THE PRODUCTIVITY OF VARIETAL MIXTURES OF WHEAT

B.R.Trenbath, M.A. (Cantab.), M.Sc. (Bangor)

Department of Agronomy,
Waite Agricultural Research Institute
15 December 1971

This thesis is submitted to the University
of Adelaide in fulfilment of the degree of
Doctor of Philosophy.

STATEMENT

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university. To the best of my knowledge and belief, the thesis contains no material previously published or written by another person, except where due reference is made in the text of the thesis.

signed

SUMMARY

The Productivity of Varietal Mixtures of Wheat

Recognising mixture yields to be the sum of the yields of components, a theoretical approach is developed to the yielding of dry matter by components of 1:1 binary mixtures of plant genotypes. The expectation according to a proposed rational model is that components in mixtures should show equal proportional increases and decreases of per-plant yield relative to per-plant yield in monocultures; the results of many published mixture experiments are reanalysed to show that such data are fitted better by a proportional model than by an additive one. A new analysis for mixture diallel experiments (McGilchrist & Trenbath 1971) is proposed to replace previous analyses based on assumed additivity.

Factors determining whether mixtures yield transgressively (i.e. beyond the limits set by the monoculture yields of their components) are examined. It is postulated, and a mathematical model is developed, that the key factors in such transgressive yielding are the uptake and the efficiency of utilization of a limiting resource. Further, it is demonstrated that these parameters quantitatively determine the value of the Relative Yield Total (RYT), an expression previously developed to express the yield relationships of species in binary mixtures.

Two 6x6 mixture diallels of wheat varieties were grown at 2 densities and a dry matter harvest was taken shortly after ear emergence. Out of 60 mixtures, 32 were recorded as yielding transgressively but none did so significantly. The results are interpreted according to the theoretical approach

developed earlier. Since 3 varieties showed in their mixtures some apparent mutual stimulation, these mixtures and monocultures were planted again in a 3x3 mixture diallel with low- and high-water treatments.

In the low-water treatment, all three of the mixtures yielded less than their lower-yielding monoculture. A pot experiment established the relationship for each of the 3 varieties between silica yield of shoots and water transpired. Analysis of the silica contents of plant material from the 3x3 mixture diallel indicated that the low yields of the three mixtures of the low-water regime were due to either aggregate water uptakes having been less than that of either monoculture (2 cases) or to a lower efficiency of water use in one of the mixture components compared with that in its monoculture (1 case).

In the high-water treatment of the 3x3 diallel, 2 out of the 3 mixtures yielded non-significantly less than their lower-yielding component monoculture. Canopy measurements made on two occasions were input to a photosynthesis model based on that of Duncan _et al._ (1967); the results suggested that the relatively low yields were not due to disadvantageous canopy structures.

Using the same model, the possibility was studied that with optimum soil conditions, mixtures might grow faster than either component monoculture. While the combination of extreme differences of leaf inclination and light response led to large predicted photosynthetic advantages for the mixtures, simulations including stems and degrees of overlapping of the canopies of the mixture components showed that the expected photosynthetic advantages would be small and dependent on light regime. Results obtained using a simple recursive growth model suggested that any yield advantage of a mixture would be small.

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1. GENERAL INTRODUCTION

Mixtures of field crops are still extensively grown under conditions of primitive agriculture, but where more advanced methods are used, the genetic heterogeneity of crops tends to be reduced and often almost eliminated. Claims have frequently been made, however, that crops with some degree of genotypic heterogeneity have advantages over monotypic stands.

Proponents of genotypic heterogeneity have claimed advantages for various types of mixtures. Claims have concerned mixtures of particular species of varieties of the same species, mixtures of specific proportions of these, or, on other occasions, mixtures of anything from two to many components. The alleged advantages have included one or more of the following : higher yields of shoots or grain, lower variability of yield from season to season, a better spreading of production over the growth period, reduced losses due to epidemic diseases, and/or an improved quality of the product. In the hope of securing such benefits, mixed pastures and multiline crops retain a place in contemporary farm practice.

To consider the criterion of higher yield in more detail, the benefit from growing a mixture has often been thought to be a production advantage for the mixture compared with the output from an equal area planted with monocultures of the components sown in the same proportion as that in which they occur in the mixture. More recently, the improvement required to justify mixed culture has been realised to be an advantage of the mixture over the better (or best) of its components grown in monoculture over the whole of the same area. In spite of the greater stringency of this latter criterion, reports of such advantages for particular mixtures continue to appear in agricultural literature. At the same time, although receiving less emphasis in reports, mixtures occasionally show the marked disadvantage of a productivity not only lower than that of the more productive monoculture, but, even below that of the less productive component.

Although a yield and quality advantage has been firmly established for forage mixtures which include leguminous and non-leguminous components, the experimental substantiation of claims for other combinations for use as field crops has proved difficult. This has been due to the usually small size of the advantage claimed and its apparent dependence for expression on relatively uncommon combinations of biological material and environment. The possibility of gaining benefits from the simple mixing of seeds holds such attractions for agriculturalists that research into the productivity of mixtures continues. Two main objectives are apparent in this research : the first is to show that the required combinations of circumstances occur sufficiently regularly in agricultural environments to justify the use of mixtures whose component genotypes have been chosen more or less empirically. The second objective is to gain an understanding of the processes which lead to mixture advantages so that a rational choice of mixtures for specific environments can allow this effect to be produced at will.

The present thesis is related to the second objective since it attempts to define, by a combination of experimental and theoretical approaches the conditions, firstly, under which a mixture advantage may be achieved by design, and secondly, the conditions under which a mixture disadvantage may instead appear by accident. Although in many environments the grain yield of temperate cereal crops is not highly correlated with the dry weight of the shoots, the photosynthetic production of dry matter is a fundamental process in the pathway to this yield. Hence, in the present work, mixture performance has been judged in terms of (dry) weight of shoots. The experimental material used was a wide range of varieties of spring wheat grown under virtually disease- and pest-free conditions; the theoretical approaches included simulations of growth using both simple and complex models of plant activity.

2. REVIEW OF LITERATURE AND CONCEPTS

The present work is a study of the production of dry matter by mixtures of wheat varieties. Since only the shoots are normally accessible, productivity is measured in terms of shoot weight. Following a convenient and common if not strictly correct usage, shoot weight is here referred to as 'biomass' *. In the mixtures here considered, components are present in a 1:1 proportion. The biomass yields of these mixtures are compared with the yields of monocultures of the component varieties planted at the same total density within the same experiment.

This review will consider the published evidence concerning the following topics: the yields of mixtures compared with those of their components' monocultures; mechanisms causing minor (non-transgressive) deviations from the 'expected' yield mid-way between the components' monocultures; mechanisms causing transgressive deviations, so that the yields of the mixtures are either less than that of the lower yielding monoculture or more than that of the higher yielding monoculture; the use of mathematical models to predict the rate of biomass production by crop communities; and the efficiency with which crops use water in the production of biomass. Models of biomass production (essentially net photosynthesis) are reviewed because a theoretical exploration is attempted of the potential yields of mixtures. The efficiency with which water is used during the production of biomass is reviewed because this factor is involved in several of the experiments reported later in the thesis.

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* Where a distinction is made between shoot weight and whole-plant weight, use of the term 'biomass' is avoided.

2.1 The yields of mixtures and monocultures

In this section reference will be made to experiments whose purpose and design conform closely to those used in this study. Reports of experiments involving mixtures of cereal varieties are very numerous but usually consider only grain yield. Since the degree of correlation between grain yield and shoot weight is uncertain, reference will be made to such reports only where a point cannot be adequately illustrated by data on shoot weight. The subject of mixtures of legumes and non-leguminous species is not considered because the special type of nutrient relationship existing between components of such mixtures is not found in mixtures of cereals.

To facilitate description, a number of terms and symbols are introduced. A mixture will be said to have 'overyielded' when the mixture biomass*, M, has exceeded that of the more productive pure culture, P_1, i.e $M > P_1$. The mixture will be said to have 'underyielded' when the mixture biomass has fallen below that of the less productive pure culture, P_2, i.e $M < P_2$. These two 'transgressive' situations will be shown to have occurred with a relatively low frequency compared with the cases where $P_1 > M > P_2$. Since a search for the possible reasons for transgressive yielding by mixtures represents the substance of this thesis, attention will be particularly focused on previous reports of its occurrence.

In his review of the performance of cereal mixtures, Simmons (1962) was concerned almost entirely with grain yield. His conclusions are of interest however because they are so similar to those of Donald (1963) who considered yields of biomass. Simmons found that often $M \quad (P_1 + P_2)/2 = \bar{P}$, sometimes $P_1 > M > \bar{P}$ and occasionally $M > P_1$. He noted that

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* M, P_1, P_2 and $\bar{P}$ have the units g/unit area.

'negative' interactions (i.e. $M < \bar{P}$) were rare.

Reviewing evidence concerning the possibility that mixtures might overyield in biomass, Donald (1963) concluded that while mixture yields were usually greater than $\bar{P}$, there was no substantial evidence to show that a mixture of two genotypes can fix more carbon than the more productive of the two genotypes in monoculture. Van den Bergh (1968) similarly concluded that 'in almost all experiments, the monoculture of the more productive species yielded more than the mixed culture'. In the same way, neither Donald (1963) nor van den Bergh (1968) found strong evidence of underyielding.

In Table 2.1, the distribution of mixture biomasses relative to those of monocultures is shown for 283 mixtures. The data are taken from those published reports of diallel experiments in which full diallel tables were presented. Although replication is not specifically mentioned by Harper (1964), it is believed that all data used in Table 2.1 were based on replicated experiments. The data of Caputa (1948, in Jacquard & Caputa 1970) were reported as being unreplicated and are therefore not included. Taken together, the data show that mixture yields tend to lie <u>above</u> the mean yields of the monocultures; the difference between 61% (above) and 39% (below) is very highly significant ($P < .001$). Presumably reflecting this difference, the frequency of overyielding is significantly ($P < .05$) greater than underyielding. According to these results, apparently transgressive yielding is by no means uncommon, comprising 37% of all the mixtures considered. However, although differences between overyielding mixtures and their higher-yielding monocultures have not often been examined for statistical significance, of those so examined, very few have reached even the 5% probability level.

There seem to be only two individual cases of significant overyielding reported to this author's knowledge, in the literature. The first case (Whittington & O'Brien 1968) concerns the significant overyielding by three mixtures of grass species in the third year of a field experiment. This overyielding affected only the treatment with frequent cutting, but there was also a trend towards it in the less-frequently cut treatment. It has been noted that these results of Whittington & O'Brien concern selected data; van den Bergh (1968) has noted that apparently highly productive mixtures in some cuts may be quite the reverse in other cuts. If the mixtures of Whittington & O'Brien had been relatively low yielding in the first two years of the experiment, there might have been greater reserves of nutrients in the soil to provide the high yields of the third year. It must also be realised that since measures of the overyielding of several mixtures may be affected by the monoculture yield of one high-yielding genotype, the measures of overyielding of mixtures in the same diallel may not be independent; the multiple overyielding in the diallel of Whittington & O'Brien does not, therefore, provide any strong grounds for believing that the overyielding was a real effect.

The second case in which overyielding achieved significance ($P \ll 0.01$ in two independent comparisons) was reported by Rhodes (1968). In a diallel of ryegrass varieties, under each of two regimes of cutting (high and intermediate frequency), a particular mixture overyielded by 12.5% and 14.6%. In the frequently-cut treatment, this mixture's yield was below $\bar{P}$. The plots with the different cutting regimes were independent and so there seems reason to accept this result as due to a real effect. It is important that this experiment should be repeated in a range of conditions to find whether the effect is a stable one.

One other instance of overyielding has been reported which, although lacking clear statistical treatment, seems possibly due to a real effect. Data of Khan (in Harper 1964) and data of an independent experiment by Harper (1964) both show that in pot culture, mixtures of various flax and/or linseed varieties overyielded. Khan's data show two flax-linseed mixtures as overyielding ('significantly', Harper 1964, p.471) by 13% and 14%. Harper's own experiment included the same two mixtures. At low density, one mixture overyielded by 38% while the yield of the other was non-transgressive; at high density, neither mixture yielded transgressively. Since, at low density, only two plants were present in each pot, the errors may have been large. Furthermore, Harper mentioned neither replication nor significance levels and so the value of this experiment as an independent confirmation of Khan's results is uncertain. If Harper's experiment was in fact adequtely replicated, the high proportion of overyielding mixtures (40%) would suggest that his mixtures were worth further investigation. The flax-linseed (Weira-Valuta) mixture of Khan and Harper remains, however, the only mixture which has to this author's knowledge, ever been shown to overyield in two separate experiments *. Since the light relationships are so different between cultures in spaced pots and in field plots it would be of interest to know whether the same result could be obtained in plot conditions.

Little consideration has been given by authors to the possibility that mixtures may underyield. No significant cases appear to have been reported although Ahlgen & Aamodt (1939) found that all three mixtures in an incomplete diallel of grass species underyielded (by 11%, 23% and 26%). The

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* The single analogous case in <u>grain</u> production is the mixture of rice varieties (BK and 2A) of Roy (1960).

ERRATUM : Page 9, line 1. For 'The biomass yields...' read 'Frequency distribution of the biomass yields...'

line 12. For '$P_2 \quad \begin{array}{c} P_2 \\ \text{to} \\ \bar{P}- \end{array} \quad \begin{array}{c} \bar{P} \\ \text{to} \\ P \end{array} \quad \begin{array}{c} \bar{P}- \\ \text{to} \\ \bar{P}+ \end{array} \quad \begin{array}{c} \bar{P}+ \\ \text{to} \\ P_1 \end{array} \quad P_1$' read

respectively '$P_2 \quad \begin{array}{c} P_2 \\ \text{to} \\ \bar{P}- \end{array} \quad \begin{array}{c} \bar{P}- \\ \text{to} \\ \bar{P} \end{array} \quad \begin{array}{c} \bar{P} \\ \text{to} \\ \bar{P}+ \end{array} \quad \begin{array}{c} \bar{P}+ \\ \text{to} \\ P_1 \end{array} \quad P_1$

<u>Table 2.1</u> The biomass yields of varietal or interspecific mixtures compared with yields of their components' monocultures, based on published data of 283 mixtures. P_1 and P_2 are the yields of the higher- and lower yielding monocultures respectively.
$\bar{P}$ is the mean monoculture yield, i.e. $\bar{P} = (P_1 + P_2)/2$.

The symbol $\bar{P}+$ represents a value slightly above $\bar{P}$; it is greater than $\bar{P}$ by the quantity $0.2\ (P_1 - \bar{P})$; the value of $\bar{P}-$ is less than $\bar{P}$ by the same quantity. The multiplier 0.2 was chosen arbitrarily to provide categories to include mixture yields which lay 'close' to $\bar{P}$.

Crop	P_2	P_2 to $\bar{P}-$	$\bar{P}$ to P	$\bar{P}-$ to $\bar{P}+$	$\bar{P}+$ to P_1	P_1	Author
Wheat				1	1	1	Sakai 1953
Rice	9	7	5	2	9	4	Sakai 1955
Either grasses or legumes		3		1		2	Aberg *et al.* 1943
	1	1		2	7	3	Donald 1946
?	1	1	1	2	12	4	Williams 1962
Legumes	1				1	1	Williams 1963
Flax & linseed	3	5	2	1	7	12	Harper 1964
Grasses	12	28	10	10	32	28	England 1965
Barley	1	4		3	2		Norrington-Davies 1967
Grasses	5	5	4	2	9	15	Norrington-Davies 1968
Totals	33	54	22	24	80	70	

%

63%

39%

61%

errors in the experiment were very large and these effects were not significant. Donald (1946) repeated this experiment but none of the mixtures underyielded.

As mentioned previously, Donald (1963) and van den Bergh (1968) have both concluded that there is no firm evidence that a mixture can have an advantage over the higher-yielding component monoculture (mixtures of legume and non-legume are excepted). Also, Woodford (1966) has expressed the same opinion. The additional evidence presented in this review is consistent with these conclusions. However, it seems that 'firm evidence' has rarely been sought. Experiments showing transgressive yielding by mixtures have either seldom been repeated or if they have, the results have not been published. Until the transgressive yielding of some mixtures can be shown to be repeatable, the addition of further data concerning once-performed experiments can add little to what is already known about mixture performance.

2.1.1. Mechanisms leading to non-transgressive deviation of mixture yields from mean monoculture values (RYT = 1)

Let us assume that a 1:1 mixture of the seeds of two genotypes has been sown along with monocultures of the components. If plants of each component yield the same as they do in their respective monoculture, the yield of the mixture will be exactly mid-way between the yields of the monocultures, i.e. M will have the value of $\bar{P}$.

Writing the per-plant yield of genotype i in mixture with genotype j as Y_{ij}, the average per-plant yield, M_{ij}, in the ij mixture will be :

$$M_{ij} = (Y_{ij} + Y_{ji})/2$$

If per-plant yields of i and j in the mixture are the same as in their monocultures, i.e. $Y_{ij} = Y_{ii}$, $Y_{ji} = Y_{jj}$, the average per-plant yield in the mixture is given by

$$M_{ij} = (Y_{ii} + Y_{jj})/2 = \bar{P}/n$$

where n is the number of plants per unit area. The per-plant yields just defined can be similarly expressed in terms of the M, P_1 and P_2 which were introduced in Section 2.1:

$$M_{ij} = M/n$$
$$Y_{ii} = P_1/n$$
$$Y_{jj} = P_2/n \qquad (\text{for } Y_{ii} > Y_{jj})$$

However, as many early experiments showed (e.g. Montgomery 1912, Tansley 1917, Clements & Weaver 1924, Sukatschew 1928) per-plant yields of genotypes in mixture and monoculture are seldom the same. From this springs the tendency for mixture yields to deviate from the mid-monoculture values.

The biological processes responsible for the deviation of per-plant performance in mixture from that in monoculture are complex and varied. A general term which has been applied to them is 'interference' (Crombie 1947, Harper 1961). They result in what may be called either 'interference effects' or 'neighbour effects' ('Nachbarwirkungen', Lampeter 1960). The latter is a more objective and neutral term and hence perhaps preferable. Clements (1904) laid a firm foundation for the study of such effects by asserting that the reaction of a plant to neighbouring individuals is not a direct response to the neighbour itself, but to the plant's own microenvironment insofar as it has been altered by the presence of the neighbour.

The best understood and perhaps the most important mechanism which can cause the microenvironment of plants of a genotype to differ between mixture and monoculture, is the process of 'competition' (Clements 1904). Competition between plants for the limited resources of any environment, results in an uneven sharing of these resources and therefore in unequal growth (Clements et al. 1929, de Wit 1960, Donald 1963).

De Wit (1960) has presented a model based on the simple assumption that biomass yield of each component is strictly proportional to the share of environmental resources it can acquire. According to this model, if the sharing is uneven, plants of one component, say i, will be larger in mixture than in monoculture. Plants of the other component, j, will be smaller than in monoculture. Thus, $Y_{ij} > Y_{ii}$ and $Y_{ji} < Y_{jj}$. In such a case, genotype i is termed the 'aggressor' (Donald 1946) and subsequently the yield of the aggressor will be subscripted with A. The genotype showing depression in mixture will here be termed the 'subordinate', and subscripted with S. Thus, according to this simple model of unequal sharing of environmental resources, $Y_{AS} > Y_{AA}$ and $Y_{SA} < Y_{SS}$. This appears to be the commonest situation in mixtures, for of 70 results reviewed by Donald* (1963), 51 (74%) were of this type. Of the additional 283 results reviewed in Section 2.1, 229 (81%) showed the same pattern. The predictions of the de Wit (1960) model have also been shown to apply quantitatively in many field and pot experiments using gramineous species (de Wit 1960, van den Bergh 1968).

When both an aggressor and a subordinate can be identified in a mixture, the behaviour of the components is said to be of a 'compensating' type (Aberg et al., 1943, Donald 1963). If the Plant Relative Yield (based on the per area Relative Yield of de Wit & van den Bergh 1965) of a component is the ratio of per-plant yield in mixture to that in monoculture,

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* Of the 70 mixtures, 34 were of a grass and a legume; in 10 mixtures the density was not closely controlled.

then in such a mixture, the Plant Relative Yield (PRY) of the aggressor will be greater than unity; that of the subordinate will be less than unity. Thus $Y_{AS}/Y_{AA} > 1$ and $Y_{SA}/Y_{SS} < 1$.

The terminology for this relationship has unfortunately been confused by Schutz & Brim (1967) who have applied the term 'complementary' to mixtures in which deviations of PRY from unity have been of the type (+,-). 'Complementary' as applied to mixture components had already been used in the literature to refer to something rather different (Salisbury 1929 and see Section 2.3). Among other terms which they introduced, Schutz & Brim use 'neutral' for cases where both components give their 'expected' yields, i.e. cases of the type (0,0) Mixtures of the type (+,0) and (-,0) are described Schutz & Brim as showing 'over-' and 'under-compensation' respectively. While neutral and over- and undercompensation seem useful terms, the original term 'compensating' (noun 'compensation') will here be retained for cases of the type (+,-).

From the point of view of mixture productivity, the common occurrence of compensation tends to keep mixture yields close to mid-monoculture values. According to the de Wit (1960) model, when components in a mixture are competing for the same supplies of environmental resources, the proportional increase of one component will tend to equal the proportional decrease of the other. This implies that the means of the plant relative yields will have a value close to unity. In terms of the per-area relative yields of de Wit & van den Bergh (1965), this index is a total which they have called the Relative Yield Total. The Relative Yield Total (RYT) is given in the present notation by

$$RYT = \frac{1}{2}\left(\frac{Y_{AS}}{Y_{AA}} + \frac{Y_{SA}}{Y_{SS}}\right)$$

Van den Bergh (1968) showed that if RYT =1 , the mixture yield must lie between the yields of the pure cultures (strictly $P_1 \geqslant M \geqslant P_2$). The general scatter of observed RYTs around the value of unity is shown for 532 mixtures in Table 2.2. These data seem to provide ample basis for expecting RYTs to lie close to unity, and incidentally provide support for the wide applicability of de Wit's (1960) model. The slight asymmetry of wide deviations from unity (12% compared with 21%) is not significant at the 5% probability level.

This section (2.1.1) was introduced as being a consideration of mechanisms whereby yields of mixtures may deviate from $\bar{P}$. Having introduced the concept of RYT, it can now be made clear in fact, that for the sake of a logical development, only those mechanisms are treated here which cause deviations of M from $\bar{P}$ without any accompanying deviation of RYT from unity. This restriction implies, as mentioned above, that mixtures affected by such mechanisms will yield non-transgressively.

The environmental resources for which plants compete are principally the light, water and soil-nutrient supplies necessary for growth (Clements et al.1929, Harper 1961, Donald 1963). Although carbon dioxide is required for shoot photosynthesis and oxygen is needed for the respiration of the roots, competition for these seems normally unlikely to occur. The probable absence of competition for CO_2 is due to the generally efficient mixing of the air within the canopy (Monteith 1963, Impens et al.1967); all leaves are surrounded by air of approximately the same CO_2 concentration. Similarly, except in almost waterlogged soils, the diffusion of oxygen in soil is usually fast enough to maintain adequate supplies to all roots (Greenwood 1969).

If cases of allelopathic influence (see below) are discounted, it seems that investigators of neighbour effects mostly appear satisfied that these effects have been due

Table 2.2 Distribution of Relative Yield Total (RYT) based on published data of biomass of components in 532 mixtures.

Crop	.5 to.7	.7 to.9	.9 to1.1	1.1 to1.3	1.3 to1.5	1.5 to1.7	1.7	Author
Grasses	1	2						Ahlgren & Aamodt (1939)
Grasses or legumes		1	4	1				Aberg *et al.*(1943)
Grasses or legumes		3	9	2				Donald (1946)
Wheat			2	1				Sakai (1953)
Rice		6	26	4				Sakai (1955)
Grasses*		5	41	11	1			Lampeter (1960)
(not stated)		4	11	4	1		1	Williams (1962)
Subterranean clover			3					Williams (1963)
Flax & Linseed	2	5	5	9	3	3	3	Harper (1964)
Grasses*		3	95	22				England (1965)
Barley			10					Norrington-Davies (1967)
Grasses*		3	106	4				Van den Bergh(1968)
Grasses*		7	20	9	2	2		Norrington-Davies (1968)
Grasses*	3	21	26	21	4			Whittington & O'Brien (1968)
Totals	6	60	358	88	11	5	4	
%	1	11	67	17	2	1	1	
	12%			21%				

* Data derived from a series of cuts.

to competition for one, or a combination of, light, water and the nutrients nitrogen, phosphorus, potassium and sulphur. Since it is relatively easy to measure and explain the unevenness of the sharing of light between the foliage of two components in a mixture, the studies involving competition for light have been generally the most conclusive.

Clements and many others have related differences in success in mixture to differences in height between the leaves of the components of mixtures, simply stating that leaves of the shorter component must be experiencing some degree of harmful shading. More recent analytical approaches are based on techniques suggested by Monsi & Saeki (1953). Working with monocultures, Monsi & Saeki introduced techniques for the measurement of profiles of light intensity and leaf area index (LAI). Since then, these techniques have been used very successfully in mixtures to relate the differences in growth rates of the two components to differences in the proportions of the total incident light intercepted by leaves of the two components (Black 1958, Iwaki 1959, Stern & Donald 1962a,b, Williams 1963, Jennings & Aquino 1968). The general conclusion from all experiments involving competition for light is that the component with its leaf area higher in the canopy is at an advantage. If the leaves are horizontal, the advantage is greater than if they are erect. This is because horizontal leaves intercept more of the total downward light flux per unit area of leaf than do erect leaves (e.g. Stern & Donald 1962a). Also, if the taller component has a greater leaf area, its advantage is correspondingly greater (Iwaki 1959).

In most of the experiments cited above, the investigators have attempted to exclude the possibility of competition for soil factors. By providing optimal soil conditions or by separating the roots of the mixture components, it was hoped that neighbour effects would be interpretable in terms of competition only for light. In most agricultural environments however, soil conditions are sub-optimal and root systems interpenetrate each other freely. Hence, the possibility of competition for water and/or nutrients exists. Where the soil is very infertile or the density of planting very low, competition between root systems for soil factors may decide which component becomes the aggressor; the LAI produced may never become great enough to lead to significant competition for light. Indeed, large depressive effects have been reported in cases where shading was allegedly absent (Pavlychenko & Harrington 1935 , Myers & Lipsett 1958). In pot experiments where competition for light has been prevented, competition for soil factors has similarly been shown to produce large effects (Donald 1958, Aspinall 1960).

The principles involved in competition between root systems have not been as well worked out as in the case of competition between shoots. A general theoretical approach was made by Bray (1954). In contrast with supplies of light, nutrient supplies are usually not greatly added to after the beginning of growth of an annual crop although subsequent rainfall or irrigation normally supplements the initial store of soil moisture. Whereas success in competition for light depends on a species having a large absorptive area closer to the light source than the leaves of the other component, the variable and complex geometry of the sources of soil factors result in the components of competitive success being less easy to define.

Bray (1954) noted that competition between root systems for nitrogen is likely to start at lower root densities, i.e. earlier in growth, than competition for phosphorus and potassium. This is because nitrogen is much more mobile in soil than the others; zones of nitrogen depletion round individual roots will begin to overlap relatively quickly. The mobilities of N and water in soil are similar (Fried & Broeshart 1967), so that competition for these factors may be expected to occur early in growth. Competition for these may determine the outcome of competition for light (Donald 1958, Aspinall 1960).

If Bray's propositions are correct, they allow the identification of the characteristics which would lead to success in competition for nutrients and water. If two genotypes were competing only for soil factors and both had the same weight of root tissue, the genotype having the more widely spreading, less branched root system would be at an advantage. There would probably also be an additional advantage in having thin roots, thus allowing the available root material to be present as a greater length of root; theoretical considerations suggest that the rate of nutrient uptake by a whole root system of given weight would be greatest if the roots were as thin as physically possible (Olsen et al. 1962). Abundant, long root hairs (see Olsen & Kemper 1968) and a high root 'demand' factor (Drew et al.1969) are also likely to contribute to competitive success.

This theoretical consideration of competition for soil factors has treated competition between root systems ('root competition'). However, Donald (1958) has suggested that in well developed agricultural crops of uniform genotype, both shoot and root competition are usually occurring. The relative importance and times of onset of root and shoot competition will depend on conditions (Aspinall 1960); the nature of the genotypes involved will also have an effect. To compare, for a particular set of conditions and genotypes, the contributions of the effects of root and shoot competition to the overall effect of being grown in mixture, pot experiments have been designed in which partitions separate either roots or shoots or both or none. Although such a design was mentioned in Tansley (1917) and used by Grümmer (1958), the first experiment testing all the combinations given above was that of Donald (1958).

Using a mixture of two grasses, Donald showed that the proportional reduction in the subordinate's yield due to shoot competition was greater when root competition was occurring than when it was absent. Similarly the proportional reduction due to root competition was greater when shoots were competing for light than when they were separated. Donald suggested that the failure of, say, the roots to acquire sufficient nitrogen caused leaf development to suffer. This in turn reduced the supplies of assimilate for the roots which grew less and so were less able to compete for nitrogen. Donald proposed a similar set of causes and effects for a component of a mixture which was unsuccessful in competition for light. The important conclusion was that the effects due to competition, once initiated, would tend to be magnified by a system of positive feedback, if simultaneous shoot and root competition were occurring.

Aspinall (1960) reported an experiment designed with the same intention as Donald's. His results were similar to those of Donald in that in the conditions of both experiments, root competition had a greater effect. Judging by the reported data of biomass, however, the subordinate species did not show the positive-feedback effect found by Donald. This appears surprising since the degree of shading of the subordinate was likely to have been more intense than in Donald's experiment. Aspinall did, however, accept the likelihood of an accelerated depression of the subordinate where both shoots and roots were at a disadvantage in competition.

Milthorpe (1961) has discussed the effects of the onset of competition for soil factors in a mixture where competition for light has already caused some depression of the growth of one component. Arguing from the depressive effect of shading on root/shoot ratio (e.g. Brouwer 1966). Milthorpe considered that any deficiency of soil-water or nutrients would cause the accelerated suppression of the subordinate if any previous shading had reduced its root's growth or uptake capacity relative to the size of its shoot. The writer has recently presented results (Trenbath 1970) showing that a slight deficiency of soil factors occurring where competition for light already existed, caused an approximately threefold increase in the depression shown by a series of subordinates.

While competition for resources has seemed to explain the results of most mixture experiments, a number of workers believe that neighbour effects are sometimes caused by other processes. This belief has been expressed by workers well acquainted with the mechanisms of competition (e.g. Warne 1953, Welbank 1963), has been implied by apparently open-minded investigators (Sakai 1955) and used as a convenient explanation of unexpected results by others (Ahlgren & Aamodt 1939, Went 1942).

The process frequently proposed as an alternative to competition is the exudation from root or shoot of biologically active substances which enter neighbouring plants and affect their metabolism. The process is termed allelopathy (Winter 1961). While exudations of a range of organic substances from roots certainly do occur (Rovira 1969), conclusive evidence of their influence on the production of neighbour effects in crop mixtures is apparently lacking (Harper 1964). With regard to exudations of active substances from shoots, Sandfaer (1968) has shown with a series of experiments that there is a strong possibility that the shoots of certain barley varieties affect the grain-setting of associated varieties by liberating a volatile toxic substance which is then carried to other plants in the air. As Harper (1964) points out, however, research into the role of plant toxins in mixtures is beset with extreme technical difficulties and to treat the subject with adequate detail would greatly extend this review. In the interpretation of the experimental data presented in this thesis, appeal will not be made to exudate effects in order to explain the aggressiveness of one genotype to another in mixture. It seems preferable to exhaust the possibilities of simpler hypotheses, such as those concerned with competition for resources rather than resorting almost directly, as some authors have done, to a consideration of possible exudate effects.

Whether caused by competition or by exudate effect, the unequal sharing of resources between components affects the yields of mixtures. If the aggressor is the higher-yielding component in monoculture, then with RYT = 1, the mixture yield will lie between $\bar{P}$ and P_1. The greater the depression of the lower-yielding component, the closer the approach of M to P_1; With its complete suppression, $M = P_1$. Similarly, if the lower-yielding component in monoculture is the aggressor in the mixture (the so-called Montgomery effect, Gustaffson 1951), then M lies between $\bar{P}$ and P_2. With complete suppression of the subordinate, $M = P_2$.

The finding of Donald (1963) that mixture yields usually lie between $\bar{P}$ and P_1 suggests that there is a general positive correlation between aggressiveness in mixtures and biomass production in pure stands. This is in agreement with the ideas discussed earlier, namely that a large leaf area displayed at a sufficient height gives advantage in competition for light (e.g. Donald 1961). Iwaki (1959) has suggested a case in which the correlation might break down : a species might become the aggressor due to the diversion of a particularly large share of photosynthetic product to the building of tall stems; the associated species might be shaded and suppressed. On the other hand, in monoculture, the low proportion of the species' dry matter invested in productive leaves might mean that its biomass production was relatively low. Again, if productivity is measured in terms of a particular part of the shoot, for instance the yield of grain, the correlation might be reversed. This has been demonstrated by Jennings & Aquino (1968) and others with rice.

Under some suboptimal conditions, a low growth rate may have a selective advantage (Antonovics et al. 1967). Van den Bergh (1968) suggested that since less favourable conditions usually result in lower leaf areas, the shorter component will be less at a disadvantage in such conditions. The positive correlation between aggressiveness in mixture and yield in monoculture might again become a negative one.

The aggressiveness of a species is well known to depend on environmental conditions. Different soil treatments have often been reported to reverse the dominance-suppression relationship between genotypes (van Dobben 1955, Sakai & Iyama 1958, Stern & Donald 1962a, van den Bergh & Elberse 1962, Cavers & Harper 1967); the less easily definable differences between seasons have marked effects on aggressiveness, at least where the index used to measure it is based on seed yields (Laude & Swanson 1942, Sakai & Oka 1955, Allard & Workman 1963, Workman & Allard 1964, Lin & Torrie 1968). Allard et al. (in Edwards & Allard 1963) showed from the data of Suneson (1949) that taking the value of Atlas as 100, the selective advantage of Vaughn ranged from 40 to 173 in 13 seasons. Transfer from the field to the greenhouse may also cause reversals of dominance (Aberg et al.1943, Syme & Bremner 1968),

The apparent lack of repeatability in experiments involving mixtures suggests a finely balanced and unstable system.

Harper (1964) concluded that under his particular experimental conditions, the outcome of the interaction between two Lemna species depended on chance alone. Apparent indeterminism has been found also in some mixture experiments with animals (Park 1954). This variability of results adds to the technical difficulty of mixture experiments.

2.1.2 Mechanisms capable of causing transgressive yielding by mixtures (RYT $\neq$ 1).

The results reviewed in Section 2.1 show that mixtures have quite frequently been recorded as apparently yielding transgressively; furthermore, the data indicate that records of mixtures overyielding are significantly more frequent than records of those underyielding. Two interpretations of this situation can be envisaged.

It might be suggested that if RYT could be measured without experimental error, its value might always be close to unity; also, it could be maintained with some justification from experimental data that there is a positive correlation between a genotype's aggressiveness and its biomass yield in monoculture. In such circumstances, theoretical error-free experiments would show mixture yields lying usually between P_1 and $\bar{P}$, less frequently between $\bar{P}$ and P_2, and never outside the range P_1 to P_2. The experimental error found in actual experiments would be expected to disperse the observed results about their 'true' values so that overyielding mixtures would be recorded more frequently than underyielding ones. This view implies that observed cases of transgressive yielding are due only to experimental error.

An alternative interpretation is that at least some, though perhaps very few, of the observed cases of transgressive yielding do represent real effects. The higher frequency of overyielding compared with that of underyielding could simply be because the mechanisms which can lead to apparent mutual stimulation (see below for examples) are, given the conditions of the types of experiment commonly performed, more able to operate than mechanisms leading to inhibition. The evidence in favour of transgressive yielding as a real phenomenon has been discussed in an earlier section; in the present section, the mechanisms which could lead to transgressive yielding are considered. If they appear likely to operate under the conditions normally used for mixture experiments, this would add credibility to the second interpretation given above.

In connection with overyielding, the findings and theory of animal ecology may be relevant since they help to define conditions which might lead to this kind of transgressive yielding. Gause (1934) quoted Formosov's observations of natural mixed populations of Tern in which four species coexisted apparently because they exploited the environment in different ways. In such a case, it seems likely that a mixed population would be more productive than any monospecific population. Gause (1934) summed up his own experimental results in the principle that species of very similar requirements tend not to coexist. Using this principle, Harper (1967) and others argued that the species diversity found in natural communities implies that the component species occupy differing niches. Together, therefore, they must exploit the environment more completely. Beardmore et al.(1960) and Seaton & Antonovics (1967) reported overyielding of mixtures of Drosophila strains in controlled environments. Seaton and Antonovics suggested that in their mixtures the two genotypes were avoiding competition.

In the botanical literature, genotypes believed to be avoiding competition while they share a habitat are said to be 'complementary' (Woodhead, in Salisbury 1929). Woodhead first used the term in connection with natural woodlands where, by the sharing of environmental resources in either time or space, the various types of species seem to escape, at least partially, the effects of competition. His concept of the complementary use of resources would seem to be applicable to crop mixtures; the possible ways in which resources may be used in such a manner will now be considered.

Van den Bergh & de Wit (1960) reported an example where temporal sharing of the environment may have been responsible for a case of apparent mutual stimulation in mixture. In a mixture of two grass species which differed markedly in time of development, plants of both components had more tillers (53% and 36%) than did plants in the corresponding monocultures. Biomass yields were however not reported. Flax and linseed differ in maturity date; their significant overyielding in two mixtures was attributed to this by Khan (1963) (see Section 2.1). However, Sechler & Chapman (1967) and Syme & Bremner (1968) both reported cases of mixtures of cereal genotypes which differed greatly in flowering date yet did not overyield.

Differing temporal patterns of growth or development sometimes result in a reversal of dominance during the growth of a mixture (Harper and Clatworthy 1963, England 1965). Even if the biomass increments of the mixture over the periods before and after the reversal are not transgressive compared with the increments in the monocultures over the same intervals, the biomass accumulated by the mixture over the whole growing season may yet be transgressive. Van den Bergh (1968) gave a hypothetical example of this in which the more aggressive component in each phase was the component with the greater biomass-increment in its monoculture during that phase. In this example, the total accumulation of biomass over the two phases was the same in each component monoculture; the association of greater aggressiveness and faster biomass accumulation within each phase resulted in overyielding at the final harvest. If the direction of this association had been reversed, the result would have been an underyielding mixture. Examples of such effects have not yet been found and too few suitable sets of data exist to judge their plausibility. Van den Bergh (1968), failing to find this kind of effect in the data of England (1965), suggested that the originally suppressed species had been unable to take advantage of the sharp reduction in the vigour of the other component of the mixture. The dominance during the second phase was too weak for the mechanism described above to operate. A similar observation applies to the later-ripening component in one of Syme & Bremner's (1967) experiments.

The components of a mixture may be complementery in a spatial sense by exploiting different layers of the soil with their root systems. Although Gustaffson's (1954) discussion and vague reference to such a case cannot be taken as more than an indication, he claims the possibility of increased grain yields in cereal mixtures through stratification of root systems. Cable (1968) found that desert species were affected least by the proximity of plants of other species whose root systems did not overlap their own. The significant overyielding of grass mixtures reported by Whittington & O'Brien (1968) was accompanied by phosphorus uptake from lower depths in the mixtures than in the monocultures (O'Brien et al. 1967) but this could have been the result as well as the cause of enhanced growth. The writer (Trenbath 1970), measuring panicle weights in a field experiment involving 5 mixtures of oat species, found in one replicate that 5 out of 5 mixtures overyielded; in the succeeding two replicates in a linear sequence of three, the numbers of overyielding mixtures were respectively 2 and 1 out of 5. The reality of this trend was supported by the significance ($P < 0.01$) of the regression of panicle weight RYTs of the 5 mixtures on the position of the replicate in the linear sequence across the field. The trend in mixture yields was tentatively related to an observed soil-depth gradient. It was suggested that stratification of root systems had occurred on the deep soil, leading to high RYTs and overyielding, but this stratification had been prevented on the shallow soil. The two species making up the mixture with the highest RYT were suspected to differ the most in depth of rooting. Ellern *et al.* (1971) showed that indeed these two species had rooting depths significantly different; the other species were unfortunately not tested.

Components of a mixture may complement each other nutritionally; one component may require much of an element of which the other component needs little (see Kolb 1962). Considering a particular element, one component may be able to utilise a form which is unavailable to the other. Although mixtures of leguminous and non-leguminous species are not formally treated in this review, it is such mixtures which provide the most striking and repeatable examples of overyielding due to nutritional complementation. Since the roots of the components are drawing on different supplies of nitrogen in the soil, in conditions of short supply RYT values regularly exceed unity and overyielding is often recorded (e.g. de Wit *et al.* 1966, Ennik 1969). When nodulation is prevented, the species compete for the same supply of nitrogen, the RYT falls to unity and overyielding does not occur (de Wit *et al.* 1966). Since phosphorus is present in the soil in several forms of differing availability to different species (Richardson *et al.* 1931, Schander 1941), nutritional complementation with respect to phosphorus could also occur but has not yet been reported.

Overyielding by mixtures has in some instances been attributed to a more efficient utilization of light by their canopies. As will be discussed in a later section, the use of mathematical models has suggested that a leaf arrangement in which the steepness of the inclination of the leaves decreases with depth might lead to the highest photosynthetic rates (Wilson 1960, Verhagen et al. 1963, Duncan et al. 1967, Nilson 1968). This 'ideal' arrangement could be approached by a mixture of a tall erect-leaved genotype and a short, prostrate-leaved one. A mixture of such components might possibly overyield. Hanson et al. (1952) did not find overyielding mixtures of grass strains but suggested a possible yield benefit from a mixture of a 'high-yielding strain and a low-growing dense sod-former'.

Rhodes (1968) reported the yield of grass in a mixture whose canopy structure approached Wilson's (1960) 'ideal' configuration mentioned above. The mixture overyielded significantly in the treatments with more frequent cutting, but not in the plots which were left to grow until they intercepted 95% of the incident light. It is difficult to accept Rhodes' explanation of the overyielding being due only to more efficient light use in the mixture since, according to the mathematical models, the 'ideal' leaf arrangement gives the greatest advantage when the leaf area is the greatest. Also, other mixtures of apparently similar leaf arrangement did not overyield. In a similar way, van den Bergh (1968) and Alcock & Morgan (1966) found (non-significant) overyielding in grass mixtures where repeated cutting prevented any abundance of foliage. Although van den Bergh appealed to possibilities of better light-use by the sods of such mixtures, he gave no measurements or theoretical basis for such an explanation.

Before leaving the topic of light utilization, it might be pertinent to point out that Duncan et al. (1967) simulated the photosynthesis of a canopy of which the leaves were horizontal above, becoming more inclined with depth. According to their result it can be expected that a mixture of a tall, prostrate-leaved type and a short, erect-leaved type might underyield.

Allelopathic effects can theoretically cause transgressive yielding. Roy (1960) attributed overyielding by a mixture of rice varieties to an active substance carried in the irrigation water. Ahlgren & Aamodt (1939) suggested that underyielding in three grass mixtures was due to mutually harmful exudations from the roots. To avoid the obvious arbitrariness of such suggestions, it seems that results should be attributed to allelopathy only after exhaustive search for other explanation has failed, or, preferably, when the active substance has been isolated and shown to have the alleged effects. A set of requirements analogous to Koch's postulate should be worked out.

Mechanical factors could, again theoretically, lead to transgressive yielding by a mixture. Let us suppose that the aggressor is potentially capable of the higher yield in monoculture, but is susceptible to lodging; if the subordinate resists lodging strongly enough, the mixture will stand while the susceptible monoculture lodges. If the lodged monoculture yields less then the resistant component's monoculture, the mixture would be expected to overyield. Lodging in mixtures commonly follows the behaviour of the more resistant component (Atkinson 1900, Tsedik-Tomashevich 1951, Stringfield 1959, de Wit 1960, but see Probst 1957).

The effects of disease on mixture yield may be positive or negative. Several authors have reported that when a stand of susceptible plants is 'diluted' with resistant plants, as in a suitable mixture, the chance of an individual susceptible plant being infected is reduced (Hanna 1956, Borlaug 1959, Müller in Lampeter 1960, Browning 1966). If both components are suffering simultaneously from a disease to which the other is resistant, disease escape in the mixture would be likely to result in the mixture overyielding. If, as is more usual, only one component is affected, the mixture is more likely to yield intermediate between the monocultures. Whether the mixtures yield close to P_1 (as in Suneson 1960), or closer to $\bar{P}$ (as in Klages 1939) or between $\bar{P}$ and P_1 (Borlaug 1959), is decided by several factors such as time of onset of the disease, the degree of disease escape due to the dilution effect mentioned above and whether the affected plant is the aggressor or the subordinate (see de Wit 1960, Sibma *et al.* 1964).

It was suggested by van den Bergh & Elberse (1962) that a substantial depression of RYT in a grass mixture was due to a virus, latent in one component, attacking the susceptible component with which it was mixed. Such an effect could lead to underyielding if the monoculture yields were sufficiently similar. Chamblee (1958) also reported plants in a mixture to be worse affected by disease than those in monoculture.

To end this review of the yields of mixtures, some comclusions may be stated.

1. Most mixtures have been recorded as yielding at a level between the yields of the components' monocultures. This non-transgressive yielding is what might be predicted on the assumption of competition between components for the same resources. Such competition would be expected, as a first approximation, to lead to equal proportional increases and decreases of plant biomass compared with per-plant performance of the components in monocultures. This is indeed found to be so (see Table 2.1)

2. A minority of mixtures has been recorded as yielding transgressively. This suggests that the above model may not always apply, but the frequent lack of repetition of the experiments and the peculiarly large errors associated with mixture experiments usually make it impossible to say whether

a given case of transgressive yielding is due to experimental error or to a systematic effect. Since a series of plausible mechanisms can be suggested which could lead to systematic, mutually beneficial effects on mixture components, it seems likely or at least possible that some of the observed cases of overyielding are due to such effects. The lack of strong experimental evidence in favour of the operation of the hypothetical mechanisms may be partly due to the lack of sustained investigations of specific cases of overyielding and partly due to their extreme sensitivity to variations of environmental conditions. Also, few informed attempts have yet been made to increase the likelihood of overyielding by conscious choice of conditions and genotypes. Similar remarks apply to underyielding by mixtures although rather fewer mechanisms have been suggested to account for it.

3. The operation of mechanisms resulting in stimulation or inhibition beyond expectations based on the proportional model, only produces transgressive yielding if the monocultures are sufficiently similar. A convenient index of such stimulations or inhibitions, and thus of the mechanisms underlying them, is the RYT. This index has the advantage that it takes account of the observed monoculture yields in such a way that it may be able to detect the operation of these mechanisms even in mixtures which do not overyield.

2.2 The use of mathematical models to predict crop growth rates and yields

The quantitative prediction of crop responses to limiting conditions was pioneered by Liebig (reviewed in Russell 1961). Later, the development of regression equations stating yield as a function of the levels of several factors provided crude 'models' through which to predict future responses (e.g. Brenchley 1920, Gregory 1926).

Although these empirical models could indicate the relative importance of the various environmental factors in determining growth and yield, these models were essentially descriptive. They were founded only on statistical correlations and their construction involved no insight into the processes which led to the observed results. Since the measure of agricultural yield is usually the dry weight of some part of the plants making up the crop, attention has subsequently become focused on the plant processes, basically photosynthesis and respiration, which limit the production of this dry matter. These limiting processes, and the way in which they, in turn, are themselves limited, have become key studies of crop physiology.

Recently, a sufficiently advanced understanding of the plant has been acquired for many of its physiological processes to be approximated by mathematical relationships showing the rates of the processes as functions of environmental and plant parameters. The plant has been seen to behave with some appearance of the determinism expected in physical systems. Prediction of yield can be put on a rational, and therefore more certain, basis,

Although 'dynamic' models for predicting growth over periods of several weeks have been constructed (e.g. Sande-

Bakhuyzen 1937, Iwaki 1958, de Wit & Brouwer 1968, Paltridge 1970), the model used extensively in the present work predicts only one day's photosynthesis. This review is therefore confined to models giving short-term predictions of photosynthesis and growth. The efforts which have been made to show that the models give valid predictions (i.e. efforts to 'validate' the models) will be considered along with each model. However, in the case of the predictions concerning the effect of leaf inclination on growth, attempts at validation are considered in a separate section.

The more analytical approach to yield prediction was founded by the work of Boysen Jensen (1932). Boysen Jensen provided a basis for understanding how crop growth rates are related to the intensity of solar radiation and the arrangement of the green surfaces within the leaf canopy. He demonstrated that the rate of net photosynthesis of individual leaves showed a hyperbolic (law of diminishing returns) dependence on the illuminance * of their surface. He next studied the net production rate (i.e. net photosynthesis rate of the photosynthetic parts minus the respiration rates of other parts, Monsi 1968) of the whole stand of plants; this rate increased linearly with light flux density over the whole range used. He showed that the two observations could be reconciled by taking into account the inclination of the leaves and the large area of the leaf surface (3.4 times that of the soil surface under it). He explained, using a simple mathematical model, that a spreading of the light flux over a larger leaf area may give lower illuminances of individual leaves, but will give a greater overall photosynthesis rate under the high radiation conditions found in nature.

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* The degree of illumination produced by a given light flux density ('light intensity') at the surface of a body (see Denmead's discussion in Saeki 1963).

2.2.1 The early models developed by the Japanese school

Monsi & Saeki (1953) developed a detailed geometrical approach to the problem of the distribution of the light flux between the leaf surfaces of ideal plant communities. Their model for the prediction of crop growth rates included so many of the refinements added by subsequent authors that it will be treated fairly fully. Many simplifying assumptions had to be made to bring the complex geometry of surfaces in a real canopy into a form amenable to mathematical analysis. The principal assumptions were that the effect of all aerial parts other than leaves could be neglected; that all leaves had the same gross photosynthesis-illuminance relationship, the same respiration rate and the same inclination to the horizontal; and that the leaves could be represented as small flat elements of area which were distributed randomly, without preferred azimuth, within any horizontal layer. The light regime considered was that of an overcast day; light came from a sky represented as a hemisphere of uniform luminance. The illuminance of the leaves, which was calculated as described below, was taken to be constant throughout any layer. In common with nearly all the other models to be treated in this review, Monsi & Saeki's model assumed that soil and aerodynamic factors were non-limiting. Thus no adjustment was made in the specified gross photosynthesis-illuminance (P:I) relationship to correct it for water stress or for change of CO_2 content of the air.

The leaf area in each layer was defined in units of m^2 (one sided) leaf area/m^2 of soil surface (now known as Leaf Area Index, LAI, Watson 1947). Geometrical considerations showed that the expected light flux density, I, at any horizontal surface in the canopy depended on the leaf area, L, above that surface in a way that would approximate the Beer-Lambert law,

$$I = I_0 e^{-KL} \qquad (2.1)$$

where I_0 is the light flux density at a horizontal surface just above the crop and K is an extinction coefficient. The extinction coefficient for leaves of any inclination angle, α , measured from the horizontal, could be calculated from a consideration of the shadow cast by a unit area of such leaves integrated over all possible azimuths. This value would then be integrated with respect to all possible angles of incidence of light from the sky hemisphere.

While the use of Eqn. 2.1 gave the expected light flux density at a horizontal surface at any depth in the canopy, the average illuminance of leaves inclined at α had still to be calculated. The illuminance of the leaves was estimated by calculating the incident flux at a horizontal surface at the required depth in the canopy, repeating the calculation for a 'slightly' greater depth, and then dividing the difference in flux density by the leaf area in the thin layer between the two heights. The light flux was thus considered to be spread evenly over the leaves in the layer that had intercepted it. Since illuminance is proportional to normally-directed light flux density, the illuminance of the leaves had therefore been determined.

Given the calculated illuminance of leaves and the specified area of leaf in each layer, the P:I relationship was used to calculate an expected P rate for the whole canopy. Since the P:I curve was approximated by a rectangular hyperbola passing through the origin, the calculated P rate was a gross rate; the predicted net P rate was obtained by subtracting a canopy respiration rate which was proportional to the area of leaf present.

Monsi & Saeki validated their model in three stages. The light interception part was checked on overcast days with a photometer using a range of communities whose 'productive structures' (essentially profiles of LAI) were determined by stratified clipping. The approximately linear plots of $\log_e(I/I_o)$ against L showed that Beer-Lambert's law applied to light penetration into canopies and that K was approximately constant with depth. This finding has since been confirmed by Davidson & Philip (1958), Takeda & Kumura (1957), Takeda (1961) and others. However, marked variation of K with depth has sometimes been found e.g. by Brougham (1958) and Stern & Donald (1962a). While some curvature is expected on theoretical grounds (Monsi & Saeki 1953), some may be caused by variation of leaf inclination or interception by stems, petioles and reproductive structures.

Values of K calculated by Monsi & Saeki (loc.cit) from measured leaf inclinations (method of measurement not described) agreed excellently with K values derived from measured light profiles in five out of seven cases. Lastly, using Boysen Jensen's (1932) data on leaf areas and P:I curves for individual leaves, and assuming (rather arbitrary) values for leaf inclinations, these authors calculated predicted rates of canopy photosynthesis. The fit of these predicted rates to Boysen Jensen's observations was reasonably good for two out of three sets.

Using their model to specify the conditions leading to high production, Monsi & Saeki predicted the existence of an optimum LAI which would depend on light level and K (i.e.leaf inclination). At high light levels, greatest growth rates were expected from crops with erect leaves; at low light levels, horizontal leaves were expected to give an advantage.

When Kasanaga & Monsi (1954), using a simplified model, had shown that light transmission by leaves might be important in determining photosynthesis rates, Saeki (1960) introduced a treatment of transmission suitable for insertion into the

the original model (Monsi & Saeki 1953). Saeki (1960) extended the model to give rates of daily net photosynthesis. He calculated maximum possible rates of growth under various natural conditions. His values agreed well with observed rates cited by Blackman & Black (1959); to make the comparison, he assumed (quite arbitrarily) that 24-hour respiration of non-photosynthetic tissue was equal to 1/6 of the surplus production of photosynthate by leaves.

A serious shortcoming in this Monsi & Saeki model is that the uniform average illuminance assumed for all the leaves of a layer must cause the model to overestimate actual photosynthesis in any layer (Saeki 1960, Monteith 1965). This is due to the curved nature of the leaf P:I relationship and the enormous horizontal variation in illuminance of leaves at any level within a canopy (Norman & Tanner 1968).

As mentioned above, Monsi & Saeki (1953) suggested that beyond a certain LAI, the rate of net photosynthesis of a canopy might be reduced. Clear LAI optima have been demonstrated by Davidson & Donald (1958) and Black (1963) using subterranean clover and by Watson (1958) using kale. Tanaka *et al.* (1966), basing their use of the Monsi & Saeki model on data for rice, showed a calculated optimum LAI such as that already reported for that species by Kanda & Sato (1963). However, many other experiments have not shown such optima (Wasserman 1964 with wheat, Ludwig *et al.* 1965 with cotton, Williams *et al.* 1965 with maize, Stoy 1965 with wheat, King & Evans 1967 with lucerne and wheat). The conflicting results are suggested by King & Evans (1967) to be due to the canopies in the second group of investigations either being more deeply penetrated by light at high LAIs or having less young tissue deep in the canopy that could fall below its light compensation point and thus make a negative contribution.

Ludwig et al. (1965) showed that the lack of decline of net photosynthesis at high LAI was associated with reduced respiration rates of the shaded lower leaves; these authors and McCree & Troughton (1966) showed considerable reductions of respiration rates when leaves experienced low illuminance. In the Monsi & Saeki model, the strict proportionality between foliage respiration rate and LAI will need to be revised at least for some species. It has led to qualitative errors in some of the model's predictions.

2.2.2 Models developed by groups in Europe, USA and Australia.

Although Japanese workers pioneered the use of mathematical models in the prediction of crop growth, other schools, principally in Europe and the USA, have developed their own versions.

In 1959, de Wit introduced the first model which considered the great variation in irradiance of leaves at any one level according to whether they are in the sun or not. He assumed a simplified, Blackman-type P:I relationship; leaves were assumed to be arranged at random with respect to position, inclination and azimuth; the LAI was assumed ta be large enough to absorb practically all incident light. The photosynthesis of sunlit leaves was calculated from strict geometrical considerations while the treatment of diffuse light was more approximate. The sky-light flux density on a horizontal surface above the crop was spread evenly over the shaded leaf area in any layer; this shaded leaf area was the area of surface which would be visible from a vertical direction. From de Wit's account, it seems that the rest of the leaves in the layer would be treated as being in complete darkness.

Using this model, de Wit (1959) predicted the maximum possible montly rates of photosynthesis throughout the year in the Netherlands. Subtracting an arbitrary 20% for respiration loss, his estimates were over twice as high as the observed maximum rates of production by grassland. The difference he attributed mainly to the low LAIs and effects of water shortage in actual swards.

Monteith (1965) proposed a model for predicting light penetration which at first sight seems unrelated to Monsi & Saeki's (1953) approach. If transmission of leaves is ignored, however, his equation for light flux reduction by a layer can be put into the exponential form of Eqn. 2.1. Although Monteith opened the way for a detailed treatment of transmission dependent on wavelength, Wilson (1967) pointed out that an assumption of vertically-falling sunlight has unwittingly been introduced. To represent the changes in light level through the day, Monteith (loc.cit.) had assumed a sinusoidal variation in the vertical flux of sunlight. Since the proportions of sunlit and shaded leaf-area in any layer did not change with the time of day, the sun was effectively at the zenith throughout the day. In spite of this obvious flaw, it is instructive to note that Monteith's predictions of the effect of LAI and latitude on growth-rates were similar to those of authors whose more complex models took account of hourly changes of solar altitude. In his comparisons of predicted and observed crop growth-rates, Monteith emphasised that large errors were to be expected when so little information was available concerning respiration rates and root/shoot ratios.

In the same year, de Wit (1965) presented a model of light penetration with which to calculate the area of leaf which was sunlit for any specified distribution of the inclination of leaf are (DILA) (see also Isobe 1962 and Kuroiwa 1968). Again, the equation used by de Wit to calculate the penetration of sunlight can be expressed in the form of Eqn.2.1 His formula for finding K is a special case of that of Monsi

& Saeki; hence, it contains their parameter s, which is an index of the degree of the non-randomness of the distribution of leaves within the horizontal layers. In view of the common occurrence of non-random distributions in natural canopies (Wilson 1959), this seems to be valuable as a parameter to include in a photosynthesis model. However, de Wit showed that, for a LAI of 5, the variation of s within observed limits had a negligible effect on the expected rate of photosynthesis. It seems likely, nevertheless, that at lower LAIs, aggregation of leaves, as within individual plants or the rows of a row-crop, might have a greater effect.

Several other features of de Wit's (1965) model deserve mention. The distribution of illuminance of sunlit leaf surfaces was calculated from geometrical principles, but the illuminance of shaded leaves within a layer was found as in Monsi & Saeki (1963). Skylight was therefore assumed to be totally diffuse within a layer and spread evenly over other leaves of all inclinations. A proportion (usually 30%) of the incident light flux in any layer was assumed to be scattered equally upwards and downwards; the scattered light in a layer was added to the skylight whose treatment was mentioned above.

A simple treatment was given to allow for levels of CO_2 depletion within the canopy to be affected by windspeed. That this is perhaps necessary is suggested by the correlations occasionally found on rather still days between the rate of CO_2 uptake by a crop and the wind speed (Lemon 1963 with maize, Denmead 1968 with wheat). A model to assess the effects of turbulent exchange coefficients on CO_2 depletion and canopy photosynthesis has also been presented by Uchijima (1966) with supporting experimental data (Uchijima *et al.* 1967). On the other hand, at normal wind speeds, atmospheric turbulence seems likely to remove most of the effects of local CO_2 depletion (Monteith *et al.* 1969, Impens *et al.* 1967, Kanemasu *et al.*1969).

Since photosynthesis is proportional to CO_2 concentrations at the low levels found in nature (Gaastra 1959), an additional correction appears to be urgently required for variation of CO_2 concentration in the bulk air above the crop. Depletion on a continental scale can give CO_2 concentrations in the bulk air above the crop as low as 200 ppm (Lemon 1960 in eastern USA). Also, Denmead (1968) regularly found concentrations of 230-290 ppm near Canberra.

Having defined 'standard conditions', de Wit (1965) used his model to estimate the effect of variation in each of ten parameters. He concluded, as did Saeki (1960), that the light-saturated rate of photosynthesis of individual leaves, P_{max}, was expected to be highly influential indetermining (gross) rates of crop photosynthesis. This accorded well with the finding of an approximate proportionality between growth rate at high light levels and values of P_{max} (Waggoner *et al.* 1963, Cooper & Tainton 1968). Another conclusion, was that at high LAI's, senescence of lower leaves might reduce crop photosynthesis rates by 20% (however see Saeki 1959). De Wit's conclusions about leaf inclination were similar to those of Monsi & Saeki (1953). Using climatic data, he predicted maximum photosynthesis rates thoughout the year for all latitudes.

The model of Duncan *et al.* (1967) showed certain improvements over that of de Wit (1965) but ignored the possibility of local depletions of CO_2. The authors assumed whole-plant respiration to be a constant proportion (40%) of daily gross photosynthesis in accordance with the findings of Ludwig *et al.* (1965). Their treatment of the illuminance of shaded leaves took account of leaf inclination but, in contrast with the presentation given by de Wit (1965), photosynthesis under overcast conditions was not considered. The treatment of reflection and transmission was more complex than in any previous model. The authors experimented with the effect of varying leaf inclination with depth in the canopy. As Verhagen et al. (1963) had shown previously using a Monsi & Saeki model, increased production rates were predicted by Duncan et al. when, above about LAI 4, the upper leaves of the canopy were erect and the lower leaves were inclined horizontally. The results referred only to a sunny day near mid-summer at latitude 38°N.

The fullest and most sophisticated model of this type so far published is that of the Estonian group led by J.K.Ross (Ross & Bichele, 1968, 1969). It is based on a long series of publications indicating a strongly independent development (e.g. Ross 1957, Ross & Nilson 1963, 1965). The most recent model (Ross & Bichele 1969) treated the light fluxes within the canopy with about the same degree of detail as did the Duncan model, but introduced a number of important refinements not found elsewhere. Tooming & Niliisk (1967) had found that the proportions of photosynthetically active radiation in sky- and sun-light are very different, i.e. 0.6 as opposed to 0.2 - 0.43. The greater photosynthetic effectiveness of skylight was therefore included in the Ross-Bichele model. Since sunlit leaves are usually light-saturated with respect to photosynthesis, while the rest of the leaves, lit by skylight, are not (e.g. de Wit 1959, Kumura 1968), models assuming uniform average effectiveness of the two sorts of light (e.g.de Wit 1965, Duncan et al. 1967) seem likely to underestimate photosynthesis by the shaded leaves. The higher proportion of photosynthetically active radiation in sunlight when the sun is low in the sky (Tooming & Niliisk 1967) may have caused previous models also to underestimate photosynthesis at the beginning and end of the day. In the Ross-Bichele model, the light-saturated rate of leaf photosynthesis was made to decrease with depth in the canopy in accord with observations of Saeki (1959) and others. Similarly, decreases with depth in leaf transmissivity and CO_2 content of the air were included to simulate the effects reported respectively by Brandt & Tageyeva (1967) and Uchijima et al.(1967). The authors considered that their treatment of respiration was the weakest point in the model due to lack of data. Nevertheless, they felt justified in dividing the respiration rate of a leaf into two components: one depending (indirectly) on its photosynthesis rate and the other representing a maintenance rate depending on its position in the canopy and on air-temperature.

Although the checking of predictions against reality is of vital importance, no such test of the Ross-Bichele model has yet been attempted. However, a set of simulated data testing the influence of temperature on the appearance of an optimum LAI showed a striking similarity to the results obtained by Ludwig et al.(1965). Other conclusions were similar to those of other authors.

A further model for predicting crop photosynthesis has been outlined by Denmead (1968). Instead of accepting the usual hyperbolic P:I relationship, he used Gaastra's (1959) formula involving CO_2 concentrations and diffusive resistances. Since so many parameters were assumed rather than measured, the good fit to a selected day's data was not surprising. On the other hand, such an approach carries the modelling process one stage closer to a concern with fundamental mechanisms rather than superficial correlations.

The models so far discussed have considered the growth of canopies limited by light level and CO_2 supply. Temperature effects have been occasionally included. The development of process-orientated models concerning limitation by water and nutrient supply has hardly commenced owing to the lack of suitable data relating photosynthesis rates to water and nutrient status. On the basis of hardly adequate data, Idso (1968)

(1968) presented a model to predict the effect of soil moisture stress on photosynthesis rates. With a well validated model (Waggoner & Reifsnyder 1968) now available to simulate the microclimate of a canopy, further advance in this direction is soon to be expected. Process models linking soil nutrient status and plant growth still belong to the future although Visser (1969) provided a yield model which relied to some extent on a consideration of underlying processes.

2.2.3 The treatment of respiration in growth models.

Considering the efforts which have been made to model the anabolic (synthetic) aspect of growth, the scant attention given to the katabolic aspect is surprising.

Estimates of the rates of 24-hour respiration of whole plants vary widely. Expressed as percentages of the gross photosynthesis over the same time interval, Gaastra (1963) concluded that for field crops a range of 25% to 50% was frequently measured; Bonner and Galston (1959) carry their lower limit to 10% (not specifically for field crops) and Tanaka et al.(1966) have estimated that for rice crops grown in the tropics, respiration may exceed 60% of the gross daily photosynthesis. Respiration rate is clearly a most important yield-determining factor.

As has been noted, the crop respiration rate has been estimated in models either by assuming that it is linearly related to the LAI (Monsi & Saeki 1953, Davidson & Philip 1958, Saeki 1960, Tanaka et al.1966, de Wit 1966) or by assuming it is a fixed proportion of the gross photosynthesis (McCree & Troughton 1966, Duncan et al. 1967). An experimental justification for the first method was given by Tanaka and Kawano (1966) while the use of the second method is supported by the findings of McCree & Troughton (1966), Ludwig et al. (1965) and King & Evans (1967). The possible reasons for the apparent differences of behaviour between stands have been briefly discussed in Section 2.2.1. In view of the uncertainty involved, it is difficult to decide which is the preferable method in any specific case.

A third approach to respiration is that of de Wit (1959, 1965); by explicitly designing his models to predict only gross photosynthesis, he apparently avoids the problem altogether. However such models have the disadvantage that they cannot be validated: to compare the predictions of growth models with experimental findings, the predictions must be given in a directly measurable form as net production rates.

While the concept of net photosynthesis needs no revision, the understanding of its components has recently been so improved that a brief explanation of the physiological basis for their modelling needs to be given.

The discovery (e.g. Moss 1966) that respiration rates of leaves in the light are, in many temperate-zone species, higher than those in the dark, complicates any fundamental approach to the modelling of net photosynthesis rates. An additional component of respiration, 'photorespiration', occurring in leaves exposed to light, uses a different metabolic pathway from that of dark respiration and requires separate modelling (Zelitch 1967, Hofstra & Hesketh 1969).

Since the models discussed in this review are less fundamental, their original mathematical forms can be retained provided the meanings of some of the original terms are changed. 'Respiration' must be defined strictly as dark respiration; 'gross photosynthesis' used in the present work in the sense of the older textbooks (e.g. Thomas 1947), must be regarded as the resultant of CO_2-fixation in the chloroplasts and CO_2-production by the pathways of dark respiration and photorespiration. Only in those tropical species (e.g. maize and sorghum) where photorespiration seems to be absent (Jackson & Volk 1970) can gross photosynthesis keep its original meaning.

When required for use in a model, the gross photosynthesis rate is calculated from the net rate by adding the rate of respiration in the dark. It seems therefore that de Wit's (1959, 1965) models, in common with those of other authors, do in fact rest on assumptions concerning the rate of dark respiration

What evidence there is suggests that the rate of respiration of a tissue depends closely on its general level of physiological activity. Thus, young tissues respire faster than old ones and organs with a high proportion of actively growing tissue respire faster than organs with little. Again, in step with general physiological activity, the rate of respiration rises with increasing temperature (over the range 0°to 30°C, Meyer & Anderson 1940) and falls in tissues suffering water-stress (Kramer 1969). Of the short term models, only that of Ross & Bichele (1969) attempts to include any of these factors.

2.2.4 The testing of predictions concerning the effect of leaf inclination on growth.

Since the same predictions relating productivity and leaf inclination have been made by Monsi & Saeki (1953), Duncan et al.(1967) and Ross & Bichele (1969) on the basis of their models, it would seem that the field confirmation of this relationship is of vital importance. Unfortunately, there are technical difficulties so far which have prevented definitive confirmation.

