GERMINATION, ESTABLISHMENT, AND INTER-SPECIFIC COMPETITION IN TWO ANNUAL PASTURE GRASSES.

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STATEMENT

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

P. S. Cocks

SUMMARY

The annual grass *Hordeum leporinum* has been studied as a pasture plant in southern Australia. Study was directed to germination, establishment, and early vegetative growth following the first seasonal rains of autumn. Comparisons were made with *Lolium rigidum*, a less successful annual grass in pastures, and experiments were conducted on the competition between the two species.

Non-dormant seeds of both *H.leporinum* and *L.rigidum* are able to germinate over a similar temperature range, with an optimum of about 25°C. Both species can resist germination at high temperature without losing all viability. At all temperatures, *H.leporinum* germinates much more rapidly than L.rigidum.

The germination rate of both *H.leporinum* and *L.rigidum* is stimulated by short periods of pre-soaking. *L.rigidum*, which germinates more slowly than *H.leporinum*, requires a longer period of pre-soaking to achieve its maximum germination rate. Light rains which fall before the first seasonal rains usually wet seeds only for short periods, and this increases the advantage of *H.leporinum* over *L.rigidum* in rate of germination.

H.leporinum germinates much more readily from the soil surface than *L.rigidum*. The reasons are firstly its rapidity of germination which allows it to establish

before the soil surface dries out, and secondly its ability to germinate at high moisture tensions.

Seed of *H.leporinum* has a dormancy mechanism relieved by leaching, and decreasing with time. The inhibitor is located in both the sterile florets and in the central, fertile floret.

The seedling growth of *H.leporinum* and *L.rigidum* was studied at three temperatures in a controlled environment. At all temperatures tested (10°C, 17°C, and 24°C) the relative growth rate of *L.rigidum* is greater than that of *H.leporinum* with the difference greatest at 17°C. Seedling growth rate is more rapid during the period the endosperm is available then after endosperm exhaustion.

In spite of the superior relative growth rate of *L.rigidum*, seedlings of *H.leporinum*, because of the greater seed size, are larger in terms of total weight, leaf area, root weight, root depth and plant height, for a considerable period following seedling emergence. The length of this period of greater weight depends on temperature, being least at 17°C, when the advantage of *L.rigidum* in relative growth rate is greatest.

An hypothesis was developed about the outcome of vegetative competition between the two species based on these differences in seed size and relative growth rate. This hypothesis states that at high densities of *H.leporinum*, seedlings of *L.rigidum* will be shaded as they emerge, and because of their inferior root system at this stage, their roots will be less able to extract

nutrients from the soil. Thus they will be suppressed in competition with *H.leporinum*. At lower densities of *H.leporinum* however, interspecific competition may not begin until *L.rigidum* plants are the superior in size, and in this case *H.leporinum* seedlings will be suppressed. Consequently the outcome of competition will depend on the density of *H.leporinum*, but will be independent of the density of *L.rigidum*.

The hypothesis outlined above successfully predicted the outcome of competition between *H.leporinum* and *L.rigidum*. At high densities of itself, *H.leporinum* proved aggressive, but at low densities it was not aggressive, regardless of the density of *L.rigidum*. An "Index of Aggression" was devised to analyse the results, and the usefulness of this index compared to the usefulness of de Wit's (1960) "relative crowding coefficient".

Vegetative competition between *L.rigidum* and *H.leporinum* with separation of below ground parts was studied. The results suggest that *H.leporinum* competes successfully with *L.rigidum* because its roots explore the nutrient environment first. It thus depletes the supply of nutrients available to *L.rigidum*, and this leads to the suppression of the *L.rigidum* through an interaction between the competition for light and for nutrients.

Finally these experimental results are discussed in relation to the annual pastures of the Mediterranean environment of southern Australia. Various management practices which may assist in the control of the botanical composition of these pastures are assessed.

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1.0.0. INTRODUCTION

Annual plants are widespread throughout the pastures of the Mediterranean-type environment of southern Australia. Rossiter (1966) has estimated that more than 40 million acres of pasture have been sown to annual species in this area, while a considerably greater area has unsown annuals by natural ingress.

Mediterranean-type environments have cool, wet winters and hot, dry summers. The period during which pastures grow is restricted to the autumn, winter and spring, summer being a period of total, or almost total drought. The growing season begins following the first effective rainfall of the autumn, and ends during the spring or early summer. The length of the growing period depends on the locality and season, but ranges from 5 months to 9 months (Prescott and Thomas 1948-49).

The life-cycle of annual pastures in this environment is of interest. Following germination they grow rapidly during the autumn, more slowly in the winter when temperatures are lower, then very rapidly in early spring, reaching maturity when the soil dries out, usually in mid to late spring. The persistence of an annual species depends on its ability to set seed in spring before the onset of summer drought, to establish rapidly in the autumn so that it is potentially in a favourable competitive situation relative to other species, and to grow in the presence of the grazing animal for the remainder of the rainfall season.

One of the notable features about annual pastures is the great variation in their botanical composition, not only from site to site, but also from year to year.

This thesis is about the contribution to this variation of events at the beginning of the annual life-cycle, the phase of germination, establishment, and seedling competition which occurs each autumn. These events have been studied in relation to two annual grass species, *Hordeum leporinum* (barley grass) and *Lolium rigidum* (Wimmera ryegrass).

H. leporinum was apparently introduced into Australia soon after European settlement, and is now almost ubiquitous in the annual pastre zone of southern Australia (Smith 1966). It is a native of the Mediterranean region but now also occurs in North and South America (Covas, 1949, Rajhathy and Morrison 1962). Although it is never sown, it is considered a useful pasture plant by many farmers (Smith 1966), but the long, barbed awns of the seed have the disability of irritating the mouth, eyes and nose of cattle and sheep, or becoming entangled in wool. *L.rigidum*, on the other hand, is the only annual grass species which is commonly sown in annual pastures. It too, is a native of the Mediterranean region (Black 1952).

The literature review which follows this introduction is divided into several sections. Following a consideration of the Mediterranean environment, factors affecting the dormancy and germination of annual species are discussed. Then follow sections on seedling growth, and the effect of seedling density. The effect of climate is discussed, and the review ends with a brief recapitulation.

2.0.0. REVIEW OF THE LITERATURE

2.1.0. The Mediterranean environment and its plants

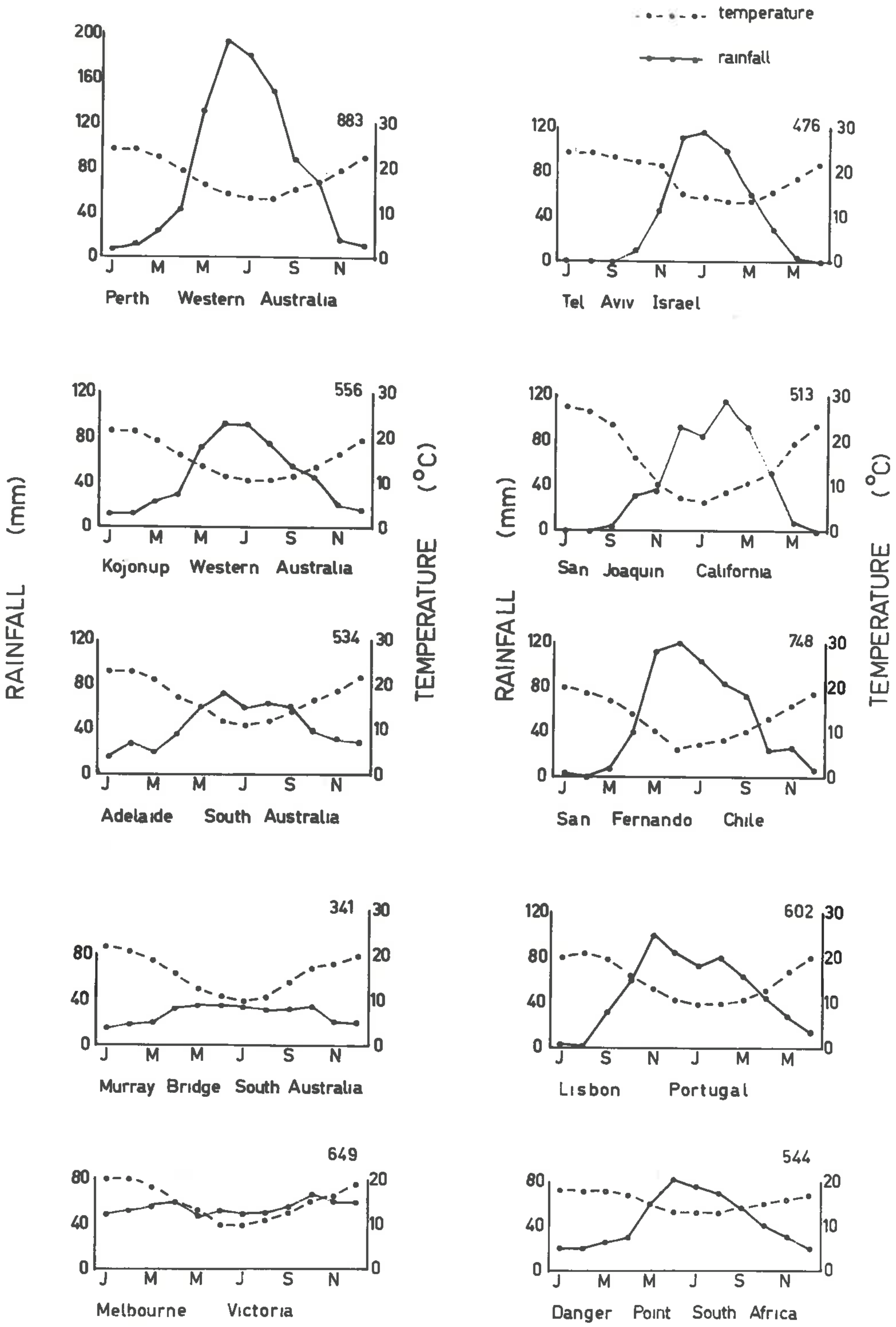
Annual pastures grow in south west and much of south east Australia, that part of Australia which experiences hot, dry summers, and cool, wet winters. This climate, typical of the Mediterranean basin, central and northern California, central Chile, and the south western tip of South Africa is known as the "Mediterranean climate".

Figure 1 shows a number of places with Mediterranean climates, in Australia and elsewhere. The Australian localities are shown in the column on the left, the chart at the top representing Perth, furthest west, and the chart at the bottom, Melbourne, furthest east. The column on the right shows localities from other parts of the world. Note that, in Australia, the western sites are more typical of Mediterranean environments elsewhere, than are the eastern sites.

The climate of south western Australia is similar to, but not as extreme, as that of the eastern Mediterranean. For example Tel Aviv has absolutely no summer rain, but at Perth, though summer is a period of intense drought, it is not rainless. In South Australia, (e.g. Adelaide) thunderstorms are frequent in summer, but rainfall is ineffective because of high temperatures and rapid evaporation. Further east (e.g. Melbourne), the climate comes under the influence of south east trade winds which bring rain in summer, and at least in some seasons, perennial pasture plants can grow throughout the year. Nevertheless great areas of southern Australia experience summers in which rainfall is insufficient to support pasture growth, and the successful pasture plants

Figure 1. Monthly rainfall and temperature at various centres with Mediterranean-type climate. The figure in the top right-hand corner of each chart is the annual rainfall in mm. Latitudes are as follows :

Perth	32°South	Tel Aviv	32°North
Kojonup	34°South	San Joaquin	37°North
Adelaide	35°South	San Fernando	34°South
Murray Bridge	35°South	Lisbon	39°North
Melbourne	38°South	Danger Point	34°South


temperature
rainfall
RAINFALL (mm)
TEMPERATURE (°C)
Perth Western Australia
883
Tel Aviv Israel
476
Kojonup Western Australia
556
San Joaquin California
513
Adelaide South Australia
534
San Fernando Chile
748
Murray Bridge South Australia
341
Lisbon Portugal
602
Melbourne Victoria
649
Danger Point South Africa
544
J M M J S N
J S N J M M
0 40 80 120 160 200
0 10 20 30

are mainly annual species of Mediterranean origin.

Except in parts of south eastern Australia, winter temperatures are rarely so low that plant growth ceases. Whereas in northern Europe the growing season can be defined as that part of the year when temperature is above 10° C (Alberda 1966), in Australia it is defined as that part of the year when the soil is wet (Trumble 1937, Prescott and Thomas 1948-49, Black 1964).

In the Mediterranean basin the olive (Olea europaea) and the evergreen oak (Quercus coccifera) are accepted as indicator plants of the limits of the Mediterranean environment (Rossiter 1966). Few areas of climax vegetation remain. It is interesting to note (Black 1952) that the olive is now "spontaneous on Adelaide foothills and sandhills at Encounter Bay". Conditions are sufficiently similar at Adelaide to those in the Mediterranean basin to encourage colonisation by this species.

It is still possible to find examples of every climax vegetation type in Australia. The genus Eucalyptus is ubiquitous and dominates three broad vegetation groups in the regions in which we are interested (Wood 1937). The first of these is dry sclerophyll forest which grows on leached soils where rainfall is between 25 and 40 inches. In other parts of the world these sclerophyll communities are given such distinctive names as maquis or macchia in the Mediterranean basin, chapparal in California, espinol in Chile and scrub in South Africa. In Australia the trees are from 30 to 100 feet high and there is a dense undergrowth of various shrubs of the Proteaceae, Myrtaceae, Epacridaceae, Cyperaceae and Leguminosae.

The second principal vegetation type is savannah woodland, found where the rainfall is about 20 to 35 inches and usually where the soil type is heavier than under dry sclerophyll forest. The widely spaced trees are 30 to 50 feet high, and between them grow tufted perennial grasses, dwarf shrubs, or both.

The third vegetation type is locally known as mallee, a reference to the habit of the trees, which produce several stems from large underground lignotubers. Trees grow to 40 feet in a rainfall zone of from 8 to 20 inches. Soils are typically alkaline, though not universally so. There is an enormous variation of undergrowth, from a complete lack of it in some of the drier areas to a dense heath-like scrub in the wetter areas. Some of Australia's most beautiful wildflowers occur in this association.

Since Australia was colonized by Europeans in 1788, much of the Mediterranean region has been cleared of its native vegetation. The first areas to be widely used for grazing were those supporting savannah woodland, where the livestock grazed the native grasses. However, the introduction of Mediterranean annual species soon followed. Seeds were distributed by various means and the introduced species became dominant over considerable areas. The most common genera among the grasses were (and still are) Bromus, Festuca, Hordeum (H.leporinum is studied in detail in this thesis) and Vulpia, among the legumes Trifolium and Medicago, and among the herbaceous genera Erodium. In addition to these Mediterranean genera, the annual herb Arctotheca calendula, a native of southern Africa, has become widespread, especially in Western Australia.

Cereal crops were grown in Australia from the time of first European settlement, but with decreasing success. In the late nineteenth century the soil was found to be deficient in phosphorus, and superphosphate has been used on cereal crops since that time. Its application to pastures was delayed until the discovery that subterranean clover (*Trifolium subterraneum*) was well adapted to the local environment, if supplied with phosphorus. The development of pasture lands, and thus the input of phosphorus and rhizobial nitrogen, became the most important component of agricultural progress in southern Australia. Leys were introduced into cereal rotations and crop yields further increased. Some Mediterranean grass species have been sown, notably *Phalaris tuberosa* (perennial) and *Lolium rigidum* (annual).

As soil fertility rose following the fertilization of subterranean clover with superphosphate, the volunteer annual species, which had previously been introduced from the Mediterranean region, invaded the now productive clover pastures. A phase of clover dominance was succeeded by a phase of dominance by various annual species. Botanical composition fluctuated from year to year, and from place to place. Some account of this variation is given in the data of Tiver and Crocker (1951) in Table 1. Much of the year to year variation, of which the figures in Table 1 are typical, is commonly explained in terms of such climatic aspects as time of seasonal rains, especially first or opening rains, and occurence of false starts to the growing season (autumn rains followed by a return to summer conditions).

TABLE 1

Showing variation of botanical composition in annual pasture in the Lower South East of South Australia between years and sites. The figures show percentage of each species present, using a Levy point quadrat.

A) Year to year variation at the same site (Tiver and Crocker (1951), page 73)

Year	Percentage botanical composition Trifolium subterraneum	Annual Grasses	Arctotheca calendula	Other species
1945	12	24	59	5
1946	89	4	5	2
1947	47	9	43	1
1948	72	20	6	1
1949	34	51	12	0

B) Site to site variation* (Tiver and Crocker, (1951) page 51)

Site	Percentage botanical composition Lolium rigidum	Trifolium subterraneum	Trigonella ornithopodioides	Other species
Crabhole	33	51	10	6
Puff	77	8	0	15

* Variation within a pasture on a crabhole or gilgai soil which forms depressions (crabhole) and ridges (puff) as a constant microrelief.

2.2.0. DORMANCY

2.2.1. Dormancy as a survival mechanism.

Dormancy mechanisms are physiological adaptations which increase the potential of a species to survive, although this is difficult to prove (Koller 1964). Consideration of three examples from environments other than Mediterranean will illustrate this and at the same time serve to highlight differences between environments.

In deserts, dormancy of many species is relieved by heavy rain which leaches inhibitors from seeds or seed coats (Went 1949). Thus plants cannot germinate after light rain which would otherwise be sufficient for their establishment, but would not allow completion of their life cycle.

In continental environments seeds which experience winters so cold that seedlings would be killed if they germinated in the autumn, usually require a period of cold to break dormancy. This is provided when the seeds remain moist and in contact with snow or ice through the winter, and germinate when the weather is warmer in the spring. Examples are many deciduous trees, aquatic plants (Crocker and Barton 1953), Stipa viridula (Rogler 1960a) and Oryzopsis hymenoides (Rogler 1960b).

Many plants which inhabit pond edges have seeds with a light requirement. Examples are Typha latifolia (Sifton 1959) and Juncus maritimus (Tadmore et al (1958) quoted by Koller (1964)). This requirement probably restricts their germination to the very edge of open water, which is free of dense vegetation.

If, in a Mediterranean environment, winters were always wet and summers were always dry, species whose seeds were dormant in summer would possess no ecological advantage over those species whose seeds were not dormant. Such is the case at Tel Aviv. In other parts of the Mediterranean, and in Australia, however, summers are not always dry, and when rain comes in summer, it is followed by drought and high temperatures, resulting in almost certain death of newly established seedlings. Ideally, then, dormancy mechanisms will be so adapted that germination is resisted during summer, but proceeds unchecked after the first seasonal rains of autumn.

The results of Morley (1958b) are interesting in respect to the hypothesis that dormancy will be ecologically less significant in an environment which has constantly dry summers (e.g. Tel Aviv). Although his results were not statistically significant, they do suggest that strains of subterranean clover collected from what he terms cool, moist environments have a greater degree of dormancy than strains from cool, dry environments. In warmer environments, all strains had a high degree of dormancy.

2.2.2. Dormancy of subterranean clover

Of the dormancy mechanisms of species growing in Australian annual pastures, most is known about those of subterranean clover. This species possesses two kinds of dormancy. The first, hard seededness, which is common to many other legumes (Rossiter 1966), was described by Aitken (1939) and is a resistance to imbibition. It is reduced by fluctuating temperature, or any physical breaking of the seed coat. It is a mechanism whereby seed can survive for several years, thus providing a reservoir of seed in the soil independent of the growing conditions of any particular year. The second, *embryo dormancy*, was described by Loftus Hills (1942, 1944a,b,c). Here the embryo does not germinate after the imbibition of water. *Embryo dormancy* is of a more temporary nature, and is relieved by low temperature (Woodforde 1935) or higher than normal atmospheric concentrations of carbon-dioxide (Ballard 1958). From the point of view of summer survival and autumn establishment, *embryo dormancy* is obviously of more importance than *hardseededness*. Consequently, hardseededness will not be discussed further, and where I use the word dormancy, it will refer to embryo dormancy.

Let us now examine how embryo dormancy helps the survival of subterranean clover in a Mediterranean environment. First an examination of the facts. No subterranean clover seed will germinate at temperatures above 30° C (Toole and Hollowell 1939, Loftus Hills 1944a). While non dormant seed will germinate below 30°C, dormant seed will not germinate unless the temperature is below 10° C (Woodforde 1935, Loftus Hills 1944a). Carbon dioxide relieves dormancy between 10°C and 25°C (Ballard 1958, 1961). Lastly, the removal of the testa from soft seed (that is seeds not showing hardseededness) will overcome dormancy, at least at a temperature of 20°C (Loftus Hills 1944c).

Before formulating a model, I will discuss briefly the significance of carbon dioxide in relieving dormancy in subterranean clover. Ballard (1958, 1961) who first noticed the effect, felt that its significance was confined to the laboratory. In the field, he said, carbon dioxide levels are usually higher than the 0.5% level that he had found was required to break dormancy. As an example, he quoted Russell (1950), who stated that one measurement of carbon dioxide concentration under grassland was 1.5%. An examination of Russell's source (Russell and Appleyard 1915) revealed however, that this measurement was taken at 6 inches depth under permanent pasture, in England. Furthermore, carbon dioxide concentration increased with depth, suggesting that at shallower depths it may have been less than this level.

Burford (personal communication) has shown at Adelaide, that only after heavy rain in summer and autumn, when the soil is very wet in winter, or when there is much root activity in spring, does carbon dioxide concentration rise to 0.5% or more at a soil depth of two inches, the shallowest depth he measured. This is probably due to micro-organism activity, root activity and soil pore saturation. Thus subterranean clover seeds buried at a shallow depth beneath the soil surface will experience the required concentration of carbon dioxide in the summer and autumn only after heavy rain.

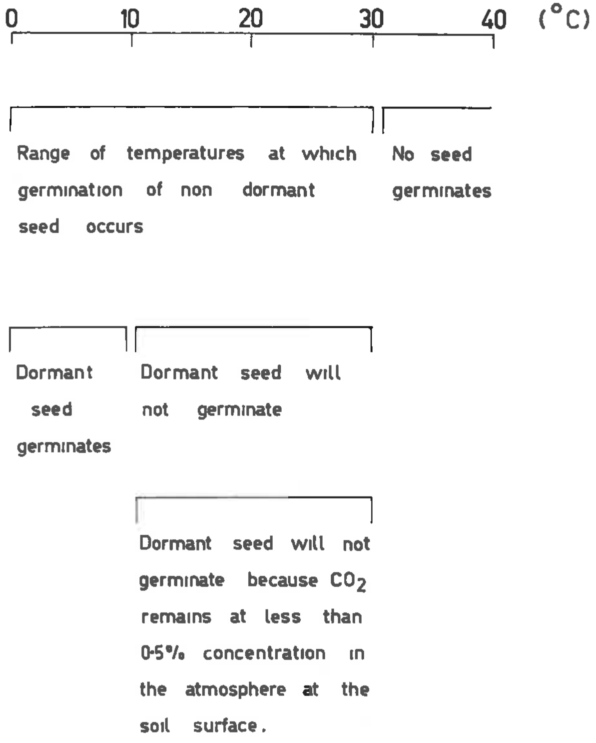
The question as to whether carbon dioxide levels at or just above the soil surface ever rise to 0.5% is difficult to resolve. Wright and Lemon (1966) measured carbon dioxide concentrations at various heights above 25 cm from the ground in a maize crop, and though concentration rose as height fell towards the surface, it was little above 0.03% even at night (when there was no photosynthesis). If there is no vegetation, levels of carbon dioxide above atmospheric concentration will be due to soil and surface litter micro-organism activity, and diffusion of carbon dioxide from these sources . Consequently, concentration at the surface will never be above that in the soil, and because of air movement will usually be well below it. Thus subterranean clover seeds, whether lying on the surface of the soil, or buried at a shallow depth beneath it, either never experience the required concentration of carbon dioxide (on the surface) or experience such a concentration only after heavy rain (beneath the surface). This mechanism then, apparently does have ecological significance.

The proposed ways in which embryo dormancy in subterranean clover is relieved in the field are shown in Figure 2. It is suggested that dormant seeds lying on the soil surface only germinate at low temperatures in late autumn or winter when the chances of the soil drying out are small. Those beneath the surface can germinate in warmer weather after heavy rain, if the carbon dioxide concentration becomes sufficiently high. Seeds beneath the surface are less likely to dry rapidly than those on the surface, hence the value of the carbon dioxide response, in allowing these buried seeds to germinate in warmer conditions.

The effect of testa removal in relieving embryo dormancy (Loftus Hills 1944c) suggests either that a germination inhibitor is present in the testa, or that the testa limits entry of carbon dioxide into the seed. If the first proposition were correct, then germination would be stimulated by rains heavy enough to leach the inhibitors. Thus if this mechanism replaced the carbon

Figure 2. Models illustrating the ecological significance of embryo dormancy in subterranean clover.
The model on the left is of dormant seeds lying on the soil surface, and the model on the right is of dormant seeds buried beneath the soil surface.

SEED ON THE SURFACE



Range of temperatures at which germination of non dormant seed occurs

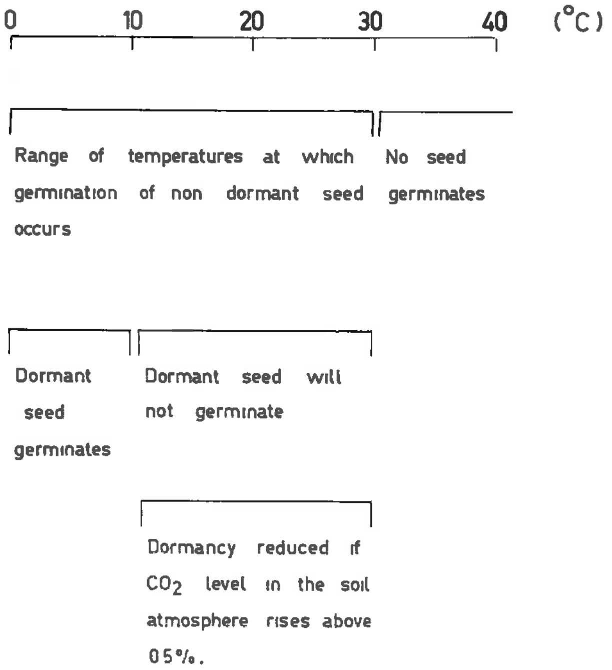
No seed germinates

Dormant seed germinates

Dormant seed will not germinate

Dormant seed will not germinate because CO_2 remains at less than 0·5% concentration in the atmosphere at the soil surface.

SEED BENEATH THE SURFACE



Range of temperatures at which germination of non dormant seed occurs

No seed germinates

Dormant seed germinates

Dormant seed will not germinate

Dormancy reduced if CO_2 level in the soil atmosphere rises above 0·5%.

RESULT Dormant seed on the surface germinates following rainfall only when temperatures are below 10°C, which usually occurs only in late autumn and winter.

Dormant seed beneath the surface germinates following rainfall provided that the temperature is below 30°C. This occurs throughout the autumn months and in summer.

dioxide requirement, seed lying on the surface may be able to germinate at temperatures above 10°C, after very heavy rain, even though carbon dioxide levels remained low.

2.2.3. Dormancy in other Mediterranean annual species.

Some degree of summer dormancy is possessed by some other Mediterranean annual pasture plants. Meadly (1936) in Western Australia found that germination of *Lolium rigidum* was much quicker at the onset of autumn (mid March), than it was in the preceeding summer. This slowness of germination may be an effective kind of dormancy if conditions revert rapidly to normal (hot and dry) following rain: that is if the soil dries out before germination begins. Rossiter (1966), also in Western Australia, gives germination percentages of four grass species (*Bromus rigidus*, *B.arenarius*, *Hordeum leporinum*, and *Vulpa myuros*) which showed that seeds were dormant in midsummer (January), but that after this time dormancy was rapidly lost. His figures, however, did not reveal whether germination *rate* in February and March was less than later in the autumn. His results infer that if rains fell in February and March there would be some risk of germination and seedling death. Laude (1956) found that several annual grasses (*Bromus rigidus*, *B.mollis* *Hordeum leporinum*, *H.hystrix* and *H.glaucum*), all of Mediterranean origin, were dormant for at least five weeks after maturity, but like Rossiter, he made no observations of rate of germination. Laude also found that *Erodium botrys* was highly dormant in summer. Similarly, Rossiter (1966) found that both *Erodium botrys* and *Arctotheca calen-*

dula were dormant in summer.

Apart from the dormancy mechanisms of subterranean clover already discussed, two other mechanisms have been reported for Mediterranean pasture species. The first, a diurnal temperature variation requirement, has been reported for the biennial grass *Lolium multiflorum* (Collery et al 1961) and the perennial grass *Oryzopsis miliacea* (Koller and Negbi 1964).

The second mechanism is a requirement for heavy leaching rains, to leach germination inhibitors present in hulls and seeds. Germination of the perennials *Phalaris arundinacea* (Vose 1962) and *Cenchrus ciliaris* (Stiles 1960) is known to be improved by the removal of hulls, a treatment which may remove the inhibitors. Black (1959) found that leachable inhibitors occur in the hull and caryopsis of the annual *Avena fatua*. Waisel and Adler (1959) found that extracts of matured spikelets of the desert annual *Aegilops kotschyi* inhibited germination both of that species and of lettuce. Amongst plants normally occurring in a Mediterranean environment, Waisel and Adler claimed that *Hordeum murinum* behaved similarly to *Aegilops kotschyi* (but they gave no details) and they thought that the phenomena may be widespread. Unpublished data of Walker (Rossiter 1966) showed that dormancy of *Bromus mollis* can be overcome by prolonged leaching. Mc Gowan (1957) found that extracts from the seed of *Hordeum leporinum* suppressed the germination of *Lolium rigidum*.

It is possible that inhibitors occur commonly in the seeds of Mediterranean annual pasture plants. That the phenomenon has not been reported more widely may be due to several factors. Firstly, hulls may be removed in the threshing process when seed is harvested and inhibitors be present in the removed hulls. Secondly, if rain falls before the seed is harvested, the inhibitor may already have been leached from the seed. Thirdly, the inhibitor may cause germination to slow down, and tests have measured only total germination, not rate. Fourthly, there may be variation within species, only some varieties showing dormancy (Loftus Hills (1944b) and Morley (1958) with subterranean clover, Imam and Allard (1965) with Avena fatua). Lastly, many species have simply not been tested.

The effect of high temperature on the germination of subterranean clover has been noted. Trumble (1937) produced data for other annuals growing normally in a Mediterranean environment (Table 2). Both maximum and optimum temperatures for Mediterranean species are below those of the summer growing species in the table. The Mediterranean species do not germinate well above 25°C, but whether they are dormant at the higher temperatures, or whether they are killed was not stated.

TABLE 2

Temperature at which germination was most rapid, maximum temperature at which complete germination occurred, and maximum temperature at which any germination occurred for various Mediterranean species contrasted with species from some other environments. (See next page)

References from next page

1) Trumble 1937
2) Schroeder and Barton 1939
3) Gordon 1951
4) Sprague 1940
5) Quail and Carter 1968

* *Avena ludoviciana* and *Avena fatua* are European, both northern and Mediterranean.

n.a. - not available

TABLE 2

Species	Temperature at which germination was most rapid. (°C)	Maximum temp at which complete germination occurred (°C)	Maximum temp at which any germination occurred (°C)
a) Mediterranean			
Lolium rigidum 1)	20	24	32
Vulpia myuros 1)	17	17	25
Erodium botrys 1)	20	28	30
Trifolium subterran. 1)	18	24	33
Medicago denticulata 1)	14	14	23
b) Cool temperate			
Phleum pratense 3)	25	30	33
Dactylis glomerata 4)	15	15	n.a.
Lolium perenne 1)	20	26	30
c) Alpine			
Camassia leichtlinii 2)	n.a.	5	5
Calochortus 2) macrocarpus	n.a.	5	5
Lewisia rediviva 2)	n.a.	1	25
d) Warm temperate			
Echinochloa 1) crus-galli	38	38	n.a.
Sorghum sudanense 1)	35	35	n.a.
e) Others *			
Avena fatua 5)	n.a.	15	25
Avena ludoviciana 5)	n.a.	10	25

2.3.0. Germination

Germination in a Mediterranean environment normally occurs with the first autumn rain. Rate of germination depends on moisture, temperature and rarely, on aeration or carbon dioxide level. The influence of temperature and moisture are here reviewed.

2.3.1. Influence of temperature

Opening rains may fall at any time from very late summer to early winter (February to June), and consequently seed populations experience a wide range of temperatures at which moisture conditions permit germination. For example, mean temperature over a period of 30 years at Adelaide was 21°C for March and 15°C for May, but temperatures as high as 43.6°C (1934) and as low as 6.6°C (1933) have been recordedin March, and as high as 31.9°C (1921) and as low as 2.7°C (1895 and 1904) in May. (Commonwealth of Australia Year Book 1966).

There is little information on the response of germination to temperature of Mediterranean annual species, but information is available for other species, so that some indication of responses by seeds to temperatures can be obtained. Perhaps the most important point is that temperature affects both total germination and rate of germination, and may affect them differently. A good example of the two effects is provided by *Gymnarrhena micrantha*, an annual dwarf composite of wide occurence in the steppe and desert regions of the Negev (Israel). Maximum percentage germination of seeds occurred throughout a temperature range from 5°C to 20°C, but germination was most rapid at 16°C (Koller and Roth 1964).

Optimum temperature of germination varies widely among plants from different environments, the alpine plant *Camassia leichtlinii* germinating well only at temperatures below 5°C (Schroeder and Barton 1939), while the tropical grass *Sorghum sudanense* germinates best at 35°C (Trumble 1937). Several species germinate best when temperature alternates; furthermore, some species, for example *Aquilegia canadensis*, germinate quite well even if the maximum temperature used in an alternating sequence will, if maintained, inhibit germination (Crocker and Barton 1953).

Of work on the Mediterranean annuals, Trumble's (1937) data are perhaps the most relevant. He obtained some measure of rate by counting germinated seeds at two and five days. His results appear in Table 2, together with some results obtained from other environments. It can be seen that the warm temperate species have temperature requirements rather higher, and the alpine species have temperature requirements rather lower, than the Mediterranean or cool temperate species. The Mediterranean and cool temperate species, together with the two *Avena* species which occur in both environments, have similar temperature requirements, optimum temperature (that is temperature at which germination is most rapid) being about 15-20°C. That they are similar is not surprising, as Mediterranean autumn and winter temperatures (the seasons of germination in that environment) are not dissimilar to cool temperate spring and summer temperatures (seasons of growth in cool temperate environments).

For example, mean October and November temperatures at Lisbon, Portugal, are 15°C and 12°C, while at Frankfurt, Germany, mean May and June temperatures are 11°C and 14°C.

2.3.2. Influence of water

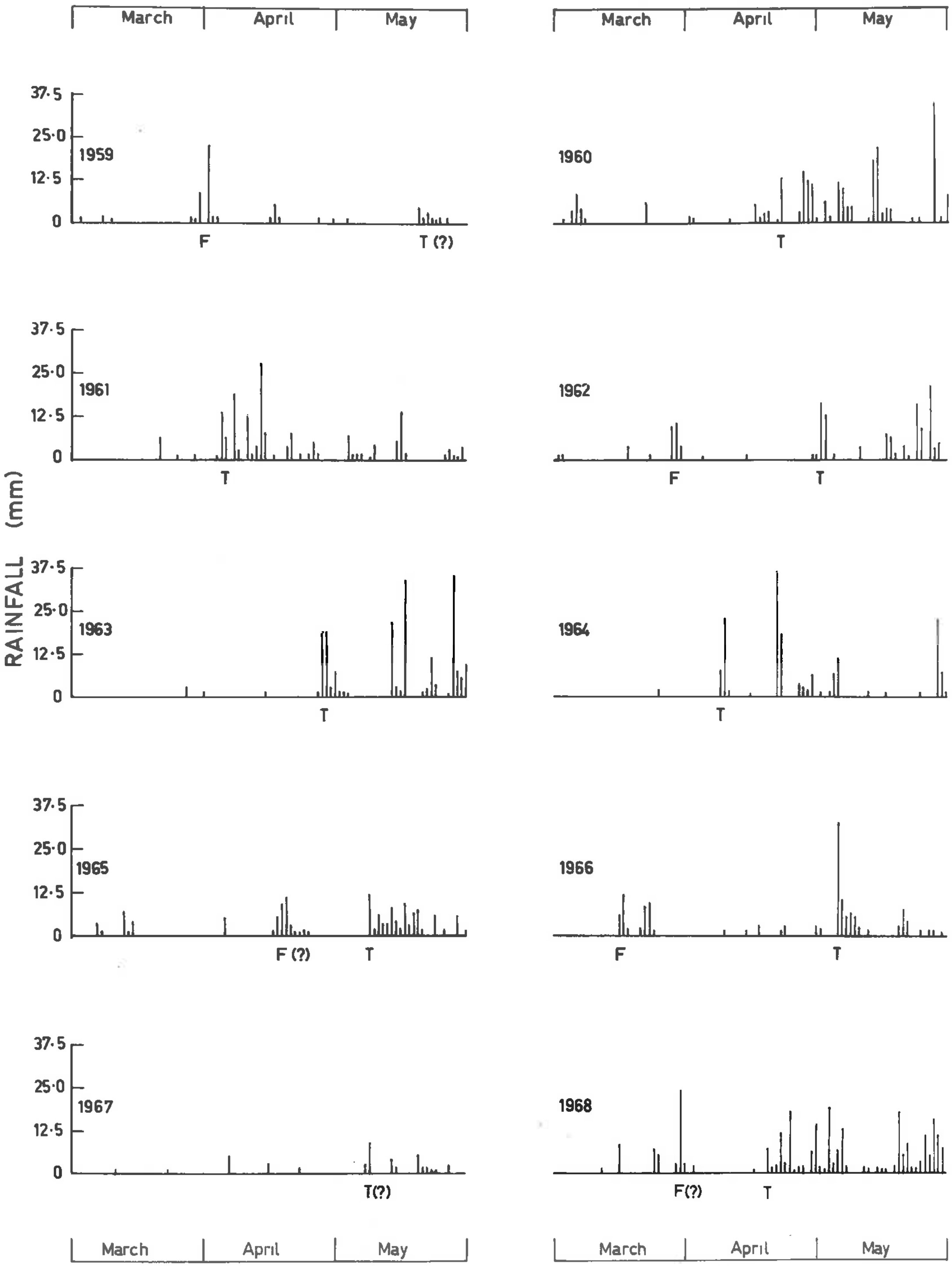
The second factor affecting rate of germination is moisture tension. Rains in autumn are not necessarily either heavy or reliable. The growing season may begin with heavy rain or with a series of light rains, or one light rain followed by low temperatures. (Light rain followed by high temperatures cannot be counted as an opening because the soil dries too quickly for any germination to occur). Heavy rains can be followed by 2, 3 or even 4 weeks of drought (Figure 3). Thus seeds may have adequate water for germination, water may be marginal, or tension may be so great that only some species or some seeds of some species germinate. Moreover, most seeds of Mediterranean pasture plants lie on the soil surface, so that water cannot pass readily from the soil to the seed.Far from having wet soil particles surrounding the seed, seeds may make contact with the soil at only one or two points on the seed surface. Even if the soil is quite wet, dry hot air may be able to evaporate water from a seed lying on the soil surface faster than water can pass from soil to seed. Hence an examination of the effect of water on germination rate, and of the passage of water from soil to seed is desirable.

An interesting example of the effect of moisture stress on germination and consequent establishment was

Figure 3.

Daily rainfall distribution in the autumn months of the years 1959-1968 at the Waite Institute, Adelaide, South Australia. An opening of the season (denoted by "T" in the figure), was said to occur if 13 mm (0.50 inches) of rain fell in a 7-day period. A false opening (denoted by "F" in the figure) was assumed to have occurred if the rain was followed by 3 weeks with less than 3 mm (0.10 inches) of rain on any one day. A question mark indicates that conditions were not quite fulfilled for either a false or a true opening, depending on whether the question mark accompanied an "F" or a "T".

In the period 1959 to 1968, 3 years in 10 had false openings. A further 4 years had false opening in the previous 10 year period.


March
April
May
March
April
May
RAINFALL (mm)
37·5
25·0
12·5
0
1959
F
T (?)
1960
T
1961
T
1962
F
T
1963
T
1964
T
1965
F (?)
T
1966
F
T
1967
T(?)
1968
F(?)
T
March
April
May
March
April
May

provided by Lazenby (1955), in an experiment with the rush (Juncus effusus). He found that if the water table was at the soil surface the rush established freely, but that establishment was reduced when the water table was 5 cm below the surface, and that there was virtually no establishment when the water table was 10 cm below the surface. Seedlings of the grasses Agrostis tenuis and Lolium perenne however, established in all cases. Thus the chance of Juncus effusus being a serious weed was greatly increased when the water table was at the soil surface. Lazenby's observation that Juncus effusus seeds are very sensitive to increase in water tension has since been confirmed by Collis-George and Sands (1959).

Water stress in the soil can be produced physically, as a result of suction by the soil matrix, and chemically, by solutes in the soil solution. In non-saline soils matrix forces are normally more important. The matrix potential of available water has been shown to vary from - 0.05 atmospheres at field capacity to about - 15 atmospheres at permanent wilting percentage (Salter and Haworth 1961). Traditionally we are used to thinking in terms which denote the inverse of potential, namely water tension, suction or stress.

The ability of a seed to germinate in mannitol or other solutions of various osmotic pressures, has often been used to indicate its moisture requirements (Helmerick and Pfeifer 1954, Knipe and Herbel 1960). This work can be criticised on the ground that it does not represent tension forces that exist in normal soils. Further, it assumes that the seed coat is intact and impermeable to the solute used. Manohar and Heydecker (1964) have shown that solutions can enter the seed through the micropyle, and that solutions of different compounds behave differently from each other and from water supplied by a tension plate.

There have been several studies of the effect of water stress produced by physical means on germination. Collis-George and Sands (1959) found that by increasing suction up to 10,000 cm of water they slowed down, and at the highest tensions, stopped the germination of three *Medicago* species and *Juncus vaginatus*. They also found that both suction and hydraulic conductivity of the soil affected germination, and concluded that soil moisture characteristics as well as moisture content must be considered in germination experiments. Later work (Collis-George and Sands 1962) with lucerne, *Lolium perenne*, and oats, suggested that for some osmotic systems 100 cm of matric tension is as effective as 10,000 cm of osmotic tension in retarding seed germination rates. They considered that there was no effect of degree of contact between seed coat and matrix, provided that pores remained full of water. Their results supported the proposition that osmotic potential does not permanently manifest itself in biological systems, because there is no truly semi-permeable membrane.

Sedgeley (1963) found that rates of water uptake and rates of seed germination on a suction plate apparatus are increased by improving the degree of contact between liquid water and seed. He criticised the conclusion of Collis-George and Sands (1962) that low matrix tensions are equivalent to high osmotic tensions. He considered that their results could be explained in terms of soil permeability. However, the conclusions of Collis-George and Sands (1959, 1962) are supported by the work of Manohar and Heydecker (1964). There seems little doubt that osmotic tension and matrix tension are differentially effective, because of imperfections of the semi-permeable membranes. However, Sedgeley's criticism is justified, and the effectiveness of matrix tension in retarding germination is likely to be considerably less than reported by Collis-George and Sands.

Consideration of the results discussed above apparently led Harper and Benton (1966) to experiment with seeds which present different surface areas, and which have some mechanism of improving liquid seed contact. They found that mucilaginous seeds are least sensitive to water tension, and that spiny and reticulate seeds are specially sensitive. Not only was contact between liquid and seed important, but also the degree of exposure to the atmosphere. Harper and his colleagues (1965) also found that roughness of the soil surface affected water uptake and germination. They sowed seeds of *Bromus rigidus* and *Bromus madritensis* on to surfaces of varying roughness. The number of seedlings established was proportional to the number of seeds sown except when the surface was smooth and cracked. Then the number of seedlings became proportional to number of sites (cracks) available for germination. Further, it was shown that the dart-like seed dispersal units of *Bromus rigidus* gave this species an advantage over *Bromus madritensis*, which had flat seeds that did not fall into cracks.

The work of Harper et al (1965, 1966) quoted above has special relevance to annual pastures in the Mediterranean environment of Australia. Firstly, seeds that are buried, even partially, have better contact with the moisture supply than seeds lying at the soil surface. An example of a species whose seeds are buried is subterranean clover. Following fertilization of the flowers of this species, peduncles elongate towards the ground, burying a variable proportion of burrs in the soil (Yates 1957, 1958). It is likely that the seed dispersal units of some annual grasses become partly buried because they have sharp points and because of the arrangement of their awns which allows movement in only one direction, that is in the direction following the sharp point. *Hordeum* species, *Bromus rigidus* and *Vulpia myuros* are examples of such grasses. Smith is one who (1968a) states that the awns of *Hordeum leporinum* appear to play a part in anchoring the seed to the soil surface.

Secondly, round seeds have poorer moisture relationships with the soil surface than flat seeds. This, however, is likely to be less important than the third point, namely seed size. Large seeds on the surface will tend to have less contact with the surface, relative to their total surface area, than small seeds, because small seeds will be better able to occupy favourable germination sites like cracks, crevices and small depressions. Fourthly, awned seeds or seeds otherwise spiny will have poorer moisture relationships than plain seeds, because the awns or spines will restrict contact with the surface to their tips. This will not occur, however, if the awns aid seed burial as in the examples quoted above. Fifthly, the seeds which germinate quickly will have less opportunity to lose water before seedling roots reach water supply beneath the surface, than seeds which germinate slowly.

One other aspect of the influence of water needs to be noted, that of the effect of wetting and drying. Whenever light rain is followed by drought, seeds imbibe water and then dry out again. Depending on the length of the soaking period, this may increase or decrease the rate of subsequent germination following the drought period (Kidd and West 1918). Lang (1965) points out that among different species there is a wide variation in tolerance to soaking followed by drought. The main reason for stimulation of germination rate following a short period of soaking before drying is the action of enzymes in the endosperm and conversion of starch to sugar, a process which normally precedes germination. However, the possible removal of inhibitors during the presoaking cannot be ignored. Suppression of germination, if the presoaking period is longer than this, is probably due to the effect of subsequent drying on the embryo which had commenced growing during the presoaking treatment. This is confirmed by the harmful effect of presoaking in oxygenated water (Barton and McNab 1956). Presumably, in this case, the presence of oxygen stimulated embryo growth causing the seed to be more vulnerable when the drying period commenced.

2.3.3. The effect of rate of germination on competition among annual pasture plants.

All the seeds on the surface of the soil in a Mediterranean annual pasture are wetted by the rain at the same time. Buried seeds will be wetted later, the interval depending on depth of burial. They may not, however, germinate at the same rate. Thus some plants will appear above the ground before others, and the leaves of these plants will expand so that latecomers will be shaded and the ability of their leaves to photosynthesize reduced. Similarly, those plants whose roots are deepest have more soil from which to draw their nutrients, and a greater reservoir of water in case of drought.

Thus, rate of germination is potentially of great importance in plant competition, as has been demonstrated by several workers. Lazenby (1961) found that growth of Allium vineale was greatly reduced when it was sown into established swards of Lolium perenne, compared to sowing the two species at the same time or sowing Lolium perenne later. Harper delayed sowing Bromus rigidus by up to 32 days in an association of that species with Bromus madritensis, and found that the greater the delay the smaller was the contribution of B.rigidus. Sagar (quoted by Harper 1961) sowed lolium perenne 21 days before, at the same time, and 21 days after Plantago lanceolata, and found that the species planted first was aggressive. Mann and Barnes (1947) published similar results for barley and Holcus mollis. Black and Wilkinson (1963) working with pure cultures of subterranean clover, varied sowing dates by smaller amounts, and recorded actual dates of emergence. Their results confirmed those of previous workers, and showed in addition that the day of emergence was of more importance than pre-emergence growth rate. They also found that some seeds of subterranean clover, though wetted at the same time as others, emerged up to 16 days later.