Although, at low LAI, models predict slightly higher growth rates in horizontal-leaved crops than in crops with erect leaves, at high LAI a much larger advantage is predicted for the erect-leaved type. The cross-over point is at about LAI 3.5 according to Duncan et al.(1967) and between LAI 3 and LAI 5 according to Monteith (1965). Above this point, the advantage of the erect-leaved crop is expected to rise with increasing LAI.

For a critical test of the models the ideal material would consist of two or more communities which differed only in leaf inclination. Growth-rate measurements would be carried out over an interval in which LAI did not exceed about 3 and also over another interval in which all communities would have similar LAIs, considerably greater than 4. The ideal plant material would undoubtedly be a set of genotypes differing only in the gene(s) determining leaf inclination (isogenic lines). Unfortunately such material has not yet been available for long enough for this test to have been satisfactorily performed. As a consequence, the experiments to be reported do not fully meet the requirements stated above. Hence, their results, although suggestive, are in some degree ambiguous. Experimental efforts have been concentrated on testing the effects predicted at high LAI.

The evidence against the validity of the models will be examined first. The net assimilation rate of erect-leaved sugar beet was found by Watson & Witts (1959) to be higher than that of a prostrate-leaved wild form. Saeki (1960) quoted this in support of his model. Monteith (1965) however pointed out that the LAI of the crops used by Watson & Witts only reached 2.8. If the P:I relations of the two forms were assumed to be similar, all models would predict that the wild form would have had the higher assimilation rate. The result thus tells against the validity of the models, but until the P:I curves have been demonstrated to be the same it cannot be considered to be strong evidence. It is possible that the clustered leaves of wild beet seriously transgressed the condition of random arrangement assumed by the models; if so, the models could not be expected to predict with accuracy.

A more serious objection to the models is that crops of widely differing canopy structures and P:I curves, grown under near-optimum conditions in one location, may all have the same maximum growth rate. Sibma (1968) has shown this from records of the growth of grass, oats, peas, barley, potatoes, maize, sugar beet and algae in the Netherlands; they all grew at a maximum rate of about 200 kg/ha/day. The great difference of leaf inclination between, say, grass and potatoes is not reflected in Sibma's data. Also, apart from considerations of leaf inclination, maize with its higher light-saturated rate of leaf photosynthesis might be expected to grow faster than the other crops (de Wit 1965), but in fact, in the Netherlands it does not. However, without a formal prediction of growth rates using the most recent models and measured crop and weather parameters, these data do not constitute very strong evidence against the validity of the predictions concerning leaf inclination. Some unconscious bias could have entered into the selection of the crops with the fastest growth.

Recently, Puckridge and Ratkowsky (1971) compared the photosynthetic response of canopies of two wheat varieties to horizontally-measured light flux density; one variety had erect leaves and the other had droopy ones. The LAIs achieved in both cases were up to about 6. No difference in the patterns of response was found even on sunny days although the models of de Wit (1965) or Duncan et al. (1967) would have predicted higher midday gross photosynthesis by an erect-leaved than by a more horizontal-leaved canopy. Unfortunately, the distribution of the inclination of photosynthetic area (here called DIPA) was not measured, nor were the P:I curves of leaves of the two varieties. It is thus impossible to apply, say the

Duncan model to these canopies to obtain a formal prediction.

Results of the same kind have been obtained by other workers using similar material and techniques (J.Angus, D.J. Connor pers.comm.). In the case of Connor's experiment, the leaf P:I curves were shown to be effectively the same. Although the wheat varieties differed markedly in the droopiness of their leaves, actual measurements of DIPA showed them to have nearly the same mean inclination of their photosynthetic area; however, the inclinations showed greater variability about the means in the droopy-leaved variety (D.J.Connor & C.Cartledge pers.comm.). The similarity of light response found by Puckridge & Ratkowsky (1971) could thus have been due to similarity of the DIPA and leaf P:I curves in the two varieties.

We turn now to the evidence which seems to support the predictions of the models. Using a densely planted rice crop, Matsushima et al.(1964) showed that the net photosynthesis rate was lower in a variety whose naturally erect leaves had been caused to droop by the attachment of paper-fasteners to the tips. Although the value of LAI was not given , it was probably greater than 4. Concerning the result, however, it might be argued that the lower leaves in the artificially 'drooped' canopy would have had a higher respiration rate than leaves low in a naturally 'drooped' canopy; their previous relatively good illumination would have deferred the normal reduction of respiration found in chronically shaded leaves (e.g.Ludwig et al.1965, McCree & Troughton 1966). On the other hand, there are indications that shading may not cause such large reductions of respiration rate in rice (Tanaka & Kawano 1966).

A similar kind of experiment was performed by Pendleton et al.(1968) who mechanically lifted the upper leaves of a horizontal-leaved maize community to an erect position. The treatment was applied at the time of pollination and was maintained until maturity. Although the grain yield of the maize with lifted leaves was found to be significantly higher than that of the control, the biomasses were not recorded *. Since the LAI harldy exceeded 4, the models would not, in any case, have predicted a marked advantage for an erect-leaved crop (Loomis & Williams 1969). The higher grain-yield was attributed by Pendleton et al. (1968) to the improved illumination of the leaves near to the ears (see Allison & Watson 1966).

A similar explanation seems to apply to Pendleton's (1968) comparison of two isogenic lines which differed only in leaf inclination. Biomasses were not reported but it was found that the grain yield of the erect-leaved form was 41% higher than that of the prostrate-leaved type. If, as is likely, the biomasses reflected this large difference of grain yields, these results would be far from what would be predicted by the models since the maximum LAIs attained were again close to 4. Such a discrepancy between observation and theory would suggest that the models no longer apply when the crop has entered the reproductive phase. Indeed, data of Osman (1968, in Milthorpe 1970) concerning wheat point to the same conclusion; 'source-sink' relationships and not whole-plant potential for photosynthesis may be controlling the rate of increase of biomass during this phase.

A further experiment in which natural leaf inclinations were modified experimentally was reported by Pearce et al. (1967) who grew seedlings of barley in seed-boxes tilted at various angles. For the measurement of photosynthesis, the seed-boxes were laid horizontally; the leaves of the barley seedlings were thus directed at different angles from the horizontal. Since the phyllotaxy was unaltered, the differences in the distribution of the inclination of the leaf surfaces were presumably not as great as might be suggested by the differences

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* The same is true for the report of erect-leaved selections of maize showing higher grain yields in Indian trials (CIMMYT 1969).

in the angle towards which the shoots were directed. Nevertheless, large differences between treatments were found in the light extinction coefficient, K (of Eqn. 2.1). Over a wide range of LAI (2 to 10), the measured rates of net production in the treatments were found to be quite well approximated by predictions based on the model of Saeki (1960). There were large differences in the rates of net production between tilting treatments: the more erect the shoots, the higher the rate.

A defect of the design, admitted by Pearce <u>et al</u>, was that in the treatments where the shoots were more nearly horizontal, the leaves were packed more densely. The accompanying variation in height of the top of the canopies caused differences in the distance of the tops of the swards from the artificial light source. The resulting differences in incident light (71:68:61) have therefore greatly exaggerated the differences between the treatments. A further criticism of the experiment is that the leaf area densities in the high LAI treatments were many times greater than found in field crops of similar LAI.

Nevertheless, taking into account the disparities of illumination, the predicted differences between the treatments were realised and were consistent over the two (unreplicated) experiments.

An alternative approach has been used by two other groups. Hayashi & Ito (1962) showed that within a group of 14 rice varieties, the steeper the inclination of the upper leaves, the greater the LAI reached at the time of flowering. This was shown to apply within three flowering-date categories. Steeper leaf inclination was also found to be associated with a greater increase of biomass over the succeeding three weeks and with a reduced rate of leaf senescence. The results concerning LAI at flowering (showing a range of LAI 3.8 to 9.7) support the predictions of the models, but the frequent observations of 'sink' effects during grain-filling in cereals (e.g. Nösberger & Thorne 1965, Bingham 1967, King et al.1967, Puckridge 1968) make interpretation of the other results less certain. If growth during the three weeks after flowering was truly limited by supply of assimilates, this experiment would provide strong evidence in favour of the general reliability of the models.

A second investigation of this type was carried out at Guelph where Gardener (1966) compared the growth rates of three erect-leaved and three droopy-leaved varieties of barley. After the point at which 95% of the incident light was intercepted, the growth rates were greater in the erect-leaved forms. Before this point, growth proceeded faster in the droopy-leaved forms. Following up this work, Tanner et al.(1966) classified 300 varieties of wheat, barley and oats according to erectness of foliage and leaf width. This grouping agreed almost perfectly with a grouping according to yield of grain. However, as Heslehurst (1970) pointed out, the high grain yield of the erect-leaved group was not necessarily associated with increased biomass; it might have been simply due to a greater density of fertile ears or better ear development. J.Angus (pers.comm.) has suggested that greater penetration of light into an erect-leaved canopy might allow more tillers to survive and produce ears. The results of Tanner et al.(1966) could thus be interpreted as a 'sink' effect (Heslehurst 1970, King et al.1967) : a greater number of 'sinks' (developing grains) per area of soil in the erect-leaved crops might have induced higher photosynthetic efficiency in the surfaces supplying them with carbohydrate. The same interpretation might be applied to the post-flowering results of Hayashi & Ito (1962).

A more satisfactory experiment was performed by Tsuno & Fujise (1965, quoted from Monsi 1968). These authors showed firstly that the P:I curves of leaves of rice and sweet potato were similar and then showed that the more erect-leaved rice crop had a higher optimum LAI than the horizontal-leaved sweet potato. As LAI increased, the advantage of the rice with respect to growth rate became greater. These observations agree closely with predictions based on the model of Saeki (1960). At low LAIs, the predicted advantage of horizontal leaves was, however, not discernible.

Although the evidence as discussed above is inconsistent and in most instances open to alternative explanations, it seems that there is reason to accept, provisionally at least, the predictions concerning leaf inclination. When more experiments have been performed using genotypes isogenic for leaf inclination, the position will become clearer.

2.2.5 Concluding remarks on the use of growth models.

Mathematical models of plant processes allow knowledge from various types of investigation to be integrated into a pseudo-plant system (Duncan 1967, Loomis 1969, Milthorpe 1970). By basing theoretical experiments on such a system, the investigator can assess the likely importance of each real process and parameter involved in the model. If a model has been well validated within a certain range of conditions, it can be used fairly confidently for predicting the growth of a crop under untried combinations of conditions, providing these are at levels within the original range. Assuming conditions outside this range, predictions can still be made, but with less certainty. Such extrapolations may be valuable where actual experiments are either impossible or too costly to perform (Duncan 1967).

To be of really practical use, however, photosynthesis models of the type discussed in previous pages must be incorporated into dynamic models of plant growth and development.

The building and validation of such a model has been undertaken by the Wageningen school (de Wit & Brouwer 1968, Brouwer & de Wit 1968). Although the model is still in an early stage of development, its predictions of growth in the field seem definitely promising. When this, or similar models have been sufficiently refined, they will be of help in choosing selection criteria for the breeding of new crop varieties. Another use will be in the definition of suitable areas for the culture of particular varieties.

The building of rational models also has heuristic value. The model-builder is usually faced with a multiplicity of factors, all known to affect to some extent the process which he hopes to simulate. Although he may feel tempted to include all factors in his model, economic considerations often oblige him to restrict his attention to only a few of them. He therefore chooses those factors which appear to him to be the most important in the situation with which he is concerned.(Writing of the modelling of plant growth, Brouwer & de Wit (1968)point out that it is not the plant but opinions which are simulated). In this way, the modeller's opinions are crystallised and made explicit, while the flexibility of the simulation procedure allows the testing of alternative approaches. In addition to this, during the assembly of the information on which the model is to be based, the gaps in available knowledge become more clearly defined (Duncan 1967). Research reports are reviewed in depth and published data are reevaluated. The attendant clarification of thinking, along with experiments using the completed model, help in the design of really critical experiments.

Over recent years, attempts to model plant growth have disclosed a number of particularly difficult aspects. These are listed below with some comment.

1. <u>The percentage of the incoming radiation which is photosynthetically active radiation (% PAR)</u>. Values assumed to apply to total radiation have ranged from 50% (de Wit 1965) to 44.4% Williams <u>et al</u>.1968). Until more is known of the action spectra of different species, the choice of a value for %PAR within this range will be rather arbitrary.

2. <u>The effect on photosynthesis of fluctuations in the irradiance of the leaf</u>. Fluctuations of the level of incident radiation are caused by clouds passing over the sun. Fluctuations of the irradiance of individual leaves within the canopy are also caused by the changing elevation of the sun and by the wind changing the relative positions of the leaves in the canopy. Although perhaps the total sunlit leaf area in any layer of a canopy remains roughly constant over intervals of a few minutes on cloudless days, leaf movements result in rapid changes of the distribution of the layer's foliage between the sunlit and shaded categories. Fluctuations of irradiance of various frequencies are clearly very common (Ross 1968, Norman & Tanner 1969).

The question arises as to whether these fluctuations alter the efficiency with which light is utilised. Variation of the incident light flux, as caused by passing clouds leads to a loss of efficiency in terms of photosynthesis per unit of energy received. This was demonstrated by Evans (1963), Denmead (1968) and McCree & Loomis (1969). The loss of efficiency is due partly to the behaviour of the stomata; they respond faster to decreases of irradiance than they do to increases (Evans 1963). Thus, predictions of production based on average radiation incomes may tend to be too high if radiation conditions fluctuate. McCree & Loomis (1969) showed that with a suitable light sensor, predictions of net production can, however, be brought very close to the observed values.

Concerning short-term fluctuations, Huxley (1969) using

5 species, tested the effect on growth of alternations between being in the sun and being in the shade, with various rates of alternation. The growth rate under a regime of alternations every two seconds was the same as that with a fixed pattern of light and shade. Similarly, McCree & Loomis (1969) showed that alternations between high and low light with periods of between 10^{-2} and 10^{-3} seconds did not affect efficiency of light-use providing the low-light level remained above a certain minimum. On the other hand, Pollard (1970) working with aspen found that the efficiency of light-use was increased by rapid alternations between high and low light. This agreed with the 20% increase of efficiency obtained by McCree & Loomis (1969) using rapid alternations of sunlight and complete darkness.

Norman & Tanner (1969) suggested that if the period of fluctuation is long enough and the irradiance during the low light phase is low enough, the stomata will close and the effect noted above will reduce the efficiency. If stomata remain open there would seem to be a chance of an increased efficiency. An important conclusion is that if, under field conditions, the wind keeps long droopy leaves in motion, increased efficiency of light-use within the canopy might compensate for the less even spread of light over the leaves compared with that in a canopy with stiff, erect leaves.

3. Non-random distribution of leaves within layers. Although most stands of plants show a degree of non-randomness in the horizontal distribution of leaves (Wilson 1959), the models of Duncan et al. (1967) and the Estonian group rely on the simplifying assumption that leaves are randomly distributed. Calculations by de Wit (1965) suggested that when the LAI is about 5, the variation in the degree of randomness of distribution observed by Monsi & Saeki (1953), may not affect greatly the accuracy of the predictions of photosynthesis models. Tooming & Ross (1964) found that light extinction at two solar elevations was the same in square- and row-planted maize crops and agreed well

with predictions based on the assumption of random distribution. However, Laisk (1969) found that skylight penetrated more freely than predicted into stands of sunflower, sorghum and maize; he attributed this disagreement to the aggregation of leaves around individual plants. Attempting to meet this difficulty, Saeki et al (1965, quoted from Monsi 1968) introduced a model in which leaves were treated as randomly-dispersed clusters. Although this was a promising approach, it has apparently not yet been shown that a prediction of growth rate based on it is more accurate than one based on the standard model of Saeki (1960). In general, the difficulty of the mathematics involved has prevented any rigorous treatment of non-random leaf distributions. The effect on growth rates of such distributions is probably considerable in extreme cases.

4. Sink effects. In certain circumstances, photosynthesis rates of green surfaces may be affected by the rate of utilization of carbohydrate in the parts of the plant which act as sinks for it. (King et al. 1967) have reviewed evidence which shows that a wide range of organs, vegatative as well as reproductive, may act in this way. These affects are extremely difficult to estimate for inclusion in a model.

5. Respiration. The simple and arbitrary fashion in which respiration has been treated in otherwise sophisticated models (Duncan et al.1967, Ross & Bichele 1969) indicates the poverty of data on the subject.

A final point concerns the validation of growth models. As emphasized by Monteith (1965), the adequate validation of a model requires that all its input parameters should be measured, rather than estimated. Estimated parameters too easily become 'fudge' factors (respiration rate is the almost universally-used 'fudge' factor in growth models). The model's prediction must then be checked against the real situation of which the presumed determining variables have been measured. Unfortunately, growth rates in the field depend on many factors, and a flexible model will need many parameters, more perhaps than can be measured with the resources available on any one occasion. For this reason, the complex models produced in recent years can perhaps never be validated in the simple way presribed by Monteith. An acceptable alternative is, however, available: the breaking of the model into sub-models of a size which allows all inputs, outputs and parameters of the chosen sub-model to be measured on one occasion. The complexity which has necessarily been introduced into recent models challenges their authors to design the required critical experiments and cooperate in their implementation. The task of validation is such a large one that only cooperative ventures seem likely to succeed.

ADDENDUM : Page 58, line 23. For 'Production Ratio will be used...' read 'Production Ratio (PR) will be used...'

2.3 Growth of crops and the use of water under conditions of limiting water supply.

The shoots of living plants tend to lose water to the surrounding air. The roots take up water from the soil, and so, in favourable circumstances, the plant continues to maintain its vital activities. The growth of the plant depends on the accumulation of carbonaceous material by the process of photosynthesis. When water is in short supply, the relative rates at which transpiration and photosynthesis occur is of agronomic significance since the ratio of the rates will determine how much growth occurs during the utilization of a given quantity of water.

Various indices have been defined to describe this ratio in ways which are useful from an agronomic point of view. The commonly used term Transpiration Ratio (e.g. Klages 1942) is the weight of water transpired during the production of unit weight of biomass (usually shoot weight only). Briggs & Shantz (1913) used Water Requirement in the same sense. Maximov (1929) suggested that the redprocal of the above ratio would be a preferable index emphasizing growth rather than the use of water which accompanies it. This reciprocal of Transpiration Ratio was termed by Maximov the Transpiration Efficiency. Monteith (1966) preferred the synonymous term Production Ratio; it is this term which will be used in the present work. Production Ratio will be used as the ratio of biomass production to transpiration when each has been accumulated over an interval of at least 24 hours. The symbol P/T (Downes 1970) will be used for the ratio of instantaneous rates in preference to the symbol E/A of de Wit (1958) and Bierhuizen & Slatyer (1965).

Since transpiration cannot be measured directly in field experiments, the term Water-Use Efficiency (WUE) is sometimes measured as being a parameter of great practical importance.

Viets (1962) defined WUE as the weight of shoot or marketable yield produced per unit weight of water used. The water 'used' includes that lost by soil- and plant-surface evaporation, run-off and drainage as well as that transpired from the plants.

Although the rates of photosynthesis and transpiration of a plant community may be combined in a meaningful ratio, the two processes are largely independent (Penman & Schofield 1951, Monteith 1963). Transpiration occurs since the water of the shoots tends to evaporate; it is then carried away as vapour into the bulk atmosphere by diffusion and turbulent transfer (e.g.Slatyer 1967). The rate of transpiration of a leaf is determined by a driving force and by the resistances in the transfer pathway (Gates 1968). The driving force is essentially the difference in water vapour concentration between the substomatal air-space and the bulk air above the canopy. The greater this difference, the faster will the loss occur. The two resistances in the pathway, r_s and r_a, represent resistances to the diffusion and turbulent transfer of water vapour along two parts of the path; r_s is concerned with passage through the stomata and r_a with movement through the external air (Gaastra 1959). Although the resistance of the cuticle, r_c, is relatively very large (Waggoner 1966), some transpiration occurs through it (Oppenheimer 1960), and so r_c may be treated as a resistance in parallel with r_s (Gates 1968).

Photosynthesis causes carbon dioxide to be incorporated into organic substances in the chloroplasts of green parts of the shoots. The consequent lowering of the CO_2 concentration in the chloroplast creates a difference between the concentration at the site of photosynthesis and that in the bulk air. This concentration difference acts as the driving force for the transfer of CO_2.

As with transpiration, most CO_2 exchange occurs along a pathway involving the stomata; the resistances to CO_2 transport are analogous to those described above for water vapour. However, in this case a further resistance, the 'mesophyll' resistance, r_m, is added to the resistance to water-vapour transfer. This includes several components such as resistances to entering the water-phase in solution, to intracellular transport and also a biochemical resistance to carboxylation (Troughton & Slatyer 1969).

The presence of a third resistance, r_m, in the path of CO_2 transport, has led Gaastra (1959, 1963), Waggoner (1966) and Slatyer & Bierhuizen (1964) to suggest that increase in r_s might cause an increase in production ratio. If the concentration differences of water vapour and CO_2 remain constant, the production ratio (PR) is proportional to $\Sigma r / \Sigma r'$, where Σr is the sum of the two resistances to water-vapour loss, and $\Sigma r'$ is the sum of the three resistances to CO_2 uptake (Bierhuizen & Slatyer 1965). Since the presence of r_m makes r_s a smaller fraction of the total in the denominator than in the numerator, an increase in r_s is expected to cause $\Sigma r / \Sigma r'$, and therefore PR, to rise. This was demonstrated experimentally by Slatyer & Bierhuizen (1964); by raising r_s artificially, they obtained a 40% increase in PR in cotton plants over a 4 week period (growth as measured by biomass increase per unit of leaf area was however reduced, relative to that of controls, during this period).

Most estimates suggest that the mesophyll resistance is larger than the minimum r_s (Penman & Schofield 1951, Gaastra 1963, Cowan & Milthorpe 1968a), that the minimum value of r_s is much greater than r_a under field conditions (Monteith 1963, Kanemasu *et al*.1969), and that r_m may not be much affected by water stress (Troughton 1969, Troughton & Slatyer 1969). Thus, water stress by causing stomata to close when the potential rate of evaporation is high (e.g. Kanemasu & Tanner 1969), might be expected to result in plants using water more efficiently in the production of biomass.

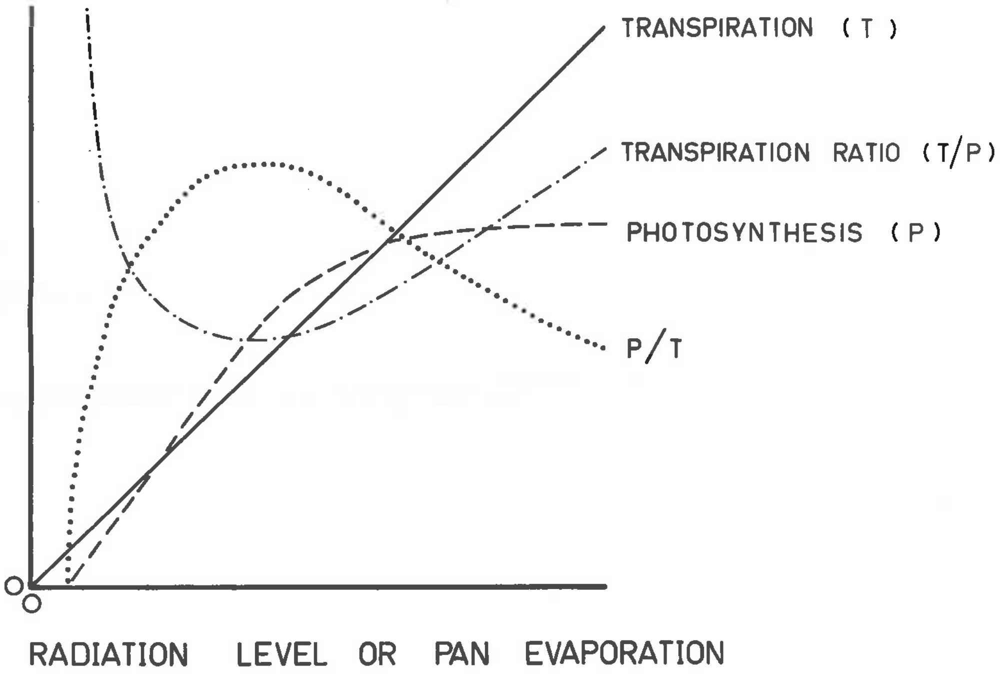
Working with an arid zone species, Hellmuth (1969) observed a three-fold increase in PR in the course of a rainless summer. This appeared to substantiate Slatyer's (1964) suggestion for this type of species. For mesic crop species, however, the evidence of changed production ratios in water-stressed plants is rather contradictory. This is discussed below under the headings of long-term measurements of PR in field crops, long-term measurements in container-grown plants and measurements over short periods. Finally the available evidence regarding the water use efficiency of mixtures is considered.

2.3.1 Long-term measurements of PR in field crops.

In semi-arid or arid regions, where crops are likely to suffer some degree of moisture stress, yields of dry matter depend more or less linearly on the amount of water falling as rain or applied as irrigation (Cole & Matthews 1923, Clements & Weaver 1924). This observation suggests that the production ratio remains substantially constant over a wide range of water stress situations. However, a graph of Cole & Matthews' data (see Black 1957) of biomass of wheat against water used shows a considerable scatter of points about the regression line. This scatter suggests that the production ratio may depend somewhat on weather and soil conditions.

In a thorough review of crop yields as related to water supply, de Wit (1958) showed that the transpiration ratio or a modified form of it, was in fact remarkably constant over all stress treatments of experiments concerning a particular species, no matter whether they were performed in the field or in containers. Arguing from the relationships shown in Fig.2.1, he suggested that in regions with abundant sunshine, as in Cole & Matthews' study, the water transpired should be standardised by being divided by evaporation from an open pan of water. This would have the effect of removing the dependence of transpiration

Fig. 2.1 The expected variation of rates of photosynthesis and transpiration, Transpiration Ratio and P/T as affected by radiation level. Pan evaporation is assumed to be proportional to radiation level (after de Wit 1958).


TRANSPIRATION (T)
TRANSPIRATION RATIO (T/P)
PHOTOSYNTHESIS (P)
P/T
O
O
RADIATION LEVEL OR PAN EVAPORATION

ratio (reciprocal of PR) on radiation. According to Fig.2.1, this dependence would be a close one in sunny regions. Thus, soil-surface evaporation was estimated and subtracted from the soil-water income to give estimated transpiration; this was divided by pan evaporation arrived at from meteorological data. Cole & Mathews' data, and several sets of similar field data (using various species), were replotted and in each case compared with regression lines calculated from pot experiments of other authors who had used the same respective species. The agreement was often remarkably good.

The curves of Fig. 2.1 suggested that at medium radiation levels, transpiration ratio and PR are relatively independent of radiation level. Confirming this suggestion, de Wit found that the analysis of experiments conducted in more cloudy regions did not require the transpiration to be standardised. The graphs of biomass plotted directly against estimated transpiration lay close to the regression lines derived from pot experiments using the same species. The results from both types of region agreed in showing that the biomass:transpiration* relationship was linear while water supply was limiting growth; the slope of the line depended only on the species. When water was not limiting growth, a plateau was reached whose height depended on the fertility (nutrient status) of the soil. De Wit suggested that the alternation of periods of water shortage and excess and also the interdependence of nutrient uptake and water supply may result in the plateau being approached by a curve rather than by a straight line. The results of wheat shoot weight of Widstoe (1912) and of wheat grain yield of Fortier (1925) showed marked curvature before the plateau was reached. In these cases greater stress apparently resulted in higher production ratios.

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* standardised or not, as appropriate.

Presumably because of the difficulty of estimating losses of water by drainage and soil-surface evaporation (de Wit 1958, Black et al.1970), de Wit's analytical approach has not been developed in subsequent experimentation. Without such estimates, the numerous data on water-use efficiency (reviewed by Pendleton 1966) give only an uncertain indication of the effect of stress on PR. These results will therefore be treated with some caution.

Several reports have suggested that stressed crops have a higher WUE than unstressed ones (Carlson et al.1959 with maize, Musick et al.1963 with maize, Stanberry & Lowery 1965 with barley, Doss et al. 1970 with forage maize). Viets (1966) concluded that there is 'some evidence' of higher WUE in conditions of water shortage, especially if biomass is the yield considered. It seems that greater surface evaporation or drainage from more frequently wetted soil might explain some of the lower WUE at higher moisture supplies, though evaporation from the soil surface under pastures or fodder crops is likely to be less than the 50% of the total evapotranspiration found sometimes in cereals (Penman & Long 1960, Tanner et al.1960). In addition, irrigated plots will be more affected by advected heat (Viets 1962). More simply, these plots may lie on de Wit's (1958) yield plateau where further water only reduces the apparent WUE.

Other reports suggest, however, that the WUE of stressed crops is either the same or lower than that of unstressed crops (Stanberry et al.1955 with lucerne. Ustenko 1963 with maize, Doss et al.1964 with sorghum). The results are not decisive though; for example Doss and colleagues found the WUE of their high-watering treatment to be enhanced in one year but not in the next.

In contrast to the uncertainty of the effect of water stress, an improvement of nutrient status gives large and fairly consistent increase of WUE (Penman 1956, Viets 1962, Cohen & Strickling 1968, but see Doss et al.1970). While increases in WUE may result from fertilizer application at low levels of moisture supply, the effect is greater in a higher moisture regime (Smika et al.1965). Wind (1954) reported an instance where fertilizer application led to a four-fold increase in yield of grass while the evapotranspiration increase by only one quarter. It seems possible that some of the improvement of WUE often seen under irrigation (see above) may be attributed to an indirect effect upon nutrient uptake; moisture stress impairs the nutrient uptake capacity of roots (Olsen & Kemper 1968) and dry surface soil denies roots access to the soil-layer where nutrients are most plentiful (Troughton 1962, Cowan & Milthorpe 1968a).

2.3.2 Long-term measurements of PR of plants grown in containers

In his review of investigations of production ratio using sealed containers, de Wit (1958) assembled the results of 18 water stress experiments. When graphed as shoot weight against transpiration, the points of 7 experiments lay on a linear regression lines through the origin; in 9 experiments, a regression line would make an intercept with the shoot weight axis; in 2 experiments the intercept would be with the transpiration axis. De Wit concluded that there might be a slight indication that the production ratio of plants very short of water is higher than for less stressed plants.

The only sealed container experiment in which whole-plant weights (i.e. including roots) were reported, showed a linear regression of total weight on transpiration (Boonstra 1934 with peas). The line passed through the origin.

Since the level of water stress experienced by a plant is affected by the evaporative demand of the air (Denmead & Shaw

1962), the response of the production ratio to this factor is of importance. Montgomery and Kiesselbach (1912) found that the production ratio of corn in a humid greenhouse was 80% higher than in a dry one; the difference of relative humidity was about 20%. Using two growth cabinets with a relative humidity difference of 40%, de Wit & Alberda (1961) found that the PR of the oats and barley in the more humid cabinet was more than double the PR of plants in the dry one. Briggs & Schantz (1913) observed that the production ratio of lucerne was reduced in 'hot weather'. This could either be an effect of temperature but could as well be an effect of correlated radiation intensity (see Fig. 2.1).

2.3.3 Shorter term measurements of PR

Two field studies have shown that in maize the growth rate is more sensitive than transpiration to low levels of moisture stress (Baker & Musgrave 1964, Shinn & Lemon 1968). Baker & Musgrave found that net photosynthesis was reduced at stress levels at which transpiration was unaffected. Shinn & Lemon (1968) confirmed this using increase of biomass as an integrated measure of net production over a drought period.

Denmead (1968) reported two days' records of aerodynamic measurements of vapour and CO_2 fluxes over a wheat field, in which net assimilation of CO_2 was reduced in the middle of the day with no simultaneous reduction of transpiration. By removing the effects of the measured fluxes due to the soil, Denmead showed that a large decrease of P/T had occurred over the midday period. Rather significantly, net P had decreased while stomata were apparently wide open; this seemed to imply a possible direct action of some kind of stress (water- or heat- stress) on photosynthesis rate. In terms of diffusive resistances this would be accounted for by an apparent increase of r_m. Boyer (1965) has observed a similar effect in cotton under laboratory conditions of osmotic stress (but cf. Troughton & Slatyer 1969).

Slatyer (1957) examined biomass increase and transpiration at lethally high stress levels, using tomatoes grown in pots. He found that although growth had ceased, transpiration continued at a measurable rate. This and the previous examples in the section suggest that P/T, and hence PR, may be reduced at times of water stress.

Several studies have included simultaneous short-term measurements of photosynthesis and transpiration made on pot-grown plants suffering degrees of water-stress. Three investigations of this kind (Schneider & Childers 1941, with apple, Loustalot 1945 with pecan, Brix 1962 with pine seedlings and tomato) have shown that as stress increased, net photosynthesis and transpiration decreased in parallel. Kanemasu & Tanner (1969) used a less satisfactory index of growth i.e. leaf area expansion, but similarly showed that during a drying cycle, 'growth' and transpiration of snap beans decreased closely in step. Although they did not demonstrate a correlation between their index of growth and net production, they felt able to suggest that the parallel reduction of 'growth' and transpiration, presumably caused by the observed increase in r_s, showed that r_m must be relatively small.

Only one study has reported that stress affected transpiration more than photosynthesis (Zavitkowski & Ferrell 1968). Using seedlings of two ecotypes of Douglas fir, these authors showed that transpiration was proportional to soil moisture tension over the whole range used, but photosynthesis only declined when the soil tension reached 1 atmosphere.

Although Totsuka (1963) has enumerated the other components of long-term production ratios (e.g. night-time respiration and transpiration rates), it would seem that day-time exchanges of CO_2 and water, by virtue of their greater magnitudes, are likely to dominate in the determination of long-term PR. Although the short-term studies of P/T have given conflicting results, the tendency towards parallel responses by photosynthesis and transpiration seems consistent with many authors' observation that long-term production ratios are not much affected by the level of stress when water supply is limiting.

2.3.4 Production Ratio of Mixtures

In a consideration of the way in which mixture components might contribute to the water-loss from a mixed sward, Milthorpe (1961) quoted an anonymous author who suggested that the reduced transpiration of the subordinate 'would possibly lead to a greater proportion being lost from the aggressor due to the redistribution of available energy'. The implication of this proposition is that in terms of the energy balance (e.g. Lemon 1966), closure of stomata of the subordinate's leaves will increase the proportion of their net radiation income which will be dissipated as sensible, rather than latent, heat. The leaves of the subordinate will act as local sources of advected heat for the leaves of the aggressor. The PR of the aggressor might, in this case, be lower than in its monoculture. Concerning the overall PR of a mixed community, Milthorpe (loc.cit.) quoted a suggestion by Penman (1953) that if the canopy of the taller component projects markedly above that of the shorter, as in an orchard with grass sward, the increased ventilation may well produce a greater loss than from a complete cover of the taller species.

According to the literature, no measurements of the overall PR of mixtures seem to have been made. However, Lampeter (1960) reported WUEs for 9 mixtures of which 4 were grass+grass and 5 were legume+grass. They were grown in containers of soil at 70% field capacity, with no control of soil surface evaporation. Lampeter calculated an expected WUE for the mixtures based on the proportions of each component in the total shoot weight and the components' WUEs in monoculture. Basing WUE on shoot weight, 5 mixtures showed a significant depression of WUE below that expected. Basing WUE on whole-plant weight, only 1 mixture had a significant depression of WUE. However, the WUE of all other 8 mixtures fell below expectation. In Lampeter's results, the two different kinds of mixture seemed to be behaving similarly.

The measurement of the separate PRs of components in a mixture has recently become a possibility. Jones & Handreck (1965) found that silicon is carried into oat plants passively in the water taken up for transpiration; Handreck & Jones (1968) suggested that this property, shown also by some other species including wheat, might be used to estimate a crop's transpiration.

3. A CONTRIBUTION TO THE THEORY OF THE GROWTH OF MIXTURES

In this Section, an attempt is made to construct a theoretical basis for the treatment and interpretation of the experimental data reported in the thesis. The Section does not aim to provide a comprehensive model to explain all neighbour effects. Rather, it aims at elaborating those aspects which seem vital to the understanding of transgressive yielding. It is hoped both to develop a theoretical approach to mixture productivity and to assist the presentation of the experimental material in later sections.

Since any case of transgressive yielding is inevitably accompanied by a deviation of RYT from unity (though the reverse is not necessarily true), the first part of the Section (see 3.1) is devoted to examining why RYT might be expected, on theoretical grounds, to be usually close to unity. Section 3.1 continues by exploring the possible reasons for deviations from this expected value and concludes by showing that although a RYT deviation is a vital prerequisite for transgressive yielding, the latter only occurs when certain other conditions are also fulfilled.

The second part of the Section (3.2.1 and 3.2.2), shows how the analysis of mixture experiments has suffered in the past from various deficiencies. Either the data have been analysed using a rational model but no proper statistical treatment, or, on the other hand, the analysis has been adequate statistically, but based only on an empirical model. The advantage of an analysis combining the positive features of the two approaches is outlined and such an analysis is described (Section 3.2.3).

3.1 Some extensions of the de Wit model for the special case of 1:1 mixtures.

The distribution of RYT values has been shown in Section 2 to be centred on unity (Table 2.2). If this distribution can be assumed to be analogous to a normal probability distribution, the mean value of RYT may be taken as the 'expected' value. Little error seems to be involved if 1.0 is presumed to be this expected value.

De Wit (1960) based his model of the effects of competition on the assumption that the growth of a species was proportional to the 'space' it acquired. This abstract 'space' was defined as being equivalent to the growth factors, light, water and nutrients, when these are homogeneously distributed over and in the field where the plants grow. When the outcome of competition for one particular factor is mainly determining growth rates in a mixture, it seems that de Wit's 'space' can be identified as the supply of this 'principal' factor. In the field, competition for one factor (a 'one-factor' system) is only found when the soil is highly fertile and well watered (e.g. Iwaki 1959, Stern & Donald 1962a, Jennings & Aquino 1968); the 'principal' factor is then light. By artificial means (partitions, nutrient application to leaves or the regulation of humidity), experimental communities could however be produced where growth would be limited by only water or just one nutrient.

In such one-factor systems, yield seems likely to be strictly proportional* to the quantity of 'principal' factor absorbed when this factor is in limited supply. For example, in Section 2, evidence was reviewed which showed that when water-supplies are limiting, yield responds linearly to water uptake over a wide range of uptakes. For light, Shibles &

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* 'Strict' proportionality implies a linear relationship with the line passing through the origin.

Weber (1965) and Baker & Meyer (1966) showed, for soybeans and cotton respectively, that crop growth rates respond linearly to radiation intercepted over a wide range of conditions. Similarly, Singh et al. (1967) found that the yield response of cocksfoot to nitrogen uptake was almost linear up to an uptake of 50 kg N/ha. In these four cases, linear regression lines drawn through the graphed points at medium and low levels of factor uptake pass through or close to the origin.

If it is assumed for the present that yield is strictly proportional to the uptake of a 'principal' factor over the observed range, the de Wit model seems to have a simple graphical interpretation (see Fig. 3.1). In a one-factor system, the factor whose absorption is given as the abscissa will be light, water or a nutrient.

In Fig. 3.1, monoculture plants of two species are shown as absorbing the same quantity of the 'principal ' factor, Q, However, because they differ in the efficiency with which they utilise it, their monoculture yields differ. As in Section 2.2, species A and S will always be taken as being the aggressor and subordinate respectively; here, species A also gives the greater monoculture yield (i.e. $Y_{AA} > Y_{SS}$). If, in both monocultures, the uptake of Q per plant is 1 unit, the aggressor in the mixture has a per-plant uptake of $(1 + F_{AS})$ units. If total uptake is the same in all communities, the subordinate's per-plant uptake is $(1 + F_{SA})$ units, where $F_{SA} = -F_{SA}$. Thus, if A's per-plant uptake in mixture is $(1 + F_{AS})$ times that in its monoculture, and the yield is strictly proportional to uptake, then

$$Y_{AS} = Y_{AA}(1 + F_{AS}) \quad .$$

Similarly, for species S,

$$Y_{SA} = Y_{SS}(1 + F_{SA}) \quad .$$

Fig. 3.1 Simple graphical interpretation of de Wit's (1960) model when competition is for only one growth factor, Q. The scale of uptake of Q has been adjusted to give plants of the monocultures of the two species, A and S, unit uptake. Small single-headed arrows by the monoculture points lie in the direction of the points of the same species grown in the mixture. For explanation, see text.

Y_{AA} - per-plant biomass in monoculture of A (○)

Y_{SS} - per-plant biomass in monoculture of S (□)

Y_{AS} - per-plant biomass of A in mixture with S (●)

Y_{SA} - per-plant biomass of S in mixture with A (■)

P_1 - per-plant biomass of higher-yielding monoculture

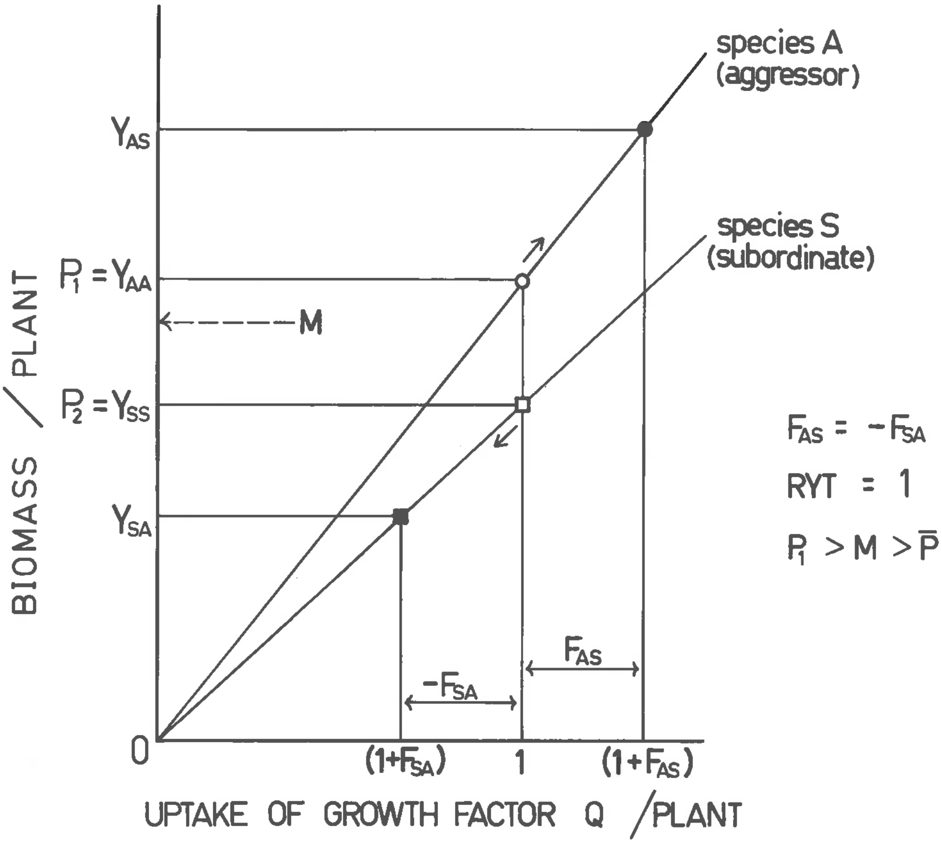
P_2 - per-plant biomass of lower-yielding monoculture

M - average per-plant biomass in the mixture

F_{AS} - proportional increase in per-plant uptake of Q by plants of A in mixture, compared with their uptake in monoculture

F_{SA} - proportional decrease in per-plant uptake of Q by plants of S in mixture, compared with their uptake in monoculture

RYT - Relative Yield Total of mixture


species A
(aggressor)
species S
(subordinate)
Y_{AS}
$P_1 = Y_{AA}$
M
$P_2 = Y_{SS}$
Y_{SA}
BIOMASS / PLANT
0
$(1+F_{SA})$
1
$(1+F_{AS})$
$-F_{SA}$
F_{AS}
UPTAKE OF GROWTH FACTOR Q / PLANT
$F_{AS} = -F_{SA}$
RYT = 1
$P_1 > M > \overline{P}$

The RYT of the mixture is now given by

$$RYT = \left[\frac{Y_{AA}(1 + F_{AS})}{Y_{AA}} + \frac{Y_{SS}(1 + F_{SA})}{Y_{SS}} \right] /2$$

$$= (1 + F_{AS} + 1 + F_{SA}) / 2 = 1 .$$

From this last equation it is clear that this simple model provides a theoretical basis for the observation that RYT values of mixtures tend to lie close to unity.

3.1.1 Deviations of RYT from unity (gain or loss of growth factor).

Among the situations requiring adaptation of his basic model, de Wit (1960) considered mixtures in which the components were exploiting more or less different sources of the same 'principal' factor, i.e. the components were competing for the same factor but were obtaining it in part from differing sources. In a mixture of this type, when only factor Q is the subject of competition, the increase in the per-plant uptake of Q by the aggressor (compared with that in monoculture) will exceed the reduction of uptake by the subordinate (compared again with uptake in monoculture). This is shown diagrammatically in Fig. 3.2a, where F_{AS} is seen to be greater than $-F_{SA}$. There has been a 'factor-gain' by the mixture as a whole since the total uptake of Q has been greater in the mixture than in the monocultures. This factor-gain is indicated by a positive deviation of the mixture's RYT :

$$RYT = 1 + \frac{F_{AS} + F_{SA}}{2} , \quad (F_{AS} + F_{SA}) > 0 .$$

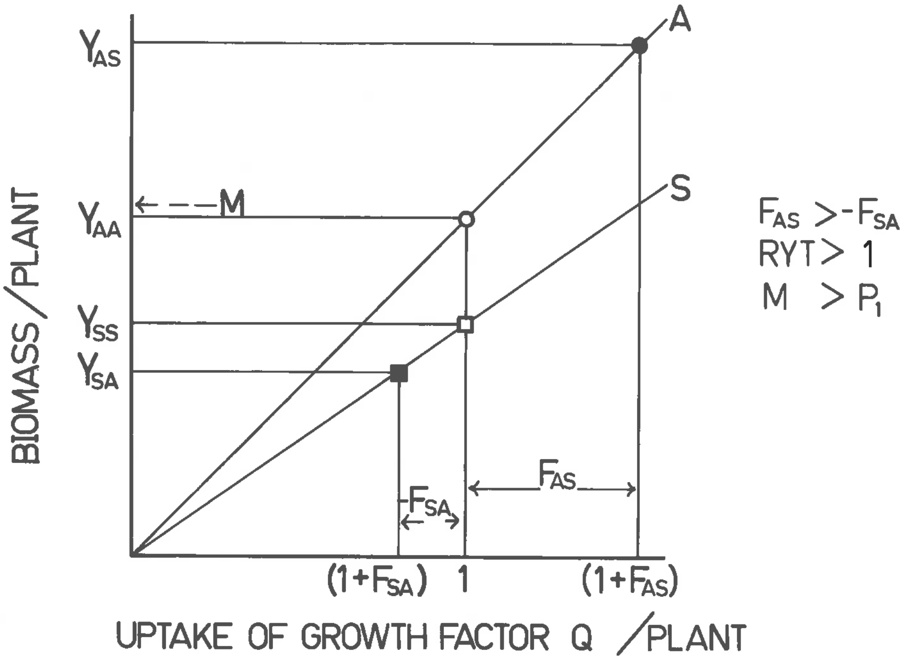
Corresponding to a factor-gain, a 'factor-loss' by the mixture is also possible. In such a case, the increase of uptake of Q by the aggressor, resulting from being in mixture,

Fig. 3.2 Graphical interpretation of de Wit's (1960) model in the cases of factor-gain and factor-loss by mixtures. Gains and losses by individual species are relative to the uptake of factor in the species' own monoculture. Symbols as in Fig. 3.1 .

(a) Factor-gain; in mixture, the gain of Q by species A exceeds the loss by species S. The mixture over-yields in this example, but factor-gain by the mixture would not necessarily be accompanied by overyielding (this is explained in a later section, 3.1.5).

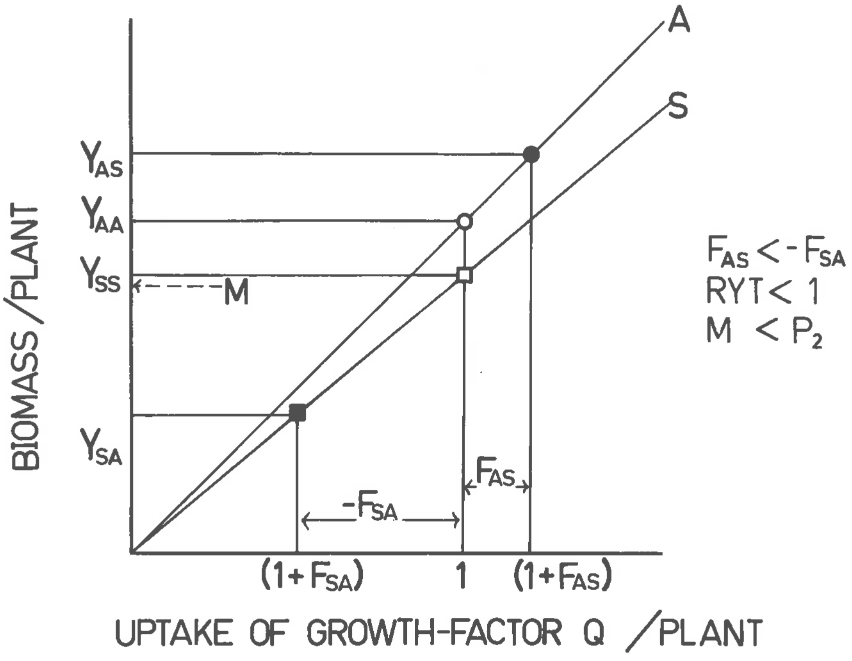
(b) Factor-loss; in mixture, the gain of Q by species A is less than the loss by species S. The mixture underyields in this example, but again factor-loss by the mixture would not necessarily involve underyielding.

(a)



Y_AS
Y_AA
Y_SS
Y_SA
M
A
S
F_AS
-F_SA
(1+F_SA)
1
(1+F_AS)
BIOMASS /PLANT
UPTAKE OF GROWTH FACTOR Q /PLANT
F_AS > -F_SA
RYT > 1
M > P_1

(b)



A
S
Y_AS
Y_AA
Y_SS
M
Y_SA
F_AS
-F_SA
(1+F_SA)
1
(1+F_AS)
BIOMASS /PLANT
UPTAKE OF GROWTH-FACTOR Q /PLANT
F_AS < -F_SA
RYT < 1
M < P_2

is less than the reduction of uptake suffered by the subordinate (see Fig. 3.2b). The RYT here will fall below unity:

$$\text{RYT} = 1 + \frac{F_{AS} + F_{SA}}{2} \quad , \quad (F_{AS} + F_{SA}) < 0$$

The practical situations in which transgressive yielding by mixtures might occur have been reviewed in Section 2.1.2. Most of the cases where there is a possibility of overyielding due to a complementary use of the environment, may now be seen to be situations which might lead to factor-gain (e.g. temporal sharing or root stratification). Mutual allelopathic stimulation could have the same effect.

On the other hand, situations likely to lead to factor-loss are less easy to envisage. One possibility is a mixture in which each component gives out substances which inhibit the growth of the other component. A factor-loss could also occur in a mixture of components which differed greatly in height (see Section 2.3.4). The increased atmospheric turbulence within the mixture canopy might increase the loss of water by surface evaporation so that less water would be available for plant use in the mixture than in either monoculture.

3.1.2 Deviation of RYT from unity caused by changes of efficiency of utilization.

The deviations of RYT so far considered have been due to overall factor-gains or factor-losses, in which

$$F_{ij} \neq - F_{ji}$$

It is proposed here that the observed deviations of RYT from unity may also be due, to some extent, to deviations of yield from the strictly proportional dependence on factor uptake which has been assumed up to this point. When such a dependence is maintained in a species in both mixtures and monoculture, the ratio of yield to quantity of factor taken up has the same value in all cases. Since this ratio is a direct measure of how efficiently plants use the growth factor in the production of biomass, it follows that strict proportionality of yield and uptake implies a constant efficiency of utilization. When however strict proportionality is not maintained, the efficiency of factor utilization by a species in mixture may be higher or lower than that in monoculture. In general, the efficiency of utilization of a growth factor which is in limiting supply is likely to depend (a) on the level of per-plant uptake of the factor and (b) on the level of uptake and nature of any other factors also in limiting supply. For the present, a one-factor situation will continue to be assumed.

3.1.2.1 Efficiency of utilization as affected by the level of uptake of factor concerned.

For many species, experiments with monocultures have established the form of dependence of yield on the level of per-plant absorption of various growth factors (e.g. Black 1963, de Wit 1958, Singh et al.1967). The design has normally involved the use of varied levels of supply of the factor while the quantity of factor absorbed has been either calculated or measured. Other factors have usually been at high, non-limiting levels. The result has been a one-factor system.

The general finding of these investigations is that the relationship between yield and per-plant uptake of any factor is at first linear; it then becomes curved and asymptotic to a maximum at high uptakes. Russell (1961) and de Wit (1958) considered this effect with respect to soil factors and Kumura (1965) explained it in the case of light.

Curvature of response curves is important in the present context for it indicates changes in the efficiency with which growth factors are utilised, according to the level of uptake. Any change in this efficiency, occurring within the range of uptakes encountered in a mixture and its corresponding monocultures, will cause RYT values to deviate from unity even though no overall factor-gain or loss has occurred. Let us define e_{ij} as the relative efficiency of utilization of the 'principal' factor by species i in mixture with species j ; it will be expressed as a fraction of the efficiency in monoculture. The RYT of a mixture is then given by

$$RYT_{ij} = \left[\frac{Y_{ii}\ e_{ij}\ (1+F_{ij})}{Y_{ii}} + \frac{Y_{jj}\ e_{ji}\ (1+F_{ji})}{Y_{jj}} \right] /2 \quad . \qquad (3.1)$$

Although F_{ij} may equal $-F_{ji}$, values of e_{ij} and e_{ji} differing from unity will in general cause RYT to deviate from unity. From this expression it is clear that the usefulness of RYT as an indicator of whether species are competing for the same 'space' (de Wit _et al_.1966, van den Bergh 1968) depends on e_{ij} and e_{ji} remaining constant at a value of unity. In other words, conclusions about the way in which species interact in mixture can only validly be based on RYT if it is known that the components respond to uptake of the factor(s) according to linear relationships (at least over the range of uptakes within the monocultures and the mixtures), with lines passing through the origin*.

The effect of varying efficiencies of utilization of growth factors on RYT can be seen by partitioning the value of

---

* If, in a one-factor situation, the linear response lines of the components to the principal factor do not pass through the origin, but yet are identical in intercept and slope, conclusions may still be based on RYT values, at least when $F_{ij} (=F_{ji})$ is small. This however is a special case and the requirement for lines to pass through the origin applies in general.

RYT as follows. Eqn. 3.1 simplifies to

$$RYT_{ij} = \left[e_{ij} + e_{ij}\,F_{ij} + e_{ji} + e_{ji}\,F_{ji}\right]/2$$

Rewriting this equation as

$$\begin{aligned} RYT_{ij} = \Big[&2 + F_{ij} + F_{ji} + e_{ij} - 1 + e_{ji} - 1 \\ &+ e_{ij}\,F_{ij} - F_{ij} + e_{ji}\,F_{ji} - F_{ji}\Big]/2 \end{aligned} \qquad (3.2)$$

four meaningful components appear :

$$RYT_{ij} = 1 + \frac{F_{ij} + F_{ji}}{2} + \frac{(e_{ij}-1)+(e_{ji}-1)}{2} + \frac{F_{ij}(e_{ij}-1)+F_{ji}(e_{ji}-1)}{2}$$

The first term (unity) is the value of RYT obtained in the simplest case, i.e. when the conditions implicit in Fig. 3.1 are fulfilled; the remaining terms are potential causes of deviation. The second term is the average proportional change of per-plant uptake of growth factor due to the mixing of the genotypes. The third is the average change of efficiency of utilization of growth factor relative to the genotypes' efficiencies in monoculture. The fourth term represents the average effect of the interaction between the unequal sharing of growth factor and the changes in efficiency of utilization.

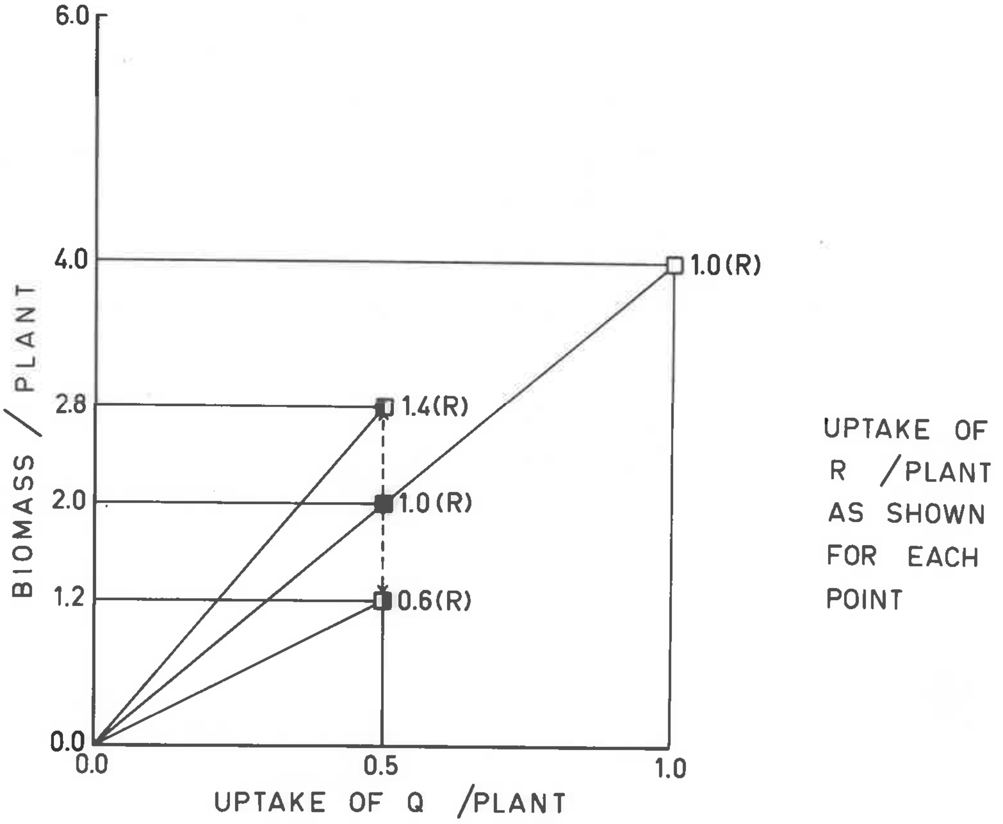
In Section 6.2, data will be presented which allow the estimation of these four components of RYT for 3 mixtures. The results of a 3x3 diallel, grown under conditions in which water could be assumed to be the 'principal' factor, will be considered with respect to per-plant biomass and estimated water uptake by monocultures and mixture components. For each mixture, the values of F_{ij}, F_{ji}, e_{ij} and e_{ji} will be calculated and the contribution of the three terms given above to the deviant values will be compared.

3.1.2.2 Efficiency of utilization as affected by the level of other factors.

While the morphology and physiology of a genotype together determine its response curve to the uptake of a factor in monoculture, when the same genotype is grown mixed with another under the same environmental conditions, the pattern of uptake of other factors may be different enough to cause its response curve to the first factor to change. Prediction of yield in mixture made on the basis of measured factor uptake and a response curve established in pure culture may be seriously in error. Since also competition for more than one factor is likely to develop in crop mixtures (Donald 1958), the one-factor approach is now extended.

Accepting with Clements (1904) that neighbour effects are purely the outcome of specific patterns of microenvironmental modification, we now consider the behaviour of a genotype in a mixture where the associate produces an environment which causes the genotype's per-plant absorption of two factors (both in limiting supply) to differ between mixture and monoculture. For illustrative purposes, the much idealised situation shown in Fig. 3.3 is taken to represent the growth responses of a plant in monoculture to relatively low levels of two factors. A similar system of radiating lines has been shown to apply for example to the response of the net photosynthesis of whole young wheat plants to low levels of radiation and CO_2 concentration (Hoover et al.1933). In Fig. 3.3 biomass has been supposed to be strictly proportional to the uptake of the 'principal factor' Q, with the uptake of R affecting the response of Q through a second proportionality factor. According to this example, the biomass of a monoculture plant is 4 units, attained by the uptake of 1 unit of Q and 1 unit of R. In three different mixtures, plants of this

Fig. 3.3 Idealised responses of a genotype to the uptake levels of two growth factors, Q and R, in monoculture (□) and in three mixtures where it is the subordinate component. In one mixture (▩), this component has the same uptake of factor R as in monoculture. In another mixture (◧) its share of factor R has increased, and in the third mixture (◨) its share has decreased, relative to monoculture. The vertical broken arrows indicate the extent of the deviation of the points from the monoculture response line.


6.0
4.0
2.8
2.0
1.2
0.0
BIOMASS / PLANT
0.0
0.5
1.0
UPTAKE OF Q /PLANT
1.0(R)
1.4(R)
1.0(R)
0.6(R)
UPTAKE OF R /PLANT AS SHOWN FOR EACH POINT

genotype do not compete effectively for Q and, in each case, the per-plant uptake of Q is only 0.5 units. In one mixture, the form and physiology of plants of the associate are such that per-plant uptake of factor R is the same as in the genotype's monoculture (black square in Fig. 3.3); the efficiency with which Q is used in the production of biomass is 2 units of biomass per 0.5 units of Q. This is the same as in monoculture. In a second mixture involving a different associate, plants of the genotype acquire 40% more R than they did in monoculture (pied square with the left side black in Fig.3.3; this partly offsets their competitive disadvantage with respect to Q. While the uptake of Q is as in the first mixture, here the 0.5 units of Q are used more efficiently in the production of biomass. In terms of the <u>relative</u> efficiency of utilization of Q, the value of e_{ij} is unity in the first mixture, but 2.8/(0.5x4)=1.4 in the second. In a third mixture, the uptake of R is reduced almost as much as is that of Q (pied square with right side black in Fig. 3.3). As a result, the efficiency of utilization of Q is less than in monoculture with the value of e_{ij} being 1.2/(0.5x4)=0.6 . This example indicates how differences between mixture and monoculture in the availability, and hence uptake, of any factor R could affect the apparent efficiency with which Q is used. A reciprocal effect of Q on the efficiency of utilization of R is also envisaged. No attempt will be made to quantify these effects but in graphs analogous to Fig. 3.3, the action of subsidiary factors (here factor R) will be recognised by the points representing mixture components lying away from the line of the monoculture response to the factor used in the drawing of the graph. Such deviations may occur in the aggressor as well as in the subordinate component of mixtures.

Changes of efficiency of utilization caused by two or more factors varying from monoculture levels, seem likely to affect RYTs either positively or negatively. Some hypothetical examples will be suggested, followed by others based on real data. The hypothetical examples all involve water as the 'principal' factor, and so the monoculture response lines of the corresponding graphs (Fig. 3.4), being based on water uptake, may be assumed to be straight and to pass through the origin (see Section 2.3).

Three hypothetical examples are now given of the effect of subsidiary factors on the efficiency of utilization of the 'principal' factor :

a) *Water and light* - A mixture of a tall aggressor with a shorter subordinate in a water-limiting situation. The aggressor has the tropical-grass type of photosynthetic mechanism (Cooper & Tainton 1968) and so with its photosynthetic capacity less easily saturated by high light levels, the greater share of light absorbed per plant in the mixture does not lower its PR significantly (Fig. 2.1 was based on the photosynthesis curve of plants with the less efficient mechanism). It is supposed that the shading of the subordinate makes its PR higher in mixture than in monoculture (as in Fig. 2.1). The situation is summarised in Fig. 3.4a.

b) *Water and Nitrogen* - A mixture of an aggressive, fertility-responsive pasture grass and a wild grass, growing on a soil of moderate N content with limited water-supply. The aggressive grass gains an advantage in water uptake due to faster leaf growth. Since N is carried in the soil solution, advantage in water uptake leads to an advantage in N uptake. Increased availability of nutrients increases the PR (de Wit 1958) probably through an effect on photosynthesis rate (Ryle & Hesketh 1969). The subordinate grass is an undomesticated type , of the kind found by Bradshaw *et al.*(1964) to be diminished relatively little in yield at low nitrogen levels. Thus, as a

Fig. 3.4 Hypothetical examples of the effect of varying levels of uptake of subsidiary factors on the efficiency with which a 'principal' factor (water) is utilized. Several of the points representing performance in mixtures are shown as deviating from the lines of the monoculture responses to water uptake. For explanation, see text.

A - species A, the aggressor

S - species S, the subordinate

F_{AS} - proportional increase in per-plant uptake of 'principal' factor by plants of A in mixture, compared with their uptake in monoculture.

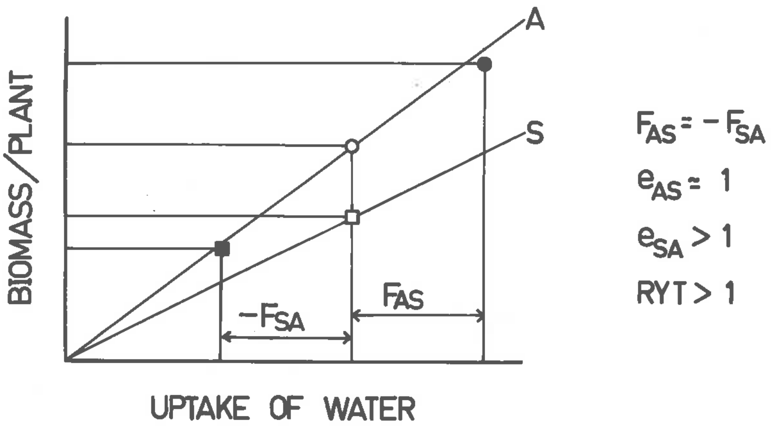
F_{SA} - proportional decrease in per-plant uptake of 'principal' factor by plants of S in mixture, compared with their uptake in monoculture.

e_{AS} - relative efficiency of utilization of the 'principal' factor by plants of A in mixture with S

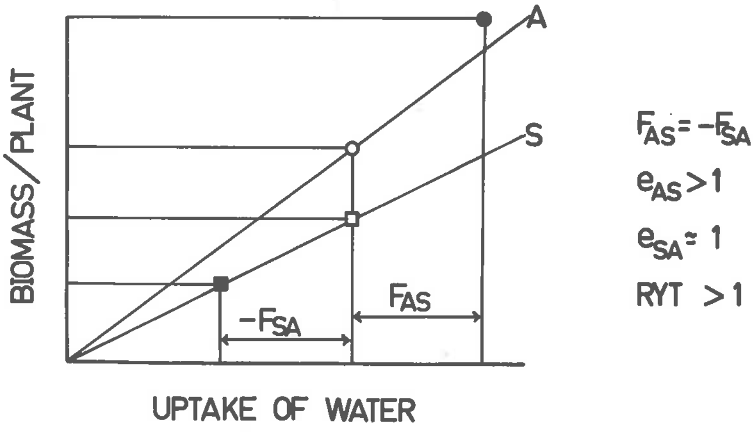
e_{SA} - relative efficiency of utilization of the 'principal' factor by plants of S in mixture with A.

RYT - Relative Yield Total of mixture

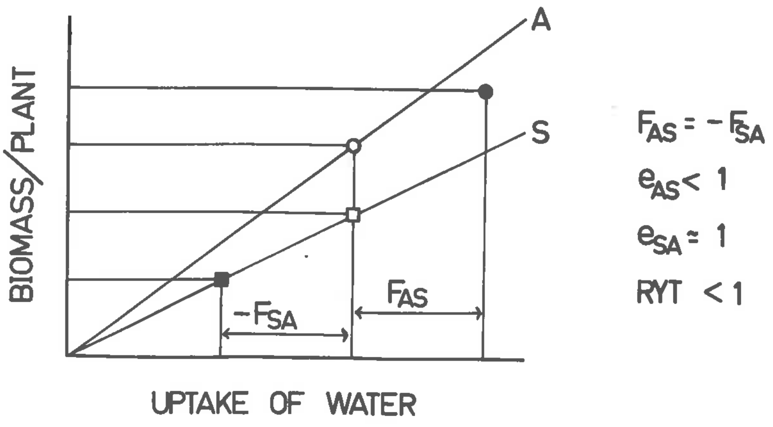
(a)


A
S
BIOMASS/PLANT
UPTAKE OF WATER
$-F_{SA}$
F_{AS}
$F_{AS} = -F_{SA}$
$e_{AS} \simeq 1$
$e_{SA} > 1$
RYT > 1

(b)


A
S
BIOMASS/PLANT
UPTAKE OF WATER
$-F_{SA}$
F_{AS}
$F_{AS} = -F_{SA}$
$e_{AS} > 1$
$e_{SA} \simeq 1$
RYT > 1

(c)


A
S
BIOMASS/PLANT
UPTAKE OF WATER
$-F_{SA}$
F_{AS}
$F_{AS} = -F_{SA}$
$e_{AS} < 1$
$e_{SA} \simeq 1$
RYT < 1

result of the unequal sharing of nitrogen and water in the mixture, the PR of the aggressor may be higher than in its monoculture, while that of the subordinate may not be much decreased (see Fig. 3.4b).

c) Water, Nitrogen and Light - A mixture of a tall and a short grass growing on soil of low nitrogen content with a limited water supply. The tall grass has a higher per-plant light absorption in the mixture and its PR declines (as in Fig. 2.1). The tendency for an increase in the PR of the subordinate is offset by an opposite tendency due to a shortage of nitrogen.