2.4.0. Seedling growth

2.4.1. Pattern of growth

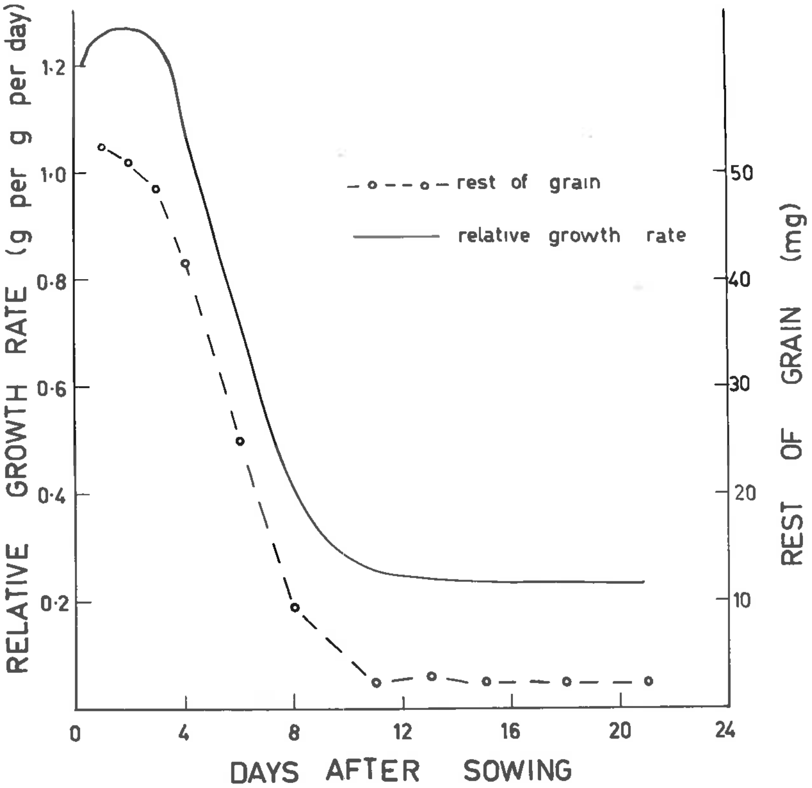
After germination, seedlings grow to the soil surface where they come under the influence of light. Friend (1966) considered that seedling independence, that is independence from endosperm reserves, occurs when total seedling weight equals original seed weight. Although this may be arbitrarily true, seedling independence strictly occurs when the seedling is no longer dependent on reserves in the seed. A seedling is capable of independence, though growth rate may be reduced, once it has produced sufficient photosynthetic surface to maintain itself; that is to meet respiration needs and provide a margin for growth.

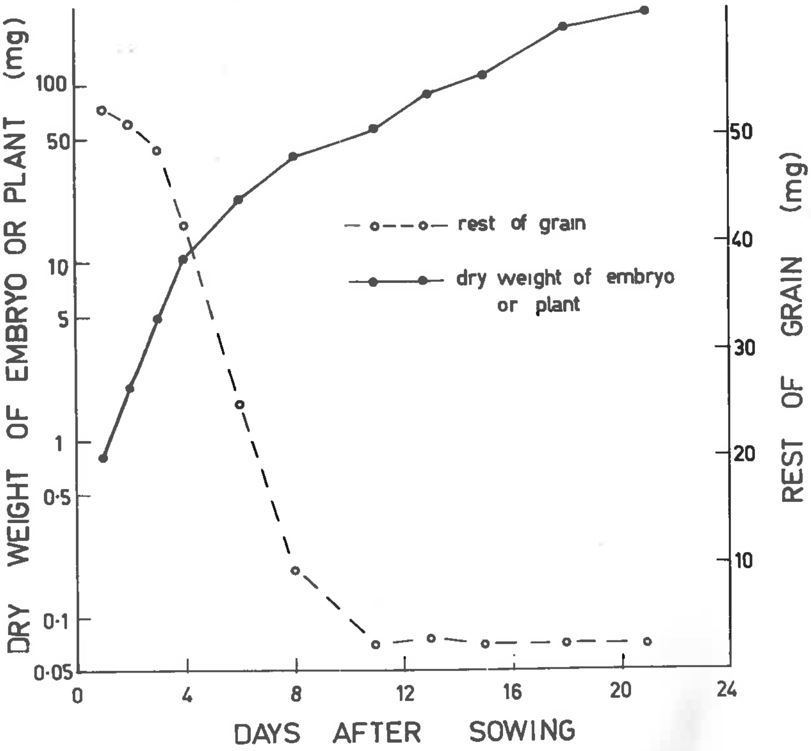
Williams (1960) studied the early development of the wheat plant. He found that the relative growth rate of the embryo was initially high, but when seed reserves were exhausted fell to a level which thereafter remained constant (Figure 4 - top). Note in Figure 4 that relative growth rate was apparently proportional to the weight of the rest of the grain, that is to the weight of seed reserves. Figure 4 (bottom) shows weight of embryo, from which Williams calculated relative growth rate. The first leaf was produced when about 20% of the seed reserves had been used. Thus the plant was able to produce nutrients from its leaf, and at the same time continue to use nutrients from its seed.

Williams' (1960) results, obtained using a species

Figure 4 (top) Change in relative growth rate of the embryo of a wheat plant, and decrease in weight of the rest of the grain, excluding the embryo, with time (Williams 1960).

(bottom) Increase in dry weight of the embryo of a wheat plant, and decrease in weight of the rest of the grain excluding the embryo, with time (Williams 1960).


RELATIVE GROWTH RATE (g per g per day)
1·2
1·0
0·8
0·6
0·4
0·2
REST OF GRAIN (mg)
50
40
30
20
10
rest of grain
relative growth rate
0
4
8
12
16
20
24
DAYS AFTER SOWING


DRY WEIGHT OF EMBRYO OR PLANT (mg)
100
50
10
5
1
0·5
0·1
0·05
REST OF GRAIN (mg)
50
40
30
20
10
rest of grain
dry weight of embryo or plant
0
4
8
12
16
20
24
DAYS AFTER SOWING

with hypogeal germination, contrast sharply with Black's (1956) results, using subterranean clover, a species with epigeal germination. Black found that while the growth of subterranean clover after emergence apparently depended on variations of cotyledon weight caused by variations in the seed size, it did not depend on variations of cotyledon weight caused by variations in depth of seeding. This seeming anomaly was explained by the fact that cotyledon area, unaffected by the use of seed reserves during emergence from depth, did affect subsequent growth. Seed reserves, depleted by emergence from depth, ceased to contribute to further development after emergence. Thus we have two situations, firstly that recorded by Williams for wheat, where seed reserves continued to influence growth after emergence, and seconly that recorded by Black for subterranean clover, where seed reserves did not continue to influence growth after emergence.

Bremner et al (1963) studied the relative effects of embryo size and endosperm size on seedling size of wheat. They found that though small embryos grew slightly quicker than large embryos, the effect of embryo size was small. However, following removal of part of the endosperm mechanically, large differences in seedling size resulted, directly related to differences in residual endosperm size, and independent of embryo size. Further, large endosperms were used quicker even in absolute terms than were small endosperms. Following exhaustion of the endosperm, rates of growth were parallel, and seedlings from seeds with large endosperms maintained their advantage in size. These results are suspect, however, because the effect of mechanical removal of part of the endosperm is assumed to be zero, except for its effect on endosperm size, and this assumption is quite likely to be incorrect. Resistance to attack by micro-organisms would surely be reduced by such a treatment, and the possibility of the presence of growth substances in the endosperm has been disregarded (e.g. Paleg et.al.1962, considered that the endo sperm was the primary site of action of gibberellic acid when it activated enzymes before germination). Nevertheless the conclusion of Bremner and his colleagues agree with that which can be drawn from the work of Williams (1960); that is that growth rate is dependent not only on the availability of seed reserves but also on the amount of seed reserves (Figure 4).

Whalley and his colleagues (1966) found that seedling size depended on both seed size and speed of germination. They also found that seedlings from large seeds grew more quickly, and they attributed this to the effect of greater seed reserves. However, the slope of the line relating seed size to seedling size was steeper for species with small seeds, and this, they considered, indicated that in large seeded species some endosperm is not used. Another explanation is that endosperm is not used so efficiently in large seeded species. However, there is nothing in their data to show that t e relative growth rate of the small seeded species was not greater than that of the large seeded species, and this could have accounted for the different slopes.

There have been a number of other studies of the relationship between seed size and seedling size.(Kogler

1954, Kneebone and Cremer 1955, Thomas 1966). None of these have attempted to differentiate between the effects of embryo and endosperm size.

2.4.2. The influence of light and temperature on seedling growth.

The effects of light and temperature on plant growth have been studied by relating variations of growth attributes to fluctuations in the environment over a period of time (Watson 1947, Black 1955), by the use of artificial shading (Blackman and Black 1959) and in controlled environments (Thorne 1960, Silsbury 1966). These studies, however, did not commence until the seedling was well established.

Wellington (1966) states that there is little or no photosynthetic activity by the first leaf of an oat seedling for some time after it has emerged and turned green. This lag, he explains, is due to slow translocation of nutrients from the endosperm because it is not shown by species with cotyledons which are also storage organs. If this is true, light will not affect seedling growth until the leaf begins to photosynthesize. However, Friend (1966), found that both increased light and higher temperature reduced the time needed for wheat to reach seedling independence. Evidently this species at least, photosynthesizes before seed reserves are exhausted.

Silsbury (1966) studied the effect of light and temperature on the growth of seedlings of *Lolium perenne* still partly dependent on seed reserves (some reserves were present at the beginning of his experiment which was designed to study later growth). He found that even after the formation of the first leaf, temperature affected seedling growth more than did light. After reserves were exhausted however, (about 8 days after sowing), seedlings were comparatively more strongly influenced by light than previously. It seems reasonable to conclude that until leaves are formed and become photosynthetic, only temperature will affect seedling growth, but that after this both light and temperature will affect growth.

2.4.3. The influence of seedling growth on competition among annual pasture plants.

First, it is pertinent to state that there is little or no influence of competition on seedlings as they emerge. Any factor of the environment which is limiting, such as water or oxygen, will limit all individuals equally because seed environments, except in rare circumstances, do not overlap. For the same reason, allelotrophic effects (toxic effects of one seed or seedling on another) occur only rarely. Temperature is not a factor which has a supply level, so cannot be the subject of competition. Competition will begin when leaves first shade each other or roots first mutually deplete the water or nutrient supply.

I turn now to the influence of seedling growth on subsequent competition.

The effect of sowing mixtures of species or plants of different seed size will be essentially similar to that of sowing mixtures of seeds with different germination times. The principle is that the largest seedling or the seedling establishing first will be able to use the environment either better or earlier than its smaller or later competitor, thus modifying the environment to the detriment of the latter. It will, however, be able to do this only if its largeness or earliness gives it a mechanism by which it can compete. Thus seed size will not lead to success in competition unless it gives superior height or greater root proliferation. It will give these advantages when two individuals of the same species compete, and probably also when plants of similar habit compete, for example two grasses or two legumes of like ecology and habit.

How height and seed size are correlated when plants of the same species compete has been shown by Black (1958), who grew subterranean clover swards from two seed sizes. He showed that when the two were grown in separate dense swards, they yielded about equally, but that when they were grown together, seedlings from large seeds suppressed seedlings from small seeds by shading them to such an extent that by the last harvest small seedlings were receiving only 2% of the incident light. Thus superior seed size led to taller plants which suppressed the shorter plants resulting from inferior seed size.

The work of Stern and Donald (1962a,b) emphasised the importance of height rather than seed size in interspecific competition between unlike species. By using four nitrogen levels to promote various amounts of grass (Lolium rigidum) relative to subterranean clover, and by measuring the amount of light which penetrated to various levels of the sward, they were able to show a direct shading effect of grass on clover, leading to the suppression of clover. They related level of light reaching the clover canopy to clover growth rate, showing clearly that reduction in clover growth, directly caused by a reduction of light intensity, could be attributed to grass growth above the clover canopy. Yet the grass had smaller seed than the clover, and the grass seedlings were barely one quarter the size of clover seedlings a few days after emergence.

Aspinall and Milthorpe (1959) found that barley, with its larger seed was a better competitor than white persicaria (Polygonum lapathifolium) although the two had similar relative growth rates. "Seed size", they said, "together with the relative times of germination, would appear to be among the most important criteria influencing competition between annual plants".

2.5.0. The influence of density on the growth and development of annual pastures.

2.5.1. Plant numbers in annual pasture

Few estimates of plant numbers in Mediterranean annual pastures are available. Rossiter (1966) quoted two Californian sources indicating populations as high as 20.0 plants per sq cm in a pasture mainly of Festuca sp. Heady (1958) found up to 4.0 plants per sq cm in annual pasture at the beginning of the growing season at Hopland Field Station, California (Table 3). Carter (unpublished) estimated plant numbers in an annual pasture at Adelaide, South Australia; his study was on the effects of various stocking rates fora period of years. Some of his results are summarized in Table 4 which shows plant numbers present at the beginning of several seasons. The range in values recorded by Carter (0.3 to 2.3 plants per sq cm) is similar to that measured by Rossiter and Pack (quoted by Rossiter 1966) in Western Australia, whose counts, presumably at the beginning of the season, varied from 0.3 to 1.5 plants per sq. cm.

Californian and Australian figures are not directly comparable. For example, both Heady, and Rossiter and Pack found that plant numbers decreased with time during the growing season. In Heady's case this was presumably due to inter-plant competition as the plots were not grazed, but in the case of Rossiter and Pack the effect of the grazing animal may have contributed to this decline in plant numbers. Different species

TABLE 3

*Plant numbers per sq cm * at three ungrazed sites of annual pasture at Hopland Field Station, California (Heady 1958). The plots were sampled at four times during the growing season.*

	+ Site 1	Site 2	Site 3
Dec	1.75	2.36	4.00
Feb	1.43	1.18	3.30
April	1.30	1.04	3.21
June	1.12	0.78	2.15

* Mean of 40 samples per year over a 5 year period.

\+ *Site 1* had not previously been grazed for several years and the pasture consisted mainly of *B.mollis* and broad leafed herbs. *Site 2* had been "moderately" grazed in previous years, and the pasture, like that at Site 1 was mainly *B.mollis* and broad leafed herbs. At *Site 3* previous grazing had been more intense, and the pasture consisted of various short grasses, namely *Aira caryophyllea*, *Briza minor*, *Gastridium ventricosum*, and *Festuca dertonensis*

TABLE 4

Plant numbers in annual pasture at Adelaide, grazed continuously at three stocking rates from early 1963. Figures are plant numbers per sq cm at the beginning of each season, and are the mean of 2 replicates with 20 sample sites in each replicate. Sample size was 89 sq cm.

	3 sheep/acre	6 sheep/acre	9 sheep/acre
1964	1.28	0.99	0.37
1965	2.29	1.41	0.55
1966	1.15	0.92	0.30

were involved, which may have produced different amounts of seed in the previous season or be able to maintain different plant numbers in the sward. Some idea of the effect of different species can be obtained by comparing Heady's three sites (see again Table 3), which had, however, had different grazing treatments in previous years. At site 3, which had twice as many plants throughout the growing season as at the other two sites, the principal species were short grasses eg. _Aira caryophyllea_, _Briza minor_, _Gastridium ventricosum_, and _Festuca dertonensis_. The principal species at the other two sites were the taller growing _B. mollis_ and broad leafed herbs.

The higher figures obtained by the Californian workers is probably due in part to the fact that counts were taken from ungrazed plots. Carter's figures in Table 4 show the effect of grazing. All plots in his experiment had been continuously grazed since the beginning of 1963, when the plots were very uniform (they had been established in the previous year). By the beginning of 1964, heavily grazed plots had less plants than others and this difference was maintained throughout the experimental period.

In conclusion, it seems that pasture stocked at low to medium stocking rates (stocking rates as high as 6 sheep per acre are uncommon in South Australia) have high plant populations, possibly in excess of 1.5 plants per sq cm. Plant numbers decrease as the season progresses (Heady 1958, Rossiter 1966) and are less at the beginning of the season if stock numbers were high during the preceding season (Carter unpublished).

2.5.2. Influence of density on the growth and development of pure cultures.

Although most pastures, unlike crops, are composed of several species of plants often quite different in habit, I shall consider first the effect of density on the growth and development of a pure culture. In a later section the effect of density on mixtures will be discussed. I shall consider biological yields or total yield of dry matter, which is the economic yield of pastures, rather than seed yield which is the economic yield of most crops. At the same time, it must be remembered that seed yield is of great importance to annual pastures, because of their dependence on natural reseeding for reproduction, and that seed yield ultimately determines plant numbers.

The relationship between biological yield and density is that yield increases with density until a ceiling is reached and thereafter remains constant, no matter how many more plants are present. The results of Donald (1951) are typical. He grew pure cultures of subterranean clover and Lolium rigidum at a wide range of densities. At the final harvest, the yield of each species depended on density only at low densities. At higher densities, increase in plant numbers was accompanied by a compensating decrease in plant size and resulted in a constant yield. Once constant, or ceiling yield was reached, yield per plant was inversely proportional to density. This relationship did not hold at earlier harvests (Donald harvested at three dates) because plants interferred less with each other when thy were smaller. Similar relationships have been found by Holliday (1953) using Lolium perenne, and Aspinall and Milthorpe (1959) using barley and Polygonum lapathifolium.

Some mathematical descriptions of the relationship between yield and density have been proposed, and these have been discussed by Donald (1963). The formula of Shinozaki and Kira (1956) is perhaps the most satisfactory expression. The expression is :

$$\frac{1}{w} = Ad + B$$

where w is the yield per plant, d is the density, and A and B are constants. This expression states that there is a linear relationship between the reciprocal of yield per plant and density. The expression depends on four assumptions :

1) That the growth of a plant, in terms of dry weight increase, is represented by the simple logistic equation

$$\frac{1}{w} \frac{dw}{dt} = r \left(1 - \frac{w}{W} \right)$$

where w is the weight per plant, W is the asymptote of w, r the initial relative growth rate, and t is the time.

2) That the initial relative growth rate (r) is independent of density.

3) That final yield is constant at high densities.

4) That time is measured from a common date of sowing.

The assumptions, discussed by Donald (1963) and Harper (1967), seem reasonable, and the expression fits data from a range of sources.

Where density changes in a sward due to plant mortality, the empirical relationship

$$w = Cp^{-\frac{3}{2}}$$

where w = weight per plant, p = existing plant density, and C is a constant,

$$\text{or } y = wp = Cp^{-\frac{1}{2}}$$

where y = weight per unit area, accounts for such mortality (Yoda et al, quoted by Harper (1967)). Yoda et al tested this relationship in a number of populations including pure populations of *Betula* sp., *Pinus densiflora*, *Erigeron canadensis*, and *Plantago asiatica*.

Density affects the growth of individuals because of its effect on the plant's environment. If, by some means, each plant could be supplied with all its requirements, density and yield would be linearly related. The effect of supply of nutrients (one factor of the plant environment) is illustrated by the work of Donald (1951), who established plants of *Bromus catharticus* at several densities and three nitrogen levels. He found that at low nitrogen, plants shared the nutrient supply irrespective of number, that is, that nutdent level governed final yield. Only at high nitrogen was more than one plant needed to exploit fully the nutrient environment. At this nitrogen level (or perhaps at some other higher nitrogen level), it can be assumed that some other factor (ultimately light) will limit further increase of yield. Similar results have been obtained by Holliday (1953) who varied nitrogen supply to swards of *Lolium perenne*. The important point is that the plant's environment , which is altered at high density by the presence of other plants, will limit yield by limiting the growth of each individual member of the sward.

That light, as an environmental factor, can affect the relationship between density and yield in the same way as nutrient supply, is shown by the work of Black (1963). He studied the growth of swards of subterranean clover at three light levels (obtained by shading), and several densities. In his experiment 3, ceiling yield occurred at a lower density for shaded swards than for unshaded swards. Thus when light intensity was low, less plants were needed to intercept all the light; that is, there was less light penetrating into the sward, and leaf area required to intercept it all was also less. This effect was less obvious in his other 2 experiments partly because ceiling yield was not always attained. Nevertheless, even in these experiments his results are indicative, especially if the response of leaf area to density, instead of the response of dry weight to density, is considered.

2.5.3. The influence of density on the growth and development of individual plants.

We have seen that the effect of increasing density is to reduce the environment which each individual can exploit. Let us now examine the consequences of this in terms of individual plants.

The first point is that relative growth rate (r) of individuals within a species may not vary greatly when they are non competing. Black (1957) found that subterranean clover plants from large seeds maintained their advantage in size over small seeded plants for the whole of the growing season. Apparently, *r* was constant no matter what the seed weight. Silsbury (1966) however, measured the growth of *Lolim perenne* plants in a controlled environment and found no correlation between seed size and plant size. Presumably, this can be attributed to differences in *r*. Thus for this cross fertilized species at least, variation in *r* may have potential importance as a mechanism in competition between individuals. However, even within this species there is disagreement between workers on this point. For example, Thomas (1966) obtained results for *Lolium perenne* similar to those of Black (1957) for subterranean clover, but he did find that the correlation between plant weight and seed size fell with time, suggesting that there was some variation of *r*.

If *r* within a species does not vary, plant size of spaced plants presumably depends on seed size. In a mono-specific sward of such a species where individuals have various seed sizes, those individuals from the largest seeds will dominate the sward. If, however, *r* varies as well as seed size, then in a sward composed of such individuals the most successful plants will be those with greatest *r* and greatest seed weight, or if high *r* and high seed weight are not correlated, will be those with the greatest *r* if the environment allows potential *r* to be exploited; that is, if interplant competition does not reduce *r* in those plants which potentially have the greatest r. Put another way, successful plants in swards of low density will be those able to grow quickly (have high r), but in more dense swards, successful plants will be those with large seeds, large seedlings, and capacity for early dominance.

The question as to whether r is constant within a species, or varies, possibly depends on the species, though some variation is surely present in all species. The very small amount of variation in r recorded by Black (1957) in subterranean clover was probably due to the fact that he worked with only one strain of a predominantly self fertilizing species. A cross fertilized species like *Lolium perenne* is far more likely to show larger variation of r.

Whether individual plants, competing with each other or not, become more or less similar, has occupied the minds of two Japanese workers, Kyoma and Kira (1956), and is relevant to this discussion. They begin with the premise that the distribution in size of spaced plants would not be normal, but skewed. This view was based on Blackman's (1919) definition of relative growth rate :

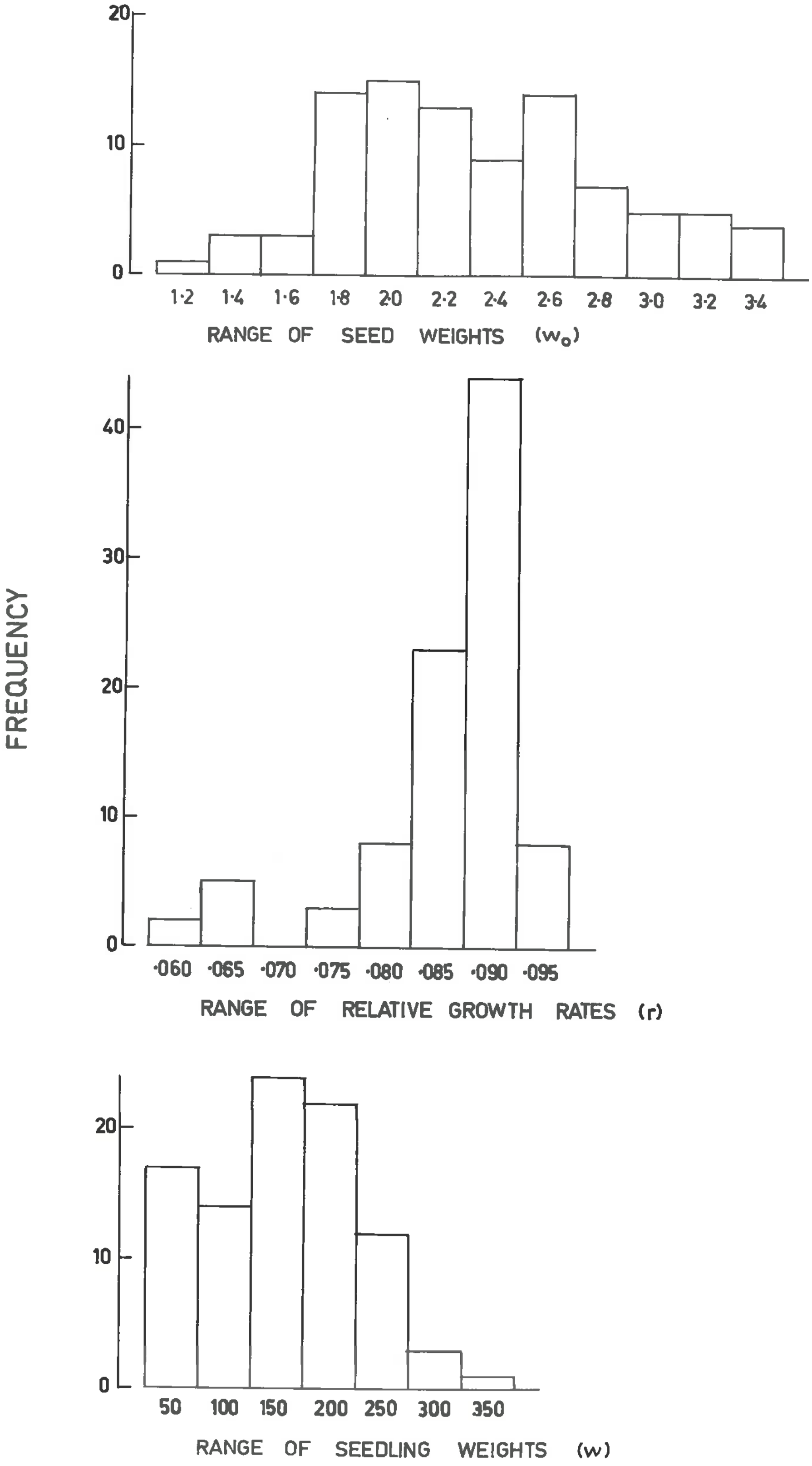
$$r = \frac{1}{w} \frac{d\,w}{d\,t} \quad \text{or} \quad r = \frac{1}{t} (\log w - \log w_o)$$

where w is plant weight, t is time, and r is the relative growth rate. If both w_o (initial plant weight or seed weight) and r are constant, plant weight (w) will be invariable at any time. If w_o is distributed normally at any time and r constant, then w will be distributed normally at any time. If however, either r is normally distributed, or both r and w_o are normally distributed, then because log w is related to r, distribution of w will be skewed (that is log normal). They regard a normal distribution of seed weight as usual, and present evidence that the distribution of r in non competing plants of rose mallow (*Hibiscus moschentos*) is normal. They present a considerable body of evidence to show that plant size in a dense community has a skew distribution, and propose that this is due to an increase in variability of r in crowded communities.

In Figure 5, data from Silsbury (1966) for isolated plants of *Lolium perenne* grown in a controlled environment have been redrawn to give the distribution of w_o , W , and r (I have derived r from Silsbury's values of w_o and w, but as w represented weight of tops only, r is actually underestimated). Although w_o was apparently normally distributed, the distribution of both r and w was skewed, r skewed towards higher values of r, W skewed towards lower values of w. Thus the development of skewness in w of isolated plants did not depend on a normal distribution of r, but on a variation of r.

On logical grounds, however, the development of skewness of individual plant size in a population need not depend on the distribution of r at all. Relative growth rate within swards is not related to log w but to w_o (where w_o = plant weight when competition begins), because, as soon as plants commence competing with each other, the largest plants tend to depress growth of the smaller plants by restricting light or some other factor of the environment, and r of the smaller plants becomes less. Distribution becomes skewed not because of increased variability of r but because larger plants have larger

Figure 5 Distribution of seed weight (mg), relative growth rate (g/g/day), and seedling weight (mg) of non competing plants of *Lolium perenne* after 49 days in a controlled environment (Silsbury 1966). Values for relative growth rates are derived from Silsbury's seed and seedling weights. Figures on the x axis are the top of the range for each column.


20
10
0
1·2
1·4
1·6
1·8
2·0
2·2
2·4
2·6
2·8
3·0
3·2
3·4
RANGE OF SEED WEIGHTS (w_o)
FREQUENCY
40
30
20
10
0
·060
·065
·070
·075
·080
·085
·090
·095
RANGE OF RELATIVE GROWTH RATES (r)
20
10
0
50
100
150
200
250
300
350
RANGE OF SEEDLING WEIGHTS (w)

w than smaller plants, and so large plants will become even larger, smaller plants will/increase by lesser amounts, the population will become dominated by less and less larger plants, and a pronounced skewness will develop with the bulk of the population being, relative to the few large plants, small.

That skewness of distribution of *w* in populations actually occurs was verified by Koyama and Kira for rose mallow (*Hibiscus moschentos*) and soybeans. They found that there was increased skewness at high density, a result which would follow from the above hypothesis. This work has since been confirmed by Obeid (quoted by Harper 1967) working with flax at three densities. Skewness was greatest at the highest density, but scarcely present at the lowest density. The work of Sterm (1965) is interesting because it shows that variation of plant size is higher at high densities and increases with time. This confirms Koyoma and Kira to the extent that variation is greater at high densities. However, his results are not in disagreement with the hypothesis here presented, as variation in a skewed population formed in this way probably would be greater (in terms of standard deviation) than in a normally distributed population.

The growth and development of individual plants in a community has been studied by other Japanese workers in association with Kira. Their technique was to measure individual plant weights and heights, and to correlate them with earlier measurements or those of neighbouring plants. They found (Hozumi et al 1955) that the individual plant height of competing maize plants at the end of a three day period was negatively correlated to height at the beginning of the period. In other words plants elongated under shading, and rate of elongation was reduced when their light environment became more favourable. They found that the size of one plant was negatively correlated with the size of a neighbouring plant. Thus they presented direct evidence that large plants were successful competitors at the expense of their smaller neighbours. Yoda et al (1957), working with rose mallow, found that these effects were intensified with density, and further suggested that communities of herbaceous plants would experience more severe interplant competition than grasses because of the spatial arrangement of their leaves.

2.5.4. The influence of density on the outcome of competition in species mixtures.

I have discussed the mechanisms which lead to dominance of some individuals over others in monospecific swards, and have concluded that the most important are seed weight and relative growth rate before the onset of competition. These attributes give a plant tallness or deepness and ramification of the root system which in turn give it success in subsequent competition with its lesser neighbours. In a species mixture where the two species have closely similar habit, the same reasoning holds good. Where species are of different habit, potentially taller species, those with deep roots, more favourable leaf disposition, or any other mechanism which leads to competitive success, will eventually dominate those species which are shorter or those with lesser root systems etc, regardless of seed weight and relative growth rate.

The effect of density on competition between barley and white persicaria (*Polygonum lapathifolium*) was studied by Aspinall and Milthorpe (1959). Barley was a good competitor at all densities, and the authors attributed this to its larger seed and embryo. The effect of higher density was to increase the competitive advantage of barley. White persicaria, however, remains a weed of barley crops in England because it matures later. In their experiment, after barley began to senesce, white persicaria was able to grow further and produce seed. Perhaps at higher densities than those used by these authors, the complete suppression of white persicaria would occur. However, difference in maturation time is a mechanism whereby an apparently "less aggressive" species is able to maintain itself in a population.

Black (1960) grew red clover (*Trifolium pratense*) and lucerne (*Medicago sativa*) at eight densities, alone and together. He found that the species sown at low density tended to gain in any mixture where the other species was sown at high density. The explanation seems to be that within species competition of the species sown at high density was so great that individual plant size was reduced to a level which allowed the other species to gain. This explanation assumes that the two species are competing for different parts of the micro-environment. If the same part of the micro-environment were involved, individual plants of the species sown at low density would be affected by the high density of the other species in the same way as individuals of the dense species. This was not so.

Turning now to competition between plants with more similar habit, we examine the results of Harper (1963). He sowed varieties of flax and linseed (Linum usitatissimum) at two densities. The yield of seed in pure culture of some varieties (mainly flax) increased at high density, and of other varieties (mainly linseed) decreased. When sown as mixtures, the linseed varieties gained in competition with flax varieties at low density, and the flax varieties gained at high density. Here then, is a case where the outcome of competition depends on density. Harper did not explain his results, but it seems that at low densities, linseed is able to branch at the base forming many shoots able to compete favourably with a lesser number of flax shoots. At high densities, such branching is suppressed and the larger shoots of flax dominate those of linseed. In addition, flax can branch all along the stem rather than just at the base as linseed does, and so branching is less suppressed by high density. Thus differences in plant habit, though not great, were sufficient to enable one variety to compete successfully with the other at a particular density.

In conclusion, we can only say as a generalization that density will affect the outcome of competition between mixtures of species. The way in which it affects competition will depend on the species concerned, and in particular, on the habit of those species. Probably, the level of supply of any of the factors needed for growth will also affect the influence of density.

Finally, I will consider the question of equilibrium in species mixtures. Donald (1963), after studying the data of Mann and Barnes (1953) and Black (1960) came to the conclusion that above a certain density, mixtures of species come to an equilibrium no matter what further increase in density takes place. In both examples cited by Donald, the density of one component was held constant, and the other varied. His conclusion seems logical because, if one species is held constant there may be a relationship between density and yield of the second species somewhat similar to that in a pure culture. The optimum density in pure culture and the density of constant composition in a mixture will presumably not be the same. Botanical composition in a mixture will be constant if either both species are above the density at which no further yield increase of the mixture takes place when the density of either species is increased, or if one is held constant and the other is raised above such a density. It follows that the density to give constant composition of a mixture will vary with time from sowing just as does density for optimum yield.

2.6.0. The influence of the climatic environment on competition among seedlings of annual pasture plants.

2.6.1. Influence of time of opening of the growing season

There are two aspects of the Mediterranean climate which affect the botanical composition of annual pastures. These are the time of the first effective rains and reliability of following rains.Time of seasonal rains is important because of the different temperature and light regimes which occur after germination, while reliability of following rains is important because of the effect of water stress on growth following germination. The two are linked, as early rains are far more likely to be followed by drought than are late rains.

Let us first consider the time of the opening rains. In Figure 6(a), the mean maximum temperature for the 14 days following opening rains has been plotted against date of opening rains (opening rains are defined as 13mm of rain in a 7 day period) at the Waite Institute, Adelaide, South Australia for the period 1947-1966. There is a negative linear relationship between time of first seasonal rains so defined and temperature during the following 14 days, with a mean fall of 0.75°C per week. Hours of sunshine in the same period show a similar relationship. Thus after an early opening of the growing season, temperatures are higher, and more light is available for plant growth. Until water is exhausted, pasture growth will be more rapid, and if different species have different temperature and light requirements

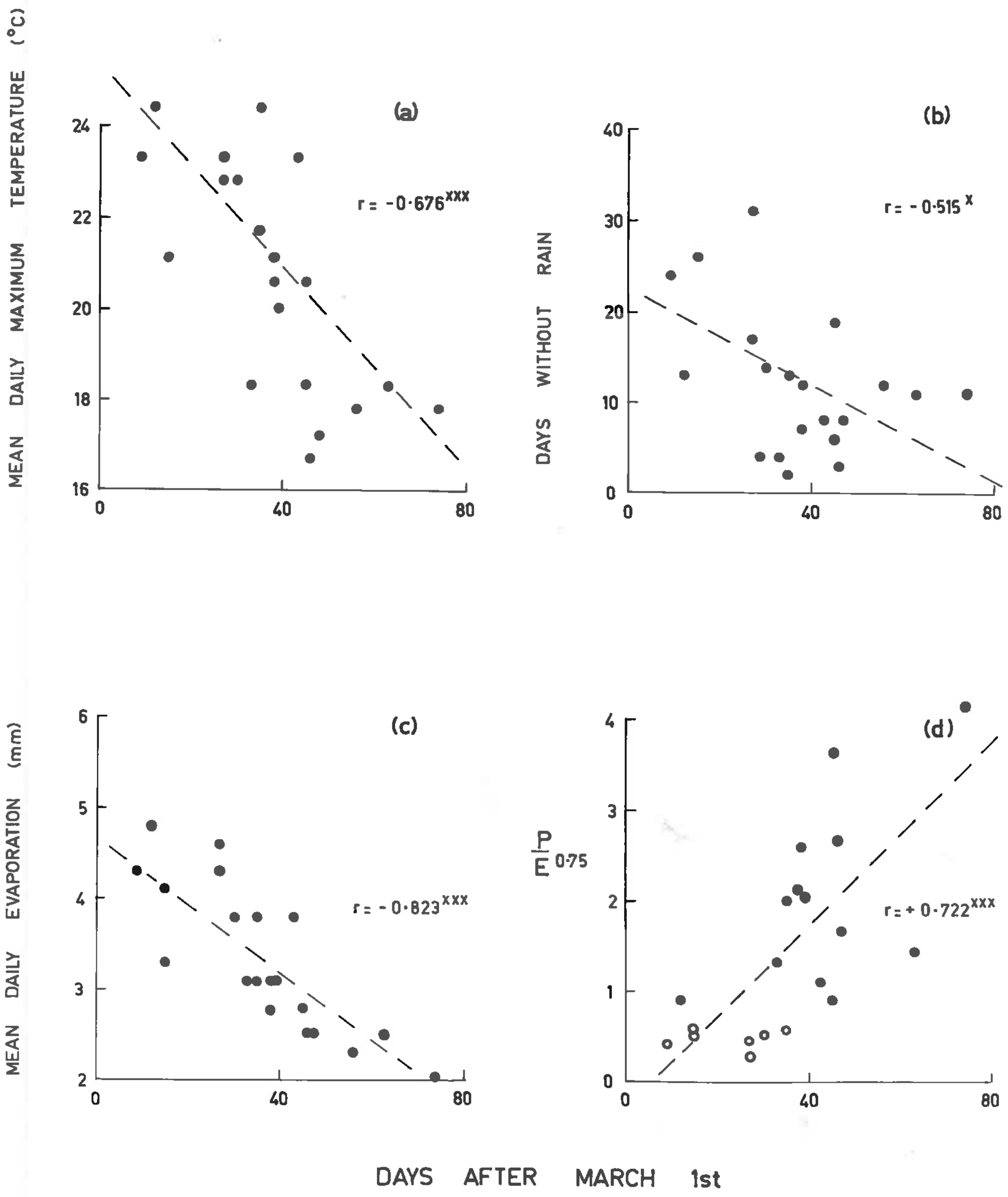
Figure 6 (a) The mean daily maximum temperature in the 14 day period following opening rains at different times of the year.

(b) The number of days with less than 3mm of rain before a further fall of rain greater than 3mm, following opening rains at different times of the year.

(c) Mean daily evaporation in the 14 day period following opening rains at different times of the year.

(d) The effectiveness of opening rains as defined by Prescott and Thomas (1948-49) when those rains fall at different times of the year. In the calculation of the index, rainfall and evaporation for 28 days following (and including) opening rains were used.

The period under study was the 20 year period between 1947 and 1966, and the place was the Waite Institute, Adelaide, South Australia.


MEAN DAILY MAXIMUM TEMPERATURE (°C)
(a)
r = -0·676xxx
24
22
20
18
16
0
40
80
DAYS WITHOUT RAIN
(b)
r = - 0·515 x
40
30
20
10
0
0
40
80
MEAN DAILY EVAPORATION (mm)
(c)
r = - 0·823xxx
6
5
4
3
2
0
40
80
P/E 0·75
(d)
r = + 0·722xxx
4
3
2
1
0
0
40
80
DAYS AFTER MARCH 1st

we have a potential mechanism to explain variation in botanical composition between years.

This variation between years has been more observed than measured. However, the work of Tiver and Crocker (1951) provides perhaps the best examples of what we have come to believe are typical variations. They measured the percentage ground cover of species growing in annual pastures in the South East of South Australia, an area of good rainfall and long growing season. (This data was shown in Table 1). In one year, (1946), rains as early as January were followed by good subsequent rains and the pasture became dominated by subterranean clover. In a later year, (1949), opening rains came in April, and the pasture was dominated by annual grasses. This is the kind of relationship which, despite the meagre data available, is thought by most people to be typical.

Rossiter and Pack (unpublished work quoted by Rossiter, 1966), studied botanical composition on a dry weight basis of a grazed area at Kojonup, Western Australia. They found marked fluctuations between years, and thought that this was due, partly at least, to time of opening rains. Like Tiver and Crocker, they found that peak years for subterranean clover content were associated with early March and April openings. Willoughby (1954) too, presented data from Canberra, from which he concluded that early openings favoured subterranean clover, and later openings <u>Lolium rigidum</u>, in a mixture of the two. It was his opinion, like that of other authors quoted, that this kind of response to early rains is general.

Not all work, however, has associated early opening rains with clover dominance. Rossiter and Pack (quoted by Rossiter 1966) irrigated annual pasture at Kojonup, Western Australia, at various times after February 21. Although a March opening resulted in subterranean clover dominance, an opening as early as February 21 resulted in dominance by the composite Arctotheca calendula. However, this finding has limited meaning because a February 21 opening would be extremely rare in the Kojonup area. Rossiter (1966) also quotes Talbot and Biswell (1942) as finding that Bromus mollis and Erodium botrys were abundant following early rains, while late rains favoured many species including legumes.

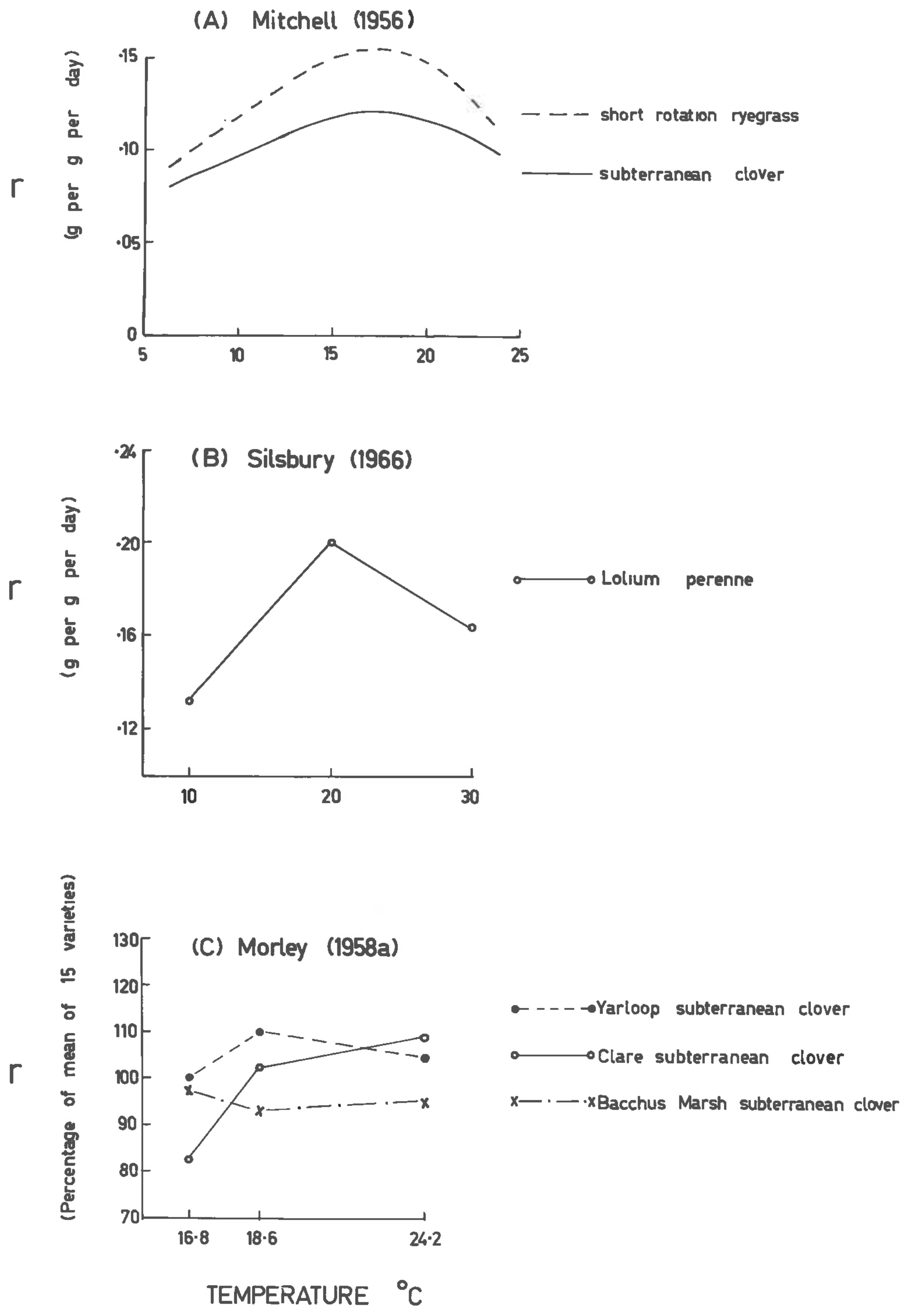
Reasons for the dependence of botanical composition on the time of opening rains must now be sought. The first is that it is due to the variations of temperature already noted (Figure 6a). The logic behind this theory is simply that species of plants vary in their response to temperature. Thus if species A grows quicker than species B at low temperatures, A will become dominant in a mixture of the two when opening rains are late. This is the theory put forward by Willoughby (1954) where species A = Lolium rigidum and species B = subterranean clover.

However, the evidence for such variation in temperature response is not persuasive. Several people have measured the response of subterranean clover to temperature, and have found, either that over the range which occurs during the growing season of southern Australia there is little response to temperature (Black 1955) at Adelaide), or that it has an optimum temperature of about 20°C (Mitchell 1956, Morley 1958) similar to some grasses (Mitchell 1956, Silsbury 1966) (Figure 7). Data from the experiment of Rossiter and Pack (Rossiter 1966) suggests that the growth rate of subterranean clover after early rains (that is, at higher temperature) is no greater than annual grasses and may be considerably less than <u>Arctotheca calendula</u>, although growth rate in winter may be lower than these species. Thus from a consideration of temperature responses, it seems unlikely that superior growth rate of subterranean clover after early opening rains is the explanation of its frequent success in these conditions.

Even if the response curve to temperature of one species did differ from other species when both were grown as spaced plants, it does not necessarily follow that such differences would be maintained in sward conditions. A plant, or community of plants can only grow as well as the environment will allow, and if one aspect limits growth, then variation of another will have little effect. Swards may well be limited by light intensity (Black 1963) even if spaced plants are not (Osanne 1955) and while light is limiting there will be little response to change of temperature. Thus we have a second reason for questioning a temperature effect.

However, the effect of temperature cannot be quite so easily discarded. Rate of germination and seedling growth before competition, are affected by temperature (see Sections 3 and 4 of this thesis), but there is

Figure 7 Response of the relative growth rate of various pasture species to temperature at constant light. Morley's (1958) results are expressed as the percentage of the mean of all relative growth rates, at all temperatures, of 15 varieties of subterranean clover, of which the three varieties shown are representative.



(A) Mitchell (1956)
r
(g per g per day)
·15
·10
·05
0
5
10
15
20
25
short rotation ryegrass
subterranean clover
(B) Silsbury (1966)
r
(g per g per day)
·24
·20
·16
·12
10
20
30
Lolium perenne
(C) Morley (1958a)
r
(Percentage of mean of 15 varieties)
130
120
110
100
90
80
70
16·8
18·6
24·2
Yarloop subterranean clover
Clare subterranean clover
Bacchus Marsh subterranean clover
TEMPERATURE °C

insufficient evidence about these responses to predict what will happen in the field. A similar comment can be made about the effect of changes in light intensity. Although it is known that swards respond to light to very high intensity levels (Black 1963), the significance of such a response in terms of botanical competition is difficult to estimate. There is obviously a great need to study changes in temperature and light intensity in relation to individuals among populations of plants rather than to individuals alone.

A second explanation is that most grass and herb seeds may be dormant in summer andearly autumn, but populations of subterranean clover seed may include only a few dormant individuals. A variant of this theory is that subterranean clover seed loses its dormancy before other annual pasture plants. There is little evidence to support this theory, however, simply because no study has been made of these seed populations.

A third theory to explain the influence of time of opening rains on botanical composition is that there may be changes in soil nutrient status. There are two effects operating, firstly there may be a high degree of mineralization of organic matter associated with the high temperatures of an early opening, and secondly there is an increased possibility of leaching by heavy rains following a late opening. There could be an interaction too, because there may be less nutrient available to be leached after a late opening, as well as the greater leaching potential. The nutrients nitrogen and sulphur are most likely to be affected, because when available to plants they are present in water in soluble form.

While high levels of nitrogen are associated with grass dominance, high levels of sulphur are associated with clover dominance (Walker and Adams, 1958, Fowrie 1967, McLachlan and de Marco 1968). If seasonal changes of either nutrient occurs in the way described above an early opening of the season may lead to grass dominance if nitrogen levels are high, or clover if sulphur levels are high.