The above examples, although based wholly on supposition, illustrate ways in which the effets of several factors could combine to influence the efficiency with which a particular growth factor is used in the production of biomass. They also show how changes of efficiency of utilization between monoculture and mixture may affect the RYT value and hence the likelihood of transgressive yielding by a mixture. Since the same graphical approach will be used in Section 6.2 in connection with original data, it is of interest to give two further examples of its use, in these cases applied to published data. Although neither set of data is entirely suitable for this treatment, some of the effects postulated in the hypothetical examples above are demonstrated. Since the graphs (Fig. 3.5) are based on nitrogen uptakes covering a wide range of values, monoculture responses have been drawn with Mitscherlich-type curves.

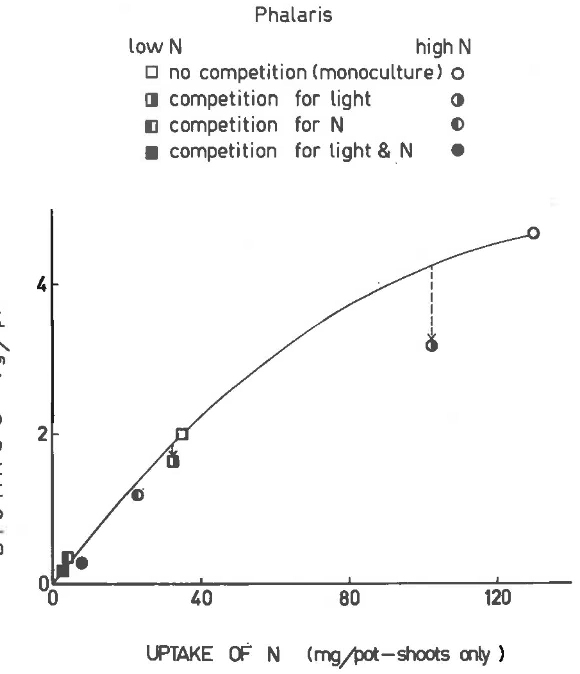
a) Nitrogen and Light - In Fig. 3.5a, the data of Donald (1958) concerning phalaris grass in monoculture and mixture have been plotted using similar axes to those used in Fig. 3.4. The curve was drawn by eye through the origin and the monoculture values at the two levels of nitrogen. In the treatments where competition was for nitrogen only, or for nitrogen and

Fig. 3.5 Examples based on published data showing how, in some mixtures, the efficiency of utilization of nitrogen deviates from the value expected in a monoculture with the same nitrogen intake. The particularly large deviations of efficiency, apparently due to differences of light interception between mixture and monoculture, are shown by vertical arrows with broken lines. Mitscherlich-type curves have been drawn by eye through the monoculture points.
For explanation, see text.

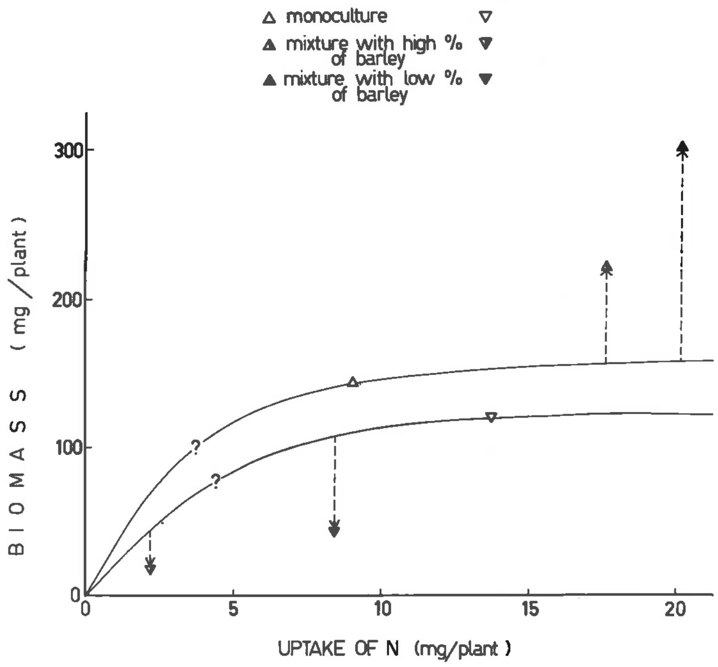
(a) Response of biomass to nitrogen uptake of phalaris grass at two levels of nitrogen application. In the mixture treatments, three different kinds of competition for growth factors are allowed to occur between phalaris and ryegrass; the phalaris is the subordinate component. (Data of Donald 1958).

(b) Response of biomass to nitrogen uptake of Barley and Charlock, on a soil rich in nitrogen, in monoculture and in two mixtures with differing proportions of the components. (Data of Idris and Milthorpe 1967).

(a)


Phalaris
low N
high N
□ no competition (monoculture) ○
◨ competition for light ◑
◧ competition for N ◐
■ competition for light & N ●
BIOMASS (g/pot)
0
2
4
0
40
80
120
UPTAKE OF N (mg/pot—shoots only)

(b)


Barley
Charlock
△ monoculture ▽
▲ mixture with high % of barley ▼
▲ mixture with low % of barley ▼
BIOMASS (mg/plant)
0
100
200
300
?
?
0
5
10
15
20
UPTAKE OF N (mg/plant)

light, the points lie close to the monoculture response curve. It is where competition was not for nitrogen, but for light only, that the points deviate most from the curve. The points representing the treatments with competition for both factors are close to the nitrogen response curve.

The addition of competition for nitrogen either to the monoculture or to the system in which competition was for light only, was shown by Donald to have caused large and significant increases of efficiency of N-utilization in Phalaris (measured in terms of biomass production per unit of N uptake). These particular changes of efficiency appear to be the most obvious features of the data when the criterion used is the direct comparison of the reciprocal of nitrogen content between treatments.

However, it is considered here that a change of efficiency from a monoculture value is more properly judged by a comparison of biomass per unit of factor uptake, in this case nitrogen, between the treatment and the monoculture <u>at the same level of intake</u> (see vertical broken arrows in Fig. 3.5a). In such a comparison, the most striking feature of Donald's data is the effect of adding competition for light to the 'no competition' monoculture at high nitrogen. Evidently, in this mixture treatment, the shading of the leaves of Phalaris by the taller ryegrass caused the nitrogen taken up by Phalaris to be used less efficiently for dry matter production than in its monoculture. The deviation of this treatment's point (pied circle with right side black in Fig. 3.5a) from the curve of the monoculture response to nitrogen exemplifies the comment made above that the action of other varying factors can be recognised by such deviations.

b) <u>Nitrogen and Light</u>. Idris & Milthorpe (1967) grew monocultures and mixtures containing two proportions of barley and charlock at constant density in soil of very high fertility.

The barley grew much taller than the charlock, and in mixture, the suppression of the charlock was thought to be mainly the result of competition for light. Using the data of the penultimate harvest (because those of the last are slightly ambiguous), Fig. 3.5b was drawn. Since there was only one nitrogen level used, the hand-drawn lines through the monocultures are arbitrary except that they have been drawn in such a way as to suggest that nitrogen supply was non-limiting in monocultures (the nitrogen supply was clearly abundant since the LAIs of the barley and charlock monocultures were 21 and 13 respectively.

Comparing the value of 1/(N%) of barley in the low-barley mixture with that in the monoculture, the improved light supply to the barley in mixture apparently improved the efficiency of N-utilization by barley hardly at all. In the other mixture, the value of 1/(N%) is actually lower than in the monoculture. Considering the charlock, even when the proportion of barley in the mixture was low, shading reduced charlock's efficiency of N-utilization a good deal. In the high-barley mixture, the efficiency of N-utilization by charlock was the same as that in its monoculture.

However, assuming that the hand-drawn lines are approximately correct, if the comparisons are made between mixture components and estimated monoculture values at the same level of N uptake, the conclusions to be drawn are radically different. The efficiency of N-utilization now seems to have differed greatly in both species between monoculture and mixture components. The barley plants' relative freedom from self-shading in the mixtures apparently allowed them to use N much more efficiently than they would if they had been in monoculture with the same N uptake. Conversely, the efficiency of N-utilization by the charlock in mixtures was apparently reduced to values much below the potential monoculture values (see Fig. 3.5b). Assuming that these reductions in the efficiency of N-utilization by charlock were caused by shading, they would correspond closely to the strikingly deviant high-nitrogen point in the graph based on the data of Donald (Fig. 3.5a).

Comparing the efficiency of N-utilization by charlock in mixture and in monoculture, Idris & Milthorpe did not find the large decrease of efficiency in mixture which they expected. The not improbable hand-drawn curves suggest on the other hand that comparisons with the efficiencies in monoculture at equivalent levels of uptake, had they been made, would have shown that the expected decrease of efficiency had in fact occurred.

Two conclusions may be based on these applications of the response-curve approach to real data. Firstly, Donald's results suggest that in a truly one-factor situation, where experimental manipulation can confine competition to just that factor, a compoment's biomass in mixture can be closely predicted from its monoculture's response curve to the same factor provided that the uptake is known. This result concerning competition for nitrogen is consistent with a similar conclusion regarding competition for light which can be made on the basis of investigations carried out at Adelaide: Stern & Donald (1962a,b) showed that the growth of subterranean clover, in mixture with grass, was dependent on the radiation it received, and Black (1963) showed that in pure culture, subterranean clover responded to radiation level in an essentially similar way. In Section 6.2, the possibility of a correspondence between behaviour in mixture and monoculture will be examined with respect to competition for water.

Secondly, in a 'one-factor' situation, when the data are plotted as in Fig. 3.5b using as abscissae the uptakes of a factor which is not the 'principal' one (this was light), the data points will probably lie away from the monoculture response curve. This is seen also in Fig. 3.5a, when competition is not for nitrogen. The closeness of the data points to monoculture response curves for different factors might possibly indicate the importance of competition for the various factors. The use of efficiency of factor-utilization alone, without taking into account the shape of the monoculture response curve could lead to unwarranted conclusions.

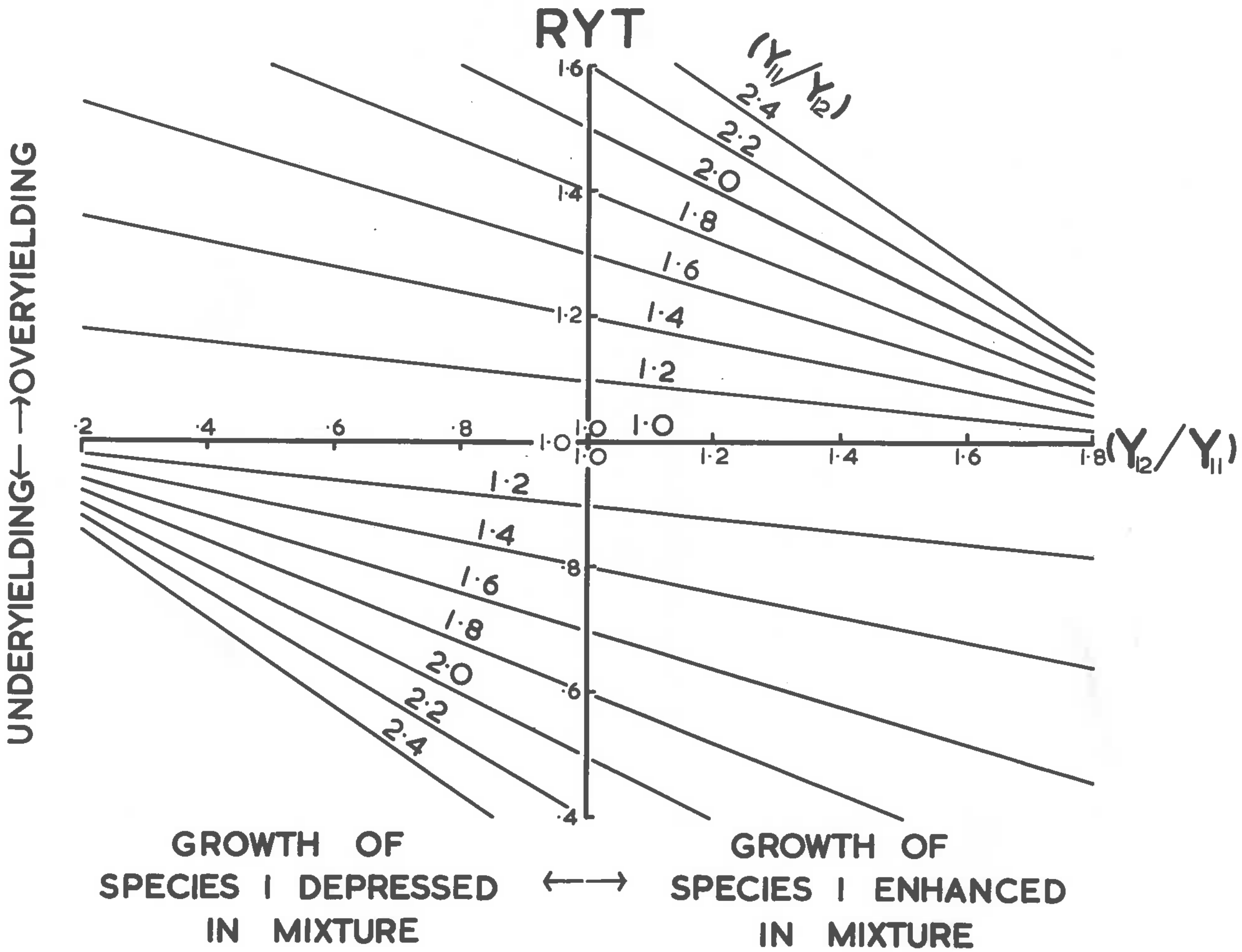
Having considered how factor uptake and efficiency of factor utilization by mixture components may affect the value of RYT (see Sections 3.11. and 3.1.2), we continue by examining the relationship between deviations of RYT from unity and transgressive yielding by mixtures.

3.1.3 RYT deviations and transgressive yielding by mixtures

Much attention has been given to RYT in this section because its value expresses one aspect of the biological situation which leads to over- or underyielding by a mixture. As explained in quantitative terms in Section 2, a mixture with a RYT deviating from unity only over- or underyields if the monoculture yields are sufficiently similar. Van den Bergh (1968, van den Bergh & Elberse 1970) presented a graph showing that with greater deviation of Y_{ii}/Y_{jj} from unity, transgressive yielding involves greater deviation of RYT. (In fact, van den Bergh used the product of the crowding coefficients (de Wit 1960) which, as he showed, is a non-linear index of RYT; also in his figure, there is no restriction on the proportions of the components in the mixtures).

To show the same effect, but in terms of RYT and 1:1 mixtures, Fig. 3.6 has been drawn. It shows the lowest or highest RYT required to give either over- or under-yielding respectively, for a given relative yield of the species with

Fig. 3.6 Relationships between the minimum RYT required for overyielding to occur (upper half of the graph), the degree of dissimilarity of the monoculture yields and the magnitude of the neighbour effects in the mixture. The lower half of the graph gives the corresponding relationships for the maximum RYT necessary for underyielding to occur. The degree of dissimilarity of the monoculture yields is measured by the quotient of the higher and the lower monoculture yields; taking species 1 as having the higher monoculture yield and species 2 the lower, this quotient is (Y_{11}/Y_{22}). The magnitude of the neighbour effects is measured by the plant relative yield in the mixture (Y_{12}/Y_{11}) of the species with the greater monoculture yield.


RYT
(Y_{11}/Y_{12})
2·4
2·2
2·0
1·8
1·6
1·4
1·2
1·0
·2
·4
·6
·8
1·0
1·0
1·0
1·2
1·4
1·6
1·8
(Y_{12}/Y_{11})
1·6
1·4
1·2
·8
·6
·4
1·2
1·4
1·6
1·8
2·0
2·2
2·4
UNDERYIELDING ⟵ ⟶ OVERYIELDING
GROWTH OF SPECIES I DEPRESSED IN MIXTURE
⟵⟶
GROWTH OF SPECIES I ENHANCED IN MIXTURE

the higher-yielding monoculture and a given difference between the monoculture yields. From Fig. 3.6, it can be seen that besides RYT and the quotient of the monocultures yields, there are two other factors which determine whether a given mixture yields transgressively. These are the degree of unevenness in the sharing of growth factors in the mixture, and which of the two species gets the bigger share. In Fig.3.6, these factors are represented by Y_{12}/Y_{11} ($Y_{21}/_{22}$ would have served quite as well). The Figure shows that if it is the species with the higher yield in monoculture which is the aggressor, over-yielding can be achieved with a lower RYT, especially if this species is very aggressive. The figure also shows that when the monocultures differ more in yield, a greater RYT is required for overyielding to occur. Similar considerations apply for underyielding. A proof of the assertions on which Fig. 3.6 is based is given in the Appendix, Section 11.1 . This graph will be used in the interpretation of the results of two 6x6 diallels presented in Section 4.

3.2 The analysis of mixture experiments

The ideal statistical analysis of a biological experiment has the following characteristics :

a) it is based on a rational, rather than empirical, model;

b) the parameters have direct biological interpretations;

c) confidence intervals are available for all parameters.

3.2.1 Analyses using a rational model

It appears that only the Wageningen school has attempted to base analyses of mixture experiments on a rational model. De Wit (1960) described a method whereby curves could be calculated from such a model and fitted to the experimental points of a replacement* series. A method of trial and error was suggested for the estimation of values of the parameters. Although this method could have been based on a least squares approach, apparently goodness of fit continues to be based on visual estimates. No statistical tests seem to have been carried out on the data published by this group.

The lack of statistical treatment was justified by de Wit (1960, and 1966 pers.comm.) on the basis of the intractable error-structure of mixture experiments; the yields of components within a single plot share the same plot error but are themselves likely to be negatively correlated. A statistical analysis suitable for experiments using varied proportions of components was presented by McGilchrist (1967) but because the parameters estimated were not those of the de Wit model, it has not been used by de Wit or his colleagues.

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* A series of mixtures, of equal density, differing in the proportions of their components (de Wit 1960).

3.2.2 Statistical analysis of mixture diallel based on empirical models.

While a variety of designs has been used in experiments investigating neighbour effects (e.g. Sakai 1955, Schutz & Brim 1967, de Wit *et al.* 1966), in recent years a diallel design has often been used in mixture experiments. Only this sort of design, here termed a mixture diallel, is considered in what follows. To indicate the shortcomings of published analyses, it is necessary to describe first the main features of a diallel design. Results of mixture diallels are reported in Sections 4 and 5.

In a p x p mixture diallel, p genotypes are grown in monoculture and in all the possible binary combinations in mixture. The mixtures contain only 1:1 proportions of the components and these are normally planted within a plot in a 'chess-board' arrangement (plants of one genotype in the white-square positions and plants of the other in the black-square positions). The treatments involved are therefore p monocultures and p(p-1)/2 mixtures. The results are usually presented as a square pxp diallel table (see Table 3.1). The performance of the i-th genotype growing in association with the j-th genotype is given as the ij-th element, Y_{ij}, of the table. Consistent with the notation developed in Section 2.1.1, the first subscript, denoting the row of the table, refers to the genotype (the 'producer', Jacquard & Caputa 1970) whose yield is being considered; the second subscript identifies the genotype with which it is growing (the 'associate', Norrington-Davies 1967). A row of the table thus contains yields of just one producer grown with each of the p genotypes in turn. A column of the table contains the performances of all p genotypes when grown with one particular associate. The monoculture values, Y_{ii}, lie on the NW-SE diagonal.

Table 3.1. The form of a diallel table showing the notation for identifying the elements of the table and the marginal means.

		Associate					Row means
		1	2	3		p	
Producer	1	Y_{11}^{*}	Y_{12}	Y_{13}	......	Y_{1p}	$\bar{Y}_{1.}$
	2	Y_{21}	Y_{22}^{*}	Y_{23}	......	Y_{2p}	$\bar{Y}_{2.}$
	3	Y_{31}	Y_{32}	Y_{33}^{*}	......	Y_{3p}	$\bar{Y}_{3.}$
		.	.	.		.	.
		.	.	.		.	.
		.	.	.		.	.
	p	Y_{p1}	Y_{p2}	Y_{p3}	......	Y_{pp}^{*}	$\bar{Y}_{p.}$
column means		$\bar{Y}_{.1}$	$\bar{Y}_{.2}$	$\bar{Y}_{.3}$	......	$\bar{Y}_{.p}$	$\bar{Y}_{..}$

* Monocultures

A row mean, $\bar{Y}_{i.}$, is the mean yield of the i-th producer grown with each of p associates. A column mean, $\bar{Y}_{.j}$, is the mean yield of p producers grown with the j-th associate. It should be noted that some authors (Sakai 1961, Jacquard & Caputa 1970) use a transposed version of this table with rows and columns interchanged. The form used here is that of Aberg et al.(1943).

Since the results of a mixture diallel have the same form as results of a genetic diallel, only a slight adaptation of the analyses worked out for genetic diallels was necessary to make them applicable to mixtures. Thus, Harper (1964) used the analysis proposed by Hayman (1954) and Jinks (1954) to establish the pattern of 'ecological dominance' in mixtures of Linum varieties. However, a parameter based on a genetic model may not have a direct ecological interpretation. For instance, England (1965) found that a calculated 'ecological dominance' did not correspond to any actual domination of the mixture by the component indicated as being 'dominant'.

Norrington-Davies (1967) used the adaptation of a genetic analysis suggested by Durrant (1965); only one of the two main parameters estimated has any fundamental biological significance. This parameter, 'the effect due to beta competition' measures the tendency for a component's aggressiveness in mixture to be proportional to its monoculture yield. The estimates of the two parameters cannot, apparently, be derived independently and great ambiguity can exist in the interpretation of results (e.g. Norrington-Davies 1967).

Another adaptation of an analysis originally devised for a genetic diallel was used by Jensen & Federer (1965) and Laubscher et al.(1967). Griffing's (1956) analysis measuring general and specific combining ability was applied to mixture yields and both groups of workers found general, but not specific, combining ability. (Jensen & Federer applied the unfortunate term 'competing ability' to this index). There is some difficulty in the interpretation of these indices, however, for a genotype can show high combining ability in two ways: either through a general effect on the yields of mixtures of which it is a component or by being a component in a few mixtures which have exceptional yields. Since this last effect is also considered as high specific combining ability, the two indices are not fully independent.

Hanson et al.(1961) and Helgason & Chebib (1963) tested differences between $\bar{Y}_{i.}$'s and between $\bar{Y}_{.j}$'s by treating the p x p table of results as if they came from a p^2 factorial experiment. Their analysis was based on the model

$$Y_{ij} = \mu + r_i + c_j + rc_{ij}$$

where μ is the overall mean, r_i the effect of the i-th row, c_j the effect of the j-th column and rc_{ij} the statistical 'interaction' or special effect due to the combination of r_i and c_j (for simplicity, the terms due to block effect and error have been omitted). However, although this analysis has the merit of simplicity, it can only properly be used when the ij-th and ji-th elements of the table are independent and when all elements are liable to the same degree of error. In a mixture diallel, neither of these conditions is fulfilled.

A similar model was the basis for the analysis of Eberhart et al.(1964) except that these authors separated an averaged value of $(M-\bar{P})$ over all mixtures. They made row effects and 'interactions' relative to this. England (1965) used their analysis but found that 'interactions' were so frequent that it was difficult to interpret the row effects. This appears to be the same problem as was noted in Griffing's analysis. England therefore calculated whole-plot and half-plot error mean squares and used them to judge the significance of any comparisons which seemed useful.

The Eberhart analysis was used by Lin & Torrie (1968) but they introduced three further parameters. One, equal to $(Y_{ij} - Y_{ii})$, measured the difference of a genotype's yield between mixture and pure culture, another averaged this quantity over all mixtures containing genotype i, and the third was $(M-\bar{P})$ for each mixture. Although the three new parameters were not independent, they seemed able to describe adequately the differences between a series of diallel results.

A parallel line of development was initiated by Williams (1962) with an analysis again based on the genetic diallel. McGilchrist (1965) proposed an essentially similar analysis but he chose parameters which were easier to interpret biologically. Two measures of aggressiveness of one species towards another were obtained. One was arithmetic increase in the per-plant yield of the aggressor in mixture above its monoculture value; the other was the corresponding decrease in yield in mixture of the subordinate below its monoculture value. These two estimates of aggressiveness were averaged, since several authors had concluded that, for grain yield at least, they were usually similar in value (Stringfield 1959, Hanson <u>et al</u>.1961, Hinson & Hanson 1962). Thus, the aggressivity* of genotype i with respect to genotype j was

$$C_{ij} = (Y_{ij} - Y_{ii} + Y_{jj} - Y_{ji}) /2 \qquad (3.3)$$

The second principal parameter, D, measured the depression of the mixture yield below the mid-monoculture value, i.e. it was $(\bar{P} - M)$.

Paying considerable attention to the error structure of the mixed plots, McGilchrist allowed for further components

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* 'Competitive advantage' was used by McGilchrist (1965) but its use makes an unnecessary assumption about the causes of the neighbour effects. The term 'aggressivity' will refer to a specifically defined index of aggressiveness. 'Aggressiveness' will always be used in general sense.

of variability. One was the increase of variance of the yields of genotypes in mixtures due to their being estimated from only half the number of plants used in the estimation of monoculture yields. Another was the increase (or decrease) of variance of yields of mixture components due to the plants of a genotype in mixture being systematically more (or less) variable than those of the same genotype in monoculture.

A numerical example used by Williams (1962) and McGilchrist raises the question of the effect of log-transformation of data prior to analysis. Following Williams, McGilchrist used log-transformed data since in this form the variances were more homogeneous. The effect of the transformation on the interpretation of the parameters could however be large; theoretically, results could be obtained which, when log-transformed, give a zero value McGilchrist's D parameter but which, on a natural scale, show the mixture to be overyielding by 25%. Norrington-Davies (1967), reanalysing Williams' (logged) data, showed a tendency for mixture yields to be below $\bar{P}$. His own (unlogged) data, obtained from a field- rather than from a pot-experiment, showed the opposite tendency. Although, as Norrington-Davies suggested, differing patterns of interference may be expected from experiments conducted in pots and in the field, at least some of the difference in this case is due to the log-transformation.

3.2.3 An analysis based on a rational model

As mentioned above, Stringfield (1959) and others have concluded that neighbour effects are additive in the sense that

$$Y_{AS} - Y_{AA} \simeq Y_{SS} - Y_{SA} \qquad (3.4)$$

In the light of the preceding sections, however, there seem to be strong rational grounds for expecting

$$\frac{Y_{AS} - Y_{AA}}{Y_{AA}} \simeq \frac{Y_{SS} - Y_{SA}}{Y_{SS}} \quad . \qquad (3.5)$$

Eqn. 3.4 could be considered to be a special case of Eqn. 3.5 where $Y_{AA} \simeq Y_{SS}$. Neither Stringfield (1959) nor Eberhart et al. (1964) mention any strong correlation between yield in monoculture and aggressiveness in mixture. In their experiments, the cases where the aggressor had the higher-yielding monoculture may have been about as frequent as the cases where it had the lower-yielding monoculture. If so, Eqn. 3.4 would have indeed seemed to fit the data approximately. Unfortunately their raw data were not reported and so no test can be made.

More recently, reporting on biomass rather than on grain yields, two authors have independently concluded that the aggressor usually gains more than the subordinate loses and that aggressiveness and monoculture yield are positively correlated (England 1965 with grasses, 4 mixture diallels each with $p = 4$; Norrington-Davies 1967 with barley, $p = 5$; 1968 with grasses, $p = 5$). These two conclusions taken together suggest that Eqn. 3.5 (and thus the de Wit model) would fit their data more closely than would Eqn. 3.4. The same conclusions are consistent with the findings of Donald (1963) that mixture biomasses usually lie between $\bar{P}$ and P_1 (see Section 2.1). The clustering of RYT values about unity (van den Bergh 1968 and see Table 2.2) provides further support for the applicability of Eqn. 3.5. It must be pointed out though that an RYT of unity is only support for Eqn. 3.5 rather than Eqn. 3.4 when the monoculture yields are strikingly different.

Since a new analysis, to be described below, is based on the applicability of Eqn. 3.5, it is necessary to establish the wide validity of this equation and to show that it is at least as good an approximation as Eqn. 3.4. Using data of the mixture diallels cited in Table 2.1, the left hand side of Eqn. 3.4 was first plotted against its right hand side; this tests the 'additive' model. Secondly, the left hand side of Eqn. 3.5 was plotted against its right hand side to test the 'proportional' model. Fig. 3.7 shows the data from eight investigations plotted in the two ways. In the preparation of the graph based on the additive model, the data of different experiments were brought on the same scale by dividing them by the general mean of each experiment respectively. Data derived from long series of cuts have not been used since van den Bergh (1968) has shown that they are well fitted by the proportional model. The data of Norrington-Davies (1968) are of only two cuts and have been included; all others are based on single harvests.

Fig. 3.7 shows that the data points of the 133 mixtures plotted are fitted considerably better by the proportional model than by the additive model. To allow a statistical test * of this difference to be made in each graph, since neither variable depended on the other, the data points were treated as an elliptical cloud of points and the position of the major axis of the ellipse was calculated. The details of the resulting 'regression' lines are given in Table 3.2. By rotating each line about the position of the mean and calculating the goodness of fit of the data to the line at 5° intervals, approximate confidence limits were found for the slopes of the major axes. For the additive model, the 98% confidence range of the slope is 18° to 28° and for the proportional model the corresponding range is 30.5° to 43°. The two slopes differ

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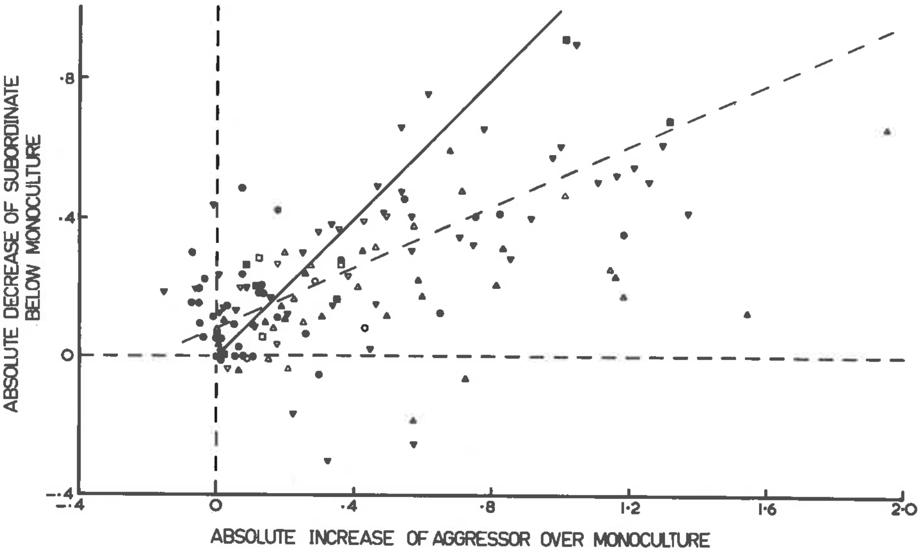
* These tests were kindly suggested and carried out by Mr. L.G.Veitch, C.S.I.R.O., Division of Mathematical Statistics, Adelaide. The treatment was based on techniques given in Anderson (1963).

Fig. 3.7 Test of fit of published results of 133 mixtures to the 'additive and 'proportional' models. The additive model postulates the equality of arithmetic increases and decreases in per-plant yield of the components in mixture; the increases and decreases are presented relative to yields in the respective monocultures. The proportional model postulates the equality of the corresponding proportional increases and decreases. For a perfect fit, the data points should lie on the solid 45° line drawn from the origin (0, 0). The major axes fitted to the clouds of points are shown as dashed lines. Statistical details of the lines are given in Table 3.2 and in the text.

■ Aberg et al. (1943)
▴ Donald (1946)
○ Sakai (1953)
● Sakai (1955)
▴ Williams (1962)
□ Williams (1963)
▿ Norrington-Davies (1967)
▾ Norrington-Davies (1968)

(a) Additive model



(b) Proportional model

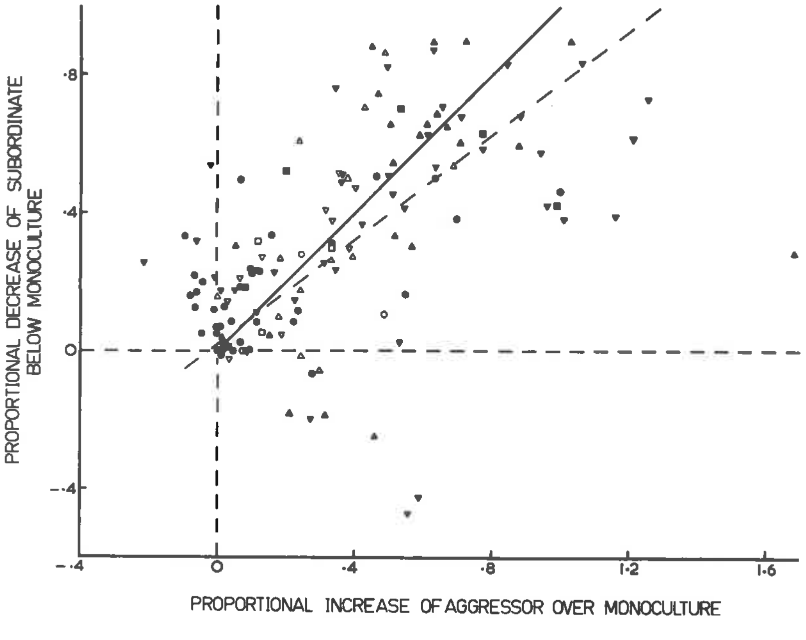


Table 3.2 Details of the major axes calculated for the clouds of points in Fig. 3.7 , with corresponding data for the results of Harper (1964).

Data used	no. of mixtures	slopes of fitted major axes	
		additive	proportional
Data of Fig. 3.7 (8 investigations)	133	+ 22.9° (r = .5451)⊕ ($\bar{x}$, $\bar{y}$=.325, .223)*	+ 37.0° (r = .5830) ($\bar{x}$, $\bar{y}$=.311, .264)
Harper (1964)	30	- 8.5° (r= -.0840) ($\bar{x}$, $\bar{y}$=.343, .181)	0.0° (r = -.0405) ($\bar{x}$, $\bar{y}$ =.512, .126)

⊕ Correlation coefficient between the pair of variables used to draw the graphs of Fig. 3.7 .

* Coordinates of the means of the clouds of points; the major axes pass through these points.

significantly from each other at the 5% level; with the slope of the line on the graph using the proportional model being closer 45°. Although the slope of the line of the 'proportional' graph is itself significantly different from 45° ($\chi^2 = 11.01$, d.f. = 1, $P < 0.001$), that of the graph based on the additive model deviates from 45° at a very much higher level of significance ($\chi^2 = 117.4$, d.f. = 1, $P \ll 0.001$). While clearly not providing a perfect fit to the data, the proportional model seems to give a more satisfactory basis for an analysis than does the additive model.

The data of Harper (1964, 30 mixtures) were not included in the above comparison since they seemed to be anomalous. They contained a particularly high proportion of mixtures which yielded transgressively (50%), and, when analysed in the same way as the other data, gave no indication of a fit to either model. The details of the calculated major axes are given in Table 3.2.

An analysis is now proposed which is based on the method of McGilchrist (1965, see Section 3.2.2), but with the parameters revised by the present author to make them interpretable in terms of the model developed in Section 3.1. Working with these revised parameters, C.A.McGilchrist has elaborated a new analysis, similar in statistical approach to the one he described previously (1965). This work (McGilchrist & Trenbath 1971) has now been published. Since this analysis is used in Sections 4 and 5, it is briefly described below.

The aggressivity, A_{ij}, of genotype i with respect to genotype j is estimated as the average of the proportional changes from monoculture values, seen in mixture, in the yields of aggressor and subordinate; the second deviation term is used with its sign reversed. Thus, (Cf. McGilchrist's original C parameter defined in Eqn. 3.3),

$$\begin{aligned} A_{ij} &= \left(\frac{Y_{ij} - Y_{ii}}{Y_{ii}} + \frac{Y_{jj} - Y_{ji}}{Y_{jj}}\right)/2 \\ &= \left(\frac{Y_{ij}}{Y_{ii}} - \frac{Y_{ji}}{Y_{jj}}\right)/2 \end{aligned} \qquad (3.6)$$

If the two terms entering the estimate of aggressivity are expected to be equal, this 'two-term' estimate of aggressivity will be a more satisfactory index of it than any 'one-term' measure. The two-term method was introduced by McGilchrist (1965). To allow the estimation of an overall measure of each genotype's aggressivity, each A_{ij} is decomposed according to the following statistical model :

$$A_{ij} = \hat{k}_i - \hat{k}_j + \hat{\theta}_{ij} \quad , \quad (i \neq j). \qquad (3.7)$$

Further assumptions are :

$$A_{ij} = -A_{ji}$$

$$\sum_i \hat{k}_i = \sum_{j(\neq i)} \hat{\theta}_{ij} = 0 \, ,$$

$$\theta_{ij} = -\hat{\theta}_{ji}$$

The parameter $\hat{k}_i$ represents the tendency for genotype i to increase in mixtures and cause a decrease in yield of the other component. The parameter $\hat{\theta}_{ij}$ represents departure from the value expected according to the previously fitted parameters $\hat{k}_i$ and $\hat{k}_j$. The 'genotype aggressivity effects', $\hat{k}_i$, and the table of $\hat{\theta}_{ij}$ $(i \neq j)$ are calculated by a least squares method.

The D parameter of McGilchrist (1965) which measured the depression of mixture yield below $\bar{P}$ is replaced by a measure of RYT depression below unity. This is $(1 - RYT_{ij})$, where

$$RYT_{ij} = \left(\frac{Y_{ij}}{Y_{ii}} + \frac{Y_{ji}}{Y_{jj}}\right)/2$$

It will be noted that the two-term expression which gives RYT_{ij} is closely analogous to the expression which gives A_{ij}. As with A_{ij}, a statistical model is assumed for $(1-RYT_{ij})$:

$$(1-RYT_{ij}) = \hat{\mu} + \hat{\lambda}_i + \hat{\lambda}_j + \hat{T}_{ij} \qquad (3.8)$$

where $\hat{\mu}$ is the overall mean, $\hat{\lambda}_i$ is the 'genotype RYT effect, and $\hat{T}_{ij}$ is an 'interaction' term analogous to $\hat{\theta}_{ij}$ above. Additional assumptions are made, viz.

$$RYT_{ij} = RYT_{ji} \quad ,$$

$$\sum_i \hat{\lambda}_i = \sum_{j(\neq i)} \hat{T} = 0 \quad ,$$

$$\hat{T}_{ij} = \hat{T}_{ji}$$

The parameter $\hat{\lambda}_i$ measures the tendency for genotype i to cause a depression of RYT, positive or negative, in its mixtures. The parameters are again estimated by a least squares method.

By entering RYT as (1-RYT), McGilchrist has been able to use exactly the same model and variance structure as in the original analysis (McGilchrist 1965). Similarly, the model and variance structure for his original C_{ij} has been applied directly to A_{ij}.

An analysis of variance tests the significance of differences between values of the various monoculture yields, $\hat{k}_i$'s and $\hat{\lambda}_i$'s. It also tests overall interactions affecting A or (1-RYT), and the overall deviation of RYT from unity. Individual interaction terms in Eqns. 3.7 and 3.8 can be tested for significance using standard errors. A significant $\hat{T}_{ij}$ would be analogous to a finding of specific combining ability in the sense of Jensen & Federer (1965).

3.3 Concluding remarks on theoretical approaches to mixture experiments.

Considering the broad foundation provided by the theoretical formulations of de Wit (1960), it is surprising that so few further developments have been attempted of his fundamental approach to the processes occurring in mixed communities. The recent theoretical advances have tended to be more of a descriptive than a truly analytical nature (e.g. de Wit & van den Bergh 1965, Jones 1967, van den Bergh 1968, Jacquard & Caputa 1970).

Apart from the ad hoc physiological explanations of particular experimental results, only few attempts (e.g. Donald 1961, 1963, Milthorpe 1961) appear to have been made to construct general theories to bridge the gap between the abundant knowledge of physiological responses to microenvironment and the observations of neighbour effects made in mixture experiments. The present Section has attempted to develop some aspects of de Wit's formulations into the form of a model which may help in the understanding of neighbour effects and the way they affect yields of mixtures. By breaking down the observed yields of genotypes into directly measurable components, i.e. quantity of growth factors absorbed and the efficiency with which they are transformed into biomass, it is hoped to clarify some of the factors which determine the observed yields of mixtures. The possible usefulness of this approach will be judged in relation to the results of experiments which are described in the Sections which follow.

4. MIXTURE DIALLEL EXPERIMENTS IN THE FIELD

4.1 Introduction to the field diallels

The aim of these experiments was to examine the biomasses of a large number of varietal mixtures of spring wheat in the hope of finding some overyielding combinations. These mixtures could then serve as material for later experimentation seeking to establish the causes of the overyielding. A wide range of contrasting varieties was used; also, the diallels were sown at two densities. In this way it was hoped to maximise the chance of finding pairs of genotypes which utilised the environment in different ways and which would thus possibly give overyielding mixtures.

4.2 Materials and methods

To make up two 6x6 diallels, two groups of 6 varieties were chosen from the Waite Institute world collection of spring wheats. Within each group, contrasts of flowering-date, height at flowering, tillering capacity, and droopiness of foliage were present. The varieties used in the experiments are listed in Table 4.1.

The site of the experiments was paddock W5 at the Waite Agricultural Research Institute, Adelaide. During the previous season a crop of peas had been ploughed in to leave a bare fallow over the summer months. The seedbed received the customary preparation and an application of 242 kg/ha of superphosphate.

The two 6x6 diallels were located in separate parts of the field; the two density treatments were introduced as subplots of the main plots, each of which contained a particular mixture or monoculture. The design for each 6x6 diallel

Table 4.1. Varieties used in the two 6x6 mixture diallels performed in the field. In some of the Tables which follow, varieties will be referred to by the numbers given here.

Experiment	Number	Name	Origin
Diallel 1	1	DES 0043	Crete
	2	India 50	India
	3	Napo 63	Colombia
	4	Pitic 62	Mexico
	5	Selkirk	Canada
	6	Summit	Victoria, Australia
Diallel 2	1	CT 144	Canada
	2	Giza	Egypt
	3	Heron	N.S.W., Australia
	4	Justin	Canada
	5	Klein Petiso Rafaelo	Argentine
	6	Mentana	Italy

was thus a 4-replicate randomised block experiment with each replicate containing 6 monoculture plots and 15 mixture plots, each being split for the density treatment. The end of the plot to be occupied by the high density subplot was chosen at random.

The positioning of the plants (seeds) in a mixture plot is shown in Fig. 4.1b. The rows of plants were set north-south over both experiments. The 5 rows of each plot were 15 cm apart, and the distance between plants within the row was 15 cm in the low-density subplot and 4cm in the high-density subplot. Plants of the two components of the mixture alternated within the N-S rows, but as Fig. 4.1b shows, they did not alternate in the E-W direction. The monoculture plots were similar in all respects except that all seeds were of the same variety.

The plots were arranged into tiers such that each of the four blocks of each diallel had the form of a square. The tiers were two plots wide, and hence each plot had one of its long sides adjoining another plot while the other long side bordered a path.

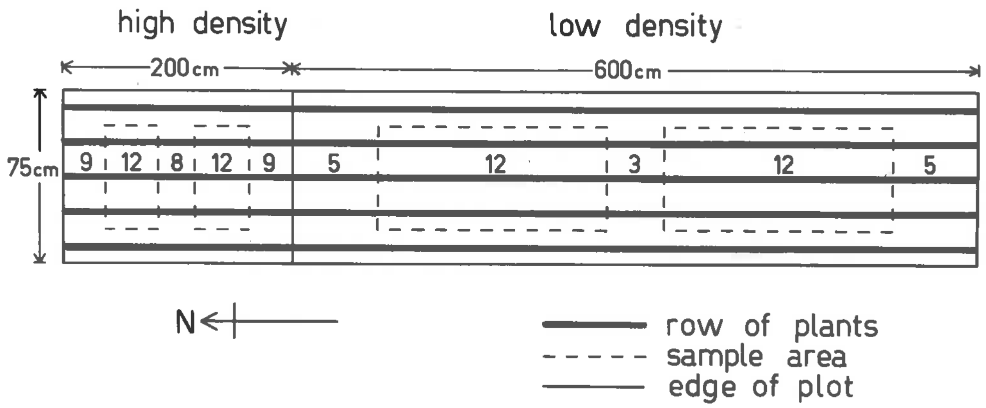
Provision was made in each subplot for two harvest areas, each containing 36 plants (see Fig. 4.1a). These harvest areas were assigned to harvest occasions at random. Along the path side of each harvest area was one guard-row of the same composition and a second guard-row (not shown in Fig. 4.1a) of cultivar (cv.) Summit. On the opposite side, bordered by another plot, there was just one guard row of the same composition as the harvest area. In the other direction, the harvest areas were bordered at each end by 3 or 5 plants in the low density, and 8 or 9 plants in the high density part of the plot. In monocultures the harvest plants were all of the same varieties, and in mixtures the 36 plants

Fig. 4.1. Layout of a mixture plot in the field diallel experiments.

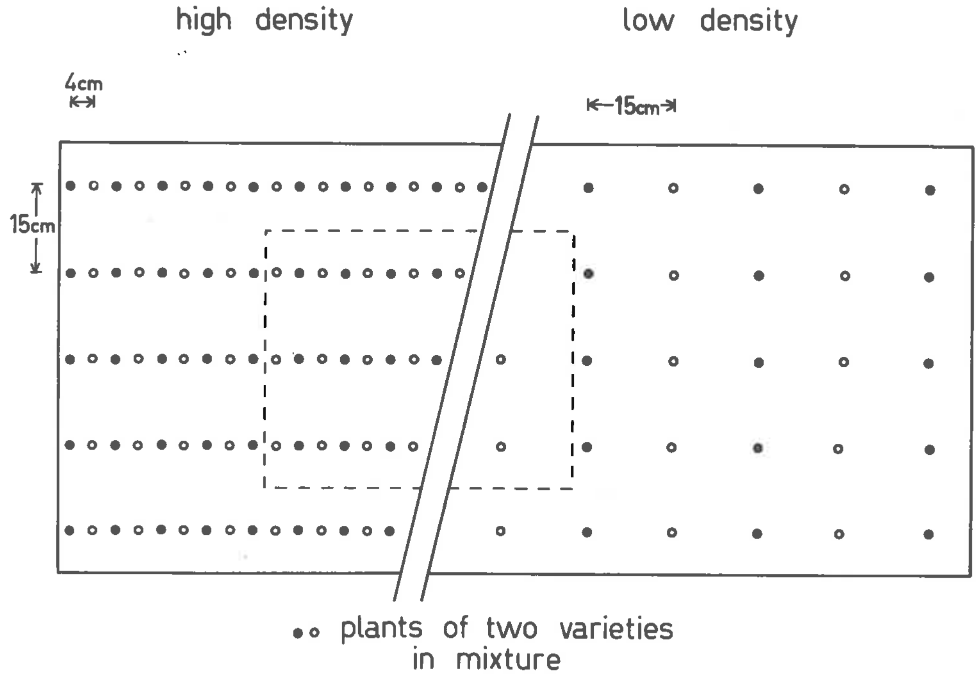
(a) General arrangement of the plot. The high-density subplot has been assigned to the north end in this plot. Sample areas are shown by broken lines. The numerals indicate the numbers of plants within one row which lie in the various parts of the plot. (borders and sample areas). The outer row on each side of the plot is a border row. The scale in the east-west direction is twice that in the north-south direction.

(b) The ends of the main plot, drawn on a larger scale (the same scale in both directions) showing the arrangement of individual plants. A part of a sample area is shown in each density. (See also Plate 4.1

(a)


high density
low density
200 cm
600 cm
75 cm
9
12
8
12
9
5
12
3
12
5
N
row of plants
sample area
edge of plot

(b)


high density
low density
4cm
15cm
15cm
plants of two varieties in mixture

were made up of 18 of each component.

Successive replicates of the experiments were sown over the period 27 June - 3 July 1967. As a convenient reference point, the date 30 June will be taken as the date of sowing. The seedbed had been left as a series of ridges and furrows, with 15 cm between furrows. The seeds were placed in the bottom of the furrows, in the low density subplots by hand, and in the high density subplots using a special device (suggested by K.P.Barley). This was a metal tube with holes at 4 cm intervals, and attached to a vacuum cleaner. Seeds were sucked out of a gutter onto the holes and deposited where required by turning off the suction. The seeds were then covered evenly with a layer of sand about 5 cm deep. A total of about 70,000 seeds was planted. The 100-grain weights of the 12 varieties were measured using random samples of the seed used for planting.

Although the seeds of all varieties had been carefully graded to eliminate all small or broken seeds, and had been tested for seedling emergence under the conditions of planting described above, only about 95% emerged. The missing plants (about 1200 in the harvest areas) were replaced soon after seedling emergence with transplants of the appropriate variety. A preliminary trial of 5 methods had shown that the best method for high density plots was a tracing-paper tube (diameter 3 cm) filled with a medium loam, with the germinated seed planted under sand at the top. The roots of the young plant, in the cylinder of soil, were inserted carefully into a hole in the ground made at the point where a plant was missing, with a soil-corer. This method was used for the high density subplots while transplants grown in cardboard beakers (diameter 5 cm) of loam were used for the low density ones. The cardboard was removed before the cylinder of soil and roots was inserted into the hole prepared for it. Transplanted plants were marked, and were not included in the harvested sample. Perhaps due to the dryness of the season, they did not grow as well as the preliminary experiment had suggested that they might.

Attacks of caterpillars, millipedes and cut-worms were controlled by spraying with 2% DDT and 'Imadan'. Being a dry season, weeds were easily and completely controlled with hand hoeing and spraying with 'Buctril'. The appearance of the plots 52 days after 'sowing date' is shown in Plate 4.1.

The number of days to 50% ear emergence was estimated for each component in each density of all plots in one replicate of each diallel. The first harvest was started when most varieties had reached the early dough stage of ripeness, since about this time, the shoots were expected to have reached their maximum biomass (Puckridge & Donald 1967). This harvest continued, at the rate of about a replicate per two days, over the period 9-29 October (101-102 days after the 'sowing-date'). In each subplot, the two rows of the harvest area with fewest transplants were harvested as individual plants : they were cut at ground level, bound with elastic bands and stored in a closed polythene bag at 1°C prior to being measured. The plants of the third row (omitting transplants) were harvested as a bulk sample for each variety and similarly stored in a closed polythene bag at 1°C.

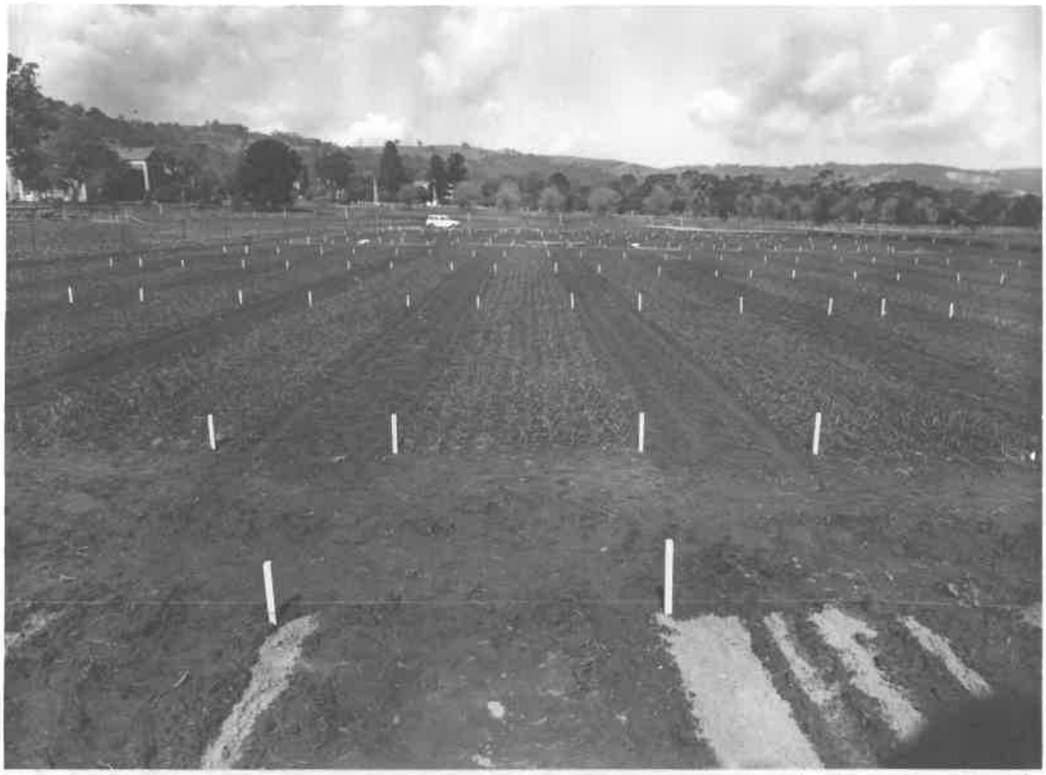
The second harvest, for grain yield, was taken when all varieties were mature. It lasted over the period 29 November-16 December (152-169 days after the 'sowing date'). All plants (other than transplants) were uprooted and stored until they could be processed.

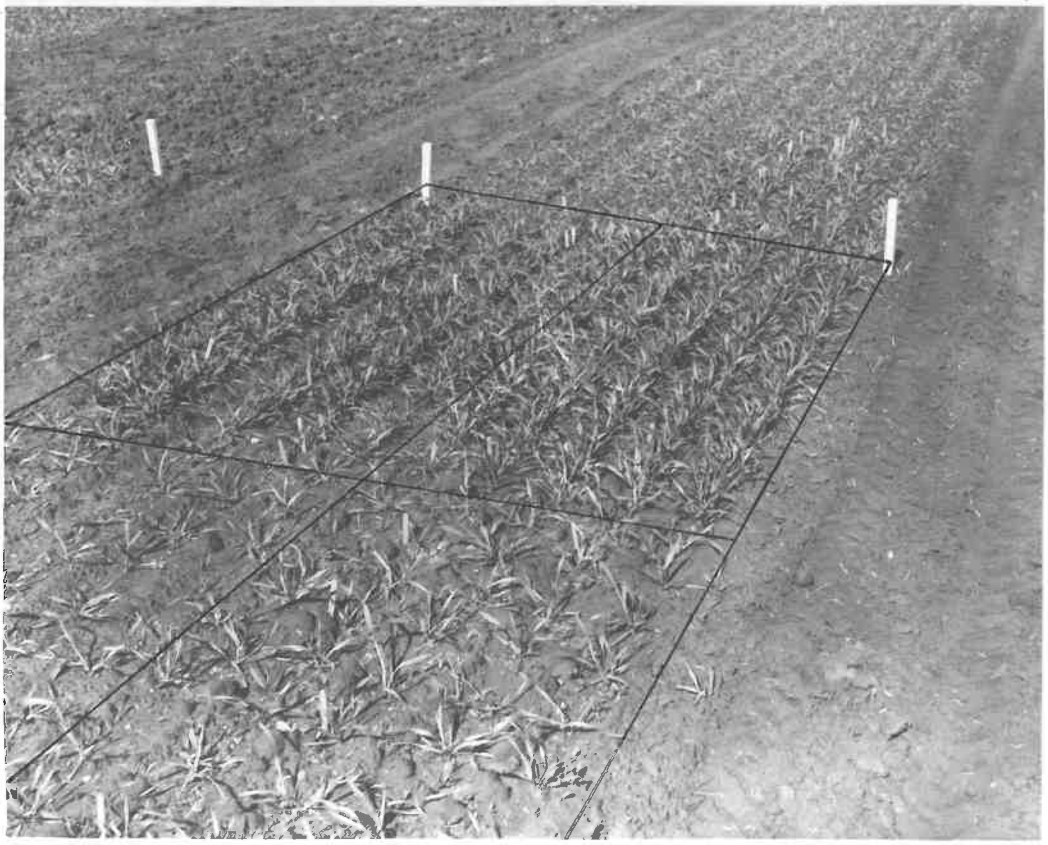
The processing of plants of the first harvest commenced with the drying of the bulk sample of one row from each subplot

Plate 4.1. The appearance of the plots of the field diallel experiments 52 days after 'sowing date'.

(a) General view of the plots looking south.

(b) Close-up view of the ends of two plots. The high-density subplots, next to the large pegs, are enclosed within the black lines. The plants of the immediate foreground are in the low-density subplots. The positions of missing plants awaiting transplants are indicated by small pegs. (see also Fig. 4.1)





for 24 hours at 80°. The individual plant sample of two rows, after being measured (see below), was similarly treated and the average per-plant biomass for each subplot was calculated. The observations made on each plant of the individual-plant sample were of number of tillers (counting only those longer than 5 cm to their highest ligule) and height to the highest leaf ligule.

The processing of the plants of the second harvest was as follows: the ears of each component of a subplot were threshed to produce a bulk grain sample which was dried, weighed and expressed on a per-plant basis. Unfortunately, the season was an extremely dry one (the lowest rainfall during the growing season for 81 years), and this, combined with the effects of hot winds, shattering of the heads and unevenness of run-off due to undulations in the surface of the field, caused the results of the second harvest to have very high errors. Accordingly, only the results of the first harvest (biomass) are reported.

4.3. Results

4.3.1 Biomass *

The biomasses of the mixtures were distributed rather uniformly about $\bar{P}$ (see Table 4.2a). In the first diallel, transgressive yielding was relatively uncommon, but in the second diallel, mixtures yielding transgressively were over twice as common as mixtures which yielded between P_1 and P_2. This difference between the two diallels was significant at the 5% level (approx. $\chi^2 = 5.40$, d.f.= 1, see below). The pattern of mixture yields was much the same in the two densities within the same diallel except that there was a (non-significant) tendency in Diallel 2 for more mixtures to underyield in the low density than in the high density. In none of the 32 mixtures which over- or underyielded was the transgressive yielding significant at the 5% level.

The frequencies with which the varieties were components of the different kinds of transgressively-yielding mixture are given in Table 4.2b. Within each diallel, there was a suggestion that the presence of certain varieties tended to be associated with one particular kind of mixture performance. There was also a suggestion that the same pattern was present at both densities, but this could have been because the low- and high-density subplots shared the same mainplot error. The coefficients of variation of subplot yields were between 10% and 14% and so this possibility is not to be ignored. The intercorrelation of the results from plots of the high and low density makes the chi-square value, calculated above, only approximate.

Since RYT values based on biomass are of theoretical importance, their distribution over all the mixtures is shown

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* The diallel tables may be found in the Appendix, Section 11.2.

ADDENDUM : Page 116, caption of Table 4.2b. The second column gives the numbers of the varieties; these correspond with the numbers given in Table 4.1

Table 4.2. Biomasses of mixtures relative to those of component monocultures.

a) Number of mixtures in each diallel and density which under- and over-yielded, and of which the yield lay intermediate between the yields of the component monocultures.

Diallel	1		2		
Density	low	high	low	high	Totals
Underyield	3	2	7	5	17
Intermediate	9	10	5	4	28
Overyield	3	3	3	6	15

b) Number of under- and over-yielding mixtures in which the various varieties were present as components, in each diallel and density.

Diallel		1		2	
Density		low	high	low	high
Under-yield	1	1	-	3	1
	2	1	1	3	2
	3	1	1	1	1
	4	-	-	3	3
	5	2	2	3	3
	6	1	-	1	-
		6	4	14	10
Over-yield	1	1	-	1	2
	2	2	1	1	1
	3	-	-	1	2
	4	2	3	-	1
	5	-	1	-	2
	6	1	1	3	4
		6	6	6	12

in Fig. 4.2. When values are calculated plot by plot, using only the values within the replicate in question, errors accumulate since each value is based on ratios of yields derived from three independent plots. The distribution of these values is shown as a broken line in Fig. 4.2. When the RYTs are based on yields averaged over the four replicates, the scatter around the value of unity due to experimental error is reduced considerably (see solid line in Fig. 4.2). The distributions can clearly be said to be centred on unity although the scatter is considerable.

To find whether individual varieties mainly contribute to the same tail of this distribution, Table 4.3 was drawn up. To take account of the magnitudes, rather than just the frequencies, of the two types of departure from RYT, the results of the McGilchrist-Trenbath analysis (described in Section 3.2.3) are given in Table 4.4. Although the original analysis was carried out using values of (1-RYT), the values of the parameters have, for ease of interpretation, been back-transformed. Although in two cases RYT variety effects deviated from unity by more than twice their standard error, differences among variety effects were not significant. The four means of RYT averaged over whole diallel tables were all close to unity, none deviating by more than 3.2%. There was not strong evidence of the appearance of deviant RYTs in particular mixtures since the variance ratios of the RYT interactions ($\hat{T}_{ij}$) were never more than 1.42 .

The monoculture yields of the twelve varieties are given in Table 4.5. They are presented as log-transformed yields, since in Section 3.1.3 it appeared that it was the ratio of the components' monoculture yields which determined whether a mixture with a given RYT yielded transgressively (see Fig. 3.6) Arithmetic differences between the log-transformed values are measures of Y_{ii}/Y_{jj} . In Table 4.5, it

Fig. 4.2. Distributions of values of Relative Yield Total (RYT). Two of the distributions are based on the results of the field diallels and a third is based on the published results of 532 replicated mixtures.

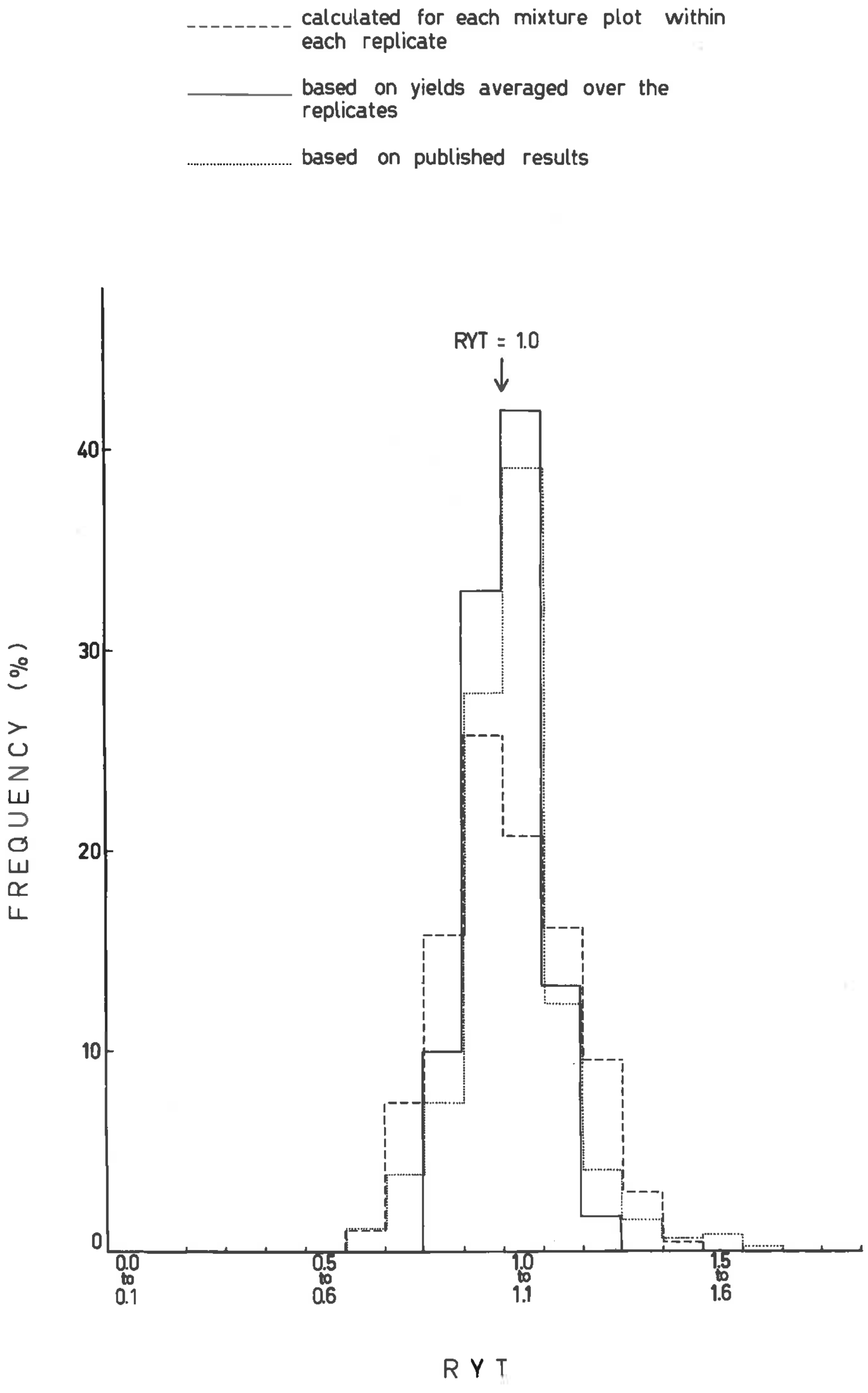

calculated for each mixture plot within each replicate
based on yields averaged over the replicates
based on published results
RYT = 1.0
FREQUENCY (%)
0
10
20
30
40
0.0 to 0.1
0.5 to 0.6
1.0 to 1.1
1.5 to 1.6
RYT

Table 4.3. Contribution of the various varieties to the two tails of the distribution of RYT, by diallels and densities.

Diallel		1		2	
Density		low	high	low	high
	1	1	3	3	1
	2	2	3	4	2
RYT < 1	3	3	3	3	1
	4	-	1	4	3
	5	3	2	5	3
	6	1	-	1	-
	total	10	12	20	10
	1	4	2	2	4
	2	3	2	1	3
RYT > 1	3	2	2	2	4
	4	5	4	1	2
	5	2	3	-	2
	6	4	5	4	5
	total	20	18	10	20

Table 4.4. Values of the McGilchrist-Trenbath parameters concerning RYT, and the results of significance tests based on the data of the two field diallels.

Diallel		1		2	
Density		low	high	low	high
RYT variety effects *) ($\hat{\lambda}_i$)	1	.995	.971	.995	1.014
	2	1.014	.962	.963	.959
	3	.973	.970	1.037	1.1021
	4	1.027	1.046	.967	.965
	5	.935	.943	,948	.979
	6	1.056	1.108	1.090	1.062
S.E. of variety effects		± .047	±.046	±.036	±.033
Mean RYT with S.E.		1.032 ±.035	1.017 ±.035	.970 ±.027	.988 ±.024
Results of F tests in AOV tables e)					
Mean effects		NS +)	NS	NS	NS
Variety effects($\hat{\lambda}_i$)		NS	NS	NS	NS
Interaction ($\hat{T}_{ij}$)		NS	NS	NS	NS

*) $\hat{\lambda}_i$ have been back-transformed (see text).

e) The complete tables are given in the Appendix, Section 11.3.

+) Here and elsewhere, NS denotes 'non-significant'.

Table 4.5 The monoculture yields of the two groups of 6 varieties used in the field diallels. The values refer to $\log_e$(biomass, g/plant).

diallel		1		2	
density		low	high	low	high
varieties	1	2.647	1.454	2.454	1.425
	2	2.322	1.325	2.502	1.371
	3	2.670	1.561	2.386	1.423
	4	2.511	1.348	2.500	1.378
	5	2.279	1.316	2.581	1.472
	6	2.193	1.111	2.492	1.381
L.S.D.(5%)		0.222	0.228	-	-
Results of F tests in AOV tables *)		$P < .01$	$P < .05$	NS	NS

*) See Appendix, Section 11.3

can be seen that there were large and significant differences among the monoculture yields in Diallel 1, whereas in Diallel 2, the yields were remarkably uniform (the variance ratios of the 'effects due to differences between monocultures' were 1.33 and 0.62 at low and high density respectively). This difference between the diallels in the uniformity of their monoculture yields was quite unexpected and was not the result of any conscious selection of the varieties to compose them.