That soil sulphate levels do vary during the year has been shown by Barrow (1966), and that soil nitrogen varies, by Storrier (1962), and Richardson and Fricke (1931). They found that, following heavy rains in winter, sulphate and nitrate levels fell to a quarter of the autumn level, but sulphate levels especially, rose again during spring, presumably due to mineralization or upward movement of water as the soil dried out. While this work did show nutrient variations it did not show that early rains leach less quickly than late rains, merely that rains reduce nutrient levels. The whole topic needs further investigation.

2.6.2. Moisture stress after early opening rains.

The second, and perhaps more important aspect of climate effect is that effect known in Australia as the "false break". This occurs when rains sufficient to cause germination are followed by drought. By defining such rains as 13mm over a 7 day period, and examining meteorological data over an ensuing period, some idea of the frequency of "false breaks" can be obtained.

This has been done in Figure 6.

Figure 6(b) shows the number of days following 13mm of rain in which no further rain fell. The relationship in Figure 6(b) indicates that 15 days without rainfall can be expected even if the first seasonal rains fall on April 1, and that more than 20 days without rain can be expected following similar rains in March. It can be seen that if temperatures are high during March, newly established seedlings are very likely to experience moisture stress.

Figure 6(c) shows that evaporation from a free water surface also declines as time during the season progresses, just as does the number of days without rain (Figure 6(b)). An expression which combines evaporation and rainfall is the expression

$${}^{P}/_{E} \quad 0.75$$

derived by Prescott and Thomas (1948-49), where P = precipitation and E = evaporation from a free water surface. Prescott and Thomas considered that if the value of this expression was equal to or greater than 0.4, rainfall was effective. In Figure 6(d), this expression, calculated using rainfall in the 28 day period including and following 13mm of rain, has been plotted against days after March 1 when 13mm of rain fell. In only 2 years in the period 1947-1966 was this value less than 0.4, and the relationship shows that after March 13 rainfall is likely to be effective. This indicates a close agreement between the index of Prescott and Thomas and the definition of opening rains used in this thesis in predicting the opening of the growing season. However, if we refer back to Figure 5, some of these openings have been subsequently defined as false because of the long periods of dry weather which followed the initial rainfall. These years have been shown as open circles in Figure 6(d), and all have Prescott and Thomas values of less than 0.6 . Consequently, it seems that if the value of this expression is greater than 0.6 in the 28 day period following 13 mm of rainfall, then that rainfall can safely be said to be the opening seasonal rains. This rainfall is likely to be effective after March 18.

Years in which fairly severe drought periods have followed rains in early autumn are shown in Figure 8. In 1957, rain was followed by high temperature and drought, and in 1959, though temperatures were lower than in 1957, the drought period was exceptionally long (only 8 mm of rain in 50 days). There was obviously no moisture stress after opening rains in 1952 which is included for comparison with the other years (April rainfall in 1952 was 77 mm compared with an average April rainfall of 53 mm).

That death of seedlings of annual pasture plants occurs under drought conditions is demonstrated by data from Carter (unpublished) and Rossiter (1966) appearing in Table 5. Note that Carter's results (Table 5a) show that, following early rains, a reserve of seeds remains in the soil capable of germinating later in the season. Grass and clover seedlings both suffered severely

Figure 8 Showing two seasons (1957 and 1959) when autumn rain was followed by long dry periods, and a "normal" season (1952) at the Waite Institute, Adelaide. Opening rains occurred on April 16 1952, March 9 1957, and March 30 1959. The dotted line is the daily maximum temperature (°C) and the columns the daily rainfall (mm).

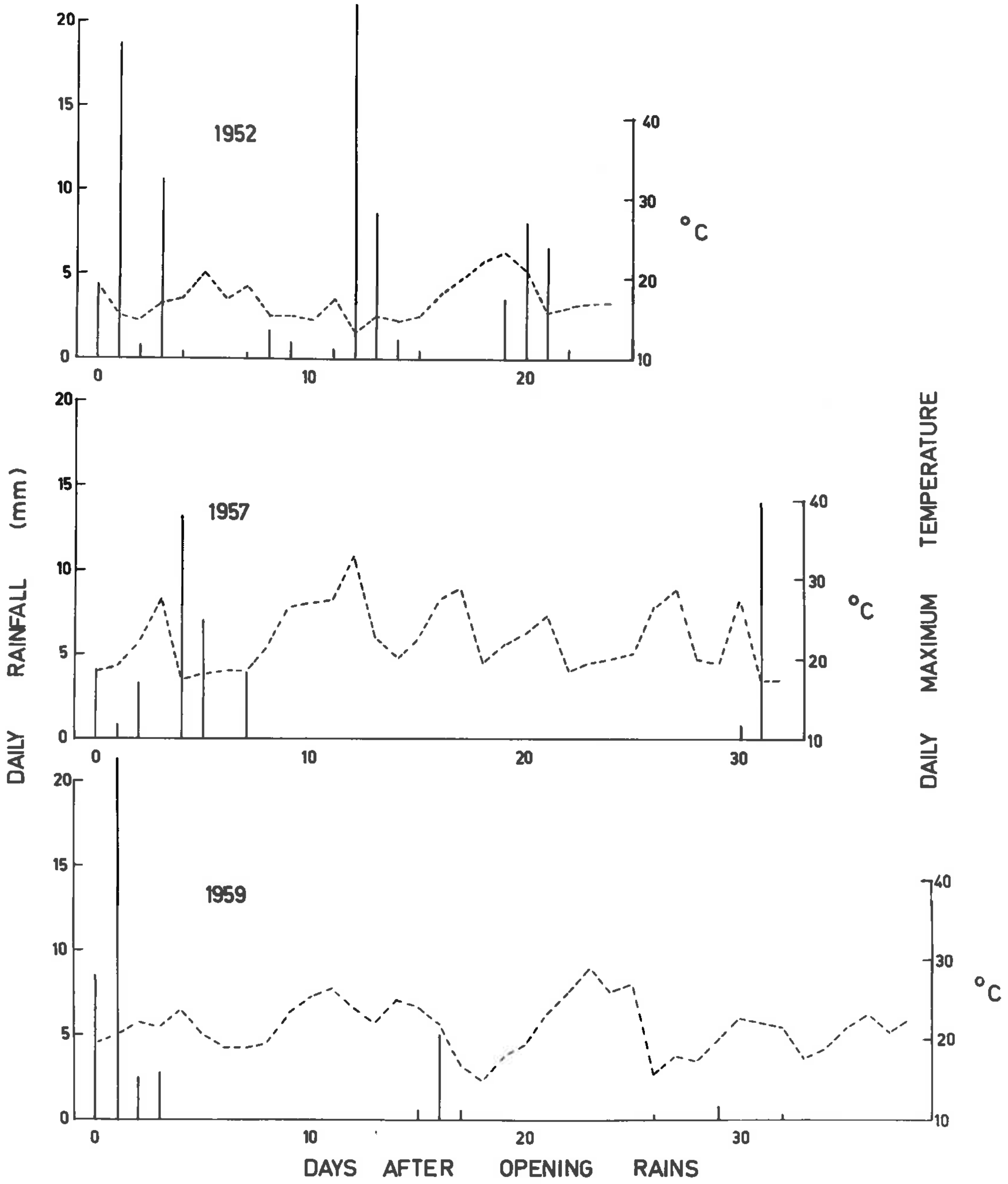

1952
1957
1959
DAILY RAINFALL (mm)
DAILY MAXIMUM TEMPERATURE
°C
0
5
10
15
20
10
20
30
40
DAYS AFTER OPENING RAINS

TABLE 5

(a) Seedlings established after rains in March 1966 and those surviving after 42 days in which 40 points of rain fell (Carter, unpublished).

	Species	3 sheep per acre	6 sheep per acre	9 sheep per acre
Seedlings present on 28/3/66	T.subterraneum	6	10	9
	grass	106	71	7
	other	3	10	14
Seedlings survived on 10/5/66	T.subterranemm	2	2	1
	grass	27	19	2
	other	1	2	2
New seedlings established on 10/5/66	T.subterraneum	13	22	6
	grass	24	19	1
	other	0	1	0

(b) Percentage of seedlings surviving following heavy early rains and a long drought period in 1955 and 1956 at Kojonup, Western Australia (Rossiter and Pack quoted by Rossiter 1966)

Year	Trifolium subterran.	Arctotheca calendula	Erodium botrys	Bromus rigidus	Vulpia myuros
1955	9	28	53	45	10
1956	12	85	62	41	5

in Carter's plots. Rossiter's data (Table 5b) indicates that subterranean clover seedlings are more sensitive to water stress than the seedlings of some other annual species. Other evidence includes that of Black (quoted by Donald 1960), who found that in the summer of 1954-55 at Adelaide, 83% of the seed of Bacchus Marsh subterranean clover was lost by germination and subsequent seedling mortality. Smith (1965) too, found that subterranean clover survived a moisture stress period less well than *Hordeum leporinum*, with the result that the latter became dominant

The importanceto a plant of surviving drought periods is clear, When further rain does fall, those seedlings still alive have leaf area and root already formed and will probably dominate later germinating plants. As well as this, total population in a sward resulting from later rains may be considerably reduced.

The explanation of differential drought resistance among seedlings of annual pasture plants probably lies in differences in development of their root systems. Ozanne, Asher and Kirton (1965) have shown that plants of *Erodium botrys* and *Arctotheca calendula* root deeper than plants of *Lolium rigidum*, subterranean clover (Yarloop strain) and *Vulpia myuros*. Re-examination of Table 5(b) shows that these deep and shallow rooted species, are drought resistant and drought susceptible respectively.

Total depth of rooting may be less important than rate of penetration. If the top soil does not remain damp until the next rains, then roots must penetrate to the sub soil before the top soil dries. Ozanne and Asher (1965) found that root penetration of a number of annual pasture species depended on seed size. Thus *Bromus rigidus* (seed weight 10.5 mg) penetrated to a depth of 35 cm in 10 days, while *Vulpia myuros* (seed weight 0.5 mg) barely reached 5 cm in the same period. These seeds were growing in potassium deficient sands, so that differences recorded were doubtless higher than if no deficiency existed (presumably *Vulpia* seedlings exhausted reserve potassium before *Bromus* seedlings). But I think it is still valid to assume that differences of some magnitude dependent on seed size would occur.

It is possible that some species can extract moisture from drier soils than others, but to my knowledge no such difference has been demonstrated among annual pasture plants.

2.7.0. Concluding remarks

When the first autumn rains fall after the long summer drought, very large numbers of seeds are simultaneously wetted. These seeds, if they are not dormant, begin to germinate very quickly. They lie on the surface of the soil or just beneath it and soon become established as young seedlings. The environment in which these seedlings will live is one which is intensely competitive. Because they are so dense, competition between them begins soon after they established. Very small differences in seedling size may have quite profound influences on their success in the subsequent pasture. Very small differences in rate of germination, seedling growth rates, seed sizes and responses to the environment will affect seedling size and hence competitive ability.

The events which occur in the period after the opening seasonal rains in a Mediterranean annual pasture are the events which concern me in this thesis. I have studied factors affecting germination of seeds and survival of seedlings, and the mechanisms whereby differences in these processes affect subsequent botanical composition.

Of the annual pasture grasses which have invaded southern Australian pastures, Hordeum leporinum (known in Australia as barley grass) is one of the most common. (Tiver and Crocker, 1951, Rossiter 1966, Smith 1968a). It was apparently introduced by Europeans, and was almost ubiquitous in southern Australia by the beginning of the 20th century (Smith 1965).

Hordeum leporinum is considered an undesirable plant in pastures mainly because of the morphology of its seed dispersal unit. This unit consists of three florets, the outer two being sterile, and the inner one fertile. On each floret there are long awns and lanceolate glumes with ciliate margins. The whole unit has a strong point, the rhachilla. Because of the ciliate margins of the awns and glumes, the unit can move in only one direction, that is towards the point. When lodged in the wool of sheep it can become a severe health problem, especially if there are large numbers of these "grass seeds" affecting the animal. The eyes, mouth and ears of the sheep are most vulnerable. In addition, the value of the fleece is reduced.

Accordingly, annual pastures are here studied with particular attention to *Hordeum leporinum*. In many cases comparisons have been made with *Lolium rigidum*, the only annual grass which is widely sown. It is a high producing grass with none of the "grass seed" worries of *Hordeum leporinum*. Its main fault is its inability to regenerate in permanent pasture (Table 6), though it successfully maintains itself as a weed in cereal crops, especially in Victoria (McGowan 1967).

The experimental programme can be divided into four parts. In the first part, factors affecting germination and establishment have been studied. In the second, emphasis has been on the growth of seedlings with special reference to the effect of temperature.

In the third, the effect of seedling density on competition between H.leporinum and L.rigidum has been studied. In the fourth, plant competition between these two species with reference to competition for light and nutrients has been examined.

TABLE 6

The percentage of *Lolium rigidum* and other grasses (mainly *Hordeum leporinum* and *Vulpia myuros*) in the period 1959 to 1963, in plots grazed by sheep at Kybybolite, South Australia. The plots were sown in 1958 with 10 lb of *Lolium rigidum* seed per acre. Percentages were measured using Levy point quadrats (Cocks 1966)

Year	Lolium rigidum	Other grasses
1959	70.9	10.6
1961	30.1	28.4
1962	11.0	34.9
1963	8.9	61.1

3.0.0. GERMINATION AND ESTABLISHMENT.

3.1.0. Experiment 1. Dormancy of Hordeum leporinum.

Dormancy tests were conducted on a strain of H.leporinum known to be very dormant in midsummer. This strain had been collected from Semaphore, a seaside suburb of Adelaide with 17-18 inches of rainfall per annum. Plants of this strain had been grown at the Waite Institute for one year previously, and it was from these plants that seed was gathered.

3.1.1. Procedure.

Seeds of H.leporinum were collected during November (for description of seed dispersal unit, see page 72, and also Covas, 1949). At two dates, 9th April and 12th June in the following year, samples of the seed were washed in a strong jet of water for various times up to 30 minutes. The various treatments simulated light to fairly heavy rain. A control sample was not washed. Twenty seeds were counted out from each washing and placed on filter paper in a Petri dish in a germination cabinet at 20°C. The number of seeds germinated were counted each day. There were five replicates.

At the first date, sterile florets were removed from an unwashed sample, and five replicates of twenty seeds counted and germinated as above.

3.1.2. Results

The effect of leaching seeds was to hasten germination (Figure 9). Significantly more washed seeds than controls had germinated at days 2, 3, 4, 5 and 8 for the 9th April test, and at days 1 and 2 for the 12th June test. Comparison of the two dates shows that dormancy was less strong at the latter date.

Removal of sterile florets partially relieved dormancy, though not to the same extent as washing for 30 minutes (Figure 10). This test was conducted on 9th April.

3.1.3. Discussion

To my knowledge this is the first demonstration that leachable inhibitors occur in the seed dispersal units of *H.leporinum*. At the dates tested, the inhibitor slowed down rather than stopped germination, though complete suppression of germination was observed earlier in the summer. It has been shown that much of the inhibitor occurs in the sterile florets, but also that some occurs in the central or fertile floret.

FIGURE 9 The effect on subsequent germination of washing seeds of *H. leporinum* in a strong jet of water. The numbers in the circles indicate the number of days after the commencement of the test at which the germination was measured. The bars indicate least significant differences ($P = 0.05$) between any two points on a particular day of measurement.

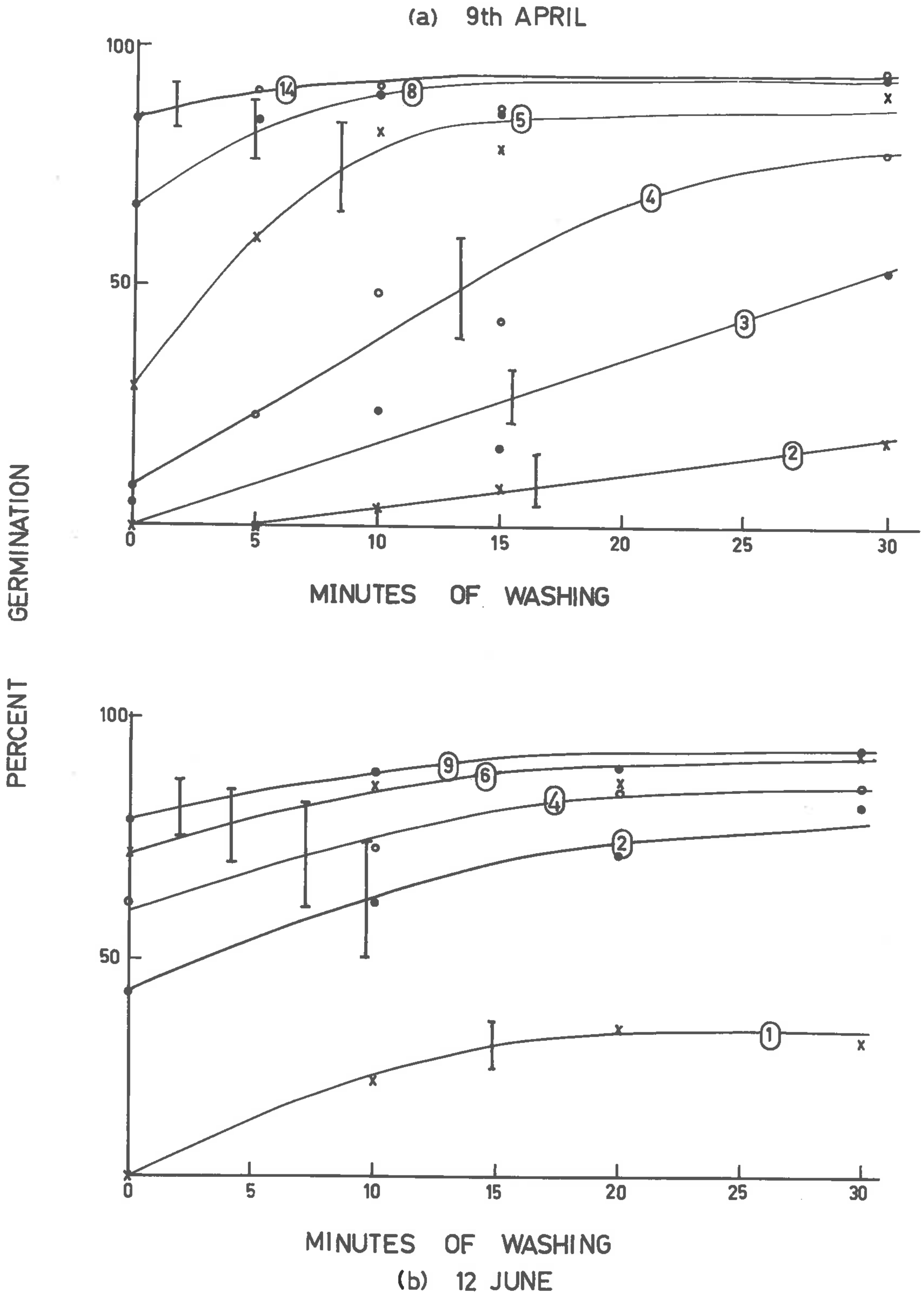
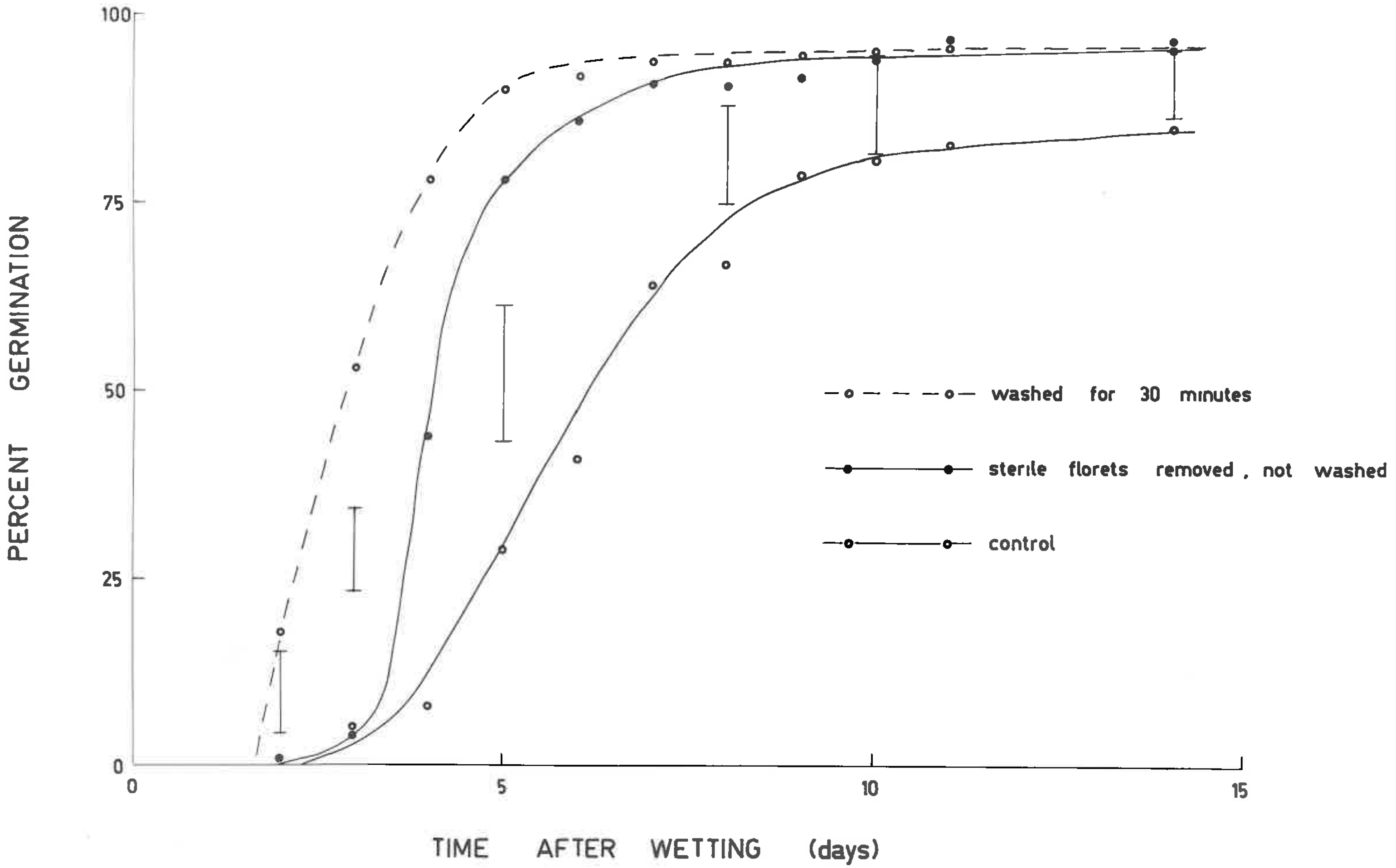

(a) 9th APRIL
100
50
0
5
10
15
20
25
30
14
8
5
4
3
2
MINUTES OF WASHING
PERCENT GERMINATION
100
50
0
5
10
15
20
25
30
9
6
4
2
1
MINUTES OF WASHING
(b) 12 JUNE

Figure 10 The effect of removal of sterile florets, and of washing for 30 minutes, on the rate of germination of dormant seeds of *H. leporinum*. The bars represent least significant difference ($P = 0.05$) between the curves at a particular time after wetting. The test was begun on 9th April.


PERCENT GERMINATION
100
75
50
25
0
0
5
10
15
TIME AFTER WETTING (days)
washed for 30 minutes
sterile florets removed , not washed
control

3.2.0. Experiment 2

Effect of constant and alternating temperature on germination of seeds of H.leporinum and L.rigidum.

The effect of temperature on germination is two-fold: an effect on total germination and an effect on rate. Consideration has been given to both criteria in the following experiment.

3.2.1. Procedure

A multiple temperature incubator was used, similar to that described by Andrewartha and Andrewartha (1935) except that a refrigerator unit was used instead of ice, and that the incubator stood in a constant temperature room. Fourteen compartments were available and the temperature range could be varied either by adjusting the temperature of the heating end or of the cooling end of the incubator. Typical temperature variations within each compartment are shown in Table 7. Temperatures used to described results are means, as in Table 7.

Two hundred seeds of each species were used for each treatment and placed on moist filter paper in Petri dishes. Deionized water was added as needed. Seeds were counted as 'germinated' on the appearance of the radicle.

To test the effect of alternating temperature, dishes were placed in the multiple temperature incubator during the day (for 12 hours) and placed in one of

TABLE 7

Examples of temperature variation in compartments of the multiple temperature incubator used to test response of germination to temperature.

Compartment	Day										
	1	2	3	4	5	6	7	8	9	10	Mean
1	39.5	38.1	39.1	39.1	38.9	39.4	40.4	40.4	39.3	39.3	39.4
5	23.3	23.9	23.8	23.5	23.5	24.1	24.6	24.6	24.2	24.1	24.0
9	16.4	17.0	17.0	17.0	17.0	17.4	17.4	17.6	17.3	17.0	17.1
12	10.0	10.9	10.7	10.6	10.9	10.9	10.9	11.1	10.8	10.7	10.8
14	4.0	4.0	4.0	4.0	4.3	4.1	4.5	4.6	4.1	4.1	4.2

four cabinets maintained at 6°C, 12°C, 20°C and 26°C at night (for 12 hours). Light was excluded from all treatments.

A commercial sample of *L.rigidum* seed was used. Seed of *H.leporinum* was obtained from Pinaroo in the South Australian Murray Mallee district, a locality where rainfall is about 14 inches. The seed had been threshed to remove sterile florets. This made the seed much easier to handle, and also eased dormancy problems, but unfortunately reduced total germination.

A second experiment was conducted to see whether seeds which failed to germinate at high temperature were killed or remained viable. Seeds were germinated in Petri dishes as before, but after several days at 38°C were removed to a cabinet held at 20°C. The results to be shown in Table 8 indicate that a temperature as high as 38°C inhibits germination of both species. Seeds of *H.leporinum* used in this experiment were unthreshed because it was thought that damaged seed would be far more likely to be subject to attack by micro-organisms.

3.2.2. Results

1) Total germination

Complete germination of both species occurred in 12 days at constant temperatures ranging from 8°C to 29°C (Table 8). Germination at temperatures below 9°C would probably have been greater if the test had continued for a longer period. Germination of both species was inhibited at temperatures above 30°C.

Figure 11 shows the effect of alternating temperature on total germination. The x axis represents the higher of the two temperatures (day temperature), the y axis the drop in °C between the high and the low temperature (night temperature), and the figures, the number of seeds expressed as percentage of total seed which germinated after 10 days when subjected to the two temperatures shown on the x and y axis. The lines, iso-germination lines, are lines connecting temperature treatments of equal seed germination.

Both species show a response to alternating temperature. Highest germination of H.leporinum occurred when a high temperature of 25-32°C was followed by a temperature fall of between 2°C and 8°C. Apart from this treatment (represented by a closed isoline in Figure 11) the positions of the isolines suggest that there is less alternating temperature requirement at high temperatures than there is at low temperatures. This is shown graphically in Figure 12, where various day temperatures between 17°C and 30°C have been plotted against the fall in temperature at night which gave optimum germination at that day temperature.

Best germination of L.rigidum occurred when a day temperature between 20°C and 27°C was followed by a fall of temperature at night of between 8°C and 16°C. This indicates that some seed of L.rigidum was 'dormant' at fixed temperatures, and that this seed has an alternating temperature requirement. In this species the optimum alternation of temperature is apparently greater

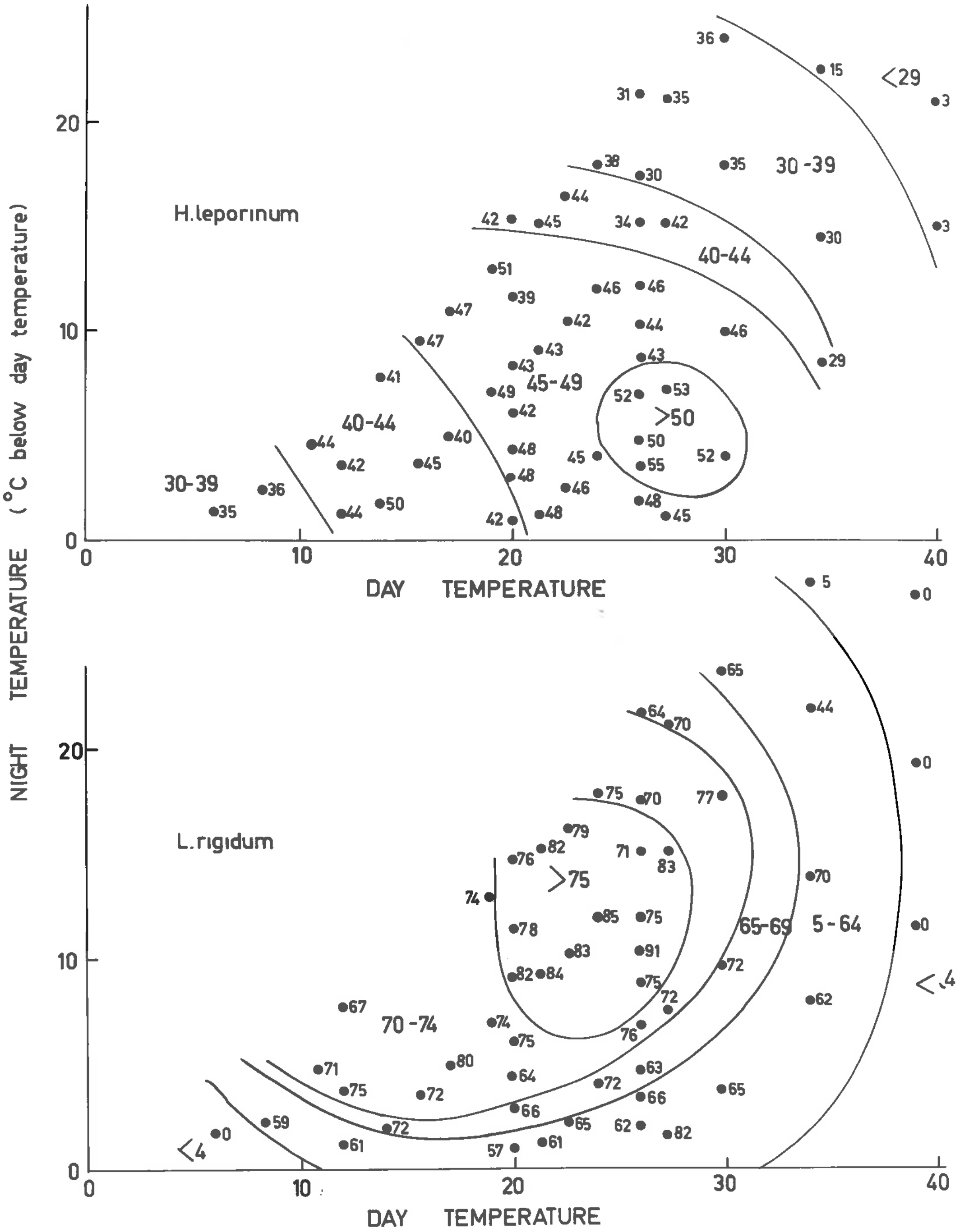
TABLE 8

Percentage germination after 12 days at the indicated constant temperatures.

Hordeum leporinum		Lolium rigidum	
Temp. °C	Germination	Temp. °C	Germination
37.3	0	36.8	0
32.8	23	31.8	43
29.3	51 *	28.0	65 *
27.3	49	26.0	72
24.4	57	23.0	70
23.0	58	21.6	71
22.1	56	20.6	62
19.8	59	18.3	68
17.8	59	16.4	66
16.0	51	14.6	76
14.0	57	12.7	76
10.9	59	9.8	71
8.4	50	7.3	45
4.0	1	3.0	0

* The figures within the brackets represent maximum germination percentage. The span of the brackets represents the range of temperature at which maximum germination occurred.

Figure 11 Showing lines of equal germination (iso-germination lines) in relation to day and night temperature. The figures are the percentage of all the seeds in the test which had germinated after 10 days when subjected to the two temperatures shown in the x and y axes.


H.leporinum
L.rıgıdum
NIGHT TEMPERATURE (°C below day temperature)
DAY TEMPERATURE
DAY TEMPERATURE
0
10
20
30
40
<29
30-39
40-44
45-49
>50
40-44
30-39
36
15
3
31
35
38
30
35
44
42
45
34
42
3
30
51
46
46
39
47
42
44
46
47
43
43
29
41
49
52
53
42
40
50
44
48
45
52
42
45
55
36
48
46
50
44
48
35
42
48
45
>75
70-74
65-69
5-64
<4
<4
5
0
65
64
70
44
0
75
70
77
79
82
76
71
83
70
74
85
75
78
0
83
91
72
82
84
75
72
67
62
74
76
75
80
63
71
64
72
75
72
66
65
66
72
59
65
0
62
82
61
57
61

at high day temperatures than it is at low day temperatures, in marked contrast to *H.leporinum* (Figure 12).

Table 9 shows the effect of soaking for several days at a temperature high enough to inhibit germination (38°C), on subsequent germination at a constant lower temperature (20°). The Table shows that both species were able to germinate under these conditions, but at a reduced level compared with controls, the reduction in germination depending on time of exposure to the high temperature. The Table also shows that *L.rigidum* was markedly better able to tolerate such conditions than was *H.leporinum*. The latter species was killed after 7 or more days at 38°C, yet 35% of *L.rigidum* survived 10 days high temperature exposure.

ii) Rate of germination

Rate of germination was more rapid for both species at 25°C (Figure 13). Rate of *H.leporinum* was greater than *L.rigidum* at all temperatures. Figure 13 shows that after 24 hours no seeds of *L.rigidum* had germinated, and that even after 48 hours, germination of that species had only commenced if night temperature was 20°C or 26°C. Rate of germination curves of both species at two constant temperatures are shown in Figure 14. Note that at 23°C *H.leporinum* began germination at least one day before *L.rigidum*, and that at 10°C this difference was 4 days.

3.2.3. Discussion

It is apparent that both species have an alter-

__Figure 12__ Optimum fall of night temperature below day temperature at various day temperatures for maximum germination of __H.leporinum__ and __L.rigidum__. The lines showing the relationship between day temperature and optimum fall in temperature at night were hand fitted.

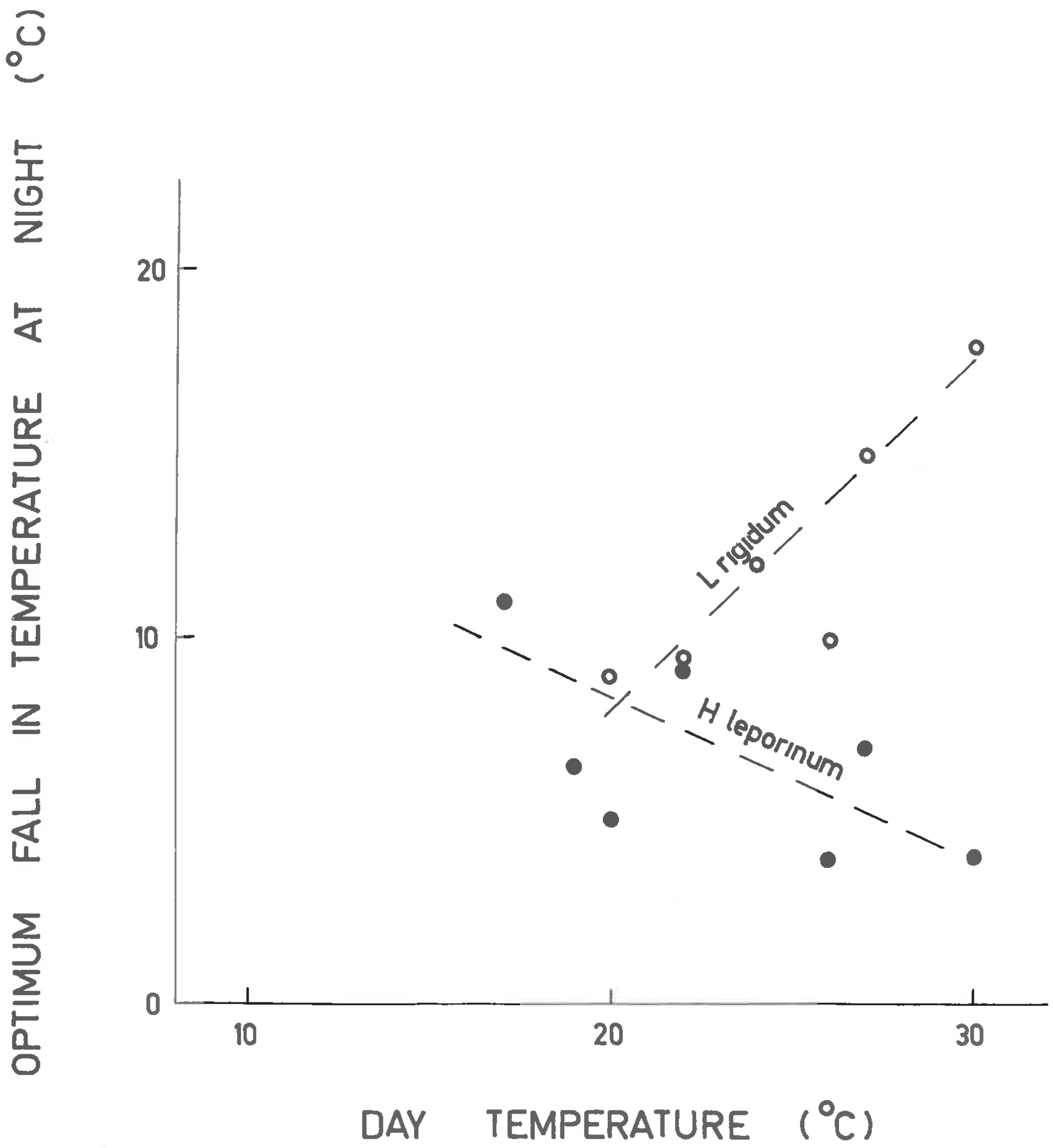

OPTIMUM FALL IN TEMPERATURE AT NIGHT (°C)
20
10
0
10
20
30
DAY TEMPERATURE (°C)
L rigidum
H leporinum

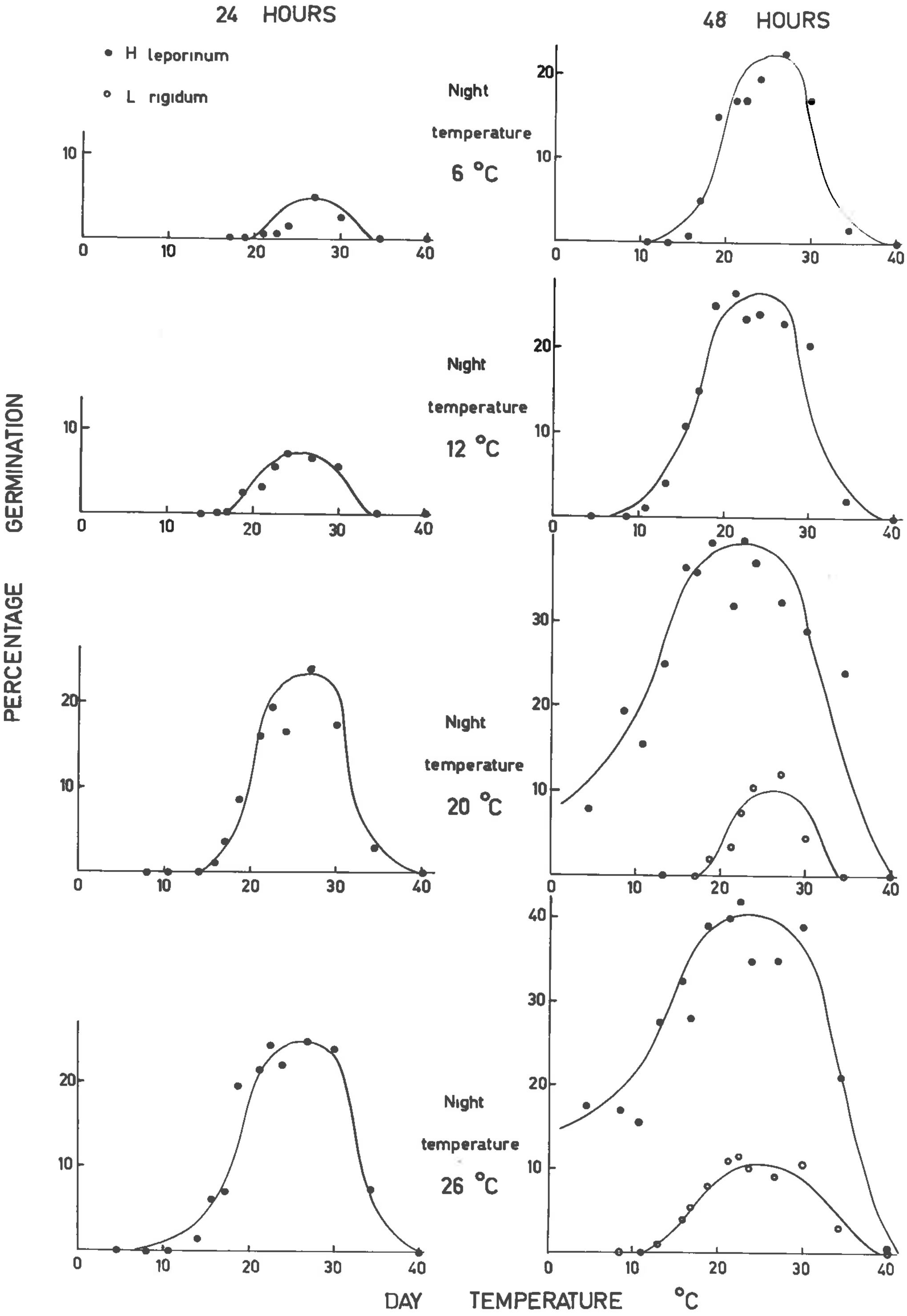
TABLE 9

The percentage of all seeds tested of H.leporinum and L.rigidum which germinated following soaking for various periods at 38°C and transfer to a constant 20°C.

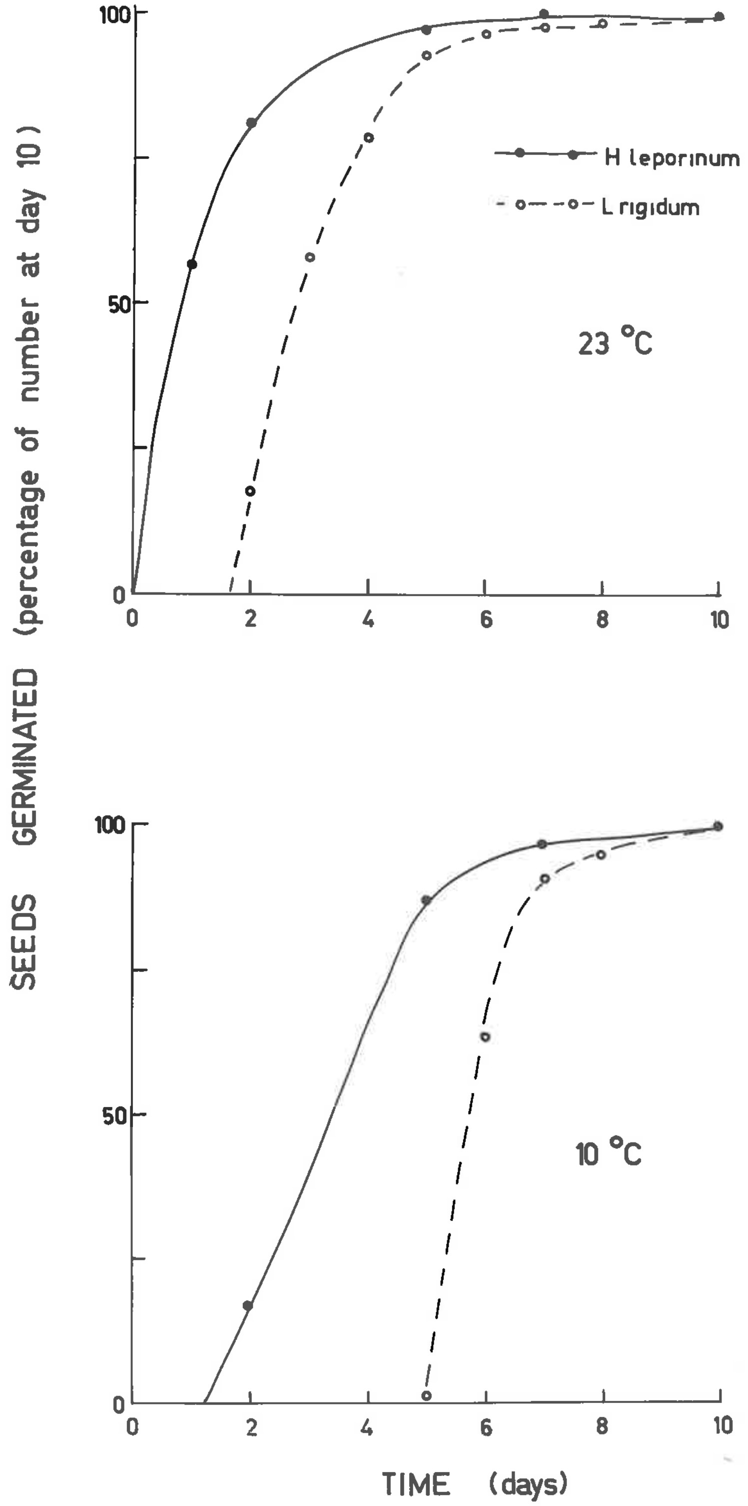
Length of period at 38°C	Length of period at 20° C					
	2 days		4 days		14 days	
	H.lep	L.rig	H.lep	L.rig	H.lep	L.rig
0 days	85	80	98	92	98	92
1	83	83	93	96	94	98
2	57	75	63	91	74	94
5	12	36	14	61	26	66
7	0	16	0	36	2	44
10	0	0	0	21	0	35
*L.S.D. P=0.05	13.4		15.2		16.5	

* L.S.D. between species and between periods of soaking at 38°C.

<u>Figure 13</u> Germination of <u>H.leporinum</u> and <u>L.rigidum</u> 24 hours and 48 hours after the commencement of the test, at various day and night temperatures, as shown. Curves were fitted by hand.


24 HOURS
48 HOURS
● H leporinum
○ L rigidum
Night temperature 6 °C
Night temperature 12 °C
Night temperature 20 °C
Night temperature 26 °C
PERCENTAGE GERMINATION
DAY TEMPERATURE °C
0
10
20
30
40

<u>Figure 14</u> Showing rate of germination of both species at two constant temperatures.


SEEDS GERMINATED (percentage of number at day 10)
100
50
0
0
2
4
6
8
10
H leporinum
L rigidum
23 °C
100
50
0
0
2
4
6
8
10
10 °C
TIME (days)

nating temperature requirement. Except at lower temperatures (below about 20°C), *L.rigidum* requires a greater fall in temperature at night than does *H.leporinum*. Whereas at high temperatures *L.rigidum* requires a greater amplitude of alternation than it does at low temperatures, the reverse is true for *H.leporinum* .

The possibility that some seeds require a period of low temperature before germination, similar to the low temperature requirement of dormant seeds of subterranean clover, can be dismissed on the grounds that germination is no better at a constant low temperature than it is at a constant high temperature. For example germination of *L.rigidum* after 10 days at a constant temperature of 16°C was 71%, and at 26°C was 61%, but if the temperature alternated between 26°C and 16°C the germination was 90%. If there was a requirement for the seed to spend a period at 16°C, the the seed which was held at that temperature would presumably germinate as well as the seed which had 12 hour periods at that temperature, though not as quickly if the other seeds spent the other 12 hours at a higher temperature. For similar reasons, a high temperature requirement can be dismissed. The requirement is in fact for alternation of temperature.

The ecological significance of a response to alternating temperature may be two fold. Firstly, germination is limited to the season in which the requirement is met, and secondly, because diurnal change of temperature decreases with depth (Geiger 1959), the depth from which the seeds germinate may be limited. The mechanism may result in a continuing reserve of seed in some circumstances. However, it does not seem well adapted to aid survival in a Mediterranean climate or in annual pastures. Diurnal temperature changes are of the order required all the year round (Table 10) and in annual pastures, seed normally falls on the surface, or is buried only beneath surface litter.

Of more significance is the ability of both species, particularly L.rigidum, to survive soaking at a temperature (38°C) which had been shown earlier (Table 8) to inhibit germination. This indicates a high temperature dormancy mechanism which will presumably restrict germination after summer rains, of great importance in the southern Australian environment, where risk of such rains is high. Treatments applied were extreme, but L.rigidum demonstrated great ability to survive even these.