The aggressiveness of a particular component in a single mixture is measured in the McGilchrist-Trenbath analysis by the aggressivity parameter, A. This parameter was defined mathematically for an ij mixture in Eqn. 3.6, but A_{ij} can be verbally defined as the average of the deviations of the plant relative yields of i and j from unity, where the deviation of j is used with its sign reversed. The analysis assumes a statistical model (see Section 3.2.3, Eqn. 3.7) giving A_{ij} in terms of $\hat{k}_i$, $\hat{k}_j$ and an interaction term $\hat{\theta}_{ij}$. The least-squares solutions for these parameters, obtained from the diallel data, are given in Table 4.6. The overall measure of the aggressivity of a given variety in its various mixtures is the $\hat{k}_i$ parameter, the 'aggressivity variety effect'. Judging by the absolute magnitudes of these variety effects, it is seen (Table 4.6) that in both diallels, the neighbour effects were clearly much greater in the high density than in the low. By far the greatest neighbour effects concerned the least aggressive variety, number 5 of Diallel 1. This variety, Selkirk, was the subordinate of all mixtures in which it was present, but its plant relative yields were usually much smaller at the higher density.

A notable feature of the data is their apparently simple structure. They are fitted quite well by only the first two terms of the model given in Eqn. 3.7. The interaction terms,

Table 4.6 Values of the parameters concerned with aggressiveness and the results of significance tests, based on the data of the two field diallels. The greater the aggressiveness of a variety the greater the value of its $\hat{k}$.

Diallel		1		2	
Density		low	high	low	high
Aggressivity variety effects ($\hat{k}_i$)	1	−.043	.076	−.041	−.093
	2	.034	.116	.084	.185
	3	.032	.046	.024	−.071
	4	.025	.079	−.066	−.091
	5	−.129	−.309	−.028	.029
	6	.080	−.009	.027	.041
S.E. of variety effect		±.039	±.039	±.030	±.029
Results of F tests in AOV tables *)					
Variety effects($\hat{k}_i$)		NS	$P < .01$	NS	$P \leq .01$
Interaction($\hat{\theta}_{ij}$)		NS	NS	NS	NS

*) See Appendix, Section 11.3

$\hat{\theta}_{ij}$, are very small since the variance ratios for interaction effects, indicated in Table 4.6 as non-significant, are infact all less than unity. The F values, in the order of the columns, are 0.87, 0.94, 0.42 and 0.16. A similar observation has already been made regarding the interactions in the model for (1-RYT).

4.3.2 Comparisom of models

In Section 3.2.3 an attempt was made to distinguish which of two models, the additive model (Eqn. 3.4) or the proportional model (Eqn. 3.5), summarised better the published results of individual mixtures. The biomass data of the wheat diallels were of the same type as used earlier, and hence they were plotted in the same way (Fig. 4.3a,b). These graphs are thus comparable with those of Fig. 3.7a & b. In contrast to the graphs using other authors' results, the points representing the various mixtures of the wheat diallels are seen to be widely scattered about the line of unit slope in both graphs.

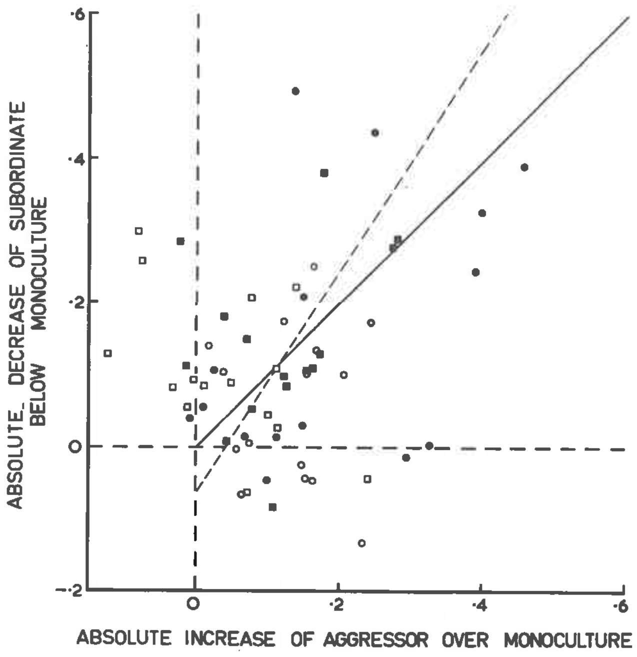
Treating the clouds of 60 points as being roughly elliptical, the slopes of the major axes of the ellipses were calculated using the techniques already described in connection with Fig. 3.7. The results, comparable with those given in Table 3.2 for data of 133 mixtures, were as follows : slopes of major axes 57.3° (additive) and 56.1° (proportional); correlation coefficients 0.2143 (additive) and 0.2232 (proportional); the coordinates of the population means, $(\bar{x}, \bar{y})$, were 117.6, 119.0 and 121.2, 119.2 for the points on the 'additive' and 'proportional' graphs respectively. Since the correlation coefficients are very low, the 98% confidence intervals for the slopes are wide, stretching for both graphs from approximately 18° to include 90° (i.e. including a slope indicating zero correlation). In terms of the results of individual mixtures, the data seem then to be fitted by both models rather poorly.

Fig. 4.3 Test of fit of results of the 60 mixtures in the two field diallels to the 'additive' and 'proportional' models. The additive model postulates the equality of arithmetic increases and decreases in per-plant yield of the components in mixture; increases and decreases are relative to yields in the components' respective monocultures. The proportional model postulates the equality of the corresponding proportional increases and decreases. For a perfect fit to a model, the data points should lie on the solid 45° line from the origin (0, 0). The major axes fitted to the clouds of points are shown as dashed lines. Statistical details of the lines are given in the text. Note the difference of scale when comparing these graphs with those of Fig. 3.7 .

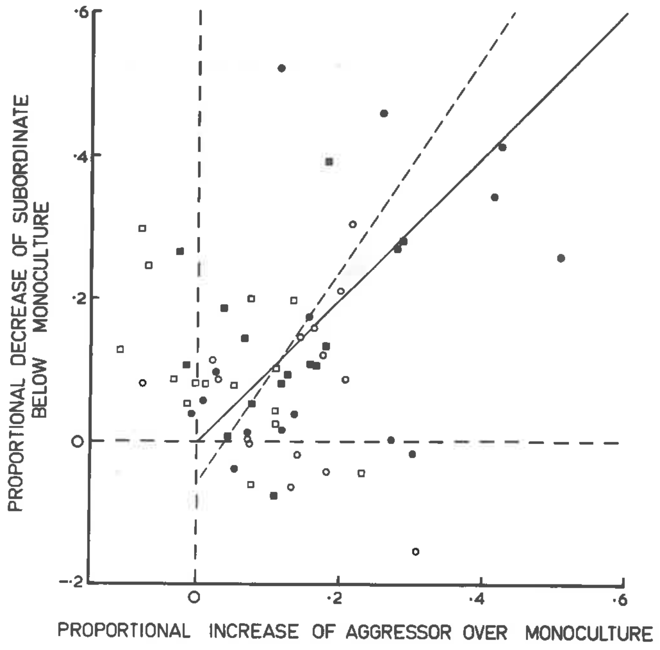
Diallel 1
○ low density
● high density

Diallel 2
□ low density
■ high density

(a) Additive model



(b) Proportional model



In terms of the results of complete diallels, again, the data are fitted hardly better by the McGilchrist-Trenbath model than by the standard factorial model used by Helgason & Chebib (1963, see Section 3.2.2). This is suggested by the relative sizes of the variance ratios of the 'interaction effects' in the analysis of variance tables. These are shown in Table 4.7 along with variance ratios of the interaction effects calculated according to the analysis of McGilchrist (1965) using log-transformed data. Only the values derived from the second (McGilchrist-Trenbath) and third (McGilchrist) analyses of Table 4.7 are strictly comparable but the general impression is of little difference between models in the importance of the apparent interaction effects.

4.3.3 Morphological characteristics and aggressiveness.

In an attempt to discover what characteristics, or combination of characteristics, determined aggressiveness in the diallels, the values of several possibly important characters (measured in the monocultures) were used as independent variables in a multiple regression analysis.

These characters were tiller number, height and (shoot) biomass at the harvest 110 days after planting, 100-seed weight measured on the seed sample used for planting, and the number of days from planting to 50% ear-emergence. The values of these measurements averaged over replicates are given in Table 4.8.

The aggressivity variety effect, $\hat{k}_i$ (see Table 4.8), estimated from the performances of the varieties in all of the mixture plots, was used as the dependent variable in the calculation of multiple regression equations; the independent variables were the five characters mentioned above. According to the stepwise procedure used in these calculations, at each

Table 4.7 A comparison of the variance ratios of 'interaction effects' in analysis of variance tables resulting from analyses of the diallel data performed in 3 different ways.

Source of data	Type of analysis				
	Factorial	McGilchrist-Trenbath(1971)		McGilchrist (1965)	
	Rows x Columns interaction (d.f.= 25)	$\hat{\theta}_{ij}$ (d.f.=10)	$\hat{T}_{ij}$ (d.f.=10)	$\hat{\theta}_{ij}$ (d.f.=10)	$\hat{T}_{ij}$ (d.f.=10)
Diallel 1					
Low D.	1.314	.938	1.019	1.100	1.123
High D.	1.331	.874	.997	.927	.921
Diallel 2					
Low D.	1.359	.417	1.142	.451	1.349
High D.	.693	.162	.869	.145	.914

Table 4.8 Aggressivity variety effects ($\hat{k}_i$) and the values for the five characters of the monocultures used as independent variables in stepwise regression calculations.

a) <u>Diallel 1, low density</u>

Variety	$\hat{k}_i$	Wt. per 100 seeds (g)	Tiller no.	Height (cm)	Y_{ii} (g)	Days to ear emergence
DES	-.043	3.80	5.7	63.9	14.25	96.9
India	.034	3.16	8.5	60.5	10.32	93.3
Napo	.032	3.80	7.4	61.9	14.62	90.3
Pitic	.025	3.47	5.8	61.1	12.44	97.4
Selkirk	-.129	2.40	7.9	58.0	9.91	114.6
Summit	.080	3.56	6.1	49.1	9.04	107.1

b) <u>Diallel 1, high density</u>

DES	.076	3.80	3.8	64.3	4.30	96.9
India	.116	3.16	3.4	57.9	3.82	93.3
Napo	.046	3.80	3.2	63.1	4.77	90.3
Pitic	.079	3.47	3.0	56.8	3.85	97.4
Selkirk	-.309	2.40	3.9	56.8	3.79	114.6
Summit	-.009	3.56	3.7	49.1	3.06	107.1

(Table 4.8 - continued)

c) Diallel 2, low density

Variety	$\hat{k}_i$	Wt. per 100 seeds (g)	Tiller no.	Height (cm)	Y_{ii} (g)	Days to ear emergence
CT	-.041	3.08	6.8	51.1	11.76	111.0
Giza	.084	3.91	6.4	61.2	12.22	98.2
Heron	.024	4.23	7.3	50.5	10.95	100.8
Justin	-.066	2.52	8.1	59.9	12.24	112.9
Klein	-.028	3.38	5.8	57.3	13.25	93.2
Mentana	.027	3.53	4.7	56.8	12.15	97.6

d) Diallel 2, high density

CT	-.093	3.08	3.8	50.7	4.22	111.0
Giza	.185	3.91	2.8	56.8	3.94	98.2
Heron	-.071	4.23	3.6	53.4	4.16	100.8
Justin	-.091	2.52	3.4	58.0	3.97	112.9
Klein	.029	3.38	3.4	60.2	4.38	93.2
Mentana	.041	3.53	2.7	57.9	3.99	97.6

step a further variable out of those presented is added to the equation currently being produced. The variable added is the one which causes the greatest reduction in the error sum of squares. The process stops when no other variable, when included in the equation, shows an individual F-value greater than a specified level (here this level was 2.5).

The results of the stepwise regression are given in Table 4.9. Weight per 100 seeds was the first variable included in the regression equation in both diallels, at low density and high density; the correlation coefficient, r, between 100-seed weight and $\hat{k}_1$ was always greater than +0.45. Tiller number was always negatively correlated with aggressivity, possibly due to its generally positive correlation with flowering date (see below). In diallel 2 at high density, tiller number was the only variable included in the final equation; no other single variable could be found to increase the predictive power of the equation sufficiently to pass the (not at all stringent) test criterion for entry. Height (at 110 days after planting) had low positive r values at high density and at low density the r was inconsistent. In spite of the importance of height growth in competition for light (see Section 2.1.1), height at harvest was apparently of little importance in these diallels.

The monoculture yield had little predictive value on its own since the absolute values of r were small and inconsistent in sign. 'Vigour', as seen in monoculture, was therefore not important in determining aggressivity. Lateness of flowering was always negatively correlated with $\hat{k}_1$ (r values were -0.524, -0.869*, -.601, and -0.673) and so flowering date seems to have been the variable second to weight per seed in consistency of predictive power.

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* Significant at the 5% level.

Table 4.9 Results of stepwise regression of aggressivity variety effect, $\hat{k}_i$, of two sets of six varieties, on five characters. r = simple correlation coefficients of $\hat{k}_i$ with each of the characters (d.f. = 4). R^2 = square of the multiple correlation coefficient representing the proportion of the variance accounted for by the multiple regression equation.

Diallel & density		Wt. per 100 seeds (g)	Tiller no.	Height (cm)	Monoculture yield/plant (g)	Days to ear emergence	R_2
1, low	r	+.665	-.222	-.346	-.030	-.524	
	Order of inclusion	1			2	3	
	Coefficients of final equation	+.124			-.0310	-.00465	.915
1, High	r	+.804	-.597	+.248	+. 220	-.869*	
	Order of inclusion				2	1	
	Coefficients of final equation				-. 151#	-.0209	.936
2, Low	r	+.827*	-.417	+.191	-. 212	-.601	
	Order of inclusion	1		2			
	Coefficients of final equation	+.0868		+.00565			.876

Continued

Table 4.9 (continued)

Diallel & density		Wt. per 100 seeds (g)	Tiller no.	Height (cm)	Monoculture yield/plant (g)	Days to ear emergence	R^2
2, High	r	+.457	-.801	+.447	-.315	-.673	
	Order of inclusion		1				
	Coefficients of final equation		-.197				.642

* Significant at the 5% level.

\# The difference in sign between the r value and the coefficient of the final equation is due to the correlation coefficient reflecting inter-correlations between independent variables whereas in the calculation of the multiple regression such inter-correlations have no effect on the values of the coefficients.

To summarise, aggressivity seems to have depended on the same characters in both densities of Diallel 1 but not in the two densities of Diallel 2; the only similarity of the final regression equations between the two diallels is that weight per seed was included first in the equations of both low densities. A general impression, based on simple correlations, suggests a positive dependence of aggressivity on weight per seed and earliness of flowering. 'Vigour' in monoculture was surprisingly not an important determinant of aggressivity.

4.4 Discussion

4.4.1. Yields of mixtures

Although 32 out of the 60 mixtures examined in these diallels yielded transgressively, it is remarkable that none did so significantly at the 5% level. A similar situation has been noted among the published data reviewed in Section 2.1. The results of the two wheat diallels indicate that the largest percentages by which the mixture biomasses exceeded the higher-yielding monocultures in the two densities were 15% (Summit + India, low density) and 6% (Summit + Pitic, high density). The greatest percentage by which underyielding mixtures fell short of the lower-yielding monocultures were 17% (Giza + CT, low density) and 10% (Gize + Justin, high density). Although these percentage differences were large, the variability in the data was such that they could all be ascribed, within the conventional limits of probability, to experimental error.

Comparing the results of the present diallels with those of the published reports, it appears that the ratio of under- to over-yielding mixtures (1:0.88) is rather different from the ratio (1:2.12) found in the published data (χ^2=3.78, d.f.=1, $P < 0.06$). This suggests that the present data are somewhat atypical. In Section 2.1.2, two explanation of the generally observed greater frequency of overyielding were proposed. One depended on a positive correlation between aggressiveness and monoculture yield, while the other depended on the conditions leading to apparent mutual stimulation simply being met more commonly than those leading to mutual depression. The first suggested mechanism could operate with the distribution of RYT centred on unity whereas the second mechanism would require values greater than unity. To test whether either of these mechanisms could explain the difference between the present data and the published data concerning the relative frequencies of the two kinds of transgressive yielding, each set of data was examined with respect to, firstly, the correlation between aggressivity and monoculture yield, and secondly, the distribution of RYT.

The data of the two diallels showed no consistent correlation between aggressivity and monoculture yield. The correlation coefficients (d.f.= 4) within the low and high densities of Diallel 1 were -0.030 and +0.220 respectively. The corresponding values for Diallel 2 were-0.212 and -0.315. Using the negative values * of the diallel column means as 'one-term' measures of aggressivity gave somewhat different results: the correlation coefficients calculated between column means and monoculture yield, in the same order as above, were +0.120, +0.430, +0.118 and -0.315. Using the z-transformation, these last 4 values give a pooled value of +0.124 with d.f.= 4(p-3) = 12.

Using the same index (negative values of column means), the pooled correlation coefficient was calculated for the published data of 283 mixtures and was found to be +0.289 (d.f. = 42) with a 95% confidence range of -0.013 to +0.678. Six 3 x 3 diallels, all with positive correlation coefficients, could not be ligitimately included in the pooling since at least (p-3) degrees of freedom were required for each value entered; their correlation coefficients (d.f. = p-2 = 1)were +0.846,+0.876, +0.816, +0.826, +0.395 and+0.820. The correlation coefficient for the published data considered is therefore certainly more positive than +0.289. The published data thus show a weak but almost significant tendency for aggressiveness to be positively correlated with monoculture yield while in the 2 wheat diallels, the correlation was shown above to be

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* Since diallel column means are inverse measures of aggressiveness, using their negative values allows them to be treated as direct measures of aggressiveness.

rather less (+0.124). Since the distributions of RYT are so similar, it seems that only the slight difference between these degrees of correlation is available to explain the marked difference of pattern of transgressive yielding in the two sets of data.

Examination of Fig. 3.6 suggests however a further possibly contributing factor, namely the value of Y_{12}/Y_{11}. In the low density treatments of the wheat diallels the neighbour effects were relatively slight (see Table 4.6) so that Y_{12}/Y_{11} was often close to unity. If true mixture yields were close to $\bar{P}$, random experimental error would cause under- and over-yielding to be almost equally frequent (e.g. Diallel 1, low density). Experimental error apparently caused a relatively high frequency of downward deviations of RYT in the low density treatment of Diallel 2 (see Table 4.3); the general closeness of Y_{11}/Y_{22} to unity caused such RYT deviations to be especially effective in producing cases of underyielding (see Fig. 3.6 and Table 4.2a). It was from this density of Diallel 2 that the preponderance of underyielding cases in the wheat diallels originated.

The significant difference between the frequencies of transgressive yielding in the two wheat diallels can similarly be explained by reference to the factors considered in Fig. 3.6. In Diallel 1, the Y_{11}/Y_{22} ratio showed significant deviations from unity in 8 pairs of monocultures at the low density and in 5 pairs at the high density. In Diallel 2, no Y_{11}/Y_{22} ratios differed significantly from unity. The highest values of these ratios were 1.62 and 1.56 in Diallel 1 (low and high density respectively) while corresponding values in Diallel 2 were only 1.21 and 1.11. As Fig. 3.6 shows, when Y_{11}/Y_{22} is far from unity, transgressive yielding is unlikely unless the deviation of RYT from unity is large. When $Y_{11}/Y_{22} \simeq 1$, almost any deviation of RYT from unity will cause transgressive yielding. This effect is to be seen in the present data for when all 60 mixtures are classified according to their values of Y_{11}/Y_{22}, the frequency of transgressive yielding falls off steadily as $Y_{11}/_{22}$ deviates further from unity (see Table 4.10).

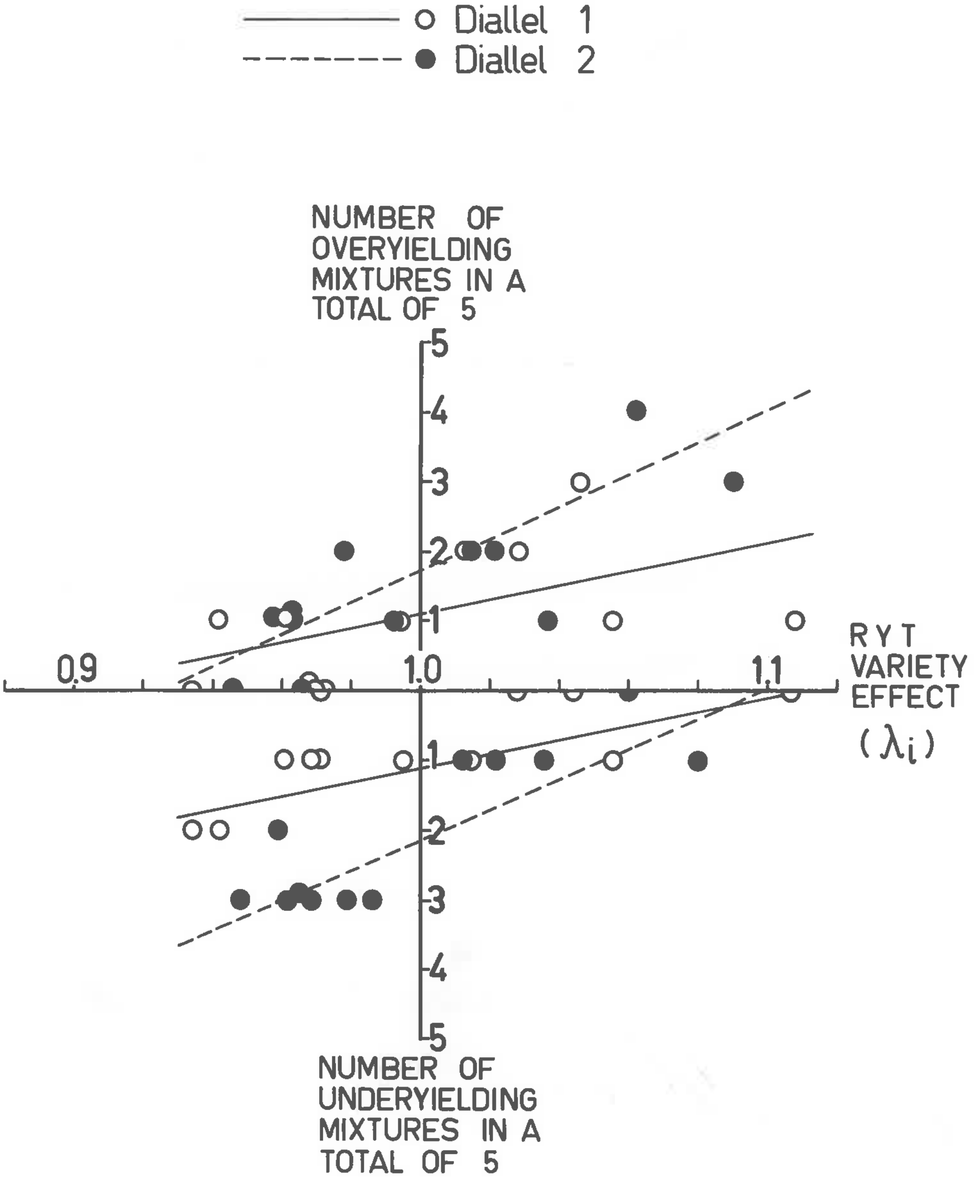
The relationship between RYT deviation and number and type of transgressively-yielding mixtures produced is shown for the wheat diallels in Fig. 4.4. The Figure has been constructed by plotting each variety's RYT effect ($\hat{\lambda}_i$) against the number of overyielding and underyielding mixtures of which it was a component. At any density, a variety was only grown in five mixtures and hence this is the highest number of, say, overyielding mixtures possible. The regression line of each diallel has been based on 12 points (6 varieties at 2 densities), and they differ significantly ($P < 0.05$) with respect to the numbers of both overyielding and underyielding mixtures; in Diallel 2, more transgressively-yielding mixtures are expected from a given varietal value of $\hat{\lambda}_i$ than in Diallel 1. The significance ($P < 0.01$) of both regressions of Diallel 2 and one of the lines ($P < 0.05$) of Diallel 1 shows the close association between RYT value and transgressive yielding by mixtures.

This discussion of the results of the wheat diallels and of the published data has illustrated and confirmed the value of some of the concepts introduced in Section 3. It appears that transgressive yielding by mixtures is a complex phenomenon since it is only achieved when several independant factors are favourable. The factors which have been particularly useful in explaining the distribution of cases of transgressive yielding by mixtures are: the type of ecological interaction involved (apparent mutual stimulation or depression, measured by RYT_{ij} or $\hat{\lambda}_i$); the unevenness of the sharing of environmental resources (measured by Y_{12}/Y_{11}, A_{ij}, $\hat{k}_i$ or the

Table 4.10 Relationship between the value of the ratio of the monoculture yields (Y_{11}/Y_{22}) and the frequency of transgressive yielding in the corresponding mixtures.

Y_{11}/Y_{22}	1.0 - 1.09	1.1 - 1.19	1.2 - 1.29	above 1.3
number of mixtures	28	15	9	10
% of mixtures yielding transgressively	71.3	60.0	33.3	0

Fig. 4.4 Relationship between the values of the varieties' RYT effects ($\hat{\lambda}_i$) and the number of over- and under-yielding mixtures of which the corresponding varieties were components. The regression lines were calculated separately for each diallel and mixture type. The upper and lower halves of the graphs are indppendet.



○ Diallel 1
● Diallel 2
NUMBER OF OVERYIELDING MIXTURES IN A TOTAL OF 5
NUMBER OF UNDERYIELDING MIXTURES IN A TOTAL OF 5
RYT VARIETY EFFECT (λ_i)
0.9
1.0
1.1
5
4
3
2
1
1
2
3
4
5

diallel column mean); the degree of similarity of the monoculture yields (measured by Y_{11}/Y_{22}); and whether the genotype with the higher yield in monoculture is the aggressor or the subordinate (Montgomery effect). The last factor is measured by the correlation between aggressivity variety effect, $\hat{k}_i$ (or the diallel column mean, as an inverse index of $\hat{k}_i$), and monoculture yield. Fig. 3.6 summarises the manner in which these factors act together to produce a specific case of transgressive yielding.

4.4.2 Comparison of models

In Section 3.2.3, published data on many individual mixtures were tested for fit to the proportional and additive models (Fig. 3.7). The fit to the proportional model was generally superior, although when neighbour effects were only slight, mixture data were fitted equally well by either model. The neighbour effects in the wheat diallels were not very great, for in Diallel 1 the largest plant relative yields observed were 1.31 and 1.51 (at low and high density respectively). Neighbour effects were still less marked in Diallel 2, since the corresponding values were 1.23 and 1.28. The slightness of these effects partly explains why the data of the wheat diallels were not fitted noticeably better by either model. A further reason is provided by the striking uniformity of monoculture yields within oneof the two diallels (Diallel 2); if the monoculture yields of a series of genotypes were identical, the graphs plotted according to the two methods of Section 3.2.3 would also appear to be identical. Hence, the lack of a superior fit of the present data to the 45° line in the 'proportional' graph of Fig. 4.3 seems not to affect the previous conclusion concerning the general superiority of the proportional over the additive model.

A further test of models was to compare the goodness of fit of complete diallel tables to two models, one additive and the other proportional. This test also was inconclusive, partly for the same reason, i.e. that when monoculture yields are similar the two models predict similar results.

4.4.3 Morphological characteristics, aggressiveness and mixture yield.

Since with a given difference between monoculture yields greater aggressiveness of the more productive genotype reduces the RYT deviation required for overyielding (Fig. 3.6), it would seem that any attempt to produce overyielding for agricultural purposes would be best made with mixtures in which the more productive component was the more aggressive. Since 'vigour' as measured by monoculture yield has been shown above to be only a poor indicator of aggressiveness, the choice of suitable genotypes for testing in combination would be easier if more perfect indicators of aggressiveness were available. Although it is known that extremely small differences of environment may nullify or reverse the effect of various characters on aggressiveness (see Section 2.1.1), is nevertheless of interest to investigate the characters which have been associated with aggressiveness under the conditions of particular experiments.

The regularly positive correlations found in the wheat diallels between aggressivity and seed-size are consistent with the results of numerous experiments (e.g. Montgomery 1912, Christian & Gray 1941, Black 1958) although the observations of Bal <u>et al</u>.(1959) suggest that other characters can compensate for the disadvantage of small seeds. Since advantages gained early in growth may be very influential in determining later patterns of dominance in mixtures (Bleasedale 1959), seed size may have acted by affecting the rate of establishment. Indeed, using a range of pasture species, Asher & Ozanne (1966) demonstrated a close correlation between seed-size and early rates of penetration of soil by roots. Similarly, Borojevic (1964) showed that the early size and growth of shoots of wheat was affected by seed-size,

Fairly high positive correlations were found in the present data between earliness of flowering and aggressiveness but the mechanism underlying this association is not certain. When competition for soil factors is not important, a positive correlation is to be expected in grasses and other species in which height of growth is associated with flowering. This follows from the results of the elegant experiment of Nguyen Van (1968) which involved a monogenotypic mixture of ryegrass; the seeds of one component, having been vernalised, gave early flowering plants which were more aggressive than unvernalised non-flowering plants. With competition for soil-factors occurring, the correlation of earliness and aggressiveness could be due to earlier height growth causing associated genotypes to be shaded, but could also be due to some advantageous feature of the development of the root-system associated with early flowering.

In the wheat diallels, the number of tillers (suggested as possibly important by Jensen & Federer 1964) only once entered a regression equation, with a negative coefficient. However, it does not seem likely that the absence of tillers directly favoured aggressiveness. Height entered an equation only once although in several mixture diallels it has been shown to be important (e.g. Knapp & Thyssen 1952, Williams 1963, Jensen & Federer 1964, Bell _et al_.1968). On the other hand, natural selection experiments and other diallels have shown that tallness may not be a necessary feature of aggressive genotypes (e.g. Bal _et al_.1959, Pal _et al_.1960, Allard

& Jain 1962, Jensen & Federer 1965). Since competition for light ceases to be the sole determinant of neighbour effects as soil conditions become less favourable, a low correlation between aggressiveness and height possibly indicates the occurence of competition for soil-factors. Considering the exceptionally dry conditions during the growth of the wheat diallels, the low correlation with height seems understandable.

It is clear that explanations can be offered for the apparent importance in the wheat diallels of most of the characters selected by the regression procedure, but it must be noted that the explanations are not actually in terms of the characters themselves but rather concern characters believed to be associated with them. In spite of the uncertainties involved in the interpretation of the effects, the agreement between the results of two independent groups of varieties picked for their contrasting characters, does suggest the importance of seed-size and earliness in the determination of aggressiveness in the environment in which they were tested.

5. SOIL BENCH EXPERIMENT

5.1 Introduction

Although many comparisons of biomasses of mixtures and monocultures have been published, remarkably few attempts have been recorded in which interesting results obtained on one occasion have been tested for repeatability (see Section 2.1.2). In this project, the intention was to find a mixture which yielded transgressively in a repeatable fashion and then to study the causes of its truly transgressive yielding.

The results of the 6 x 6 diallels did not produce any significant cases of transgressive yielding and so it was thought that attention should be concentrated on three mixtures which had either overyielded non-significantly or had high RYTs. Three varieties, Pitic (Pt), Selkirk (Sl) and Summit (Sm), were selected from Diallel 1 because their mixtures at high density had overyielded by 3% (Pt + Sl, RYT = 1.035) and 5% (Pt + Sm, RYT = 1.160) and because the third mixture (Sk + Sm) had a RYT of 1.124. The diallel table of the results of these 3 varieties taken from the 6 x 6 table, is given in Table 5.1. The lack of significance of the overyielding cast doubts on the possibility of repeating the results, but the almost complete absence from the literature of statistically significant cases of transgressive yielding suggested that any real effects tending to produce transgressive behaviour are normally so small that they cannot be separated from experimental error in trials having the usual 3-4 replications.

On the other hand, the indications of the reality of the RYT deviations were slightly stronger. In Table 4.4, the RYT effect ($\hat{\lambda}_i$) of Summit is seen to deviate from unity by more

Table 5.1 Results of the varieties Pitic, Selkirk and Summit in mixtures and monocultures within Diallel 1 (grown in 1967). The data on the three lines in each entry are 1) biomass of individual component (g/plant) 2) biomass of mixture or monoculture (g/two plants) in brackets, and 3) RYT.

a) <u>Low density</u>

	Pitic	Selkirk	Summit
Pitic	12.44 (24.9) 1.000	14.44 (22.8) 1.001	12.48 (22.2) 1.039
Selkirk	8.33 (22.8) 1.001	9.91 (19.8) 1.000	6.90 (17.9) 0.955
Summit	9.72 (22.2) 1.039	10.98 (17.9) 0.955	9.04 (18.1) 1.000

b) <u>High density</u>

Pitic	3.85 (7.7) 1.000	5.44 (7.9) 1.035	5.02 (8.1) 1.160
Selkirk	2.49 (7.9) 1.035	3.79 (7.6) 1.000	2.81 (7.4) 1.124
Summit	3.11 (8.1) 1.160	4.61 (7.4) 1.124	3.06 (6.1) 1.000

than twice the standard error of the $\hat{\lambda}_i$'s (although the overall test of differences between the $\hat{\lambda}_i$'s shows them not to differ significantly among themselves). In addition, it might be pointed out that RYT values of 1.160 and 1.124 represented apparently strong tendencies towards overyielding since if the monoculture yields of the mixture's components had been the same, such values of RYT would have been associated with overyielding by 16% and 12% respectively.

A 3 x 3 diallel of Pitic, Selkirk and Summit was therefore grown in the following season (1968) at the same high density as used previously. To test the stability of any effects observed, two moisture-level treatments were imposed.

The low-water treatment accorded to some extent with the conditions of the 6 x 6 diallel field experiment of the previous year (1967); by causing plants to grow using only the limited and unreplaced supplies of water present in the soil at planting, it was hoped to produce a crop in which water would be clearly the principal factor. Results would depend on uptakes and efficiency of utilization of water.

The high-water treatment aimed at providing near-optimum conditions of soil water and nutrients so that again a one-factor situation would be produced; any overyielding (or high RYTs) in the mixtures of that treatment would be presumably explicable in terms of the interception and efficiency of utilization of light.

5.2 Materials and methods

5.2.1 General description

Two soil benches were used for the experiment; they stood end-to-end in a north-south direction, each 850 cm x 120 cm x 65 dm deep (internal dimensions) and were constructed of hollow Besser blocks 23 cm thick. The bench was built with a 'soft bottom' of Urrbrae loam about 15 cm thick. This rested on a layer about 100 cm thick of assorted 'filling' material (mostly stone), resting in turn on Urrbrae loam.

A 2:1 mixture of Gawler loam and coarse sand was well blended, sieved and on 3 June 1968 put into the soil benches to make a layer 50 cm deep over the 'soft bottom' of loam. Between additions the soil mixture was thoroughly pressed down. In the top 15 cm of the benches was then placed a similar but sterilised soil mixture containing a dressing of John Innes basic fertilizer. This dressing supplied 180 kg N/ha in the form of hoof and horn, 230 kg P/ha as superphosphate and 350 kg K/ha as muriate of potash.

The moisture content of the soil mixture when put into the benches was 14%. The beds were left open for 33 days and received 8.4 cm of rainfall together with 2.5 cm of irrigation water given to aid the setting of the soil. It was decided that the north bench would receive the 'low-water' treatment (no further rainfall or irrigation) and so it was covered on 6 July to await planting.

Each bench was divided into 18 plots, each measuring 60 cm x 90 cm, arranged in pairs along the bench. The plots of the 6 treatments (3 monocultures of the varieties Pitic, Selkirk and Summit, and 3 pair-wise mixtures) were arranged in 3 blocks (replicates) within each soil bench.

Within each plot there were 6 east-west rows, 15 cm apart and each containing 15 plants set 4 cm apart within the row. The density and planting pattern were thus similar to those in the high density of the 6 x 6 diallels of the prævious season except that the row direction had been changed through 90° and in the mixtures, plants of the two components were alternated in both directions. The harvested area of each plot was bordered by one guard row and by 4 plants at the end of each row. Thus 28 plants were harvested in each plot; in the mixtures, the 28 plants were made up of 14 of each component.

The seeds to be used in planting were carefully graded to exclude small or broken grains; the weights of random samples of 100 seeds were Pitic 3.76 g, Selkirk 3.58 g, and Summit 3.61 g.

The experiment was planted on 20 July 1968. Germinated seeds were placed at the bottom of dibbed holes, 2 cm deep, which were then filled to the top with dry sand and lightly watered. Gaps where seedlings had not emerged were filled with transplants of the appropriate variety, prepared in the same way as for the 6 x 6 diallel experiments. They were marked and disregarded in later measurements.

To prevent the entry of further rain, the north bench was covered after seeding with a sheet of transparent PVC. By the time the seedling emerged, a sloping roof of 'crystal clear' PVC sheet had been erected over this low-water bench. The proportion of the visible light intercepted by this roof was about 20%. It sloped towards the west (the direction of the prevailing winds) and was large enough to prevent all rain from reaching the soil surface. As the crop grew, vertical screens of hessian were raised round the perimeter of each soil bench; their tops were kept roughly level with the top of the leaf canopy. The height of the roof of the low-water bench was adjusted to leave a distance of about 30 cm between it and the top of the screen of the west side. On the east side, the gap was about 60 cm. Since the benches were situated in a place fully exposed to wind, the canopies were well ventilated. The general appearance of the benches on 14 October (Day 83) is shown in Plate 5.1 .

Mildew was controlled by sulphur dusting, and by spraying with a piperaldehyde preparation (ICI, not yet released commercially). The monoculture plot of Selkirk in Block C of the high-water bench showed 'juvenile' lodging on day 60; although it was immediately supported on strings, its canopy was never

Plate 5.1 Soil bench experiment on 14 October 1968 (Day 83).

(a) General view looking north-west. The high-water bench is nearest the camera; the low-water bench with its slanting roof is beyond.

(b) Close-up view of the foliage of monoculture plots of the three varieties in the high-water bench:

1 Selkirk - foliage erect
2 Pitic - foliage drooped, ears emerging
3 Summit - foliage of intermediate type

1
2
3

restored to a natural appearance. This plot was therefore omitted from the measurements of canopy structure and light profile.

Since the results in the high-water treatment would need to be interpreted in terms of light utilization and shading of one component by another, an attempt was made to measure the canopy structure of the monocultures in this treatment on two occasions during growth. The canopy structures in the mixtures were estimated from the directly measured structures of the monocultures; the methods are given below.

Canopy structure can be characterised by the distribution, in the various layers, of the inclination of photosynthetic area (DIPA). The photosynthetic area of a wheat canopy is made up of the leaf area index, LAI, the stem (and leaf sheath) area index, SAI, and the ear area index, EAI, each area of photosynthetic surface being expressed as a proportion of the area of ground over which it occurs. The canopy structure is conveniently represented by a table of m rows and n+1 columns where m is the number of layers into which the canopy has been divided and n is the number of inclination classes among which the LAI has been taken to be shared. In the present work, up to eleven 10-cm layers were used, i.e. $m \leqslant 11$; n was 3 and hence the first three columns contained the LAI which fell into the inclination classes 0° to 30°, 30° to 60° and 60° to 90° (measured from the horizontal). The last column of the table, the fourth in this case, contained the summed areas of stem and ear; these were taken to have an inclination of 90°.

Since the measurements required to measure DIPA were extremely time consuming, DIPA tables were based on replicate representative plants. These plants were chosen as follows : the tiller number (counting those longer than 5 cm to the highest ligule) and the pulled height were measured for all plants in the harvest areas of the monoculture plots. The plant in each plot, of which the measured tiller number and height most closely matched the measured plot averages, was taken as the representative 'test plant' for that plot. Measurements of tiller number and pulled height were also made at the same time on all plants in the harvest areas of the mixture plots, and of all plots in the low-water bench. These measurements of tiller number and height were made on two occasions: the first (T1) was on days 51 and 52, and the second (T2) was on days 101 and 111.

The treatment of the 'test plants' and the procedure for producing the m x 4 DIPA tables from the resulting data were rather complex. The details are given in the Appendix, Section 11.4 and so here the methods are described only in outline. Firstly, for each leaf of the plant, the leaf's position in space and its approximate geometrical form were defined by appropriate measurements; the areas of the parts of the leaf in the three inclination classes were then determined and their areas assigned to the layers in which the parts occurred. The contributions of all leaves to the cells of the required m x 3 table were summed and converted to LAI units. Secondly, the stems and ears were approximated respectively by vertical cylinders and four-sided columns. From measurements of their dimensions and their positions with respect to the boundaries between layers, the total area of roughly vertical photosynthetic surface was arrived at for each layer. When the resulting values had been converted to units corresponding to LAI, they constituted the fourth column of the DIPA table.

Since the canopy structures of the mixtures had not been measured, DIPA tables were estimated for them based on the tables of their components' monocultures. The total areas (cm^2/cm^2 soil surface) of leaf and stem organs of each component in a mixture were roughly estimated as 0.5 times the

the values in the corresponding monoculture. The height relations of the two canopies within a mixture were approximated by expanding or contracting the vertical scale of each monoculture DIPA array according to how the height of the variety measured in the mixture compared with that in its monoculture. The two DIPA arrays of each mixture were then recalculated using standard 10 cm layers to make them comparable with those of the monocultures. Since in the high-water bench all differences between the heights of mixture components and corresponding monocultures proved to be small and non-significant, these adjustments of scale did not in fact introduce any marked differences between the DIPA tables of plants of the same variety in mixture and monoculture.

This technique of estimating the DIPA tables of the communities in the high-water bench was used on two occasions, T1 and T2, associated with the measurements of tiller number and height referred to earlier. The dates on which the DIPA measurements were performed are given in Table 5.2.

The period over which the various measurements of each occasion were made was much longer than desirable and this was principally due to the lack of suitable windless days. The siting of the soil benches in an exposed position and a particularly cold and windy season were unfortunate. The delays between the measuring of the replicates made it impossible to average the results of the three Blocks and hence, only the averaged results of Blocks A and B are reported in entirety.

Associated with the investigation of DIPA, measurements of 'light' profiles (strictly profiles of the irradiance of a flat horizontal sensor) were made in the canopies of the same monocultures. The two occasions were over the periods Days 59-63 and Days 107-111. The sensor (Barrowman 1956) consisted of 6 silicon cells mounted on a probe under a diffuser. (The readings integrated the outputs of the 6 sensors.)

Table 5.2 Times at which the operations related to the measurements of canopy structure were performed. The two measurement occasions are referred to as T1 and T2. Times are given as number of days after planting.

	T1	T2
Measurement of tillers and pulled height of all plants	51 - 52	101 - 111
Measurement of canopy structure	59 - 65	101 - 111
Measurement of light profiles	59 - 63	107 - 111

Profiles were measured in still, sunny weather within 1.5 hours of apparent solar noon. Readings were taken with the probe parallel to the rows; starting above the canopy, the probe was moved downwards by withdrawing it and reinserting it, 10 cm lower each time, until it reached ground level. Profiles were taken down through the middle of a row, 5 cm to the north of a row and 5 cm to the south. This series was repeated three times within each plot, using the northernmost three of the four inner rows. The results of each level were averaged to produce the profiles shown in the Figures.

The purpose of the measured profiles was to check, for one solar altitude, the predictive power of a new model of light penetration into canopies; this model, DAYP, is described in the next Section (5.2.2). Since the model was designed to also give predictions of canopy photosynthesis, its application to the calculated DIPA tables resulted in predictions of daily P rates of the monocultures and mixture components in the high-water bench. Two sets of simulations were performed corresponding to the two occasions, T1 and T2, on which canopy structures were measured.

The time at which 50% of the plants of each component in each plot had reached ear emergence was estimated by counts made every few days.

Both treatments were harvested on 20 November, 123 days after planting. At this time, the plants of the low-water bench were almost mature while those of the high-water bench had seeds at the milky-stage or dough-stage, depending on the variety.

The plants were uprooted and sorted into the two bags (for a mixture) or single bag (for a monoculture) assigned to each plot. The material was dried in an oven at 80°C for 24 hours and then individual plants were treated as follows.

The shoots were cut from the crown and roots at a point 2 cm above the top of the crown, and the culm with the highest leaf ligule was selected: the height of this culm's highest ligule was recorded. The ears were cut from the rest of the shoot (here called the straw) and the samples of ears and straw were redried and finally weighed.

5.2.2 Outline of the operation of the photosynthesis simulation programme 'DAYP'.

The programme DAYP relies heavily on the theoretical approach to canopy photosynthesis developed by Duncan et al. (1967). A full account of the structure of the DAYP programme is given in the Appendix, Section 11.5; however, in the present Section, only the general features are described.

The environmental conditions to be specified in the input to the programme are the latitude, date and sky conditions (sunny or overcast). Temperature effects are ignored. The plant factors which must be specified are the DIPA table of the genotype composing the stand, and the two constants (P_{max} and K_m, see Appendix, Section 11.5) which determine the gross photosynthesis:irradiance relationship of its leaves. In the case of a mixed stand, a double DIPA table and two sets of constants are input. A number of tables are read in at the beginning of each series of simulations; these are prinipally the tables giving sun and sky brightness (W.G.Duncan, pers. comm. 1968) for all possible elevations of the sun, and the table of the Warren Wilson-Reeve shadow ratio for all possible leaf inclinations and sun elevations (Warren Wilson 1960).

Taking account of the latitude and date, the programme calculates the sun elevation at hourly points throughout the day. The hour round each time point is assumed to be represented adequately by the situation at the time point and the prediction of the whole day's gross photosynthesis is obtained by summing the quantities calculated to have been accumulated in each daylight hour.

The rate of canopy photosynthesis at a time-point is the sum of the rates of the sunlit and non-sunlit leaves. These are considered separately. If the day is specified as sunny, the sunlit leaf area in each of the DIPA inclination classes is calculated for each layer. Assuming that leaves are pointed equally in all possible compass directions (azimuth angles), the distribution of irradiance is calculated for leaves in each of the inclination classes in each layer.

The non-sunlit leaves, or all leaves on an overcast day, receive radiation from a hemispherical sky. This hemisphere is taken to have been divided by a horizontal planes into a series of equal-angle sky zones. The radiation from each zone is regarded as coming from an elevation equal to the mid-zone angle. The interception of radiation from each of the sky zones is treated separately and the total irradiance of the leaves due to the whole sky is calculated for each inclination class in each layer.

On sunny days, the radiation scattered by the leaves, i.e. reflected and transmitted, is found for each layer by an approximate method (Duncan et al.1967). This gives rise to a further component of irradiance which, being due to radiation assumed to be completely diffuse, is added equally to all leaves within the same layer.

The total irradiance of sunlit leaves is the sum of that due to 'direct' radiation together with 'sky' and 'scattered' components. The irradiance of non-sunlit leaves on a sunny day is the sum of the latter two components, while the irradiance of all leaves on an overcast day is only that due to the sky. Using the leaf P:irradiance relationship defined by P_{max} and

K_m, the rate of gross photosynthesis of the sunlit and/or non-sunlit leaves in each inclination class and each layer is calculated; these hourly rates are summed to give the quantity of photosynthate accumulated by the whole canopy in the hour considrred. Assuming that rates are symmetrical about noon, the day's accumulation is found by doubling that calculated for the hours from noon to sunset. Twilight is ignored.

5.3 Results

5.3.1 High-water treatment observations made during growth

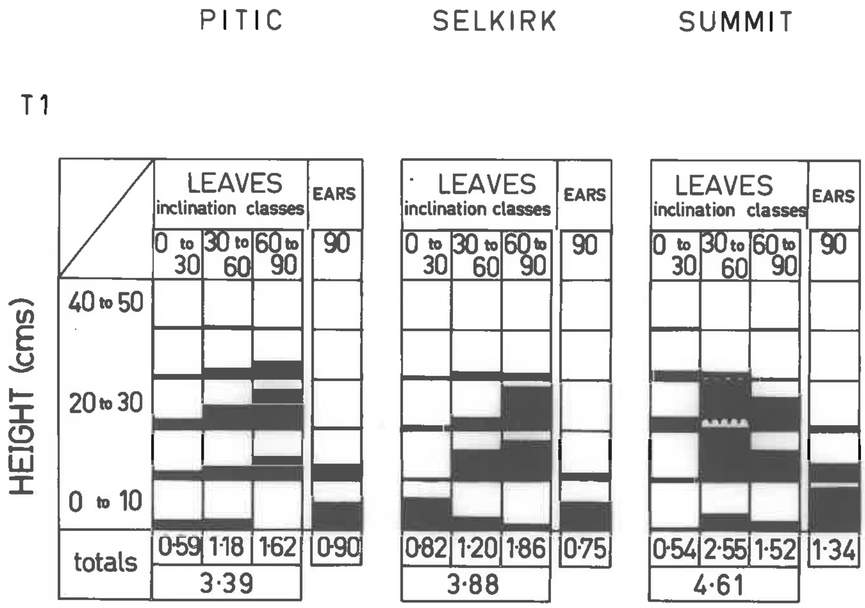
The results of the measurements of canopy structure are given in Fig. 5.1. From this Figure (or from Fig. 5.2) it can be seen that at T1, Selkirk was the shortest variety; at T2 on the other hand, it was the tallest. Using average height of the highest ligule on the 'test plant' as an index of tallness, this change of ranking appeared as a significant ($P < 0.05$) interaction between occasions and varieties.

Comparing the varieties with respect to the way in which their leaf areas were distributed between the inclination classes, From Fig.5.1a it is clear that at T1, at the top of their canopies, Pitic and Selkirk had a preponderance of foliage in the most steeply inclined class while Summit's foliage was less erect. (This conclusion, based on measurement, agrees with the appearance of the three varieties grown in a pot experiment the following year; the photograph of Plate 6.2a which shows the varieties to differ in just this way was taken at about the same stage of development as at T1). Between T1 (about Day 62) and T2 (about Day 106) the situation was reversed; Fig. 5.1 shows that the foliage of Pitic and Selkirk became less steeply inclined while the leaves of Summit became more so.

The differences between T1 and T2 in the posture of the varieties' upper leaves could nearly all be accounted for by abrupt changes occurring in the few days around ear emergence. The photograph of Plate 5.1b was taken when the ears of Pitic were emerging (Day 83). The marked droopiness of the flag-leaves (visible in the photograph, canopy number 2) had appeared only in the previous 2 or 3 days. The tendency of Pitic to produce a less erect canopy after ear emergence was also seen in the pot experiment (compare Plate 6.3a with

Fig. 5.1 Distribution of the inclination of photosynthetic area (DIPA) in the canopies of three varieties in the high-water treatment of the soil bench experiment. Inclination classes are defined by angles given in degrees. A filled square represents one unit of Leaf, Stem or Ear Area Index. The DIPA tables are given for two occasions, T1 (Day 59-65) and T2 (Day 101-111); the table of each canopy is based on two replicate plants selected as explained in the text.

(a) T1


PITIC
SELKIRK
SUMMIT
LEAVES
inclination classes
EARS
0 to 30
30 to 60
60 to 90
90
HEIGHT (cms)
40 to 50
20 to 30
0 to 10
totals
PITIC: 0·59 1·18 1·62 0·90 / 3·39
SELKIRK: 0·82 1·20 1·86 0·75 / 3·88
SUMMIT: 0·54 2·55 1·52 1·34 / 4·61

(b) T2

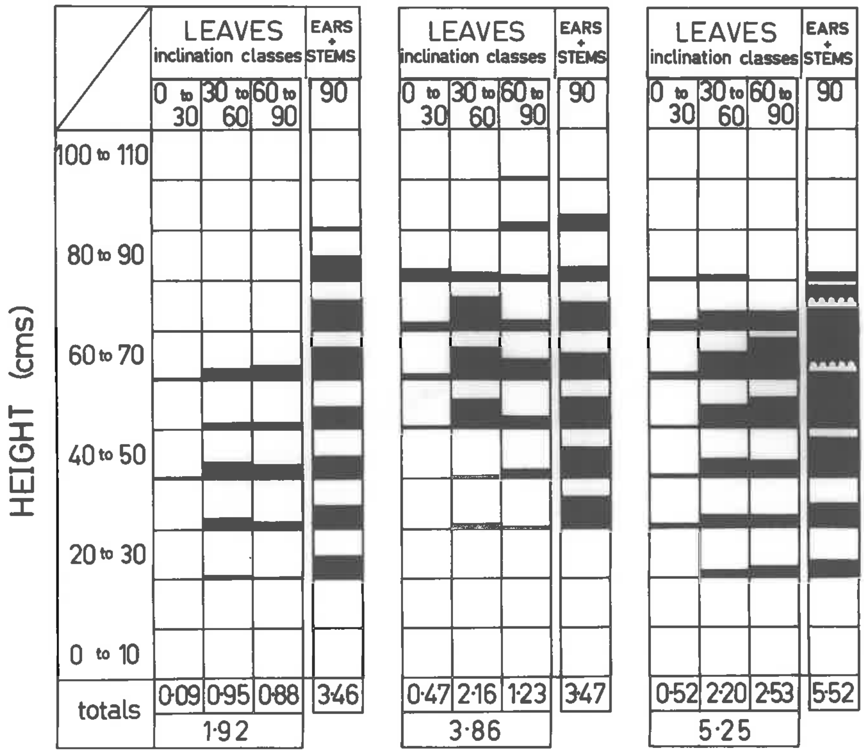

LEAVES
inclination classes
EARS + STEMS
0 to 30
30 to 60
60 to 90
90
HEIGHT (cms)
100 to 110
80 to 90
60 to 70
40 to 50
20 to 30
0 to 10
totals
PITIC: 0·09 0·95 0·88 3·46 / 1·92
SELKIRK: 0·47 2·16 1·23 3·47 / 3·86
SUMMIT: 0·52 2·20 2·53 5·52 / 5·25

Plate 6.2a). In Selkirk a sudden drooping of the upper leaves was noted to be similarly associated with the emergence of the ears. The case of Summit is however less simple. In the field and also in the pot experiment to be described in Section 6, the previously drooped leaves of Summit (Fig. 5.1a, Plate 6.2a) became erect shortly before ear emergence (Plates 5.1b and 6.3a). Possibly because the experiment in the soil bench was continued to a later physiological stage than the pot experiment, a reversion of Summit's foliage to a drooped posture was observed. However, a peculiar feature of this reversion was that although the tendency for leaves to be drooped was stronger at T2 (71% of leaves drooped) than at T1 (only 45% drooped), the DIPA table of Fig. 5.1b shows that at T2 the foliage was markedly more erectophile than at T1. A canopy of drooped leaves is thus not necessarily less erectophile than a canopy of undrooped leaves.

In Figs. 5.2 and 5.3, the measured light profiles are plotted in two ways, with observed values shown as black-filled symbols. (The predicted values shown in these Figures are discussed in a later Section). At T1, the value of I/I_o was reduced to 0.5 at 15 cm from the ground in the Selkirk plots while this degree of reduction was achieved at 18 cm in the plots of Pitic and Summit. In mixture with either of the latter varieties, Selkirk would seem likely to have been at a disadvantage in competition for light at this stage.

At T2, the opposite applied, with extinction starting higher in the Selkirk plots. The heights at which I/I_o equalled 0.5 in the plots of Selkirk, Summit and Pitic were 60 cm, 50 cm and 38 cm respectively. In mixture with the other varieties, Selkirk would be expected to have enjoyed a competitive advantage at this stage provided that earlier shading had not greatly reduced the capacity of its internodes to extend. Whereas at T1, the degree of light extinction at

Fig. 5.2 Predicted (on left) and observed (on right) profiles of light extinction in the canopies of three varieties in the high-water treatment of the soil bench experiment. The profiles are given for local noon on two occasions, T1 (Day 59-65) and T2 (Day 101-111); they are plotted in a different way in Fig. 5.3.

I/I_o is the observed irradiance (I) of the sensor relative to the value (I_o) above the canopy.

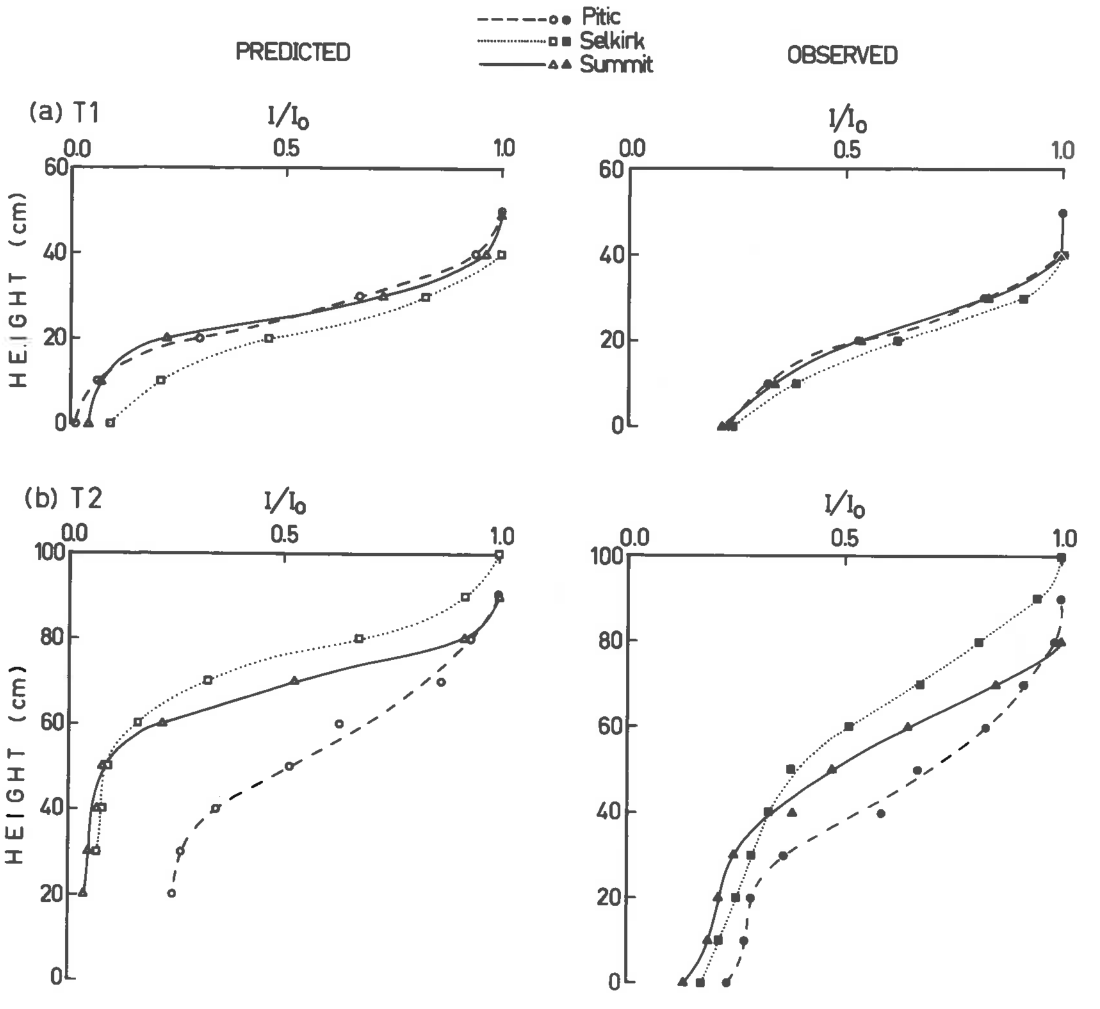
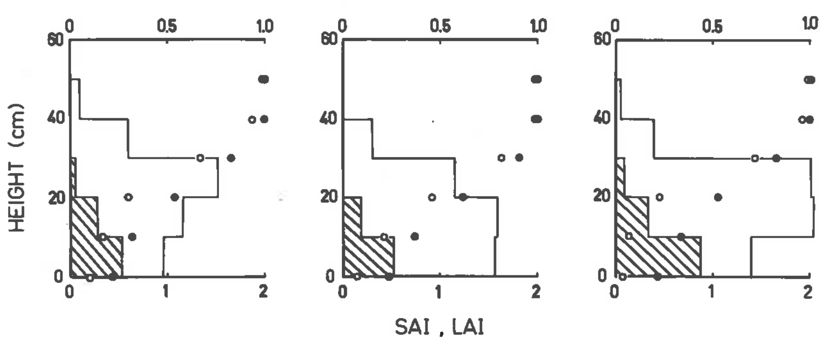
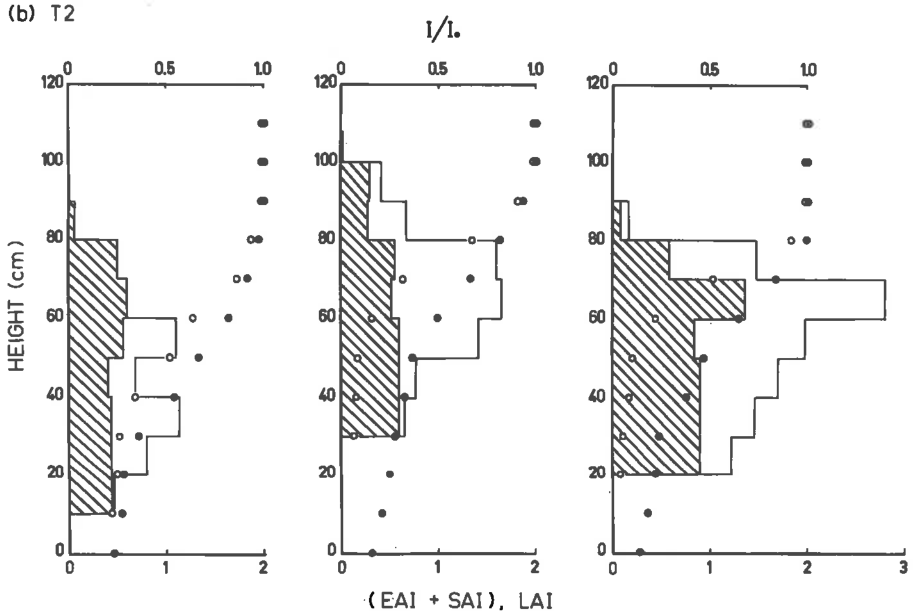

Pitic
Selkirk
Summit
PREDICTED
OBSERVED
(a) T1
I/I0
0.0
0.5
1.0
60
40
20
0
HEIGHT (cm)
(b) T2
100
80
60
40
20
0

Fig. 5.3 Observed (●) and predicted (○) profiles of light extinction in the canopies of three varieties in the high-water treatment of the soil bench experiment. The observed profiles are given for local noon on two occasions, T1 (Day 59-65) and T2 (Day 101-111). Each of the observed profiles is based on two replicate plots; the programme DAYP produced the predicted profile, based on the corresponding DIPA table. The LAI and summed Stem Area Index (SAI) and Ear Area Index (EAI) in each 10 cm layer are shown by blank and hatched areas respectively.

(a) T 1


I/I₀
0
0.5
1.0
HEIGHT (cm)
60
40
20
0
0
1
2
SAI , LAI

(b) T2


I/I₀
0
0.5
1.0
HEIGHT (cm)
120
100
80
60
40
20
0
0
1
2
3
(EAI + SAI), LAI

the bottom of the three canopies was very similar, at T2 the shading was greatest under Summit and was least under Pitic.

The differences between the light profiles seem to be readily relatable to differences in the measured leaf and stem area profiles. To facilitate comparison, these profiles have been superimposed on the graphs of Fig. 5.3 .

The dates at which 50% of the plants had emerged ears are given in Table 5.3. Although treatment and varietal effects on time of ear emergence were highly significant ($P < 0.001$) there was no effect of associates.

5.3.2 High-water treatment : harvest results.

The biomass data for the 3 x 3 soil bench diallels are given in Fig. 5.4. In this Section, only data of the high-water treatment will be discussed. In each of the 3 mixtures, plant yields of both components were lower in mixture than in monoculture. Two out of the three mixtures underyielded, but not significantly; the RYTs of the three mixtures were 0.884, 0.936 and 0.968.

The biomass data were analysed according to the McGilchrist-Trenbath method and the estimates of the various parameters are given in Table 5.4. The analysis of variance which was used, took into account the intercorrelation between estimates of RYT within one diallel; it showed that neither the individual negative deviations of RYT from unity, nor the overall deviation, were significant at the 5% level (for the analysis of variance table see Appendix, Section 11.6).

The neighbour effects on biomass in mixtures in this treatment were slight and far from being significant. Similarly, the difference among the variety aggressivity effects (Table 5.4) were not significant. To find whether the components of

Table 5.3 Number of days from planting to ear emergence in the two treatments of the soil bench experiment. The data given in the rows of the tables refer to plants of the 'producer' varieties listed at the left side.

(a) <u>High-water treatment</u>

In the presence of :

	Pitic	Selkirk	Summit	Means
Pitic	86.0	86.3	85.7	86.0
Selkirk	99.3	101.0	100.7	100.3
Summit	94.7	98.0	91.7	94.8
Means	93.3	95.1	92.7	93.7

(b) <u>Low-water treatment</u>

In the presence of :

	Pitic	Selkirk	Summit	Means
Pitic	85.0	85.3	84.3	84.9
Selkirk	95.0	90.7	94.7	93.4
Summit	90.3	90.0	90.3	90.2
Means	90.1	88.7	89.8	89.5

Comparisons between row means within treatments :

L.S.D.s (5%) = 2.56, (1%) = 3.52, (01%) = 4.67

The varieties x treatments interaction was significant at the 5% level.

Fig. 5.4 Shoot weights (biomass per plant) in the monocultures and mixtures of the two treatments of the soil bench experiment. The monoculture values are shown above the variety symbols, Pitic (Pt), Selkirk (Sl) and Summit (Sm). The mixture values are shown above the mark indicating the 1:1 proportion of the mixtures. The point showing the per-plant value of a component of a mixture is identified with respect to variety by the solid line joining it to the point of its monoculture yield. The point showing the mean per-plant yield of the mixture, averaged over both components, is indicated by the broken line joining it to both monocultures.

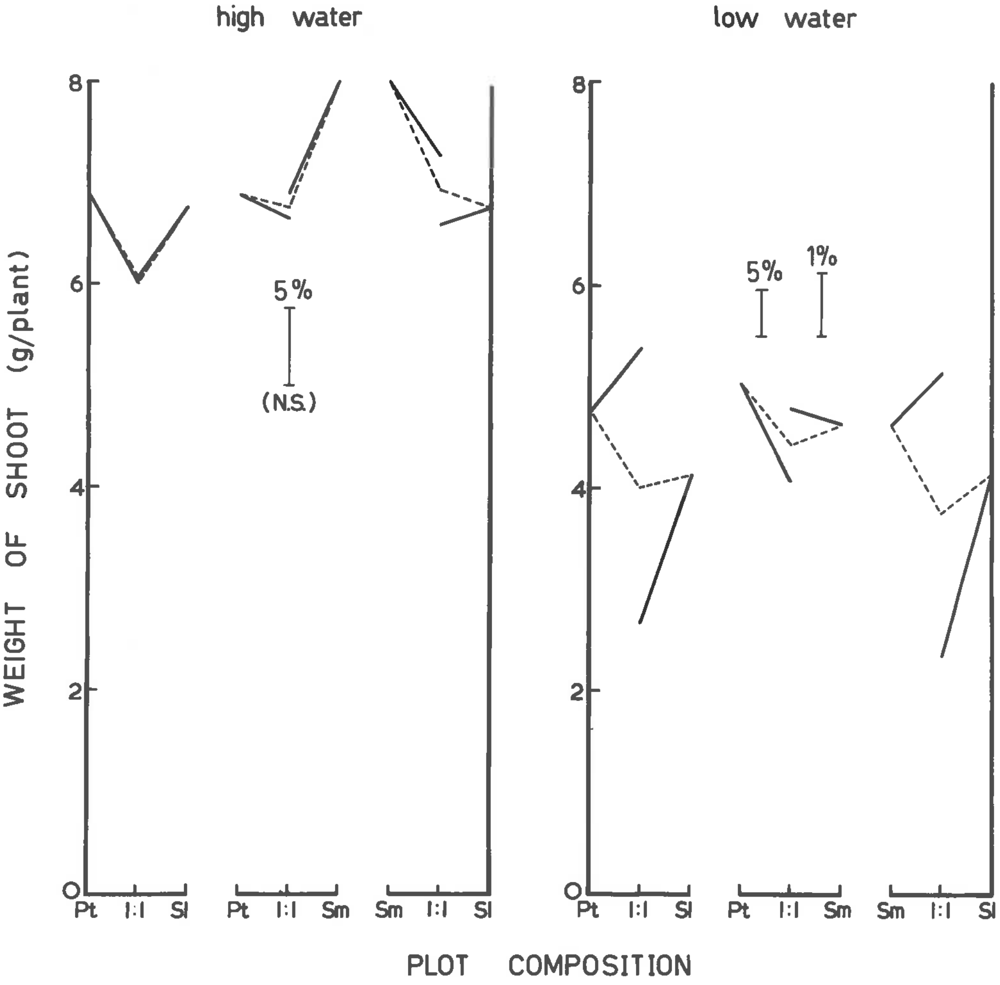

high water
low water
WEIGHT OF SHOOT (g/plant)
0
2
4
6
8
5%
(N.S.)
5%
1%
Pt
1:1
Sl
Pt
1:1
Sm
Sm
1:1
Sl
PLOT COMPOSITION

Table 5.4 Estimates of the McGilchrist-Trenbath parameters for the biomass data of the two water regimes of the soil bench experiment. Values of RYT and A are given as 3 x 3 diallel tables.