Both species germinate most rapidly at 25°C, but it is evident that germination of H.leporinum proceeds more rapidly than that of L.rigidum at all temperatures. The consequences of a difference of this kind have been discussed in the literature review. To recapitulate, species with more rapid germination tend to dominate mixtures in which they occur with species of less rapid germination (Sagar, quoted by Harper 1961, Milthorpe 1961, Lazenby 1961, Black and Wilkinson 1963).

TABLE 10

Mean monthly maximum and minimum temperatures ($^{\circ}C$) at Adelaide and Berri (in the Murray Mallee district 120 miles from the coast).

Adelaide												
Max	29	30	27	23	19	16	16	17	19	23	26	28
Min	16	17	15	12	11	8	7	8	9	11	13	15
Berri												
Max	31	30	28	23	19	16	16	17	21	24	27	30
Min	15	15	13	10	8	6	6	6	8	10	12	14

3.3.0. Experiment 3 The effect of soaking and drying on subsequent germination.

Light summer and autumn rains, or heavy rain followed by very dry conditions, are common in the late summer and early autumn in Adelaide. Seeds of annual pasture plants may be wetted for several hours or even days, then be completely dried. The ability to germinate after such a soaking obviously has ecological significance. The following experiment was conducted to test such ability.

3.3.1. Procedure

Samples of 200 seeds of each species were placed on moist filter paper in Petri dishes and put in a germination cabinet set at 17°C. The samples were left in the cabinet for varying times from 2 hours to 48 hours (*Hordeum leporinum*) and 2 hours to 96 hours (*Lolium rigidum*) At the end of the predetermined period the seeds were taken out of the Petri dishes, dried between filter paper, placed in envelopes, and dried for 24 hours at 30°C in a forced draught oven. All samples were then replaced in the Petri dishes, moistened, and the number of seeds germinated were counted each day. A control sample was dried (without being pre-wetted) and germination measured in the same way. The experiment was replicated three times.

Seed of *L.rigidum* was obtained commercially, seed of *H.leporinum* was obtained from Kybybolite, an area of 21 inch rainfall in the South East of South Australia. Sterile florets were carefully removed, but the seed coat was undamaged and consequently a high germination percentage was recorded.

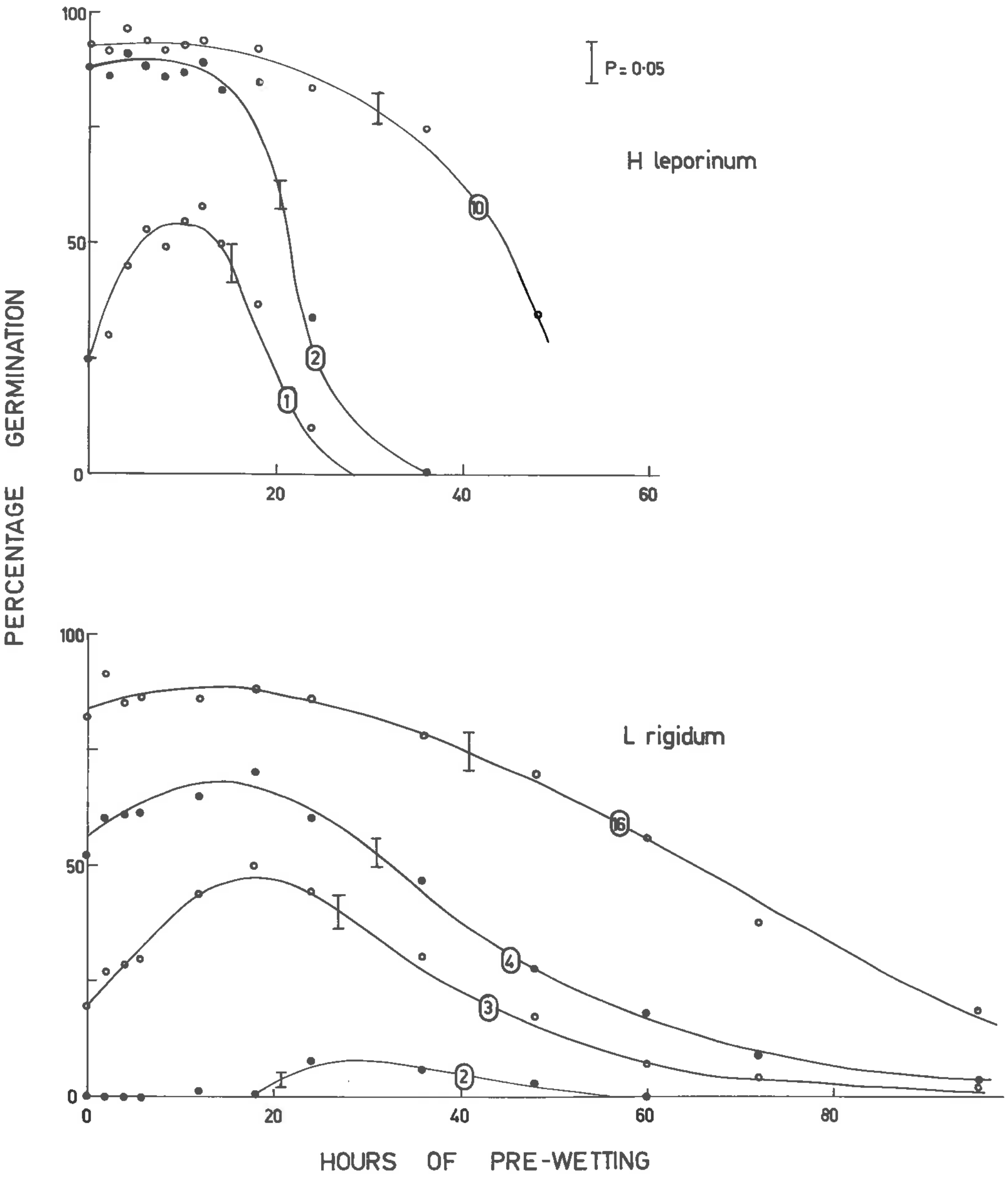
3.3.2. Results

As shown in Figure 15, pre-wetting for short periods resulted in a stimulation of rate of germination of both species. Optimum length of presoaking was 10 hours for *H.leporinum* and 20 hours for *L.rigidum*. Longer periods of pre-wetting depressed rate (longer than 15 hours for *H.leporinum* and 25 hours for *L.rigidum*). At the last count, ungerminated seeds were apparently dead (they had been attacked by micro-organisms), and it is clear that total germination of seeds subjected to long periods of pre-wetting was depressed. However, it was noticeable that seeds which had commenced germination during the pre-wetting period were not necessarily killed when dried. Radicles which had been produced did not survive the drying period, but some seeds were able to produce primary roots or a plumule from the base of a killed radicle. This kind of abnormal germination was slow, but may be extremely valuable as a survival mechanism in the field.

3.3.3. Discussion

The most likely reason for a positive rate response to pre-soaking is the breakdown of reserve material which normally precedes germination. However, the possibility that inhibitors are removed in the pre-soaking period cannot be ignored, especially in the light of germina-

Figure 15 Number of seeds germinated at the times indicated in the circles (days after commencement of germination test) for each of several pre-wetting treatments. Bars represent least significance differences (P = 0.05) between pre-wetting treatments on any days.


P = 0·05
H leporinum
L rigidum
PERCENTAGE GERMINATION
HOURS OF PRE-WETTING
100
50
0
20
40
60
80
1
2
3
4
10
16

tion rate responses to leaching in *H.leporinum*, recorded earlier in this thesis (Figures 9 and 10).

The most likely reason for injury to seeds after prolonged soaking is, in the opinion of Lang (1965), the removal of materials necessary for germination. However, because the length of soaking period necessary to cause damage is approximately the same as the time needed for the first radicles to appear, it seems that damage begins after the embryo has begun to grow. Just as an emerged seedling is susceptible to drought, so is a newly germinated seedling, the beginning of growth being the end of the drought escape phase of an annual plant. It is worth noting, however, that many of the seeds which had long soaking periods were attacked by micro-organisms after re-wetting.

If the reasoning above is correct, that is, that damage begins when embryo growth begins, then the results of this experiment give a measure of the time before such growth begins, at 17°C. Maximum stimulation and the beginning of damage occurs after 10 hours soaking for *H.leporinum* and 20 hours for *L.rigidum*. At this temperature then, the difference is a mere 10 hours, though differences in growth rate will affect actual germination times. Ten hours, however, may be quite significant when the two species are sown together in a mixture.

I shall now discuss the ecological significance of germination response to prewetting. Falls of rain of *less* than 13 mm (13 mm is the arbitrary definition of opening rains used in this thesis) occurred on an average of 3.8 times a year in the 20 year period from 1947 to 1966. The mean amount of rainfall on these occasions was 1.6 mm. Falls were thus usually very light and may have had little effect, although if they were able to keep seeds wet for 2 hours, some stimulation of germination rate of both species would result. Rains sufficient to keep seeds wet for 10 hours would increase the advantage in rate that *H.leporinum* has over *L.rigidum*, longer periods would decrease its advantage. Unfortunately, from an examination of meteorological data, it is difficult to estimate the length of time which the soil surface remains wet after light rains. I consider that periods of more than 10 hours would be uncommon unless light showers occurred at intervals over this period. In general, light rains will favour *H.leporinum*, while heavier rains, sufficient perhaps to constitute a "false opening" will favour *L.rigidum*. Because false openings occur 0.4 times a year (Figure 3), and light rains occur 3.8 times a year, the survival patterns would seem to favour *H.leporinum*, even considering the cumulative effect of several light rains.

The ability of both species to remain viable after long periods of pre-wetting is quite remarkable. They can actually survive even after radicles have been produced, though germination rate is already affected. However, provided that the seeds of other species have been similarly affected, reduction in rate of germination will not affect their ability to produce a seedling which ultimately sets seed. That is, reduction in rate of germination will adversly affect seedling survival only if the rate of some competing species is less affected.

3.4.0. Germination and Establishment on the soil surface

Because annual pastures are self regenerating, the ability of a species to establish itself when its seed lies on the surface of the soil will affect its success. Clearly, if one species is better able to establish under these conditions than its competitors, its subsequent success is assured. Accordingly, in Experiment 4, the effect of the different rates of germination of H.leporinum and L.rigidum on their ability to germinate on the soil surface is examined. In Experiments 5 and 6, the effects on surface germination of the seeds' ability to absorb water, and to germinate in conditions of moisture stress, are studied.

3.4.1. Experiment 4 - The effect of the different germination rates of H.leporinum and L.rigidum on their ability to germinate and establish on the soil surface.

1) Procedure

Soil from the field at the Waite Institute was placed in large pots in the glasshouse. The soil was from the surface 6 inches of a red brown earth (Urrbrae loam). Chips were placed in the bottom of the pots, and the soil firmly tamped.

Four treatments were applied. Firstly and secondly, 100 seeds of H.leporinum and L.rigidum were placed on the surface, and water equivalent to 13 mm of rain was applied through a sprinkler. The next two treatments were chosen because it was thought that if comparison of the first two showed that *H.leporinum* was better able to establish under the conditions of the experriment, a possible reason for its success would be its more rapid germination. Accordingly, groups of 100 seeds of *L.rigidum* were placed on moist filter paper in covered Petri dishes for one and two days before placing on the soil surface on the same day as the first two treatments. This had the effect of putting forward the date of germination of *L.rigidum* by one and two days respectively, hence increasing its rate of germination. Thus the treatments were :

1. *H.leporinum* germinating on the surface.
2. *L.rigidum* germinating on the surface
3. *L.rigidum* germinating on the surface after having been wetted for one day in a Petri dish.
4. *L.rigidum* germinating on the surface after having been wetted for two days in a petri dish.

There were 8 replicates of all treatments.

Seed of *L.rigidum* was from a commercial source, that of *H.leporinum* from Kybybolite. Sterile florets of the latter were removed so that there was no dormancy problems and more importantly, so that each species had equal contact between its seed and the soil surface, that is, they were removed to avoid confounding a contact effect with a rate of germination effect.

The weather during the experiment was warm, and temperatures as high as 90°F were recorded in the glasshouse, even though it was cooled. Although pots were protected from the direct sun by white-washing the roof of the glasshouse, conditions were very drying. Nevertheless pots were not watered after the initial simulated rain.

Plants with one or more leaves were counted after all germination had apparently ceased.

ii) Results

The results show that *H.leporinum* was strikingly better able to germinate from the surface of the soil than *L.rigidum* when the seeds of the two species were wetted at the same time (Table 11). They also show that by increasing the rate of germination of *L.rigidum* (by wetting seed one or two days earlier), its establishment becomes as good or better than that of *H.leporinum*, depending on when the seeds were wetted.

iii) Discussion

The results of this study and of Experiment 2 (which compared germination rates) suggest that the reason *H.leporinum* was so successful at germinating from the surface was its more rapid germination. The soil surface dried out rapidly, and only seeds which germinated quickly and sent roots beneath the surface could establish. This hypothesis was verified by the results from pre-wetting treatments with *L.rigidum*. If seeds were pre-wetted for one day, which meant that they germinated at approximately the same time as *H.leporinum*, or for 2 days, which meant that they germinated

TABLE 11

Plants established (as percentage of seed sown) after seed was sown on the surface of the soil and watered with 13 mm of simulated rain (in pots in a glasshouse)

Treatment	Percentage
Hordeum leporinum	34.1
Lolium rigidum	0.5
Lolium rigidum previously wetted for 1 day	32.8
Lolium rigidum previously wetted for 2 days	49.0
L.S.D. P = 0.05	10.7
= 0.01	14.6

a day earlier, then their establishment was equal or superior to that of *H.leporinum*.

The improvement due to pre-wetting may, however, have been due to the fact that pre-wetted seeds had absorbed more water than seeds not pre-wetted. Against this, it can be said that under the conditions of the glasshouse, seed moisture content would rapidly reach equilibrium with the soil surface. The significant increase in establishment caused by the second day's wetting is unlikely to be due to the greater amount of water absorbed in the second day, and very likely to be due to the more rapid germination once placed on the surface, compared with seeds wetted for only one day before being placed on the surface.

3.4.2. Experiment 5 - To compare the ability of seeds of *H.leporinum* and *L.rigidum* to absorb water from the soil surface.

i) Procedure

This experiment was similar to Experiment 4, except that there were two soil types, moisture content of the seed was taken at two daily intervals, and plant weight as well as plant number was recorded. The second soil type used was Waikerie sand, a coarse river sand of low water holding capacity. Thus a comparison could be made of water absorption from a fairly heavy soil (25% clay - Piper, 1938) and a very light soil, Waikerie sand (0% clay). There were eight replicates.

The water content of seeds during the ensuing days was measured by taking at random 25 seeds, placing them in a container which could be sealed, weighing the sealed container plus seed, drying the seed at 85°C, then weighing in the container once again. As in the previous experiment, those plants with at least one leaf at the end of the experimental period were counted as established. Their total weight was measured by drying at 85°C in a forced draught oven for 24 hours. Any seed which showed only a radicle at the end of the experiment was counted as germinated but not established.

The percentage germination and establishment were calculated as the percentage of the total number of seeds sown, corrected for viability. When taking seeds for moisture determinations, established, as opposed to germinated seeds were excluded on the grounds that these had access to water reserves not available to seeds without a root system.

At all harvests, seeds which lodged next to the edge of the pot were excluded by placing a circular quadrat in the centre of the pot and harvesting only those seeds within the circle. The gap between the quadrat and the edge of the pot was 1 cm.

Seed of H.leporinum was obtained from Kybybolite. In this experiment, sterile florets were not removed from the seed dispersal unit because it was desired to measure water uptake of the whole unit, and because removal of the florets would have allowed the seeds to enjoy rather better contact with the soil surface than they would in a natural situation. Seed of L.rigidum was obtained commercially.

Conditions were cooler and less drying than in the previous experiment, and pots were placed in the sun in a glasshouse. Pots were watered with the equivalent of 13 mm of rain applied through a sprinkler at the beginning of the experiment.

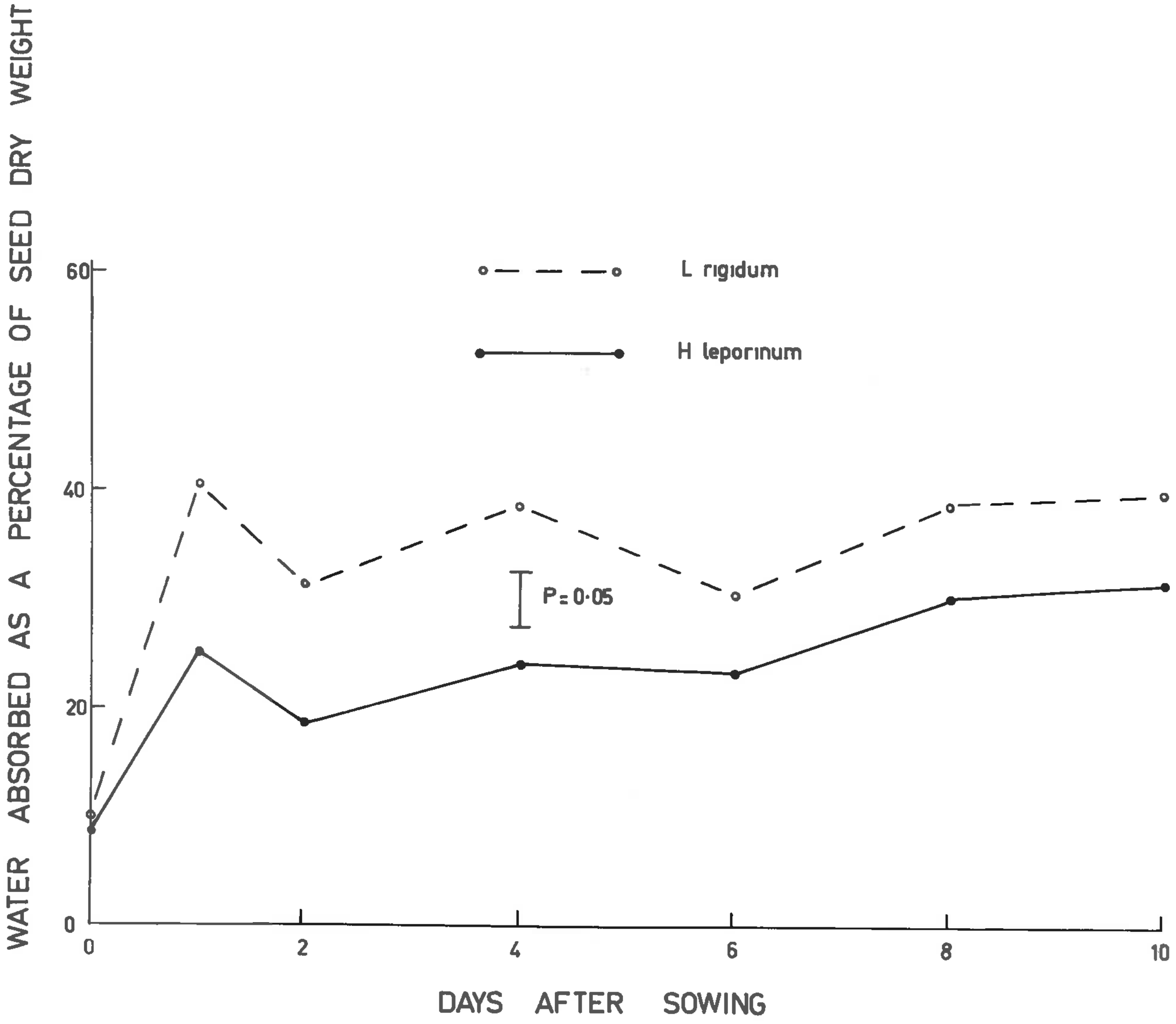
ii) Results

L.rigidum absorbed significantly more water than H.leporinum at every harvest. There was no significant difference between water uptake of seeds on sand and in loam of either species. Figure 16 shows water content of the seeds of each species at each harvest. Points on the figure were calculated from means of results for the two media.

Germination of H.leporinum was significantly better than that of L.rigidum at the end of the experimental period, and in this case there was a significant difference between mean germination on sand and loam. Establishment, that is, number of plants with one or more leaves, was similar to germination but differences between media did not reach statistical significance. Table 12 shows germination and establishment numbers of both species.

Plants of H.leporinum weighed more than plants of L.rigidum regardless of medium. Plants of this species grown on loam weighed significantly more than plants grown on sand. There was no significant effect

<u>Figure 16</u> Water absorbed by seeds of each species lying on the soil surface as a percentage of seed dry weight. The bar represents the least significant difference (P = 0.05) between any 2 estimates of water absorbed by seeds of either species.



WATER ABSORBED AS A PERCENTAGE OF SEED DRY WEIGHT
60
40
20
0
0
2
4
6
8
10
DAYS AFTER SOWING
L rigidum
H leporinum
P = 0·05

of medium on weight of plants of L.rigidum. Table 13 shows weights of both species grown on both media.

iii) Discussion

Although H.leporinum absorbed less water, it was far better able to germinate from the soil surface than L.rigidum. However, depending on the amount absorbed by its sterile florets, the amount absorbed by the seed itself may have been more, or less than that recorded here. This point has been checked in Experiment 6, where it will be shown that H.leporinum can in fact germinate under conditions of higher moisture stress, as imposed by a solution of high osmotic pressure, than can L.rigidum, suggesting very strongly that H.leporinum can germinate when its true seed has absorbed much less water than the true seed of L.rigidum

The reason for the poorer uptake of water by seed of H.leporinum is probably the very poor contact between seed and soil caused by the presence of awns and sterile florets. These appendages caused the seed in many cases to be held from the soil surface on the tip of the awns. There seemed no advantage to the seed in respect to water uptake in its possession of awns and sterile florets. However, the very different conditions which exist in the field could result in considerable advantage through possession of these awns, quite apart from their use in seed dispersal, and as a protection from being consumed by animals.

TABLE 12

Percentage germination and establishment of *Hordeum leporinum* and *Lolium rigidum* from the surface of a loam and of a sand ~~(see also Appendix Table 12)~~.

Species	Medium	Germination	Establishment	Germinated not established.
H.leporinum	loam	20.6	20.3	0.3
	sand	33.5	29.3	4.2
	mean	27.1	24.8	
L.rigidum	loam	2.6	2.5	0.1
	sand	9.3	5.0	4.3
	mean	6.0	3.8	
mean of species on loam		11.6	11.4	0.2
mean of species on sand		21.4	17.2	4.3
L.S.D.*	.05	6.7	6.6	
	.01	9.1	9.0	
L.S.D.**	.05	9.4	9.4	
	.01	12.8	12.8	

* L.S.D. between mean species or between mean media

** L.S.D. between any two figures in each column

TABLE 13

Weights of seedlings of *Hordeum leporinum* and *Lolium rigidum* 10 days after seeds were sown on the surface of a loam and of a sand.

species	medium	weight (mg/plant)
H.leporinum	loam	3.22
	sand	1.97
L.rigidum	loam	1.10
	sand	0.82
*L.S.D. P = .05		0.49
.01		0.67

*L.S.D. between any figures shown in the Table.

The difference in plant weight between plants from sandy and loamy surfaces (Table 13) was probably due to continued germination over a longer period from the sandy surface, the later smaller plants reducing the average size. Another possible explanation is that nutrient differences between media caused depression of plants grown on the sand. This, however, seems unlikely, as the experimental period was only 10 days.

Both species germinated better on the sandy surface, though not significantly so in the case of L.rigidum. The better germination was probably due to better water transportation properties of the sand. The fact that there was no significant difference in water absorption from sand and loam does not mean that such differences did not occur. In fact, the evidence points strongly to the presence of such differences.

3.4.3. Experiment 6 - Germination from solutions of different osmotic pressure.

After consideration of the results of the last experiment, it was decided to conduct a further test of the ability of the seeds of the 2 species to germinate at high moisture stress. Although germination of seeds in solutions of different osmotic pressure is not considered to be identical with their ability to germinate in soils of different moisture stress, their relative abilities can be assessed.

1) Procedure

Solutions of mannitol giving osmotic pressures of

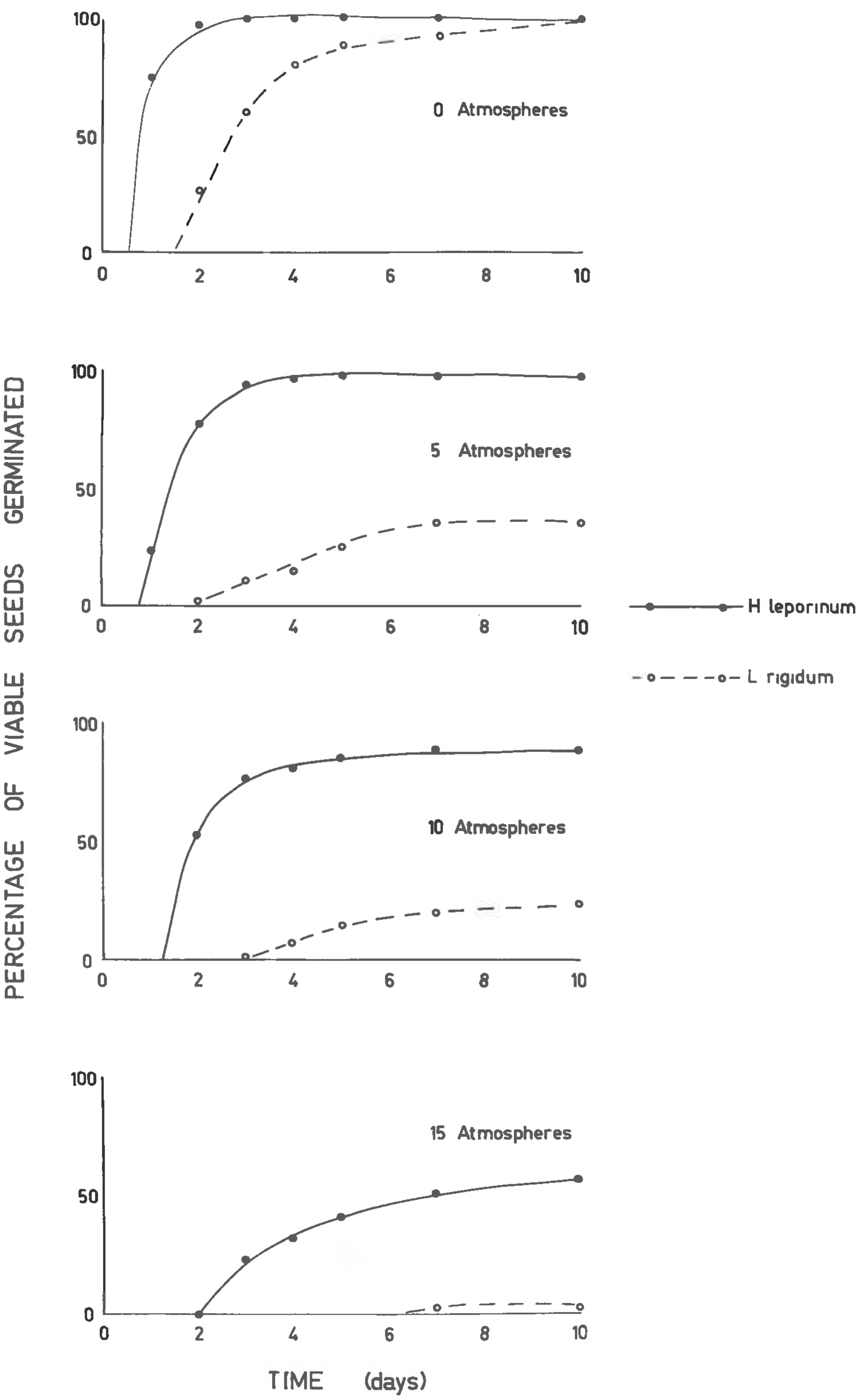
5, 10 and 15 atmospheres were used (Helmerick and Pfeifer 1954). One hundred seeds of each species were counted on to filter paper in Petri dishes containing the various solutions, and a control of pure water. Seeds were germinated at 20°C in the dark and the number germinated counted daily. Seed sources were the same as the previous two experiments, and sterile florets were removed from seed dispersal units of H.leporinum.

ii) Results

The results show that H.leporinum was strikingly better able to germinate in solutions of high osmotic pressure (Figure 17) than was L.rigidum. In solutions where osmotic pressure was as high as 15 atmospheres, 50% of viable seed of H.leporinum germinated in a period of 10 days compared to negligible germination of L.rigidum. In each of the less strong solutions, germination of L.rigidum was inhibited, but there was barely any effect of 5 atmospheres of osmotic pressure on germination of H.leporinum, and only a small effect of 10 atmospheres.

The solutions also affected rate of germination. At osmotic pressures higher than 10 atmospheres, germination of H.leporinum was slower than controls (0 atmospheres), but it was always faster than L.rigidum, and the amount it was faster increased with increasing osmotic pressure. Note the very much faster rate of germination of H.leporinum compared with L.rigidum in the control solutions.

Figure 17 Rate of germination of both species in solutions of mannitol giving different osmotic pressures. The number of viable seeds was that number of seeds of each species germinated by day 10 in pure water (0 atmospheres).


PERCENTAGE OF VIABLE SEEDS GERMINATED
0 Atmospheres
5 Atmospheres
10 Atmospheres
15 Atmospheres
100
50
0
0
2
4
6
8
10
TIME (days)
H leporinum
L rigidum

iii) Discussion

These results, considered with these of the previous experiment, show that *H.leporinum* is able to germinate at lower moisture levels than *L.rigidum*. This fact, together with its more rapid germination, explains the success of *H.leporinum* in germinating from the soil surface, even though it is apparently less able to absorb water under these conditions.

3.4.4. Discussion about germination on the surface

That germination and establishment from the surface will affect later botanical composition seems obvious. Poor establishment of a species results in low plant numbers, and hence a less important role for the species in the resulting sward. The two species studied did vary considerably in their ability to establish from the soil surface. This was attributed to the ability of *H.leporinum* to germinate in conditions of high moisture tension, and to germinate quickly before further increase in tension prevented germination. It was found that this species was less able to absorb water and this was thought to be due to the presence of awns and sterile florets preventing close contact between the soil surface and the seed.

The effect of rate of germination on ability to germinate from the surface has been overlooked in the past. However, the importance of retention and loss of water by seeds lying on the surface as the reason why germination rate is likely to be important was stressed by Harper et al (1965). Their experiments showed that part of the effect of soil surfaces of different roughness on germination was the degree of protection rough surfaces offered against water loss. In fact no germination occurred from flat surfaces; all germination which occurred from this treatment in their experiment came from cracks in the surface.

The fact that most annual grasses which persist in Australian annual pastures possess awned seeds, suggests that these awns are useful. This may be for several reasons. Firstly the awns make the seeds heavier and more awkward for micro-predators to manage. For example, McGowan (1967) in a study of the removal of seeds by ants, noticed that they cut off the long awn of *Vulpia myuros* before moving the seed. Secondly, the presence of awns make the seed more obnoxious for grazing animals or at least this is the assumption that has generally been made, and seems valid. Thirdly, awns aid in the penetration of the seed into suitable sites for germination, as was noted by Harper et al (1965). Against these factors can be placed the disadvantage of poorer seed-soil contact reported here and by Harper and Benton (1966) who found that uptake of water was poorer for spiny, reticulate seeds.

3.5.0. Concluding remarks

A comparison of the behaviour of *H.leporinum* and *L.rigidum* in respect to their germination and establishment is shown in Table 14. Perhaps the most significant comparisons are in rate of germination and ability to germinate from the surface. *H.leporinum* is superior in both, though its superior establishment from the surface is due in part to its more rapid germination. The ecological significance of these features has been discussed.

Of the other features compared in Table 14, none show a very great advantage to either species. *L.rigidum* is better able to resist wetting at very high temperatures. Both species can resist wetting and drying at lower temperatures, though short periods of wetting may favour *H.leporinum* and longer periods may favour *L.rigidum*. Both species have similar optimum temperatures for germination.

TABLE 14

A comparison of the behaviour of *H.leporinum* and *L.rigidum* in respect to their germination and establishment

Feature	Comparison between *H.leporinum* and *L.rigidum*
Presence of leachable inhibitors	Present in *H.leporinum*, but not tested in *L.rigidum*
Temperature requirements for germination	Complete germination in both species occurred over a constant temperature range of 8°C to 29°C
Response to alternation of temperature	Both species respond to alternating temperature. Alternation requirement for *L.rigidum* is greater at high temperatures, but for *H.leporinum* it is greater at low temperatures.
Speed of germination	*H.leporinum* germinates more rapidly than *L.rigidum* at all temperatures
Germination at high temperature	Neither species germinates at temperatures above 37°C
Germination after long exposure to 38°C	Germination of both species proceeds at 20°C after exposure to 38°C for 1 day, but longer exposure reduces viability. *L.rigidum* is better able to resist such exposure.

TABLE 14 (continued)

Feature	Comparison between *H.leporinum* and *L.rigidum*
Germination after wetting and drying	Wetting for up to 10 hours (*H.leporinum*) and 20 hours (*L.rigidum*) stimulates subsequent germination after drying. Longer wetting periods reduces germination, both total and rate. Summer and autumn rains probably increase rate of germination of *H.leporinum* more than *L.rigidum*.
Germination on the soil surface	*H.leporinum* germinates far better on the soil surface than does *L.rigidum*. The reasons it does so are its more rapid germination, and its ability to germinate at lower moisture levels

4.0.0. SEEDLING GROWTH OF HORDEUM LEPORINUM AND LOLIUM RIGIDUM

4.1.0. Introduction

Having considered germination and establishment of H.leporinum and L.rigidum I now turn to a consideration of their seedling growth. In the experiments described in this section, seedling growth and the influence of temperature were studied while the seedling was still using endosperm reserves, and also following exhaustion of these reserves.

Provided that there is sufficient moisture, the environmental factor which most affects seedling growth is temperature. Temperature affects mobilisation of endosperm, growth of the embryo, and photosynthesis of the shoot. The intensity and quality of light will not affect seedling growth until the production of photosynthetic material. Thus seedling growth at three temperatures has been studied.

Root development, leaf growth, and tiller production, which occurs before competition commences, may affect subsequent competition as much or more than total seedling growth. Accordingly seedling growth under conditions of no competition has been studied in some detail.

The use of controlled environments is essential for a precise understanding of seedling growth. Williams (1960) and Williams and Rijven (1965) have studied growth of the wheat plant, and Silsbury (1966) has examined the vegetative growth of Lolium perenne using such controlled environments. I have used techniques similar to these workers.

4.2.0. Experimental Procedure (Experiment 7)

4.2.1. The growth cabinet

1) Internal measurements

The cabinet measured 120 x 120x180cm inside, with a working area of one square metre on a movable platform. The walls were covered with reflecting plastic to maximise the area of uniform illumination.

2) The light source

Light energy was provided by a bank of 14 high pressure mercury vapour fluorescent lamps (MBF/U,400 watt) separated from the rest of the cabinet by a sheet of rippled glass and ventilated by a forced draught. The lights provided high intensity illumination of up to 3000 lumens per square foot for long periods without replacement.

Silsbury (1966) discussed the use of these lamps as a source of artificial light for plant growth. He concluded that there is no reason for expecting growth under mercury lamps to be markedly different from that obtained under a fluorescent source. There was some suggestion however, that photosynthesis rate was a little less than under incandescent light.

The intensity of light was checked regularly using a "Weston" barrier layer photocell with a quartz filter, and calibrated by the National Standards laboratory, Sydney. There were 16 hours of daylight, and the movable platform was placed so that light intensity reaching the plants was 2700 lumens per square foot, equivalent to 130 cal. per sq.cm per day.

3) Temperature control

Temperature control was achieved by a direct expansion refrigerator coil and a single bar heater. This resulted in the maintenance of a constant temperature ± 1°C. Temperature was recorded at plant level.

4) Air movement and humidity

Air movement was maintained in an upward direction within the cabinet. Silsbury (1966) had previously found that differences of air movement within the cabinet had little effect on dry weight over the range of temperatures used here.

Humidity was not controlled except by maintaining water in a large tray in the bottom of the cabinet. H.leporinum and L.rigidum were grown in the cabinet at the same time for any temperature treatment, so that differences between species at any temperature were not due to differences in humidity. At any rate the effect of differences in humidity would probably not be great. For example, Silsbury (1966) grew Lolium perenne at 30°C, and recorded no differencesin growth rate when saturation water vapour pressure deficit was doubled from 5.1mm of mercury to 10.2mm of mercury.

4.2.2. Treatments

H.leporinum and L.rigidum were grown at 10°C, 17°C and 24°C. The seed of H.leporinum was obtained from

Kybybolite in the South East of South Australia and the seed of L.rigidum from a commercial source.

There were four replicates of each species at each temperature.

4.2.3. Growing the plants

Five-inch pots, filled with a coarse river sand (Waikerie sand) were used. A complete nutrient solution (Table 15) was added every second day, and the pots watered twice daily. Waikerie sand was used because of its good drainage properties, and the ease of washing it from the roots. The sand remained moist even when plants were quite large, and it can safely be assumed that water was non limiting.

Seeds were germinated in Petri dishes placed in the cabinet after it had been running at the required temperature for two days. The dishes were covered with aluminium foil to exclude light. When radicles were no longer than 2mm, germinating seeds were selected from the dishes and sown half an inch deep in thepots. Because H.leporinum commenced germination sooner than L.rigidum its seeds were sown into the pots a corresponding amount of time sooner. Zero time in the experiment was considered to be that moment when water was added to the seeds in the Petri dishes.

Four germinated seeds were sown in each pot, different species occupying different pots. After four plants had emerged, fine gravel was placed over the surface of the sand to minimise evaporation and to prevent growth of blue green algae.

TABLE 15

The nutrient solution used in Experiment 7

Nutrient	Concentration
$Ca(NO_3)_2$	3.0 mM
$FeC_6H_5O_7\ 5H_2O$	0.15 m M
KH_2PO_4	0.7 m M
KNO_3	4.0 m M
$MgSO_4$	1.0 m M
H_3BO_3	0.09 m M
$MnSO_4$	0.008 m M
$ZnSO_4\ 7H_2O$	0.002 m M
$CuSO_4\ 5H_2O$	0.0007 m M
MoO_3	0.001 m M

4.2.4. Harvests

Because the experiment commenced when the seed was first wetted, several harvests were made before seedlings emerged in the pots. Plants (actually seeds) used in these harvests were selected from the seed placed in the Petri dishes. For each of these harvests, 25 seeds were chosen at random. Seedlings in the pots were assumed to be able to grow at the same rate as seedlings in the dishes, until their appearance above the ground in the pots.

At each harvest, after seedling emergence, four pots of each species were selected at random, and each pot was counted as a replicate.

At each harvest, the embryo (or at later harvests, the plant) was separated from the rest of the seed, and both fractions were weighed after drying in a forced draught oven at 85°C for 24 hours. Separation of the embryo from the seed was not difficult after the seed had been soaked for one hour, provided that a binocular microscope was used. The weight of embryo and seed at day 0 was actually measured after soaking seeds for one hour. The rest of the seed fraction included the closely attached lemma and palea of both species, which were very difficult to remove, but did not include the sterile florets of H.leporinum.

As soon as the embryo could be divided into root and shoot these two fractions were weighed separately. The coleoptile was included with the shoot. Later, root length (length of the deepest root), plant height (length from soil to the tip of the longest leaf), root weight, individual leaf weights, leaf areas, stem weights of each tiller, and tiller numbers were recorded. In this way, not only total seedling growth was measured, but also individual leaf and tiller growth.

Leaf areas were obtained by tracing outlines of leaves onto paper and measuring area using a planimeter. Areas and dry weights were of exposed leaf, thus underestimating leaf dry weight before leaves had fully emerged. A leaf was said to have appeared when the leaf tip became visible above the encircling leaf sheath. Tillers were whole tillers including that part concealed by the sheath of the subtending leaf. Dry weights were obtained by drying material at 85°C for at least 24 hours in a forced draught oven.

4.3.0. Results

4.3.1. Accumulation of dry matter

The results of the harvest at day 0 (that is, weights of seeds and embryos) are shown in Table 16. Both the total seed weight, and the weight of the embryo of H.leporinum are approximately three times those of L.rigidum.

Figure 18 shows the increase in weight of isolated plants (or embryos) of both species grown at three temperatures, with time. There appears to be three phases of growth: first a period of slow embryo growth, possibly negative in the case of L.rigidum, though this may have been due to experimental error, secondly a period of rapid growth, and finally a period of constant but slower growth. It will be shown later, when calculations of relative growth rate are made, that the second period of very rapid growth coincides with the period of endosperm utilisation (Figure 23).

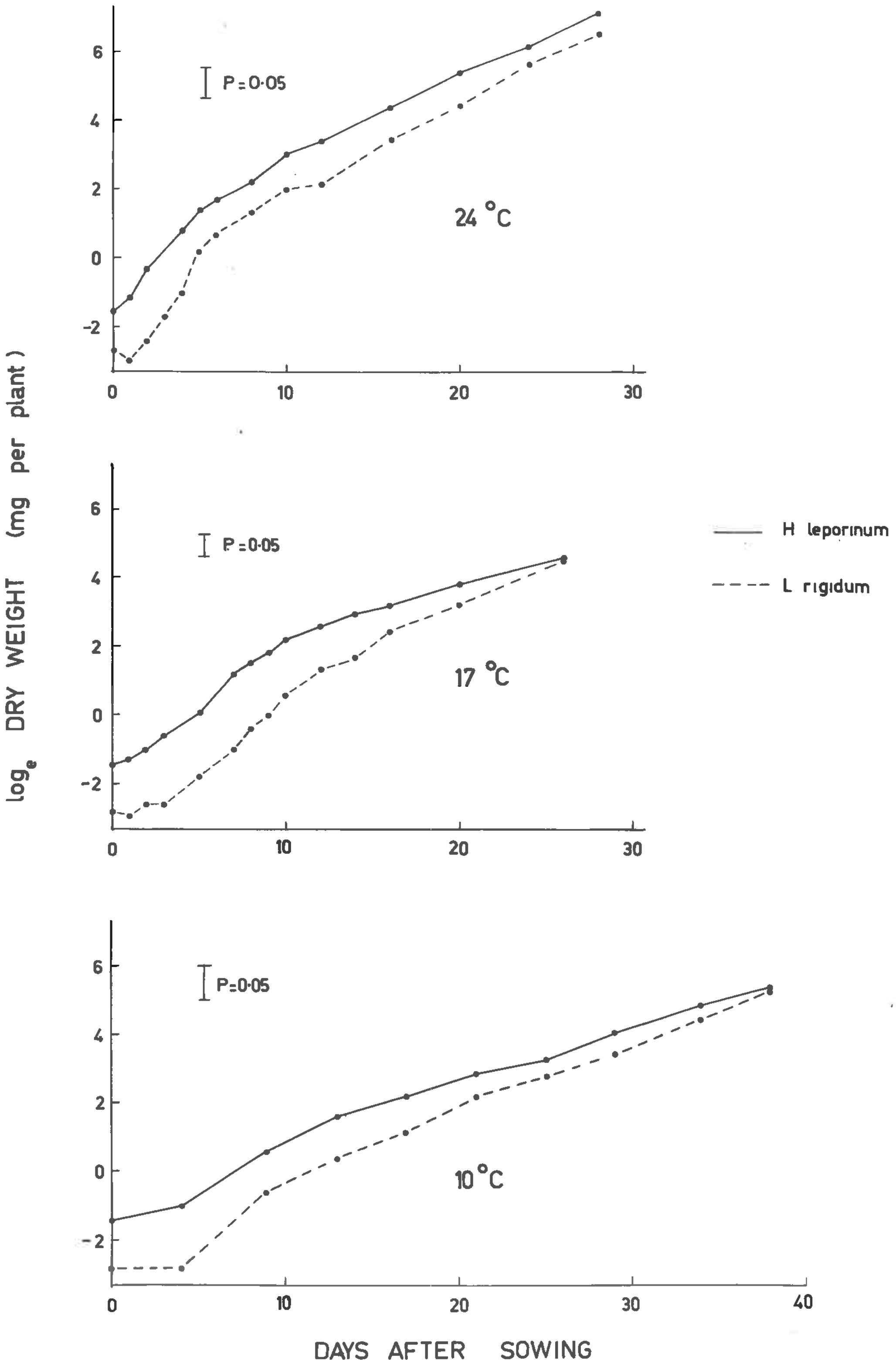
At all temperatures, the weight of L.rigidum increased more rapidly than the weight of H.leporinum, and by the end of the experimental period the weights of the two species were equal at the lower temperatures. The time needed for weights to become equal depended on temperature but the greatest time was at the highest temperature and the least time at the middle temperature, suggesting that the growth rate of the two species reacted differently to temperature over the temperature range used.

TABLE 16

Weight of the seed and of the embryo of H.leporinum and L.rigidum (mg per seed). Seed weights include embryo weights and attached glumes, but in the case of H.leporinum exclude sterile florets. L.rigidum has no sterile florets.

Species	Seed weight	Embryo weight
H.leporinum	743	0.23
L.rigidum	251	0.07

Figure 18 Increase in dry weight of isolated plants of _H.leporinum_ and _L.rigidum_ in each of three temperature environments. The bars represent least significant differences (P = 0.05) between any two measurements of dry weight at any one temperature.


P = 0·05
24 °C
17 °C
10 °C
H leporinum
L rigidum
log$_e$ DRY WEIGHT (mg per plant)
DAYS AFTER SOWING
6
4
2
0
-2
0
10
20
30
40

Seed weight (excluding embryo) has been plotted in Figure 19. At this stage it is necessary only to note that the rate of use of endosperm depends on temperature, and that endosperm use of H.leporinum begins before that of L.rigidum. The effect of endosperm availability on plant growth will be discussed later.

4.3.2. Increase in dry weight of tops and roots.

Top and root weights increased similarly to total weight. At the lower two temperatures, root and top weights of L.rigidum became equal to those of H.leporinum by the end of the experimental period, but did not become equal at the highest temperature. Root weight was 36% of total weight of H.leporinum plants and 38% of total weight of L.rigidum plants. (For top and root weights see Appendix tables 1 and 2).

4.3.3. Increase in leaf area

There was an initially rapid increase in leaf area followed by a long period where leaf area increased at a constant rate (Figure 20). The period of rapid increase, like the period of rapid increase in dry weight, coincided with the period of most rapid endosperm use.

Increase in leaf area was also similar to increase in dry weight in that the two species increased at different rates tending to become equal with time.

4.3.4. Plant height and root depth

Plant height is shown in Figure 21. Except at 24°C,

Figure 19 Change in seed weight (excluding embryo) with time, of seeds of *H.leporinum* and *L.rigidum* in three temperature environments. Bars represent least significant differences, (P=0.05) between any two measurements of seed weights in a particular temperature environment.