RYT_{ij}

High-water treatment			Low-water treatment		
*	0.8844	0.9364	*	0.8838	0.9448
0.8844	*	0.9684	0.8838	*	0.8369
0.9364	0.9684	*	0.9448	0.8369	*

	High-water treatment	Low-water treatment
S.E.	0.0417	0.0765
Mean RYT	0.9297	0.8885
S.E. of mean	0.0268	0.0564

Aggressivity A_{ij}

High-water treatment			Low-water treatment		
*	-0.0136	0.0210	*	0.2415	-0.0937
0.0136	*	0.0047	-0.2415	*	-0.2701
-0.0210	-0.0047	*	0.0937	0.2701	*

	High-water treatment	Low-water treatment
S.E.	0.0747	0.0774

Variety	High-water RYT variety effect ($\hat{\lambda}_i$)	High-water Aggressivity effect ($\hat{k}_i$)	Low-water RYT variety effect ($\hat{\lambda}_i$)	Low-water Aggressivity effect ($\hat{k}_i$)
Pitic	0.9614	0.0025	1.0516	0.0492
Selkirk	0.9933	0.0061	0.9437	-0.1705
Summit	1.0047	-0.0086	1.0047	0.1213
S.E.	0.0319	0.0358	0.0517	0.0417

biomass had behaved in the same way, the other variables which had been measured were analysed as data of a factorial experiment. Such an analysis separates 'associate effects' (equivalent to diallel column means) and 'variety effects' (equivalent to diallel row means) and provides LSDs which can be used to compare individual values in the table.

The straw weight data of Fig. 5.5 show mutual depressions in two of the three mixtures. The variety with the monoculture yielding the greater weight of straw was always depressed the more strongly. No effects were significant.

The neighbour effects on weight of ears were more marked and in two mixtures showed compensation (see Fig.5.6). The variety with the higher yielding monoculture was always depressed. The associate effect of Selkirk was 14-15% lower ($P < 0.10$) than those of either of the other varieties. This indicates that Selkirk caused a depression of the weight of ears of components with which it was growing. The effect on Pitic was significant at the 5% level.

The combination of large effects on ear weight, and small effects on straw weight, resulted in marked changes in the proportion of ear weight in the total biomass. These are shown in Fig. 5.7. All differences of this ratio between components in the Selkirk mixtures and their corresponding monocultures are significant ($P < 0.05$); perfect compensation occurred in all mixtures.

Fig. 5.5 Results of per-plant weight of straw in the monocultures and mixtures of the two treatments of the soil bench experiment (see legend of Fig. 5.4).

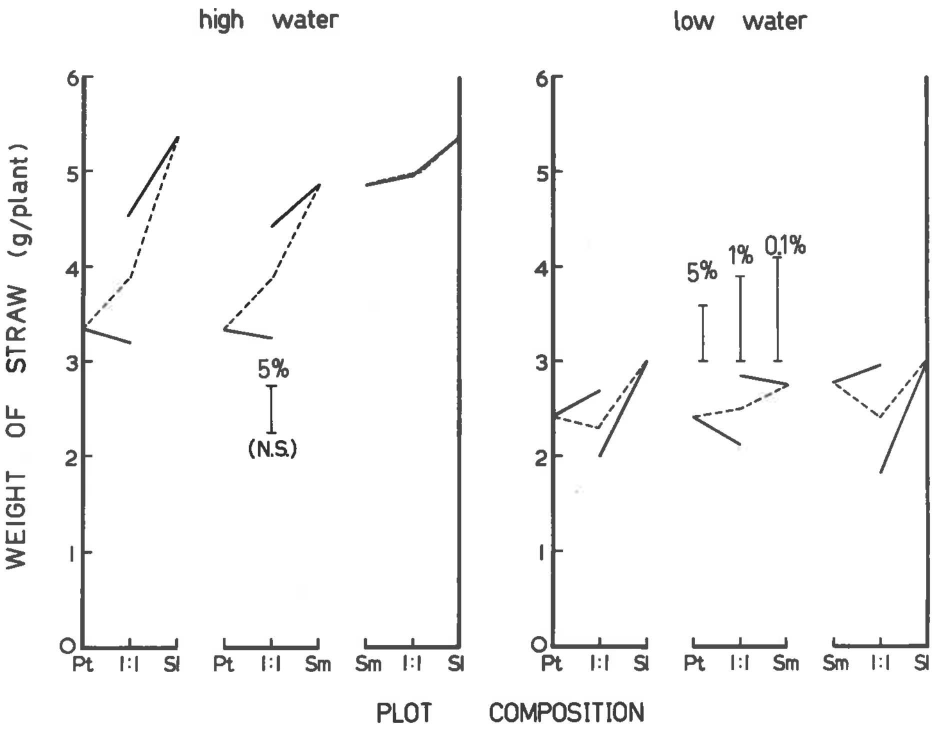

high water
low water
WEIGHT OF STRAW (g/plant)
0
1
2
3
4
5
6
5%
(N.S.)
5%
1%
0.1%
Pt
1:1
Sl
Pt
1:1
Sm
Sm
1:1
Sl
Pt
1:1
Sl
Pt
1:1
Sm
Sm
1:1
Sl
PLOT COMPOSITION

Fig. 5.6 Results of per-plant weight of ears in the monocultures and mixtures of the two treatments of the soil bench experiment. (See legend of Fig. 5.4)

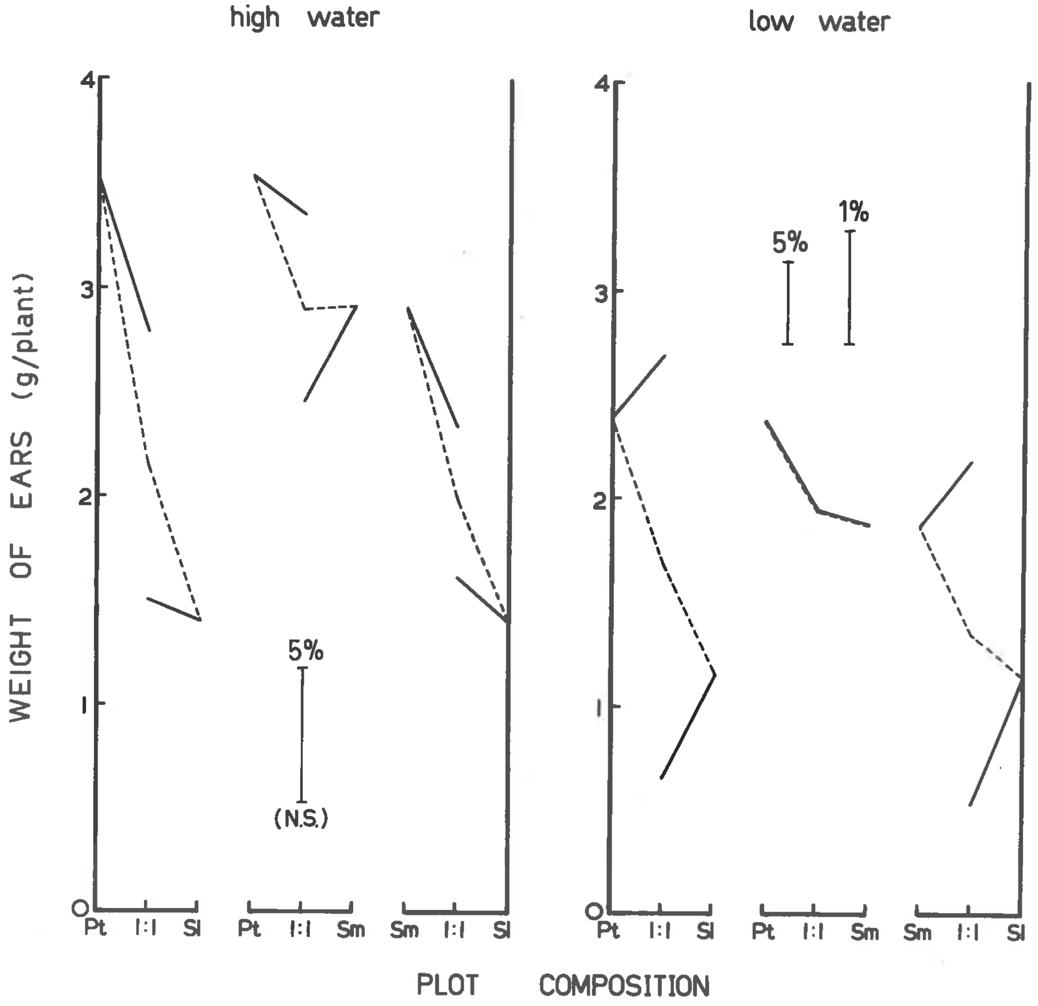
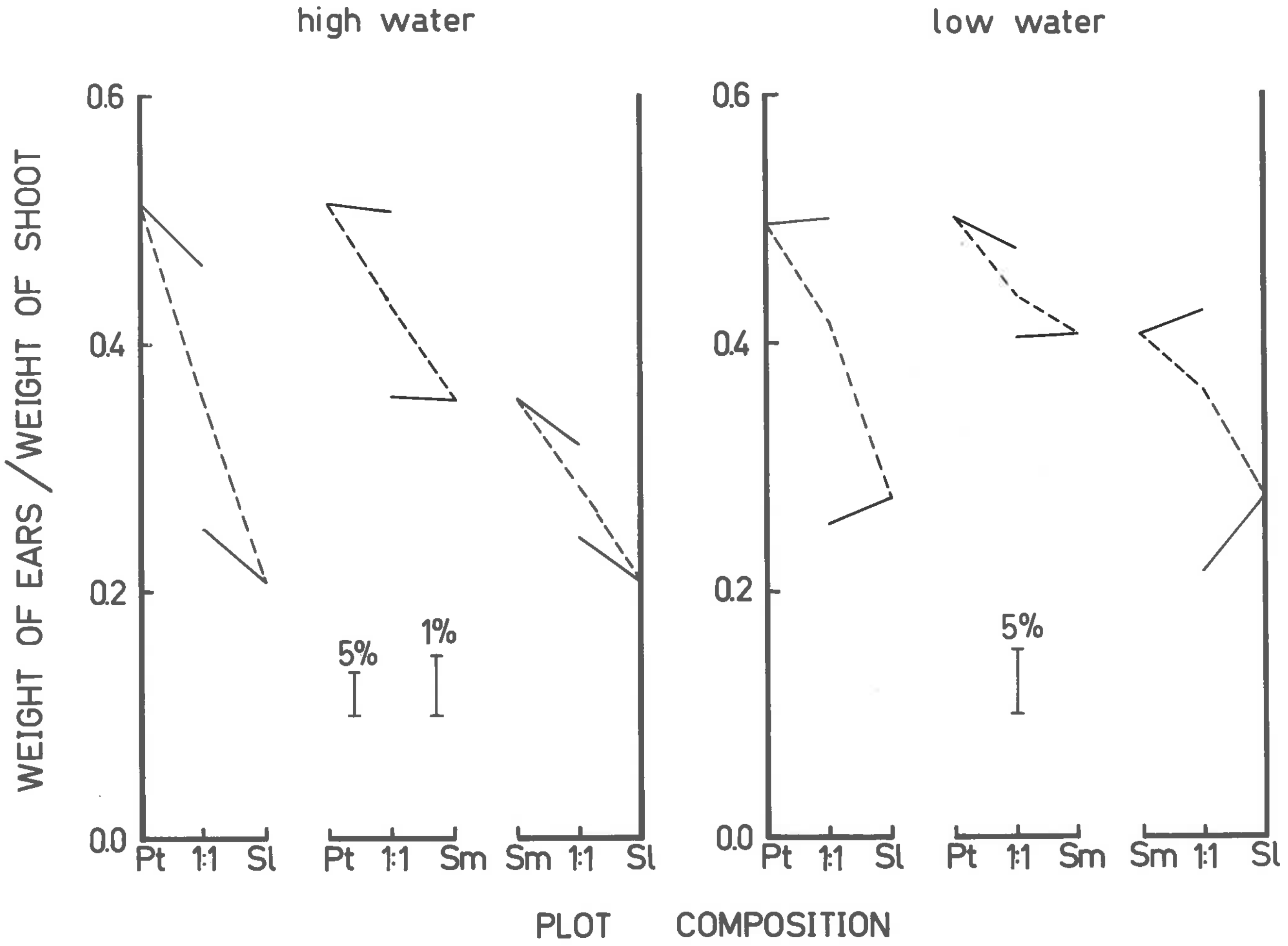

high water
low water
WEIGHT OF EARS (g/plant)
4
3
2
1
0
5%
(N.S.)
5%
1%
Pt
1:1
Sl
Pt
1:1
Sm
Sm
1:1
Sl
Pt
1:1
Sl
Pt
1:1
Sm
Sm
1:1
Sl
PLOT COMPOSITION

Fig. 5.7 Ratios of ear weight to shoot weight in the monocultures and mixtures of the two treatments of the soil bench experiment. The overall ratio for the mixtures (broken lines) has been derived by dividing the aggregate ear weight of both components by the aggregate shoot weight (see legend of Fig. 5.4).


high water
low water
WEIGHT OF EARS / WEIGHT OF SHOOT
0.6
0.4
0.2
0.0
5%
1%
5%
Pt
1:1
Sl
Pt
1:1
Sm
Sm
1:1
Sl
PLOT COMPOSITION

5.3.3 Low-water treatment : observations made during growth

The results of the measurements of pulled height at T1 and T2 are given as diallel tables in Table 5.5. For convenience of comparison, the data of height of highest ligule at harvest are presented here also.

At T1 (Day 52), there were no significant differences of pulled height between any mixture component and its corresponding monoculture. Neither were any variety effects significant, although it may be noted that the order of pulled height was Summit > Pitic $\geqslant$ Selkirk. In both mixtures, plants of Selkirk were probably shaded more than in monoculture.

At T2 (Day 106), although there were no increases relative to monoculture, the pulled height of Selkirk was significantly depressed ($P < 0.01$) in both its mixtures.

At harvest (Day 123), the height of the highest ligule showed even stronger effects on Selkirk in its mixtures than did pulled height at T2. Both values of the ligule height of Selkirk in mixture were significantly ($P < 0.01$) below that in monoculture. Furthermore, the varieties x species interaction was significant ($P < 0.05$).

Although there may have been some early shading effects on Selkirk in mixtures, by about T2 such effects would seem likely to have been slight (Table 5.5b). Since leaf senescence was proceeding rapidly after T2 in this treatment, the differences of ligule height seen at harvest (Table 5.5c) would seem unlikely to cause any appreciable shading effect.

Table 5.5 Diallel tables of measurements of plant heights in the low-water treatment of the soil bench experiment. Where an effect has been shown to be significant, an appropriate LSD is given.

(a) Pulled height (cm) at T1

	Pitic	Selkirk	Summit	Means
Pitic	37.4	36.7	37.2	37.1
Selkirk	32.8	36.9	38.0	35.9
Summit	38.4	39.2	41.2	39.6
Means	36.2	37.6	38.8	37.5

(not significant)

(b) Pulled height (cm) at T2

	Pitic	Selkirk	Summit	Means
Pitic	62.2	63.3	60.5	62.0
Selkirk	61.9	69.4	61.1	64.1
Summit	60.1	61.6	61.5	61.1
Means	61.4	64.8	61.0	62.4

Comparisons within the table: LSDs (5%) = 5.0, (1%) = 6.8

Comparisons of column means : LSD (5%) = 2.9

(c) Height of highest ligule (cm) at harvest

	Pitic	Selkirk	Summit	Means
Pitic	57.9	59.5	57.0	58.1
Selkirk	52.6	63.8	54.3	56.9
Summit	52.4	54.4	53.6	53.5
Means	54.3	59.3	55.0	56.2

Comparisons within the table: LSDs (5%) = 5.1, (1%) = 7.1
Comparisons between row means: LSDs (5%) = 2.9, (1%) = 4.1
Comparisons between column means:LSDs(5%)= 2.9, (1%) = 4.1

The varietiesXassociates interaction was significant at 5%.

5.3.4 Low-water treatment : harvest results

In this treatment all three mixtures underyielded, but as in the other soil bench, no case of underyielding was significant (Fig. 5.4) The RYTs of the mixtures were 0.837, 0.884 and 0.945 but the McGilchrist-Trenbath analysis again showed that neither the individual cases of low RYT, nor the overall deviation of 11% below unity, were significant (see Table 5.4).

In contrast with the slight and non-significant neighbour effects seen in biomass in the high-moisture treatment, in mixtures under the low-water regime, the aggressivity effects of the 3 varieties differed significantly ($P < 0.05$, see Table 5.4). Large depressions of biomass were found in some individual components. Fig 5.4 shows that in its two mixtures, Selkirk was the subordinate and suffered reductions of biomass of 35% (in Pt + Sl) and 43% (in Sl + Sm). These two reductions were significant at the 1% and 0.1% levels respectively. Although there were some compensating increases in the biomass of the aggressors, in neither mixture were these increases large enough to reach even the 5% level of significance. The combination of large decreases and small increases produced very low RYTs in these two mixtures (see Table 5.4), and although the monoculture yields differed by 30% and 12%, the effect was large enough to lead to underyielding.

In the third mixture (Pt + Sm), a similar but much less marked pattern of uncompensated decrease of biomass was found. In spite of RYT being only slightly less than unity, the monoculture yields were so similar that this mixture nevertheless underyielded.

The two major components of biomass, straw weight and ear weight both showed the same pattern as described for total shoot weight (see Figs. 5.5 and 5.6). However, all effects on the later-determined ear weight were more marked than those on straw weight.

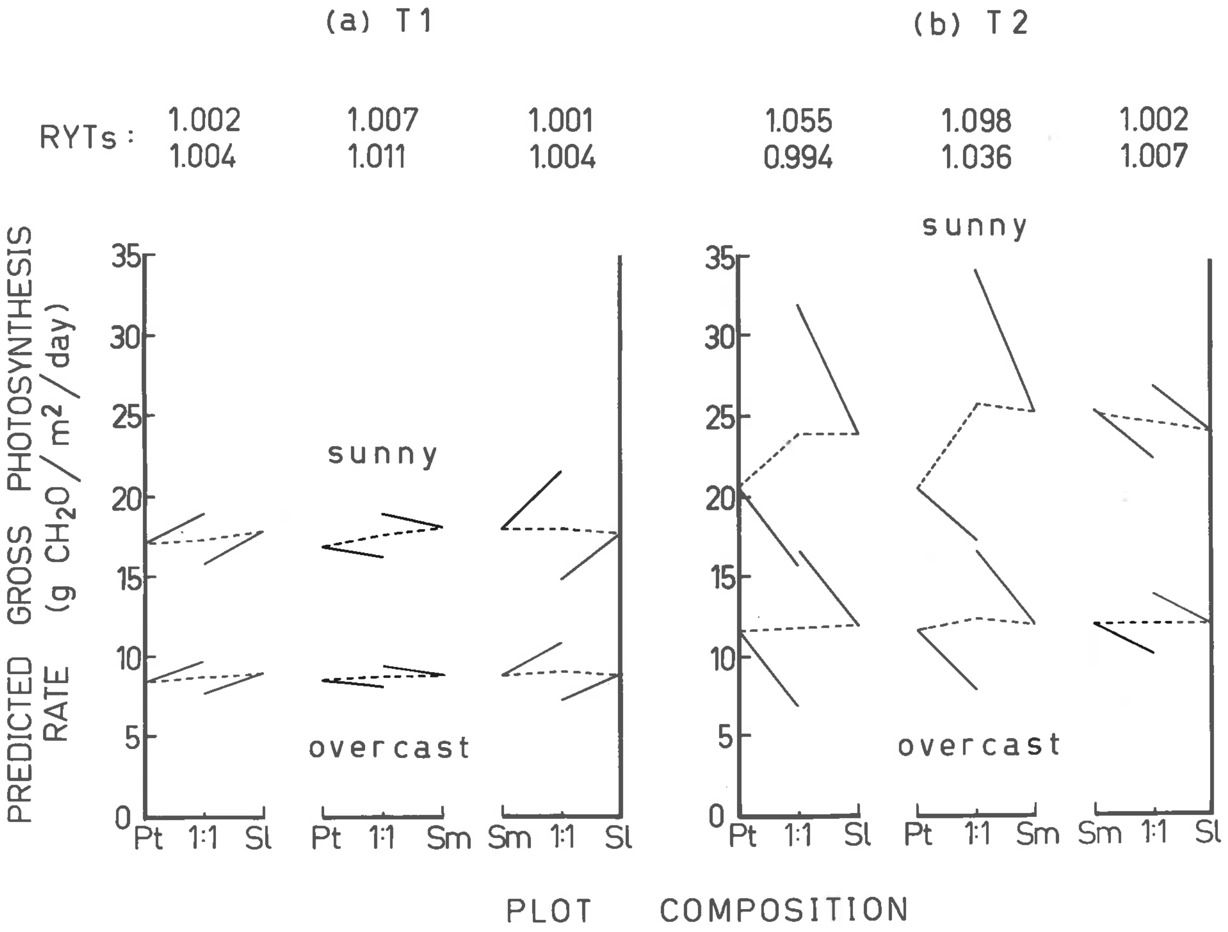
5.3.5 Simulations related to the measured canopy structures

Using the measurements of DIPA presented in Fig. 5.1, the light profiles for local noon were predicted by the simulation programme DAYP (Section 5.2.2) for the 3 monocultures on the two measurement occasions (Day 62 and Day 106). The results of these simulations are shown in Fig. 5.2 together with the observed profiles for comparison. The patterns of differences between the observed light profiles of the three varieties seem to have been rather closely predicted by the simulation technique.

A marked divergence between observation and prediction is, however, apparent in Fig. 5.3 where the predicted and actual extinctions are shown together; the predicted values are seen to be always greater than those observed. Since the infra-red sensitivity of the silicon sensor used for the measurements might be partly responsible for this discrepancy, the reflectivity and transmissivity parameters of DAYP were increased from their common assumed value of 0.1 for the visible range (Shul'gin et al.1958, Federer & Tanner 1966a) to the value of 0.3, which approximates to the magnitudes of these parameters for the wavelengths of direct solar radiation to which silicon cells mainly respond (Federer & Tanner 1966, Gaastra 1968). This change of parameters affected only the second decimal place in the values of I/I_0 and so the infra-red sensitivity of the silicon cell probably caused only a very small part of the difference between the observed and predicted profiles.

Corresponding to the predictions of the noon-time light profiles, the programme DAYP produced predictions of daily gross rates of photosynthesis for the monocultures. Using the estimates of the mixture DIPAs, predictions of the gross P rates were also made for mixture components and hence for each mixture as a whole. The results of this simulated growth-rate diallel are shown in Fig. 5.8. These simulations suggest that where competition is only for light, a pattern of compensating increases and decreases of per-plant yields would be expected in mixtures. Other predictions are that RYTs will be close to unity (the average of the RYTs of the 12 simulated mixtures is 1.018), that competitive effects at T2 will be more marked than at T1, and that at T2 the mixture of Pitic and Summit may have a marginally higher gross P rate than either of the corresponding monocultures. Reversals of dominance are predicted for the two Selkirk mixtures between T1 and T2.

Fig. 5.8 Predicted daily gross photosynthesis rates of monocultures and mixture components in the high-water treatment of the soil bench experiment. Results of simulations using the programme DAYP are given for two occasions, T1 and T2, and for two sky conditions, sunny and overcast. RYT values based on gross P are calculated for each mixture in the two conditions; upper row of values relates to sunny, and lower row relates to overcast conditions.


(a) T1
(b) T2
RYTs :
1.002
1.004
1.007
1.011
1.001
1.004
1.055
0.994
1.098
1.036
1.002
1.007
PREDICTED GROSS PHOTOSYNTHESIS RATE (g CH2O / m2 / day)
0
5
10
15
20
25
30
35
sunny
overcast
Pt
1:1
Sl
Pt
1:1
Sm
Sm
1:1
Sl
PLOT COMPOSITION

5.4 Discussion

5.4.1 Comparison of results in field and soil bench experiments.

The difference between the results in the field and in the soil benches is striking. The three varieties used in the soil benches were chosen on the grounds of the mutual stimulation observed in the earlier field experiment. In the low-water bench in 1968, the general degree of water-stress apparently approximated that in the field during 1967; the range of per-plant biomass in this soil bench was 5.37 to 2.35g while the corresponding range in the field at the same spacing was 5.44 to 2.49g. The pattern of aggressiveness was also similar in that the per-plant biomass of Selkirk was decreased in mixture with the varieties Pitic and Summit in both years. On the other hand, the apparent tendency towards overyielding seen in all 3 mixtures in 1967, became in 1968 a uniform tendency to underyield. Thus the relationship between the yields of mixtures and monocultures was apparently unstable. Since it cannot be maintained that conditions in the two experiments were more than approximately similar, it must be that the difference in conditions (e.g. seeding date, radiation, orientation of rows, etc) was sufficient to cause the differing results. Indeed, the apparent sensitivity of transgressive yielding to conditions is clearly shown by the published results of those investigators who have imposed cultural treatments on mixtures diallels (Harper 1964, England 1965 and Norrington-Davies 1968). The lack of correspondence between the results from three pairs of treatments is shown in Table 5.6. The correlation coefficients calculated between the RYTs of mixtures in the same pairs of treatments were -0.278 (d.f. = 13), 0.355 (d.f. = 4) and 0.354 (d.f.= 8). Such values similarly indicate little or no correspondence.

Table 5.6 Comparison of results of mixture biomass between pairs of treatments applied to mixtures grown in diallel experiments. Data concerning three published reports are given.

Key to symbols:

++	overyielding (above higher-yielding monoculture).
+	mixture yield between higher-yielding monoculture and mean monoculture value.
-	mixture yield between lower-yielding monoculture and mean monoculture value.
—	underyielding (below lower-yielding monoculture).

(a) Harper (1964), 15 mixtures

Density:	Low	High	Low	High
	++	—	-	++
	++	—	++	++
	++	+	+	+
	+	-	-	++
	+	-	-	++
	++	++	-	++
	++	+	-	+
	+	—		

(b) England (1965), first cut only, 6 mixtures

Density:	Low	High	Low	High
	+	+	+	-
	-	-	+	-
	+	+	+	—

(c) Norrington-Davies (1968), first cut only, 10 mixtures

Fertility:	Low	High	Low	High
	—	—	+	++
	+	++	++	+
	+	-	+	++
	-	-	++	-
	+	-	+	+

5.4.2 The effects of experimental error on the results of mixture trials.

As was pointed out in Section 2.1, few or none of the experiments which have produced transgressively yielding mixtures have been repeated under controlled conditions. Thus, with the experimental techniques so far used, the individual cases of transgressive yielding may be due to experimental error alone. The plausibility of this explanation in the present cases was tested using a Monte Carlo method.

The results of a series of experiments similar to that performed in the low-water soil bench were simulated by first assuming values for the true underlying means of the experiment, and then producing four hundred 3 x 3 diallel tables containing the assumed means as entries but with an independent random error attached to each. To represent the true means of the monocultures, the three observed monoculture means shown in Fig. 5.4 (low-water treatment) were used. Assuming that deviations of RYT from unity observed in the soil bench were due to experimental error, the true means of biomass of the components in each mixture were estimated by averaging the deviations of the components' Plant Relative Yields from unity and applying this same proportional difference to the monocultures of the two genotypes concerned. An example of this calculation is given in Table 5.7; the same table gives the theoretical biomasses used in the simulation together with the corresponding experimental data, for comparison. Since the underlying per-plant yield of each aggressor increased by the same proportion as that by which the corresponding subordinate decreased, all (underlying) RYTs were unity. The magnitudes of the error terms attached to the theoretical yields were those expected in means of 3 replicates in an experiment having a coefficient of variation of 12.3%.

Table 5.7 Diallel tables of actual and theoretical results relating to a Monte Carlo simulation of the results of the low-water treatment. The theoretical values have been derived from the actual values using the method described in the text *). The theoretical values were used as the underlying values in the simulation.

(a) Experimental results of biomass (g/plant, as in Fig.5.4)

		Associate		
		Pitic	Selkirk	Summit
Producer	Pitic	4.78	5.38	4.07
	Selkirk	2.67	4.15	2.35
	Summit	4.80	5.12	4.63

(b)

		Associate		
		Pitic	Selkirk	Summit
Producer	Pitic	4.78	5.93	4.34
	Selkirk	3.15	4.15	3.03
	Summit	5.06	5.88	4.63

*) To illustrate the derivation of the biomass yields of the mixture components, the following shows the calculation of the theoretical biomass of Pitic in mixture with Selkirk.

Average deviation of PRYs from unity $= \left(\frac{5.38-4.78}{4.78} + \frac{4.15-2.67}{4.15}\right)/2 = (0.125+0.356)/2 = 0.24$

Biomass of Pitic in mixture with Selkirk $= 4.78 \times (1 + 0.24) = 5.93$

This value * was that observed in the low-water soil bench (cf. values between 10% and 14% found in the 6 x 6 diallels of the previous season). Using a random number generator, the values of the error terms and hence the 400 simulated diallel tables were produced automatically by computer. Since each diallel contained 3 mixtures, the results of 1200 simulated mixtures were available. Among these 1200 theoretical mixtures, 21.2% underyielded and 26.7% overyielded. Only 12.25% of the diallel tables contained no transgressively yielding mixtures. Hence it seems that in experiments similar to those conducted in the benches (1968) and in the field (1967), if the underlying RYT value for each mixture is in fact unity, experimental error will be responsible for many instances of over- and under-yielding. If the bench and field experiments are a fair sample of the quality of the experiments reported in the literature, and if the degree of difference between monocultures (the range here was from 3% to 13%) can be regarded as typical, it can be suggested that most reported instances of transgressive yielding are due only to experimental error. Indeed, considering the number of mixture results which have been published, it is surprising that more mixtures have not beem reported as under- or over-yielding significantly. The explanation for this may be that monoculture yields are commonly more different than those used here.

This same Monte-Carlo simulation can throw light on the question of the reality of the three underyielding cases observed in the low-water bench since it showed that the proportion of tables in which 3 out of 3 mixtures *underyielded*

---

* The error term had the distribution N(0, V) where the variance, V, had the value of one-third of the error mean square of the low-water treatment. Thus, V = 0.268/3 = 0.0893. The constancy of the variance in all entries of the diallel table imitated the situation observed in the experiment.

was 2.50%. The 95% confidence range for this value was 0.97% to 4.03%. However, 2.50% can be treated as an estimate of the statistical probability of obtaining the observed results of the low-water soil bench under the stated assumption of underlying RYT being unity. Since this result was well within the conventional 5% level, the marked underyielding and low RYTs in the two Selkirk mixtures were taken, hopefully, as having been produced by real effects rather than by error and were made the subject of the further experimentation reported in Section 6. Since the chance probability of the results of the high-water bench seems likely to be very much greater than 5%, no attempt is made here to establish the two cases of underyielding as being due to anything but experimental error.

5.4.3 Discussion of results of the high-water treatment

Although the underyielding by two mixtures was far from being significant, other aspects of the results merit attention.

The measurements made on the plants of the high-water bench allow checking of several predictions based on mathematical models. The determinations of DIPA, although based on no more than two individual plants of each variety, appear to have been sufficiently accurate for the program DAYP to predict light profiles in which the pattern of differences between the varieties corresponded closely to the measured pattern (Fig. 5.2). This was true for both measurement occasions. A systematic difference between the predicted and the observed profiles (Fig. 5.3) could not be traced to the infra-red sensitivity of the unfiltered silicon-cell used in the determinations (see, however, Newton & Blackman 1970). The most likely reason for the unexpectedly high levels of radiation observed deep in the canopy is the markedly non-random horizontal distribution of leaves and stems in a row-planted crop (Wilson 1959, Tooming & Ross 1964). The self-shading of leaves within the rows is probably greater than would be found in a square-planted crop, where, in turn, the self-shading is greater than in a theoretically ideal canopy (as assumed by DAYP) where all photosynthetic surfaces are randomly distributed as small elements in horizontal layers. Such localised increases of self-shading will allow greater penetration of light into the canopy. The same discrepancy between predicted and observed light profile has been found by Laisk (1969) in a square-planted sorghum crop; Laisk attributed the disagreement to the clustering of leaves and stems round individual plants. Horizontal non-randomness presents a serious impediment to the successful use of most of the currently available models of light penetration into canopies.

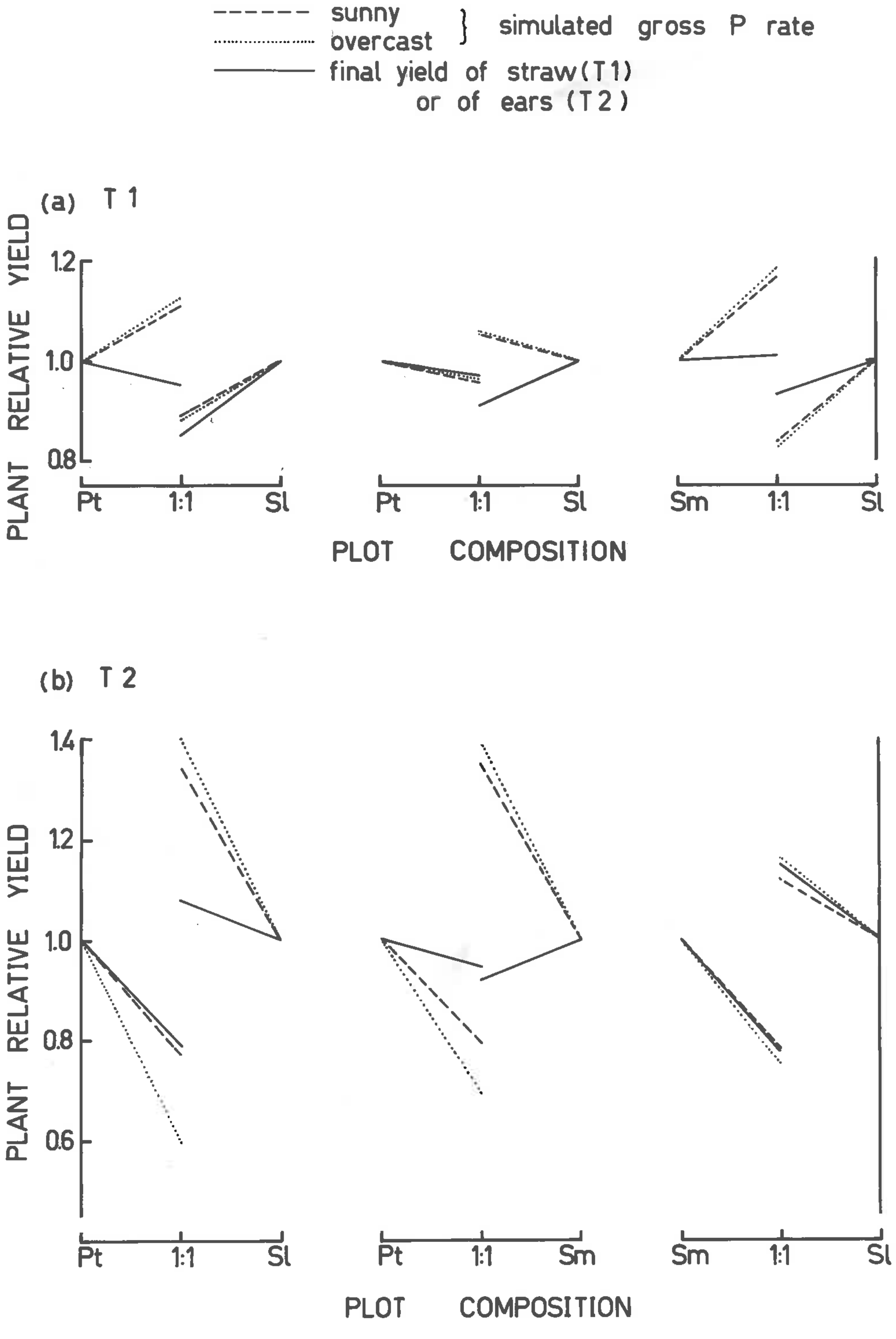
The simulated diallels of gross photosynthesis rates on the two occasions allow further predictions to be checked. The RYTs based on the gross P rates of the simulated mixtures were usually very close to unity, the average of the twelve cases being 1.018 . In the high-water bench, the RYTs of biomass were however rather below unity, although not significantly so. Similarly, the mixture of Pitic and Summit showed only mutual depression of the components and none of the beneficial effect of a favourable canopy structure as suggested by the simulation at T2 (Fig.5.9).

It is difficult to estimate how much of any discrepancy between observed RYTs of biomass and predicted RYTs of gross P may be due to effects concerned with respiration rates, distribution ratios, sink effects, etc. If it is assumed with most recent authors (see Section 2.2.3) that plant respiration rate is proportional to gross P rate, then at least RYTs based on gross and net P have the same value. This leads to the important theoretical conclusion that in spite of extreme non-linearity in most parts of the simulated system, when competition is for light alone (and nearly all of the incident light is intercepted), components of mixtures are expected to behave as if they have almost linear responses to the amount of light absorbed. Thus, for net production rates, the situation is expected to approximate to that shown in Fig. 3.1 with the growth-factor Q being light. With canopies which are more erectophile or planophile than those observed here, some modification of this conclusion may be necessary. This possibility is the subject of the theoretical study in Section 7. With the range of canopies encountered in this experiment, however, the results are expected theoretically to conform to a very simple model.

The prediction of greater competitive effects at T2 than at T1 can be tested against observed results if two assumptions are made: firstly, that competitive effects at T1 (early jointing stage) were reflected in straw weights at harvest; secondly, that effects at T2 (early grain-filling stage) were reflected in the weights of ears at harvest. Since growth in ear weight depends mostly on conditions after ear emergence (Thorne 1963, 1965, Welbank and Witts 1965), the assumption concerning ear weight may be readily accepted. The assumption relating to straw weight however requires the relationship between the weights of vegetative parts of the various varieties to be conserved over a much longer time interval. Even if the pattern of rates of photosynthesis existing at T1 continued until flowering, the post-flowering patterns of the redistribution of dry-matter undoubtedly differed between varieties. Conclusions based on straw weight will need to be treated with some caution.

In Fig. 5.9, the simulated results of gross P rates are again presented (although in slightly different form) for T1 and T2. The patterns of differences between monoculture and mixture performance may now be compared with the

Fig. 5.9 Predicted daily yields of gross photosynthate of plants of mixture components in the high-water treatment of the soil bench experiment. Results of simulations by the programme DAYP are given for two sky conditions on two occasions, T1 and T2. The weight of straw at harvest are shown on the same graph as the results of the simulation at T1; the weight of ears are similarly given with the results of the simulation at T2. To facilitate comparison between simulation results and harvest data, all results have been made relative to monoculture values and hence are Plant Relative Yields. A graph showing the simulation results in an unstandardised form together with calculated RYT values, was given in Fig. 5.8 .


sunny
overcast
} simulated gross P rate
final yield of straw (T1) or of ears (T2)
(a) T 1
PLANT RELATIVE YIELD
1.2
1.0
0.8
Pt
1:1
Sl
Pt
1:1
Sl
Sm
1:1
Sl
PLOT COMPOSITION
(b) T 2
PLANT RELATIVE YIELD
1.4
1.2
1.0
0.8
0.6
Pt
1:1
Sl
Pt
1:1
Sm
Sm
1:1
Sl
PLOT COMPOSITION

corresponding patterns of weights of straw and ears at harvest. To simplify the comparison in Fig. 5.9, these differences are compared on a relative scale, i.e. relative to the monoculture values. In the three graphs where the observed differences were of the usual compensating type, the gross P rates corredly predicted the direction of the differences in the harvest data between mixture and monoculture. In the other three graphs, where both components suffered observed depressions, only the depression of one component in each mixture was correctly predicted. With one anomalous value in the first graph of Fig. 5.9a (caused by widely differing replicate values) reversals of dominance in the two Selkirk mixtures were correctly predicted.

While the success of the predictions has not been striking where gross P rates for just two occasions have been extrapolated to weights of plant parts at harvest, the prediction of differences in light profiles between different canopies seem to be decidedly promising. Although only the noon-time profiles have been checked by observation, the programme DAYP is capable of predicting light profiles at all times of the day, once the DIPA has been determined. With more frequent determinations of DIPA and therefore more numerous estimates of the daily gross P rates of mixture components, more realistic predictions could be made of final plant relative yields. With more closely controlled experimental conditions, quantitative and not merely qualitative comparisons will become possible between theory and observation. The original intention of this part of the investigation may then be fulfilled: to relate transgressive yielding of a mixture to a particularly favourable or unfavourable canopy structure.

5.4.4 Discussion of results of low-water treatment

Since the plants of the low-water treatment were so patently affected by water stress, the underyielding of mixtures in this treatment seems likely to have been caused by some effect concerning the use of water. Competition for light was probably not very important for after some early lush growth, the canopy remained thin with soil always visible between the rows. Likewise, competition for nutrients can be assumed to have been relatively unimportant since no deficiency symptoms were observed.

Water was thus probably the 'principal' factor. In accordance with the considerations of Section 3.1, it is the negative deviations of RYT which, from an arithmetical point of view, have led to the underyielding. The RYTs of the mixtures containing Selkirk were particularly low, and suggest that a search for the cause of these low values would be worth while. Using the physiological interpretations of RYT presented in Section 3.1, the low values can be tentatively ascribed to

i) a reduced uptake of water by the mixtures and/or

ii) a reduction in the efficiency with which it was used.

A hypothesis involving decreased uptake is considered first. Let us suppose that a mixture is growing under conditions of chronic shortage of some growth factor. If an extra supply of the growth factor suddenly becomes available to a mixture component late in growth, the plants of this component may not be able to take up and respond to the extra supply. This was probably the case in the experiment of Klages (1936) who reported a rust attack on one component; it occurred too late in growth for the non-susceptible component to take advantage of it (de Wit 1960). Jensen & Federer (1965) recorded a similar lack of response when one component of a wheat mixture was removed one month before maturity. An analogous situation might have existed, in respect to water, in the mixtures containing Selkirk, for judging by the data of height (Table 5.5), the suppression of Selkirk in both mixtures occurred over a short interval in the second half of the growth period (Days 50-100).

The rapidity with which the effects were produced could have been due to the addition of competition for light to competition for water (Donald 1958). At T1, Selkirk was the shortest variety. Also, its time of 50% ear emergence was 5 or 10 days later than those of its associates in the mixtures and so its internodes presumably extended relatively late. Thus, in mixture, Selkirk seems likely to have experienced some shading during the period in which it was suppressed. Through its depressive effect on the rate of root growth (Milthorpe 1961, Brouwer 1966), shading could have reduced Selkirk's ability to compete for water at a time when the evaporative demand was increasing fast. At this stage, however, the activity of the aggressor's root system might be expected to be declining (Spahr 1960, Welbank & Williams 1968). Hence, after the rapid suppression of Selkirk, these root systems might not have been physiologically capable of expanding their uptake capacity sufficiently to compensate for the lost capacity of the Selkirk plants. Water uptake by plants of the mixture would be less than that in the monocultures. In the terminology of Section 3.1.1, this hypothesis (Hypothesis 1) postulates that the low RYTs were due to a relatively low aggregate uptake of 'principal factor' by the mixtures.

A second and a third hypotheses, paralleling the situations considered in Section 3.1.2.1 and 3.1.2.2, may also be put forward to explain the low RYTs. These involve a reduced efficiency of water utilization by mixtures. According to Hypothesis 2, it could be suggested that there was no 'factor-loss' but instead that the monoculture response curves to water of the aggressors, Pitic and Summit, showed sufficiently strong negative curvature to cause the aggressor and hence the whole mixture to be relatively inefficient in the utilization of water in biomass production.

According to Hypothesis 3, it could be that there was neither 'factor-loss' nor departure of monoculture response curves from linearity, but instead that another factor peculiar to the mixtures caused the behaviour of the components in mixture to deviate from their response to water as it would be seen in monoculture. For instance it might be suggested that during the period when Selkirk was presumed to have been shaded, Selkirk's young leaves were low enough to be in the 'hot' spot often found in the middle of canopies (e.g. Denmead 1968); unusually high respiratory losses from the subordinate and hence from the community as a whole might have led the mixture to use water less efficiently than the monoculture.

To clarify the differences between these three hypotheses, Fig. 5.10 has been drawn. The first hypothesis postulates a lower overall uptake of water by the mixture, the second postulates a curved response to water uptake in monoculture, and the third postulates that another factor (or factors) peculiar to the mixture modified the response to water from that found in monoculture. The next Section (6) is devoted to the reporting of experiments designed to distinguish which, if any, of the three hypotheses applies to this soil bench experiment.

Fig. 5.10 Three hypotheses explaining the low RYTs and underyielding of the two Selkirk mixtures in the low-water treatment of the soil bench experiment. Each mixture consists of the aggressor (variety A) and Selkirk, the subordinate (variety S). The uptake of water in all monocultures is assumed, as a first approximation, to be the same.

(a) Hypothesis 1. The total uptake of water by the mixture is less than in either monoculture.

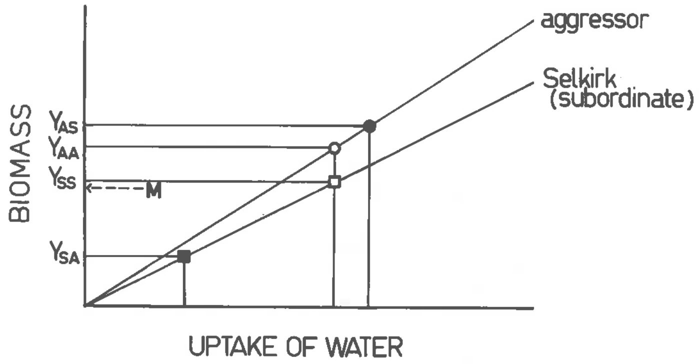
(b) Hypothesis 2. The total uptake of water by the mixture is the same as in the monocultures, but the increase in biomass of the aggressor in the mixture is less than the decrease of the subordinate, due to the form of the response curves.

(c) Hypothesis 3. The total uptake by the mixture is the same as in the monocultures but the decrease in biomass of the subordinate is greater than the increase of the aggressor due to some specific feature of the mixture.

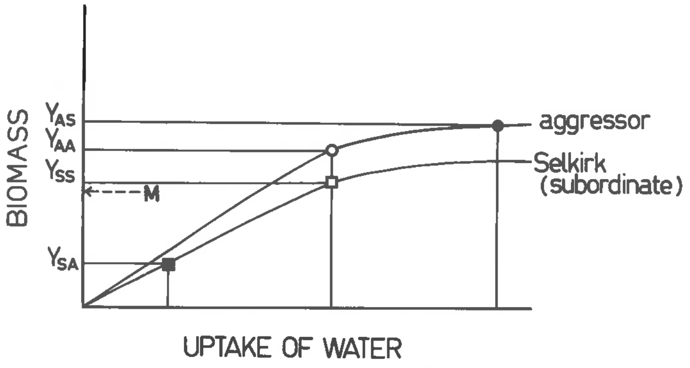
Y_{AA} - per-plant biomass in monoculture of A (○)
Y_{SS} - per-plant biomass in monoculture of S (□)
Y_{AS} - per-plant biomass of A in mixture with S (●)
Y_{SA} - per-plant biomass of S in mixture with A (■)
M - average per-plant biomass in the mixture

	monoculture	mixture
Aggressor (A)	○	●
Selkirk (S)	□	■

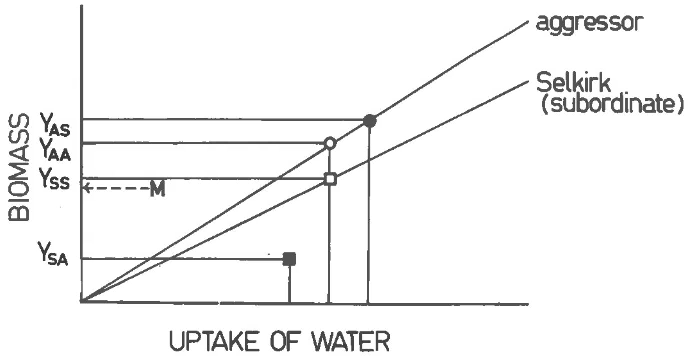
(a) Hypothesis 1



(b) Hypothesis 2



(c) Hypothesis 3



6. FURTHER STUDIES TO ELUCIDATE THE RESULTS OF THE LOW-WATER TREATMENT OF THE SOIL BENCH EXPERIMENT.

6.1 Watering experiment

6.1.1 Introduction

Under the conditions of restricted water-supply in the low-water treatment of the soil bench experiment, all three mixtures underyielded (see Fig. 5.4). The underyielding was particularly surprising in the case of the two mixtures which contained Selkirk, since the monoculture yields of the varieties composing these mixtures differed by 11% and 14% (in Section 3.1.3, it was shown that as Y_{ii}/Y_{jj} deviates more from unity, so transgressive yielding involves a progressively greater deviation of the RYT value from unity). Although the RYT values of the Selkirk mixtures were not significantly less than unity, they were remarkably low, viz. 0.884 and 0.837. Hoping to explain the appearance of the low RYTs, and hence the underyielding of the mixtures in this treatment, attention was concentrated on the two Selkirk mixtures since in these the effects seemed most marked.

In the low-water soil bench, growth seemed likely to be determined principally by the quantity of water taken up and the efficiency with which it was used in dry-matter production. Hence in Section 5.4.4, three hypotheses dealing with water uptake or efficiency of utilization were stated which might explain the low yields of the Selkirk mixtures. Briefly recapitulating, Hypothesis 1 was that in mixture, plants of the subordinate Selkirk lost more water than plants of the aggressors gained (relative to monocultues). Hypothesis 2 was that in mixture, losses and gains of water taken up were approximately the same, but that large gains by the aggressors brought them onto the plateaux of 'diminishing returns'-type response curves and so that their gains of biomass (compared with biomass in monoculture) were smaller than the losses in the other component. Hypothesis 3 was that while losses and gains of water taken up might be very similar, the action of some other factor in the mixture had an adverse effect on the normally constant production ratio (PR) of one of the components; this factor caused the biomass produced by this component to fall below what would be expected according to the actual level of water uptake achieved in the mixture and the linear response expected in monoculture.

Hypotheses 1 and 3 thus assume a linear response of monoculture biomass to water uptake whereas Hypothesis 2 assumes a negatively curved relationship. A pot experiment, the 'watering experiment', to be reported in this Section was undertaken primarily to test the linearity of the relationship between biomass and transpiratory loss (i.e. water uptake) over a range of water-stress treatments. Attempting to imitate the distribution of moisture in the soil of the low-water soil bench, in the pots where water stress was imposed, water was supplied by subirrigation.

6.1.2 Materials and Methods

Tared, white plastic pots without drainage holes were each filled with the equivalent of 11 kg of oven-dry soil. The soil was a 2:1 loam-sand mixture such as had been used in the soil bench experiment; its constituents had been obtained from the same sources. Three kilograms of soil without fertilizer occupied the bottom 6 cm depth of each pot. A PVC tube (2.5 cm diameter x 22 cm long) allowing subirrigation stood vertically upon the unfertilized soil and was embedded in the other 8 kg (15 cm depth) of fertilized soil which made up the total 21 cm depth of soil in each pot. The per-area fertilizer addition to the upper layer of soil was the same as had been used in the soil bench experiment (Section 5.2.1). The soil was tamped to achieved a bulk density of about 1.3g/cc. On top of the soil, a 3 cm layer of coarse gravel was laid to reduce evaporation of water from the soil surface; to prevent evaporative loss from inside the PVC pipe, the top of the pipe was closed with a rubber bung.

Two regimes of soil water were used in the experiment. A water-content maintained (by regular weighing) between 80% and 100% of field capacity was presumed to provide a 'no stress' water regime. A 'stress' regime was provided by a water-content maintained between 40% and 60% of field capacity.

The experiment involved three watering treatments differing in the stage (number of days after planting) at which the stress regime was applied. These treatments were 'no stress', stress regime from Day 53 ('early stress') and stress regime from Day 76 ('late stress'). Allowance was made for the three harvest occasions, on Days 33, 53 and 76. Replicate pots were harvested from the no-stress treatment on all three occasions, from the early-stress treatment on the last two occasions and from the late-stress treatment on the last occasion only. The way in which watering treatments and harvests were combined is shown in Table 6.1 .

In each replicate, one additional pot was left unplanted and maintained at 80-100% of field capacity; this pot was to act as a control with which to estimate the evaporative loss from the soil of the 'no-stress' pots. Each replicate therefore consisted of 19 pots. The pots were placed in an unheated greenhouse with evaporative coolers set to keep the air temperature below about 21°C. The pots were arranged about 10 cm apart and their positions within each replicate were reassigned at random once per week.

Table 6.1 Scheme of treatments and harvests imposed on the three varieties (Pitic, Selkirk and Summit) in the watering experiment. Before the onset of stress in the stress treatments, pots were maintained in a no-stress condition. The number of days from planting at which the three harvests were taken were H1 : 33 days, H2 :53 days, and H3 : 76 days. In the Table, the harvests at which randomly-selected pots were taken from the various treatments are indicated by asterisks. The duration of the stress regime is shown by broken lines.

	Harvest		
watering treatment	1	2	3
no stress	*	*	*
early stress (from H1)		---------*	---------*
late stress (from H2)			---------*

On the day of planting, 24 July 1969, the soil of all pots was brought to field capacity. In each of 8 regularly spaced holes in each (planted) pot, two germinated seeds of the appropriate variety were sown, covered with a standard weight of sand and lightly watered.

Fifteen days after planting (Day 15), the plants were singled by selecting at random one of the pair of shoots which had emerged from each hole and cutting it off level with the soil surface. The few holes from which only one seedling had emerged were left undisturbed; all planted positions produced at least one shoot.

As the plants grew, wire rings attached to sticks (all of standard weight) were used to support the plants. Aphids and mildew were controlled by fumigation and 'Benlate' spray respectively. Plate 6.1 shows the appearance of the experiment on Day 43.

Since the transpiratory losses (water uptake) needed to be found, the weight of water added to each pot was recorded. This weight was assumed to be equal to the loss due to transpiration from the plant shoots plus the loss due to evaporation from other parts of the pot. Water added to the no-stress (full field capacity) pots was poured onto the surface of the layer of gravel while the stress pots received water 6 cm from the bottom of the pot, through the temporarily opened mouth of the PVC tube. The evaporation from the soil surface and wetted gravel of the no-stress pots was estimated by the water lost from the unplanted, but watered, control. This amount was subtracted from the total water loss from no-stress pots to give the transpiratory loss. Evaporation from the soil surface or gravel of the stress pots was assumed to be negligible since neither were ever rewetted.

Plate 6.1 General view of the watering experiment on Day 43, looking to the South.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The first harvest took place on Day 33 when each plant had about 3 tillers. The shoots were cut off level with the soil surface, dried at 80°C for 24 hours and weighed. Crowns and roots were washed clean of all adhering soil, then dried and weighed in the same way as were the shoots. In this harvest and in subsequent ones, shoot weight was obtained as the average per-plant dry weight of shoots cut at the level of the soil surface, whole-plant weight was the shoot-weight plus the corresponding weights of crown and roots, and weight of water transpired was the average accumulated loss of water from the pot, corrected during non-stress periods for evaporation from the soil and gravel, and divided by 8 to give a per-plant value. The second harvest (H2) took place on Day 53 at the beginning of stem extension; Plate 6.2 shows the appearance of the plants in the various treatments on this day. The third harvest (H3) was on Day 76 when the ears of the latest variety, Selkirk, were about to emerge (see Plate 6.3).

At H2 and H3, the distribution of root weight within the pots was investigated. For this, the soil of each pot was moistened and divided into four parts (P1, P2, P3 and P4, see Fig. 6.1). The layer 3 cm deep at the bottom of each pot will be termed P1; this was cut off first. Next, from the remainder, the outer layer 3 cm thick which had been in contact with the almost vertical walls of the pot was cut of to constitute P2. The remaining portion, the central bulk of the pot's soil, was divided horizontally into two layers each of 9 cm thickness: the upper layer was P3 and the lower layer was P4. The roots in the various parts were washed clean of all adhering soil, dried for 24 hours at 80°C and weighed.

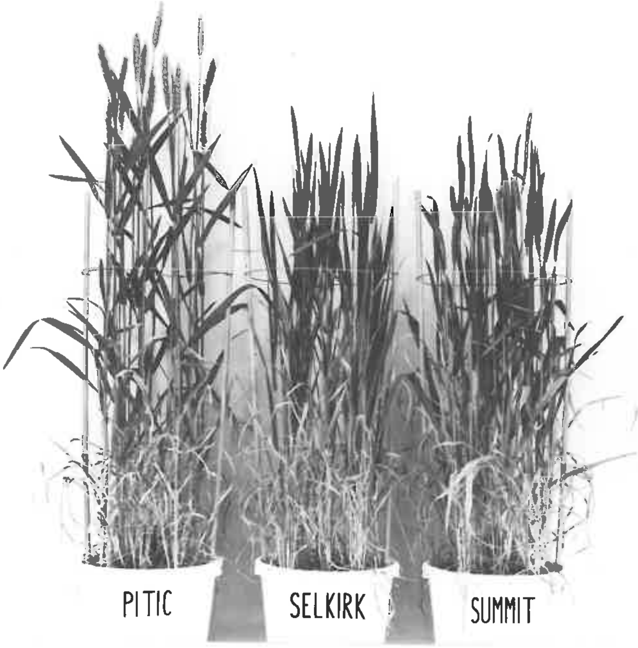
For the presentation of the results, the root weights in P2 and P3 were summed to give the weight in the 'upper half' of the pot. The weights in P1 and P4 were similarly summed to

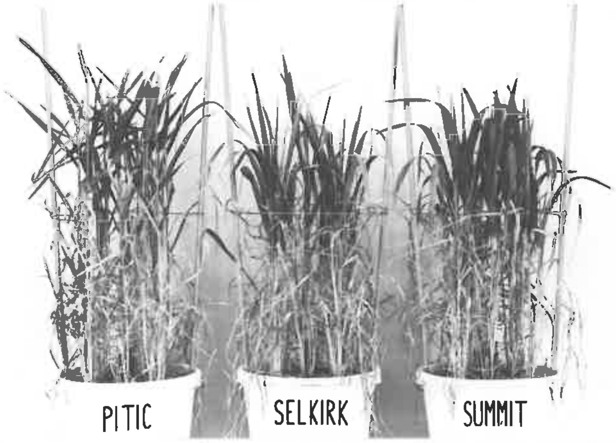
*Plate 6.2 Plants of one replicate of the pots harvested at H2 (Day 53) in the watering experiment.

a) Above : no-stress treatment

b) Below : early-stress treatment in which water stress was applied from the time of H1 (Day 33).

*See photo p. 198.


PITIC
SELKIRK
SUMMIT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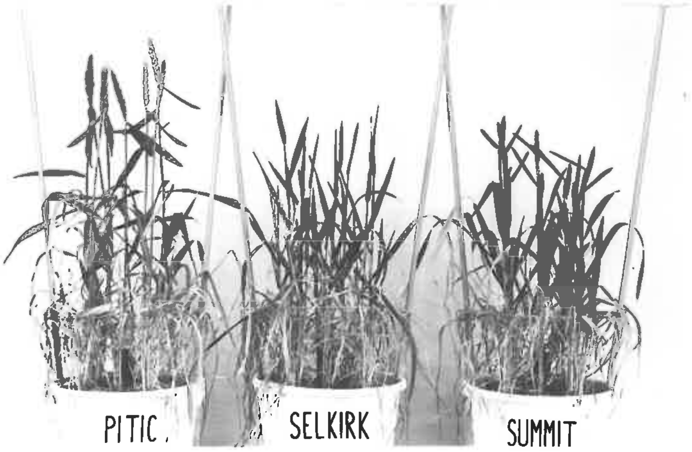

PITIC
SELKIRK
SUMMIT

*Plate 6.3 Plants of one replicate of the pots harvested at H3 (Day 76) in the watering experiment.

a) Top : no stress treatment.

b) Middle : late-stress treatment in which stress was applied from the time of H2 (Day 53).

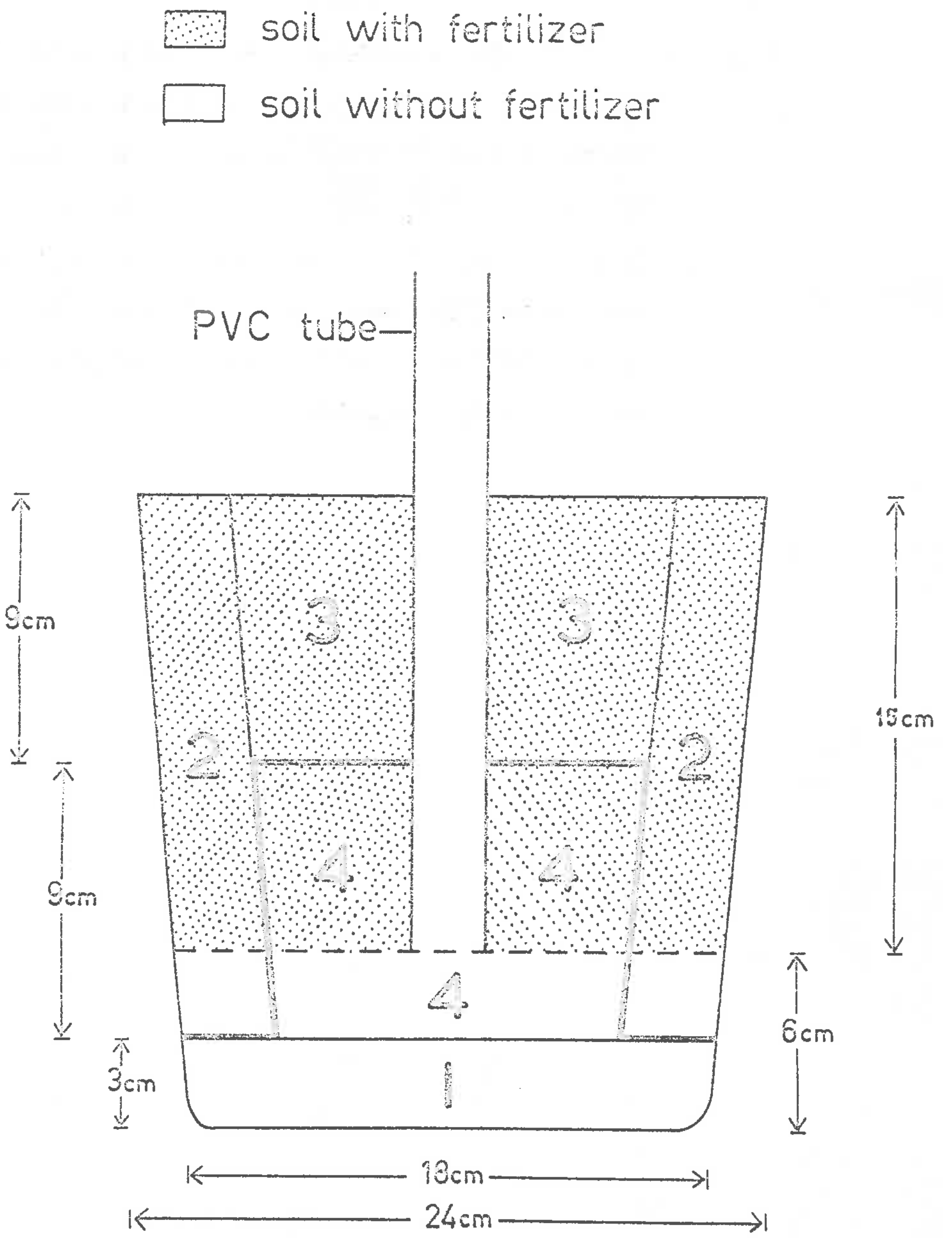
c) Bottom : early-stress treatment in which water stress was applied from the time of H1 (Day 33).

*See photo p.197.


PITIC
SELKIRK
SUMMIT


PITIC
SELKIRK
SUMMIT

Fig. 6.1 Diagram showing the four parts into which the soil of the pots were divided at H3 (Day 76). Parts 2 and 3 were combined as the 'upper half'. Parts 1 and 4 composed the 'lower half'. Also shown is the arrangement of the fertilised and unfertilised soil and the PVC tube through which subirrigation was provided for the plants under water stress.


▨ soil with fertilizer
☐ soil without fertilizer
PVC tube
9cm
3
3
2
2
9cm
15cm
4
4
4
6cm
3cm
1
13cm
24cm

give the weight of roots in the 'lower half' of the pot. The inclusion of the whole of P2 in the upper half was thought to be justified since obliquely- or horizontally-growing roots which met the side of the pot followed the wall directly downwards into P1. Hence, the root weight in P1 would be an overestimate of the weight of roots expected at and below the depth of P1 in an unrestricted rooting medium.

Wishing to compare the physiological response of the varieties to the type of restricted water-supply maintained in this experiment, relative water contents (Weatherley 1965, Slatyer & Barrs 1965, Barrs 1968) were measured on the highest two fully-emerged leaves at H3. These were the only two mature leaves which were not showing signs of senescence in the stress treatments. At harvest, these leaves were cut from the tallest culms of five randomly-selected plants from each pot. Four 1-cm long segments were immediately cut with a razor blade from the middle of each lamina. The 20 segments from each pot were stored for up to an hour in a small, sealed polythene bag at 1°C. The initial fresh weights (FW1) of the samples were measured as quickly as possible and the segments were then floated on distilled water, each sample in a separate container. The containers were then placed in the dark, in a saturated atmosphere at 20°C, for 4 hours. After this period the water on the surface of the turgid leaves was removed by placing them between absorbent tissues and applying a standard pressure. A second fresh weight (FW2) was rapidly measured. The sample was then dried at 80°C for 24 hours and a final, dry weight (DW) was taken.

The relative water content (RWC) was calculated using the formula :

$$\begin{aligned} \text{RWC} &= \frac{\text{original wt. of water in leaf}}{\text{wt. of water in leaf at full turgor}} \\ &= \frac{\text{original fresh wt.} - \text{original dry wt.}}{\text{final fresh wt. at full turgor} - \text{final dry wt.}} \qquad (6.1) \\ &= \frac{FW1 - DW}{FW2 - DW} \end{aligned}$$

Slatyer & Barrs (1965) suggested that during the soaking period, the leaves should be lit at their compensation point to prevent changes in dry weight. With the material from the present experiment however, the leaf segments from different varieties and treatments showed great variation in their tendency to become rolled; a different light intensity would have been necessary for each treatment. To avoid this difficulty, the light was dispensed with altogether.

The possible consequences of this omission need to be considered. If fresh leaf tissue at 20°C loses dry weight by respiration at the rate of $6 \times MW_{(CH_2O)}/MW_{CO_2} \simeq 4.2$ mg (CH_2O) /g dry wt/hour (a 'high' estimate, see King & Evans 1967), then in 4 hours a loss of about 2% of the original dry weight might occur. The question to be considered is whether a large difference of respiration rate between varieties or treatments might invalidate the method used. To answer this question, let us take a hypothetical example: assuming that a fresh leaf containing 80% of its fresh weight as water has a RWC of 0.8, a 2% loss of dry weight during soaking time will cause the present method to give a calculated RWC of 0.804 and a 6% loss will lead to a RWC value of 0.812. Thus, with values of absolute and relative water contents close to those observed (e.g. Barrs 1968), a 3-fold difference of respiration rate causes the estimated RWCs to differ by less than 1%. Similarly, assuming a likely respiration rate, the omission of the light treatment causes the true RWC to be overestimated by only 0.5%. Such small errors seem to be negligible compared with the other sources of error inherent in the method (see Slatyer & Barrs 1965).