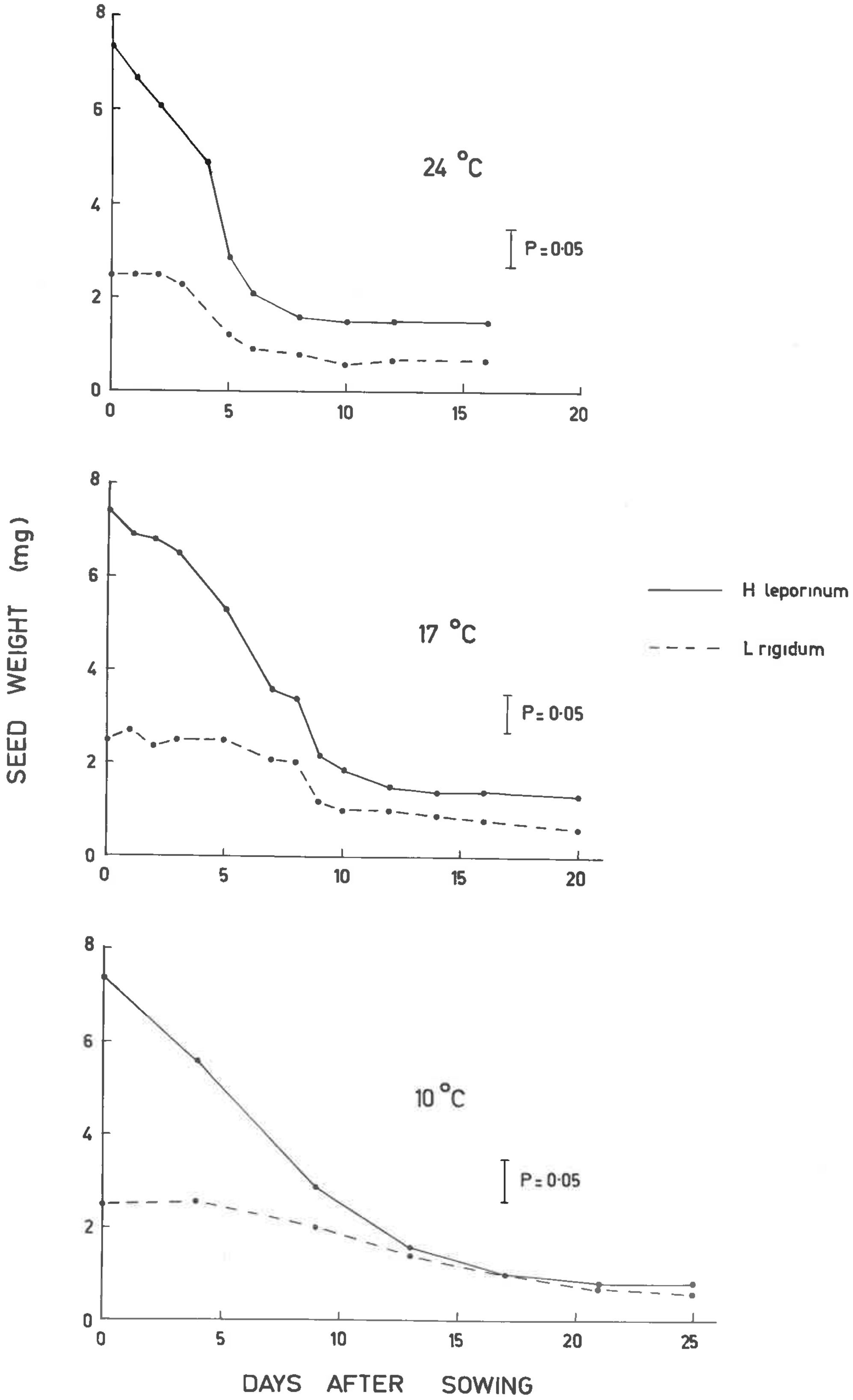
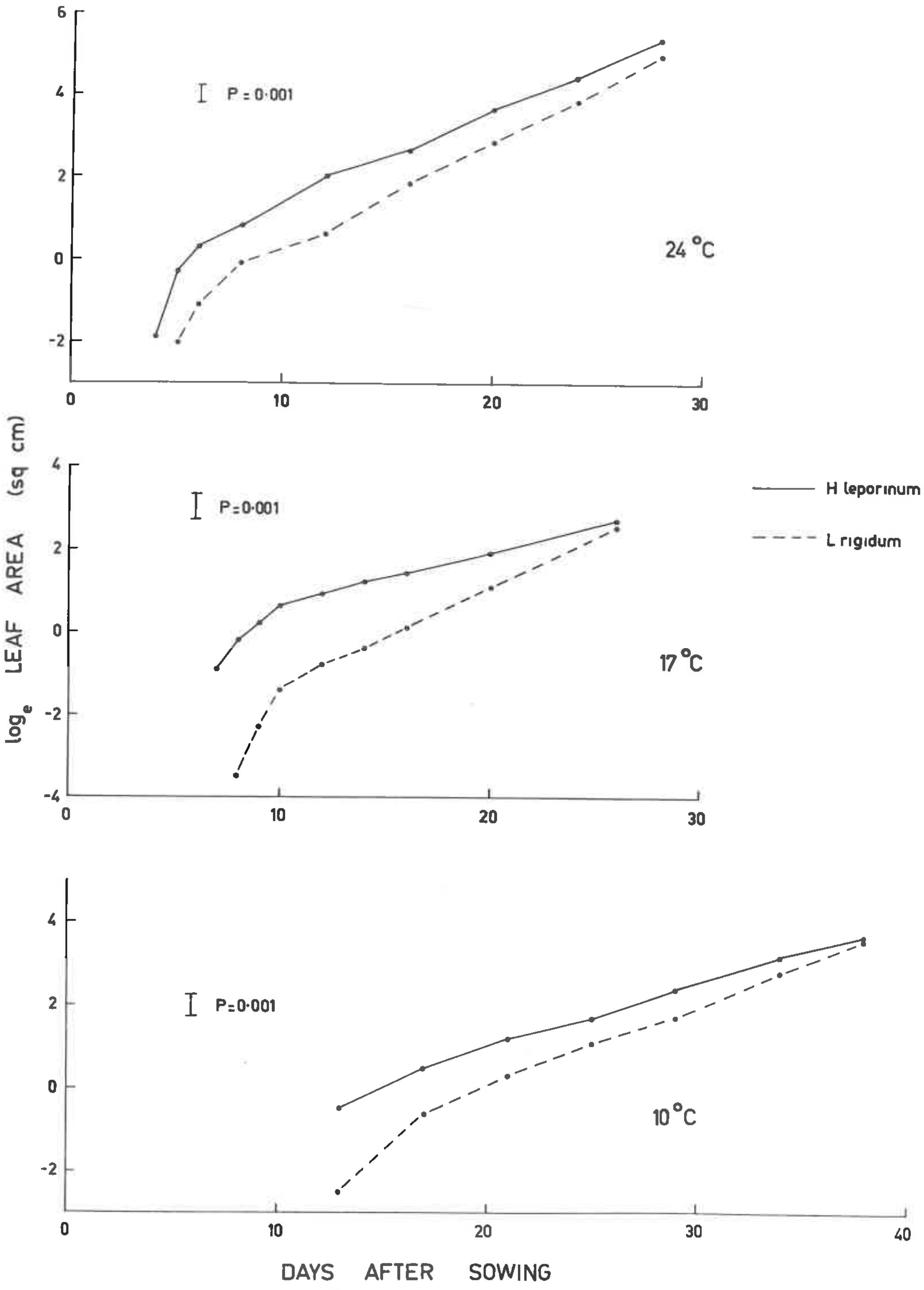
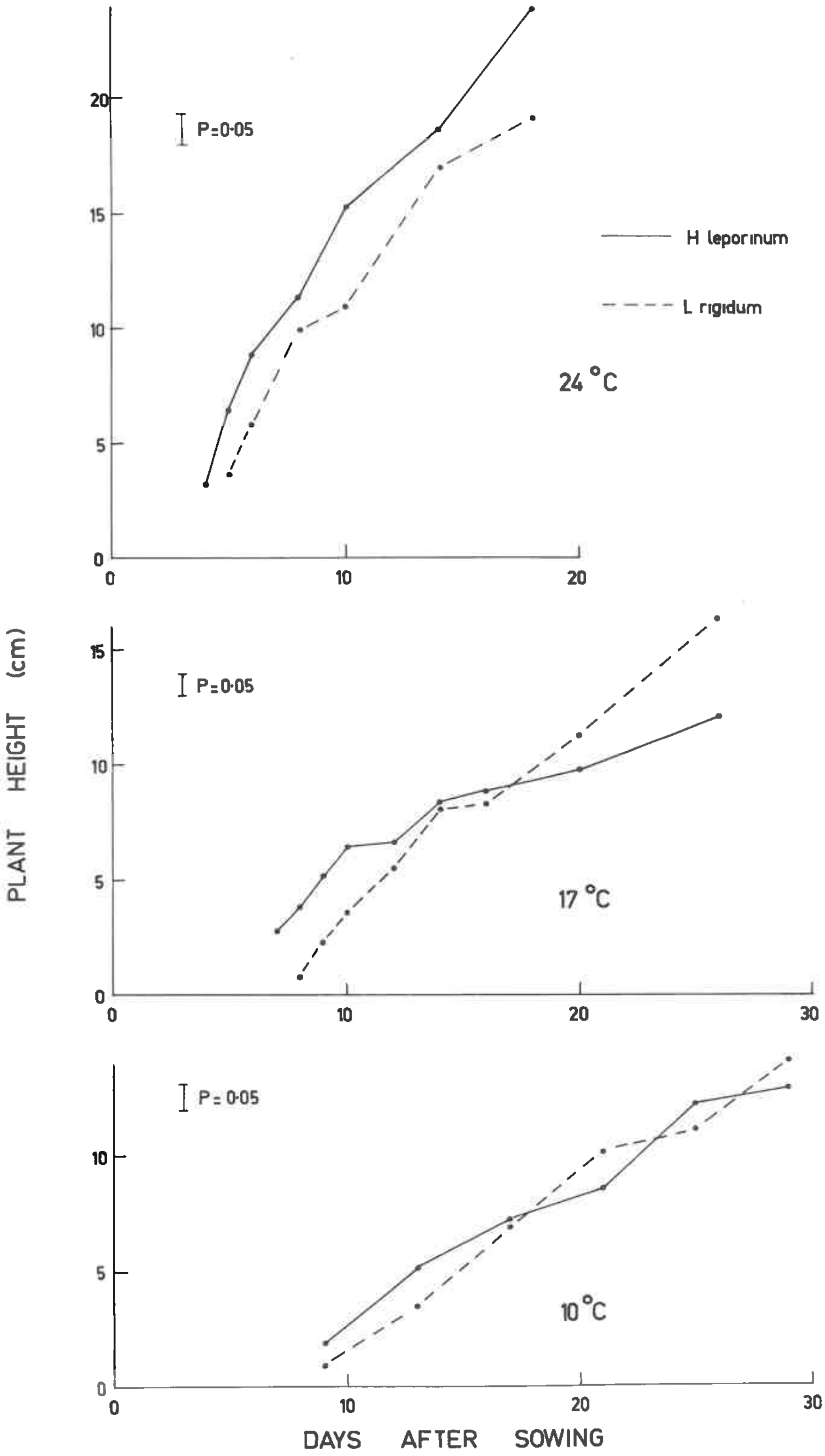

24 °C
17 °C
10 °C
P = 0·05
SEED WEIGHT (mg)
DAYS AFTER SOWING
H leporinum
L rigidum
0
2
4
6
8
0
5
10
15
20
25

Figure 20 Increase in leaf area per plant of isolated plants of *H.leporinum* and *L.rigidum* in each of three temperature environments. Bars represent least significant differences (P = 0.001) between any two measurements of leaf area at any one temperature.



24 °C
17 °C
10 °C
P = 0·001
P = 0·001
P = 0·001
H leporinum
L rigidum
log$_e$ LEAF AREA (sq cm)
DAYS AFTER SOWING
6
4
2
0
-2
4
2
0
-2
-4
4
2
0
-2
0
10
20
30
0
10
20
30
0
10
20
30
40

<u>Figure 21</u> Increase in plant height of isolated plants of *H.leporinum* and *L.rigidum* in each of three temperature environments. Bars represent least significant differences (P = 0.05) between any two measurements of plant height at any one temperature.


P = 0·05
H leporinum
L rigidum
24 °C
17 °C
10 °C
PLANT HEIGHT (cm)
DAYS AFTER SOWING
0
5
10
15
20
30

L.rigidum increased its height at a greater rate than *H.leporinum*, and plants were taller at the end of the experimental period. This pattern is similar to the patterns of increase in dry weight and leaf area. In all three categories there has apparently been a species by temperature interaction, *L.rigidum* doing best in comparison with *H.leporinum* at 17°C, and *H.leporinum* doing best in comparison with *L.rigidum* at 24°C.

In contrast to increases in dry weight, leaf area, and height, root length of *H.leporinum* is superior to that of *L.rigidum* at all temperatures, and its superiority tended to increase with time (Figure 22). This is in spite of the fact that increase in root *weight*, as noted earlier, behaved in the same way as increase in total plant weight.

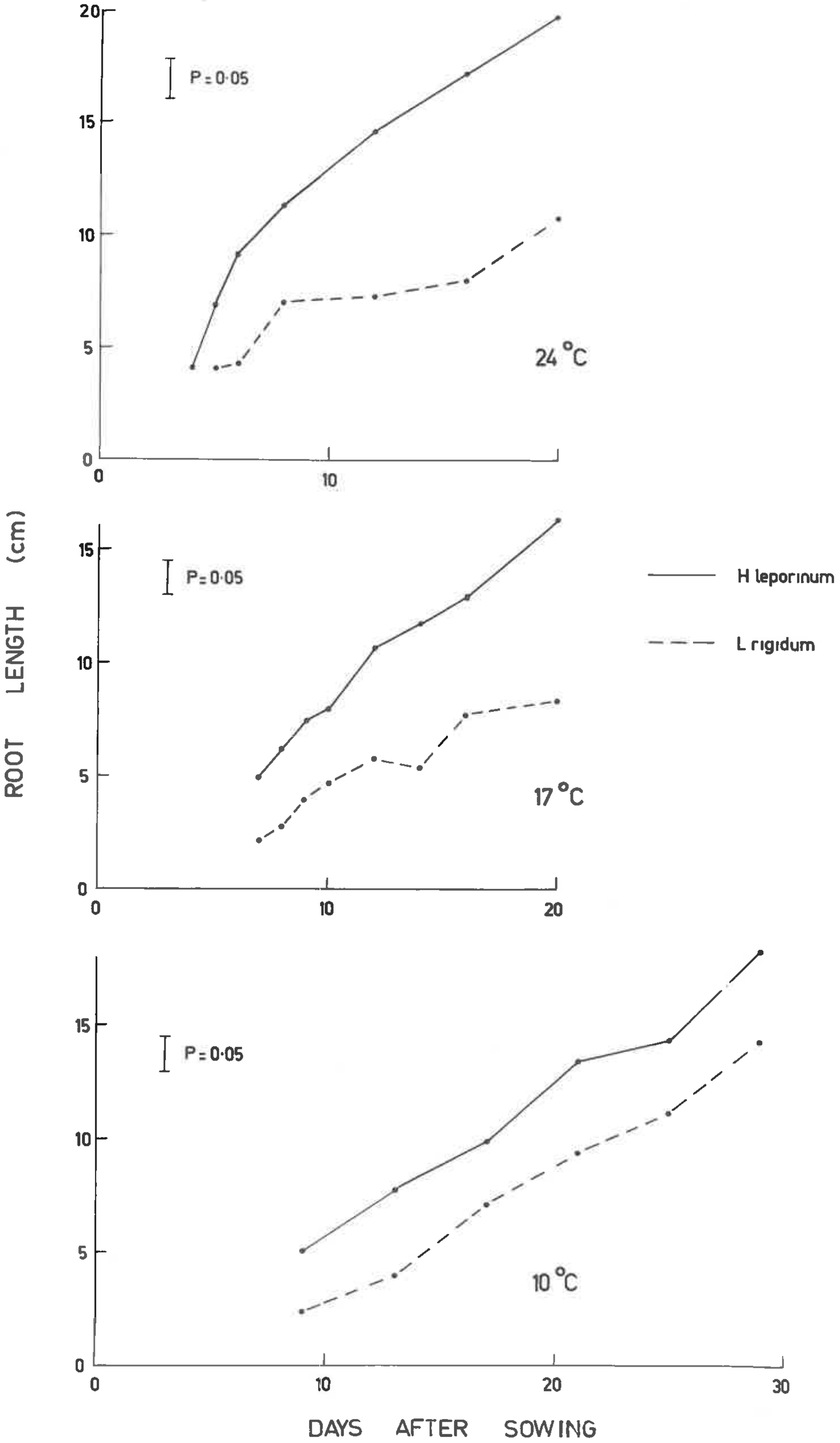
4.3.5. Growth analysis

Relative growth rates (*r*), net assimilation rates (*E*), and leaf area ratios (*LAR*) have been calculated for each species at each temperature. The use of growth analysis has been reviewed by Watson (1952) and Blackman (1960), and formulae for their calculation are as follows :

$$r = \frac{\log W_2 - \log W_1}{t_2 - t_1}$$

where W_1 and W_2 are plant weights at times t_1 and t_2

Figure 22 Increase in length of the longest roots of isolated plants of *H.leporinum* and *L.rigidum* in each of three temperature environments. The bars represent least significant differences (P = 0.05) between any two measurements of root length at any one temperature.


ROOT LENGTH (cm)
DAYS AFTER SOWING
H leporinum
L rigidum
P = 0·05
24 °C
17 °C
10 °C
0
5
10
15
20
0
10
20
30

$$E = \frac{W_2 - W_1}{L_2 - L_1} \times \frac{\log W_2 - \log W_1}{t_2 - t_1}$$

where L_1 and L_2 are leaf areas at times t_1 and t_2

$$LAR = \frac{1}{2}\left(\frac{L_1}{W_1} + \frac{L_2}{W_2}\right)$$

where L and W are as above. All logarithms are natural logarithms.

The formula for E is only valid where L/W remains constant during the period of measurement. This is acceptably so for periods of about 4 days (Blackman 1960) and has thus been used here.

Relative growth rates rose rapidly to a peak, then fell to a level which thereafter remained constant. The values are shown in Figure 23 together with a hand fitted curve. Relative growth rate can be calculated from quadratic curves fitted to the relationship between log yield and time, but this assumes that there is a continuous change of r with time, and hence does not account for exhaustion of endosperm reserves, nor does it account for slowness of commencement of germination.

Also shown in Figure 23 is endosperm loss. This is the loss in weight of the whole seed, excluding the embryo. Note that the period when r was greatest was the period during which endosperm loss was greatest.

The calculations of *E* and *LAR* were made from figures measured after the influence of the endosperm was finished, that is, during the period when *r* was stable following its initial rise and fall. These, with *r* calculated for the same period (actually for the last four harvests at each temperature), are plotted against temperature in Figure 24. Least significant differences which appear in Figure 24 were calculated on the basis that the four harvests could be counted as replicates. As neither the harvests nor the harvests x species interaction had significant variances, this was quite justifiable. The fact that the harvests did not necessarily occur at the same time is regarded as immaterial, because the more rapid growth which occurred at higher temperatures, and the nature of the change of *r* and the other fractions of the growth analysis with time, would have made such comparisons meaningless. For example, comparison of treatments at 10°C and 24°C (see Figure 23) would have shown that both species had higher *r* by day 10 at the lower temperature, but only because, at this temperature, they were still using endosperm reserves. In effect, after endosperm exhaustion, each measurement of *r*, *E*, or *LAR* has been taken as an independent estimate

Figure 24 shows that *r* of *L.rigidum* was always greater than that of *H.leporinum* as was indicated when Figure 18 was examined. At 17°C this difference was greatest (0.25 g/g/day compared to 0.14 g/g/day) and it was least (insignificant) at 24°C. Values of *E* behaved in the same way, except that differences between species were only significant at 17°C. It is interesting to note that

Figure 23 Change in relative growth rate (r) with time, and endosperm loss with time, for isolated plants of *H.leporinum* and *L.rigidum* in each of three temperature environments.

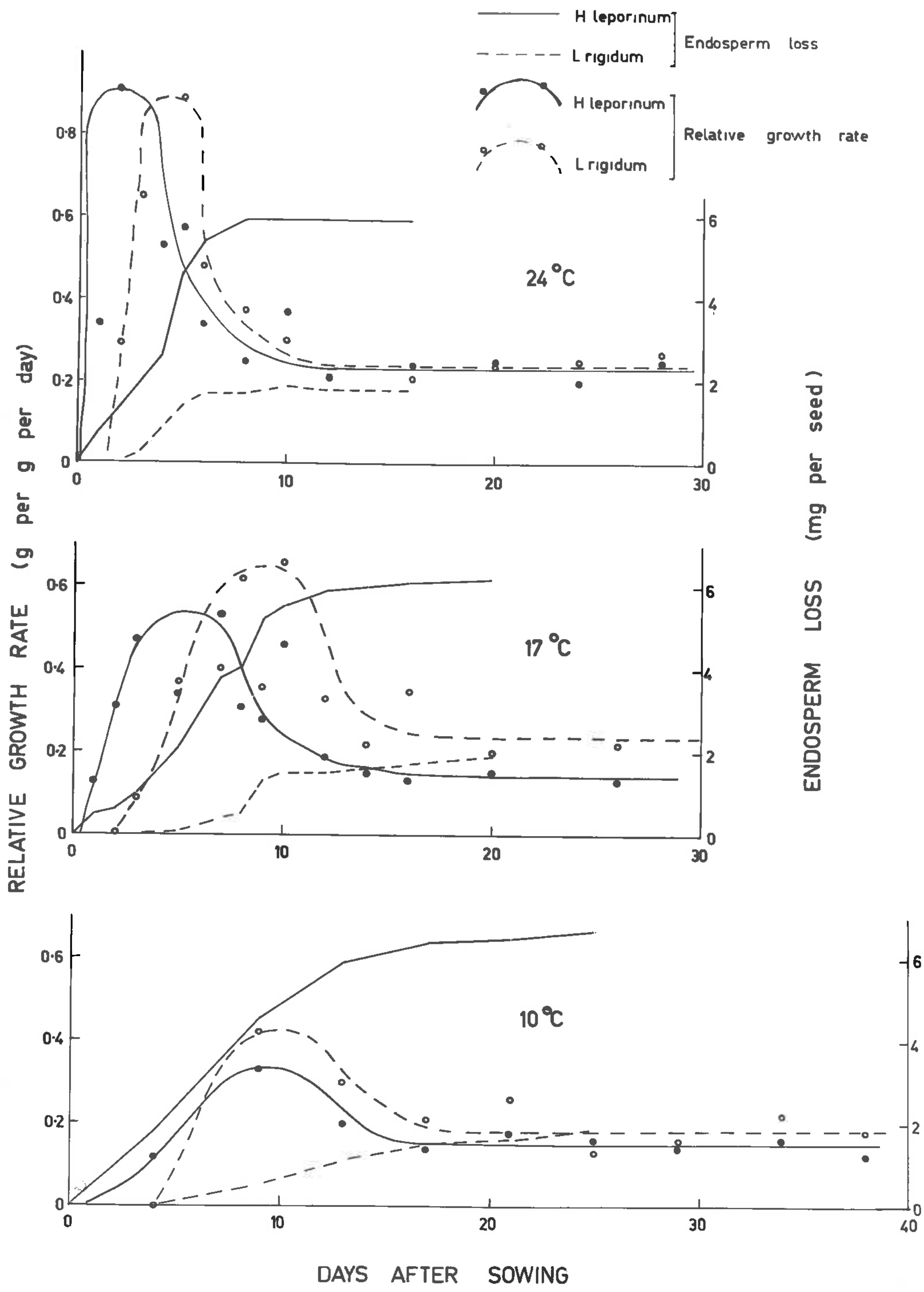
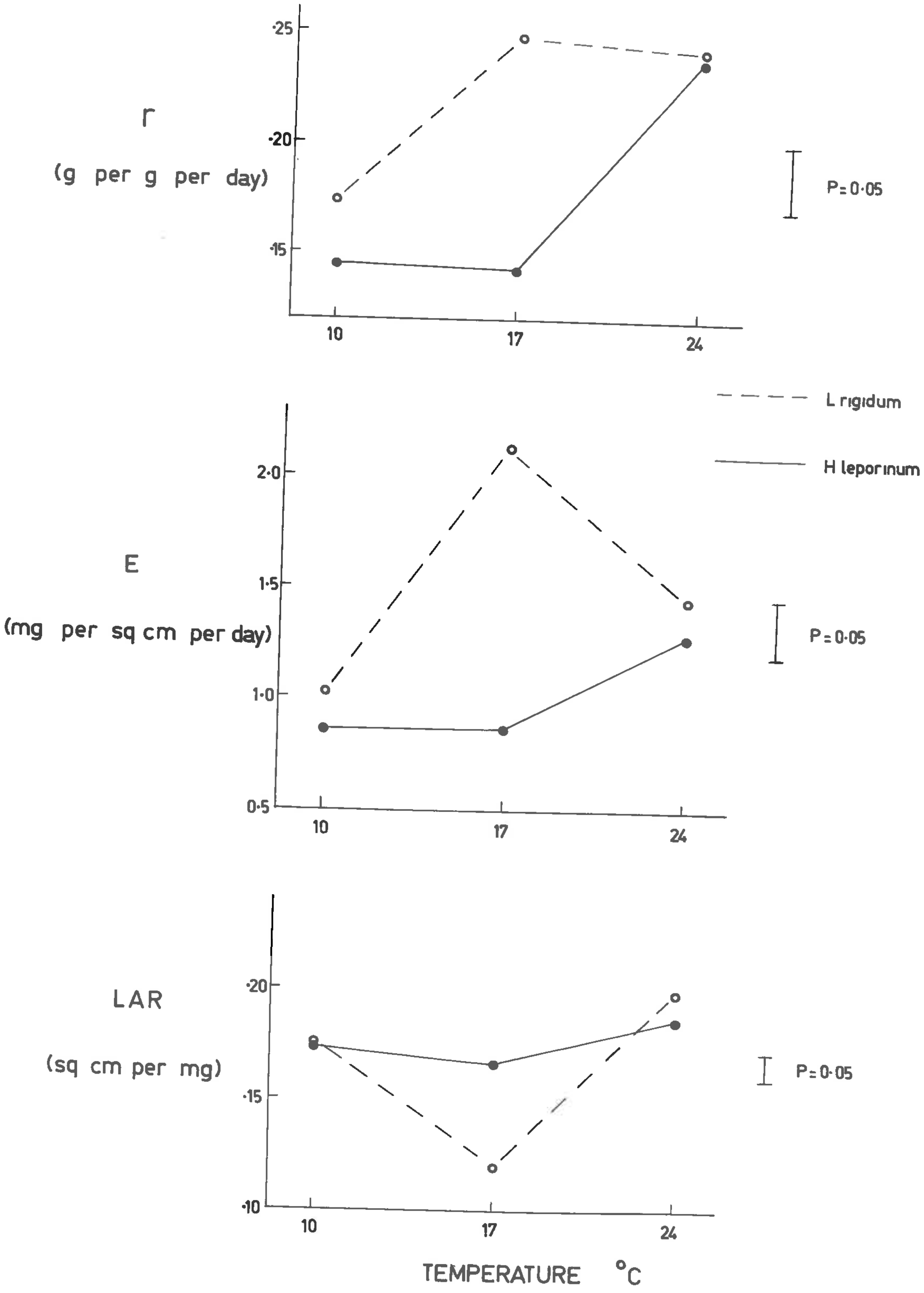

H leporinum
L rigidum
Endosperm loss
H leporinum
L rigidum
Relative growth rate
24 °C
17 °C
10 °C
RELATIVE GROWTH RATE (g per g per day)
ENDOSPERM LOSS (mg per seed)
DAYS AFTER SOWING
0
0·2
0·4
0·6
0·8
2
4
6
10
20
30
40

Figure 24 Effect of temperature on relative growth rate (r), net assimilation rate (E), and leaf area ratio (LAR), of isolated plants of *L.rigidum* and *H.leporinum*. Bars represent least significant differences (P=0.05) between both temperatures and species


r
(g per g per day)
·25
·20
·15
10
17
24
P = 0·05
L rigidum
H leporinum
E
(mg per sq cm per day)
2·0
1·5
1·0
0·5
10
17
24
P = 0·05
LAR
(sq cm per mg)
·20
·15
·10
10
17
24
P = 0·05
TEMPERATURE °C

there is virtually no effect of temperature on growth of *H.leporinum* between 10°C and 17°C, and very little effect of temperature on r of *L.rigidum* between 17°C and 24°C, although in the case of *L.rigidum* E was reduced markedly between these temperatures. The two species obviously have quite different responses to temperature.

Leaf area ratios of *H.leporinum* were not affected by temperature, or were affected very little (LAR was significantly higher at 24°C than at 17°C or 10°C). LAR of *L.rigidum* however was greatly reduced at 17°C compared to either 10°C or 24°C.

4.3.6. Leaf and tiller production

Tiller number apparently increased exponentially with time, the rate being slightly greater for *L.rigidum* (Figure 25). Rate of leaf appearance on the main stem and on tiller 1 was apparently constant with time, the rate being similar for the two tillers and the two species at each temperature (Figure 26).

The size of various leaves is shown in Figure 27. Note that the first leaf of *H.leporinum* was considerably heavier than that of *L.rigidum*, but that this difference had decreased by leaf 3, except at 24°C. Leaf areas were directly proportional to leaf weight.

Figure 25 Increase in tiller number of isolated plants of *H.leporinum* and *L.rigidum* in each of three temperature environments.

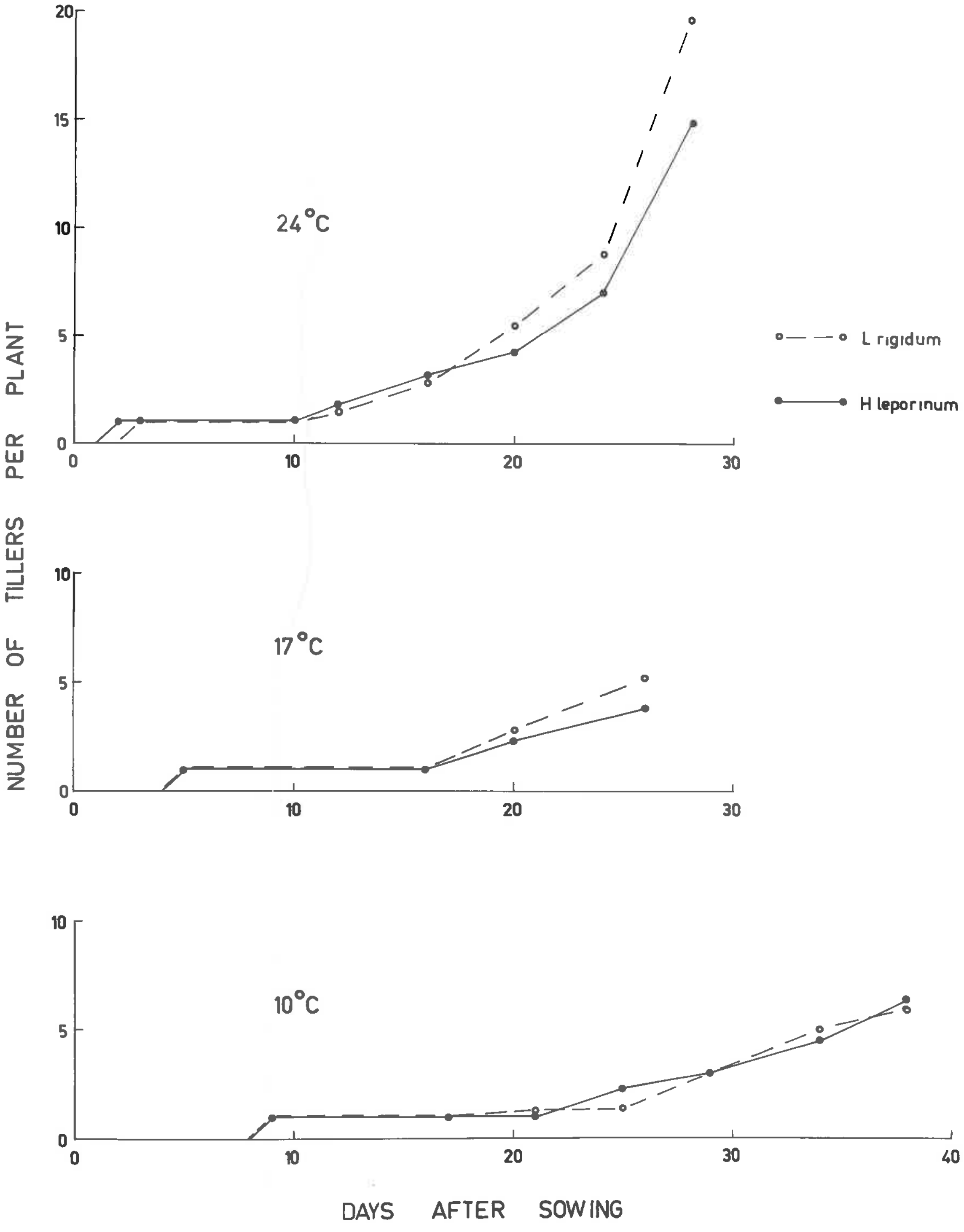

24°C
17°C
10°C
NUMBER OF TILLERS PER PLANT
DAYS AFTER SOWING
L rigidum
H leporinum
0
5
10
15
20
0
10
20
30
40

Figure 26 Number of leaves on the main stem and on tiller 1 of isolated plants of *H.leporinum* and *L.rigidum* in each of three temperature environments.

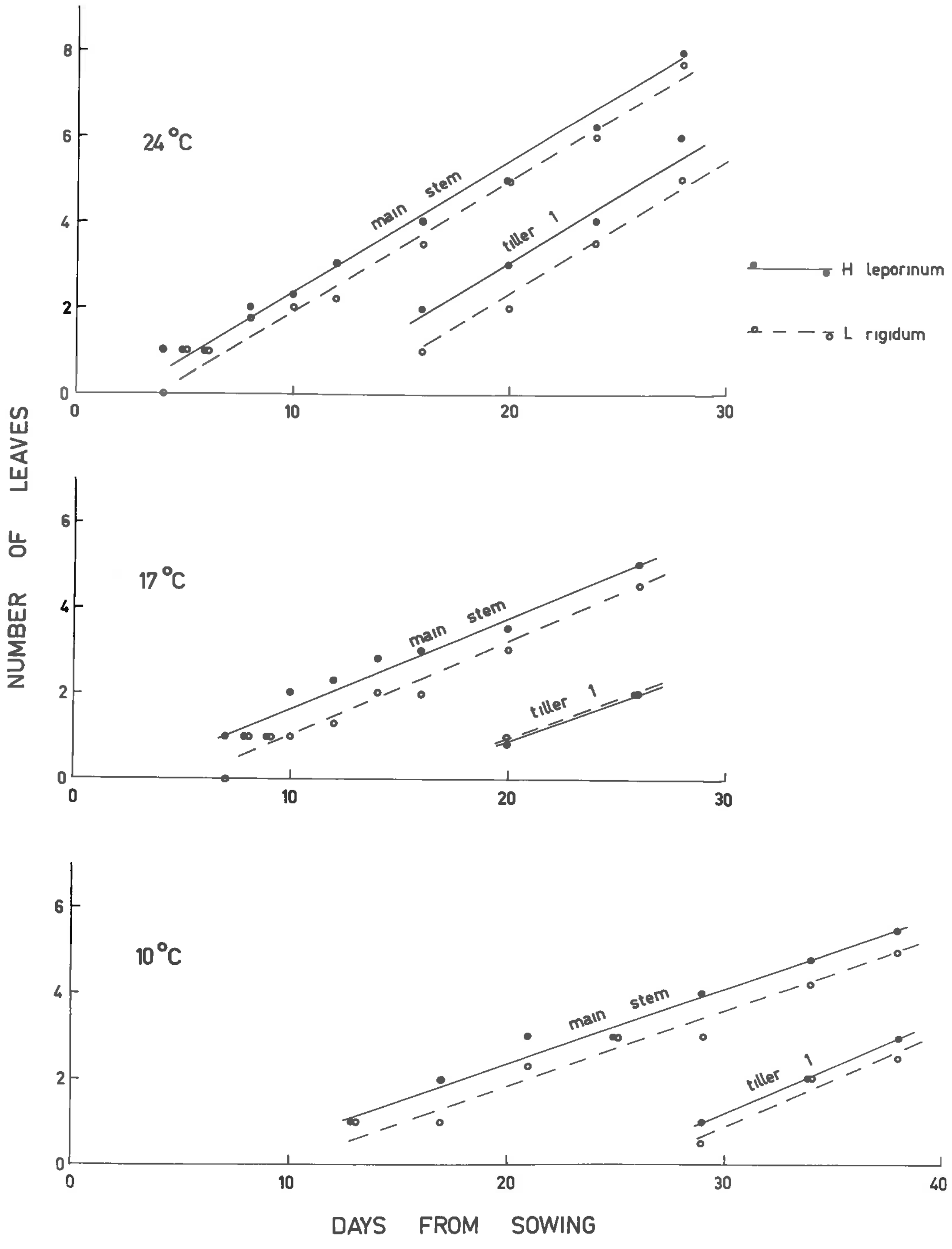
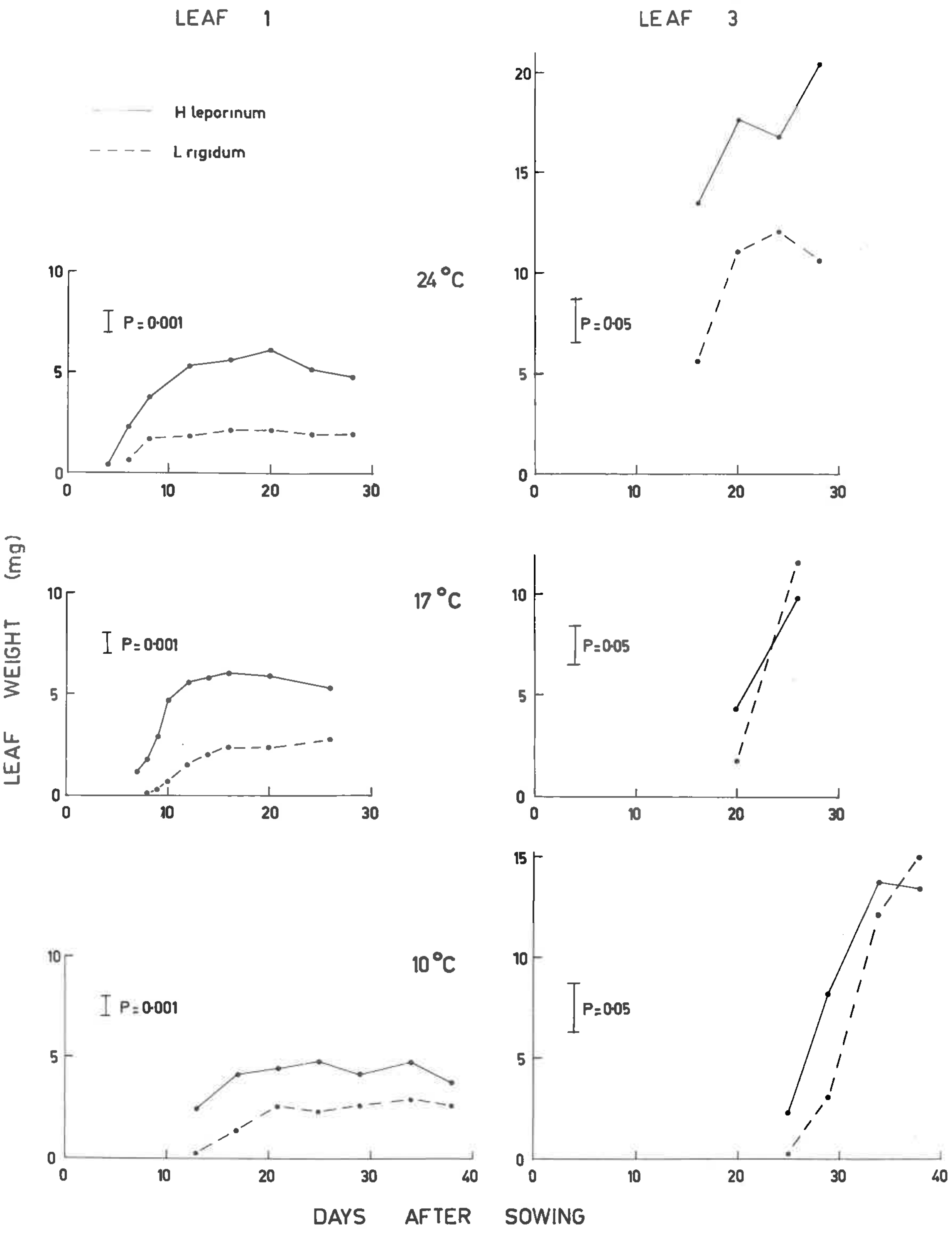

24 °C
main stem
tiller 1
H leporinum
L rigidum
17 °C
main stem
tiller 1
10 °C
main stem
tiller 1
NUMBER OF LEAVES
DAYS FROM SOWING
0
2
4
6
8
0
10
20
30
40

Figure 27 The size of leaf 1 and of leaf 3 of *H.leporinum* and *L.rigidum* in each of three temperature environments. The bars represent least significant differences (at the significance level indicated) between any two measurements of leaf weight at any one temperature.


LEAF 1
LEAF 3
H leporinum
L rigidum
24 °C
17 °C
10 °C
P = 0·001
P = 0·001
P = 0·001
P = 0·05
P = 0·05
P = 0·05
LEAF WEIGHT (mg)
DAYS AFTER SOWING
0
5
10
15
20
0
10
20
30
40

4.4.0. Discussion

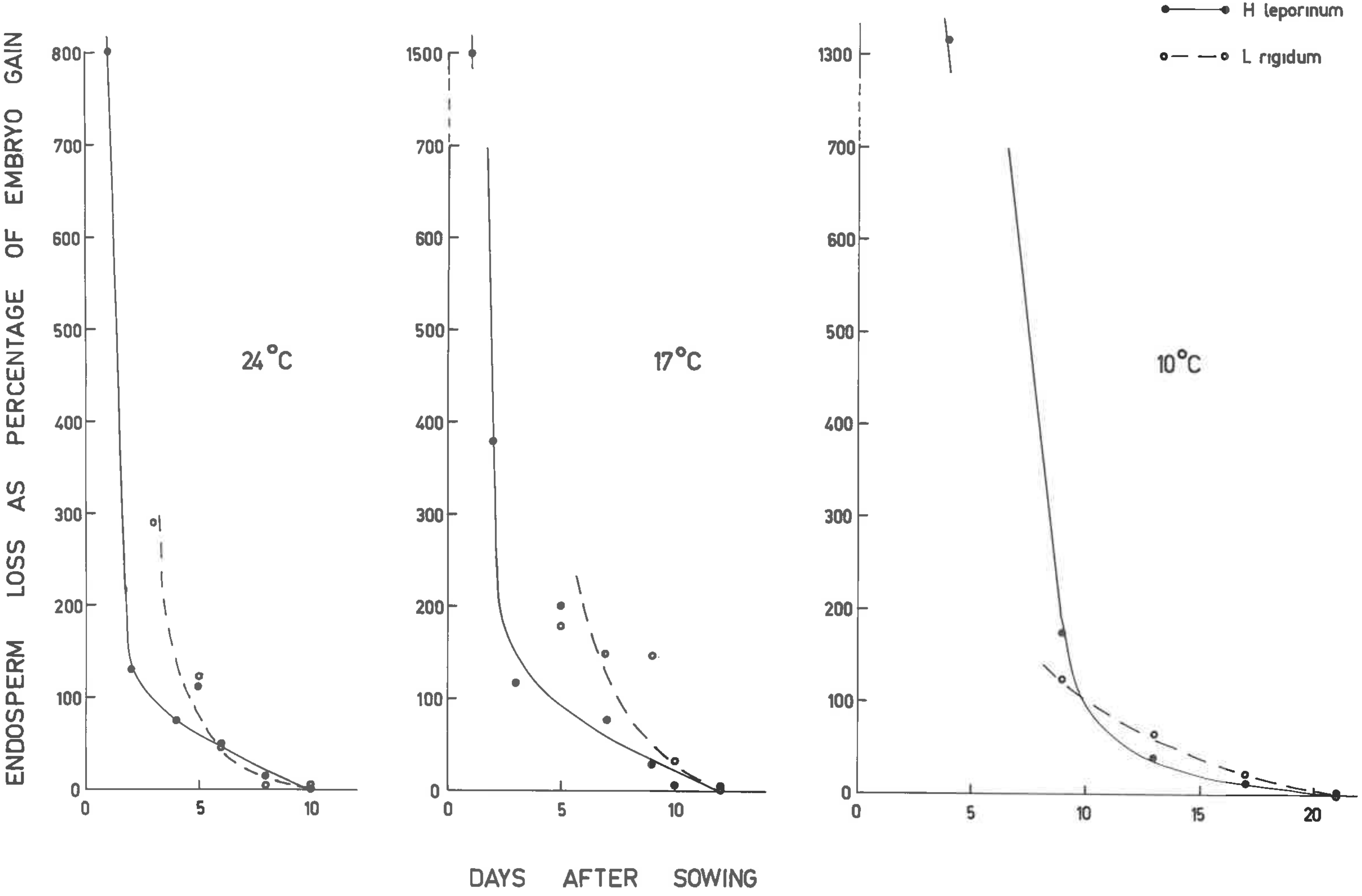
I intend discussing these results under three headings. Firstly, I will discuss the effect of endosperm on growth rate and the differences in this respect between the species. Secondly, I will discuss the effect of temperature on different aspects of growth analysis, and will formulate an hypothesis about outcome of competition between *H.leporinum* and *L.rigidum* based on their behaviour in the growth cabinet. Thirdly, consideration will be given to aspects of leaf and tiller growth.

4.4.1. The effect of endosperm availability on plant growth rate.

An examination of Figure 23 leads to the conclusion that the high relative growth rate (*r*), which occurred after germination commenced, was due to endosperm availability. The very close agreement between the time at which *r* became constant and the time when endosperm loss became zero or almost zero, strongly suggests this. So too, do the results of Williams (1960) and Foale (1968). What I shall now attempt to do is to consider the efficiency of use of these reserves at the various temperatures, and at various times after the seed was sown, and compare efficiencies of the two species.

Figure 28 shows endosperm loss as a percentage of embryo or plant gain. At first this percentage was very high, as high as 1500% for *H.leporinum* (at 17°C), and nearly 300% for *L.rigidum* (at 24°C). This presumably

Figure 28 Endosperm loss as a percentage of embryo gain in isolated plants of H.leporinum and L.rigidum in each of three temperature environments.


ENDOSPERM LOSS AS PERCENTAGE OF EMBRYO GAIN
24°C
17°C
10°C
H leporinum
L rigidum
DAYS AFTER SOWING
800
1500
1300
700
600
500
400
300
200
100
0
5
10
15
20

means that, at this stage, most of the endosperm loss was through respiration. However, neither absolute loss of endosperm (see Figure 19 which shows a gradual increase in the rate of decrease in seed weight) nor absolute gain in embryo weight was as yet very great. Efficiency of endosperm use (high efficiency can be said to occur when most endosperm can be accounted for as plant gain) increased as endosperm use became greater and the embryo became larger. Full efficiency was apparently reached when endosperm loss equalled plant gain (was 100% of plant gain). I say apparently, because it was about at this stage that the first leaf appeared.

Examination of Table 17 reveals that in every case the first leaf appeared at almost the same time as all endosperm could be accounted for as embryo gain. Probably leaf appearance occurred just before this time, as some respiration losses would surely prevent all endosperm loss being accountable in this way. Table 17 compares the dates at which endosperm loss was greatest, endosperm loss equalled embryo gain, r was highest, and first leaves appeared. The four dates were remarkably close, indicating that at the moment of emergence of the first leaf, the plant was indeed growing at its most rapid, all its endosperm reserves being used at maximum efficiency.

Table 17, does not, however, answer the question as to whether peak efficiency was due to the first input of leaf photosynthate, or whether there was in fact an increase in efficiency of use of the endosperm. That the latter explanation is most likely can be gathered from Figure 28. At all three temperatures for H. leporinum, and

TABLE 17

Comparing

A - time of most rapid endosperm loss

B - day at which relative growth rate was highest

C - day when endosperm loss was 100% of plant gain

D - day when the first leaf appeared.

Species and Temperature	A between days	B day	C day	D day
H.leporinum				
24°C	0 and 6	2	2.8	3.5
17°C	0 and 9	5	4.9	6
10°C	0 and 13	9	10.0	*
L.rigidum				
24°C	3 and 6	5	4.9	5
17°C	8 and 10	9	7.8	8
10°C	6 and 13	10	10.2	12

A - from Figure 19, where slope was greatest

B - from Figure 23.

C - from Figure 28.

D - from Figure 27.

* extrapolation inaccurate

at one temperature (17°C) for *L.rigidum*, at least two measurements of endosperm loss and plant gain were made before the appearance of the first leaf. In every case where the second measurement was taken a marked improvement in efficiency of use of endosperm had occurred, the actual figure being about 125% of plant gain in *H.leporinum* and perhaps a little more in *L.rigidum*. It seems reasonable to conclude that such an improvement in efficiency was real.

The difference between species was marked. At no stage does endosperm loss of seeds of *L.rigidum* grossly exceed plant gain in the way that this occurs in *H.leporinum*.

Indeed at the very early harvest dates when endosperm loss relative to plant gain was large in *H.leporinum*, seeds of *L.rigidum* had apparently not commenced germination, though in Figure 18 there is some suggestion of a loss in embryo weight. As remarked earlier however, this may have been due to experimental error, as differences were not statistically significant.