6.1.3 Results

(a) Shoot weights

The relationship between weight of shoot at the final harvest (H3) and the weight of water transpired is shown in Fig. 6.2. The regression was apparently linear over the range of water regimes used, with the regression lines passing close to the origin. While the lines of the varieties Summit and Selkirk were very similar, their combined data gave a line which was markedly lower than that of Pitic. The deviations of the regression constants from zero were non-significant in both cases and so the lines could be taken as passing through the origin. To test the significance of the apparently lower slope of the line of Selkirk and Summit, the production ratios (PR= shoot weight/water transpired) of all pots harvested at H3 were treated by an analysis of variance. The average PRs of Selkirk and Summit were not significantly different and their data were combined. The result was an average PR of 4.25 g/kg which was significantly ($P < 0.01$) 12.8% lower than that of Pitic (PR= 4.88 g/kg). Similarly, when the regression lines were forced to pass through the origin, their slopes differed by 11.3% ($P < 0.001$).

While the results of H3 are those most relevant to a discrimination between the three hypotheses concerning the results of the low-water soil bench, the data from all three harvests of whole-plant weight and water transpired are of interest. They have been plotted in Fig. 6.3. This graph shows that when the weight of roots was included, the difference in slope between the regression lines of the varieties was reduced. Considering regression lines which have been forced to pass through the origin, the slope of the lines based on the combined data of Selkirk and Summit was in this case only 5.4% ($P < 0.05$) below that of Pitic. Although the difference between the slopes was still significant, all varieties were closer to sharing a common regression line.

Fig. 6.2 Relationship between shoot weight at H3 (Day 76) and weight of water transpired in the period from planting to H3.

In the fitting of the linear regressions, the data of Selkirk and Summit were combined. The regression equations were :

Pitic $y = 0.272 + 4.61x^{***}$

Selkirk and Summit $y = -0.107 + 4.38x^{***}$

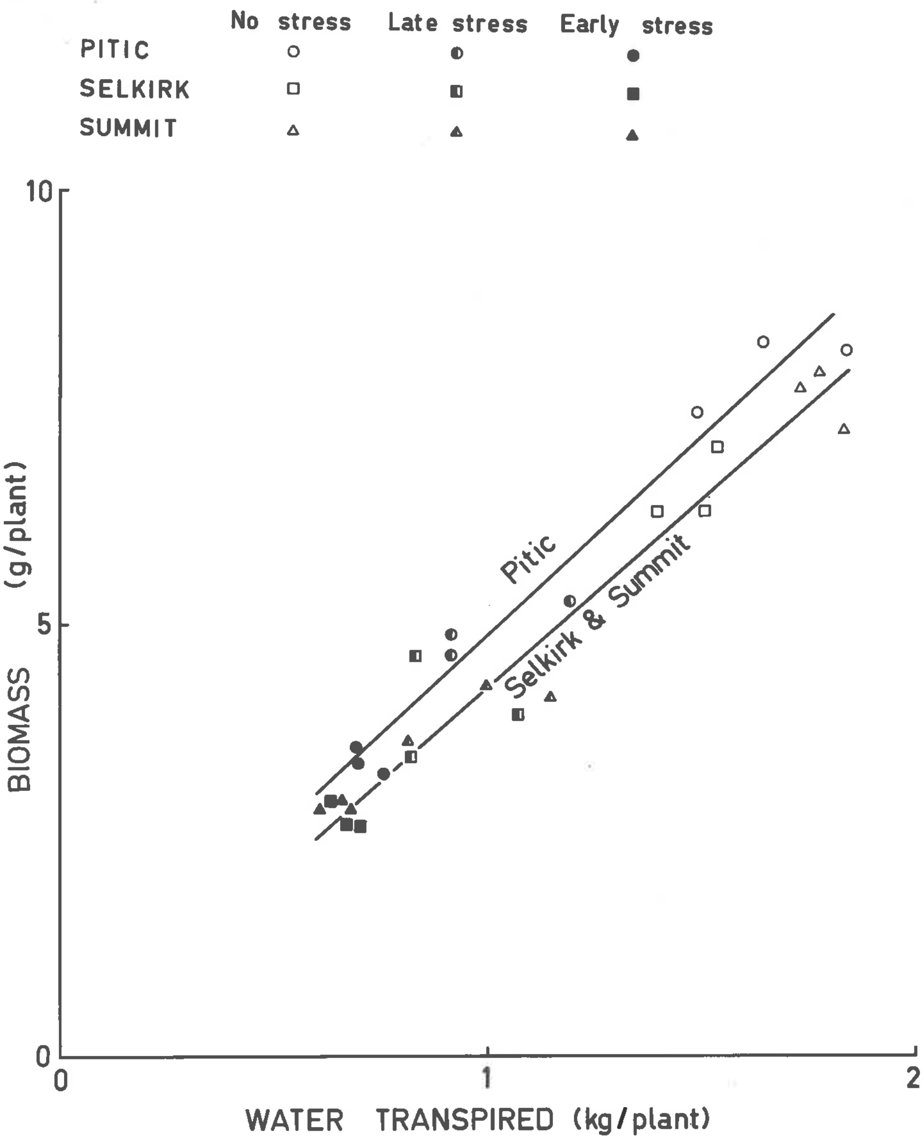
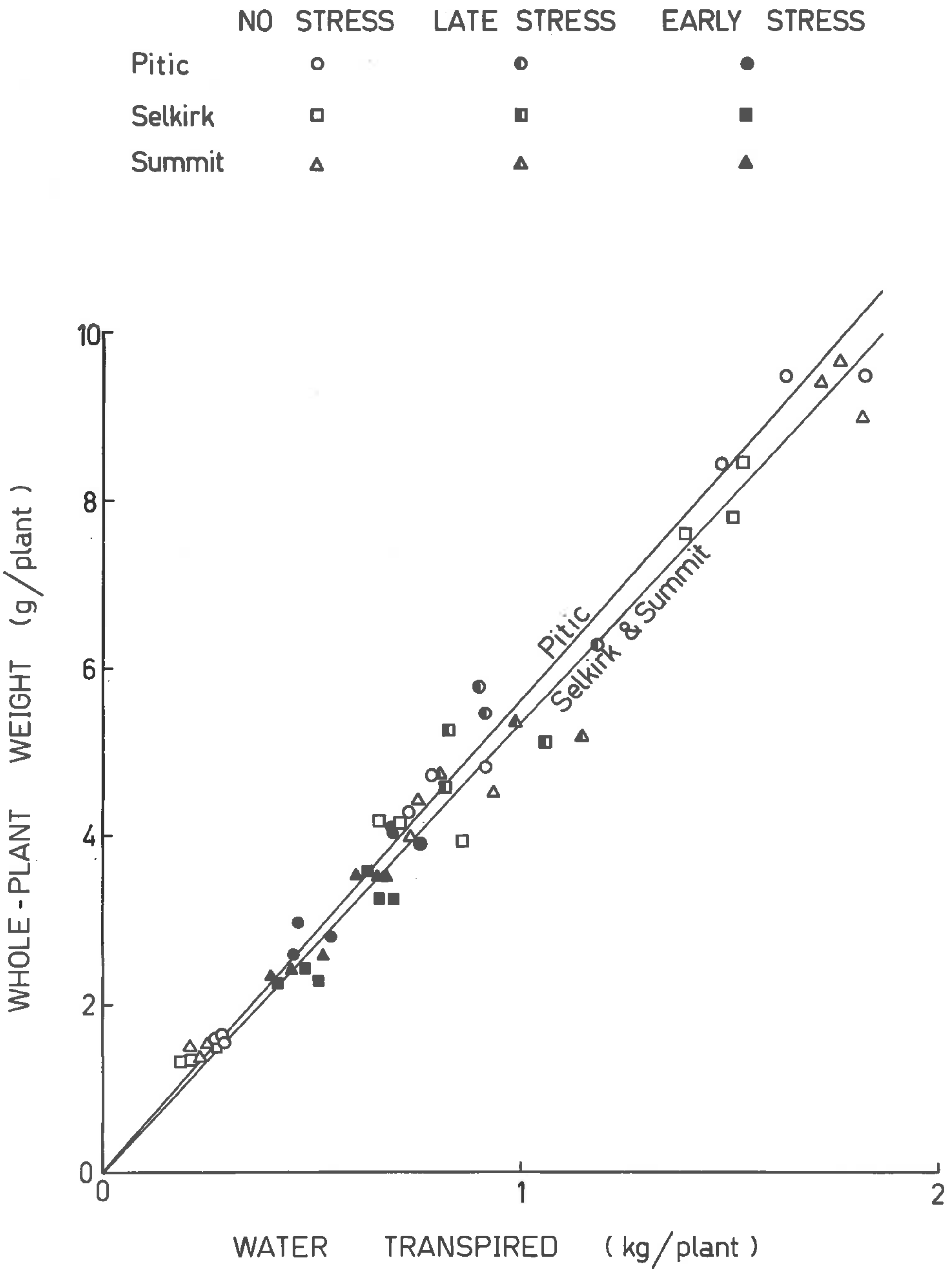

No stress
Late stress
Early stress
PITIC
SELKIRK
SUMMIT
10
5
0
BIOMASS (g/plant)
0
1
2
WATER TRANSPIRED (kg/plant)
Pitic
Selkirk & Summit

Fig. 6.3 Relationship between whole-plant weight at all harvests (H1, H2 and H3) and weight of water transpired in the period from planting to harvest. Linear regressions through the origin were fitted to the combined data of Selkirk and Summit. The regression equations were:

Pitic $y = 5.60x^{***}$

Selkirk and Summit $y = 5.30x^{***}$


NO STRESS
LATE STRESS
EARLY STRESS
Pitic ○ ◐ ●
Selkirk □ ◧ ■
Summit △ ◬ ▲
WHOLE - PLANT WEIGHT (g/plant)
0
2
4
6
8
10
WATER TRANSPIRED (kg/plant)
0
1
2
Pitic
Selkirk & Summit

The effect of the inclusion of the weight of roots was apparently due to a marked difference between Pitic and the other varieties in the way in which their dry matter was distributed between roots and shoots at H3. Table 6.2 shows that at H3 the average root/shoot ratios of Selkirk and Summit were about 40% ($P < 0.001$) greater than that of Pitic. With a greater proportion of their whole-plant weights below ground-level, the regressions of shoot weight on water transpired of Selkirk and Summit would be expected to differ from that of Pitic in the way shown in Fig. 6.2. The magnitude of the residual, unaccounted-for difference between varieties is indicated by the degree of divergence of the regression lines of Fig. 6.3 .

(b) Root weights

The data concerning the distribution of the roots within the pots at H2 and H3 are given in Table 6.3. Since the varieties x treatments interactions were small and non-significant in the cases of root weight in the lower half of the pot and upper half/lower half ratio, the varieties may be compared using the variety means given in Table 6.4 . Since attention will later be concentrated on the two Selkirk mixtures, the differences between Selkirk and the two other varieties will receive prime consideration. Comparing firstly Selkirk with Pitic, at H2 Selkirk had a 22% ($P < 0.001$) lower weight of root in the lower half of the pot; this was mostly due to the smaller fraction ($P < 0.001$) of Selkirk's total root weight which was in the lower half. At H3, the situation was similar except that Selkirk had then only 11% ($P < 0.05$) less weight of root than Pitic in the lower half of the pot.

Comparing Selkirk with Summit, Selkirk again tended to have a lesser weight of root in the lower part of the pot. However, this difference only became striking by H3 where Selkirk's value was 17% ($P < 0.01$) below that of Summit.

Table 6.2 Root/shoot ratios at the third harvest (H3) in the watering experiment. The weight of the crowns is included with that of the shoot.

Time of onset of water stress	Variety Pitic	Selkirk	Summit	Means
none	.145	.213	.220	.192
late	.178	.205	.226	.203
early	.179	.286	.262	.242
means	.167	.234	.236	.213

Comparisons of means of either water-stress treatments or varieties : LSD (0.1%) = 0.038

Table 6.3 Root weight data for two harvests of the watering experiment. The upper half of the pot consisted of P2 and P3 (see Fig. 6.1) and the lower half consisted of P1 and P4. Weights of roots (g/pot) are given for the upper half, the lower half, and the whole pot. The figures for the ratio upper half/lower half have been averaged over replicates and so do not agree exactly with the ratios calculated from entries in the Table. Results of statistical tests are given in the text and in Table 6.4 .

Varieties	Pitic			Selkirk			Summit		
Onset of water stress	None	Late	early	None	Late	Early	None	Late	Early
(a) H2									
Upper half	4.92	-	2.51	6.13	-	2.40	6.16	-	2.46
Lower half	1.91	-	1.47	1.66	-	0.97	1.96	-	1.13
Total	6.83	-	3.98	7.79	-	3.38	8.12	-	3.59
Upper/Lower	2.58	-	1.70	3.67	-	2.48	3.17	-	2.22
(b) H3									
Upper half	5.37	4.53	2.73	7.68	6.37	2.82	9.19	5.81	2.89
Lower half	3.90	2.59	2.12	3.49	2.46	1.72	4.28	2.62	2.33
Total	9.27	7.12	4.85	11.18	8.83	4.45	13.45	8.44	5.23
Upper/lower	1.40	1.76	1.29	2.23	2.69	1.64	2.15	2.22	1.24

Table 6.4 Root weight data for two harvests of the watering experiment, averaged from full data of Table 6.3

Varieties	Pitic		Selkirk		Summit
(a) H2					
Upper half	N.S.		N.S.		N.S.
Lower half	1.69	*** >	1.32	P<0.1 <	1.54
Total	N.S.		N.S.		N.S.
Upper/lower	2.14	*** <	3.08	N.S. ≥	2.69
(b) H3					
Upper half	N.S.		N.S.		N.S.
Lower half	2.87	* >	2.56	** <	3.08
Total	7.08	*** <	8.18	** <	9.05 +)
Upper/lower	1.48	*** <	2.18	P<0.1 >	1.87

+) Variety x Treatment interaction present ($P < 0.001$)

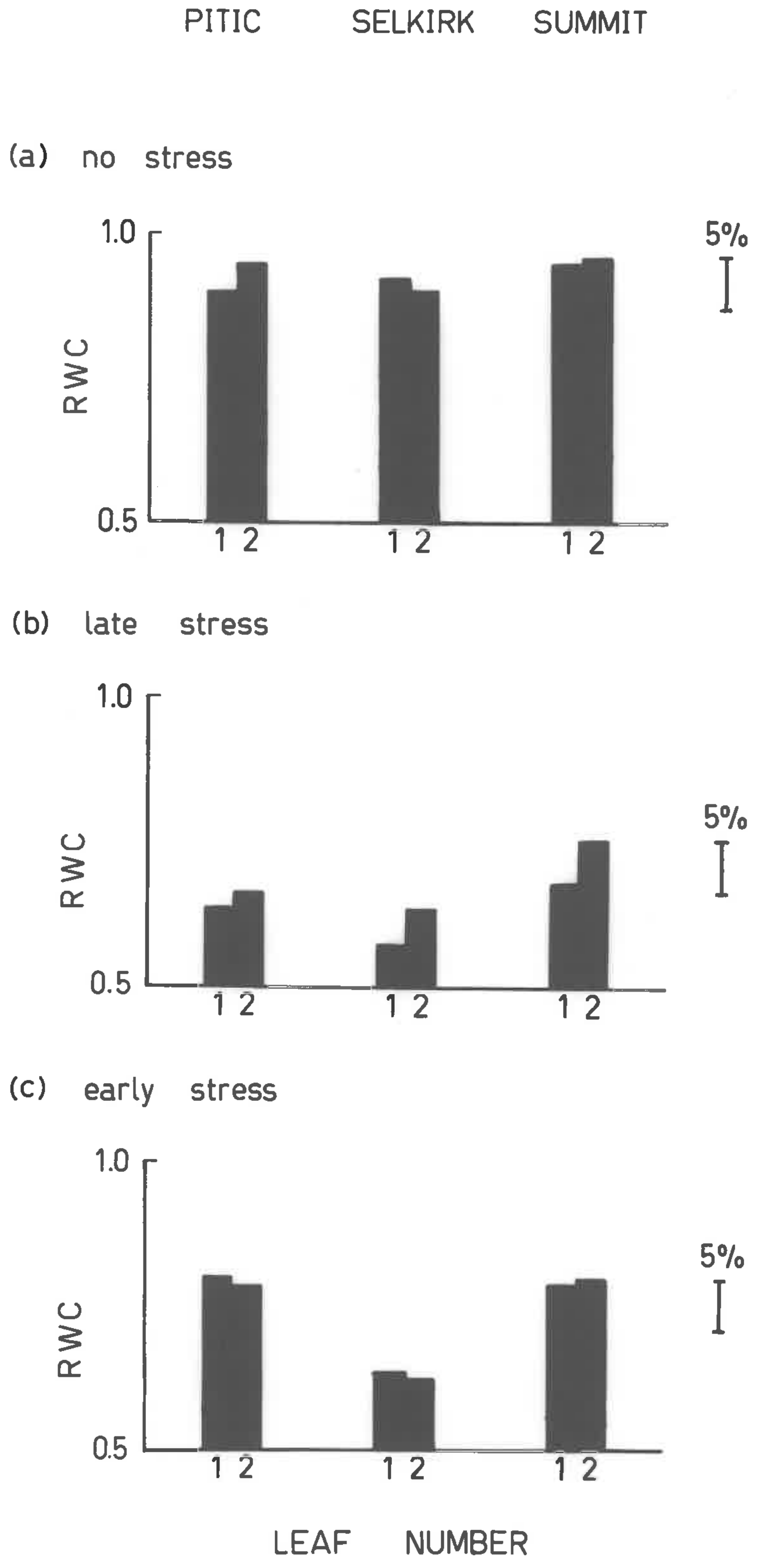
Although Selkirk had a lower proportion of its root weight in the lower part of the pot, the difference of upper half/lower half ratio did not quite reach the 5% probability level at either harvest. Instead, there was a tendency (in H3 this was obscured by a marked varieties x treatments interaction) for Selkirk's total root weight to be smaller than that of Summit. Averaged over the three treatments, Selkirk's root weight was 10% lower, but in view of the interaction (see Table 6.3), the apparent significance ($P < 0.01$) of this difference must be accepted with caution.

To summarise the data on root distribution, Selkirk had a significantly smaller weight of root in the lower half of the pot than either of the other two varieties at at least one of the two later harvests. Compared with Pitic, a significantly larger proportion of Selkirk's roots were in the upper half of the pot; compared with Summit, the significantly lower weight of Selkirk's root in the bottom half of the pot was a reflection of its smaller total root weight.

(c) Water content of leaves

The measurements of relative water content of leaves at H3 are presented in Fig. 6.4. Whereas in the no-stress pots, all varieties had similar relative water contents of their leaves, in both stress treatments (particularly in the treatment where stress was imposed early), the values for Selkirk were substantially below those of the other two varieties. This difference in behaviour when under water stress led to a significant ($P < 0.05$) interaction between varieties and stress treatments. The first and second leaves of the three varieties responded similarly to all treatments.

Fig. 6.4 Relative Water Content (RWC) of the highest two leaves on the main axis of plants at H3. The flag leaf is counted as leaf 1. The LSD ($P \leqslant 0.05$) shown is that appropriate for comparing any pair of values within the same watering treatment.


PITIC
SELKIRK
SUMMIT
(a) no stress
1.0
0.5
RWC
5%
1 2
1 2
1 2
(b) late stress
1.0
0.5
RWC
5%
1 2
1 2
1 2
(c) early stress
1.0
0.5
RWC
5%
1 2
1 2
1 2
LEAF NUMBER

6.1.4 Discussion

In the Introduction to this Section (6.1.1), three hypotheses were stated which could account for the under-yielding of the two Selkirk mixtures in the low-water treatment of the soil bench. In particular, the second hypothesis proposed that the response of shoot weight to the quantity of water taken up was negatively curved so that in mixture, while losses and gains of water uptake by the components (relative to their monocultures) might be equal, the curvature caused gains of shoot weight in one component to be less than the losses in the other. The mixture might thus underyield.

The linear relationship established between shoot weight and transpiratory loss (Fig. 6.2) shows that Hypothesis 2 must be rejected. There is little hint of any curvature in the regression lines; the lines of Fig. 6.2 both account for about 92.5% of the total variance of biomass of pots containing the varieties indicated. De Wit (1958) and others have concluded that when water is in limited supply, shoot weight depends linearly on the quantity of water taken up. The present results agree with this conclusion. The difference between the regression lines of Pitic and the other two varieties illustrates the effect of differences in root/shoot ratio which, although acknowledged by de Wit (1958) as contributing to the scatter around the regression lines, was ignored in his treatment of data.

The only experiment reviewed by de Wit (1958) in which whole-plant weight was related to water uptake was that of Boonstra (1934). Although Boonstra worked with peas, the experimental techniques used by him and those of the present study were rather similar. The graph of Fig. 6.3 confirms Boonstra's conclusion that when the supply of water is restricted, the production of whole-plant dry matter is proportional to water uptake. The fit of the points to the lines In Fig. 6.3 is remarkably good considering that experimental error is involved in the determination of positions on both axes. The lines of Pitic and of the two other varieties account respectively for 99.4% and 98.8% of the total variance. Since the points of three harvests (on Days 33, 53 and 76) lie on the same lines, it appears that the changes of conditions within the glasshouse as the season advanced were not sufficient to alter production ratios based on whole-plant weight.

While the investigation of the regression of shoot weight on water uptake has provided a reason for rejecting one of the three hypotheses concerning the soil bench experiment, the same experiment has demonstrated differences between the three soil bench varieties in their physiological responses to a restricted water supply. The data of relative water content of leaves showed that under the conditions of water supply in the stress pots, the leaves of Selkirk were experiencing an apparently greater degree of physiological stress than were those of the other varieties (Fig. 6.4).

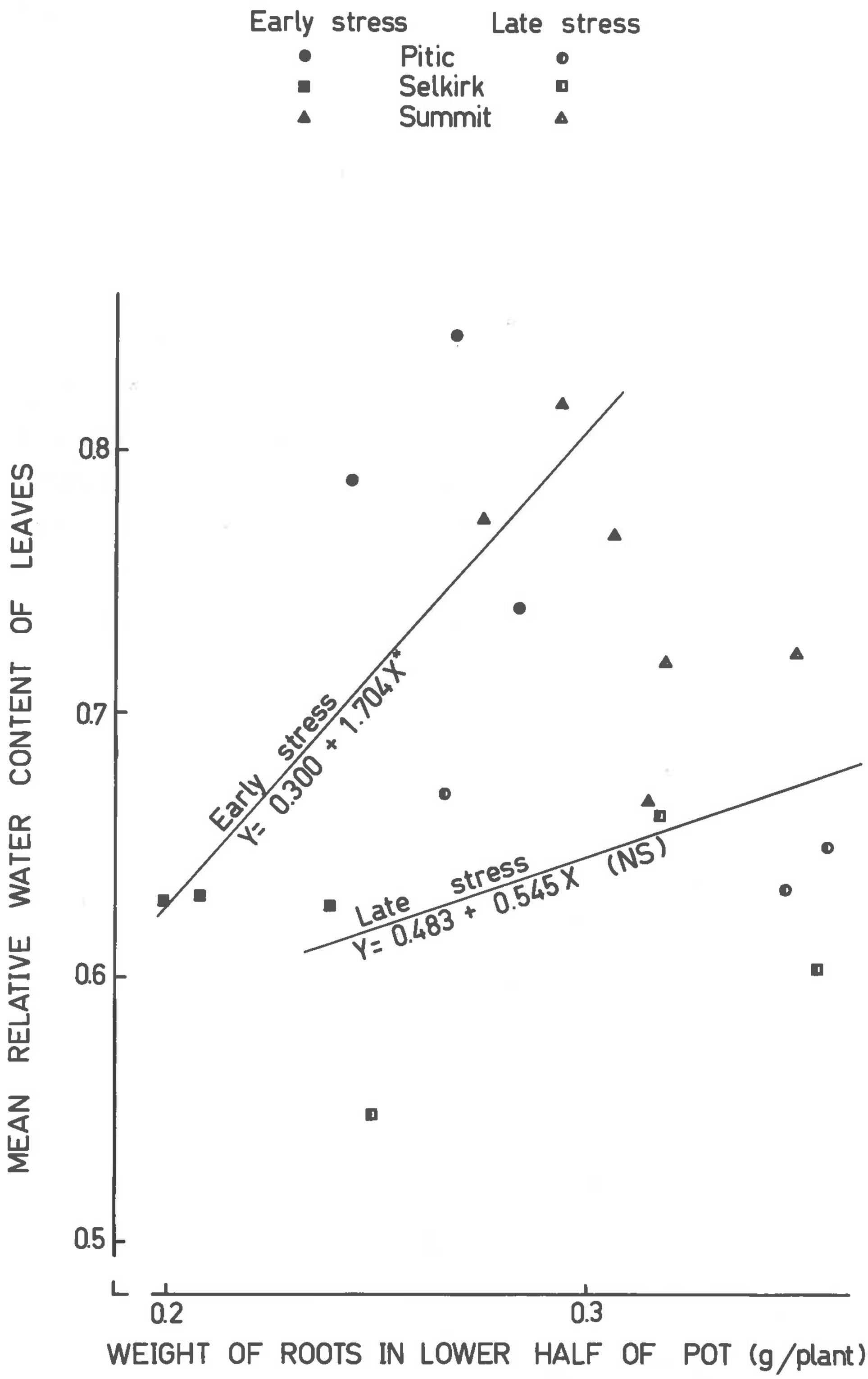
The differences in leaf RWC observed in the present experiment suggest that in the stress treatments at H3, the growth potential of Selkirk was reduced relative to that of the other varieties. In support of such a contention it is noted that Catsky (1965) found an extremely close (non-linear) relationship between the RWC of cabbage leaves and their photosynthesis rate over an RWC range of 95% to 40%; Wardlaw (1969) observed a similar relationship in ryegrass. Working with wheat, however, Wardlaw (1967) found that photosynthesis was only reduced when the leaves became wilted; in his experiment 'moderate wilting' corresponded to a RWC of 77%. In another study attesting the physiological significance of RWC, Dale (1961) showed that stomatal resistance was inversely related to RWC of cotton leaves at values of less than 85%.

If firstly, the differences in leaf RWC observed at H3 in this pot experiment also occurred in the low-water bench of the previous season, and if secondly, the physiological implications of the published work quoted above are accepted, then it becomes easier to understand why Selkirk was rapidly suppressed (at a similar stage of growth) in mixtures in the low-water soil bench. A genotype with a relatively poor supply of photosynthate for root growth, when competing in mixture for water, seems likely to suffer such a fate.

The probability of the pot experiment reproducing the RWC situation of the soil bench experiment depends on the action in both experiments of the same key factors. Before any assessment of this probability can be made, the key factors have to be identified. It is at this point that the results of the study of root distributions may be important.

At H2 and H3 the weight of root in the lower half of the pots was measured in all treatments. At H2, the weight of Selkirk's root in this part of the pot was 22% ($P < 0.001$) less than that of Pitic, and 14% ($P < 0.1$) less than that of Summit. At H3, the corresponding figures were 11% ($P < 0.05$) and 17% ($P < 0.01$). Since the water supplied to the stress pots only wetted the lower part of the soil, it seems that the weight of root in the wetted zone will be to some extent a measure of how well the soil mass was penetrated by the root-system, hence (Slatyer 1957b, Gardner 1960, Cowan 1965) of the ability of the plant to maintain the water content of its leaves during a drying cycle. The lower weight of Selkirk's root in the wetted half of the stress pots and the lower RWC of Selkirk's leaves in the same treatments seem entirely consistent with this view. To show the parallelism between the two sets of observations more explicitly, Fig. 6.5 has been plotted including all the stress pots at H3. Considering the nature of the physical connection existing between the two

Fig. 6.5 Relationship between the relative water content (RWC) of the leaves of a pot and the weight of roots in the 'lower half' of the same pot. The RWC used was the mean of the values for the two highest leaves of the main culms of 5 plants selected at random from each pot. The weight of roots was that present in parts 1 and 4 combined (see Fig. 6.1).


Early stress
Late stress
Pitic
Selkirk
Summit
MEAN RELATIVE WATER CONTENT OF LEAVES
0.8
0.7
0.6
0.5
0.2
0.3
WEIGHT OF ROOTS IN LOWER HALF OF POT (g/plant)
Early stress
Y= 0.300 + 1.704X*
Late stress
Y= 0.483 + 0.545X (NS)

variables, it seems reasonable to assert that the regressions of Fig. 6.5 depend on causal relationships. If this is so, variation of root weight in the lower half of the pot accounted for 56.3% ($P < 0.025$) of the variance of RWC in the treatment with the prolonged (early) stress. The relationship was less clear and non-significant in the case of the treatment where stress had not acted so long. The differing relationships of the treatments is not unexpected since the plants concerned differed in root/shoot ratio (Table 6.2) and in the degree of drought-hardening they had experienced.

If the key factor determining the differences in leaf RWC was indeed the quantity of roots in moist soil, the likelihood of Selkirk's leaves suffering from low RWC in the soil bench can now be considered. It may be recalled that the plants of the low-water soil bench were competing for an unrenewed supply of water which had been stored in the soil from the time of planting. Since cereal roots penetrate and deplete the surface layers of soil before the deeper layers are exploited (Conrad & Veihmeyer 1929, Linscott et al. 1962) and since evaporation from the surface must reinforce this effect (e.g.Baver 1940), it is likely that in the soil bench experimentthe profile was dried from the soil surface downwards. At any stage during growth the water content of the soil probably increased with depth.

The next question to be considered is whether the clear inter-varietal differences observed in the pot experiment can be taken to indicate that similar differences existed in the low-water soil bench. In the pot experiment, large differences of water regime had no effect on the observed varietal differences, e.g. in the analyses of root weight in the lower half of the pot, at H2 the interaction variance ratio was 1.67 and at H3 it was less than unity. It thus seems that the difference in water regime between the pot experiment and the soil bench would not be sufficient to change appreciably the pattern of differences of root distribution from that found in pot culture. Although the data of Pinthus and Eschel (1962) refer to the numbers of roots produced by a series of wheat varieties, it is pertinent to note that these authors found that the difference of conditions between culture in containers and culture in the field had little effect on varietal differences. Some other results of Pinthus & Eschel are of interest here since these workers included Selkirk in a comparison of the root systems of 14 wheat varieties, also grown in containers. After the root systems were washed clean of soil in situ, the varieties were graded visually according to type of root system. Selkirk was ranked equal with one other genotype as the variety producing the densest, most horizontally-spreading root system. The results of Pinthus & Eschel are thus consistent with the finding that Selkirk has a relatively superficial root system, at least when grown in containers (see Tables 6.3 and 6.4).

The threads of the argument can now be drawn together. It will be recalled that in the low-water treatment of the soil bench, Selkirk in both of its mixtures was suppressed, rapidly and strongly, shortly before ear emergence; if it can be accepted that Selkirk's lack of deep roots led to its critically low leaf RWC in the pot experiment, that furthermore Selkirk developed a relatively superficial root system in the soil bench experiment and that the soil bench dried principally from the surface downwards, then we have a complete hypothesis as to why Selkirk was suppressed so rapidly in these mixtures. The hypothesis may be stated as follows. After about Day 50, as the evaporative demand increased, a large part of the root systems of all varieties was located in soil from which no more water could be extracted. Selkirk, the variety with the smallest weight of roots in the deeper, still moist soil, took up and transpired smaller quantities of water than did the associated genotypes. This uneven sharing of the total water uptake resulted in Selkirk growing more slowly than its associates. A reduced rate of root growth caused its water uptake to fall further and further below that of the competing genotypes since it was caught in a feedback system: lower water uptake → lower leaf RWC → less photosynthesis → less root growth → lower water uptake. Selkirk's monoculture was not greatly affected because unevaporated soil-water, as yet not taken up, remained available in the soil to Selkirk's roots if they could reach it. In mixture however, such water would tend to be removed in advance of Selkirk's roots by the more abundant and faster-growing roots of the associates. The feedback system reduced the growth rates of Selkirk in mixtures to values much below those in its monoculture *. In Section 5.4.4, it was suggested that Selkirk, as a late variety, probably suffered some shading when its associated varieties extended their internodes. This too, by reducing root/shoot ratios (Milthorpe 1961), may have resulted in a further acceleration of the suppression of Selkirk.

This tentative account of the course of events in Selkirk's mixtures in the soil bench will receive some further clarification in the next Section (6.2). The primary purpose of the next Section is, however, to discriminate between the two remaining hypotheses concerning the underyielding by the two Selkirk mixtures in the low-water soil bench.

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* The growth of 1/4 to 1/3 of the Selkirk plants in mixture must have virtually stopped before about Day 90 since this proportion produced no ears. In contrast, only 3% of the Selkirk plants in monoculture failed to produce at least one ear.

6.2 Silicon Analyses

6.2.1 Introduction

The watering experiment showed that in the conditions of that experiment, the biomass:transpiration relationship was linear. Since this linear dependence has been shown by de Wit (1958) to be commonly found in both pot and field experiments, it seems allowable to assume that this relationship, confirmed in the watering experiment, also applies to the soil bench experiment. On this assumption, only two of the original three hypotheses concerning the cause of the underyielding of the Selkirk mixtures remain.

The original Hypothesis 1 suggested that the gains of water taken up by the aggressors in mixture (compared with their monoculture uptakes) were less than the losses of water uptake suffered by Selkirk (compared again with the monoculture value). The underyielding would in this case be attributed to the relatively low water uptake by the mixture as a whole.

The original Hypothesis 3 suggested that one (or both) of the components was subjected, in the mixture, to a level of a subsidiary factor which was sufficiently different from the level experienced in monoculture to substantially alter its response to the quantity of water taken up. This component, in mixture, would show a response to water which deviated from that which would be observed if the water-response were tested in monoculture. Since the aggregate water uptake by the mixture would be similar to that of the various monocultures, the underyielding would be attributed to a reduced efficiency of utilization of the water in one or both of the components.

In order to discriminate between these two remaining hypotheses, it was necessary to know the quantity of water taken up by each of the mixture components and by the monocultures of soil bench. This information would show whether the ryielding mixtures had taken up less water or whether the overall PRs of the mixtures were relatively low.

A technique enabling transpiratory loss, and hence water uptake, to be determined was suggested by Jones & Handreck (1965) (see also Handreck & Jones 1968). These workers concluded that silica, in solution in the soil water, is taken up passively by the roots of several cereals including wheat. The silica is apparently transported by the moving water in the xylem and when the water carrying it is lost by transpiration from some part of the plant, it is simply deposited in the tissues of that part. The silica concentration in the soil water was found to vary between soils, but in each of several soils the original concentrations remained constant in spite of the regular removal of the soil solutions and their replacement by distilled water; the equilibrium concentration was a characteristic of the soil. Jones & Handreck (1965) suggested that from a knowledge of the weight of silica in the shoot of a plant and of the concentration of silica in the soil solution, the total weight of water transpired from the plant (i.e. its water uptake) could be estimated.

Besides serving the purposes already described in Section 6.1, the watering experiment had two other functions which concerned the estimation of water uptake in the soil bench. Firstly, the conclusion of Handreck & Jones (1968) that the uptake of silica by wheat is passive could be checked with the same three varieties; the weight of silica per plant shoot ('silica yield') could be tested for strict proportionality to the water transpired. Secondly, given the simplest situation a single value of the fraction water transpired/silica yield could be calculated for use as a multiplier factor for the silica yield of the soil bench material. This factor would have a value equal to the reciprocal of the concentration of silica in water held in a soil which was very similar to that used in the soil bench. The application of such a factor to the silica yields of the plants in the soil bench would give the estimates of water transpired by plants in that experiment. In fact, as will be shown, the situation was less than simple and the watering experiment provided three calibration curves, one for each variety, rather than one multiplier factor.

6.2.2 Materials and Methods

Since the plant material was to be analysed for silica content by means of an X-ray fluorescence spectrometer, the samples were first processed to produce the compressed tablets required for use in the spectrometer.

The material of each sample was redried and passed first through a OSK mill and then through a W & G mill to make a powder which would pass a 2mm sieve. This powder was ground for 2 minutes in a Siebtechnik mill and re-dried overnight in a vacuum desiccator containing phosphorus pentoxide. After allowing the powder to regain a little moisture from the atmosphere, an approximately 1-gramme sample was formed by a hydraulic press into a tablet. This tablet was re-pressed with boracic acid powder using a force of 7000 kg (15000 lbs). The boracic acid provided an easily-handled solid backing.

A set of 6 samples was chosen as standards. These were kindly analysed by Mr. J.Hutton, CSIRO Division of Soils, Adelaide. The method of analysis of the experimental material standards used at the Waite Agricultural Research Institute was identical with that used at the CSIRO laboratory for the standards. The inclination of the PI crystal was adjusted to give maximum counts when a silica glass was inserted in the X-ray fluorescence spectrometer. Two 10-second counting periods were given for each sample, during which time a total of 2000-4000 counts were accumulated. The counts obtained at the WARI with the 6 standards were very close to being strictly proportional to the silica contents of the same samples as measured at the CSIRO Laboratory. Hence, the average value of the transformation factor (for converting counts per 20 seconds into % silica) was calculated and used with all subsequently counted samples.

The bulk of the samples was then counted, in lots of three at a time. To remove the effects of day-to-day fluctuations of power supply etc, the counts of all samples were adjusted by a factor so that the counts of a fourth sample, a standard, always had the same value. The application of the transformation factor gave the % silica in each sample.

6.2.3 Results

The dependence of the silica yield of the shoots on the weight of water calculated to have been transpired from them in the watering experiment, is shown in Fig. 6.6 . The linear regression accounted for 81% of the total variance of silica yield. The relationship was not one of strict proportionality, however, since the intercept of the regression line with the vertical axis was significantly ($P < 0.01$) below the origin. Since the line of the relationship must in fact pass through the origin, the regression was recalculated constraining the line to pass through this point; the curvature was highly significant ($P < 0.01$).

In order to test for differences in this relationship among the three varieties, unconstrained linear and quadratic regressions were calculated (see Fig. 6.7). The slopes of the linear regressions of Selkirk and Summit differed significantly ($P < 0.05$); the line of Pitic intercepted the vertical axis at a point significantly ($P < 0.05$) below the origin, and the curvature of the quadratic regression of Selkirk, although not significant, appeared to be appreciable.

Fig. 6.6 Relationship between the yield of silica (SiO_2) in the shoots at harvest and the weight of water transpired from them during growth. The results of all harvests (H1, H2 and H3) and varieties are included in the one graph.

Solid line - curvilinear regression constrained to pass through the origin.

Broken line - linear unconstrained regression.

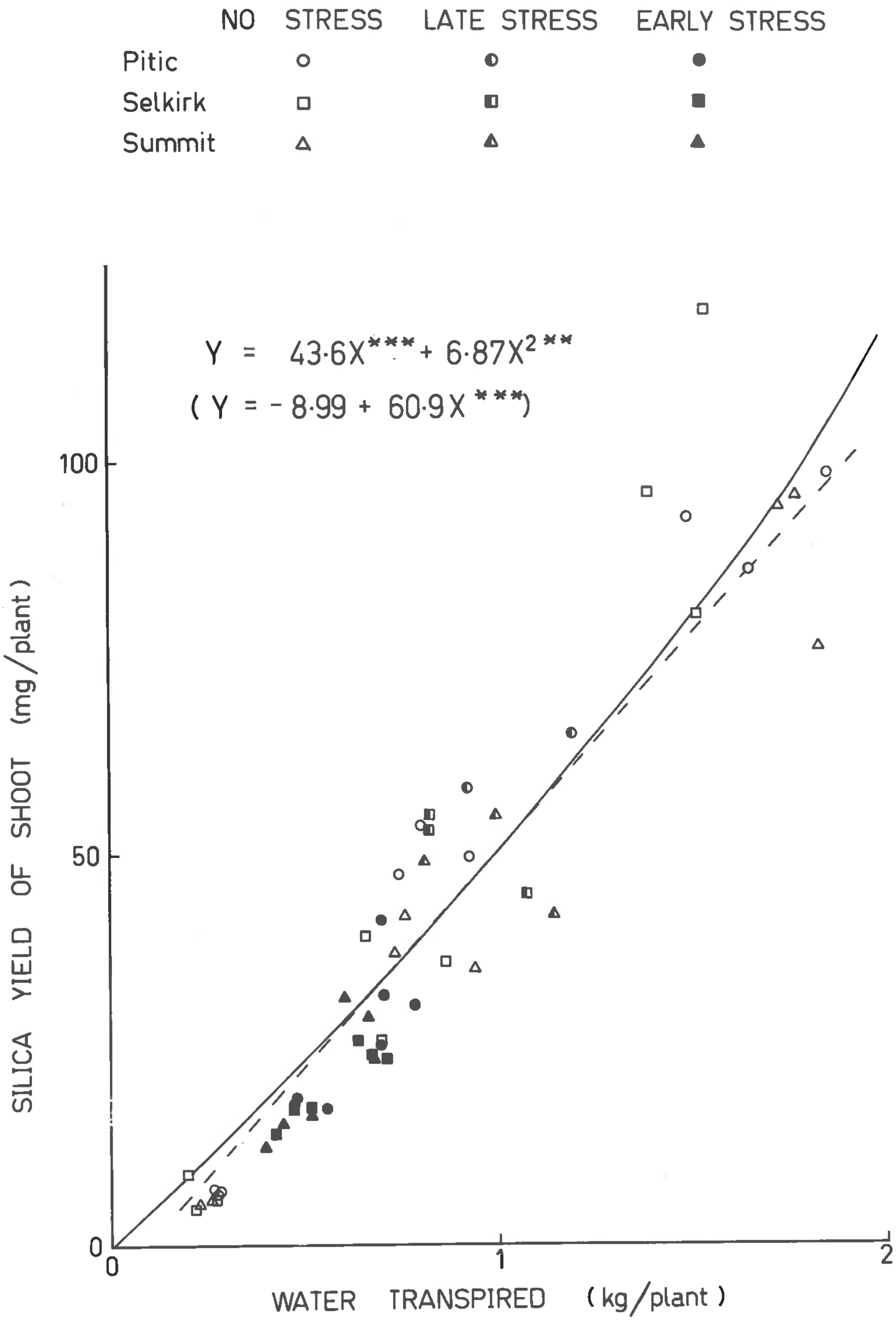
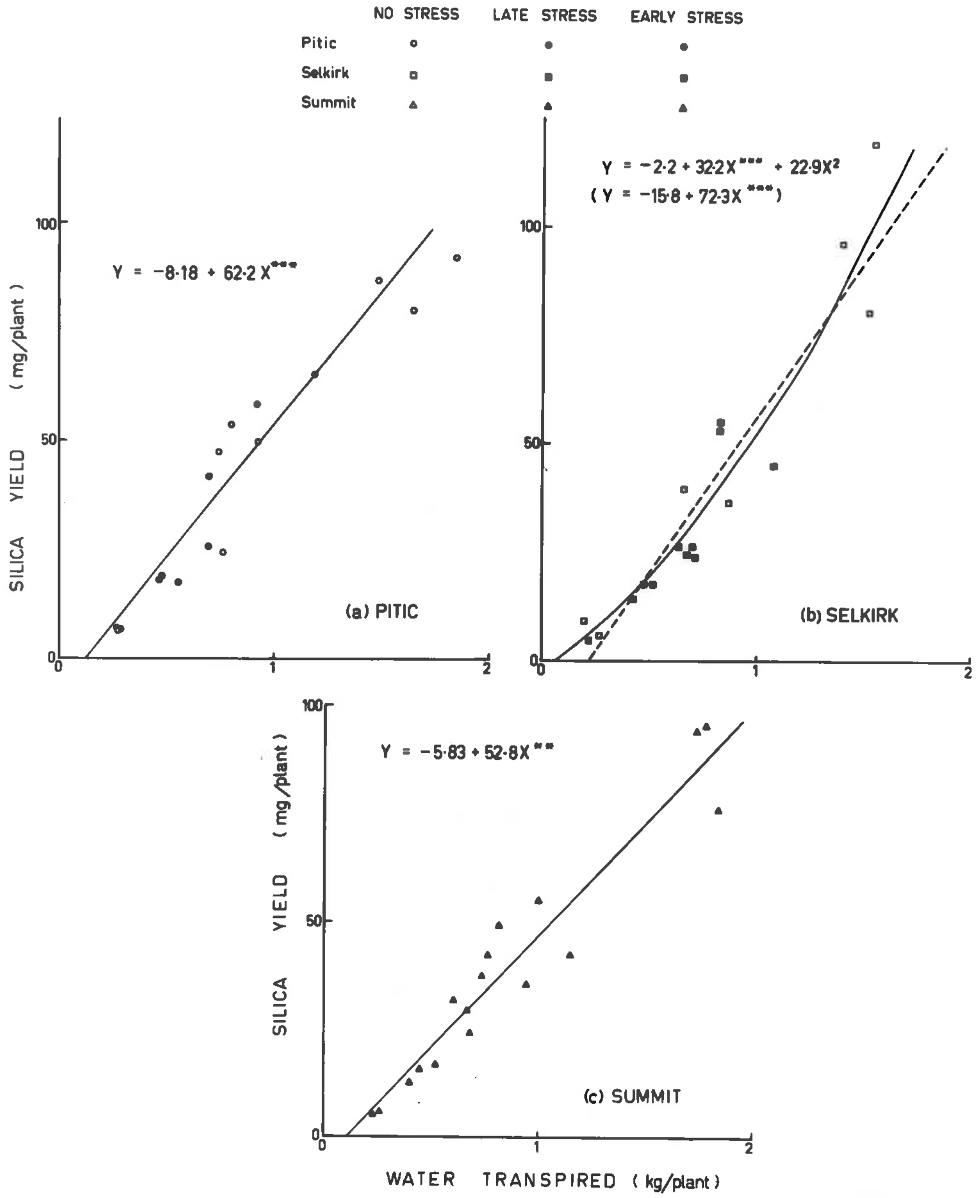

NO STRESS
LATE STRESS
EARLY STRESS
Pitic ○ ◐ ●
Selkirk □ ◧ ■
Summit △ ◭ ▲
Y = 43·6X*** + 6·87X²**
(Y = - 8·99 + 60·9X***)
SILICA YIELD OF SHOOT (mg/plant)
100
50
0
0
1
2
WATER TRANSPIRED (kg/plant)

Fig. 6.7 Relationships between the yield of silica (SiO_2) in the shoots of the three varieties at harvest and the weight of water transpired from them during growth. The results of all harvests are included on each graph. The solid regression lines are those used to convert silica yields in the soil bench experiment into estimates of water transpired. The silica yields of two pots (one of Pitic and the other of Summit) were lost and so the points of only 2 replicates are shown in these cases.

(a) Pitic

(b) Selkirk. The linear regression is shown as a broken line; the equation for it is given in brackets.

(c) Summit


NO STRESS
LATE STRESS
EARLY STRESS
Pitic
Selkirk
Summit
Y = −8·18 + 62·2 X***
(a) PITIC
Y = −2·2 + 32·2X*** + 22·9X²
(Y = −15·8 + 72·3X***)
(b) SELKIRK
Y = −5·83 + 52·8X**
(c) SUMMIT
SILICA YIELD (mg/plant)
WATER TRANSPIRED (kg/plant)
0
50
100
0
1
2

The original intention had been to use a single multiplier factor to transform values of silica yield into estimates of transpiration, but in view of the significant differences among the regression lines, it was considered preferable to apply to each variety its own observed regression line as a type of calibration curve. To achieve a better fit of the points, the quadratic curve rather than the linear relationship was used in the case of Selkirk. The three solid lines shown in Fig.6.7 were thus used as calibration curves, characteristic of the soil and the varieties, with which to estimate the weight of water transpired from the soil bench material. It is noted, in passing, that the apparent concentration of silica in the water taken up by the plants from this loam-sand mixture was 40-60 ppm; this value is well within the observed range of silica content of soil water given by Jones & Handreck (1967) but is somewhat above the common range of 30-40 ppm.

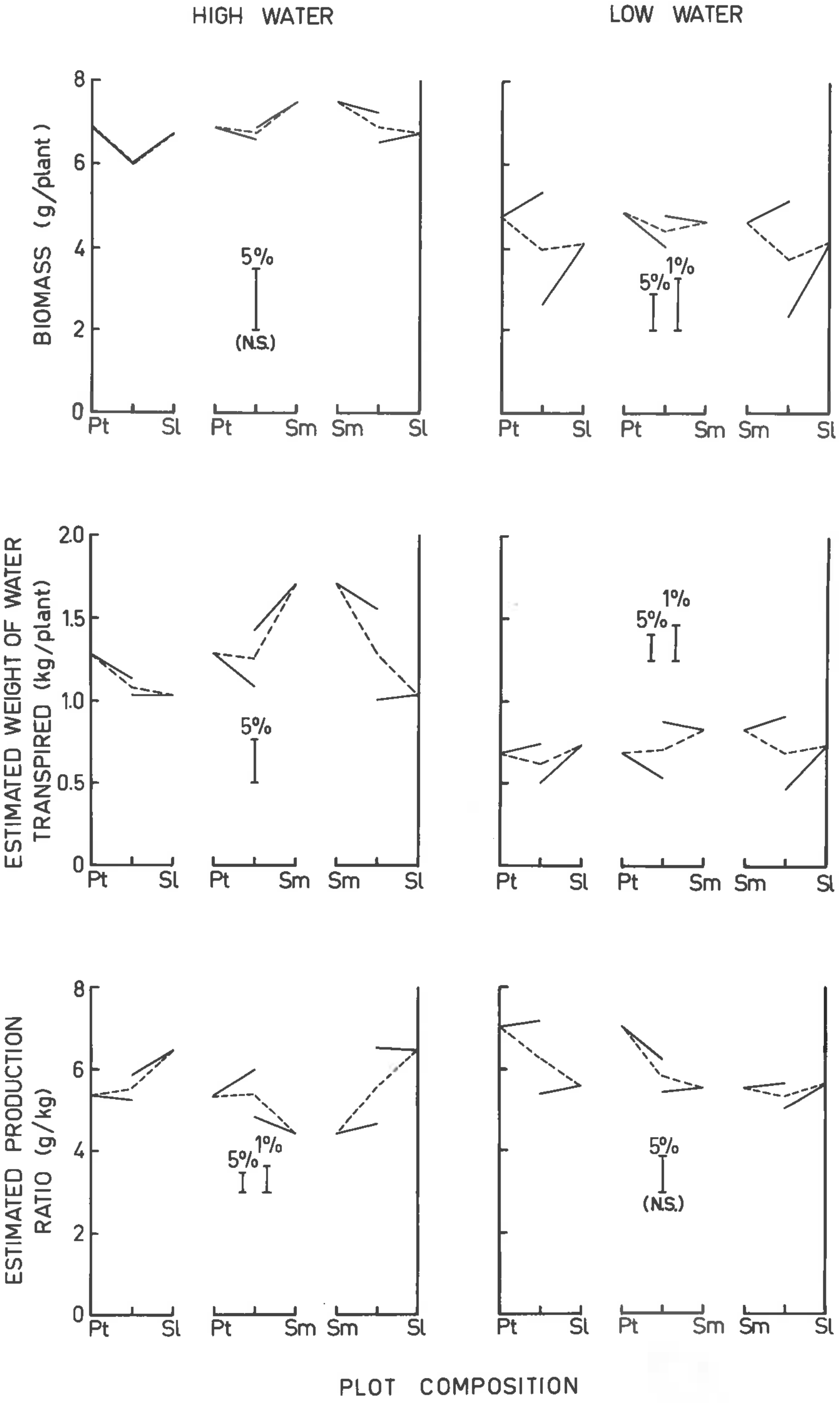
The values of silica yield obtained from the soil bench material were converted to estimated transpiration (transpiratory loss which occurred from the plants throughout growth until harvest) by the use of the calibration curves of Fig.6.7. The results of biomass (shoot weight) obtained from the two soil benches are given in Fig. 6.8, along with the estimated water uptake (= estimated transpiration) and an estimated PR (= Biomass/estimated transpiration). Biomass appears, then, together with its two multiplicative components. It can be seen in Fig. 6.8 that in the high-water bench, differences of PR and water uptake were usually in opposite directions. The cancelling-out of quite large differences resulted in observed biomasses being all relatively similar. In the low-water bench, this tendency was almost absent. Lower water uptake in a mixture was always accompanied by a lower PR. The PR of Pitic was markedly lower in Pitic's mixture with Summit than in its own monoculture, but the difference was not quite significant at the 5% level.

Fig. 6.8 Biomass results of the soil bench experiment with estimates of their multiplicative components: weight of water transpired and production ratio. Production ratio is given in units of g shoot weight (biomass)/kg water transpired.

(a) Biomass

(b) Estimated weight of water transpired

(c) Estimated Production Ratio


HIGH WATER
LOW WATER
BIOMASS (g/plant)
8
6
4
2
0
5%
(N.S.)
5%
1%
Pt
Sl
Pt
Sm
Sm
Sl
Pt
Sl
Pt
Sm
Sm
Sl
ESTIMATED WEIGHT OF WATER TRANSPIRED (kg/plant)
2.0
1.5
1.0
0.5
0
5%
5%
1%
Pt
Sl
Pt
Sm
Sm
Sl
Pt
Sl
Pt
Sm
Sm
Sl
ESTIMATED PRODUCTION RATIO (g/kg)
8
6
4
2
0
5%
1%
5%
(N.S.)
Pt
Sl
Pt
Sm
Sm
Sl
Pt
Sl
Pt
Sm
Sm
Sl
PLOT COMPOSITION

To make graphs comparable with the results of the watering experiment (Fig. 6.2), the biomass of all experimental units of the two soil benches were plotted, by varieties, against estimated transpiration in Fig. 6.9. Regression lines were fitted to the points on each graph, treating the low- and high-water benches separately. In Fig. 6.9, regression lines constrained to pass through the origin are shown as broken lines and unconstrained regressions are shown as solid lines. In none of the 6 groups of points considered (3 varieties x 2 benches) did the slopes of the constrained and unconstrained regression lines differ significantly. However, in the cases of Pitic and Summit, the constrained lines of the low water bench were significantly ($P < 0.01$) steeper than those of the high water bench. The situation was reversed in Selkirk, the difference being significant at the 5% level.

The constrained regression lines have a slope which is equivalent to an average PR. The differences in slope indicate a strong interaction between the effects of varieties and benches: Pitic and Summit apparently used water more efficiently in the production of biomass in the low-water bench than they did in the high-water bench; in Selkirk, however, the reverse was true. Since the difference between the water regimes was confounded with other differences between the benches (notably the transparent cover over the low water bench), the effects on average PR were not necessarily attributable wholly to the watering treatments.

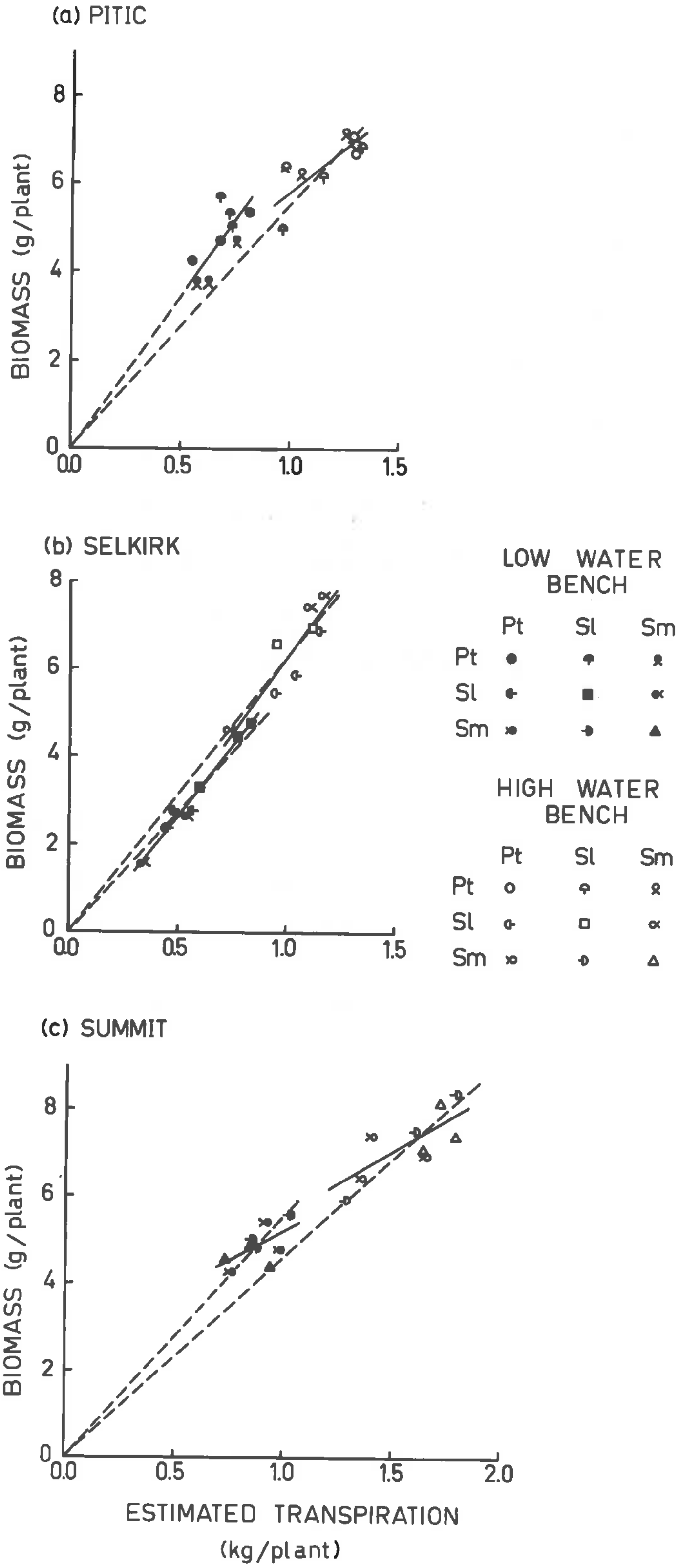
When, as in Section 6.1.3, analysis of variance is used to compare the estimated PRs of the varieties within the same treatment, in the low-water bench the average value of Pitic (6.88 g/kg) was significantly ($P < 0.001$) higher than those of Selkirk and Summit (5.34 g/kg and 5.58 g/kg respectively). This parallels a similar result obtained in pot culture (see Fig. 6.2). In the high water treatment, however, the

Fig. 6.9 Relationship between biomass of monocultures and mixture components of the three varieties in the soil bench experiment and corresponding estimates of transpiration. For each variety, the calculated regression within each soil bench is given separately as a solid line; the regressions constrained to pass through the origin are shown as broken lines.

(a) Pitic

(b) Selkirk. One monoculture plot in the high-water bench was ignored because it had lodged.

(c) Summit


(a) PITIC
(b) SELKIRK
(c) SUMMIT
BIOMASS (g/plant)
0
2
4
6
8
0.0
0.5
1.0
1.5
2.0
ESTIMATED TRANSPIRATION (kg/plant)
LOW WATER BENCH
HIGH WATER BENCH
Pt
Sl
Sm

ranking in descending order of PR was:

Selkirk (6.25 g/kg), Pitic (5.56 g/kg), Summit (4.64 g/kg); again, significant differences ($P < 0.001$) separated all varieties.

Considering the fit of the various types of points to the regression lines of Fig. 6.9, neither the points of particular mixtures nor the points of the monocultures seem to show any signs of systematic deviation from the lines appropriate to the variety and treatment.

6.2.4 Discussion

Since both the literature (e.g. de Wit 1958) and the results of the watering experiment (Fig. 6.2) indicate that the biomass of wheat is usually strictly proportional to the transpiratory loss, and since also the slopes of the constrained und unconstrained regression lines do not differ significantly within any variety and water treatment, the broken lines of Fig. 6.9 which pass through the origin would seem more appropriate to use in the present context than the solid, unconstrained lines. Although an elucidation of the results of the low-water bench is the aim of this Section, it was originally thought that the biomass-transpiration data from the high water bench should be included since they would provide information on the 'upper' end of the biomass-transpiration relationships. While the high water points appear to do this in the graph of Selkirk (Fig. 6.9b), the high water points of Pitic and Summit suggest either a strong curvature in the relationship (the curve must pass through the origin) or that the points of the two benches lie on different lines. In view of the strong evidence in favour of linearity, and considering that the higher PR of two of the varieties, when in the low water bench, accords with what would be expected in the presence of a roof which intercepted about 20% of the radiation (see Fig. 2.1), it seems that the points of the high and the low water treatments should be treated as belonging to separate regression lines. In this case, the data of the high-water treatment are not relevant to the purpose of this Section and are not considered further.

The fit of the points of the low-water treatment to the broken lines of Fig. 6.9 is reasonably good especially in the case of Selkirk which is the variety showing the greatest variation of estimated transpiration. The lack of any systematic deviations of particular mixtures or monocultures from the general regression lines shows that each variety responded to the quantity of water it took up in the same way in both monoculture and mixture. The low-water bench therefore provides what was termed in Section 3.1 a one-factor situation. In this low-water regime, growth depended only on the uptake of a single factor, water, and the changes of the levels of other factors, as experienced by plants of the three genotypes in the various mixtures, were not sufficient to alter the efficiency with which it was utilized. The efficiency of utilization of water in the production of biomass was about the same in mixtures as it was in monocultures.

The finding that the efficiency of utilization of water was nearly constant for a variety, whether it was in mixture or in monoculture, permits the rejection of Hypothesis 2 and allows a final choice to be made between the two remaining hypotheses concerning the underyielding of Selkirk's mixtures in the low-water soil bench (see Section 6.1.1 and 6.1.4). In terms of the biomass:transpiration graphs used in Fig.5.10 (and elsewhere), Hypothesis 1 requires that the points representing the yields of any one variety in mixture and in monoculture should lie on the same straight line drawn through the origin. Hypothesis 3, on the other hand proposes that the points of a variety's performance in mixture will not lie on a straight line drawn from the monoculture to the origin.

Since yields produced with the same efficiency of water utilization must lie on the same line through the origin, Hypothesis 1 is seen to apply in both of Selkirk's mixtures. Considering only these mixtures, Fig. 6.10 shows that, compared with monoculture values, the suppressed Selkirk suffered reductions of water uptake which were greater than the corresponding gains in uptake by the aggressors. Consequently, in each mixture the mean water uptake per plant (averaged over both components) was less than the water uptake of either of the corresponding monocultures.

In Fig. 6.10 the monoculture response of each variety has been approximated by a straight line joining the origin with the single monoculture point; this latter point represents the average biomass of three replicate plots in the low-water bench. Under the graphs are the calculated values of the various parameters introduced and discussed in Section 3.1. The meaning of these will be briefly recapitulated. F_{ij} in the present context (e.g. F_{12}) is the proportional increase of water uptake of genotype i in mixture with genotype j, compared with the uptake in the monoculture of genotype i. The relative efficiency of water utilization, e_{ij}, is the ratio: PR of genotype i in mixture with genotype j/PR of the monoculture of genotype i. The Relative Yield Total, RYT_{ij}, is given by the expression

$$RYT_{ij} = \left(\frac{Y_{ij}}{Y_{ii}} + \frac{Y_{ji}}{Y_{jj}}\right)/2$$

where Y_{ij} is the biomass (g/plant) of genotype i in mixture with genotype j, and Y_{ii} is the biomass (g/plant) in the monoculture of genotype i. The values of biomass, estimated

Fig. 6.10 Graphical interpretation of water uptakes and biomass yields of monocultures and mixture components in the low-water soil bench. The form of the graphs corresponds to that used in the theoretical graphs of Figs. 3.1 to 3.4. The coordinates of each point are avraged values of biomass and estimated water uptake (transpiration) of 3 plots. Straight lines estimating the monoculture responses to water uptake have been drawn from the origins to the monoculture points.

The values of the parameters introduced in Section 3.1 are given for each mixture. (Note: the order of the lists of parameters does not correspond to the order of the graphs). The units of Production Ratio (PR) are g biomass/kg water transpired.

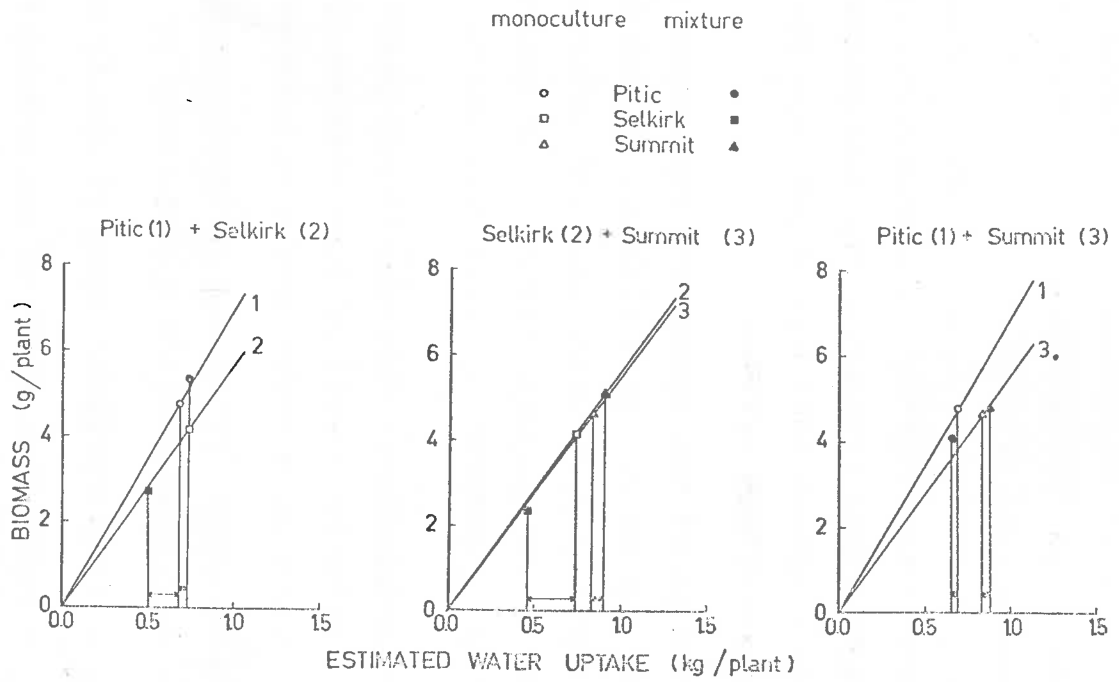
F_{ij} - proportional increase in per-plant uptake of water by plants of i in mixture with j, compared with their uptake in monoculture.

e_{ij} - relative efficiency of utilization of water by plants of i in mixture with j.

RYT_{ij} - Relative Yield Total of the ij mixture.

PR_{ii} - Production Ratio of the monoculture of genotype i.

PR_{ij} - Overall Production Ratio of the ij mixture; it is the ratio: average per-plant biomass in the mixture/average per-plant water uptake in the mixture.



F_{12} = 0.085
F_{21} = 0.327
e_{12} = 1.037
e_{21} = 0.956
RYT_{12} = 0.884
PR_{11} = 7.04
PR_{22} = 5.64
PR_{12} = 6.53

F_{13} = 0.040
F_{31} = 0.056
e_{13} = 0.886
e_{31} = 0.982
RYT_{13} = 0.944
PR_{11} = 7.04
PR_{33} = 5.54
PR_{13} = 5.78

F_{23} = 0.368
F_{32} = 0.086
e_{23} = 0.895
e_{32} = 1.018
RYT_{23} = 0.836
PR_{22} = 5.64
PR_{33} = 5.54
PR_{23} = 5.44

transpiration and PR from which the various values given in Fig. 6.10 were calculated are given in the Appendix, Section 11.7.

In Section 3.1.2.1, a method of partitioning the RYT values of mixtures was described which produced four meaningful components. These components were given by

$$RYT_{ij} = 1 + \frac{F_{ij} + F_{ji}}{2} + \frac{(e_{ij} - 1) + (e_{ji} - 1)}{2} + \frac{F_{ij}(e_{ij} - 1) + F_{ji}(e_{ji} - 1)}{2}$$

$$= 1 + F\ \text{term} + e\ \text{term} + F.e\ \text{term}$$

Reinterpreting the terms in the present context, the F term represents the deviation of the RYT from unity due to a tendency towards a gain or a loss of water taken up by the mixture compared with the uptake by the monocultures *. The e term represents that part of the deviation of RYT due to a tendency

---

*In the ideal case, the water uptakes of both monocultures are identical; a positive or negative F term then indicates that the mixture's water uptake is respectively either greater or less than that of the monocultures. Such uptakes would be analogous to over- and under-yielding of biomass. As monoculture water uptakes differ more, so the value of the F term must be more strongly positive or negative for it to indicate an uptake that is either greater than that in the monoculture with the higher uptake, or lower than that in the monoculture with the lower uptake. The situation is parallel to that described in Section 3.1.3 where it was explained that as Y_{ii}/Y_{jj} increases, a larger deviation of RYT value is required before a mixture yields transgressively. Similar considerations apply to the F and the e term; these terms measure tendencies towards transgressive behaviour in overall uptake and efficiency of utilization in the same way that RYT measured the tendency towards transgressive yielding of biomass.

towards a gain or loss of overall PR by the mixture as compared with the monocultures. The F.e term represents the overall effect on the RYT value of interactions between the F and e terms, as they affect the individual components.

The values of the four components of RYT are given in Table 6.5. Considering again only the two Selkirk mixtures, the signs of the terms which determine RYT show the same pattern but the absolute values are greater in the case of Selkirk+ Summit. The much larger e term of this mixture is due to the more marked reduction of the PR of Selkirk when mixed with Summit than when mixed with Pitic (see Fig. 6.8). However, the low RYTs of both Selkirk mixtures can be clearly traced to the low F term.

To conclude this Section, possible physiological reasons can be considered for the underyielding observed in the Selkirk mixtures in the low water-treatment of the bench experiment. The information on water uptake is consistent with the suggestions of Section 6.1.4 concerning events in these mixtures. If a combination of Selkirk's superficial root system, the drying out of the soil surface by evaporation and the shading of Selkirk's leaves by the associate varieties were the main causes of its rapid suppression, then it does not have to be concluded that the root systems of the apparently aggressive Pitic and Summit were particularly vigorous; it has indeed often been shown that root activity declines markedly at about ear emergence in cereals (Troughton 1962, Friend 1966, Welbank & Williams 1968).

All this evidence indicates therefore that at this stage of growth the aggressors were not able to expand their root systems and hence their water-uptake sufficiently to take advantage of the available soil-water left untapped through Selkirk's premature cessation of growth.

Table 6.5 Values of the four additive components of RYT for the three mixtures in the low-water treatment of the soil bench experiment. To emphasize the similarity between the two Selkirk mixtures, the conventional order of the mixtures has been changed.

Mixture	unity	F term	e term	F.e term	RYT
Pitic+Selkirk	1.000	−0.121	−0.004	+0.009	= 0.884
Selkirk+ Summit	1.000	−0.141	−0.043	+0.020	= 0.836
Pitic+Summit	1.000	+0.008	−0.066	+0.002	= 0.944

According to Fig. 6.10, the aggressors (Pitic and Summit) appear only to have taken up about one-quarter of the water made available by Selkirk's suppression. In spite of this, the uptakes of the Selkirk mixtures never fell greatly below that of the corresponding monoculture with the lower uptake. Using the data of the Appendix, Section 11.7, it can be calculated that whereas Pitic+Selkirk took up 10.2 cm of water, the Pitic monoculture took up 10.7 cm. Similarly, Selkirk+Summit took up 11.4 cm while the uptake of the Selkirk monoculture was 12.3 cm. The calculated mixture uptakes were therefore 5% in one case and 7% in the other below that of the component monoculture which had the lower uptake. Although neither difference was significant, it can be concluded that in these two mixtures, transgressive yielding was accompanied by parallel, transgressive behaviour in the uptake of water by the mixtures.

The effects leading to the underyielding of the third mixture (Pitic+Summit) in the low-water soil bench have been shown to be relatively small (Fig. 6.10 and Table 6.5). Since they may well be due to experimental error, no attempt is made to explain them in physiological terms. The Pitic+Summit mixture is nevertheless of theoretical interest in that it provides an example of a mixture conforming to Hypothesis 3; it underyielded because of an apparent difference between mixture and monoculture in the efficiency with which water was been used in the production of biomass.

7. Theoretical study of the possibility of overyielding by mixtures grown under conditions of non-limiting soil factors.

7.1 Introduction

One of the mixtures which showed a high RYT in the high density treatment of the 6x6 diallels (Selkirk+Summit, see Table 5.1b) consisted of a tall component with rather erect leaves (Selkirk) and a shorter component with markedly droopy leafes (Summit). Although it was felt that in the dry conditions of the 1967 season, RYTs were unlikely to have been affected by canopy structure, it seemed that in the high-water treatment of the soil bench experiment (1968), canopy structure could have important effects. Observation of the high-water soil bench suggested that Warren Wilson's theoretically favourable canopy structure (Warren Wilson 1960, Duncan et al. 1967) of erect leaves at the top of the canopy and more horizontal leaves in lower layers was achieved in the Selkirk+Summit mixture at a time when the LAI exceeded 4 (see Plate 5.1b and Section 2.2.4). It was therefore thought that the RYT of this mixture might, on harvesting, be found to be greater than unity.

Harvest data showed in fact that the RYT of the Selkirk+Summit mixture was less than unity. Actual measurements of canopy structure (Fig. 5.1) demonstrated that while Selkirk's foliage was more erect than that of Summit before stem extension (Day 62), after ear emergence (Day 106) the situation had been reversed. The photograph of Plate 5.1b suggests that by Day 86 the foliage of Summit was already hardly less erect than that of Selkirk. At the time when growth was likely to be proceeding fastest (at about ear emergence, Friend 1966), the mixture's canopy structure probably lacked the 'Warren Wilson configuration' originally thought to be present.

The results of the simulations using measured canopy structures (Fig. 5.8) seem able to explain why the biomass RYT of the Selkirk and Summit mixture did not significantly exceed unity; at neither measurement occasion did the combination of solar elevation and canopy structure provide any basis for believing that the mixture was achieving any advantage in gross photosynthesis.

On the other hand, the results of Fig. 5.8 suggest that another mixture (Pitic and Summit) had a favourable canopy structure at T2; the RYT based on daily gross photosynthesis was nearly 1.1. This apparently favourable canopy structure did not however cause the predicted gross P rate of the mixture to be higher than that of either monoculture because the difference between the monoculture rates was too great. The complexity of a real DIPA table (Fig. 5.1) makes it difficult to trace the reason for this high RYT, but it is possible that the abundant tall stems and ears of Pitic allowed the mixture as a whole to approximate the 'Warren Wilson configuration' more closely than either monoculture.

Since the possibility of high RYTs had been shown by this example to exist, a study was undertaken, using simplified DIPA tables and the programme DAYP (see Section 5.2.2), to investigate the conditions under which overyielding might occur in mixtures grown with non-limiting soil conditions.

7.2 Simulations using the programme DAYP.

In order to compare the results produced by DAYP with those of the programmes used by Duncan et al. (1967) and Ross & Bichele (1969), Fig. 7.1 was drawn. The results of DAYP concern the predicted daily gross photosynthesis of two types of canopy differing in leaf inclination ($\alpha = 15^o$ and 75^o), as affected by sky condition and LAI. According to Fig. 7.1a, DAYP predicts that in canopies with an LAI greater than 3, there is an advantage for an erect-leaved canopy under sunny conditions; simulations using both other models (Fig. 7.1b & c) have already led to this conclusion although the authors of the published models used somewhat different parameter values.

If the density of the clouds on an overcast day is such that the irradiance of an horizontal surface is 20% of that under a cloudless sky with full sunlight, DAYP predicts that daily photosynthesis under the overcast sky is about half of what it is with sunny conditions. This agrees with the conclusions of de Wit (1965) using an overcast sky of this same density. If a level of diffused light can be produced which gives the same irradiance of a horizontal surface as is found on a sunny day, Fig. 7.1a (the curve marked '100%') predicts production rates 25% higher than found under natural sunlight. This agrees with and extends predictions of Ross & Bichele (1969) which were made using a fixed sun elevation.

The results of the simulations using DAYP will be presented in the following order:

a) a study of the predicted photosynthetic advantage of mixtures of components differing in leaf inclination;

b) a short series of simulations to show the effect on mixture performance of the inclusion of stem area;

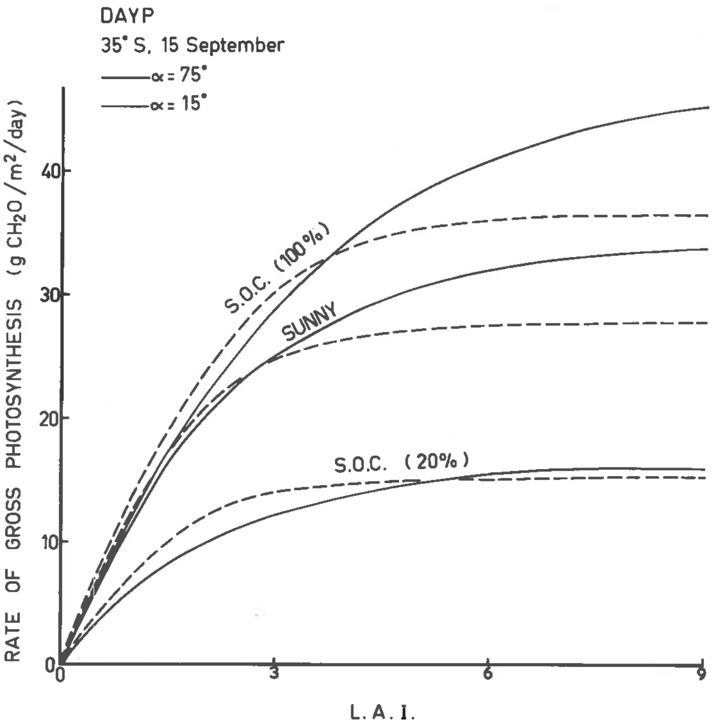
c) another short series of simulations to estimate the effect on mixture performance of the degree of overlap of contrasting canopies within a mixture;

Fig. 7.1 Predicted rates of photosynthesis according to the programme DAYP for comparison with analogous predictions given by Ross & Bichele (1969) and Duncan et al. (1967). In each graph the predicted photosynthesis rates are given for two canopies contrasting strongly in leaf inclination (α), at a range of LAI values. The environmental conditions are specified on the graphs.

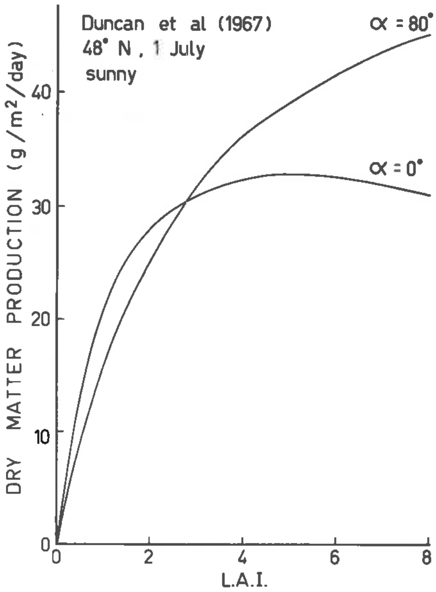
(a) DAYP Besides the curves of gross P for sunny conditions, curves are given for two types of Standard Overcast Sky (S.O.C) differing in the level of radiation which arrives at the crop surface. In the S.O.C. curves marked 100%, the irradiance of an unshaded horizontal sensor is equal to that experienced under equivalent sunny conditions; this condition could only be achieved artificially. For the S.O.C. curves marked 20%, the irradiance of the sensor is only one fifth of the value found under equivalent sunny conditions; this approximates the normal field situation under an overcast sky. The values of the leaf photosynthesis parameters are P_{max} 18 mg $(CH_2O)/dm^2/hr$ and K_m 0.05 $cal/cm^2/min$.

(b) Duncan et al. (1967). These authors' graph showed dry matter production rather than gross P.

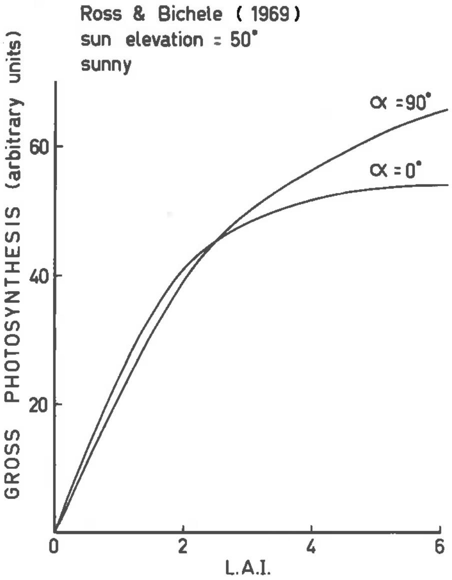
(c) Ross & Bichele (1969). The gross photosynthesis is given in arbitrary units since the Figure in the original publication is unclear on this point.


DAYP
35° S, 15 September
α = 75°
α = 15°
RATE OF GROSS PHOTOSYNTHESIS (g CH2O / m2 / day)
S.O.C. (100 %)
SUNNY
S.O.C. (20 %)
0
10
20
30
40
0
3
6
9
L. A. I.

(b)


Duncan et al (1967)
48° N , 1 July
sunny
α = 80°
α = 0°
DRY MATTER PRODUCTION (g / m2 / day)
0
10
20
30
40
0
2
4
6
8
L.A.I.

(c)


Ross & Bichele (1969)
sun elevation = 50°
sunny
α = 90°
α = 0°
GROSS PHOTOSYNTHESIS (arbitrary units)
20
40
60
0
2
4
6
L.A.I.

d) a study of predicted photosynthesis in mixtures composed of types differing in their leaf P:I curves.

7.2.1 Mixtures of genotypes differing in leaf inclination.

A community composed of a tall wheat variety with erect leaves mixed with a short variety with almost horizontal leaves would have a canopy structure approximating the ideal 'Warren Wilson configuration' (see Section 7.1). At very low LAIs, a monoculture of the variety with near-horizontal leaves might intercept more light and hence grow faster than either the mixture or the other monoculture. At high LAIs, radiation might penetrate deepest into the canopy of a monoculture of the erect-leaved variety which might therefore grow the fastest. However, at intermediate LAIs, the mixture might have an advantage over both monocultures because the mixture would combine the favourable characteristics of both monocultures. The theoretical validity of this argument was tested using DAYP.

Two genotypes with contrasting leaf inclinations were represented by canopies with leaves set at 75° (erect-leaved) and 15° (prostrate-leaved). In mixture, each component was given a canopy consisting of half the LAI present in the corresponding monoculture. All the erect-leaved canopy was taken to be above the canopy of the prostrate-leaved genotype. For this series of simulations, an equal area of foliage was assumed for each layer * and sufficient layers were used to ensure that the LAI in each layer never exceeded 1.5 units. The leaf gross

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* Tests with DAYP had shown that gross photosynthesis was only very slightly affected by the form of the LAI profile in monoculture. The values of the predicted gross P of a canopy of LAI 4.5 agreed to within 1.2% when the DIFA was input as (a) 3 layers of LAI 1.5, (b) 3 layers containing a sequence of 1.2, 2.1 and 1.2 LAI units, and (c) 9 layers of LAI 0.5. Consequently, the use of a rectangular LAI profile in these simulations does not prevent reliable extrapolation to cases with, say, parabolic leaf area profiles.

photosynthesis:irradiance relationship corresponded to that given by de Wit (1966) as 'supposed to hold for a number of common agricultural species'. To approximate this curve (see Fig. 7.4a), the values of the photosynthesis parameters P_{max} and K_m were taken to be 18 mg $(CH_2O)/dm^2/hour$ (26.4 mg $CO_2/dm^2/hour$) and 0.05 $cal/cm^2/min$ respectively. The predicted gross P rates of these 'leaf-inclination mixtures' and the values of the corresponding monocultures at various LAIs are given in Fig. 7.2 for four differing light regimes. The range of LAI over which an advantage for the mixture is theoretically expected is shown on each graph and it appears that the somewhat intuitive argument advanced above is correct in the cases of 'latitude 0°, spring/autumn equinox, sunny' and 'latitude 35°, midsummer, sunny' (Fig. 7.2a & b). As LAI increases, first the prostrate-leaved monoculture is superior, then the mixture and finally the erect-leaved monoculture. At latitude 35°, with overcast sky in midsummer (Fig. 7.2d), the superiority of erect leaves over the other two types of stand does not appear within the range of LAI used but the general pattern is similar to that in the first two cases. With the conditions 'latitude 35°, midwinter, sunny' (Fig. 7.2c), the prostrate-leaved monoculture is predicted to be superior or at all LAIs within the range studied.

This first series of simulations shows that differences of leaf inclination can lead theoretically to a mixture advantage in gross photosynthesis in certain light regimes. Out of four contrasting light regimes, three showed a theoretical mixture advantage over a range of LAI from about 2 to 7 or above. The advantage over the monoculture with the higher rate of photosynthesis reached maxima of about 6% in Figs. 7.2a, b & d. It must however be emphasised that a stemless canopy of leaves without overlap between the layers of the canopy occupied by the two leaf-inclination types is far

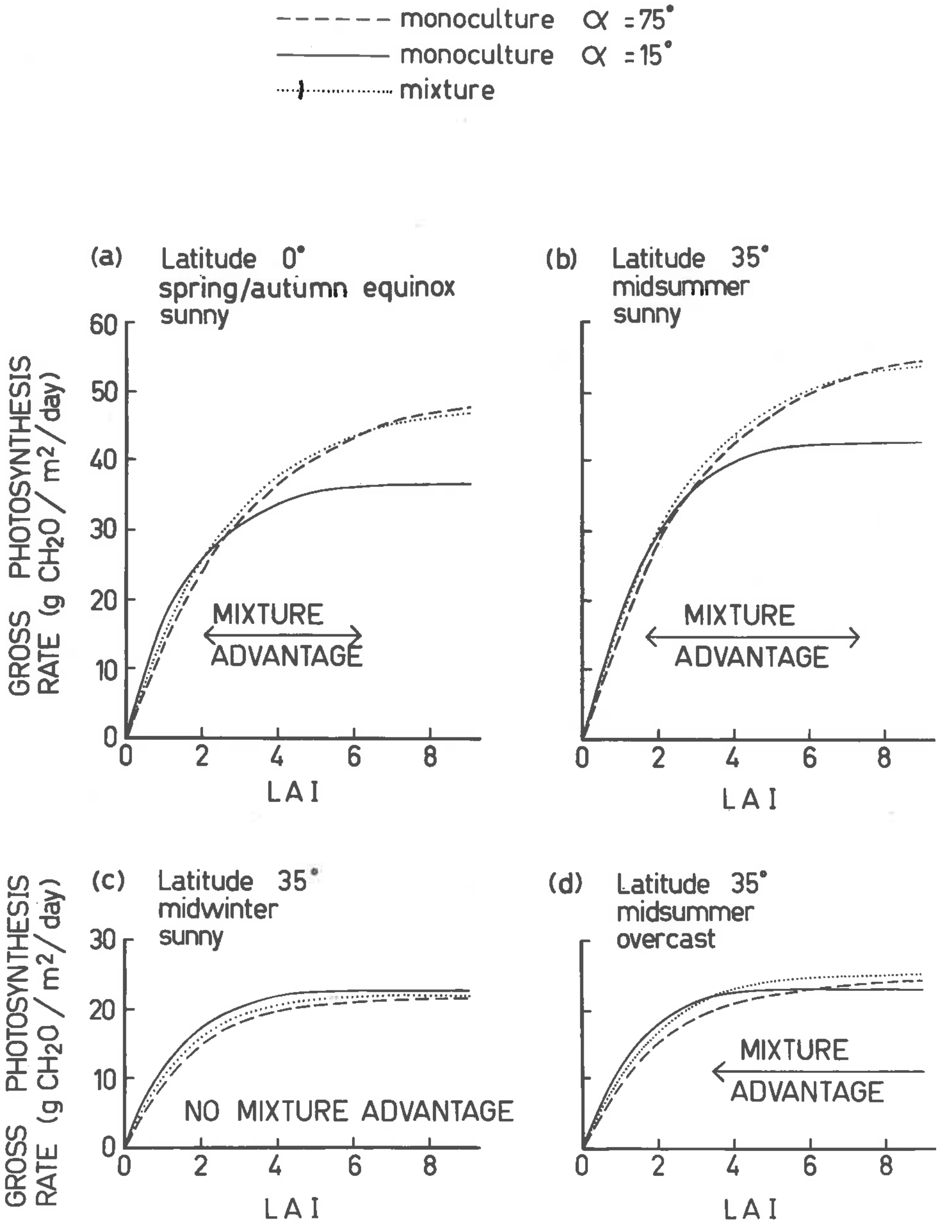
Fig. 7.2 Rates of gross photosynthesis predicted by the programme DAYP for canopies of monocultures and mixtures of genotypes with contrasting leaf inclinations. The mixtures are composed of equal leaf areas of the two types of canopy, with the 75°-foliage above the 15°-foliage. Stem area is not included and there is no overlap of canopies. The range of leaf area index over which the mixture is expected to have a photosynthetic advantage relative to both monocultures is indicated on each graph.

(a) Latitude 0°, spring or autumn equinox, sunny conditio

(b) Latitude 35°, mid-summer, sunny conditions.

(c) Latitude 35°, mid-winter, sunny conditions.

(d) Latitude 35°, mid-summer, overcast sky.


monoculture α = 75°
monoculture α = 15°
mixture
(a) Latitude 0° spring/autumn equinox sunny
(b) Latitude 35° midsummer sunny
(c) Latitude 35° midwinter sunny
(d) Latitude 35° midsummer overcast
GROSS PHOTOSYNTHESIS RATE (g CH2O / m2 / day)
LAI
0
10
20
30
40
50
60
2
4
6
8
MIXTURE ADVANTAGE
NO MIXTURE ADVANTAGE

from the actual situation in mixed cultures of wheat varieties.

7.2.2 The effect of including stem area in simulations

Taking the canopies and conditions used to produce the results for LAI 3 shown in Fig. 7.2a, two types of stem area were added to the canopies for the purpose of further simulations. The two types of stem area corresponded approximately to the distributions of Stem Area Index (SAI) given in Fig. 5.1 for T1 (Day 62) and T2 (Day 106) in the high-water soil bench. To achieve the rather unrealistic situation of non-overlapping canopies, some distortion of the original data was inevitable. The ratio SAI/LAI for the T1 simulation was 0.5/3.0 and for the T2 simulation it was 3.0/3.0. The tables of the hypothetical Distributions of Inclination of Photosynthetic Area are given in Table 7.1. The photo - synthetic activity of stem area was taken to be equal to that of the leaves.

The results of the simulation are shown in Table 7.2. The addition of stems decreases the predicted advantage of the mixture over the monoculture with the higher photosynthesis rate; the greater the SAI/LAI ratio (with constant LAI), the greater is this reduction.

Table 7.1 Canopy structures employed in simulations using the programme DAYP to investigate the effect of including stems.

The DIPA tables given below are of the monocultures only and are in LAI or Stem Area Index units. The LAI profiles are approximately parabolic while the vertical distributions of SAI follow those of the canopies of the high-water soil bench at T1 (Day 62) and T2 (Day 106). Mixture canopies were produced by taking the monoculture canopies together after halving all entries in the tables.

(a) No stem

	Short variety, prostrate leaves			Tall variety, erect leaves		
α =	15°	45°	75°	15°	45°	75°
				0	0	0.5
				0	0	1.0
				0	0	1.0
				0	0	0.5
	0.5	0	0	0	0	0.0
	1.0	0	0	0	0	0.0
	1.0	0	0	0	0	0.0
	0.5	0	0	0	0	0.0
Totals	3.0	0	0	0	0	3.0

(b) With stem (as for T1)

	Short variety, prostrate leaves				Tall variety, erect leaves			
α =	15°	45°	75°	90°	15°	45°	75°	90°
					0	0	0.5	0.00
					0	0	1.0	0.04
					0	0	1.0	0.07
	0.5	0	0	0.00	0	0	0.5	0.09
	1.0	0	0	0.05	0	0	0.0	0.10
	1.0	0	0	0.15	0	0	0.0	0.10
	0.5	0	0	0.30	0	0	0.0	0.10
Totals	3.0	0	0	0.50	0	0	3.0	0.50

(continued)

Table 7.1 (continued)

(c) With stem (as for T2)

	Short variety, prostrate leaves				**Tall variety, erect leaves**			
α =	15°	45°	75°	90°	15°	45°	75°	90°
					0	0	0.5	0.60
					0	0	1.0	0.60
					0	0	1.0	0.60
	0.0	0	0	0.60	0	0	0.5	0.60
	0.5	0	0	0.60	0	0	0.0	0.60
	1.0	0	0	0.60	0	0	0.0	0.00
	1.0	0	0	0.60	0	0	0.0	0.00
	0.5	0	0	0.60	0	0	0.0	0.00
Total	3.0	0	0	3.00	0	0	3.0	3.00

Table 7.2 Results of simulations of gross photosynthesis rates (g $CH_2O/m^2/day$) of monocultures and mixtures either ignoring stems, or including stems using a vertical distribution which approximated either that at an early stem-extension phase (T1) or that found after flowering (T2). The DIPA tables used are given in Table 7.1. The conditions are as for Fig. 7.2a.

	No stem	With stem (T1)	With stem (T2)
P rate of prostrate-leaved monoculture ($\alpha = 15^\circ$)	31.07	32.22	41.65
P rate of erect-leaved monoculture ($\alpha = 75^\circ$)	31.28	32.97	41.99
P rate of mixture	32.64	34.39	43.55
Advantage of mixture over monoculture with higher P rate	3.35%	4.31%	3.72%

7.2.3 The effect of increasing the degree of overlap between the contrasting canopies of the components in the 'leaf-inclination mixtures'

In Fig. 7.2a, the mixture advantage seems to be most marked at LAI 2.75. In the present series of simulations, this mixture, the corresponding monocultures and the same set of conditions (latitude 0°, equinox, sunny), were studied using parabolic leaf area profiles subjected to four degrees of overlap. The configuration of the canopies tested and the corresponding results of mixture gross P are shown in Fig. 7.3a. For purposes of comparison, the same set of simulations was repeated using double the leaf area (LAI 5.50, see Fig. 7.3b). It is clear that as the degree of overlap increases, the advantage of the mixture diminishes. At LAI 2.75, monoyulture yields are very similar for each leaf inclination and a mixture advantage persists with greater degree of overlap than at LAI 5.50. At both LAIs, the values of RYT based on a day's photosynthesis show a similar pattern of decline as the degree of overlap increases. According to this series of simulations, mixture advantages in gross photosynthesis due to differences of canopy structure are very sensitive to the degree of overlapping of the canopies. For a mixture advantage to exist, the difference of leaf-inclination must be accompanied by an appropriate difference in the heights and positions of the canopies of the two components.

7.2.4 The theoretical possibility of mixtures showing a photosynthetic advantage over monocultures due to differences of leaf gross P:I curves between the components.

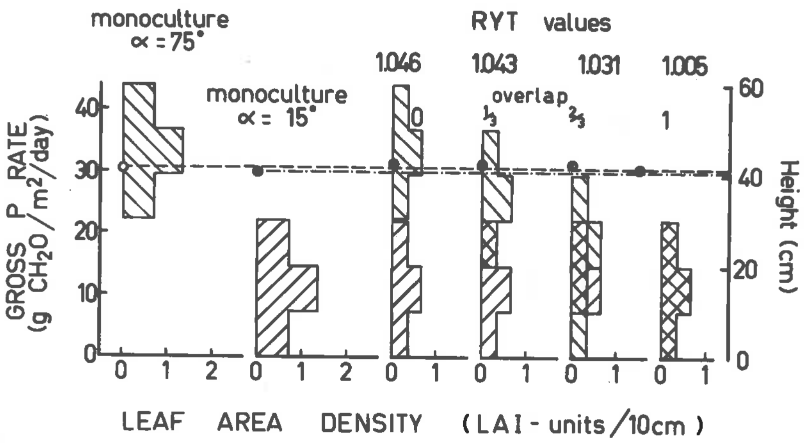
The value of P_{max} of leaves of shade-adapted genotypes has been found to be often much lower than that of sun-adapted

Fig. 7.3 The effect of overlapping of the canopies of the mixture components on the predicted rate of gross photosynthesis in mixtures. Parabolic leaf area density profiles are approximated in each monoculture and mixture component by a 3-layer profile in which the successive layers contain leaf areas in the ratio 1:1.86:1; the the total LAI in each community of the upper series (a) is 2.75, and of the lower series (b) is 5.50. Four degrees of overlap are considered : none (0), involving a third of the depth of each canopy (1/3), involving two-thirds of this (2/3), and involving the whole canopy (1). The P rates in monocultures are shown as open or black-filled circles; the P rates of the mixtures are shown as pied circles whose relationship to the monoculture rates varies with the degree of overlap of the canopy.

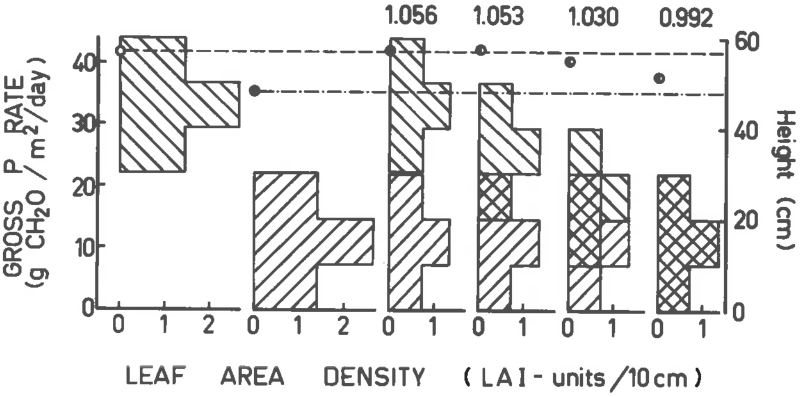
(a) Leaf area index 2.75

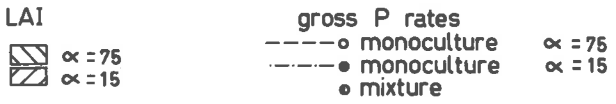
(b) Leaf area index 5.50

(a) LAI = 2.75



(b) LAI = 5.50





forms (e.g. Björkman 1970). The values of K_m usually differ in about the same proportion as those of P_{max} and so the initial slope (P_{max}/K_m) of the gross P:I curve usually does not vary much (Milthorpe 1970). The measurements of net P by Kumura (1968b) however showed that ageing, shade-adapted leaves of soybean occasionally have steeper initial slopes of the net P:I curve than do younger, sun-adapted leaves. This observation suggests the possibility of the same kind of difference existing between two varieties of a crop, rather than only between leaves within the same variety. For simplicity, it is assumed at this stage that these differences in net P:I reflect similar differences in the gross P:I relationship. If two such varieties were grown in mixture, there seems to be a chance that their mixture would overyield. This may be explained as follows: assuming that the sun-form was the taller variety, it would use the bright light at the top of the canopy with maximum efficiency because of its high P_{max}; at the same time, the dim light low in the canopy would be used most efficiently by a specially-adapted shade form with a steeper initial slope of the gross P:I curve but perhaps a lower P_{max}.

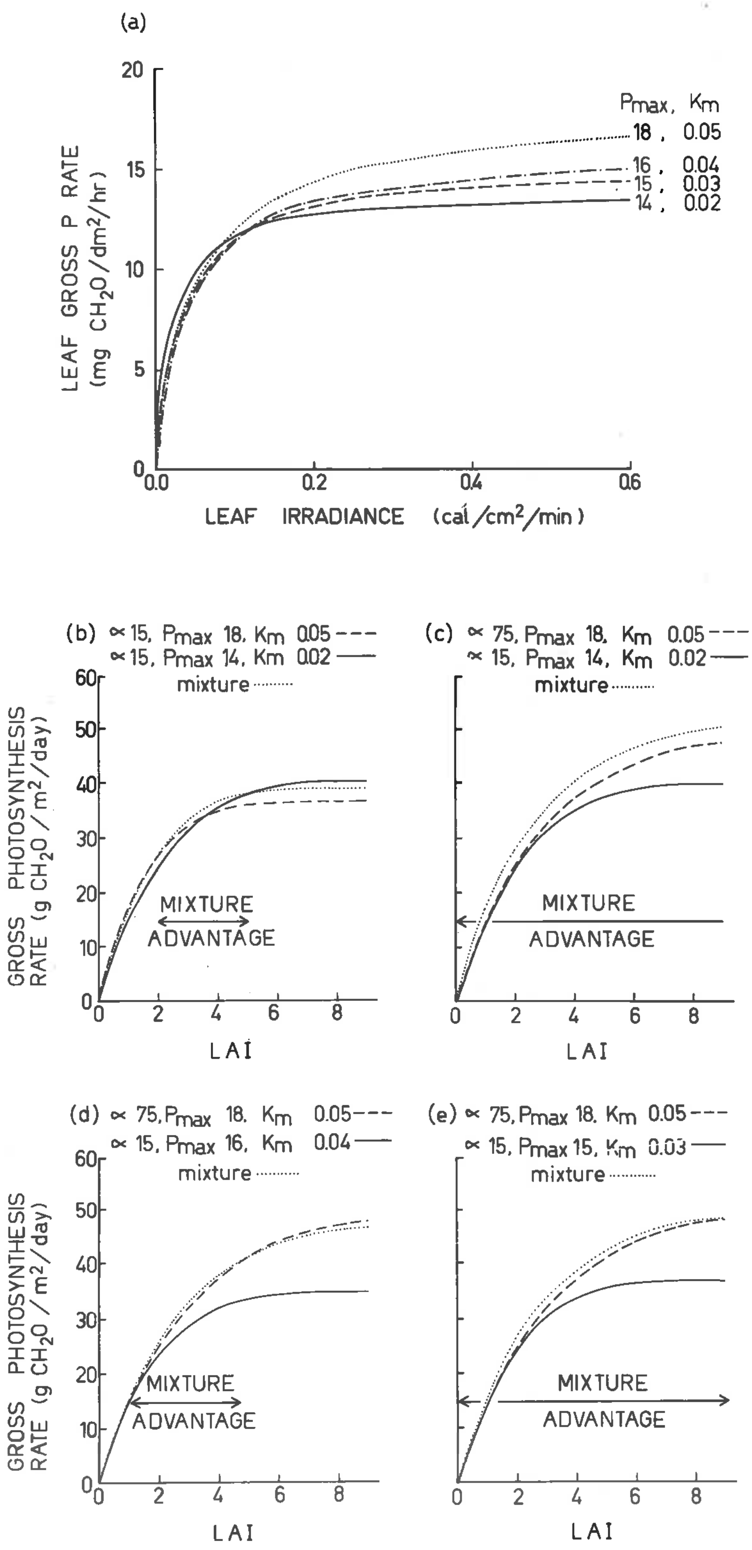
The theoretical foundation of this hypothesis was tested using DAYP. For this series of simulations, the same conditions were used as in Fig. 7.2a and 7.3, i.e. latitude 0°, equinox, and no cloud. Both components of the mixture were given a 15° leaf inclination, but the values of P_{max} and K_m given to the taller component were 18 mg (CH_2O)/dm^2/hour and 0.05 cal/cm^2/min while the corresponding values of the shorter component were 14 mg (CH_2O)/dm^2/hour and 0.02 cal/cm^2/min respectively. The P:I curves defined by these values are plotted in Fig. 7.4a. The results shown in Fig. 7.4b indicate that between LAI 2 and 5 the mixture is predicted to have an advantage. The situation is very similar to that found in the 'leaf-inclination mixtures' (Fig. 7.2) except that in the present case the taller component has the lower monoculture P rate at high LAIs.

Fig. 7.4 Predicted rates of gross photosynthesis of monocultures and mixtures of genotypes differing in leaf gross P:irradiance relationship. The mixtures are composed of equal leaf areas of the two types of canopy; where contrasting inclinations are involved, the 75°-foliage is above the 15°-foliage. There is no overlapping of canopies. The range of LAI over which the mixture is expected to have a photosynthetic advantage relative to both monocultures is indicated on each graph.

(a) The four leaf gross P:I curves used in the simulations. The values of the parameters, P_{max} and K_m, which describe the curves, are given in each case. The units of P_{max} are mg(CH_2O)/dm^2(leaf surface)/hr and of K_m are cal/dm^2(leaf surface)/min.

(b) The canopies of both genotypes have the same leaf inclination but in the mixture the canopy of the 18/0.05 component is above that of the other.

(c), (d) and (e) Monocultures and mixtures of components differing in both P:I curve and leaf inclination. Parameter values are given on the graphs.


(a)
LEAF GROSS P RATE (mg CH2O/dm2/hr)
20
15
10
5
0
0.0
0.2
0.4
0.6
LEAF IRRADIANCE (cal/cm2/min)
Pmax, Km
18, 0.05
16, 0.04
15, 0.03
14, 0.02
(b) ∝ 15, Pmax 18, Km 0.05 ---
∝ 15, Pmax 14, Km 0.02 ——
mixture ········
(c) ∝ 75, Pmax 18, Km 0.05 ---
∝ 15, Pmax 14, Km 0.02 ——
mixture ········
(d) ∝ 75, Pmax 18, Km 0.05 ---
∝ 15, Pmax 16, Km 0.04 ——
mixture ········
(e) ∝ 75, Pmax 18, Km 0.05 ---
∝ 15, Pmax 15, Km 0.03 ——
mixture ········
GROSS PHOTOSYNTHESIS RATE (g CH2O / m2 / day)
60
50
40
30
20
10
0
0
2
4
6
8
LAI
MIXTURE
ADVANTAGE

Wishing to find whether the predicted advantage of the mixture could be increased further, the photosynthesis of a mixture involving a combination of differences of leaf inclinations and P:I curves was simulated. As Fig. 7.4c shows, the mixture combining the leaf inclinations of Fig. 7.2 with the values of the photosynthesis parameters dsed in Fig. 7.4b, has a predicted advantage in gross photosynthesis at all values of LAI. The advantage over the more productive monoculture reaches a maximum of 8% at LAI 5, and this is the largest advantage observed in any of the simulations reported in this Section. Since the difference between the P:I curves for this prediction was large, the sensitivity of the mixture advantage to the exact shape of the curves was studied. Two other closely related curves were used in two further sets of simulations: the tall erect-leaved component with $P_{max} = 18$ and $K_m = 0.05$ (units as above) was combined in turn with short prostrate-leaved components, the first having $P_{max} = 15$, $K_m = 0.03$ and the second having $P_{max} = 16$, $K_m = 0.04$.

The results are given in Fig. 7.4e and 7.4d. The marked reduction in the size of the mixture advantage in these cases shows that rather extreme differences of P:I curve are needed in conjunction with extremely marked contrasts of leaf inclination and canopy height, to produce notable mixture advantages in gross photosynthesis.

7.3 Discussion

In an earlier Section (2.2.4) the published predictions of the effects of leaf inclination on canopy photosynthesis were described. It was noted that several models based on rather different approaches agreed in their predictions of large advantages for erect-leaved canopies at high LAIs and smaller advantages for prostrate-leaved canopies at low LAIs. In the same Section, it was pointed out that although these theoretical advantages had not yet been rigorously demonstrated by experimentation, there were sufficient indications of their reality to accept the predictions of the models at least provisionally. Since the predictions obtained using DAYP resemble so closely those produced according to the models of Duncan et al. (1967) and Ross & Bichele (1969) (see Fig.7.1), they appear to merit the same provisional acceptance.

Although for the present purpose, correct prediction of relative performances is the feature required of DAYP, it is of interest to compare the absolute rate of gross P predicted by this programme with one of the few measured rates; a rice crop of LAI 6 (Tanaka et al. 1966, their Fig. 16) showed a gross P rate of 49 g $(CH_2O)/m^2$/day on a sunny day in the tropics while the prediction * using DAYP is 43.4 g $(CH_2O)/m^2$/day. The 11% underestimate by DAYP could well be due to an underestimation of the rice leaf's P_{max}; rates higher than 26.4 mg CO_2/dm^2/hr have recently been measured (Tanaka & Matsushima 1971).

The choice of 15° and 75° as the only leaf inclinations to be considered in this Section was somewhat arbitrary but

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* The conditions taken for this simulation were : latitude 15°N, 15 October, 6 layers with LAI 1 and SAI 1 in each layer, leaf inclination 75°, leaf P parameters as for Fig. 7.1a.

it was thought that these values may not be far from the average leaf inclinations of the most extremely differing canopies achievable in the field. (The mechanical properties of leaves together with the action of wind virtually preclude the possibility of strictly 0°- or 90°-foliage.) Although no evidence is adduced to support the proposition, it is considered likely that the predicted positive effects of mixing 15°- and 75°-foliages are close to the maximum to be gained from combining any achievable types of canopy.

The effects of stems (including leaf sheaths) were omitted from most of the simulations of this Section for two reasons:

(a) The inclusion of stems makes the DIPA tables of contrasting canopies more similar. Since it is the contrast of canopy structures and their vertical separation which are responsible for the theoretical mixture advantages, there is a likelihood that the presence of stems will reduce the predicted effect of mixing the canopies below the maximum possible. This is confirmed by the results given in Table 7.2. Although the presence of stems low in the canopy (as at early stem extension) narrows the photosynthetic advantage of the mixture very little, the considerable amount of stem and ear area present after ear emergence causes a reduction of 14% in the mixture advantage.

(b) The ratio of stem area to leaf area index and the details of the vertical distribution of stem area are likely to be strongly influenced by temperature, density, stage of development (etc.) and hence the choice, for all simulations, of any one ratio and SAI profile would have been arbitrary.

The results presented in Fig. 7.2 show that the photosynthetic advantages predicted for 'leaf-inclination' mixtures occur, if at all, only above LAI 2. With a leaf area of less than this, in all cases examined the prostrate-leaved monoculture is expected to have a faster daily P rate. This is because at low LAI, such a canopy intercepts the greatest total of radiation during a day.

Self-shading apparently becomes important in determining productivity at LAI 2 or 3 because in each of the three sets of conditions where mixture advantages are predicted (Figs 7.2a, b & d), it is at an LAI within this range that the mixed canopy, with its 'Warren-Wilson type' configuration, becomes the canopy with the highest P rate. Although the daily total of radiation intercepted by the mixed canopy is smaller than that intercepted by the prostrate-leaved monoculture, the day's radiation is more equitably shared among the layers of the canopy when the upper layers contain erect leaves. As a number of authors argued (Warren Wilson 1960, Donald 1963, Verhagen et al.1963, Monteith 1965, Kumura 1968a) a more even distribution of radiation in conjunction with a hyperbolic leaf P:I curve results in higher expected P rates in the whole canopy.

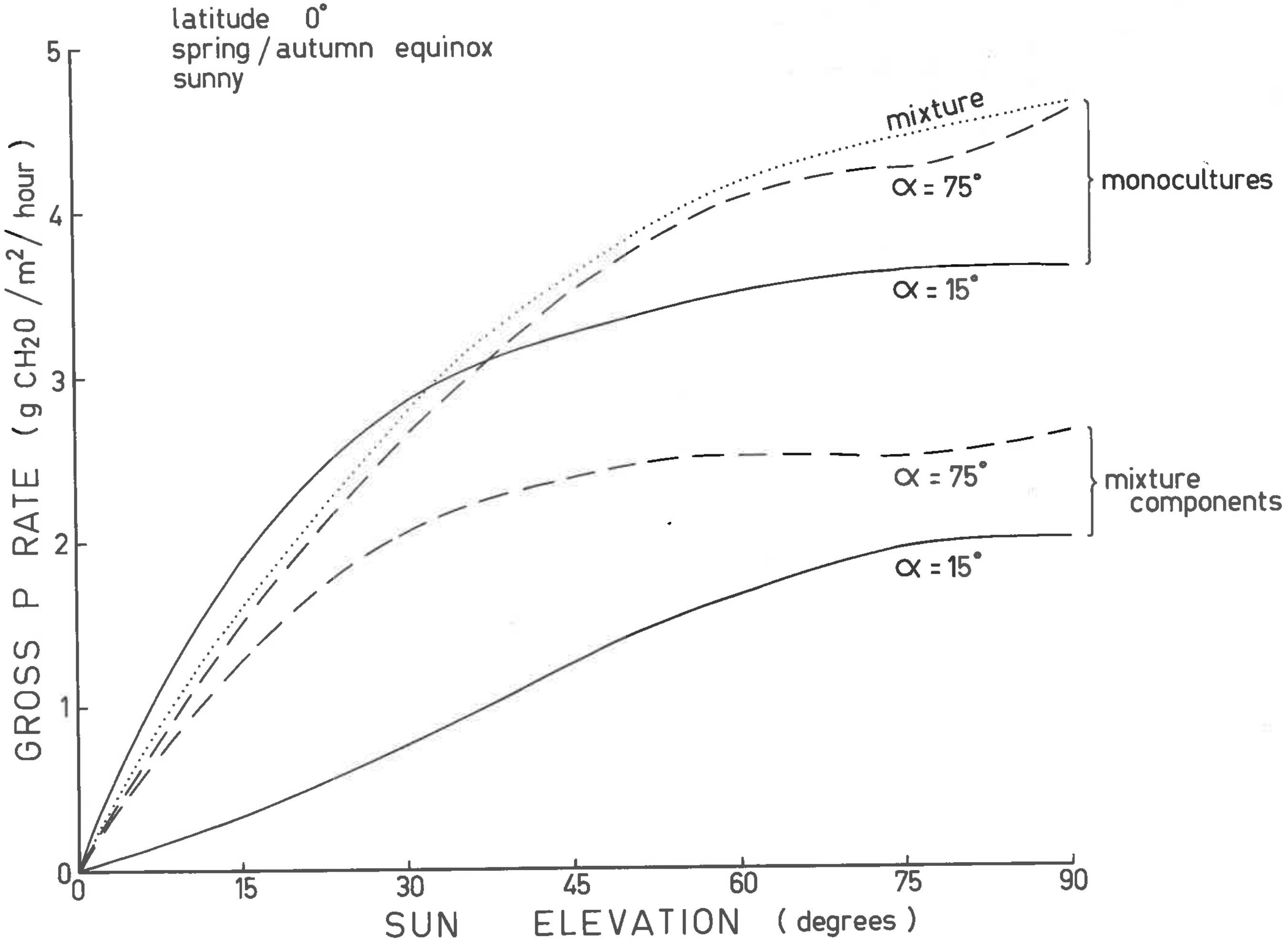
The existence of upper limits of LAI for the advantages predicted for the mixtures is explained in a similar manner. In the sunny conditions of Figs. 7.2a and b, this limit falls between LAI 6 and 7. Although the total interception of radiation by the mixture is greater than that in the erect-leaved monoculture, this monoculture is expected to have the higher daily P rate because of the more even distribution of radiation within the canopy.

In Fig. 7.2d, it is shown that under overcast conditions, the limits of LAI over which the mixture advantage is predicted is raised. This is equivalent to a prediction that the P rate of a prostrate-leaved monoculture will exceed that of an erect-leaved one up to a higher LAI under overcast conditions than under sunny conditions. That this result is not unexpected can be seen from the following argument. Direct measurement of the irradiances of individual leaves (Kumura 1968a) has shown that diffuse radiation from an overcast sky produces a more uniform distribution of radiation within the canopy than exists on a sunny day. If then, with increasing LAI, a prostrate-leaved canopy cedes its predicted superiority to an erect-leaved canopy because the latter allows more uniform lighting of the leaves, then under overcast conditions which tend to produce just such a uniformity, it follows that the more prostrate-leaved canopy will retain its superiority to higher values of LAI. The difference of form between the simulated results of Figs. 7.2a & b (sunny) and Fig. 7.2d (overcast) can thus be readily explained. To the author's knowledge, no formal quantitative prediction of the magnitude of this effect has previously been made.

A comparison of Figs. 7.2a and b with Fig. 7.2c demonstrates that the latitude and time of year greatly affect the predicted relative performance of erect- and prostrate-canopies and their mixtures. To show that the factor through which latitude and season act is solar elevation, mean weighted solar elevations were calculated for the three sets of conditions of Figs. 7.2a, b & c. This mean elevation was found by weighting the solar elevation of each hour of daylaight by the irradiance, due to sunlight only, of a surface normal to the sun. These means were 52.5°, 49.2° and 25.3° for Figs.7.2 b and c respectively.

To facilitate the interpretation of the effect of these differences, the hourly rates for the three canopies with LAI 4 of Fig. 7.2a are shown in Fig. 7.5. Under the conditions of Fig. 7.2a, at LAI 4 the mixture is predicted to have an advantage over both monocultures at all sun elevations greater than 30°. This explains the advantages predicted in

Fig. 7.5 The hourly rates of predicted gross photosynthesis of the monocultures and mixture of two genotypes differing in leaf inclination but having the same leaf P:I curve. All canopies have an LAI of 4. The mixture is composed of equal leaf areas of the two components with the canopy of the genotype with 75°-foliage completely above that of the component with 15°-foliage. The conditions (given on the graph) and P:I curve are those of Fig. 7.2a. At this latitude and time of year, the sun is directly overhead at noon. The sun elevations 75°, 60°, 45°,....,0° apply at 1, 2, 3,...,6 hours before and after noon.


latitude 0°
spring / autumn equinox
sunny
GROSS P RATE (g CH2O / m2 / hour)
SUN ELEVATION (degrees)
0
1
2
3
4
5
0
15
30
45
60
75
90
mixture
α = 75°
α = 15°
monocultures
α = 75°
α = 15°
mixture components

Figs. 7.2a & b for mixed canopies at LAIs of about 4; under the conditions indicated on these graphs, most of the day's radiation arrives from elevations greater than 30°. The absence of any mixture advantage in the winter conditions at Latitude 35° (Fig. 7.2c), is explained by the small proportion of the total radiation arriving from elevations greater than 30°. Indeed the maximum elevation reached by the sun under winter conditions at this latitude (that of Adelaide) is only 33°.

The mean weighted angle of incidence (elevation) of incoming light from a standard overcast sky (Moon & Spencer 1942) was found to be 55°, independent of solar elevation This relatively high elevation explains the predicted advantage of the mixture under the conditions of Fig. 7.2d.

While various mixtures have predicted gross P rates greater than those of either of the corresponding monocultures, there are four reasons for doubting whether such large advantages can be achieved in practice.

(a) Heights. All graphs of Figs. 7.2 and 7.4 assume that there is no overlap between the components' canopies, but in fact some degree of overlap seems likely to be always present. For instance, although Selkirk and Summit are examples of what would commonly be described as tall and short (but certainly not ultra-short) varieties, at T2 in the soil bench the estimated degree of overlap in the Selkirk and Summit mixture corresponded approximately to that shown as 2/3-overlap in Fig. 7.3. The results given in Fig. 7.3a show how much this degree of overlap may affect predictions: with no overlap present, the advantage of the mixture over the monoculture with the higher P rate is 2.6%; with the more realistic 2/3-overlap, the advantage is only 1.9%. The profiles at T1 in the soil bench (Fig. 5.3a) suggest that overlap was almost complete in all mixtures; any mixture advantage would thus be very slight.

(b) Leaf inclination. As mentioned earlier, the 15°- and 75°-foliage may represent the most extreme differences in average leaf-inclination attainable. If the leaf-inclination of the components differed less, the effect on predicted photosynthesis of mixing the components would seem likely to be less also. The presence of stems in the canopy was also found to reduce the predicted difference between the photosynthesis of the mixture and the monoculture with the faster P rate.

(c) Leaf gross P:I relationships. Since there is little evidence of differences among temprrate species in the initial slope of the gross P:I curve (e.g. Milthorpe 1970), the results of variation in this factor (Fig. 7.4) may seem to be of rather academic interest. However, differences between genotypes in the capacities of their tissues to reduce their respiration rates when the leaves are heavily shaded (Grime 1965, 1966) could possibly lead to curves of plant net production as a function of leaf irradiance having much the same form as those in Fig. 7.4. The solid line of Fig. 7.4a might approximately represent the net production curve of a 'shade type' and the dotted line might similarly represent that of a 'sun type'; the results of Fig. 7.4 would in this case reflect patterns of net production.

Whether such extreme differences of curve could be found among existing wheat varieties is very doubtful since wheat shows all the characteristics of being a sun species; in particular, gross P:I curves of wheat continue to rise at high levels of irradiance (Gaastra 1962, Stoy 1965), and varieties which contrast highly in other respects may have very similar gross P:I curves (Stoy 1965). Hence, the advantages predicted for the mixtures in Fig. 7.4 are not likely to be achieved, according to present evidence, using wheat varieties.

(d) Angle of incidence of incoming radiation. As explained above, predicted advantages for mixtures disappear when a considerable part of the daily income of radiation comes from elevations of less than about 30°. In cool temperate regions where wheat is grown as a summer crop, the period of maximum LAI and fastest growth (at about ear emergence) may coincide with the season with the highest solar elevations (e.g. in Cambridge, U.K., latitude 52°N, at the summer solstice the mean weighted solar elevation, MWSE, is 40.9°); however, the elevations are not great enough to give effects as big as those shown in Fig. 7.2a and b. In Mediterranean climates such as that of South Australia, winter-sown wheat reaches its maximum LAI shortly before the spring equinox (Puckridge & Donald 1967). Again, solar elevations at this time (e.g. at Adelaide, latitude 35°S, at the spring equinox MWSE = 40.4°) are much less than in summer and predicted results for sunny conditions are likely to be intermediate between those of Fig. 7.2b & c.

The simulations of this Section have so far concerned only gross photosynthesis rates. By assuming that plant respiration is an approximately constant proportion of gross photosynthesis (e.g. King & Evans 1967, using wheat), the patterns of rates found for gross P can be supposed to apply also to rates of net production. However in the context of the present work, it is relevant to ask whether the predicted differences of rates are likely to affect yields.

This question is difficult to answer because the crop and environment constitute a dynamic, continually changing system. During growth, the morphology and physiology of the crop are changing both in response to developmental processes and to the more or less systematic changes in environmental factors; the developmental and environmental factors usually interact strongly. Furthermore, in the 'leaf-inclination mixtures' considered earlier, the balance between the components will be changing at an accelerating rate in favour of the taller component. The gross P rate of the mixture canopy will gradually approach that of the erect-leaved monoculture.

To provide at least a crude estimate of the effects on yield of the predicted differences among the curves of Figs. 7.2 and 7.4, a very simple recursive growth model was constructed. The starting point of the simulated growth is a canopy of leaf area index L_o. Assuming a leaf area/leaf dry weight ratio of 300 cm^2/g (Wasserman 1964, Puckridge & Donald 1967), the initial weight, F_o, of leaves per m^2 of land is given by $L_o/0.03$. Assuming values for the ratios leaf weight/shoot weight, (F/S), and shoot weight/total weight, (S/T), the initial weights of stems and roots can also be calculated. The effect of the first day is estimated by referring to the appropriate curve in Fig. 7.2 or 7.4, and reading off the day's production of gross photosynthate, $P_1 = f(L_o)$, corresponding to the leaf area, L_o, which is present at the beginning of the first day. The value of P_1 is converted by a factor R to give the day's net production of dry matter, and further multiplied by S/T to give the weight of dry matter added to the shoot. This shoot-weight increment, ΔS_1, is divided between leaves and stem according to the ratio (F/S) to give the leaf-weight increment ΔF_1. The leaf weight, F_1, at the end of the first day is thus $F_o + \Delta F_1$ and the leaf area is $0.03F_1$. The system can be summarised by the following equations which refer to the i-th day:

$$P_i = f(L_{i-1})$$

$$\Delta S_i = \left(\frac{S}{T}\right) RP_i$$

$$\Delta F_i = \left(\frac{F}{S}\right) \Delta S_i$$

$$F_i = F_{i-1} + \Delta F_i$$

$$L_i = 0.03F_i$$

Since this growth model will only be used to estimate growth over short periods fairly late in the vegetative period, the shoot weight/total weight ratio will be assumed constant at 0.833 (this corresponds to a root weight/shoot weight ratio of 0.2). The leaf weight/shoot weight ratio will similarly be held constant at 0.4. Values for both ratios are based on the high-light experiments of Friend <u>et al</u>.(1965) at 20° and 30°C. The constancy of these ratios allows predicted shoot weight to be calculated from F_i at any stage.

The factor R which converts gross P to net dry matter production is taken to be 0.6. This figure represents an arbitrary choice but it is not far from the mean of estimates given by Thomas & Hill (1949), Monteith (1966), de Wit (1966), King & Evans (1967) and Kira (1968).

The results of the DAYP simulations which are most favourable to mixtures are the 7% advantage in one of the leaf-inclination mixtures (Fig. 7.2d) and the 8% advantage in a mixture involving differences of both leaf inclination and P:I curve (Fig. 7.4c). The effects of these theoretical advantages on the yields of the mixtures compared with values for the corresponding higher-yielding monocultures were predicted using the growth model.

(a) <u>Fig. 7.2a</u>. It was assumed that both the mixture and the erect-leaved monoculture reached L = 3 at the same time, and the simulation was started at this stage. It took 13 'days' for the mixture to reach L = 6; the simulation was then stopped because beyond this point no further advantage is predicted for the mixture. The predicted yield of shoots of the mixture at L = 6 was only 2% more than that of the higher-yielding (erect-leaved) monoculture. During the simulation the yield advantage at no time exceeded this figure. Similar conclusions seem likely to apply to the case of Fig. 7.2b.

(b) Fig. 7.2d. It was assumed that the mixture and the prostrate-leaved monoculture reached L = 4 at the same time, and the simulation was started with this leaf area. Under the overcast conditions, growth was slower than in (a) and the mixture increased its leaf area by 2 units in 14 'days'. At L = 6 in the mixture, the shoot weight was 1.4% greater than that of the prostrate-leaved monoculture. Further simulated growth using this model would predict a greater yield advantage for the mixture over the prostrate-leaved canopy. However the tendency for the balance between the mixture components to change, would have meant that the P rate of the mixture in a more accurately modelled system would perhaps have been close to that of the erect-leaved monoculture at L = 6. The above figure of 1.4% is therefore an overestimate of the yield advantage of the mixture at this stage.

(c) Fig. 7.4c. The mixture and the erect-leaved monoculture were taken to reach L = 2 at the same time. Starting the simulation at this point, it took the mixture 18 'days' to reach L = 6. If simulated growth had been continued, the mixture would have increased its yield advantage; already at L = 6, its shoot weight exceeded that of the higher-yielding monoculture by 7.2%.

Bearing in mind that these figures are estimates of maximum yield differences, it seems possible to conclude that there is little likelihood of any mixture overyielding significantly by virtue only of a specially advantageous canopy structure. A mixture of which the components contrasted in leaf P:I curves as well as in leaf inclination might overyield in sunny conditions if the LAI at harvest was rather high.

Van den Bergh (1968) and Rhodes (1968) have suggested that some advantageous feature of the mixture canopies was responsible for certain cases of overyielding. Since the mixtures in question were subject to frequent clipping, their canopies were unlikely to have even approached LAI 6. The relatively low LAIs in their experiments, together with the small size of the yield advantages predicted above, indicate that van den Bergh's and Rhodes' suggestion is not supported by the findings of this theoretical study. In addition, the mixtures of Rhodes (1968) which overyielded in his two most frequently cut treatments, did not overyield in the treatment with infrequent cutting. On the basis of the results of this Section, the action of some factor(s) other than light utilization seems to be required to explain these cases of overyielding.

8. FINAL DISCUSSION

The aim of the work reported in this thesis was to investigate the possibility that binary, 1:1 mixtures of wheat varieties might yield more dry matter than either component monoculture. The intention was to find such a mixture and to elucidate the mechanisms which led to the overyielding. In fact, when three mixtures chosen for their high yields in the first year were grown again under the two contrasting water regimes, five out of the six mixtures yielded less than the lower-yielding component monoculture. This final discussion therefore considers the two aspects of transgressive yielding, namely underyielding as well as overyielding, rather than only the agriculturally advantageous overyielding.

The findings reported in the thesis will be reviewed in the perspective of the literature under six main headings.

8.1 The statistical probability of a given mixture yielding transgressively.

Judging by the published records of mixture experiments (Section 2.1) the chance of any particular mixture yielding transgressively seems considerable. Out of 283 mixtures, 37% showed recorded yields lying outside the range of their components' monocultures. Overyielding accounted for 25% of the 283 cases and was significantly ($P < 0.05$) more frequent than underyielding which accounted for only 12%. The preponderance of overyielding cases seems to be a reflection of the general tendency noted by Donald (1963) for mixture yields to lie above the mean of the yields of the component monocultures. Of the 283 mixtures, 61% had yields above the mean-component value leaving 39% with yields below it. This difference was again significant ($P < 0.001$). The results from the two

ERRATUM : Page 266, line 21 _et seq_. For 'There was however...' random variable' read ' The distributions of RYT shown in Fig. 4.2 were not tested for departures from normality since RYT, being the mean of the ratios of two normal distributions, was not itself expected to have a strictly normal distribution'.

mixture diallels of wheat varieties carried out in the field in Year 1 were atypical in that among the 60 mixtures there was actually a slight excess of underyielding cases.

Wishing to clarify the arithmetical basis of trangressive yielding, the yields of mixtures were seen as the sum of the yields of the two components, and the relationships between these yields were considered. In 1:1 mixtures, the de Wit (1960) model predicts the equality of proportional increases and decreases of per-plant yields of mixture components (relative to their monoculture values). When these increases and decreases are equal, the Relative Yield Total, RYT, of the mixture is unity (see Section 2.1.1). When the increase is greater than the decrease, this index exceeds unity; when the increase is less than the decrease, RYT is less than unity. Since values of RYT strictly equal to unity would imply the absence of any transgressive yielding, the distribution of RYTs calculated from 532 published results was analysed in Table 2.2 (Fig. 4.2). The distribution was found to be centred on a value very close to unity and so confirmed the similar conclusion of van den Bergh (1968) based on a more restricted sample. There was however a considerable spread of RYT values, from about 0.6 to 1.5; the shape of the tails of the distribution caused it to bear a striking resemblance to a normal or 'error' distribution. Although no rigorous test of normality has been presented, the histograms of Fig. 4.2 suggest that RYT can be regarded as a random variable.

A notable feature of the RYT distribution was that there were rather more mixtures with RYTs above 1:1 than below 0.9. Although the difference was not quite significant, it seems that the consequent asymmetry about unity may be responsible in an arithmetical sense for some of the preponderance of overyielding mixtures which was considered above. That this does not, however, necessarily follow is shown by the results of the wheat diallels of Year 1. While the balance of RYT values above and below unity was extremely similar to that in the 532 mixtures (Fig. 4.2), overyielding mixtures did not in fact predominate.

Another factor which must act in the direction of producing mixture yields which lie above the mean-component value is the tendency for the genotype with the higher-yielding monoculture to be the more aggressive component in mixture. The correlation coefficient between an index of aggressivity and monoculture yield pooled over all the published mixture diallels was estimated to be about +0.3 (at least +0.289, see Section 4.4.1). The results of the Monte Carlo simulation of mixture yields (Section 5.4.2) can be seen to demonstrate that a positive correlation, combined only with experimental error, leads directly to an excess of overyielding mixtures. In passing, it might be noted that when the weight of grain is the measure of yield, the correlation between aggressiveness and yield has sometimes been observed to be negative (see Donald 1968); such a type of correlation is clearly absent in most data where yield has been measured in terms of dry matter.

While the difference of frequencies of mixtures which overyield and underyield seems to find an arithmetical explanation in the observed distribution of RYT and the positive correlation between aggressiveness and monoculture yield, a systematic search for further arithmetical factors influencing the likelihood of trangressive yielding provides additional insights into the results of mixture experiments. A third and a fourth factor of this type were recognised in Section 3.1.3. The third factor is the degree of difference between the monoculture yields of the mixture's components. The more similar are these monoculture yields, the greater is the chance that the mixture will yield transgressively. An example of this may be taken from the results of the diallel experiment of Year 1. It was found that there were over twice as many cases ($P < 0.05$) of transgressive yielding in Diallel 2 as in Diallel 1; however, this apparently puzzling difference could be traced to the relative uniformity of the monoculture yields in Diallel 2 compared with the significantly ($P < 0.01$ and $P < 0.05$) differing monoculture yields within the two densities of Diallel 1.

The fourth arithmetical factor is the intensity of the neighbour effects in the mixture. With a given non-zero difference of monoculture yield of the components, and with a given RYT value, the greater the aggressiveness of one component, the closer the mixture yield lies to the aggressor's monoculture yield. The likelihood of the mixture yield becoming transgressive at some point naturally increases at the same time but whether it is over- or under-yielding which becomes more likely depends on whether the aggressor is the component with the higher- or lower-yielding monoculture (i.e. whether the correlation between aggressiveness and monoculture yield is positive or negative).

These conclusions are formalised in Fig. 3.6 but they may be briefly summarised as follows. The arithmetical conditions leading to transgressive yielding are quite complex. Overyielding is most likely to occur when RYT is much greater than unity, when the aggressor has the higher-yielding monoculture, when the aggressor is strongly aggressive, and when monoculture yields are very similar. Underyielding is most liekly to occur when RYT is much less than unity, when the aggressor is the component with the lower-yielding monoculture, and when the other two factors are as above. The key factor of this type seems to be RYT, for however unfavourable the other factors seem to be with respect to producing a certain type of transgressive yielding, a value of RYT always exists such that this type of transgressive yield is observed.

On the other hand, if RYT equals, say, unity or less, then overyielding cannot occur. A value greater than or equal to unity similarly precludes underyielding

8.2 The statistical probability of finding a mixture which yields trangressively in a repeatable manner.

A survey of the literature shows that while apparent overyielding has been frequently reported, there are very few cases where mixtures have over- or under-yielding significantly (Section 2.1). The experimental results in the present work conform to this pattern. No case of observed transgressive yielding was statistically significant, neither among the 60 mixture comparisons available from the experiments of Year 1, nor among the 12 of Year 2. Since biological science has come to judge once-produced effects as 'real' and 'potentially repeatable' only when the calculated probability of their being due to chance is less than an arbitrary 5%, the lack of statistical significance in the numerous once-performed experiments seems to suggest that 'real' transgressive yielding does not occur. However, it could just as well be argued that not enough replicates have been used in most experiments to detect small but potentially repeatable differences of yield. It is thus possible that some mixtures do in fact yield transgressively, but by a rather small margin. To discriminate between these alternative interpretations of the situation would be difficult; indeed to resolve the question for even one environment would require greater resources than were available to the present project. Even granted considerable resources, the conclusion would inevitably be only in terms of probability and hence not definitive. In some other environment, as will be shown below, totally different results might be obtained.

If the results of once-performed experiments have not indicated that the observed transgressive yielding is 'potentially repeatable', it must be asked whether actual repetition of experiments has demonstrated repeatability of the results. It is here that the greatest short-coming of the published data is apparent. Very few of the mixtures which have been reported as yielding transgressively have received further study. If the experiments have been repeated the results have apparently rarely been published.

There are only two examples of the reported repetition of experiments: firstly, the 3 underyielding mixtures of Aamodt & Ahlgren (1939, in the USA) which were grown again by Donald (1946, in Australia) and found to yield non-transgressively and secondly, two flax-linseed mixtures grown by both Harper (1964) and Khan (in Harper 1964); one of these mixtures overyielded in both cases while the other only overyielded in one (see Section 2.1). The three mixtures of the present study which were grown in two seasons, with restricted water supply in each, behaved in a similarly inconsistent way. In Year 1, two of the three mixtures overyielded and the third had an RYT of 1.124, while in Year 2 all three underyielded.

These results again suggest two contrasting interpretations: either that the observed differences between the original experiment and its repetition were due to the vagaries of experimental error or alternatively that the differences in conditions were sufficient to cause the results to differ. The influence of experimental error on such comparisons may be inferred from the primary results of the Monte Carlo simulation which was described in Section 5.4.2. Having assumed that the coefficient of variation of yields in the simulated experiments had the admittedly high value of 12.3%, the average probability that an individual mixture would overyield can be calculated from the primary results to have been 0.267. The corresponding probability of underyielding was 0.212. With the probability of transgressive yielding thus almost evenly divided between over- and under-yielding and with the probabilities of these two together being not much less than the chance of non-transgressive yielding, any repetition of such an experiment, even without a change of conditions, would be likely to give results differing qualitatively from those of the original.

In view of the uncertainties introduced by experimental error, the apparent demonstrations by Harper (1964), England (1964) and Norrington-Davies (1968) (see Table 5.6) of the sensitivity of mixture-monoculture yield relationships to cultural conditions would seem not to carry much weight (it is recalled that replication is not specifically mentioned in the report of the experiment of Harper; also Norrington-Davies' experiment only included two replicates). The general similarity of the patterns of mixture yields found in the high- and low-water soil benches in Year 2 may be considered to be fortuitous rather than indicating real similarity.

While the published data thus appear not to provide particularly accurate estimates of the sensitivity of mixture-monoculture yield relationships to environmental and cultural conditions, a strong dependence can be inferred from the results of mixture experiments in which only reproductive yield has been considered. For instance, after finding that a certain mixture of wheat varieties showed highly significant overyielding of grain in a field experiment, Whitehouse and colleagues (Whitehouse <u>et al</u>.1967, Bell <u>et al</u>.1968) grew the same mixture again in the following season imitating the conditions of the previous season as nearly as possible. Neither at the original density, nor at any of a range of additional densities did this mixture overyield. To give a second example, in which the effective factor was tentatively identified, the present writer (Trenbath 1970) demonstrated a large and highly significant trend in RYTs (based on panicle weights) within 5 mixtures of oat species in an experiment grown on field soil. In the replicate on deepest soil, all 5 mixtures overyielded in panicle weight; in the two other replicates with successively shallower soils, the numbers of overyielding mixtures were 2 and 1.