The amount of the endosperm which is used in the plant can be calculated from Figure 18. This can be done if it is assumed that there are 3 stages of growth and that the plant grows at the same rate for the whole of any one stage. Thus the stage of endosperm use will be the second stage, one of rapid growth, as is shown at each temperature in Figure 18. The slope of this line is the effect of the endosperm plus the effect of any leaves which may appear before endosperm exhaustion. The slope of the line in the third stage is due only to photosynthesis from the leaves. Thus the differences between the two slopes will be the effect of endosperm. The actual calculations involved are shown in Figure 29. The results are shown in Table 18(a). Note that in all cases, most of the endosperm appears as plant material, and in some cases the calculated influence of endosperm exceeds the actual amount of endosperm lost. This is shown more clearly in Table 18(b) where plant gain apparently caused by the endosperm is expressed per unit endosperm lost. Although this last figure is always greater for *L.rigidum* than for *H.leporinum*, the figures for the two species are of the same order.

It is obviously impossible for more material to appear in the plant than is lost from the endosperm, when there are no other sources of carbohydrate for growth. The method outlined above for calculating the influence of the endosperm assumes that leaf photosynthesis rate remains constant and it assumes also that all photosynthesis occurs in the leaves. The latter assumption may be true at this stage, since Thorne (1959) found that leaf sheaths can photosynthesise at only half the rate of leaves, and since sheath area would be very low. However, the former assumption, that of a constant net assimilation rate (E) may not be true. This can be tested by calculating E's from the time of the appearance of the first leaf, and allowing for the loss in weight of the endosperm (that is, subtract change in endosperm weight from W2 - W1 in the formula for *E* on page 134).

This has been done in Figure 30, which shows a high early E at least in some cases, and especially at 17°C,

Figure 29 Example of method of calculating the absolute contribution by the endosperm to plant growth. The influence of endosperm can be measured by assessment of the value antilog (c) - antilog (d). The position of (d) can be ascertained, by measuring (a) - (b) and subtracting from (c).

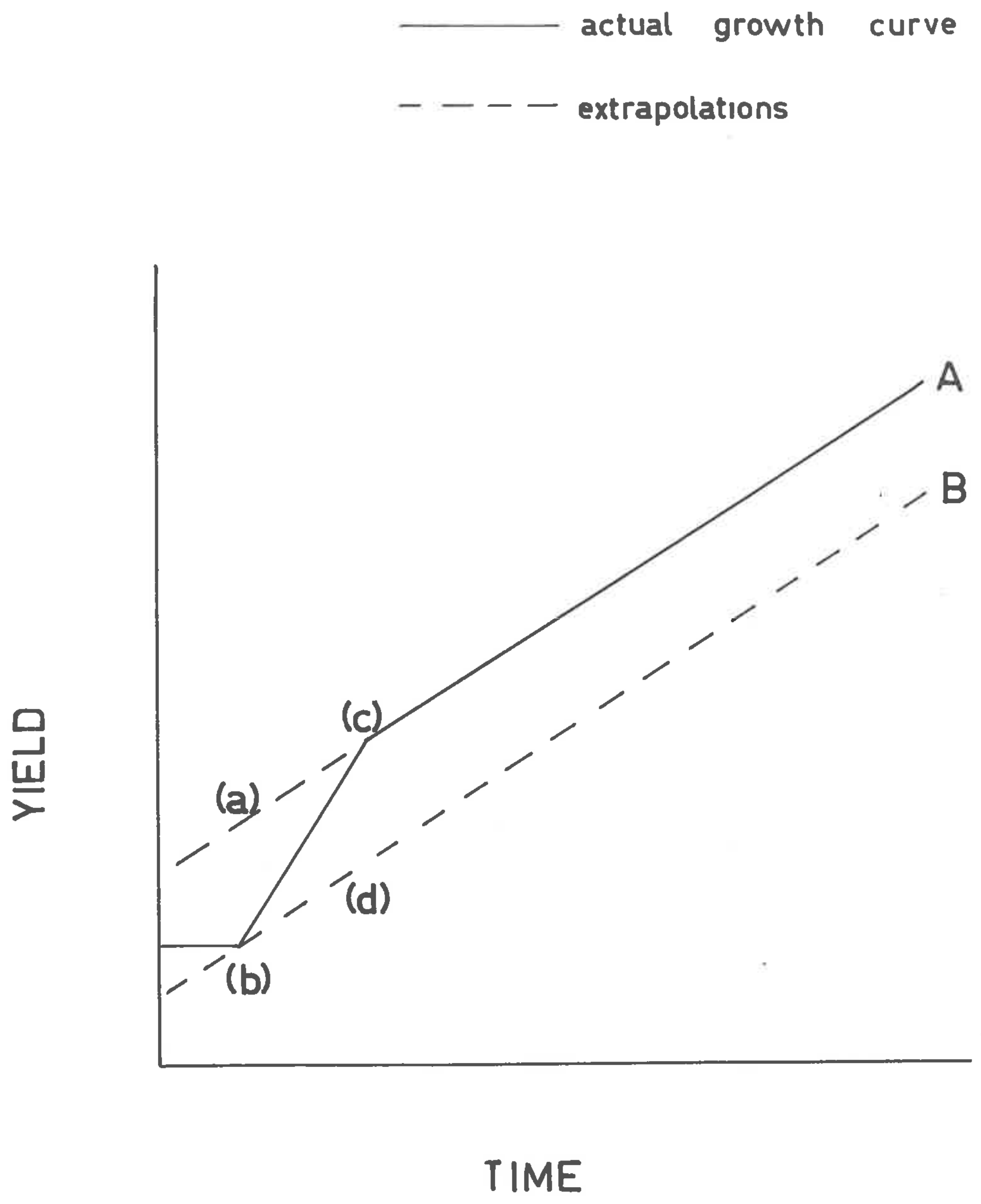

actual growth curve
extrapolations
A
B
(c)
(a)
(d)
(b)
YIELD
TIME

TABLE 18

(a) Contribution by the endosperm to embryo growth, measured as in Figure 29 (mg per plant).

Temperature	*H.leporinum*	*L.rigidum*
24	6.2	2.4
17	10.6	3.4
10	3.8	1.3
L.S.D. P=0.05	2.2	2.2

Wt. of endosperm lost = 6.3 mg per seed for *H.leporinum*, and 1.9 mg per seed for *L.rigidum*.

(b) Contribution by the endosperm to embryo growth expressed as embryo growth per unit weight of endosperm (mg per mg).

Temperature	H.leporinum	L.rigidum
24	0.98	1.26
17	1.68	1.79
10	0.60	0.68

the temperature at which endosperm contribution was apparently greatest. This evidence is rather inconclusive, but the probable explanation for the over-estimation of endosperm contribution calculated from data in Figure 18 is that the first leaf, when it first appears, is able to photosynthesize more rapidly than later. Whether this is due to a growth factor in the endosperm or whether all leaves possess the same property cannot be elucidated.

One final point about endosperm reserves can be made. Table 18 (a) indicates that the larger reserves of *H.leporinum* are part of the reason for its larger seedling at emergence as shown in Table 19. The other reasons are its earlier germination and larger embryo. Thus seedlings of *H.leporinum* are about 5 times the size of seedlings of *L.rigidum* at emergence.

4.4.2 Aspects of growth analysis

I propose firstly to discuss the uses to which growth analysis has been put in the past, secondly to use it as a means of comparing the response of the two species to temperature, and thirdly to use it to form an hypothesis about the outcome of competition between the two species.

Growth analysis, involving calculation of relative growth rate (r), net assimilation rate (E), and leaf area ratio (*LAR*) has been advocated by various authors since the concept of r was first introduced by Blackman in 1919. The term r is perhaps the most useful. The basic assumption in its calculation is that growth of plants depends on the amount of material present, or that increase in dry weight is exponential. It is in fact

Figure 30 Change in net assimilation rate with time in isolated plants of H.leporinum and L.rigidum in each of three temperature environments.

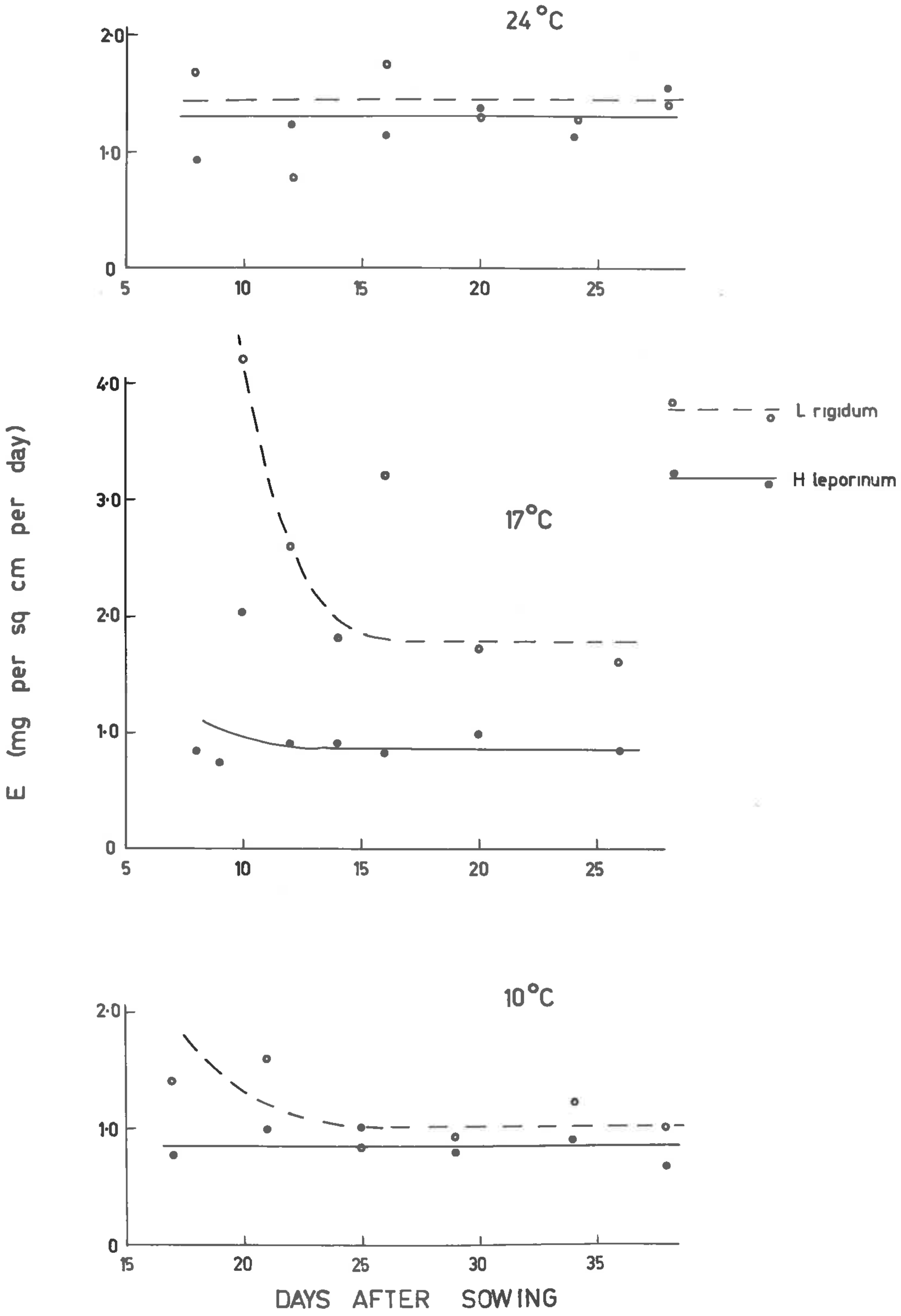

24°C
2·0
1·0
0
5
10
15
20
25
E (mg per sq cm per day)
4·0
3·0
2·0
1·0
0
17°C
L rigidum
H leporinum
5
10
15
20
25
10°C
2·0
1·0
0
15
20
25
30
35
DAYS AFTER SOWING

TABLE 19

Weight and leaf area of seedlings of *H.leporinum* and *L.rigidum*, at the first harvest following emergence of *L.rigidum* (weight in mg per plant, leaf area in sq cm per plant).

	Weight (mg)			Leaf area (sq cm)		
	10°C	17°C	24°C	10°C	17°C	24°C
H.leporinum	5.24	4.52	4.09	0.65	0.81	0.72
L.rigidum	1.48	0.71	1.08	0.08	0.03	0.14
Day of harvest	13	8	5	13	8	5
Significance	*	***	**	***	***	***

* P = .05
** P = .01
*** P = .001

analogous to compound interest rate, biological material already present being analogous to capital. The term *E* is a measure of the plants' net photosynthesis (that is, photosynthesis less respiration per unit leaf area), because it is a measure of increase in dry weight with reference to leaf area. It is thus a measure of efficiency. The third term, *LAR*, is simply the ratio of leaf weight to total plant weight. Relative growth rate can be altered either by a change in *E* or *LAR* and is the product of them (Briggs et al 1921).

Plant weight is properly total plant weight, although *r* can be partitioned into leaf *r*, stem *r*, or any other *r*, as was done by Williams (1960) for the growth of wheat seedlings. *E* and *LAR* cannot be so partitioned and *E* is grossly underestimated and *LAR* overestimated if root weight is neglected.

Growth analysis has had two uses, firstly as a physiological basis for the understanding of crop yield, and secondly to describe plant response to environmental change. Its use in studying yield was questioned by Watson (1952). He maintained that because roots of crops cannot be included in calculations of *E*, and because photosynthesis occurs in other parts of the plant beside the leaves, that there are significant errors in the estimation of *E* . For this reason, and because leaf area varies more in response to the environment and between species, he concluded that the amount of leaf area is a better method of describing crop growth potential. Since Watson's paper, emphasis has changed from a study of *E*, to a study of leaf area index, a concept he introduced in 1947.

The second use of growth analysis has been to measure whole plant response to changes of the environment. This has been strongly advocated by Blackman (1961). Where plants do not compete with each other and where vegetative growth only is considered, the technique appears to have some value as a bridge between laboratory response and field experimentation. This is especially so when controlled environments are used. Thus the whole plant's response to controlled changes in the environment can be assessed and some extrapolation to the field ventured. It is in this way that I propose to use growth analysis.

First, a consideration of response to temperature.

Very few measurements of the response of annual pasture plants to temperature have been made, and these have been confined to subterranean clover (Mitchell 1956, Morley 1958a). Depending on thevariety, this species has an optimum of between 18°C and 20°C, and there is a tendency of growth rates to be approximately constant over the range 18 - 24°C. Most varieties respond sharply to temperature below 18°C. This kind of response is similar to that recorded for *L.rigidum*. Considering that for most of the growing season mean temperature is below 18°C, growth of both *L.rigidum* and subterranean clover will be affected by temperature. The case of *H.leporinum* however, is different. Its growth is apparently unaffected by temperature over the range of temperatures occurring during the early part of the growing season. The effect of temperature in relation to the environment is discussed more fully in the general discussion.

At every temperature, *L.rigidum* grew better than *H.leporinum*, that is, its *r* was higher. This is in marked contrast to the results of Smith (1968b) who suggested that early growth of H.leporinum was much better than that of L.rigidum. In his experiment "A" however, swards of L.rigidum eventually outyielded swards of H.leporinum, suggesting that the growth rate of L.rigidum was superior to H.leporinum, the superior early growth of the latter species being due to its large seeds and early germination.

I now turn to consideration of an hypothesis about the outcome of competition between H.leporinum and L.rigidum based on their behaviour in the growth cabinet.

The net result of differences in embryo weight, endosperm weight,and relative growth rate is that, at emergence, plants of H.leporinum have substantially larger seedlings than have L.rigidum (Table 19). As discussed earlier, this was due to the differences in embryo weight and time of germination. Table 19 shows the size of the seedlings at the time at which the second species, Lrigidum emerged. This is the starting point of the effect of r, and plant size at emergence, on subsequent competition.

Because L.rigidum has greater r, its seedlings will grow more quickly than those of H.leporinum. Thus, if no competition occurs, plants of L.rigidum will eventually be larger plants. If competition occurs, then the species which will best be able to compete in a mixture of the two species will be that species whose seedlings are largest when competition begins. Thus, if competition begins at or soon after emergence, when plants of H.leporinum are larger, this species will be better able to compete. If competition begins later, when the superior r of L.rigidum has enabled its seedlings to become larger than those of *H.leporinum*, then *L.rigidum* will be better able to compete. Thus, that species which will be the most successful species in a mixture of *H.leporinum* and *L.rigidum* will depend on the time at which competition begins. This in turn will depend on density. That is, at high density, competition between individuals will begin sooner than it will at low density. Hence the outcome of competition will depend on density.

Density in a mixed sward can be stated in three ways, as total density or as density of either component. The three density estimates will not necessarily affect outcome of competition in the same way. In the case of competition between *H.leporinum* and *L.rigidum*, the important density will be that of *H.leporinum*. If density of *H.leporinum* is high, plants of *L.rigidum*, regardless of the density of *L.rigidum*, will be shaded as soon as they emerge, or before seedlings become as large as those of *H.leporinum*. Rate of photosynthesis of these seedlings will be reduced as a result and the final effect will be their suppression. If, however, density of *H.leporinum* is so low that the superior *r* of *L.rigidum* enables that species to produce larger plants before competition begins, then *L.rigidum* will suppress *H.leporinum* for the same reason as the reverse will occur at high densities of *H.leporinum*.

Thus the hypothesis can be stated in the following way : that in competition between *H.leporinum* and *L.rigidum* the outcome will depend on the density of *H.leporinum*. There will be a critical density, such that above it, *H.leporinum* plants will shade or otherwise compete with *L.rigidum* plants to such an extent that the relative growth rate of *L.rigidum* will be reduced to less than that of *H.leporinum*. Below that critical density of *H.leporinum*, the greater *r* of *L.rigidum* will enable that species to have larger plants when competition begins, resulting in the shading or suppression by other means of plants of *H.leporinum*.

Suppression of either species could be by shading or it could be by superior exploitation of the soil by the winning species, because root *r* and top *r* behave similarly to total plant *r*. Most likely, there would be an interaction between top and root competition.

This kind of reasoning can only apply in competition between species whose growth habit is similar, that is, whose root proliferation and height are correlated with *r*. For example, grass would probably dominate clover regardless of considerable variation in *r* and seedling size, because grass potentially grows taller.

It is the object of the next experiment to test the above hypothesis.

4.4.3. Consideration of leaf and tiller growth and other aspects of plant growth.

That number of tillers increases exponentially with time (Figure 25) is not surprising, as number of tillers depends on number of leaf axils which in turn depends on number of tillers already present. Whenever rate of increase of any character depends on the amount of itself already present, that increase will be exponential (as Blackman 1919 found increase of dry weight was exponential).

A constant rate of leaf appearance on a single shoot has been established for several grasses. Cooper (1951), Mitchell (1953), Patel and Cooper (1961), and Silsbury (1966) have shown this for *Lolium perenne*, Friend et al (1962) for wheat, and Aspinall and Paleg (1964) for barley, all in constant environments. Temperature, light intensity, and to a lesser extent nutrient status, affect this rate.

Silsbury (1966) has pointed out the implication of a constant leaf appearance rate on sward growth. If tillering is suppressed, as occurs at high density, leaf production will be restricted to a constant number of apices per unit area of ground, unless competitive effects reduce plant number with time. Sward growth rate will thus depend on leaf appearance rate, and hence will be linear with time once light interception is complete. The implication of this proposition on the relationship between leaf area index (LAI) and growth rate as proposed by Davidson and Donald (1958) and Black (1963), will be that little reduction of growth rate will occur at very high LAI's compared with the optimum LAI. However, reductions in sward growth rate at high LAI's will occur if there is plant mortality, or if complete shoots become shaded, as would seem likely under these conditions. It would seem likely, also, that reduction in growth rate of grassy swards will be less than clovery swards at high LAI values because of the ability of grasses to hold their shoots erect.

The implications of a constant leaf appearance rate may not be limited to the total growth of swards. By the same reasoning, success of one species in a mixture, when total density is high, may depend on its leaf appearance rate, compared to its competitor, especially if leaf size of the two species is not greatly different. This is because growth rate of each individual species will depend on its leaf appearance rate, and so the species with the greatest leaf appearance rate will have the greatest growth rate and hence be successful. This reasoning will, however, have little effect on success of *H.leporinum* or *L.rigidum* when the two are grown together, as their leaf appearance rates are identical (Figure 26).

The conclusion, drawn after consideration of relative growth rates, that outcome of competition between these two species depends on the density of one of them, could be drawn in a different way. Figure 27 shows that leaf 1 of *H.leporinum* was considerably larger than that of *L.rigidum*, and Figure 25 shows that the latter has a slightly greater tiller appearance rate. Figure 21 shows that initially *H.leporinum* was taller, and Figure 22 that it had a deeper root system. At high densities then, when tillering is suppressed, the fact that *H.leporinum* is taller, has more leaf and a deeper root system should ensure its success. At low densities, the greater tillering ability of *L.rigidum* and its greater height as it becomes older should reverse the result.

One final point can be made. The deeper root system of *H.leporinum* will probably allow this species to tolerate a greater amount of drought early in its life cycle, than will *L.rigidum*. Drought frequencies are sufficiently high in the southern Australian Mediterranean environment (Figure 6) to make early depth of root system an important ecological character.

5.0.0. THE EFFECT OF DENSITY ON THE OUTCOME OF COMPETITION BETWEEN HORDEUM LEPORINUM AND LOLIUM RIGIDUM.

5.1.0. Introduction

In the preceding section I discussed an hypothesis about the outcome of competition between *H.leporinum* and *L.rigidum*. Because of its larger seed and more rapid germination it was postulated that *H.leporinum* would suppress *L.rigidum* when *H.leporinum* was sown at high density, but that the superior relative growth rate of *L.rigidum* would result in the suppression of *H.leporinum* when the latter was sown at low density, the density of *L.rigidum* not affecting the outcome of competition. It is the aim of the experiment reported in this section to test this hypothesis.

5.2.0. Experiment 8 - Experimental Procedure

5.2.1. Treatments

The following treatments were used to examine the effect of density of each species and of total density on the outcome of competition. Eight mixtures were sown containing :

H.leporinum at 3,12,48 and 192 plants per 100 sq cm and *L.rigidum* at 12 and 192 plants per 100 sq cm,

in all possible combinations.

The wide range of densities was chosen to ensure the inclusion of the critical density of *H.leporinum*; that is, the density of *H.leporinum* above which that species is aggressive and below which *L.rigidum* is aggressive. The experiment was sown as a complete factorial (4 sowing rates of *H.leporinum* x 2 sowing rates of *L.rigidum*) with three replicates.

5.2.2. Experimental site

The experiment was conducted in the open in soil beds raised 2 feet from the ground. Bricks were placed at the bottom to assist drainage and the remainder filled with John Innes potting compost. Fertilizers had previously been added to the compost and none were added during the experiment. The beds are shown in Plate 1.

Plot size was 53 x 102 cm. Before sowing, a permanent grid of wire mesh was laid over the whole of the area delineating quadrats for harvest. The quadrat area was 28.6 cm x 8.1 cm and there was 13 cm between quadrats

PLATE 1 The raised soil beds used in Experiment 8. The photograph was taken soon after seedling emergence. Plots sown with a high density of H.leporinum can be seen as darker strips across the soil beds.

A border 15 cm wide was allowed between any quadrat and the wall of the bed and 12.2 cm between any quadrat and the edge of the next plot (Figure 31).

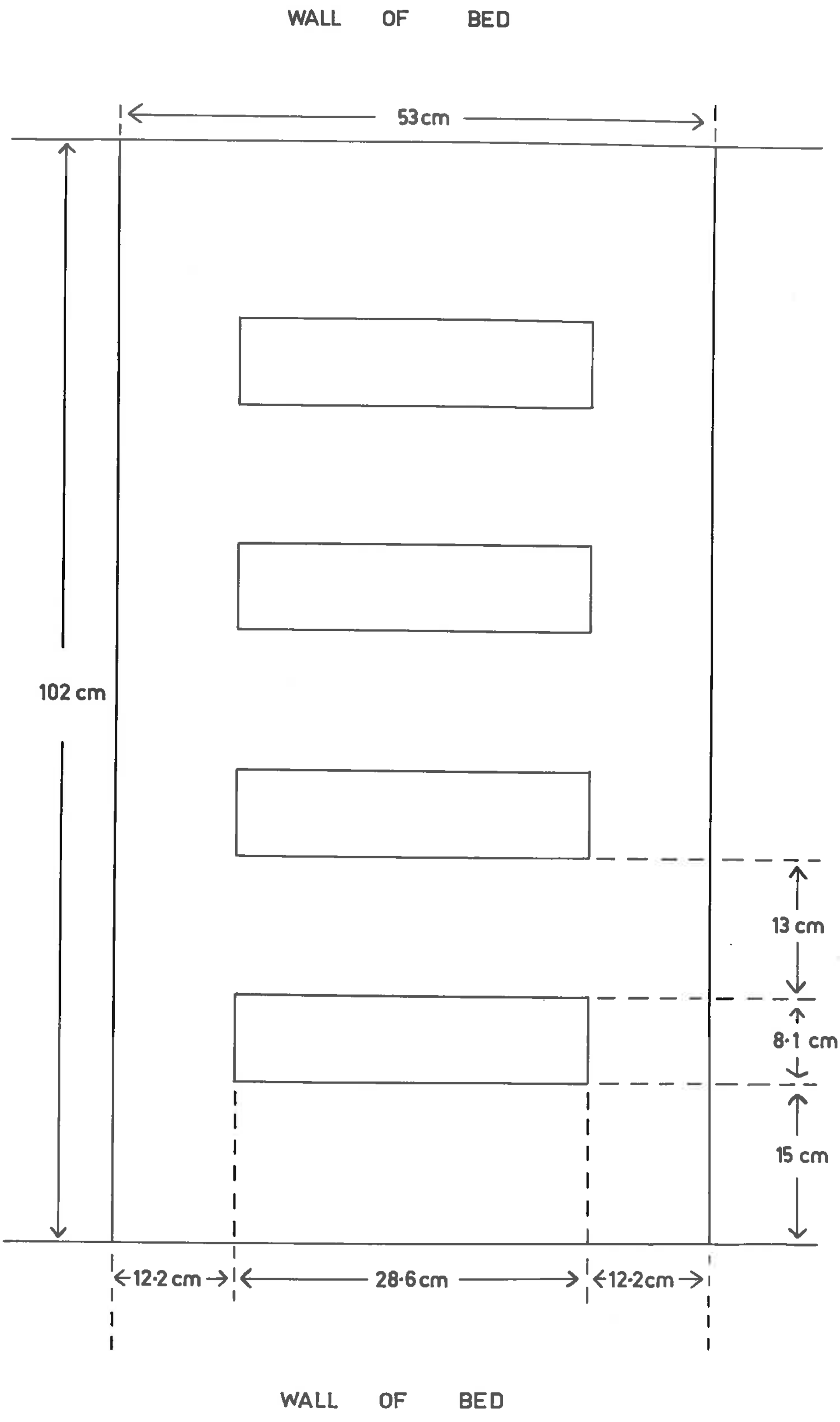
5.2.3. Method of planting

Seed of *L.rigidum* was obtained from a local seed merchant and seed of *H.leporinum* from the fields of the Waite Institute. During the threshing and cleaning process sterile florets and awns were removed from the dispersal unit of *H.leporinum*; unfortunately, some seed was damaged and potential germination thus reduced. Germination tests of both species were conducted, and the amount of seed necessary to obtain the given numbers of viable seed calculated. Germination of *H.leporinum* was 45 % and of *L.rigidum* 80 %

For densities of 48 and 192 plants per 100 sq cm, the required amount of seed was broadcast by hand. At the lower densities each seed was individually sown. Two seeds of *L.rigidum* were sown at each site, which meant that, with 80 % germination, about 4 positions in 100 would be without a plant. There were no transplants, and the second plant, where two germinated, was removed 3 weeks after sowing. Seeds of *H.leporinum* to be used in low density plots were pre-germinated at the plot site in large trays covered by hessian bags, and sown when radicles emerged. Germination of all seeds began on the same day, namely 19th May 1967.

All seeds were covered by 1cm of Waikerie sand. Those plots where seeds of both species were sown dry (namely high density plots) were covered immediately and watered, but where *L.rigidum* was to be sown with a low density of

FIGURE 31 Dimensions of a single plot showing positions of harvest sites.


WALL OF BED
53 cm
102 cm
13 cm
8·1 cm
15 cm
12·2 cm
28·6 cm
12·2 cm
WALL OF BED

H.leporinum, seed was covered with damp hessian bags which ensured it remained wet until *H.leporinum* seed was sown 3 days later. After germinated seed of *H.leporinum* had been sown these plots were covered with 1 cm of sand in the same way as other plots. The technique was successful in providing continuous growth of each species from a common date. All plots were watered when necessary throughout the experiment.

5.2.4. Harvest technique

There were three harvests of swards of high density and four when both species were planted at low density. At the third harvest of high density plots, the plants had lodged badly, and any further harvest was impossible. Harvest dates were 14 June (26 days), 28 June (40 days), 12 July (54 days) and 26 July (68 days).

At each harvest the quadrat nearest the wall was cut to prevent disturbance of the remainder of the plot. The plot edge used (east or west) was decided at random. Thus at the first harvest either quadrat may have been cut. If the west quadrat was cut, the next harvest was taken from either the east quadrat or the second from the west, and so on.

Each harvest was stratified at 5 cm vertical intervals and light measured at each level. Wire frames, of the same area as the quadrats originally laid down, were constructed with legs of heights varying from 5 cm to 30 cm. These frames were placed on the quadrats so that stratified cuts could be taken at the various levels required. Shears, with rubber strips recessed from the cutting blades, were used to cut the sward. The shears cut, and the rubbers grasped the grass, allowing none to fall or be lost.

Immediately on cutting, herbage was placed in plastic bags, sealed and put into cold storage. Processing of each harvest took up the period between harvests, but material stored for two weeks showed little sign of deterioration. Material was processed replicate by replicate, and so any loss of weight or area would appear as a block effect after analysis.

The material from each harvest was separated into leaf and stem of each species, and each component weighed after drying at 80°C. Leaf area of sub samples was measured using an air-flow planimeter (Jenkins 1959). The total number of tillers of each species was counted.

5.3.0. Results and discussion

5.3.1. Plant numbers

The predicted and actual numbers of plants established by the first harvest are shown in Table 20, which also gives the code of treatments to which I shall refer in the account of this experiment. The reasons for the variations from expectation are not known. In the case where 12 L.rigidum plants were expected, the higher numbers recorded may have been due to delayed germination, that is, germination after thinning. Further, in plots where the density of H.leporinum was high or very high, there was a high likelihood of overlooking L.rigidum plants which ought to have been removed at thinning.

Rate of establishment of each species in treatment v.high/v.high (very high density of both species) is shown in Figure 32. Numbers of plants established were counted at a harvest site (not necessarily that used in harvest 1) on the dates shown in the figure. The last count is that at the time of harvest 1. Note that complete emergence of H.leporinum occurred before that of L.rigidum, probably about 4 days before, though this cannot be accurately ascertained from the data. This confirms the more rapid germination of H.leporinum compared to L.rigidum observed by Smith (1968a) and elsewhere in this thesis.

5.3.2. Growth of swards

The effect of total density on dry matter production is shown in Figure 33. Yield has responded to density in

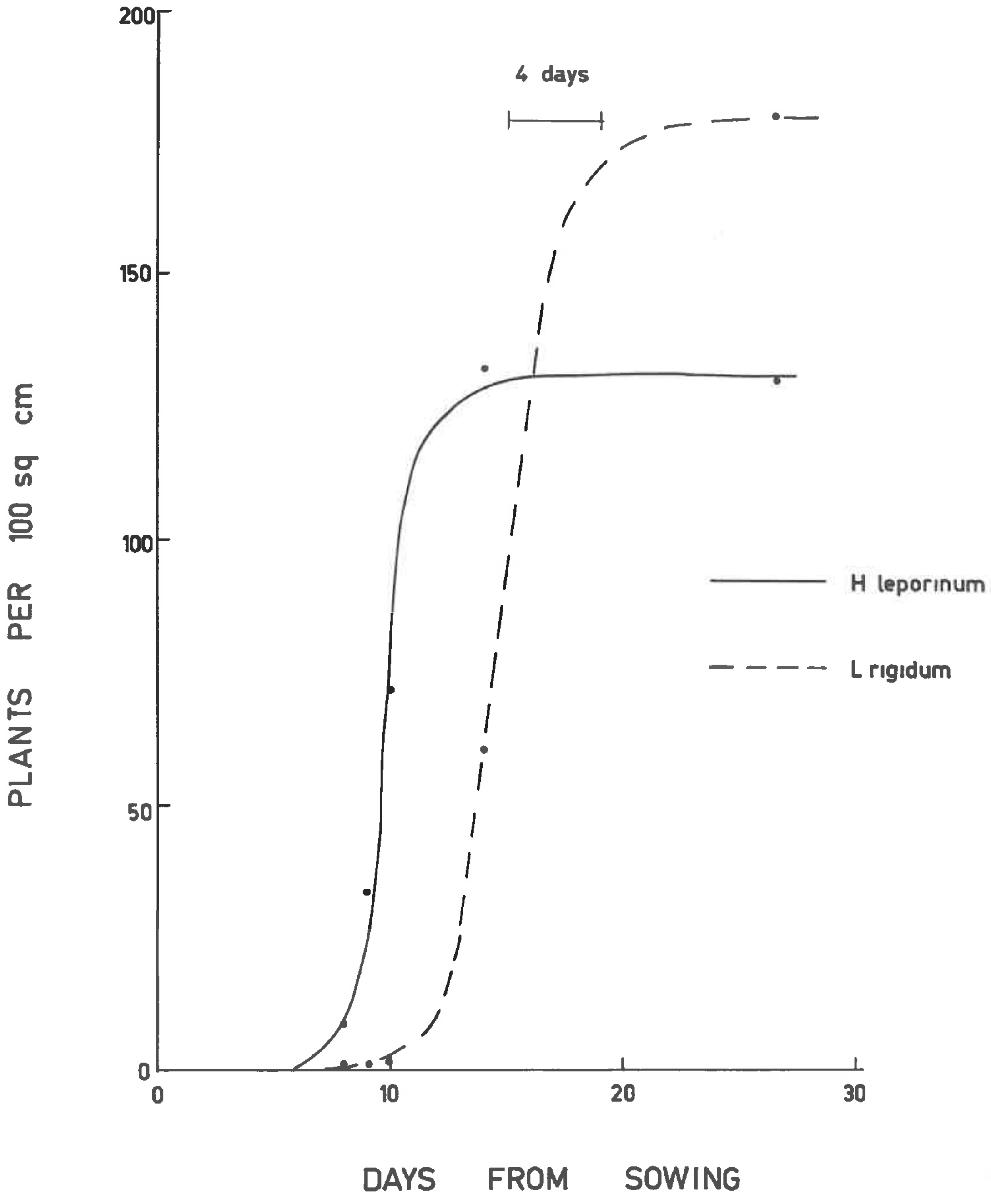
TABLE 20

Expected plant numbers, and the number of plants observed at day 26, in each treatment. The column on the left gives the treatment code referred to throughout the reporting of Experiment 8

Treatment Code	Expected plants per 100 sq.cm		*Observed plants per 100 sq cm	
H.lep. L.rig.	H.lep.	L.rig.	H.lep.	L.rig.
very high/very high	192	192	131	181
very high/ low	192	12	161	25
high/very high	48	192	39	191
high/ low	48	12	44	16
low/very high	12	192	7	208
low / low	12	12	12	16
very low/very high	4	192	3	213
very low/ low	4	12	4	15

* Mean of 3 replicates.

Figure 32 Rate of establishment of *H.leporinum* and *L.rigidum* in the very high/very high treatment. Both curves were fitted by hand. Day 0 was the day the seed was wetted.


PLANTS PER 100 sq cm
200
150
100
50
0
4 days
H leporinum
L rigidum
0
10
20
30
DAYS FROM SOWING

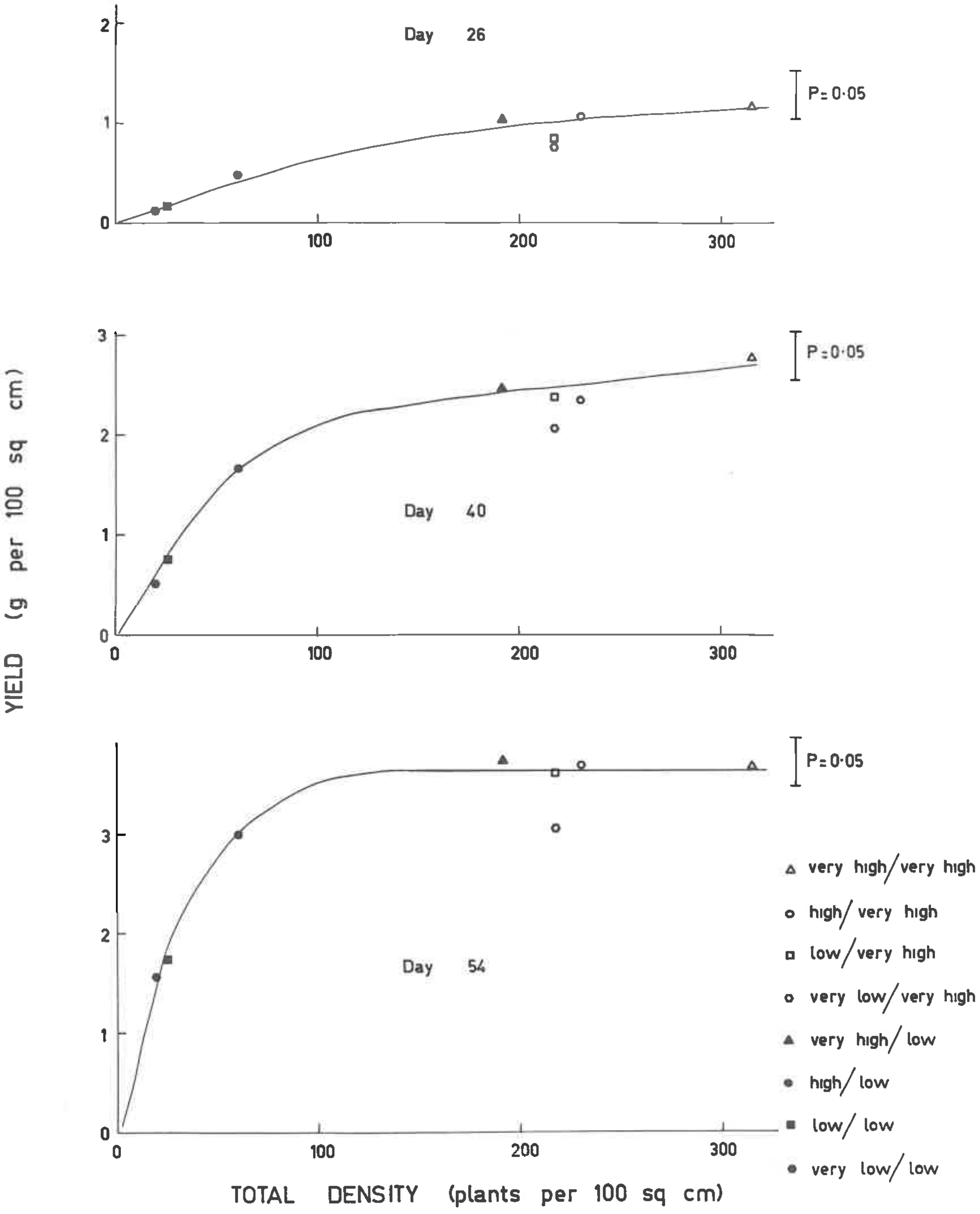
a manner similar to that recorded in previous work (Donald 1951, Aspinall and Milthorpe 1959), even though all swards were mixtures and not pure cultures. At day 26, yield increased with density to the highest density, but at day 40, though the yield still increased to the highest density, the rate of increase at very high densities was low. By day 54, yield did not increase when density was 100 plants per 100 sq cm or higher. By this date, and above this density, yield per plant had become inversely proportional to total density.

As discussed in the literature review (page 45), the most satisfactory expression governing the relationship of density and yield is the simple expression

$$\frac{1}{w} = Ad + B$$

where w is the yield per plant, d is the density, and A and B are constants (derived by Shinozaki and Kira in 1956). In Figure 34, $\frac{1}{w}$ for each species has been plotted against d, a straight line relationship resulting in each case. This is in agreement with the data of Shinozaki and Kira (1956), Reestman and de Wit (1959), and Holliday (1960b). The term d (density per 100 sq cm) as used here and in Figure 33 is actual density as recorded in Table 20, not the expected density on the basis of seed sown. It is interesting to note that the slopes do not differ greatly between harvests for the same species, though there is a tendency for the slope to decrease with time. That the slope for *L.rigidum* is always slightly steeper than that for *H.leporinum* is interesting in view of the aim of this experiment. It suggests that *L.rigidum* is favoured at low density and does not grow as well at high density, compared with *H.leporinum*.

Figure 33 The relationship between plant density and dry matter yield at each harvest. The bars represent least significant differences ($P = 0.05$) between yields at any two densities on any one day. Curves were fitted by hand.


Day 26
Day 40
Day 54
P = 0·05
P = 0·05
P = 0·05
YIELD (g per 100 sq cm)
TOTAL DENSITY (plants per 100 sq cm)
0
100
200
300
1
2
3
△ very high/very high
○ high/very high
□ low/very high
○ very low/very high
▲ very high/low
● high/low
■ low/low
● very low/low

Total dry matter yield and dry matter yield of each species at each harvest are shown in Figure 35. Yield at zero time represents weight of seed sown. Note that the growth of each species is reduced by the presence of a high density of the other species. Growth of L.rigidum at very high density was unaffected by the presence of low and very low densities of H.leporinum (Figures 35 e and g).

5.3.3. An index of aggression

The results so far considered do not confirm or deny the hypothesis that the outcome of competition depends on the density of H.leporinum. An estimate of the amount of aggression that the species are showing in each mixture is needed.

An estimate of aggression is de Wit's (1960, 1961) relative crowding coefficient. De Wit considered two species growing together in a mixture. In the first situation that he envisaged, each species gained its share of the environment without competing with its neighbours. Thus the proportion of its yield in the total yield depended on its yield in a pure culture of the same overall density, and there was a linear relationship between its yield in the mixture and the proportion of its seed in the mixture. The second situation that he envisaged more closely approached the true situation in a population of plants, that is, that plants were in fact competing with each other. One component of the mixture (say species A) gained more than its share of the environment, and the other (species B), less. The relationship between the yield of

Figure 34 The relationship between the reciprocal of yield per plant (mg per plant) and plant density. Straight line equations for each relationship are as follows :

L.rigidum day 26 $\frac{1}{w} = 0.217 + .000334\ d$

day 40 $\frac{1}{w} = 0.041 + .000520\ d$

day 54 $\frac{1}{w} = 0.011 + .000297\ d$

H.leporinum day 26 $\frac{1}{w} = 0.106 + .000309\ d$

day 40 $\frac{1}{w} = 0.021 + .000255\ d$

day 54 $\frac{1}{w} = 0.006 + .000207\ d$

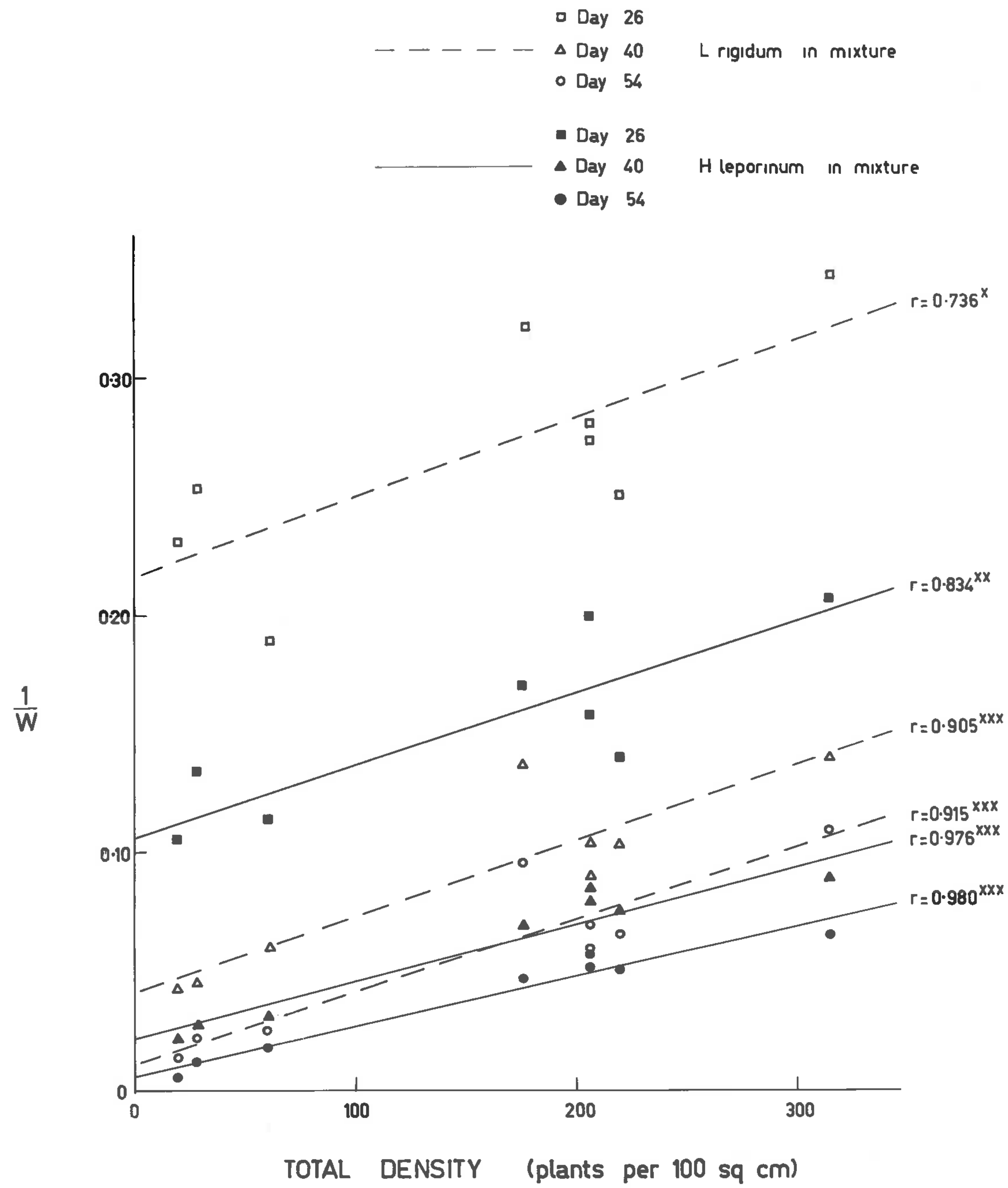
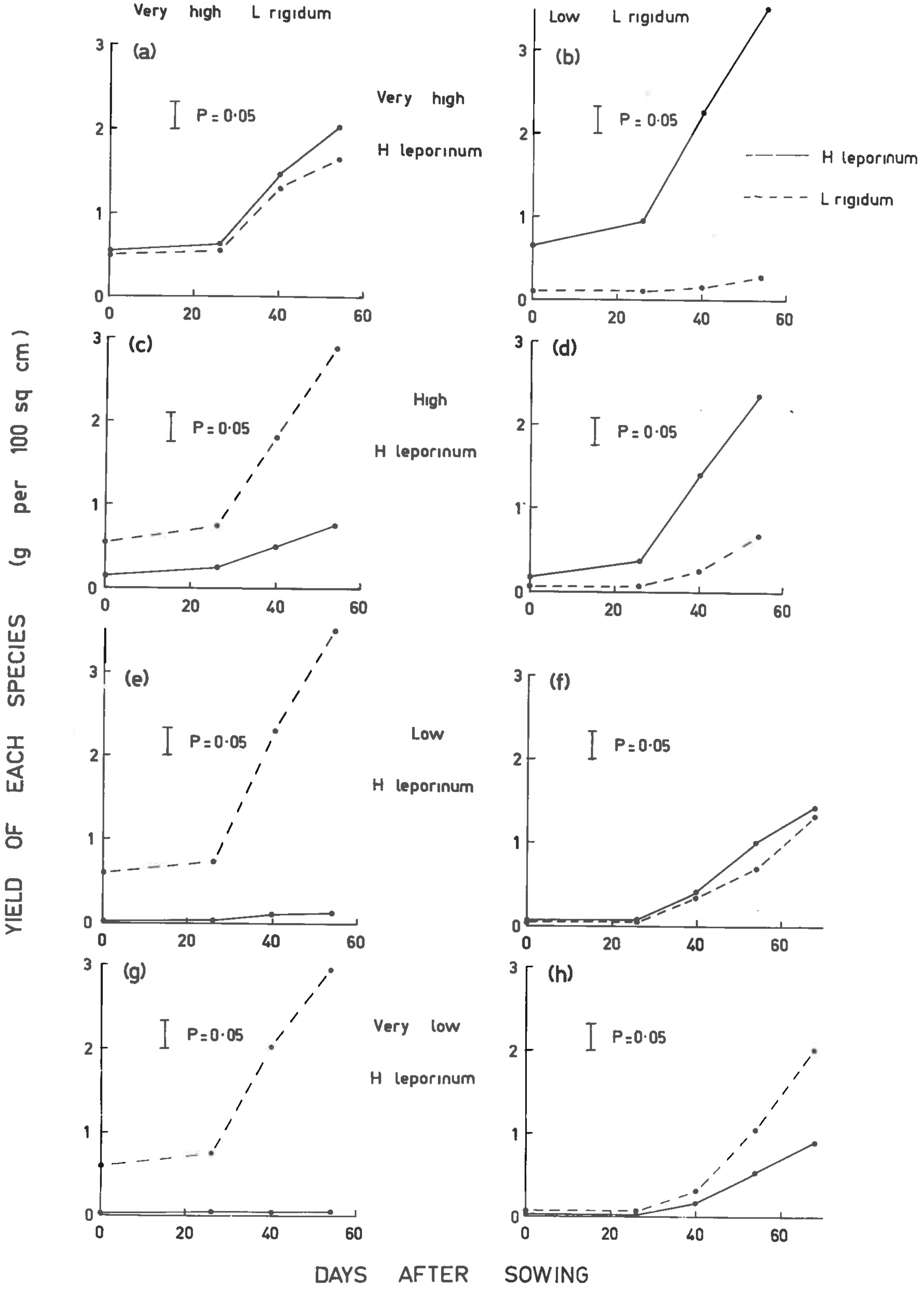

□ Day 26
△ Day 40
○ Day 54
L rigidum in mixture
■ Day 26
▲ Day 40
● Day 54
H leporinum in mixture
1/W
0·30
0·20
0·10
0
0
100
200
300
TOTAL DENSITY (plants per 100 sq cm)
r = 0·736^x
r = 0·834^xx
r = 0·905^xxx
r = 0·915^xxx
r = 0·976^xxx
r = 0·980^xxx

Figure 35 The yield of *H.leporinum* (solid line) and of *L.rigidum* (broken line) at each harvest and in each mixture. The left hand column represents those plots planted with very high density of *L.rigidum*, the right hand column those planted at low density. The four densities of *H.leporinum* are represented in the four rows, the top row being being the most dense. The bars represent least significant differences ($P=0.05$) between any two measurements of yield.


Very high L rigidum
Low L rigidum
Very high H leporinum
High H leporinum
Low H leporinum
Very low H leporinum
H leporinum
L rigidum
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
P = 0·05
YIELD OF EACH SPECIES (g per 100 sq cm)
DAYS AFTER SOWING
0
1
2
3
0
20
40
60

one component in the mixture, and the proportion of the component sown in the mixture became curvilinear, the more successful species having a convex curve to the y axis. The two cases are illustrated in Figure 36.

De Wit described the situation mathematically. In the first case (where there is no competition),

$$\frac{E_{(A)}}{E_{(B)}} = \frac{S_{(A)}}{S_{(B)}}$$

where $E_{(A)}$ is the environment available to species A (the yield of species A) , $E_{(B)}$ the environment available to species B (the yield of species B), $S_{(A)}$ the number of seeds sown of species A, and $S_{(B)}$ the number of seeds sown of species B.

In the second case (where species A gains in the competition with species B),

$$\frac{E_{(A)}}{E_{(B)}} = \frac{k_1}{k_2} \cdot \frac{S_{(A)}}{S_{(B)}}$$

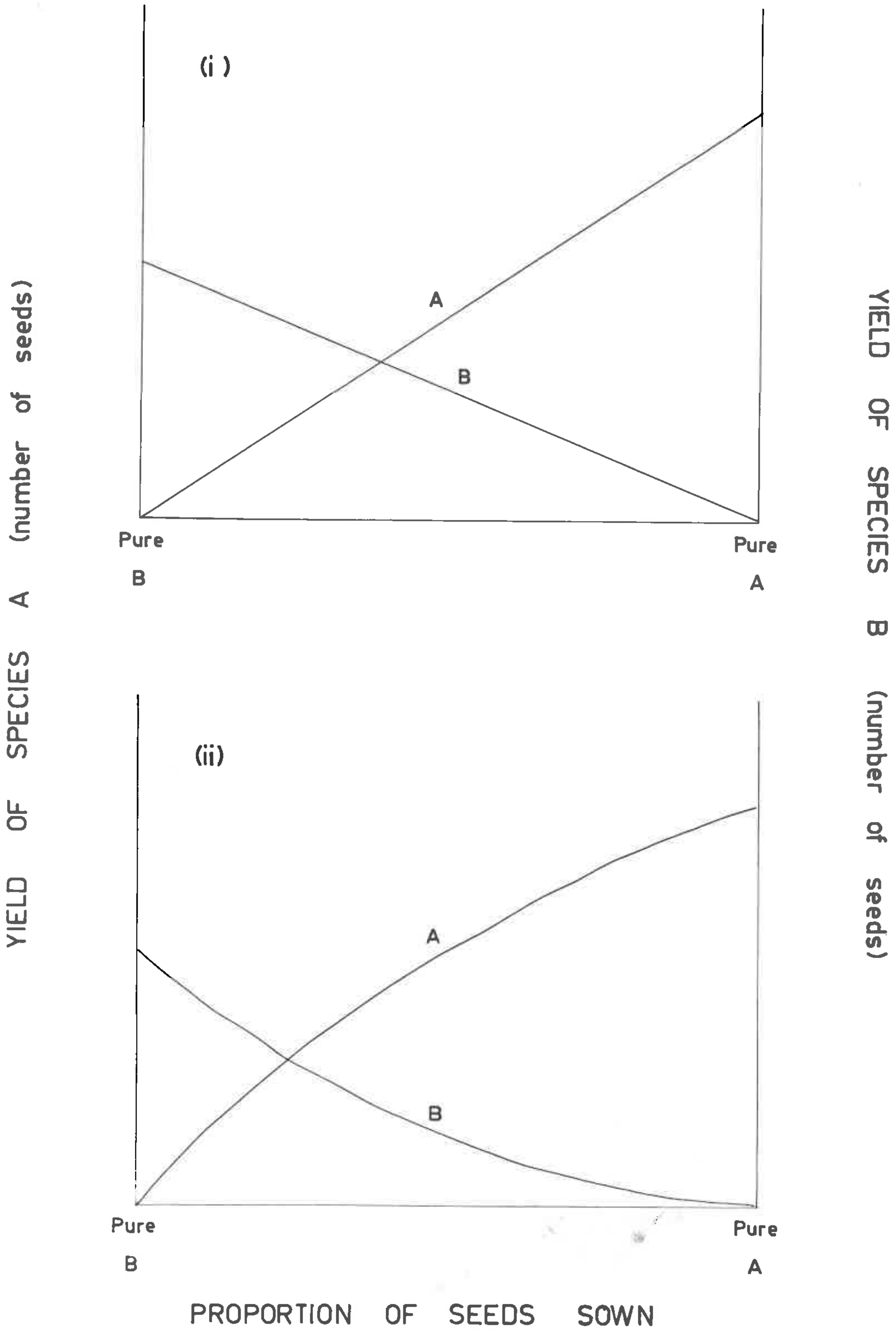
where $\underline{k_1}$ and $\underline{k_2}$ are coefficients showing the extent to which species A gains and species B loses its share of the environment. De Wit termed the ratio k_1/k_2 the *relative crowding coefficient* of the first species in relation to the second.

Thus de Wit's relative crowding coefficient is an assessment of the competitive ability of species A compared with species B in a mixture of the two species. De Wit used his expression in connection with seed numbers, that is, $S_{(A)}$ and $S_{(B)}$ were numbers of seeds of species A and B sown in a mixture, and $E_{(A)}$ and $E_{(B)}$ were numbers of seedsproduced by species A and B in such a mixture. However,

<u>Figure 36</u> The relationship of seeds planted to seeds harvested in mixtures of species when

i) there is no competition (a theoretical association)

ii) when species A is a more successful competitor than species B.


(i)
A
B
Pure B
Pure A
(ii)
A
B
Pure B
Pure A
YIELD OF SPECIES A (number of seeds)
YIELD OF SPECIES B (number of seeds)
PROPORTION OF SEEDS SOWN

there is no reason why weights of seeds or of plants should not be substituted and percentage used instead of absolute values.

It seems reasonable to regard de Wit's relative crowding coefficient as an account of the resistance which species A experiences in replacing species B. If this is so then the resistance becomes less as the percentage of species A increases. For example, k_1/k_2 decreases from 9.0 when species A increases from 50 % to 90 % of the mixture (case 1),

$$\frac{k_1}{k_2} = \frac{S_{(B)}}{S_{(A)}} \cdot \frac{E_{(A)}}{E_{(B)}} = \frac{50}{50} \times \frac{90}{10} = 9.0$$

to 5.44. when species A increases from 90 % to 98 % of the mixture (case 2)

$$\frac{k_1}{k_2} = \frac{S_{(B)}}{S_{(A)}} \cdot \frac{E_{(A)}}{E_{(B)}} = \frac{10}{90} \times \frac{98}{2} = 5.44$$

Yet in terms of the complete replacement of species B by species A, replacement from 50 % to 90 % is comparable with replacement from 90 % to 98 %, in the sense that both increases represent four fifths of the total replacement of species B.

My view of de Wit's relative crowding coefficient is that it is properly applicable to a situation where competition by the aggressor species leads to the diminution in size of each plant of the suppressed species - that is, in a 50/50 density mixture where all plants of one species are, in the postulated situation, equally suppressed through competition from the aggressor species. Thus when the suppressed species constitutes only 10 % of the sward, each individual will be only 1/9th the size of individuals of the other species. If this were the case, continued aggression by the aggressor would in fact be easier because the suppressed plants would be disadvantageously placed for the procurement of light and other resources.

This pattern of competition is illustrated in the elimination of subeterranean clover by the taller L.rigidum. This elimination has exponential acceleration as the light to the clover canopy is cut off, as was shown by Stern and Donald (1962b). These authors found that when the mean amount of light reaching the surface of the clover canopy in the previous 14 days fell below 40 cals per sq cm per day, the weight of clover in the mixture rapidly declined.

The situation described in the previous paragraphs may not, and in some circumstances will not, occur. For example, in pure cultures plant size distribution tends to be skewed and the sward dominated by a few large plants (see literature review pages 49-52) Thus it seems reasonable to suppose that in mixtures where one species is suppressed, a few plants of the suppressed species would remain as large, or nearly as large, as the largest individuals of the aggressor species, other individuals, whether alive or dead, making no further contribution to the sward. That is, although one species is aggressive and the other suppressed, it would not be true that all individuals of the first species would be aggressive and of the second species suppressed. In this situation, there would presumably be no less 'resistance' to the aggressor species in its continued replacement of the suppressed species after partial replacement had already occured, than when replacement began.

The applicability of one or other pattern of competition is also influenced by the proportion of the two species in mixtures as well as the incidence or absence of prior competition. In the experiment described in this section, I am concerned with mixtures in which the *initial* proportion of the two species (that is, *before* competition began) varied greatly from very high/low to very low/very high. In these cases the relationship between individual plants (for example relative size of seeds or seedlings at an early stage) will be the same regardless of the proportions of the two species in the mixture. There can be no question of individuals of the species sown as a larger proportion of the mixture having any greater initial advantage over the individuals of a competitor, than they would when the species was a lesser proportion of the sward. De Wit's relative crowding coefficient will thus not be applicable in its estimate of competitive ability in these situations. Accordingly, I propose an alternative index of aggression, particularly for use with mixtures of varying initial proportions ; it is based on the concept that aggression of one species in such mixtures with another meets with a constant resistance.

In a time interval t, in a mixture of 2 species A and B, the percentage of species A may change from x to y, and of species B from $100 - x$ to $100 - y$. If this change in percentage is compared to the greatest possible change, say m, we have a measure of the amount of aggression (that is, an index of aggression) which I have termed P. Thus P for species A is :

$$P_{(A)} = \frac{y - x}{m}$$

If x is larger than y, that is if the proportion of A is decreasing, $P_{(A)}$ will be negative, indicating that aggression of that species will be negative.

P can be calculated for species B in the same way, thus,

$$P_{(B)} = \frac{(100 - y) - (100 - x)}{m}$$

$$= - \frac{y + x}{m}$$

$$= - \frac{(y - x)}{m}$$

$$= - P_{(A)}$$

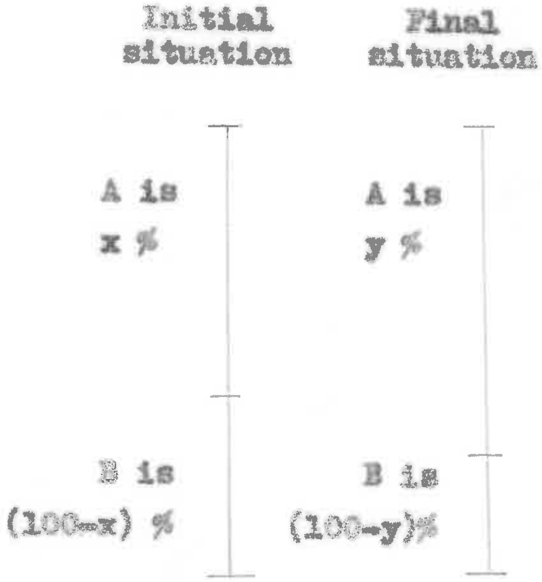
The actual calculation of P depends on the measurement of x and y (the percentage of species A at times t_1 and t_2) and on the assessment of m. Measurement of x and y though tedious is simple, and is merely the hand separation of the two species involved, and the calculation of their percentages in the sward by weight. The greatest possible change in botanical composition in terms of x and y depends on whether y is greater or smaller than x, that is on whether species A is increasing or decreasing. If species A is increasing, so that y is greater than x, then the greatest possible change from t_1 is $100 - x$ (equal to the initial amount of species B). This means that the percentage of species A can increase at most only by the total percentage of species B - it cannot do more than completely replace B. Similarly if species A is decreasing, the greatest amount it can decrease from t_1 is by the amount present at t_1, namely x. Thus for computation $m = 100 - x$ when A is increasing and $m = x$ when A is decreasing. The application of the index is illustrated in Table 21.

The index of aggression can now be compared with

TABLE 21

The application of the index of aggression

(i) Species A increasing

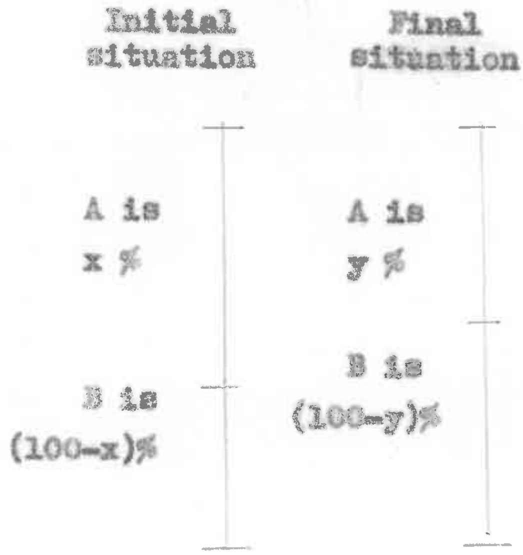


Gain by A = y − x

Potential gain by A = m
= 100−x

$$P_{(A)} = \frac{y-x}{100-x}$$

(ii) Species A decreasing



Loss by A = y − x

Potential loss by A = m
= x

$$P_{(A)} = \frac{y-x}{x}$$

de Wit's relative crowding coefficient by calculating P values for the same hypothetical examples that were used to illustrate what I considered to be limitations in de Wit's coefficient. Thus when species A increases from 50 % to 90 % (case 1)

$$P_{(A)} = \frac{y - x}{100 - x} = \frac{90 - 50}{100 - 50} = \frac{40}{50} = \underline{\underline{0.8}}$$

and from 90 % to 98 % (case 2)

$$P_{(A)} = \frac{y - x}{100 - x} = \frac{98 - 90}{100 - 90} = \frac{8}{10} = \underline{\underline{0.8}}$$

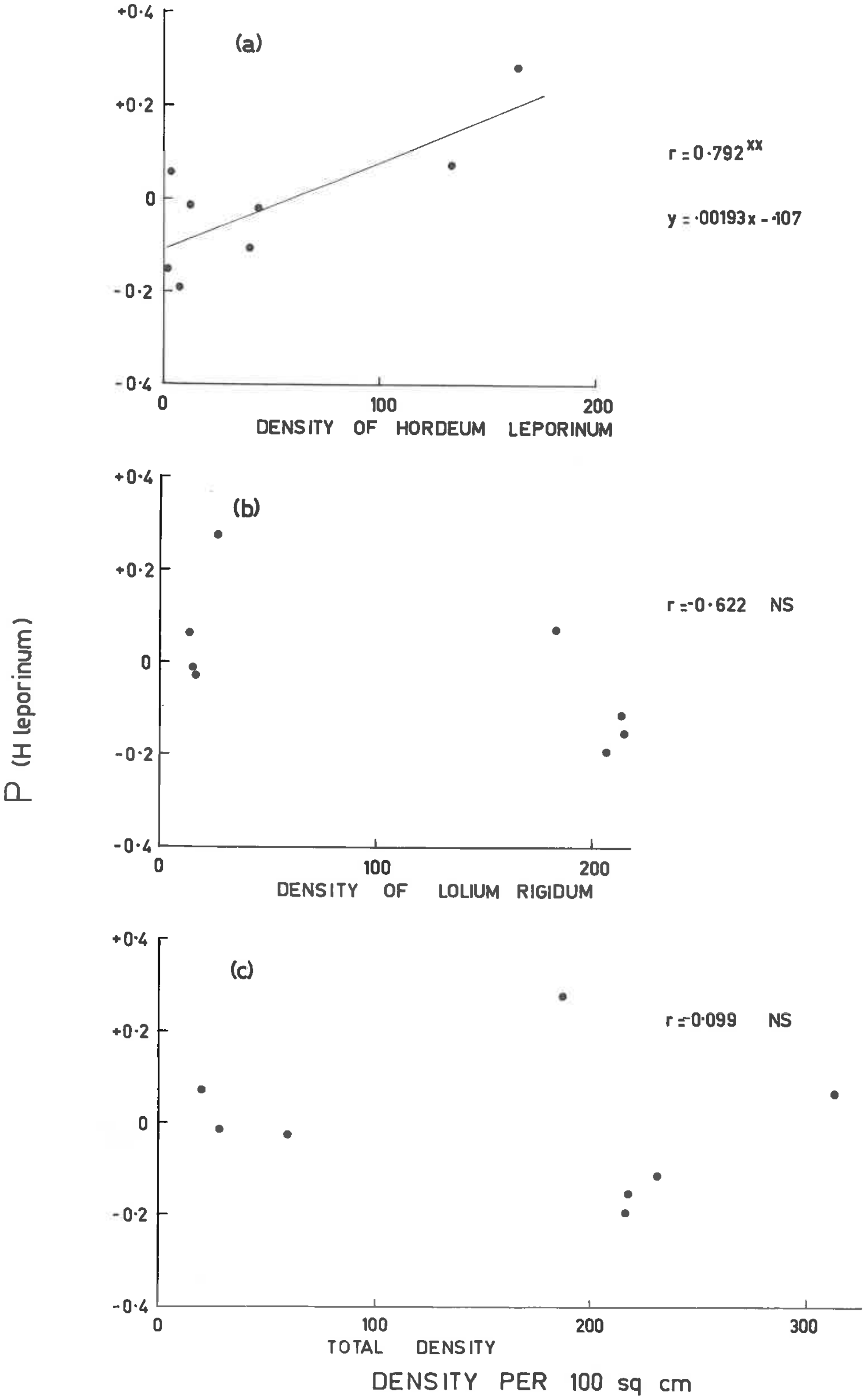
Thus the indices of aggression seem a useful assessment of competition in swards of initially different proportions of two species. When swards of initially similar proportions are assessed, de Wit's relative crowding coefficient is equally valid at least at this stage of our knowledge of the nature of plant competition. In fact, later in this thesis, when competition between H.leporinum and L.rigidum is studied in swards of the same initial proportions (50/50), I have used de Wit's coefficient to analyse the results.

5.3.4. The application of the index of aggression to the experimental results.

The index of aggression (P) described in section 5.3.3. can be calculated for any period of time. To describe the effect of density on competition I have considered that interval between sowing time (day 0) and harvest 3 (day 54), except that for low densities of both species (treatments low/low and very low/low shown in Figures 35f and h) the period between sowing time and harvest 4 (day 68) has been considered. This was done because of the low total yields in the two low density plots at day 54, and hence the lesser amount of competition which had taken place. In fact, even at day 68, total yields of the low density plots were less than total yields of the high density plots at the final, day 54, harvest. Figure 35 shows no sudden change in the accumulation of dry matter of the two species after day 54, compared to that before day 54. Also, individual mixtures tend to a stable composition with time (see literature review pages 55 and 56). For both these reasons there is not likely to be a change in the trend of competition between days 54 and 68.

When *P* for *H.leporinum* calculated in this way was plotted against the density of that species, a significant (P = 0.01) positive correlation was obtained (Figure 37). The relationship between *P* of *H.leporinum* and the density of *L.rigidum* just failed to reach significance, while the relationship between *P* of *H.leporinum* and the totaldensity was quite insignificant (Figure 37). The relationships between *P* of *L.rigidum* and the three density categories

Figure 37 The relationship between the index of aggression of *H.leporinum* and the density of *H.leporinum*, the density of *L.rigidum* and the total density. The index of aggression of *L.rigidum* is the same numerically as that of *H.leporinum* with the sign reversed.


(a)
+0·4
+0·2
0
-0·2
-0·4
0
100
200
DENSITY OF HORDEUM LEPORINUM
r = 0·792 xx
y = ·00193x - ·107
(b)
+0·4
+0·2
0
-0·2
-0·4
0
100
200
DENSITY OF LOLIUM RIGIDUM
r =-0·622 NS
(c)
+0·4
+0·2
0
-0·2
-0·4
0
100
200
300
TOTAL DENSITY
r =-0·099 NS
P (H leporinum)
DENSITY PER 100 sq cm

are not shown in Figure 37, but are the inverse of those in Figure 37. This is because *P* of *L.rigidum* is the same numerically as *P* of *H.leporinum* with the sign reversed. Thus the results are not in disagreement with the hypothesis that outcome of competition depends on the density of *H.leporinum*, although the degree of significance is far from satisfying. It is probably reasonable to say from Figure 37 that the density of both species has affected the outcome of competition as assessed by the total botanical composition at the end of the experiment, but that the density of *H.leporinum* has been the more potent factor.

For a more exacting estimate of *P*, the index can be calculated considering only that part of the sward contributing to further growth. For example if, at low densities, *H.leporinum* grew well early in the experiment, but *L.rigidum* grew taller and by the final harvest was beginning to suppress *H.leporinum*, total yields may still show that *H.leporinum* is dominant. Yield at the last harvest is thus a function of yield all through the experiment and, unless the last harvest occurs at the end of the growing season, is not an accurate measure of dominance.

The amount of each species in that part of the sward contributing most to further growth can be calculated because stratified harvests were made. What is required is an estimate of the leaf area which makes up this part of the sward. This can be done by examining the relationship between leaf area index (LAI) and growth rate. Figure 38 shows this relationship, and shows that growth rate increased fairly slowly above LAI of 4, and not at all above LAI of about 6. Thus it seems that maximum growth rate occurs at LAI of a little more than 4, and it would follow that

<u>Figure 38</u> The relationship between leaf area index and sward growth rate. Leaf area indices were calculated as the mean of two successive harvests. Thus

$$\frac{h_1 + h_2}{2}$$

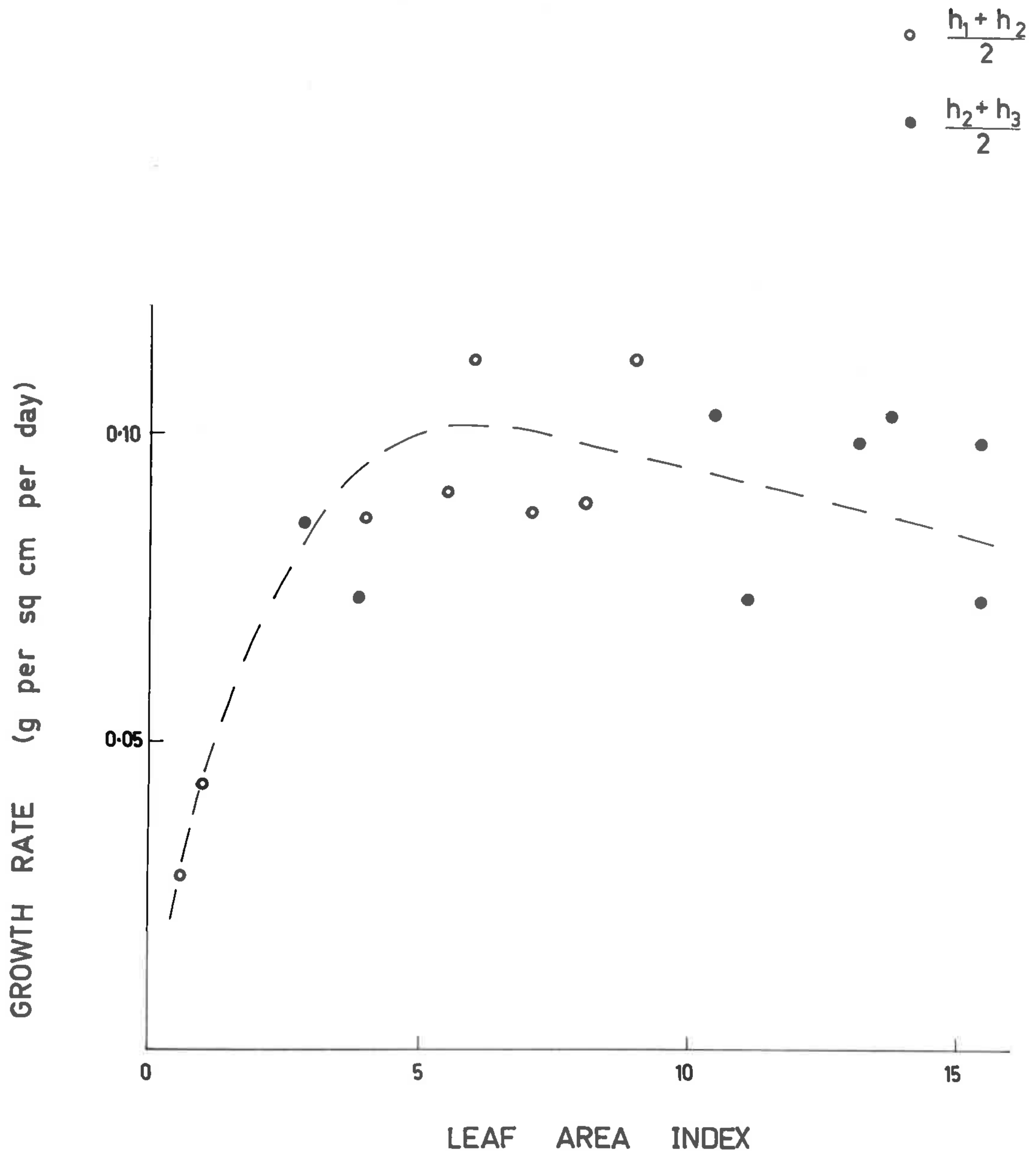
is the mean of the leaf area indices at days 26 and 40, and

$$\frac{h_2 + h_3}{2}$$

is the mean of the leaf area indices at days 40 and 54.

<u>Correction</u> :

The scale on the <u>y</u> axis should read
g per 100 sq cm per day.



$\frac{h_1 + h_2}{2}$
$\frac{h_2 + h_3}{2}$
GROWTH RATE (g per sq cm per day)
0·10
0·05
0
5
10
15
LEAF AREA INDEX

even in swards of higher LAI, the top 4 will contribute most to further growth. That the top part of the sward (though not necessarily the top 4 units of LAI) contribute most to further growth can be seen in the stratified harvests of mixtures in the work of Black (1958) and Stern and Donald (1962a). Hence the botanical composition of this part of the sward is of interest to us now. To convert LAI 4 to dry weight, Figure 39, which relates LAI to yield, must be consulted.

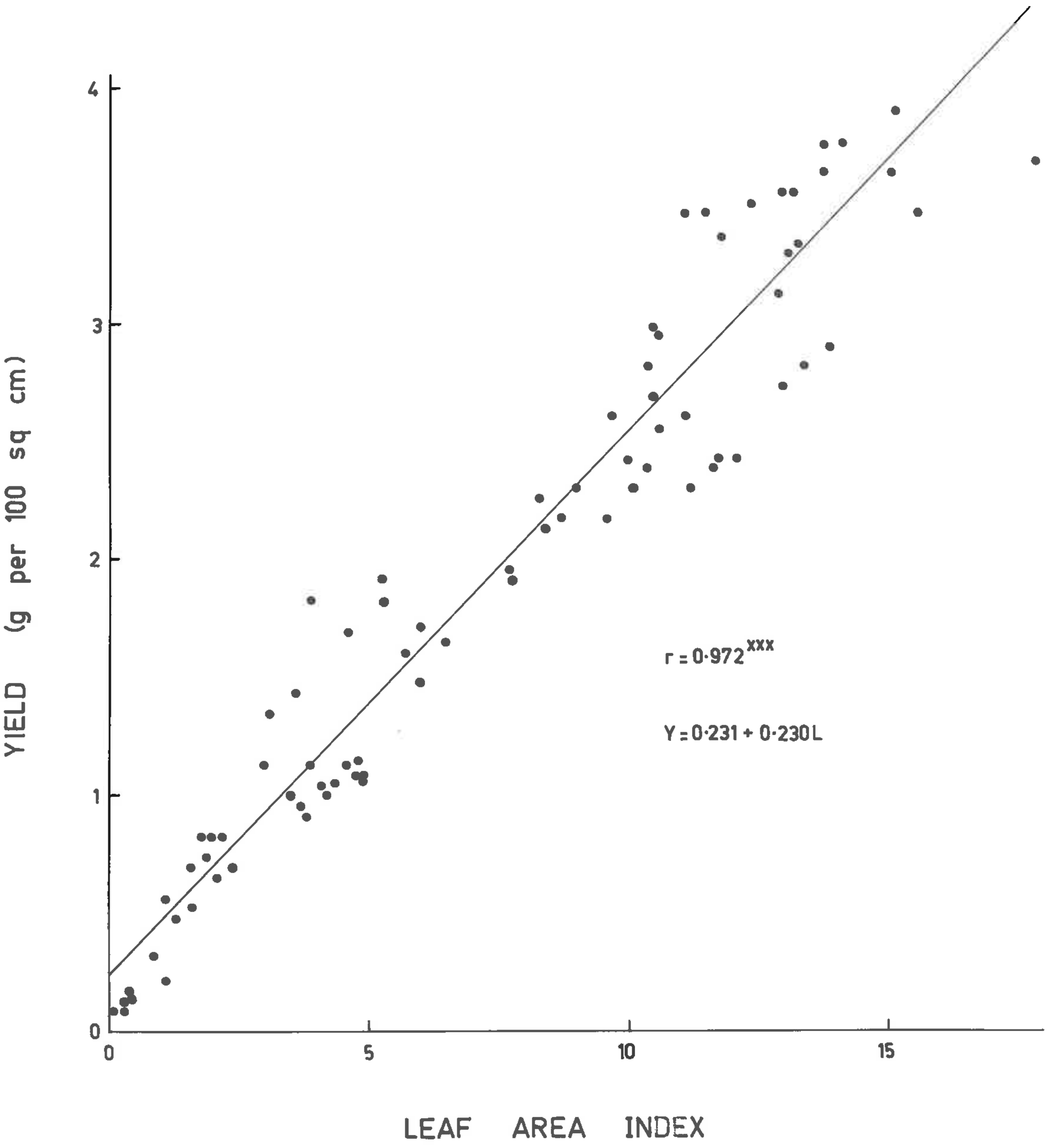
This relationship does not pass through zero, probably because of the presence of stem. The weight of leaves in the top part of the sward may thus be overestimated by a small amount. The results however, will not be affected as the relationship between growth rate and yield in Figure 38 does not show any discontinuity at LAI 4. The regression of yield on LAI in Figure 39 is

$$Y = 0.231 + 0.230\ L$$

where y is the yield and L the LAI, and hence an increase in LAI of 4 units is equivalent to 0.920 g dry matter.

The proportion of each species in the top 0.920g of the sward was calculated using data from the stratified harvest. A type example is shown in Table 22. P values from sowing to the final harvest, now using as 'final harvest' the percentage of each species in the top 0.920g of the sward, were calculated and plotted against density, as in Figure 37. The results are shown in Figure 40. The relationship between P of *H.leporinum* and the density of *H.leporinum* ($r = + 0.929$) is now significant at $P=0.001$, while the relationship between P and the density of *L.rigidum*, and between P and the total density are of no significance.

Figure 39 The relationship between leaf area index and yield.


4
3
2
1
0
0
5
10
15
YIELD (g per 100 sq cm)
LEAF AREA INDEX
r = 0·972xxx
Y = 0·231 + 0·230L

The critical density of *H.leporinum* above which *L.rigidum* is aggressive ($P = 0$) is 93 plants per 100 sq cm.

Thus it was found that although the density of both species affected the outcome of competition in terms of total dry matter at the final harvest, only the density of *H.leporinum* affected that part of the sward which contributes to further growth. These results therefore clearly indicate that the further growth of the swards would have been in accordance with the hypothesis that the success of *H.leporinum* or *L.rigidum* respectively, depended solely on the high or low density of *H.leporinum*, and not at all on the density of *L.rigidum*.

The hypothesis can be further tested by calculating slopes for the relationship between P of *H.leporinum* and the density of both *H.leporinum* and *L.rigidum* at successive harvests, using as x the proportion of *H.leporinum* sown, and as y the proportion of *H.leporinum* at each harvest

$$(\text{ remember } P = \frac{Y - X}{m})$$

As before, P of *L.rigidum* is the same numerically as P of *H.leporinum*, with the opposite sign. If the results are to be in agreement with the hypothesis, the slope of the relationship between P of *H.leporinum* and the density of *H.leporinum*, will become greater with time, and the slope of the relationship between P of *H.leporinum* and the density of *L.rigidum* will remain unchanged. Slopes (and correlation coefficients) are presented in Table 23, where it can be seen that there is an increase in the slope of the relationship between P and the density of *H.leporinum* as proposed, and little change in the slope

TABLE 22

Type example of the calculation of the proportion of each species in the top 0.920g of the sward.

Dry weight in the sward above 15 cm from ground level is:

1.050 g (1)

of which

0.644 g are *H.leporinum* (2)

0.406 g are *L.rigidum* (3)

Dry weight in the stratum of the sward between 15 cm and 20 cm above ground level is :

0.470 g (4)

of which

0.276 g are *H.leporinum* (5)

0.194 g are *L.rigidum* (6)

The amount to be subtracted from (1) is

$$1.050 - 0.920 = 0.130 \text{ g} \qquad (7)$$

of which $\frac{(5) \times (7)}{(4)}$

$= \frac{0.276 \times 0.130}{0.470} = 0.076$g are *H.leporinum* (8)

and $\frac{(6) \times (7)}{(4)}$

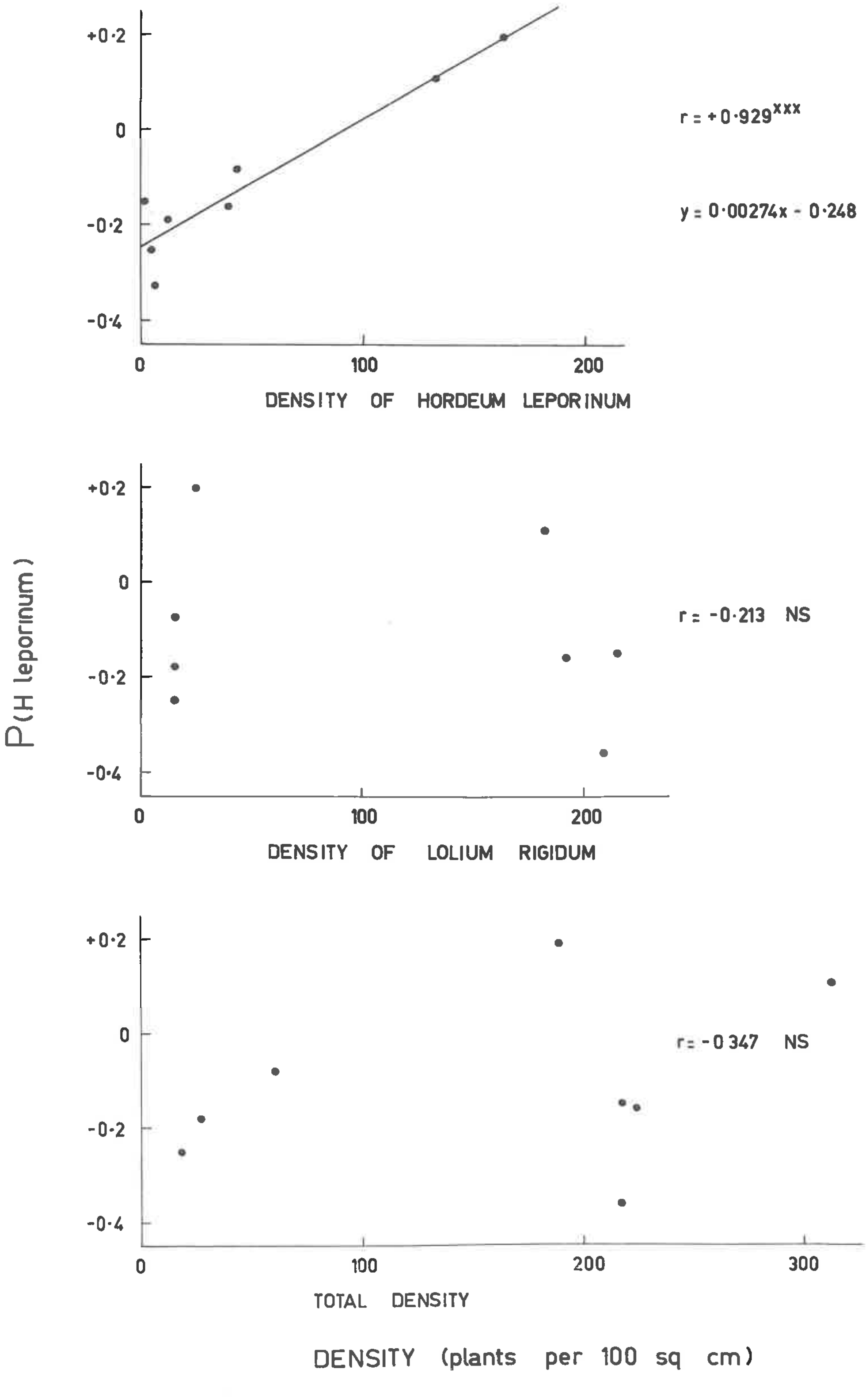
$= \frac{0.194 \times 0.130}{0.470} = 0.054$ g are *L.rigidum* (9)

Thus the top 0.920 g contains (2) - (8)

= 0.644 - 0.076 = 0.568g of *H.leporinum*

and (3)-(9) = 0.406 - 0.054 = 0.352g of *L.rigidum*

<u>Figure 40</u> The relationship between the index of aggression of *H.leporinum*, calculated using data from that part of the sward contributing most to further sward growth rate, and the density of *H.leporinum*, the density of *L.rigidum*, and the total density. The index of aggression of *L.rigidum* is the same numerically as that of *H.leporinum* with the sign reversed.


+0·2
0
-0·2
-0·4
0
100
200
DENSITY OF HORDEUM LEPORINUM
r = +0·929^xxx
y = 0·00274x - 0·248
P (H leporinum)
+0·2
0
-0·2
-0·4
0
100
200
DENSITY OF LOLIUM RIGIDUM
r = -0·213 NS
+0·2
0
-0·2
-0·4
0
100
200
300
TOTAL DENSITY
r = -0·347 NS
DENSITY (plants per 100 sq cm)

of the relationship between *P* and the density of *L.rigidum*. If consideration of the top 0.920 g of the sward is the potential for further growth, a fourth measurement of the slope can be obtained and used in lieu of a further harvest. The slope of this relationship (*P* of *H.leporinum* and density of *H.leporinum*) is significantly greater (P = 0.01) than the slope for the relationship at the first harvest. Thus as time passed, *H.leporinum* became more dominant at high densities of *H.leporinum*, and *L.rigidum* became more dominant at low densities of *H.leporinum*, while the density of *L.rigidum* did not affect the attainment of dominance. The results are thus in agreement with the hypothesis as originally proposed.

TABLE 23

The slope (b) of the relationship between the index of aggression (P) for *H.leporinum* and the density of *H.leporinum*, and of the relationship between P for *H.leporinum* and the density of *L.rigidum* in relationship to the initial proportion of the species in the mixtures.

(i) at each harvest

(ii) when considering only the upper layer (LAI=4)

	Index of aggression (P) of *H.leporinum*			
	and density of *H.leporinum*		and density of *L.rigidum*	
	b (slope)	r$^{(2)}$	b	r$^{(2)}$
Day 0-26	.00070	0.488 NS	-.00081	- 0.904***
Day 0-40	.00146	0.452 NS	-.00172	- 0.832**
Day 0-54$^{(1)}$	.00193	0.792**	-.00097	- 0.622NS
Top layer day 0-54$^{(1)}$	.00278	0.929***	-.00040	- 0.213 NS

(1) includes results from day 68 as discussed on pages 183.and 32.

(2) asterisks represent significance of correlation coefficient (r).

(3) Slopes significantly different for the relationship between P (*H.leporinum*) and density of *H.leporinum* on day 0-26 and the top layer (day 0-54). The test used was the t-test and t=3.104 (P=0.01). There were no other statistically significant differences between slopes within either species.

5.4.0. Concluding Remarks

This experiment has shown that the large seed and rapid germination of H.leporinum caused that species to be successful in competition when it was sown at high densities, but that it was suppressed when it was sown at low densities, because of the superior growth rate of L.rigidum in the pre-competition phase. The density of L.rigidum had no continuing effect on these relationships.

Density affected the outcome of competition only by its influence on the time at which competition commenced. At low density a longer pre-competition interval was available, and this gave the species which was slow to germinate and establish (L.rigidum) a chance to become as large or larger than its competitor (because of its greater growth rate), and hence the ability to dominate when competition began. The higher the density, the lesser the time available before competition began, the lesser the importance of seedling growth rate, and the greater the importance of seedling size at emergence, which in turn was dependent on seed size and the rate of germination. In these aspects, H.leporinum had clear advantage at high density.

The conclusion that can be drawn from this kind of reasoning is that in some communities the outcome of competition is decided by processes which occur before competition begins. This is not to say that the direct cause of success in competition occurs before competition begins; obviously, the direct cause is the taller plants of one species shading the other, or the root system of one species exploiting soil moisture and nutrients to the detriment of the other, or any other mechanism. But when two species begin to interfere with each other, their behaviour depends to a considerable degree on the properties of the other, properties which were developed in the pre-competition stage, and which, as shown in this experiment, may depend on the duration of the pre-competition stage. This concept was proposed in the literature review (page 50) where the reasons for skewed distribution amongst populations in mono-specific swards were discussed. It was proposed that skewness developed because relative growth rate of individual plants in a sward depended on the plant's size when inter-plant competition began.

Although there have been many reports in the literature of the effect of density on the growth and development of monocultures, experiments on the effect of density on the outcome of competition in mixtures have rarely been reported, nor has the outcome been explained in precise terms. In this experiment, the study of the growth of isolated plants has led to an understanding of their behaviour in populations. Results obtained in a growth cabinet have been applied to the field situation, and the application proven to be valid.

Most workers found that the effect of increasing density is to make more extreme an effect which was present at low densities. This is logical of course, if the same species has superior growth rate and seed size, or if the two competing species are different in only one of seedling size and seedling growth rate. The work of Mann and

Barnes (1945), Aspinall and Milthorpe (1959) and de Wit (1960) can be quoted (section 8 in de Wit's 1960 paper).

Black (1960) grew red clover (Trifolium pratense) and lucerne (Medicago sativa) in mixtures at various densities, and found that the species sown at high density was always less aggressive than that sown at low density, regardless of which species was sown at high and low density. This, he said, 'may well be only a restatement of the familiar proposition of Clements, Weaver and Hansen (1929) that competition is keenest when individuals are most similar'. By this, he presumably means that competition within the species sown at high density reduced the size of each individual to such an extent that the other species was placed at an advantage. The important point about this explanation is that it infers that the two species are competing for different parts of the micro-environment. Otherwise, the expected result would have been success of lucerne at all densities, because it normally grows taller than red clover, and because seed size at the beginning was identical.

Perhaps the only clear cut published example of an effect of density on the success of one or other varieties or species in a mixture is that of Harper (1960), who found that density affected the outcome of competition between flax and linseed varieties. Harper did not explain his results in physiological terms, but as suggested on page 55, the explanation may be in terms of the differential branching of the varieties. If this is so, the processes at work in his experiment were different from the processes at work in this experiment - in his experiment, the differential effects of branching became operative _after_ competition began, while in this experiment, growth _before_ competition was the determining factor.

6.0.0. COMPETITION FOR LIGHT AND FOR NUTRIENTS IN SWARDS OF HORDEUM LEPORINUM AND LOLIUM RIGIDUM

6.1.0. Introduction

In the previous study, density largely governed the outcome of competition in swards of H.leporinum and L.rigidum. That seedling size and seedling relative growth rate were the controlling influences was indicated; the question which follows is whether early leaf growth or early root growth was of the greater importance.

Donald and Stern (1962a and b) clearly demonstrated that competition for light alone could account for the suppression of subterranean clover by L.rigidum. However, when two grasses compete, Donald (1958) has shown that both above and below ground competition contribute to the suppression of one of them. Aspinall (1960) found in the conditions of his experiment, that below ground competition was the more important in the suppression of white persicaria (Polygonum lapathifolium)by barley.

An experiment was designed to distinguish between above and below ground competition in swards of H.leporinum and L.rigidum. When sown in mixtures, roots of the two species grew separately or together, but tops at all times grew together. Thus it was possible to measure the effect of competition for light alone, and to measure the sum of the effect of competition for nutrients and the interaction between competition for light and competition for nutrients.

6.2.0. Experiment 9 - Experimental Procedure

6.2.1. Treatments

There were three competition treatments and three nitrogen levels. The competition treatments were :

1. Competition for light.
2. Competition for light and nutrients
3. Pure cultures of each species.

Each competition treatment was at three nitrogen levels, 20, 60, and 180 mg per 100 sq cm of nitrogen (equivalent to 20, 60 and 180 kg per ha). Plant density was 24 plants per 100 sq cm throughout.

The design was a factorial with three replicates.

6.2.2. Attaining the competition treatments

The plants were grown in rows, each row in a narrow box 2.5 cm wide, 40 cm long and 43 cm deep. The boxes were clamped together to make a sward in the manner of Stern and Donald (1962b). In the pure cultures, each box of the sward contained 24 plants of the same species.

With competition for light only, a box containing 24 plants of *H.leporinum* was placed next to one containing 24 plants of *L.rigidum*, and a series of such alternating pairs were clamped together.

Competition for light and nutrients was measured by placing alternate plants of the two species in each box (12 + 12) and clamping these boxes together. The various treatments are illustrated in Figure 41 and Plate 2.

The boxes were made by nailing sheets of galvanized iron to wood slats of the required dimensions. The slats thus made the bottom and two edges of each box, and the iron the sides. The insides of the boxes were coated with "Kilrust", a tar epoxy paint intended to prevent roots from contacting the galvanized iron.