Thus it seems necessary to conclude that with experimental error in field experiments being relatively large, with transgressive yielding (if real) being only by small margins, and with mixture-monoculture yield relationships being almost certainly highly dependent on environmental conditions, the chances of finding a mixture which really yields transgressively are slight. Even if such a mixture were to be identified in a field experiment, the difference in some environmental variable between two seasons might be sufficient to prevent the specific conditions for over- or under-yielding from obtaining on a second occasion. Similarly, bringing the mixture into cultivation under controlled conditions for further study might have the same result so that the specific conditions required for transgressive yielding to occur would never be discovered. It may be significant that the only mixture which has so far been reported as overyielding in two separate experiments is one of Harper's (1964) flax-linseed mixtures which was grown on both occasions under greenhouse conditions.

8.3 Theoretical approach to mechanisms leading to transgressive yielding.

De Wit's (1960) model of plant performance in mixtures assumes that the yield of a plant in mixture is proportional to the amount of 'space' it can acquire. Although this 'space' seems to correspond fairly clearly to supplies of light, water and nutrients, de Wit (1960) suggested than any direct identification of 'space' with growth factors is 'always inaccurate and therefore inadvisable'. If this is so, de Wit's 'space' seems to be rather a numinous and possibly misleading concept. Hence, in Section 3.1 an attempt was made to restate the model in terms of real rather than abstract quantities. The argument can be briefly stated.

In the simplest case, competition between genotypes in a mixture is for just one growth factor, i.e. for light, or water, or some nutrient. Since such a factor is in limiting supply, yield in mixture and monoculture may be expected to be strictly proportional to the quantity of it which the plants absorb. The likelihood of such a relationship is shown by the results of experiments in which yield responses to per-plant absorption of these factors are tested in monoculture by varying one factor at a time and keeping the other factors at high levels; yields are close to being strictly proportional to the quantity of factor absorbed over a considerable range of absorption (e.g. for light, see Shibles & Weber 1965; for water, see de Wit 1958; for nitrogen, see Singh _et al_. 1967).

When, as is often the case, either light, water or a nutrient can be identified as the factor clearly limiting growth, the de Wit model can be restated in terms of per-plant yield being strictly proportional to per-plant uptake (absorption in the case of light) of this 'principal' factor. The model is then no longer testable only through observations of yield, as is true for an empirical model. Since the amount of 'space' acquired becomes a measurable, physical quantity, the input as well as the output of the model can be measured and hence the model is testable in all its parts.

To display the yield:factor-uptake relationships in the various communities, a simple graphical method (Fig. 3.1) was devised which was based on the assumption that yield is strictly proportional to uptake. If the total uptake of 'principal' factor is the same in all communities, in the mixture the loss of per-plant uptake (relative to the level in monoculture) of the subordinate genotype must be equal to the gain of per-plant uptake (again relative to monoculture) of the aggressor. Given such a system, in the mixture, the proportional increase and decrease of per-plant yield of the components, relative to yields in their respective monocultures, will be equal. The RYT will therefore be unity and there will be no transgressive yielding.

If, however, real transgressive yielding is to be envisaged as a possibility, it is certain to be associated with, and in an arithmetical sense caused by, real deviations of RYT from unity. Since RYT has a special importance among the arithmetical factors which can lead to over- and under-yielding (see above), in Section 3.1 the potential causes of (real) deviations of RYT were considered. If gains and losses of 'principal' factor in mixture are not quite equal, so that the aggregate uptake of factor in the mixture is greater or less than the uptakes in the monocultures, RYT will be respectively greater or less than unity. A case of RYT > 1 where the mixture apparently shows a 'gain' of utilizable resources relative to the monocultures, might occur where a complementary use of the habitat occurs through the mixture components exploiting the environment in different ways (e.g. temporal sharing or root stratification). A case of RYT < 1 might theoretically occur if there was mutual allelopathic inhibition of uptakes; however, an experimental example of 'loss' of growth factor in a mixture was explained in the present work without invoking allelopathy (see Section 8.4).

The second way in which the RYT of a mixture may deviate from unity, in the absence of any gain or loss of growth factor, is through the efficiency with which the 'principal' factor is used in dry matter production differing, in one of the mixture components, from the value seen in the corresponding monoculture. This might occur if the per-plant uptake of the factor by the aggressor was at a level at which, in monoculture, luxury consumption normally occurred. If the efficiency of factor-utilization by this component in the mixture followed the negative trend present in its monoculture behaviour at high uptakes, its efficiency of factor utilization would be lower in the mixture than in the monoculture. Unless there was a compensating increase of efficiency of utilization in the other component, the RYT would fall below unity.

Changes of efficiency of factor utilization relative to that in monocultures seem likely to occur when competition for other factors beside the 'principal' factor causes uptakes of subsidiary factors to differ from their monoculture values. Experimental data from two studies (Donald 1958, Idris & Milthorpe 1967) were found to give some support to this suggestion (Section 3.1.2.2, Fig. 3.5).

Another way in which changes of efficiency of utilization may occur due to specific features of the mixture is when lodging in a mixture follows the behaviour in monoculture of one of the components. (Lodging greatly reduces the efficiency of utilization of light (Mulder 1954)). In Diallel 1 of the field experiments of Year 1 and also in the soil bench experiment of Year 2, the variety Selkirk lodged in monocultures but was apparently held up by the other component in its mixtures. If the plants in these plots had not been artificially restored to their original posture, the mixtures would doubtless have shown high RYTs. If, with lodging corrected, Selkirk's had been the heaviest yielding monoculture, then without the correction of lodging, these mixtures might even have overyielded. The Selkirk mixtures could have shown high RYTs due to 'lodging escape'; similarly, high RYTs would be expected in cases of 'disease escape' (see Borlaug 1959) to which lodging escape is analogous.

Knowing that RYT values depend on the closeness of factor gains and losses to equality and on the efficiency of factor utilization in the mixture components as compared with that in the monocultures, the form of the mathematical dependence was studied (Section 3.1.2.1). It appeared that the RYT value has four additive components of which the first is unity; the other three components are potential causes of deviation. The first deviation term is concerned with overall gain or loss of factor in the mixture, the second with overall change of efficiency of factor utilization, and the third represents the effect on RYT of interaction between the first and second terms if both have non-zero values. Each of these three terms is further resolvable into the contributions of the individual components. These considerations show that although the value of RYT will often itself have no simple biological interpretation, its deviation from unity is the sum of three simple components each of which do have such interpretations. If de Wit's model can be validly restated in the way proposed here, a measurement of all factor uptakes leading to an evaluation of the components of a mixture's RYT would seem to offer a way of specifying rather completely the type of interaction which has occurred between two genotypes in mixture.

8.4 Underyielding in experimental mixtures

Out of the five mixtures which underyielded in Year 2, only the two containing the variety Selkirk in the low-water soil bench showed neighbour effects which were strong and consistent in pattern. In mixture with Pitic, the per-plant biomass of Selkirk was 35% ($P<0.01$) less than that in its monoculture; in mixture with Summit, the corresponding figure was 43% ($P < 0.001$). Compensating increases of biomass in the aggressors were weak and non-significant.

To explain why the proportional losses and gains in the biomasses of the mixture components were not equal, three hypotheses were proposed (for full descriptions see Fig. 5.10 and Section 5.4.4). The first involved a 'loss' of the hypothetical principal factor in the mixture, but with the efficiency of utilization remaining constant for each variety between mixture and monoculture. The second hypothesis involved a reduced efficiency of factor-utilization (luxury consumption) by the aggressive components in mixture; luxury consumption was postulated to be their normal (i.e.monoculture) response to high levels of factor uptake. The third hypothesis again envisaged a reduced efficiency of utilization by one or both components of the mixture but in this case the reduction was postulated to be due to some specific features of the mixture. In Hypotheses 2 and 3 the losses and gains of factor by the components of the mixture were expected to be equal. Since the growth of the plants in the low-water bench was so clearly limited by water supply, the principal factor was assumed to be water.

The watering experiment of Year 3 showed that the relation between biomass and weight of water transpired was linear in the three varieties (Pitic, Selkirk and Summit) over a wide range of water regimes. At least in monoculture, there was no reduction of efficiency of utilization of water at uptake levels far greater than any which could have occurred in the low-water soil bench. Hypothesis 2 thus appeared unlikely to apply.

To discriminate between Hypotheses 1 and 3 (and to confirm that Hypothesis 2 was inapplicable), the per-plant uptakes of water by monocultures and mixture components needed to be estimated. The report of passive uptake of silica by wheat (Handreck & Jones 1968) and of its subsequent deposition in the shoots, suggested a suitable method for estimating water uptakes; apparently silica yields of shoots could be transformed to weight of water transpired simply by multiplying them by a factor which depended on the nature of the soil. The watering experiment used a soil as similar as possible to that used in the soil benches and included silica analysis of shoots in conjunction with transpiration measurements. On the assumption that the silica content of the roots was negligible (Handreck & Jones 1968), the experiment could thus test whether the uptake of silica was truly passive. Since the linear regression of silica yield on transpiration intersected the silica axis below the origin ($P < 0.01$), the uptake appeared to be not strictly passive (Fig. 6.6). Moreover, there were significant ($P < 0.05$) differences among the linear regressions of the three varieties treated separately (Fig. 6.7).

Using a separate line of best fit for each variety, the regressions established in the watering experiment were used to transform data of silica analysis in the soil bench plant material into estimates of weight of water transpired by plants in the soil bench experiment. These values were the estimates of water uptake required to allow a discrimination between the hypotheses. For all monocultures and mixture components concerned in the Selkirk mixtures of the low-water bench, the calculated estimates of efficiency of water utilization were close to being constant within any variety (Fig. 6.8). The only hypothesis which could apply to the Selkirk mixtures was therefore Hypothesis 1. By plotting the biomasses against estimates of transpiration, graphs of the form of Fig. 3.1 were obtained (Fig. 6.10). These showed clearly that a very marked discrepancy between the losses and gains in water uptake of the components in each of the Selkirk mixtures was responsible for an apparent 'loss' of growth factor in the mixture. The aggregate water uptake in both mixtures was less than that of the monoculture with the lower uptake.

The analysis, described earlier, of the RYT value of a mixture into 4 additive components was carried out by calculating these components for the 3 mixtures of the low-water soil bench. The pattern of values for the two Selkirk mixtures were very similar, showing as expected that most of the effect on RYTs was due to factor 'loss' in the mixtures. The pattern of values for the third mixture showed that the RYT deviated below unity because of an apparently low aggregate efficiency of water utilization. Fig. 6.10 shows that it was the relatively low efficiency of Pitic in mixture which was responsible for this effect. The Pitic+Summit mixture thus provided, in a formal sense at least, an example of the Hypothesis 3 mentioned above.

The reason for the relatively low water uptake by the two Selkirk mixtures of the low-water bench was suggested by other results from the watering experiment. The weights of root present in different parts of the pots showed that, at Day 53, Selkirk had 22% ($P < 0.001$) and 14% ($P < 0.1$) less weight of root in the lower half of the pot than did either Pitic or Summit respectively. At a later harvest (Day 76), the corresponding figures were 11% ($P < 0.05$) and 17% ($P < 0.01$). With water only supplied to the lower half of the pot, Selkirk's lack of deeply-growing roots resulted in a particularly low Relative Water Content of its leaves in the treatment where stress had been prolonged (Fig. 6.5).

We may now consider the consequences of these differences of rooting behaviour in relation to competition for water in the low-water soil bench. If, in this bench, the soil was dried out by uptake or evaporation from the surface downwards, the deep-growing roots of Selkirk, appearing relatively late, must have encountered conditions differing greatly between mixture and monoculture. Whereas in monoculture, water would have remained in the profile until the roots of Selkirk grew down to it, in mixture this variety's roots would have grown down through soil from which the water had already been partly removed by the roots of the other component. Selkirk's share of the daily aggregate water uptake of the mixture could not but decline.

To explain the rapidity with which Selkirk was observed to have been suppressed in mixture it was suggested that plants of Selkirk must have been subject to the following cycle of causes and effects: less water uptake → lower leaf RWC → less photosynthesis → less root growth → less water uptake. Such a cycle constitutes a positive-feedback loop of the kind recognised by Donald (1958) and Milthorpe (1961); with this cycle operating, the suppression of a subordinate component would be expected to be rapid. In the Selkirk mixtures, the effect of this cycle on the growth of Selkirk may have been reinforced by a second loop: shading → less photosynthesis → less root growth → less water uptake → less stem extension → more shading.

Given this very sudden slowing down of growth by one component late in the vegetative period, it was argued (Section 6.2.4) that the root-systems of the aggressor components of the mixtures were no longer physiologically capable of expanding their uptake capacities sufficiently to take up the water which, due to Selkirk's effective demise, had been left unused; instances are known of mixture components apparently losing compensatory ability late in growth (Klages in de Wit 1960, Jensen & Federer 1965).

This proposed sequence of events, mainly directly established but in part dependent on relationships reported in other studies, seems to offer a satisfactory explanation of the reduced water uptake and growth by Selkirk, and of the 'factor-loss' and underyielding by the two Selkirk mixtures.

8.5 Prediction of neighbour effects in mixtures where competition is only for light.

The model of neighbour effects developed earlier, is a very simple one; it was based on an expected strict proportionality between yield and growth factor uptake. In spite of its simplicity, it was shown experimentally to describe adequately the situation in mixtures where competition was chiefly for water. Also, the model appears to provide a basis for predictions about the yields of such mixtures, for instance it suggests that Relative Yield Totals will tend to be close to unity.

In contrast, the prediction of neighbour effects and aggregate yields in a mixture where competition is only for light (i.e. where soil factors are non-limiting) would seem to be hazardous with some similarly simple model. The geometry of sun, sky and plant canopy are so complex that only some treatment as detailed as, say, the model of Duncan et al. (1967) would seem to present any hope of giving a satisfactory account of the process of competition for light in a mixed stand. Accordingly, the Duncan model was adapted to treat mixed canopies and a number of elaborations were incorporated so that daily gross photosynthesis rates of the components of a mixture could be predicted. Aggregate P rates of mixtures could be compared with the rates of monocultures.

As a prelude to the purely theoretical studies considered later, and in an attempt to provide at least a partial validation of the model which would be used, two aspects of the model's performance were compared with observations; these were the predicted radiation profiles in monocultures and the predicted photosynthesis of varieties in mixture and monoculture.

To generate, firstly, the expected radiation profiles, the canopy structures measured on two occasions in the stands in the high-water soil bench were used as inputs to the programme. The predicted patterns of extinction of radiation in the monocultures were remarkably similar to those observed (Fig. 5.2), except that predicted radiation levels low in the canopies were systematically lower than those observed. This systematic error was ascribed to the row planting which caused the elements of the canopies to be locally clumped. The model, with its assumption of random dispersion of leaves in a horizontal direction, would be expected to overestimate interception of light and hence underestimate radiation levels low in such canopies.

Wishing to check that the model was able to simulate successfully at least the gross features of the neighbour effects in mixtures where competition was only for light, the harvest data of the high-water soil bench were used as follows. Again employing the canopy structures measured in the high-water bench, photosynthesis by the mixture components and monocultures was estimated for two occasions, i.e. at early stem extension (T1) and at early grain filling (T2). Since it seemed likely that differences of photosynthesis at T1 would be reflected mostly in straw weights at harvest and that differences at T2 would be reflected mostly in ear weight at harvest, the predicted differences of photosynthesis rate of varieties between mixtures and monocultures at T1 and T2 were compared with corresponding differences of straw and ear weights respectively.

In three cases where harvest data showed that 'normal' compensating behaviour was present, the model correctly predicted the directions of all differences between mixture components and corresponding monocultures. In the other three cases, where double depressions were found, only the depression of one mixture component was correctly predicted. Apparent reversals of dominance between T1 and T2 were correctly predicted for the two mixtures containing Selkirk (Fig. 5.9). It seems then that, despite several potential sources of error in the comparisons, there was fair qualitative agreement between predicted photosynthesis and observed yields at harvest.

Although the above comparisons cannot be taken as justifying confidence in quantitative predictions of the model; it is of extreme interest that the RYTs (based on daily photosynthetic accumulation) of 12 mixtures predicted using measured canopy structures and corresponding light regimes, lay between 0.994 and 1.098 (Fig. 5.8); their average value was 1.018. In spite of the extreme complexity and non-linearity of all parts of the system, at least gross photosynthetic accumulation on a daily basis is predicted to have an RYT close to unity. Although it may be unsafe to extrapolate from this prediction concerning daily rates to RYTs based on biomass yields, there seems nevertheless to be a strong possibility that, in mixtures grown with non-limiting soil conditions, RYTs of biomass may lie close to unity. Results obtained using this detailed photosynthesis model may thus support the suggestion of Section 3.1 that the proportional model applies to mixtures both where competition is for light and where it is for water.

8.6 Overyielding in theoretical mixtures

Warren Wilson (1960), Verhagen et al.(1963) and Duncan et al.(1967) have recognised that under certain conditions, the optimum canopy structure might consist of having leaves erect at the top of the canopy and leaves prostrate at the bottom.

Such a structure would be approached in a mixture of a tall, erect-leaved variety and a short, prostrate-leaved one. Having a near-optimum canopy structure, this type of mixture might photosynthesise faster than any other canopy and hence might overyield.

The mixture of Selkirk and Summit grown in the high-water soil bench was originally hoped to provide an example of such a canopy. However, detailed measurements of canopy structure showed that this was not so. Although the canopy of the shorter variety, Summit, had the greater percentage of drooped leaves it nevertheless had the more erectophile canopy.

Since an experimental example of a mixture canopy with a 'Warren Wilson-type' canopy was thus lacking, the photosynthesis model mentioned in the previous Section was used to explore the possibilities of overyielding due to morphological or physiological differences between the components of theoretical mixtures.

Firstly, the effects of differences of leaf inclination were tested. Using theoretical varieties with, in one case a prostrate-leaved, short canopy and in the other, an erect-leaved, tall canopy, a study was made of the predicted photosynthesis of mixtures and monocultures as a function of LAI. In three of the four light regimes considered (Fig. 7.2), the mixture was expected to have the highest photosynthesis rate at LAIs of between 3 and about 6. At such LAIs, the prostrate-leaved monoculture was relatively inefficient because it did not allow enough light to penetrate to the lower leaves. Similarly, the erect-leaved canopy was inefficient because it let too much light pass through to the soil. In the mixture, however, it can be supposed that any excessive penetration of light was prevented by the planophile, lower canopy; similarly, uniform sharing of the light between all leaves was favoured by the erectophile upper canopy. Disadvantageous characteristics of pure canopy types were mutually compensated for.

Essentially similar results to these were obtained by Verhagen et al. (1963). In the present case, however, the use of a more elaborate light penetration model showed low light levels (as measured on a horizontal sensor) to have differing results depending on whether the low levels are caused by low solar elevation or by cloud cover (Fig. 7.2c & d). In the former case, no mixture advantage was expected at all. In the latter case a mixture advantage was predicted between LAI 3 and 9. For the mixture to have a predicted photosynthetic advantage, the mean weighted angle of incidence of incoming light must apparently be relatively high (Section 7.3).

After considering the effects of mixing canopies differing in leaf inclination, the effect of mixing genotypes with different leaf photosynthesis-irradiance (P:I) curves was tested. The gross P:I curve chosen for the shorter component imitated approximately the <u>net</u> photosynthesis:irradiance of the leaf of a 'shade' plant (Böhning & Burnside 1956) and the gross P:I curve of the taller component imitated the <u>net</u> P:I relationship of a 'sun' plant. Again in an intermediate range of LAI, a photosynthetic advantage was predicted for the mixture but the advantage was very slight (Fig. 7.4b).

When, however, differences of leaf inclination and P:I curve were combined, a maximum 8% advantage was predicted for the mixture at LAI 5. At all LAIs between 1 and more than 9, the mixture was expected to photosynthesise faster than either monoculture. The theoretical basis for Donald's (1963) suggestion that a combination of a tall sun-species with a short shade-species might overyield, has clearly been confirmed.

It may be questioned, however, whether such advantages can be realistically hoped for in varietal mixtures of wheat. The difference of leaf inclination (15° and 75°) used in the simulations is probably close to the maximum achievable through breeding; the light regime used (0° latitude, equinox) is almost certainly the one most favourable of any on earth to the attainment of a mixture advantage. The contrasts of P:I curves used (Fig. 7.4a) appear unlikely to be easily found within such an obvious sun-species as Triticum aestivum and hence represent only a theoretical possibility. Furthermore, degrees of overlap of the contrasting canopies and the presence of stems have been shown (Fig. 7.3 and Table 7.1) to reduce or nullify advantages predicted for mixtures.

At first sight, it might appear that mixture advantages of daily photosynthesis of the order of a few percent, maintained over a period of growth, might accumulate to produce quite significant yield advantages for the mixture. Results obtained with a simple growth model suggested that the overyielding due to differing leaf inclinations and leaf P:I curves might exceed 7% if LAIs exceeded 6. Other mixtures, however, were predicted to overyield by not more than 2% by the time they had reached LAI 6. Discounting the 7% case as requiring unrealistic physiological differences, and bearing in mind that all predictions are maximum estimates, it must be concluded from the present studies, that marked overyielding through the more efficient use of light in mixtures is unlikely. The attributing of cases of overyielding to such an effect (van den Bergh 1968, Rhodes 1968) may be unjustifiable.

8.7 Concluding remarks

According to the available evidence, there seems to be little chance of finding inter-varietal mixtures of cereal genotypes which regularly, across a range of conditions, give agriculturally significant overyielding of dry matter. This study has failed to find any such mixtures and further has shown that, at least under certain conditions, the yield advantage to be expected of mixtures would be small. Hence, very many replications of a field experiment may be necessary to obtain sufficiently reliable estimates of yield in any site or season to permit the identification of overyielding mixtures which offer high probability of giving the same kind of result in another, but similar, site and season. What evidence there is indicates that the ranking of mixture and monoculture yields is highly sensitive to changes of conditions. Hence, at least in the disease- and pest-free environment postulated at the outset, the use of intervarietal mixtures provides little promise of useful increases in dry matter production by cereal crops.

9. ACKNOWLEDGEMENTS

I gratefully acknowledge a post-graduate studentship provided by the Wheat Research Council of South Australia.

It is a pleasure to thank Professor C.M.Donald for his interest in the project, for long discussions, and for his numerous helpful suggestions for the improvement of drafts of this thesis. I thank Mr. G.N.Wilkinson and Dr. D.A.Ratkowsky for advice on some of the biometrical aspects of the work. Many of the staff of the Agronomy Department, W.A.R.I., have been consulted on individual points and have kindly offered comments. I am particularly grateful to Mr. J.Hutton, CSIRO Division of Soils, for his help in carrying out the silicon analysis, to Mr. L.G.Veitch, CSIRO Division of Mathematical Statistics, for performing some of the regression analyses, to Professor W.G.Duncan, Department of Agronomy, University of Kentucky, for providing a copy of this programme for the prediction of photosynthesis, and to Dr. C.A.McGilchrist, School of Applied Mathematics, University of New South Wales, for this critical reading of the parts of the thesis concerned with the analysis of mixture experiments. The staff of the Biometry Department, W.A.R.I., also gave liberal advice on details of programming and the analysis of experiments.

I am much indebted to members of the technical staff of the Agronomy and other Departments at the Waite Institute for their willing and cheerful assistance, to Mr. E.Taylor for help with the conduct of the experiments, to Mr. E.Leaney for the construction of apparatus, to Mr. T.Sherwin for help with the use of the X-ray fluorescence spectrometer, to Miss C.Norman for drawing the Figures, and to Mr. B.Palk for the photography. I thank my wife for her encouragement and forbearance, and for typing this thesis.

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11. APPENDIX

11.1 Proof of Fig. 3.6

The concept of the Relative Yield Total, RYT, of a mixture of two genotypes was introduced in Section 2.11. In a 1:1 mixture of genotypes 1 and 2, the RYT is given as

$$RYT_{12} = \left(\frac{Y_{12}}{Y_{11}} + \frac{Y_{21}}{Y_{22}}\right) / 2$$

where Y_{11} and Y_{22} are the per-plant yields of genotype 1, the higher-yielding monoculture, and of genotype 2, the lower-yielding monoculture, respectively; Y_{12} and Y_{21} are the per-plant yields in mixture of genotypes 1 and 2 respectively.

If $Y_{11}/Y_{22} = P$, we have

$$RYT_{12} = \left(\frac{Y_{12}}{Y_{11}} + \frac{PY_{21}}{Y_{11}}\right) / 2$$

Taking M_{12} as the overall average per-plant yield in the mixture, we write $Y_{21} = 2M_{12} - Y_{12}$. Substitution gives

$$RYT_{12} = \left(\frac{Y_{12}}{Y_{11}} + \frac{P(2M_{12} - Y_{12})}{Y_{11}}\right) / 2 \qquad (11.1)$$

Let us consider the relationship between these variables when the mixture yield is the same as that of the higher-yielding monoculture, i.e. $M_{12} = Y_{11}$:

$$RYT = \frac{Y_{12}}{2Y_{11}} + \frac{P(2Y_{11} - Y_{12})}{2Y_{11}}$$

$$= \frac{Y_{12}}{2Y_{11}} - \frac{Y_{12}P}{2Y_{11}} + P$$

(see on)

$$= \frac{Y_{12}(1-P)}{2Y_{11}} + P$$

The RHS can be rearranged to show more clearly that this equation describes a family of straight lines relating RYT to values of Y_{12}/Y_{11} for a series of values of P.

$$RYT_{12} = \frac{(1-P)}{2} \cdot \frac{Y_{12}}{Y_{11}} + P$$

This last equation has been used to draw the lines above the horizontal axis of Fig. 3.6; these lines indicate the RYT values which have to be exceeded for the mixture to overyield. Since $Y_{11} > Y_{22}$, $P > 1$ and the slope is negative. An exception is the special case of $Y_{11} = Y_{22}$, when the line coincides with the horizontal axis.

Similarly, to find the value of RYT below which a mixture underyields, we set $M_{12} = Y_{22} = Y_{11}/P$ and substitute into Eqn. 11.1 :

$$RYT_{12} = \frac{Y_{12}}{2Y_{11}} + \frac{P(2Y_{11}/P-Y_{12})}{2Y_{11}}$$

$$= \frac{Y_{12}}{2Y_{11}} - \frac{Y_{12}P}{2Y_{11}} + 1$$

$$= \frac{Y_{12}(1-P)}{2Y_{11}} + 1$$

$$= \frac{(1-P)}{2} \cdot \frac{Y_{12}}{Y_{11}} + 1$$

This last equation has been used to draw the family of lines below the horizontal axis in Fig. 3.6. Again, except in the case of $Y_{11} = Y_{22}$, the lines have negative slope.

11.2 Experimental results of biomass in the two field diallel experiments.

The figures in the bodies of the tables are the means of 4 replicate plots.

Diallel 1

(a) Low density

	DES	India	Napo	Pitic	Selkirk	Summit
DES	14.25	12.16	13.02	14.54	16.74	13.03
India	11.78	10.32	10.54	12.19	9.53	11.90
Napo	15.06	12.95	14.62	14.56	17.53	16.58
Pitic	14.21	12.96	13.33	12.44	14.44	12.48
Selkirk	8.71	9.12	7.83	8.33	9.91	6.90
Summit	10.90	11.82	9.60	9.72	10.98	9.04
Column means	12.48	11.56	11.49	11.97	13.19	11.65

(b) High density

	DES	India	Napo	Pitic	Selkirk	Summit
DES	4.30	3.88	4.14	4.34	6.12	4.89
India	3.92	3.82	4.41	4.09	4.80	4.27
Napo	4.74	3.94	4.77	4.95	5.31	6.07
Pitic	3.63	3.80	4.25	3.85	5.44	5.02
Selkirk	2.23	2.05	1.82	2.49	3.79	2.81
Summit	2.94	3.01	3.05	3.11	4.61	3.06
Column means	3.63	3.42	3.74	3.81	5.01	4.35

Diallel 2

(a) Low density

	CT	Giza	Heron	Justin	Klein	Mentana
CT	11.76	8.24	11.24	11.90	10.26	12.26
Giza	11.26	12.22	11.83	13.12	13.85	13.56
Heron	12.13	9.99	10.95	10.81	11.52	11.79
Justin	11.26	9.81	11.60	12.24	9.22	10.97
Klein	11.82	10.65	12.20	12.34	13.25	12.18
Mentana	14.97	11.86	12.88	13.46	12.12	12.15
Column means	12.20	10.46	11.78	12.31	11.70	12.15

(b) High density

	CT	Giza	Heron	Justin	Klein	Mentana
CT	4.22	3.04	4.19	3.77	3.88	3.82
Giza	5.07	3.94	5.04	4.65	3.84	4.64
Heron	4.34	3.03	4.16	4.48	3.56	3.72
Justin	3.91	2.42	3.76	3.97	3.24	3.54
Klein	4.89	3.22	4.67	4.54	4.38	4.71
Mentana	4.49	3.46	4.65	4.62	4.43	3.99
Column means	4.49	3.19	4.41	4.34	3.89	4.07

11.3 Analysis of variance tables for the McGilchrist-Trenbath analysis of biomass data from the field diallel experiments.

Diallel 1

Source of variation	D.F.	Low density M.S.	Low density V.R.	High density M.S.	High density V.R.
Differences between monocultures					
Varieties	5	0.1610	7.4807**	0.0914	4.0184*
Replicates	3	0.0744	3.4593*	0.0108	0.4756
Error	15	0.0215		0.0227	
RYT					
Mean (1-RYT)	1	0.1198	0.8000	0.0358	0.2391
RYT variety effects ($\hat{\lambda}_i$)	5	0.0574	0.6740	0.1288	1.5789
Interaction ($\hat{\tau}_{ij}$)	9	0.0430	1.0194	0.0360	0.9968
Replicates	3	0.3183	7.5485***	0.0586	1.6221
Error	42	0.0422		0.0361	
Aggressivity					
Aggressivity variety effects ($\hat{k}_i$)	5	0.2668	2.3340	1.1806	11.2580***
Interaction ($\hat{\theta}_{ij}$)	10	0.0466	0.9378	0.0320	0.8737
Error	45	0.0249		0.0183	

Diallel 2

Source of variation		Low density		High density	
	D.F.	M.S.	V.R.	M.S.	V.R.
Differences between monocultures					
Varieties	5	0.0165	1.3265	0.0061	0.6187
Replicates	3	0.0259	2.0685	0.0144	1.4516
Error	15	0.0124		0.0099	
RYT					
Mean (1-RYT)	1	0.1113	1.2743	0.0179	0.2507
RYT variety effects ($\hat{\lambda}_i$)	5	0.0941	1.8768	0.0500	1.1997
Interaction ($\hat{T}_{ij}$)	9	0.0361	1.4236	0.0190	0.8688
Replicates	3	0.0467	1.8427	0.0454	2.0740
Error	42	0.0253		0.0219	
Aggressivity					
Aggressivity variety effects (K_i)	5	0.1467	2.2970	0.5660	8.3656***
Interaction ($\hat{\theta}_{ij}$)	10	0.0111	0.4172	0.0062	0.1623
Error	45	0.0133		0.0190	

11.4 Measurements made on 'test plants' and the derivation of tables of the distribution of the inclination of photosynthetic area (DIPA).

Representative 'test plants' were selected in the plots of the monocultures in the high-water treatment of the soil bench and from measurements made on these, DIPA tables were constructed. The details of the procedure are described in this Appendix.

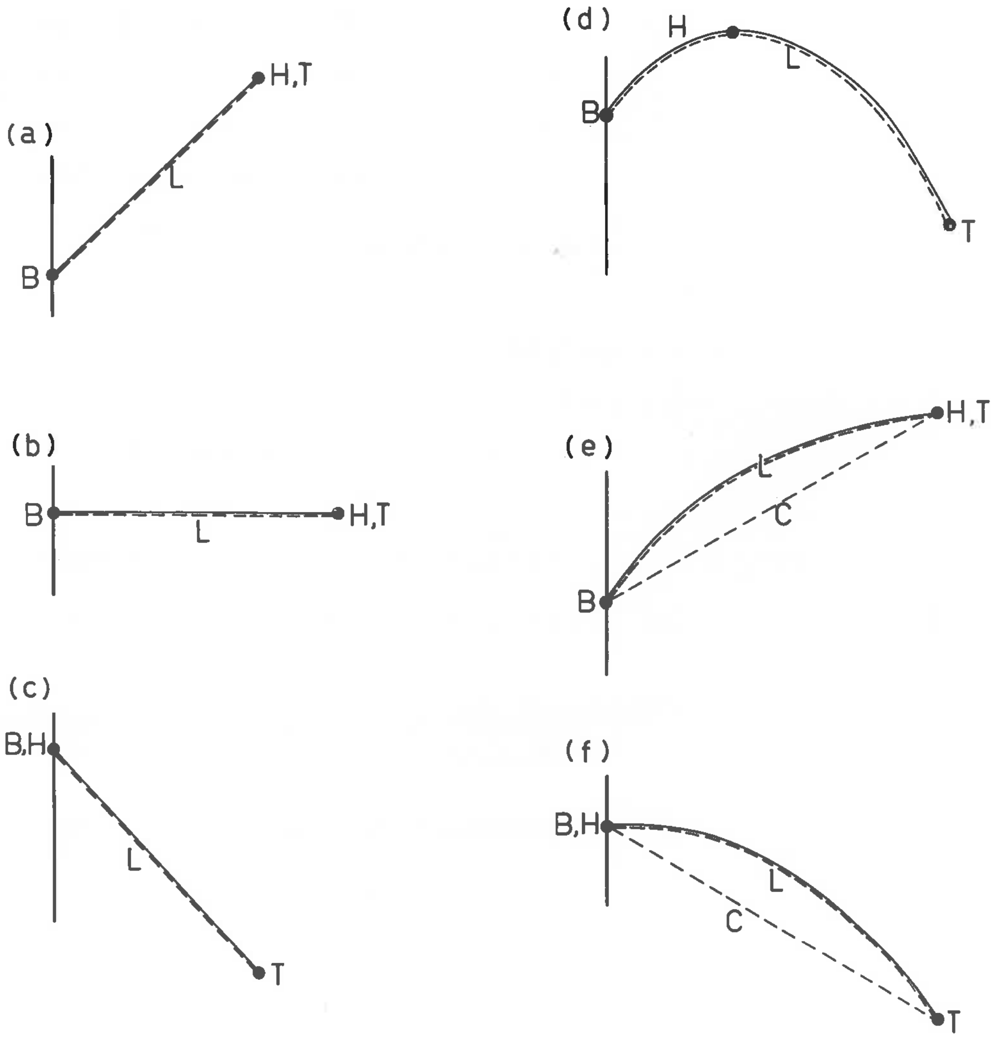
A horizontal metal bar was arranged at a standard height above the centre of the plant and a vertical pointer was lowered so that its tip made contact with certain points on the plant. A reversed scale on the pointer, read at the place where it was at the level of the top of the bar, indicated the distance from the ground of the tip of the pointer. With this device, the height of the tip of each stem and ear of the 'test plant' was determined.

The heights of points measured on various types of leaf are shown diagrammatically as black circles in Fig. 11.1. Heights were measured of the highest point of the leaf (H) and of the positions of the tip (T) and the base of the lamina (B). Leaves of the type shown in Figs. 11.1a, b & c will be termed 'straight-ascending', 'straight-horizontal' and 'straight-descending' respectively. Curved leaves may either be 'drooped' (Fig. 11.1d) or 'curved-ascending' (Fig 11.1e) or 'curved-descending' (Fig. 11.1f). The three straight types (Fig. 11.1a, b and c) are recognised respectively by measurements of height in which $H = T > B$, $H = T = B$, and $H = B > T$. The drooped type (Fig. 11.1d) is recognised by $H > \max(B, T)$. The curved types (Fig. 11.1e & f) are recognised by the addition of a further measurement to those indicating $H = T > B$ and $H = B > T$ namely the distance (C) between the leaf tip and the base.

Fig. 11.1 The measurements required to characterise six types of leaf posture. The points at which height measurements are made are shown as black-filled circles, Measurements of length are indicated by broken lines. Meaning of the letters :

H - highest point of leaf
T - tip
L - length
B - base
C - chord of a notional arc of a circle

(a) 'straight-ascending' characterised by $H = T\ B$
(b) 'straight-horizontal' " " $H = T = B$
(c) 'straight-descending' " " $H = B\ \ T$
(d) 'drooped' " " $H\ \ \max(B,T)$
(e) 'curved-ascending' " " $H = T\ \ B$; C
(f) 'curved-descending' " " $H = B\ \ T$; C


(a)
H,T
L
B
(b)
B
L
H,T
(c)
B,H
L
T
(d)
H
L
B
T
(e)
H,T
L
C
B
(f)
B,H
L
C
T

The use made of these measurements will be explained presently.

Other measurements made on the 'test' plant were the width, half-way along the ear, of the wider of the two sorts of 'face', the diameters of the top and bottom of each stem, the length (L) of each leaf and its width half-way along its length. To allow the measurements to be made with as little prior disturbance as possible, the leaves on each stem were measured from the top downwards. The measurement of L and to a lesser extent of C caused some disturbance of the canopy, but it was felt that the method caused only an insignificant change in the DIPA of the whole plot.

The calculation of the DIPA table of a plot from the measurements described above proceeded in three phases. Firstly, the forms of the individual leaves were reconstituted from the data and drawn to scale on graph paper starting at the appropriate height. The profiles of the straight leaves were easily reconstructed since B, T and L together fully defined the leaf's profile. The profiles of drooped leaves were drawn using a piece of flexible wire of length L; this was manipulated until the conditions implied by B, H and T were fulfilled and the curve approximated a parabola. Mathematically. such a curve is fully defined. A parabola was chosen since the profiles of most drooped leaves quite closely approached a parabolic form (see Plates 5.1, 6.2 and 6.3). The curved but undrooped categories were approximated by arcs of circles using the same technique. The radius of curvature was defined by the difference between L and C.

The second phase involved the assumption that the flat surfaces of the laminae of all leaves were rectangular as far as half-way to their tip, and thereafter triangular. Making this assumption the areas of the segments in each of three inclination catagories (0°-30°, 30°-60°, and 60°-90°) in each 10 cm layer were calculated and accumulated in a m x 3 array (m layers and 3 inclination classes). Multiplication throughout by a factor (1/60 = 0.0167) converted leaf area in cm^2/plant into LAI

Lastly, the stems and ears were considered. The stem area in a series of 10 cm layers was calculated on the assumption that stems had the form of vertical cylinders; the diameter taken was the mean of the values at the top and at the bottom of the stem. All stems were considered to be covered with photosynthetic surface down to the bottom of the layer in which the lowest green leaf had its ligule. If present, ears were taken to be square in cross-section and to have vertical sides. The ends of the assumed cuboids were ignored. For each 10 cm layer, the ear area was calculated and the summed value of stem and ear area was multiplied by the same factor (0.0167) as was applied to the leaves. This gave m values of 'vertical' photosynthetic area in units equivalent to these of LAI, these values constituted the fourth column of the m x 4 DIPA table.

11.5 Description of simulation programme DAYP

11.5.1 Introduction

The programme DAYP has been used in Sections 5 and 7 to predict the gross photosynthesis rate of actual and theoretical canopies. The programme itself and the underlying model are considered in this appendix.

The theoretical treatment follows closely that described in Duncan et al.(1967). W.G.Duncan has very kindly supplied a copy of a two-species version of his programme, but apart from its usefulness as a reference, only the segment on the redistribution of scattered radiation has in fact been utilized in the present programme. The detailed modelling of the photosynthetic effect of stems (and leaf sheaths) is attempted here for the first time. Other changes from the approach used by Duncan and his colleagues are mentioned below.

The course of the calculations and the experimental data on which the model is based are described in numbered sections which correspond closely to parts of the programme. A short summary of the functions of each part is given first, followed by a more discursive account.

11.5.2 Functions of the parts of DAYP

Part 1 reads input physical and biological parameters, a series of physical tables and some variables which control the form of the printed output.

The physical data specify the latitude, date and sky conditions. The biological data specify the number of genotypes, the canopy structure of the one or two genotypes (by the corresponding number of DIPA tables), the reflectivity of leaf and stem surfaces, the transmissivity of a leaf, the leaf gross P : irradiance curve (by two parameters P_{max} and K_m) for each layer, and a factor by which the photosynthesis of the stems may be reduced if a lower P:I curve is to be specified for the stems.

The physical tables read in include:

(a) Walsh's (1961) table of declination of the sun at 15-day intervals throughout the year. Values at other dates are found by linear interpolation.

(b) A table kindly supplied by W.G.Duncan (based principally on data of Kimball & Hand, 1921) giving sun and sky brightness for 1°-degree steps of sun elevation between 1° and 90°. Sun brightness is measured as the irradiance (cals/cm^2/min, all wavelengths) due to sunlight only of a surface normal to the sun's rays; sky brightness is measured as the irradiance, due to skylight only, of an unshaded horizontal surface.

(c) A table supplied by W.G.Duncan based on calculations of R. Hanau giving the fraction of reflected and transmitted light falling within vertically-directed cones whose vertices are at the point of incidence of a pencil of sunlight on a leaf surface. Since only three leaf-inclination classes are used, only three values are given, for leaves having inclinations of 15°, 45° and 75°.

(d) A table of the Warren Wilson-Reeve (Warren Wilson 1960) shadow ratio with respect to parallel rays of light arriving from an elevation β at a leaf inclined at angle α to the horizontal (α and β are given in steps of 5°). It is the average area of shadow cast by a leaf onto a surface normal to the incoming rays (when all azimuth positions of the leaf are equally probable) expressed as a ratio of the area of the leaf itself.

The possible forms which the output may take are described in Part 14. Values of the variables which control the output are read in with the data.

Part 2 finds hourly sun elevations, sun and sky brightness for the hour about noon and at hourly intervals throughout the rest of the day.

The solar elevation β is found using the equation given by Walsh (1961)

$$\sin \beta = \sin L \sin D + \cos L \cos D \cos(15H)$$

where L is the latitude, D is the declination of the sun for the time of year, and H is the number of hours away from solar noon (L and D are given in degrees). The solar elevation is found for noon and the rest of the hours in the day. The values of sun and sky brightness are drawn from Duncan's tables. To bring them to units of radiation in the range $0.4\,\mu - 0.7\,\mu$, they are multiplied by the approximate factor 0.45 (Begg & Jarvis 1968).

Part 3 finds cumulative leaf areas in the various inclination classes down to the lower limits and to the middles of the layers.

Part 4 finds, for each layer, the fraction of the skylight coming from the various sky zones which penetrates to the middle of the layer. The fractions are the 'interception factors'.

The contribution of skylight to the irradiance of leaves is treated first.

The whole sky is assumed to be a hemisphere of uniform radiance; it is divided into 6 equal-angle sky zones. The lowest zone is from elevations 0° to 15°, the second from elevations 15° to 30°, and so on. Let us consider a sky zone with a mid-angle β (measured as an elevation) and take the penetration of radiation into the canopy from this mid-angle to represent the penetration of radiation from the whole of this sky zone. Radiation entering the canopy from a very narrow sky zone of elevation $\beta \pm \Delta\beta$ in all azimuth directions will suffer interception by leaves so that when it has passed through a leaf area, A, and reached the middle of the layer under consideration, it will have been reduced by a factor, Q, so that

$$I_A = I_Z Q$$

where I_Z is the irradiance due to the narrow sky zone measured on a horizontal surface above the crop, I_A is the same measured under a leaf area index of A, and Q is the interception factor for the zone.

For a canopy of randomly dispersed, randomly orientated small leaves, inclined to the horizontal with angle α, the interception factor Q is the same for all azimuth angles, and is given by

$$Q = \exp(-A\, S_{\alpha\beta} / \sin\beta)$$

where $S_{\alpha\beta}$ is the Warren-Wilson-Reeve (1960) shadow ratio appropriate for an inclination β of the path of the radiation and an inclination α of the leaf surfaces. Since A consists of leaf areas a_1, a_2 and a_3 in the three inclination classes, three terms need to be summed to find Q :

$$Q = \exp\left[- (a_1 S_{15°,\beta} + a_2 S_{45°,\beta} + a_3 S_{75°,\beta}) / \sin\beta \right] \quad (11.2)$$

The effect of stems is introduced by adding a fourth term in Eqn. 11.2. To allow this term to be defined, some assumptions are first made. It is assumed that stems, like leaves, can be represented by small, randomly-dispersed segments. Unlike leaves, the stem segments are assumed to have only vertical surfaces (the 'cut' ends are ignored), and to be cylindrical in shape. The sideways-projected area of a stem area index of A_{stem} is A_{stem}/π . The shadow ratio analogous to $S_{\alpha\beta}$ of the leaves is $\cos\beta$, and so if only stems are present, the interception factor is

$$Q \quad = \quad \exp\,(-A_{stem}\,\cos\beta/\pi\,\sin\beta)$$

The stem term to be added to the numerator of the exponent in Eqn. 11.2 is thus $-A_{stem}\cos\beta/\pi$.

Using these expressions, interference factors are calculated to the mid-point of each layer for the six equal-angle zones of sky (contrast Duncan's equal-area sky zones).

__Part 5__ finds, for each leaf inclination class, the irradiance which is due to each of the sky zones. These irradiances are expressed as fractions of that of an unshaded horizontal surface due only to radiation from the same zone.

Hanau (appendix of Duncan __et al.__, __loc.cit__) has presented a series of expressions which allow the evaluation of the irradiance due to skylight, of a leaf surface inclined at any angle α. Suppose that the index of sky brightness is, as here, the irradiance of an unshaded horizontal plane due to the sky light; if the irradiance of the horizontal plane is B cal/cm^2/min *, Hanau's method can find the fraction, e_i, of this irradiance which the inclined leaf gains from the i-th sky zone. Thus, this sky zone contributes $e_i B$ cal/cm^2/min of irradiance to the leaf. The irradiance of a leaf due to the whole sky can then be calculated as the sum of the contributions of the six 15° sky zones, each reduced by an appropriate interference factor, Q_i $(i = 1, 2, \ldots, 6)$.

With 3 leaf inclination classes and the hemisphere of the sky divided into 6 equal-angle zones, the angle, α, of a leaf inclination class always coincides with the junction between two sky zones. Sky zones are thus of two types:

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* Derived from Duncan's table of sky brightness by multiplying it by 0.45 to bring it to cal/cm^2/min in the range of wavelengths 0.4 - 0.7 μ.

those defined by elevations greater than α and those with elevations less than α. The first expression, e_A, leads to a value for the irradiance of the upper side of a leaf due to a sky zone lying above the angle α. The other two expressions, e_B and e_C, give the irradiance of respectively the upper and lower leaf surfaces due to the parts of a sky zone which lies below α. Hanau's expressions are given below. The first is

$$\pi e_A = \pi \cos \alpha \sin (d_a + d_i) \sin (d_a - d_i)$$

where d_a and d_i are respectively the greater and smaller angles, here measured from the zenith, limiting the sky zones considered.

The second expression is

$$\begin{aligned} \pi e_B = \ & \cos\alpha \Big[\sin^2 d_a \cos^{-1} (-\tan\alpha \tan d_a)^{-1} \\ & -\sin^2 d_i \cos^{-1} (-\tan\alpha \tan d_i)^{-1} \Big] \\ & + \sin^{-1} \left[\cos d_i / \sin\alpha\right] - \sin^{-1} \left[\cos d_i / \sin\alpha\right] \\ & + \cos d_i \left[-\cos(\alpha + d_i) \cos(\alpha - d_i)\right]^{\frac{1}{2}} \\ & - \cos d_a \left[-\cos(\alpha + d_a) \cos(\alpha - d_a)\right]^{\frac{1}{2}} \end{aligned}$$

The expression for πe_C is similar to that for πe_B except that the first term with square brackets is replaced by

$$\begin{aligned} & \cos\alpha \Big[\sin^2 d_i \cos^{-1}(+\tan\alpha \tan d_i)^{-1} \\ & - \sin^2 d_a \cos^{-1}(+\tan\alpha \tan d_a)^{-1}\Big] \end{aligned}$$

Finally the total sky contribution, I_S, to the irradiance of each leaf inclination class in each layer is calculated as

$$I_S = B \sum_{i=1}^{6} e_i Q_i$$

where B is the irradiance due to the sky of an unshaded horizontal surface. Those sky zones higher in the sky than α have their e_i calculated using e_A, whereas the e_i of the others is the sum of an e_B and an e_C.

When the above calculations have been performed for the leaf classes with $\alpha = 15^\circ$, 45° and 75°, the same procedure is used for finding the irradiance of the stem class due to skylight. Since $\alpha = 90^\circ$, e_B is the appropriate expression for finding the irradiance due to each of the 6 sky zones. The other expressions are not used at all.

Part 6 finds the sunlit leaf and stem area by inclination classes and layers. A result is calculated for each of a series of relative positions of the inclination classes within the layer, and these results are averaged.

The first stage in this calculation is to find for each layer the fraction of the original area of sunlight which enters the layer (the area of sunlight above the canopy is taken as unity), the fraction which leaves it, and by subtraction, find how much of the area of sunlight has been intercepted by the layer. The intercepted area of sunlight is given by:

$$(A_{in} - A_{out}) = A_{in} - A_{in}Q = A_{in}(1-Q)$$

where A_{in} and A_{out} are the areas of sunlight, expressed as fractions of unity, entering and leaving the layer; Q is as defined in Eqn. 11.2 including the stem term, $-A_{stem}\cos\beta/\pi$, in the numerator if stems are present. This same procedure is then used for each leaf inclination class and the stem class **within** the layer. This shows how much of the area of sunlight absorbed by the layer is absorbed by each category of surface within the layer. Since the intercepted area of sunlight is calculated for the angle at which sunlight enters the canopy, a low solar elevation will mean that foliage or stem irradiated by unit area of sunlight (measured normal to the sun) will be spread out horizontally in the canopy outside the volume above the unit area of soil surface to which all leaf area and indeed, the whole model, is referred. To reduce the intercepted area of sunlight to that due to the surfaces in just that part of the layer above the reference area of soil, it is multiplied by sin β . Further, to convert the area of shadow cast by a leaf or stem class (i.e. the intercepted area of sunlight) to actual area of photosynthetic surface, the area of shadow is divided by a shadow ratio:

$$\text{area of sunlit surface} = \frac{\text{area of shadow}}{\text{area of shadow}/\text{actual area of surface in sun}}$$

For a leaf class, then, the sunlit leaf area, $A_{\odot}$, is found by using the Warren Wilson-Reeve shadow ratio*:

$$A_{\odot} = (A_{in} - A_{out}) \frac{\sin\beta}{S_{\alpha\beta}}$$

In a stem class, the sunlit stem area, $A_{stem\odot}$, is found in a similar manner:

$$A_{stem\odot} = (A_{in} - A_{out}) \frac{\pi \sin\beta}{2\cos\beta}$$

The further treatment of the inclination classes in the present programme differs somewhat from that in the programme of Duncan et al. Duncan's programme assigns each inclination class to its own individual layer and gives each of these a fixed position in the model canopy. Duncan and his colleagues admit that the order might be important if the leaf area per layer were large.

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* The parentheses in this expression appear to have been omitted in the publication of Duncan et al. (1967), although they are present in the programme supplied by Duncan.

As an illustration, with 1.5 LAI units in each of three layers having leaf inclinations 15°, 45° and 75°, insertion of the layers in different orders causes up to a threefold variation of area of sunlight intercepted by a particular layer. This sort of error is reduced in the present programme by the use of the following method. If the usual 3 leaf inclination classes are present with a stem class in addition, these four classes are treated as sublayers of the layer in which they occur. The area of sunlight intercepted by each sublayer (inclination class) is calculated for a series of relative positions of the sublayers within the layer. The first position of the sublayer will be with the 15° inclination class on top, then the 45°- and 75°-classes, and the vertical stem class at the bottom. Subsequent positions will be produced by the bottom class coming to the top and the others moving down a place. The areas of sunlight intercepted by an inclination class are averaged and provide an estimate of the area of sunlit surface in that class in the layer being considered. Although with over two classes, not all permutations enter the calculation, this procedure probably removes some of the bias which would be introduced by using a fixed order of classes.

Part 7. For 13 azimuth positions of a sunlit leaf surface, the proportions of sunlight reflected and transmitted upwards, downwards, and into the leaf's own layer, are calculated. Reflected radiation from the stems is directed into the stems' own layer. Contributions from the various inclination classes in the layer are summed.

The sine of the angle, ψ , between a leaf surface and the sun is given (Walsh 1961) by

$$\sin\psi = \left|\cos\alpha \sin\beta - \sin\alpha \cos\beta \cos\xi\right| \qquad (11.3)$$

where ξ is the difference between the azimuth angles of the leaf and the sun (cf. de Wit, 1965, where leaf azimuth angle is defined in an unusual way, see his Fig. 7). The modulus sign is introduced to produce a positive value for sin ψ whether the sun light is striking the leaf on its upper or lower surface.

Assuming that leaves behave as Lambertian surfaces for reflection and transmission, Hanau (in Duncan et al., 1967) developed a method for calculating the proportion of the total reflected and transmitted radiation from a sunlit leaf, which is expected to leave the point of incidence of the sunlight in vertically directed cones upwards and downwards. His method applies for any leaf inclination and half-angle of the cone. Sunlight striking the upper surface contributes reflected radiation into the upper cone and transmitted radiation into the lower one. The converse applies for sunlight striking the lower leaf surface.

Duncan et al. considering a layer of leaves of uniform α, used Hanau's formulations to estimate the radiant flux due to reflection and transmission upwards from the leaf layer, downwards from it, and into the layer itself; they took the proportion of radiation leaving in a direction falling inside the cones to be that moving out from the layer up or down, and the rest was taken as adding to the irradiance of surfaces within the layer. A half angle of 35° was chosen to give an albedo in 'best agreement with the accepted measurements of albedo and estimated leaf properties' (p. 187, loc.cit.).

The treatment of reflected and transmitted radiation follows fairly closely that used by Duncan et al.(1967) but is here given in more explicit detail.

We consider first a layer in a simplified, stemless canopy in which all leaves are pointed in the same direction (i.e. all leaves have the same elevation, α , and azimuth angle, ξ). The flux, I_r, of reflected radiation away from a sunlit leaf will be determined by the reflectivity and the irradiance of the surface: *

$$I_r = f\, I_{\odot} \sin \qquad (11.4)$$

where f is the average reflectivity of the leaf surface over the range of visible wavelengths, and $I_{\odot}$ is the irradiance of an unshaded surface normal to the sun's rays. If the sunlit leaf area in the layer is $A_{\odot}$ and if the fraction of scattered radiation inside the cone of chosen half-angle is f_c, then the flux of radiation reflected 'upwards', $I_{r\uparrow}$, from these leaves is taken to be

$$I_{r\uparrow} = I_r f_c A_{\odot} \qquad (\text{for } \alpha < \beta)$$

The flux of diffuse radiation transmitted 'downwards' is similarly

$$I_{t\downarrow} = (t\, I_{\odot} \sin \psi)\, f_c A_{\odot} \qquad (\text{for } \alpha < \beta)$$

$$= I_t f_c A_{\odot}$$

where t is the light transmissivity of the leaves and I_t is a transmission term analogous to I_r in Eqn. 11.4 .

If the sunlight strikes the lower surface, then

$$I_{t\uparrow} = I_t f_c A_{\odot}$$

and

$$I_{r\downarrow} = I_r f_c A_{\odot}$$

However, the fluxes of transmitted light do not need to be calculated directly since they can be derived from the fluxes of reflected light.

The total upward flux, I_T , of reflected and transmitted light is given by

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* For simplicity, the present description assumes that the irradiance of a sunlit leaf is only due to direct sunlight. In the programme, however, the value of I_r is based on the total irradiance calculated as the sum of components due to sun, skylight and scattered radiation (see Part 9). Radiation scattered by leaves not lit by direct sunlight is ignored.

$$I_{T\uparrow} = I_{r\uparrow} + I_{t\uparrow} \qquad (11.5)$$

where I_t, the upward flux of transmitted light, is calculated as

$$I_{t\uparrow} = I_{r\downarrow} t/f$$

Similarly, the total downward flux, $I_{T\downarrow}$, is given by

$$I_{T\downarrow} = I_{r\downarrow} + I_{t\downarrow} \qquad (11.6)$$

where

$$I_{t\downarrow} = I_{r\uparrow} t/f$$

If the total quantity of radiation reflected in all directions is given by $I_r A_\Theta$ and the total quantity of radiation transmitted in all directions is given by a corresponding term, $I_t A_\Theta$, then the total quantity of radiation scattered, $I_{T\ scat}$, is found as the sum of its components:

$$\begin{aligned} I_{T\ scat} &= I_r A_\Theta + I_t A_\Theta \\ &= I_r A_\Theta + I_r A_\Theta \frac{t}{f} \\ &= I_r A_\Theta \left(1 + \frac{t}{f}\right) \qquad (11.7) \end{aligned}$$

The quantity of scattered radiation left in the layer is obtained by subtracting $I_{T\uparrow}$ and $I_{T\downarrow}$ from $I_{T\ scat}$:

$$I_{T\ell} = I_{T\ scat} - (I_{T\uparrow} + I_{T\downarrow}) \qquad (11.8)$$

Substituting into this relationship Eqns. 11.5, 11.6 and 11.7, we obtain

$$\begin{aligned} I_{T\ell} &= I_r A_\Theta \left(1 + \frac{t}{f}\right) - \left[I_r \left(1 + \frac{t}{f}\right) + I_r \left(1 + \frac{t}{f}\right)\right] \\ &= \left[I_r A_\Theta - (I_r + I_r)\right] \left(1 + \frac{t}{f}\right) \end{aligned}$$

The above expressions allow the calculation of upward and downward diffuse fluxes from a leaf layer and the quantity of scattered radiation remaining within the layer. It will be recalled however that they refer to a layer of leaves all having the same value of ψ. In the model, within a leaf inclination class, ψ varies with the azimuth, ξ, of the leaf. Since all azimuth positions are assumed to be equally probable, the above calculations are made for 12 equally-spaced values of ξ ranging from 7.5° to 172.5°, using in each case a value for $A_{@}$ equal to one-twelfth of the sunlit leaf area in the inclination class.

Twelve contributions are therefore summed to give each of the terms on the RHS of Eqn. 11.8. This equation provides an estimate, $I_{T\ell}$, of the scattered radiation which would remain in the layer if the inclination class considered were the only class present in the layer. Since in the present programme three leaf inclination classes appear in the same layer, a corresponding number of terms of the type $I_{T\ell}$ are calculated and summed. To this total, $\sum I_{T\ell}$, is added a contribution of reflected radiation from the stems.

If reflection from the stems is Lambertian rather than specular, most of the reflected radiation will leave the stem surface moving in a direction more or less parallel with the ground; relatively little will leave the stem within the vertically-directed cones mentioned above. Hence, all reflection from stems is added to the diffuse scattered radiation within the layer.

To calculate the magnitude of this stem contribution, the irradiance of the sunlit stem is estimated. To simplify the treatment required here (and also when considering stem photosynthesis) the stem cylinder is approximated by a column of the same surface area which in cross-section has the form of a regular octagon. Four faces of the column are taken as being directly irradiated when the stem is in the sunlight. One vertex of the octagon is supposed to be be always directed towards the sun so that the two faces subtending this vertex have the same irradiance. This irradiance is greater than that of the other pair of faces receiving direct sunlight. The values of the angle ψ between the sun and the two pairs of surfaces are 67.5° and 22.5° at sunset (i.e. when $\beta = 0^\circ$), in general, ψ must be found using Eqn. 11.3. The irradiance of the two types of surface are calculated using the values of ψ and Lambert's law (Eqn. 11.9). The stem contribution $I_{r\ stem}$, of reflected radiation is found as

$$I_{r\ stem} = rI_s \cos\beta(\cos 22.5^\circ + \cos 67.5^\circ)A_{stem\,e}/2$$

The provisional total of diffuse scattered radiation within the layer is now

$$I'_{scat\ell} = \Sigma I_{T\ell} + I_{r\ stem}$$

<u>Part 8</u> finds how much diffuse radiation is added to each layer by the movement up and down the profile of reflected and transmitted radiation. This suffers interception as it moves.

Duncan *et al.* (*loc. cit.*) made the simplifying assumption that the radiation moving out of a layer travels vertically. They suggested that interception occurs according to an equation such as

$$I_2 = I_1 (1 - A \cos\alpha)$$

where I_1 is the diffuse flux entering a layer and I_2 is that leaving it. They suggested that by ignoring self-shading of the leaves, such an equation would compensate for the underestimating of path lengths which resulted from the assumed vertical movement. This may be a reasonable assumption, but since with large values of A the flux I_2 would appear to be negative, the interception factor Q has been used in the present programme. With $\beta = 90^\circ$, Eqn. 11.2 simplifies to

$$Q = \exp(-a_1 \cos 15^\circ - a_2 \cos 45^\circ - a_3 \cos 75^\circ)$$

Such a form of expression for Q ignores the increased interception due to the bulk of this scattered light actually travelling obliquely but the quantities of radiation involved are very small.

The programme supplied by Duncan appears to assume that the moving scattered light suffers no interception in the layer of its origin but compensating for this, it is the downwards flux of this light at the bottom of each layer which is considered to be the flux added to that incident on all leaves throughout that layer. In the present work, the site of all scattering is taken instead to be the centre of each layer, interception occurs within that layer, and it is the flux at the centre which is added to the provisional total, to give the final total, $I_{scat\ell}$, of scattered radiation within the layer. This scattered radiation is considered to be totally diffuse while it is within a layer; it contributes uniformly to the irradiance of all leaves and stems in the layer.

<u>Part 9</u> finds the irradiance of a sunlit surface in 12 azimuth positions by inclinations and layers. The normally incident radiation is the sum of sunlight, skylight, and completely diffuse light derived from reflection and transmission.

Using the 12 azimuth positions referred to earlier, and the corresponding values of sin ψ already calculated, the irradiance, I_D, due to direct sunlight is calculated according to Lambert's law :

$$I_D = I_{\odot} \sin\psi \qquad (11.9)$$

To the direct irradiance in each position is added the skylight contribution, I_S, which is independent of azimuth but not of inclination, and also the contribution from scattered radiation which is independent of both azimuth and inclination. This last contribution is found by notionally spreading the diffuse radiation, $I_{scat\ell}$, evenly over all the photosynthetic area in the layer (including both sides of the leaf area) and calculating the increase of irradiance due to this source of radiation. Since Moss (1964) has demonstrated for gramineous leaves that irradiance of either side is equally effective in causing photosynthesis, the irradiance of the two sides is summed.

Part 10 finds the photosynthesis rates for 12 azimuth positions of a sunlit leaf surface by inclination classes and layers.

The gross photosynthesis-irradiance relationship is modelled by a Michaelis-type curve (Rabinowitch 1951, Monteith 1963):

$$P = \frac{P_{max} I}{K_m + I}$$

where P_{max} and K_m are specified for the layer and genotype in the input, and where I is the irradiance of the leaf. Expanding the irradiance term gives, for a particular leaf azimuth, inclination class and layer

$$P = \frac{P_{max} (I_{\odot} \mid A + B \cos \zeta \mid + C)}{K_m + I_{\odot} \mid A + B \cos \zeta \mid + C} \qquad (11.10)$$

where $A = \cos\alpha \sin\beta$

$B = \sin\alpha \cos\beta$

$C = I_S + I_{scat\ell} \dfrac{2}{2A + A_{stem}}$

Since no satisfactory integral of this expression with respect to ζ could be found, the average photosynthesis rate, $\bar{P}$, for a particular inclination class in a layer is found by approximating the integral in

$$\bar{P} = \frac{P_{max}}{180} \int_{0}^{180} \frac{I_{\odot} \mid A + B \cos \zeta \mid + C}{K_m + I_{\odot} \mid A + B \cos \zeta \mid + C} \cdot d\zeta \qquad (11.11)$$

by Simpson's rule. When $\alpha < \beta$, there is a marked discontinuity in the curve of Eqn. 11.10 at the point where

$$\xi = \cos^{-1}\left(\frac{\sin\beta\cos\alpha}{\cos\beta\sin\alpha}\right)$$

This is the point where ψ is zero and the leaf receives radiation only from the sky or scattering in the canopy. This minimum is so abrupt that the area under the curve immediately round it is approximated by trapezia. This more accurate method of approximating the integral in Eqn. 11.11 was introduced because the method used by Duncan et al. to evaluate $\bar{P}$ (i.e. averaging the P values at six azimuth positions) produced marked irregularities in the course of hourly photosynthesis. These were traced to sampling error in the choice of the six azimuth positions. If a point happened to fall in the trough near to the minimum, the average photosynthesis rate of sunlit leaves of all layers was apparently depressed for that hour.

The photosynthesis rates per unit area of sunlit leaf surface are converted to overall rates by multiplication by the area of foliage, in each inclination class and layer, which has been calculated to be sunlit.

Part 11 finds the photosynthesis rates of the shaded leaf areas using as normally incident radiation only skylight and the completely diffuse, scattered radiation from reflection and transmission.

Since these components of illumination depend only on leaf inclination and layer, no integration with respect to azimuth is necessary.

Part 12 finds the photosynthesis rates of the sunlit and shaded stem areas in each layer.

The total irradiance of the two pairs of sunlit faces of the stem are found by adding the contributions of skylight and scattered radiation to the irradiance due to direct sunlight, calculated in Part 7. The same photosynthesis:irradiance relationship is applied to the stem and leaf sheaths as is used for the leaf laminae, but it may be scaled by a factor to imitate a lower photosynthetic activity if required (Stålfelt 1935, Thorne 1959, Stoy 1965). Each of the two resulting P rates is multiplied by half of the sunlit stem area, and the sum of these results gives the rate of gross P for the whole of the sunlit stem area of the layer.

The P rate of the shaded stem area is calculated from the irradiance resulting only from skylight and scattered radiation. The contribution of the scattered radiation is only half that given to the leaves (i.e. it is $I_{scat\ell}/(2A + A_{stem})$).

<u>Part 13</u> sums photosynthesis rates over inclination classes to find the contribution of the various layers and then over layers giving the overall estimated gross photosynthesis in the current hour. When these calculations of photosynthesis have been carried out for noon and each succeeding hour till sunset, the estimated gross photosynthesis for the whole day is found by doubling all hourly values except that of the hour about noon, and summing the results.

<u>Part 14</u> controls the printed output in accordance with the values of certain variables which have been read in with the data (see Part 1).

The 'standard' output includes calculated hourly solar elevations, hourly sun and sky brightnesses, hourly profiles of direct solar and total visible radiation and hourly profiles of the photosynthesis of each genotype.

Optional extra output includes: an hourly analysis by layers and leaf inclinations of the income of diffuse radiation (from sky, from reflection and transmission within the layer and from movement in from other layers); an hourly analysis of the irradiance of leaves due to direct sunlight according to azimuth angle, inclination class and layer; hourly profiles of direct solar radiation and profiles, by genotypes, of photosynthesis by sunlit and shaded leaves.

11.6 Analysis of variance tables for the McGilchrist-Trenbath analysis of biomass data from the soil bench experiment.

		High-water treatment		Low-water treatment	
Source of variation	D.F.	M.S.	V.R.	M.S.	V.R.
Differences between monocultures					
Varieties	2	0.0102	4.1075	0.0198	0.8946
Replicates	2	0.0025	1.0071	0.0139	0.6263
Error	4	0.0025		0.0221	
RYT					
Mean (1-RYT)	1	0.0888	6.8905	0.2238	3.9112
RYT variety effects ($\hat{\lambda}_i$)	2	0.0108	1.1735	0.0176	0.7309
Interaction ($\hat{T}_{ij}$)	0	-	-	-	-
Replicates	2	0.0225	2.8354	0.0036	0.2770
Error	4	0.0079		0.0130	
Aggressivity					
Aggressivity variety effects ($\hat{k}_i$)	2	0.0010	0.0160	0.4159	6.8393*
Interaction ($\hat{\theta}_{ij}$)	1	0.0018	0.0288	0.0085	0.3070
Error	6	0.0310		0.0138	

11.7 Data of biomass, estimated transpiration and estimated Production Ratio in the low-water treatment of the soil bench experiment.

The data of biomass and of estimated transpiration are the means of three replicates. The data of Production Ratio and RYT were calculated directly from these means. These data correspond to the low-water part of Fig. 6.8.

(a) Biomass (g/plant)

	In the presence of:		
	Pitic	Selkirk	Summit
Pitic	4.78	5.38	4.07
Selkirk	2.67	4.15	2.35
Summit	4.80	5.12	4.63

(b) Estimated transpiration (kg/plant)

	In the presence of:		
	Pitic	Selkirk	Summit
Pitic	0.679	0.737	0.652
Selkirk	0.495	0.736	0.465
Summit	0.882	0.907	0.835

(c) Estimated Production Ratio (g/kg)

	In the presence of:		
	Pitic	Selkirk	Summit
Pitic	7.05	7.29	6.24
Selkirk	5.40	5.63	5.05
Summit	5.43	5.65	5.56