After painting, the boxes were clamped into 3 groups of 30 and one of 48 as follows :

(1) Two groups of 30 were used for the pure culture treatments, namely

a) H.leporinum

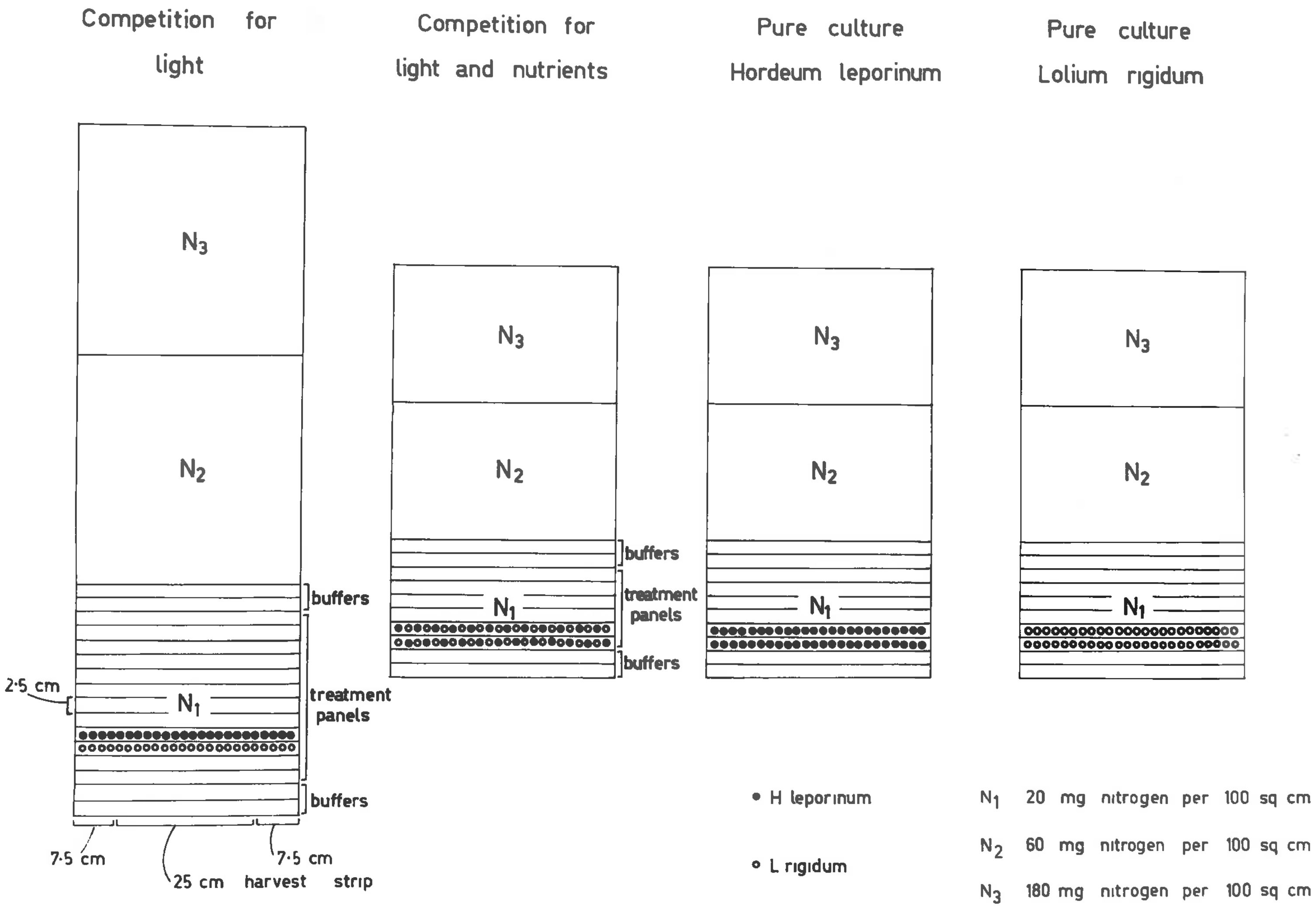
2 harvests x 3 N levels = 6 boxes + 4 border boxes
= 10 boxes x 3 replicates
= 30 boxes.

b) L.rigidum
also 30 boxes.

(2) A group of 30 boxes was used for the treatment where competition was for light and nutrients. In this case, the boxes containing H.leporinum or L.rigidum in (1) above were replaced by boxes containing alternate plants of both species.

(3) 48 boxes were necessary for the treatment measuring the effect of competition for light only namely -

Figure 41 Showing the layout of boxes, treatments and plants in the various competition treatments.


Competition for light
Competition for light and nutrients
Pure culture Hordeum leporinum
Pure culture Lolium rigidum
N3
N2
N1
buffers
treatment panels
buffers
2·5 cm
7·5 cm
25 cm harvest strip
7·5 cm
● H leporinum
○ L rigidum
N1 20 mg nitrogen per 100 sq cm
N2 60 mg nitrogen per 100 sq cm
N3 180 mg nitrogen per 100 sq cm

<u>PLATE 2</u> Showing the boxes used in Experiment 9. At the rear is the treatment where competition was for light only, then the treatment where competition was for light and nutrients, the pure culture of H.leporinum, and the pure culture of L.rigidum.

A sequence of 2 boxes, one with *H.leporinum* and
one with *L.rigidum*

x 2 harvests x 3 N levels = 12 boxes + 4 border boxes
= 16 boxes x 3 replicates
= 48 boxes

Randomization was restricted to allow replicates of each nitrogen level to be placed together (Figure 41). This saved considerably on buffer boxes, and was felt to be justified because there was no reason to expect a positional effect on treatments. At each harvest, 3 replicates of each treatment were chosen at random.

6.2.3. Method of planting

After clamping the boxes together, each was filled with a fine sand very deficient in all nutrients. The sand was chosen because of this deficiency, and also because there would be no problems of drainage. To prevent distortion of the boxes, and hence to prevent some boxes having more sand than others, the boxes were filled in the following way. Three thousand grams of the sieved sand (enough to half fill a box) were added to every alternate box. The sand was placed in the centre box of each group first, and then in alternate boxes to the edge. Boxes in between were then half filled and all boxes tamped, the tamping pattern being the same as the filling pattern. A second 3000 g of the sieved sand was then added and tamped, and all boxes filled to within 6 cm of the top. A further 750 g of sand, to which complete fertilizer less nitrogen had been added (Table 24a) made up the remainder, so that sand level was approximately 1 cm from the top. Final bulk density of sand in each box was $\frac{6750\ g}{4300cc} = 1.57$ g/cc.

Commercial seed of L.rigidum was used in the experiment, and seed of H.leporinum was obtained as cleanings from commercial barrel medic seed. Because of threshing, viability of H.leporinum seed was low (50 %) and a considerable excess was planted.

The boxes were sown to allow for 24 plants per 100 sq cm (per box). One hundred seeds of H.leporinum and 70 seeds of L.rigidum were sown to allow for poor germination, and for a harvest to be taken at thinning. Where the two species were sown in the same box, 50 and 35 were sown respectively. The experiment was sown on 29th June 1966.

Nitrogen (as ammonium nitrate) was added in solution form on 26th July (Table 24b), at rates of 20, 60 and 180 mg per box (100 sq cm). The plants were thinned on 1st August. A further 20 mg of nitrogen per box was added to the N2 treatment after the second harvest (26th September), because the treatment was not growing much better than the N1 treatment at that stage.

6.2.4. Harvest technique

Plant tops were first harvested when the plants were thinned on 1st August. At this stage, the plants were very small, and it was considered unlikely that competition between plants had commenced. Yields were calculated on a per plant basis and multiplied by 24 to

TABLE 24

a) Ingredients of sand-fertilizer mixture

60 g	superphosphate
15 g	potassium chloride
15 g	magnesium sulphate
0.50g	copper sulphate
0.50g	boric acid
0.50g	manganese sulphate
0.20g	ammonium molybdate
0.20g	cobalt sulphate
120 kg	sand

750g of this mixture was added to each box.

b) Amounts of ammonium nitrate added to each box on 6th July.

Treatment	Application (mg per 100 sq cm)	
	NH_4NO_3	Nitrogen
N1	57.2	20
N2	171.6	60
N3	514.8	180

A furher 57.2 mg NH_4NO_3 (20 mg N) was added to N2 boxes after the second harvest (26th September).

compare them with subsequent harvests. Height, leaf area, leaf weight and stem weight were measured.

For subsequent harvests, three boxes were removed from each treatment and the remaining boxes clamped together again. At each end of each box 7.5 cm of sward was left as a buffer, and the middle 25 cm (62.5 sq cm) harvested (Figure 41). The sward in each box was cut at 3.5 cm intervals from the top to the soil surface. Thus a stratified yield was obtained (Monsi and Saeki 1953, Black 1958), and dry matter, leaf area, leaf weight etc. of each 3,5 cm vertical interval measured. Total root growth in the pure culture, and in the components of the mixture where competition was for light only, was estimated by washing the sand from the boxes. Total root growth was measured in boxes where the two species grew together, but because their roots could not be distinguished from each other, species separation was not possible.

Total nitrogen percentage of the tops was measured by Kjeldahl digestion using K_2SO_4 - HgO as catalyst, followed by distillation with NaOH - $Na_2S_2O_3$. Leaf area was measured using a light scanner technique, where light beams were interrupted by passage of the leaf, and impulses recorded on an electronic counter. Dry weights of material were obtained after drying in a forced draught oven at 85°C for at least 24 hours.

Light interception was measured at the last two harvests using an omni-directional light meter with a single silicon cell. The measurement was made before boxes were removed for harvest. The meter was placed in the sward at two pre-determined distances from the edge of each box (13 and 26 cm), and the mean of these two measurements calculated. The vertical profile of light interception was measured at the same intervals as the stratified cuts were subsequently made.

Harvest dates were 1st August (day 33) at thinning, 26th September (day 89), and 24th October (day 117).

6.3.0. Results

6.3.1. Growth of pure cultures

When grown with high nitrogen *Lolium rigidum* out-yielded *Hordeum leporinum* (though not quite significantly) at all harvests but the first. At low nitrogen the yield of dry matter of both species was greatly depressed, though *Hordeum leporinum* grew better than *Lolium rigidum*, presumably because of its bigger seed (more nitrogen reserves). Table 25 shows yield of dry matter at each harvest and each nitrogen level for both species.

Leaf area index (LAI) was highest at day 89 (Table 26). At this stage LAI of *L.rigidum* was greater (not significantly) than that of H.leporinum at high nitrogen but less at lower nitrogen levels (not significantly). However if head area is added to leaf area (Table 27) the resulting total area index of *H.leporinum* continued to rise at least until harvest 3 (except at N2), although that of *L.rigidum* did not (except at N2). Head area was calculated on the basis that head shape was cylindrical but the areas of the ends of the theoretical cylinders were ignored because heads tapered to a point. Thus head area was calculated as

$$A = \pi d l$$

where *d* was diameter and *l* was length.

The decline in leaf area at day 127 was associated with an increased (not significant) amount of dead leaves (Table 28a) and with an increased (significant)

TABLE 25

Yield of dry matter of pure cultures at each harvest (g per 100 sq cm. mean of 3 replicates).

		Harvest 1 (33 days)	Harvest 2 (89 days)	Harvest 3 (117 days)
N1	H.leporinum	0.165	0.593	1.151
	L.rigidum	0.121	0.326	0.737
N2	H.leporinum	0.160	1.535	2.759
	L.rigidum	0.179	1.362	2.836
N3	H.leporinum	0.191	2.870	6.341
	L.rigidum	0.165	3.595	8.181
SE of difference		0.009	0.387	1.267
L.S.D.	P = 0.05	0.019	0.790	2.587
	0.01	0.025	1.066	3.485

TABLE 26

Leaf area index of pure cultures at each harvest

		Day 33	Day 89	Day 117
N1	*Hordeum leporinum*	0.070	.92	.52
	Lolium rigidum	.005	.30	.38
N2	*Hordeum leporinum*	.085	3.07	1.37
	Lolium rigidum	.022	1.97	1.34
N3	*Hordeum leporinum*	.103	5.90	3.06
	Lolium rigidum	.035	6.16	3.13
SE of difference		.007	.77	.45
*LSD	P = .05	.015	1.56	.91
	.01	.020	2.11	1.25
	.001	.026	2.79	1.63

*LSD for comparing nitrogen treatments and species at any one harvest.

TABLE 27

Leaf area index plus head area index of pure cultures at day 117.

	N 1	N 2	N 3
Hordeum leporinum	1.10	2.81	6.27
Lolium rigidum	.40	1.42	4.02

S.E. of difference = .63

L.S.D.	P = .05	1.28
	.01	1.73
	.001	2.29

proportion of stems (Table 28b). The increase in dead leaves was greatest in *H.leporinum*, probably because this species tends to mature earlier. The increase in proportion of stem was greatest in *L.rigidum* and at the last harvest was above 60 % of total dry weight of this species at the two highest nitrogen levels.

The highest amount of nitrogen in the tops was recorded at day 89 (except at N1). Nitrogen uptake by *H.leporinum* was higher than that by *L.rigidum* except at the highest nitrogen dressing, at day 89. Nitrogen uptake by tops is shown in Table 29, and the percentage of nitrogen in the tops in Table 30. *H.leporinum* at all times had shoots richer in nitrogen (except days 89 and 117, treatment N1).

Both species responded to applications of nitrogen, and there appears to be little difference in the way they respond. Figure 42 shows the response of top dry weight to nitrogen at each of the three harvests, dry weight being calculated as the percentage of dry weight at N180 for any harvest. The response of both species at the last two harvests was linear on the nitrogen application. I refer the reader to Table 25 for actual dry weight values and measures of statistical significance.

The response of leaf area to nitrogen application was similar to that of dry weight. Figure 43 shows this response, leaf areas being calculated as the percentage of theleaf area at N180 for any harvest. Note that in Figure 43 both species have responded at harvest 1 (for statistical significance see Table 26). This is

TABLE 28

a) Amount of dead leaves (as a percentage of total dry weight) in pure cultures of H.leporinum and L.rigidum at days 89 and 117.

Species	Day 89			Day 117			Mean species
	N20	N60	N180	N20	N80	N180	
H.leporinum	17.5	6.1	9.9	19.2	18.4	14.5	14.3
L.rigidum	15.5	5.6	7.1	14.0	9.7	10.2	10.4
Mean days	10.3			14.3			

LSD (P = 0.05) between species and between days = 4.9

LSD (P= 0.05) between any figures in the table =12.0

b) Amount of stem (as a percentage of total dry weight) in pure cultures of H.leporinum and L.rigidum at days 89 and 117.

Species	Day 89			Day 117			Mean Species
	N20	N60	N180	N20	N80	N180	
H.leporinum	35.8	40.4	40.8	44.9	45.2	44.8	42.0
L.rigidum	37.5	34.3	35.3	47.4	60.7	62.5	46.3
Mean days	37.4			50.9			

LSD (P = 0.05) between species and between days = 6.6

LSD (P = 0.05) between any figures in the table =16.3

TABLE 29

Total nitrogen (mg per 100 sq cm) in the tops of pure cultures of H.leporinum and L.rigidum for each harvest and each nitrogen level.

Species & treatment	Harvest 1(day33)		Harvest 2(day89)		Harvest 3(day 117)	
	mg	$\log_e$mg	mg	$\log_e$mg	mg	$\log_e$mg
N1 H.leporinum	5.44	1.694	11.87	2.477	12.94	2.558
L.rigidum	2.62	0.963	7.71	2.043	7.52	2.018
N2 H.leporinum	6.61	1.889	39.22	3.669	31.95	3.466
L.rigidum	6.06	1.802	28.19	3.339	23.65	3.165
N3 H.leporinum	9.55	2.257	78.21	4.359	66.72	4.200
L.rigidum	6.88	1.929	81.46	4.401	61.15	4.114
L.S.D.P= 0.05		0.281		0.538		0.464
= 0.01		0.378		0.724		0.624

TABLE 30

Percentage of nitrogen in the tops of pure cultures of both species at all harvests.

		Day 33	Day 89	Day 117
N1	Hordeum leporinum	3.3	2.0	1.1
	Lolium rigidum	2.2	2.2	1.1
N2	Hordeum leporinum	4.3	2.6	1.2
	Lolium rigidum	3.2	2.1	0.8
N3	Hordeum leporinum	4.9	2.7	1.1
	Lolium rigidum	4.2	2.4	0.8
SE of difference		.25	.26	.10
L.S.D. P =	.05	0.5	0.5	0.2
	.01	0.7	0.7	0.3
	.001	0.9	0.9	0.4

in contrast to the dry weight data in Figure 42. This result suggests that leaf area is a more sensitive measure of a species response to nutrient application, at least when the plants are young and before competition has commenced.

The response of the amount of nitrogen in the tops to nitrogen application was similar to that of dry weight and leaf area (Figure 44).

The response of root weight to nitrogen application is shown in Figure 45. The response and yield of both species were similar at day 89, but by day 117, the amount of root at N180 of *L.rigidum* was much greater than that of *H.leporinum*. This was due to the apparent cessation of root growth of *H.leporinum* between days 89 and 117, the dry weights of roots of this species being the same (or nearly so) at each of these harvests. Unlike top weight, root weight of neither species responded to nitrogen application above 60 mg at day 89. Apparently, maximum root growth was achieved at nitrogen levels which were insufficient for maximum top growth at this date. Similarly, at day 117, the results indicate a declining response to nitrogen while yield of tops was increasing linearly with increased nitrogen application.

Figure 42   Response of yield of pure cultures of *H.leporinum* and *L.rigidum* to nitrogen application. Yield is expressed as the percentage of yield at N180.

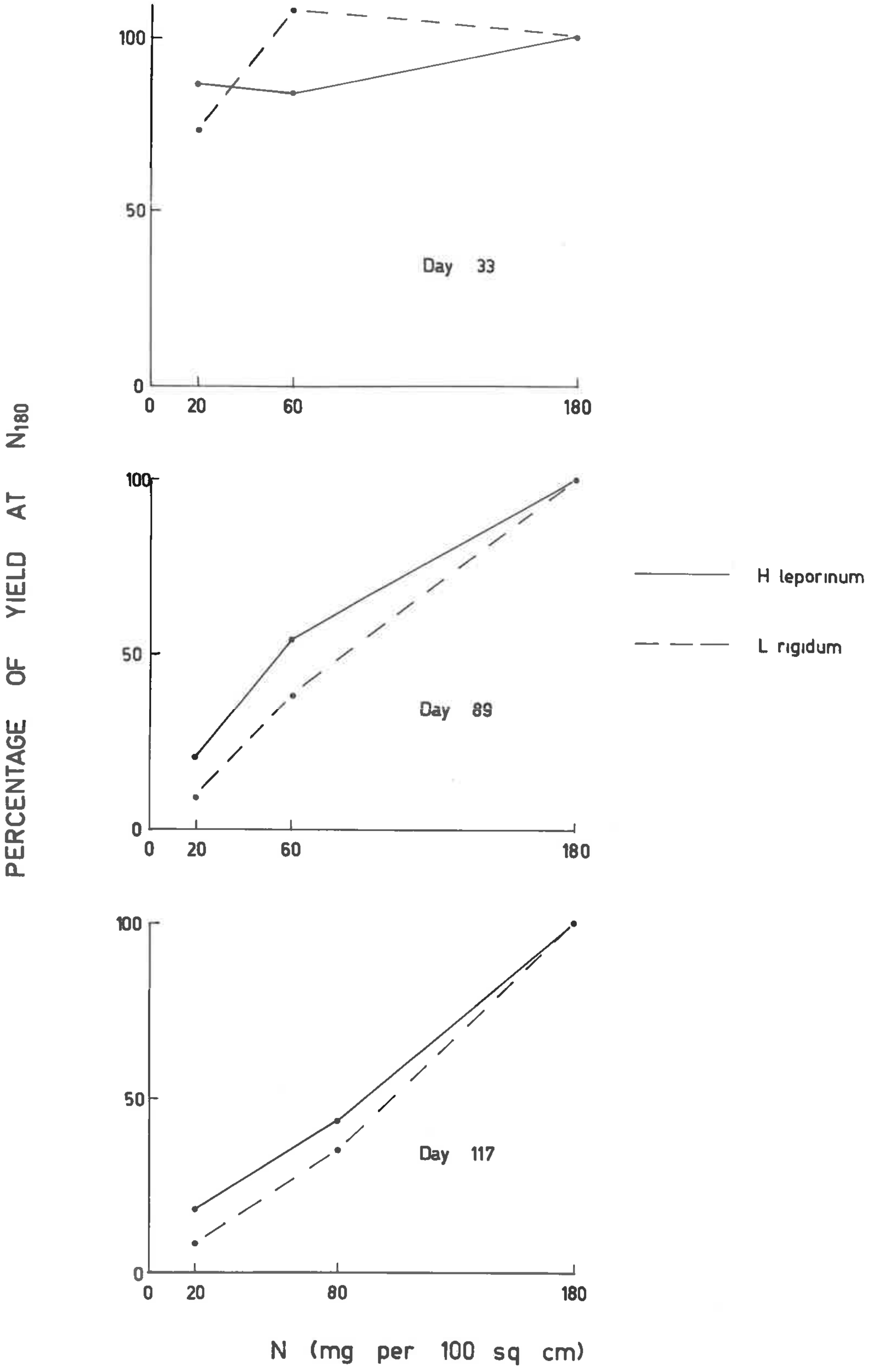

PERCENTAGE OF YIELD AT N180
Day 33
100
50
0
0
20
60
180
Day 89
100
50
0
0
20
60
180
Day 117
100
50
0
0
20
80
180
N (mg per 100 sq cm)
H leporinum
L rigidum

Figure 43 Response of the leaf area of pure cultures of *H.leporinum* and *L.rigidum* to nitrogen application. Leaf area is expressed as the percentage of leaf area at N180.

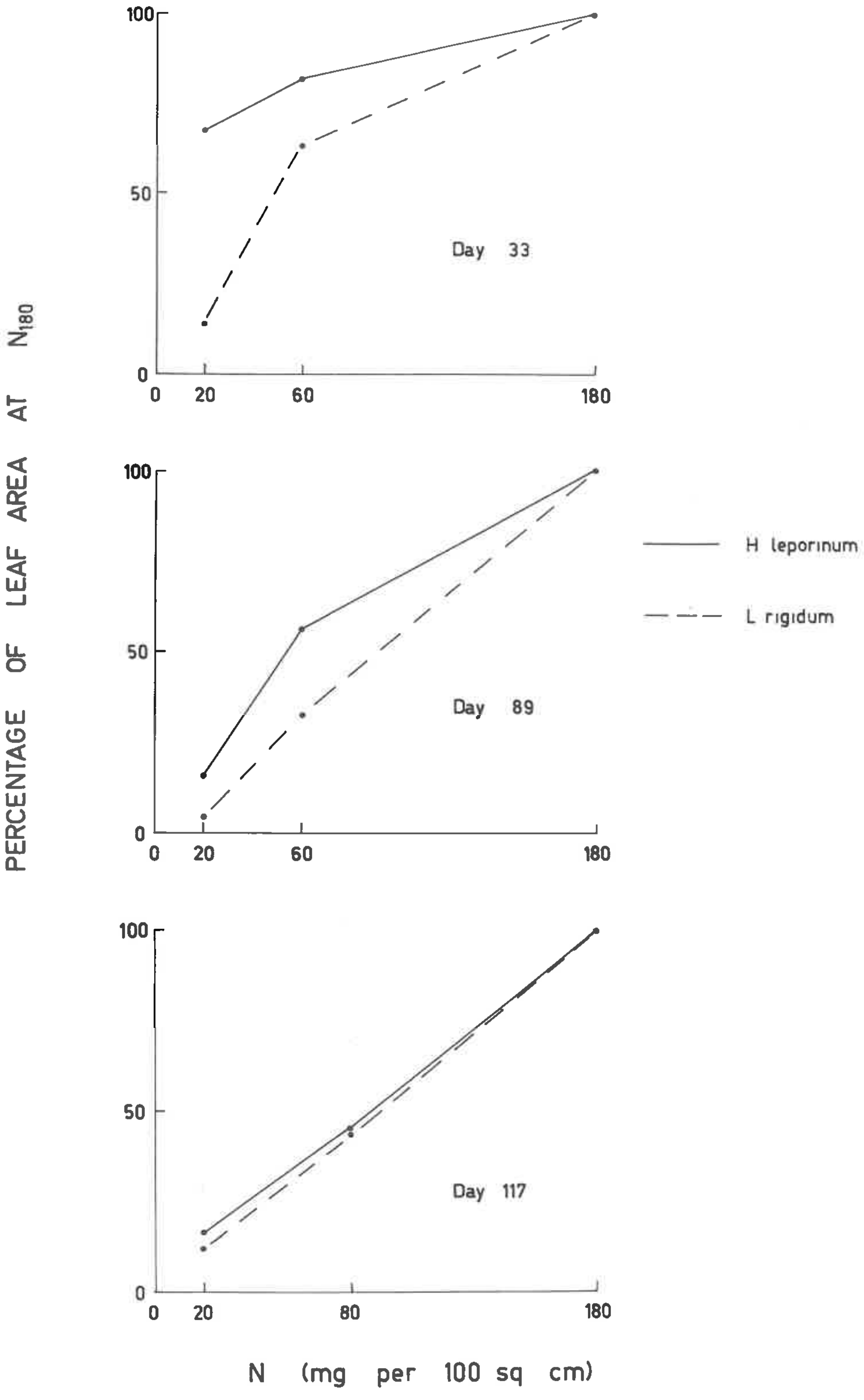

PERCENTAGE OF LEAF AREA AT N180
Day 33
Day 89
Day 117
100
50
0
0
20
60
80
180
H leporinum
L rigidum
N (mg per 100 sq cm)

Figure 44 Response of the amount of nitrogen in the tops of pure cultures of H.leporinum and L.rigidum to nitrogen application. The amount of nitrogen in the tops is expressed as the percentage of nitrogen in the tops at N180.

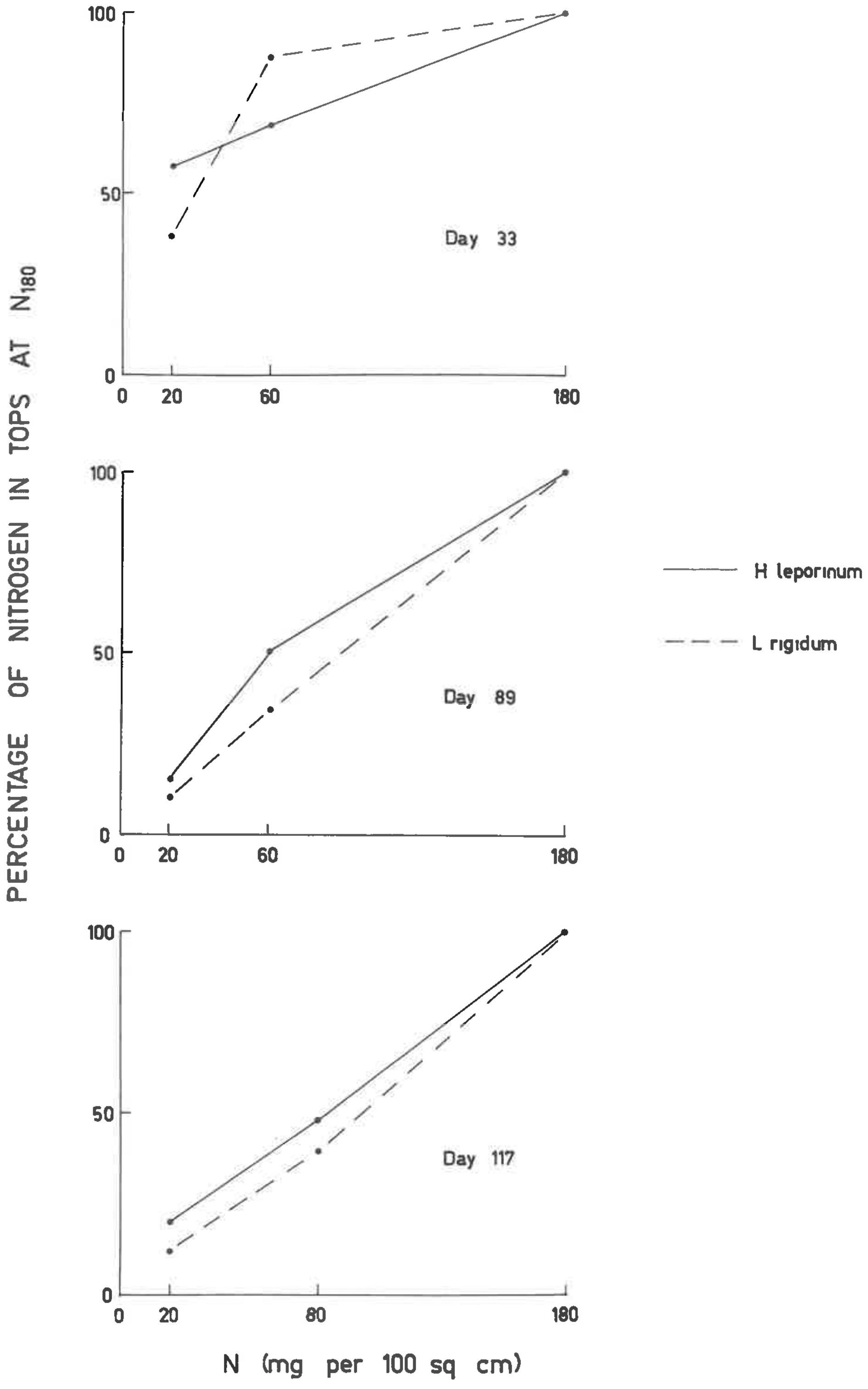
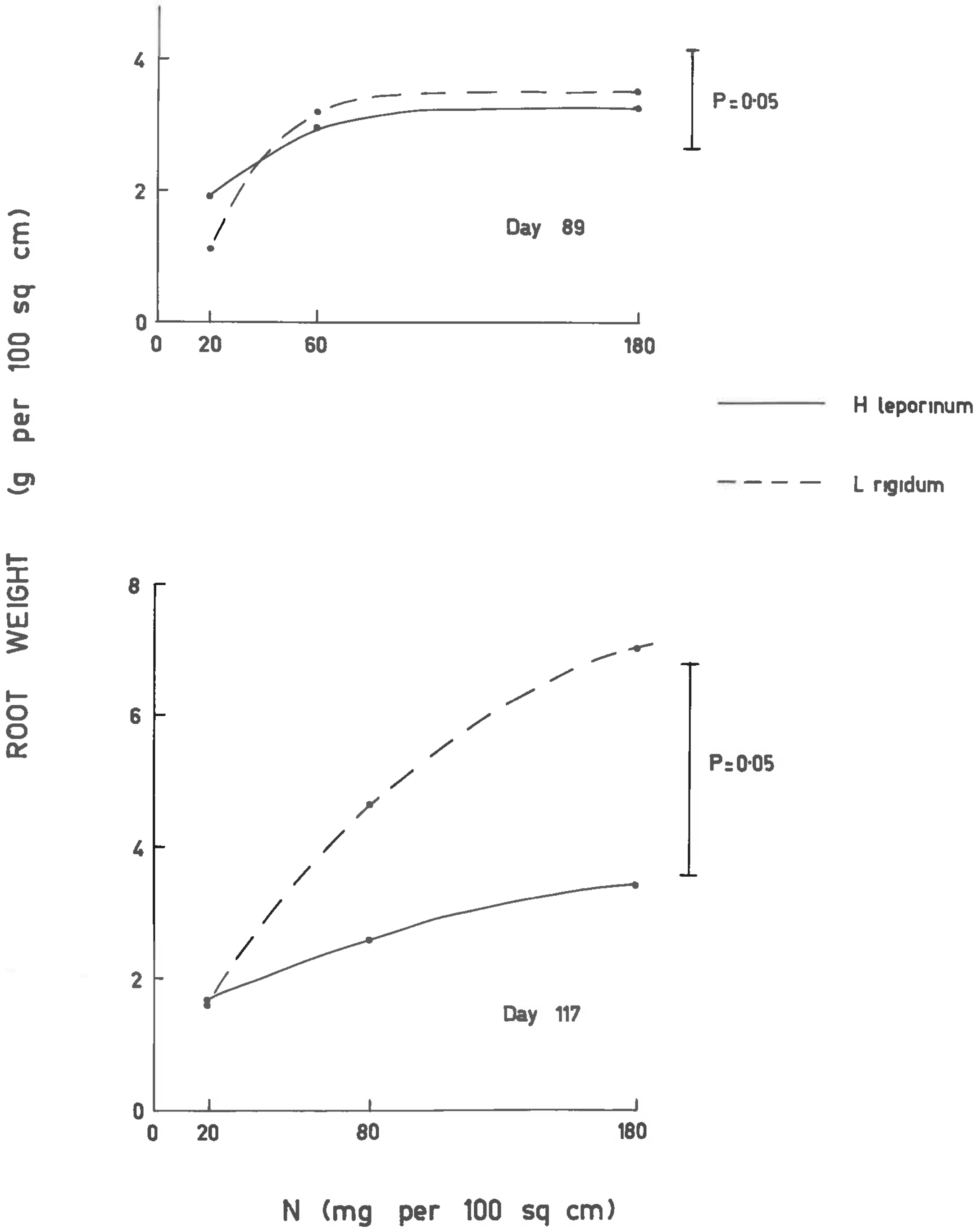

PERCENTAGE OF NITROGEN IN TOPS AT N_{180}
100
50
0
0
20
60
180
Day 33
100
50
0
0
20
60
180
Day 89
100
50
0
0
20
80
180
Day 117
N (mg per 100 sq cm)
H leporinum
L rigidum

Figure 45 The response of root growth of pure cultures of *H.leporinum* and *L.rigidum* to nitrogen application. The bars represent least significant differences between any two measurements of root dry weight at any one harvest. The curves were hand fitted.


ROOT WEIGHT (g per 100 sq cm)
4
2
0
0
20
60
180
P=0·05
Day 89
H leporinum
L rigidum
8
6
4
2
0
0
20
80
180
P=0·05
Day 117
N (mg per 100 sq cm)

6.3.2. Growth of mixtures

The effect of growing the species in mixtures has been described in the way devised by de Wit (1960). This technique has been described in section 5.3.3. The reader will remember that de Wit's relative crowding coefficient was not used to desc~~r~~ibe the results of that experiment, and that an index of aggression was devised. He will also remember that the objection to the relative crowding coefficient was that it was not considered to be applicable in comparisons of swards sown to different initial proportions of each species. In this experiment, however, 50/50 mixtures were sown in all treatments. It is thus reasonable to use de Wit's treatment of the data.

Replacement diagrams have been plotted for several characters, namely dry weight, leaf area index, nitrogen uptake, and tiller number in Figures 46, 47, 48 and 49 respectively, for mixtures where competition was for light alone, and where competition was for light and nutrients. Examination of the figures show that, when competition was for light alone, expression of the various characters, whether those of H.leporinum or L.rigidum, depended on the proportion of the species sown in the mixture (one possible exception was treatment N180 at the first harvest). That is, the effect of competition on a plant in a mixture was the same as the effect of competition on a plant in pure culture. For example, if dry matter yield (Figure 46) is considered, L.rigidum outyielded H.leporinum at day 117 in the mixture under the same conditions as it did in pure culture, namely at high nitrogen. Similar conclusions can be drawn if leaf area (Figure 47), nitrogen uptake (Figure 48) and tiller number (Figure 49) are considered.

However, when competition for the two species was for light and nutrients, there was a marked deviation from linearity in the relationship between yield or other character, and the proportion of seed sown in the sward. This deviation can be tested statistically by comparing, in the case of yield of dry matter, the yield of half the pure culture of a species with its yield in the mixture. These two figures should be identical if the relati onship between seed sown and yield in the mixture, is linear. If they differ significantly, then there is a significant deviation from linearity in the relationship. The degree of significance, where it exists, is indicated in Figures 46, 47, 48 and 49. The deviation of the recorded yield from the expected yield (half the yield of a pure culture) is indicated by a brecket, and the degree of significance by crosses. It will be noted that, with a few exceptions, the only significant deviations from linearity occur in the treatment where high nitrogen was applied to plants competing for light and nutrients.

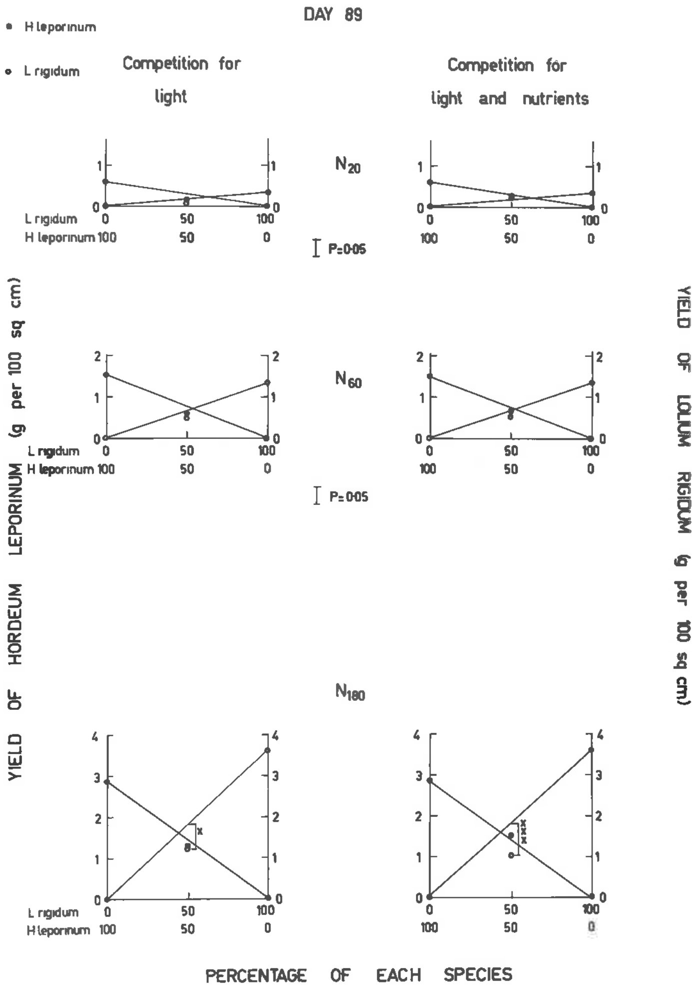
Where competition was for light and nutrients and where nitrogen application was high, the position of *H.leporinum* improved, and the position of *L.rigidum* deteriorated in the mixtures. If the total yield of mixtures was equal to that of pure cultures, it would follow that the amount by which *H.leporinum* improved and the amount *L.rigidum* deteriorated would be equal. Generally, this was so at day 89, but by day 117 the improvement of *H.leporinum* was generally greater than the deterioration of *L.rigidum*. The explanation of this is probably that the

Figure 46 Effect of kind of competition on yield of dry matter of H.leporinum and L.rigidum in mixtures at three nitrogen levels. Significance of deviation from linearity, where it exists, appear as crosses thus :

x represents P = 0.05

xxx represents P = 0.001

Bars represent least significant difference (P = 0.05) between any two points in the figure.


DAY 89
● H leporinum
○ L rigidum
Competition for light
Competition for light and nutrients
N20
N60
N180
P=0·05
P=0·05
x
xxx
L rigidum 0 50 100
H leporinum 100 50 0
YIELD OF HORDEUM LEPORINUM (g per 100 sq cm)
YIELD OF LOLIUM RIGIDUM (g per 100 sq cm)
PERCENTAGE OF EACH SPECIES

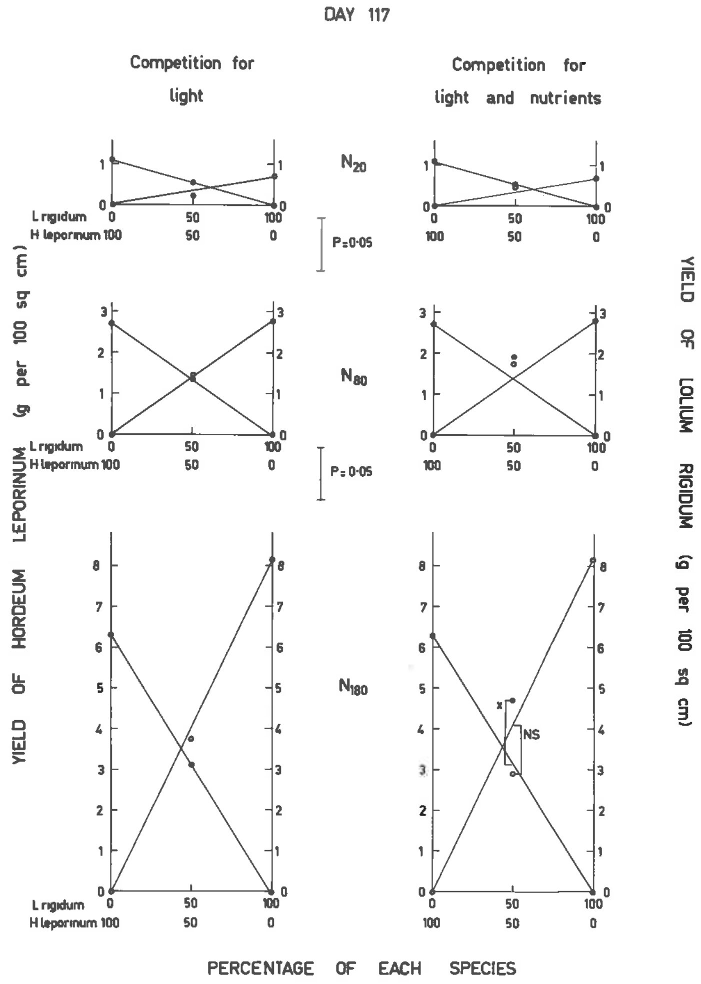

DAY 117
Competition for light
Competition for light and nutrients
N20
N80
N180
P=0·05
P=0·05
x
NS
L rigidum 0 50 100
H leporinum 100 50 0
YIELD OF HORDEUM LEPORINUM (g per 100 sq cm)
YIELD OF LOLIUM RIGIDUM (g per 100 sq cm)
PERCENTAGE OF EACH SPECIES

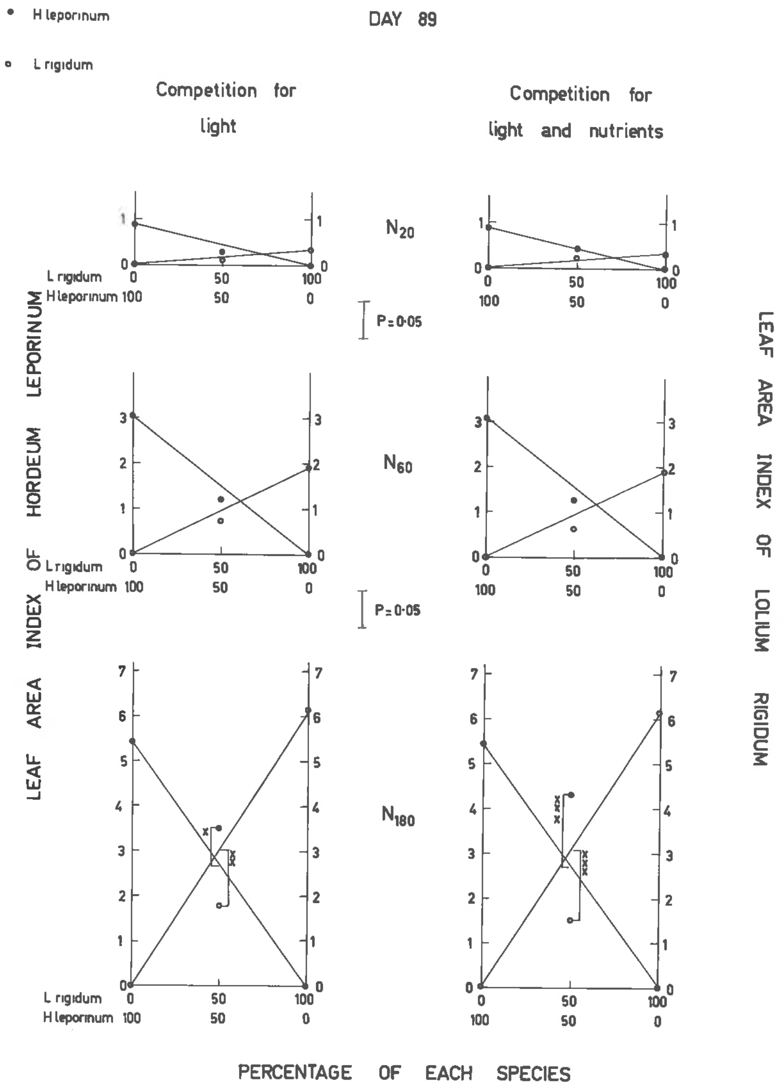
Figure 47 Effect of kind of competition on leaf area index of *H. leporinum* and *L. rigidum* in mixtures at three nitrogen levels. Significance of deviation from linearity, where it exists, appears as crosses thus :

x represents P = 0.05

xx represents P = 0.01

xxx represents P = 0.001

Bars represent least significant difference (P = 0.05) between any two points in the figure.


● H leporinum
○ L rigidum
DAY 89
Competition for light
Competition for light and nutrients
N20
N60
N180
P = 0·05
P = 0·05
L rigidum 0 50 100
H leporinum 100 50 0
x
xxx
LEAF AREA INDEX OF HORDEUM LEPORINUM
LEAF AREA INDEX OF LOLIUM RIGIDUM
PERCENTAGE OF EACH SPECIES

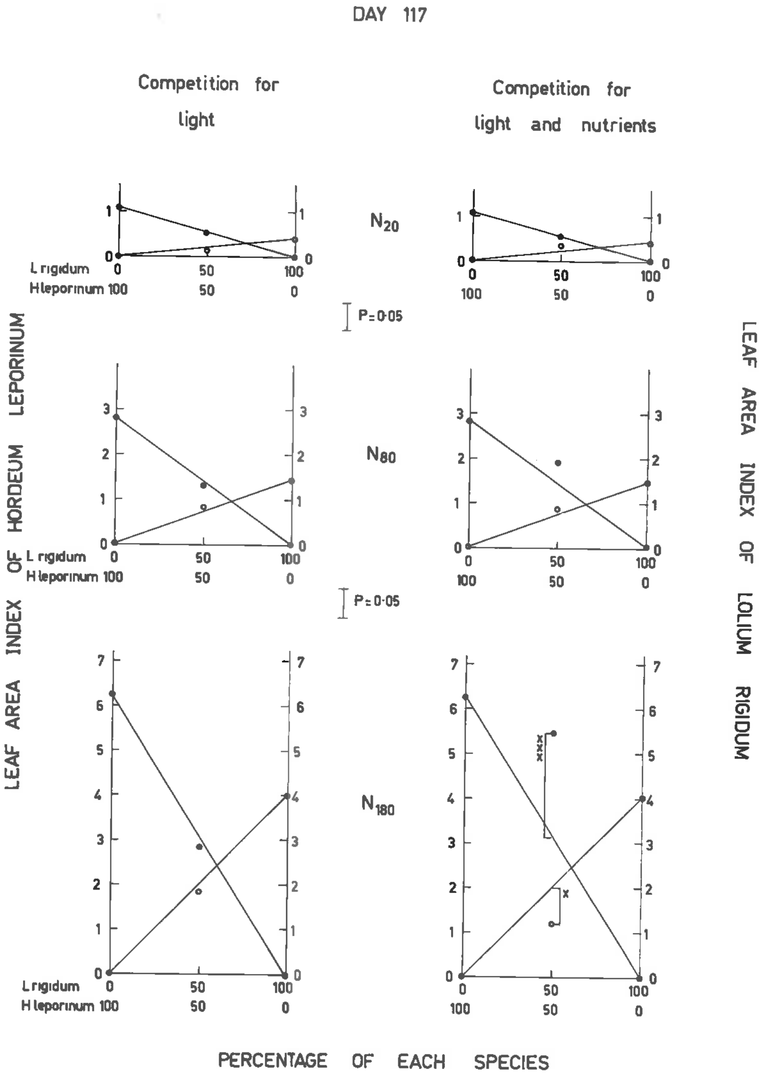

DAY 117
Competition for light
Competition for light and nutrients
N20
N80
N180
P = 0·05
P = 0·05
L rigidum 0 50 100
H leporinum 100 50 0
xxx
x
LEAF AREA INDEX OF HORDEUM LEPORINUM
LEAF AREA INDEX OF LOLIUM RIGIDUM
PERCENTAGE OF EACH SPECIES

Figure 48 Effect of kind of competition on nitrogen in the tops of *H.leporinum* and *L.rigidum* in mixtures at three nitrogen levels. Significance of deviation from linearity, where it exists, appears as crosses thus :

x represents P = 0.05
xx represents P = 0.01
xxx represents P = 0.001

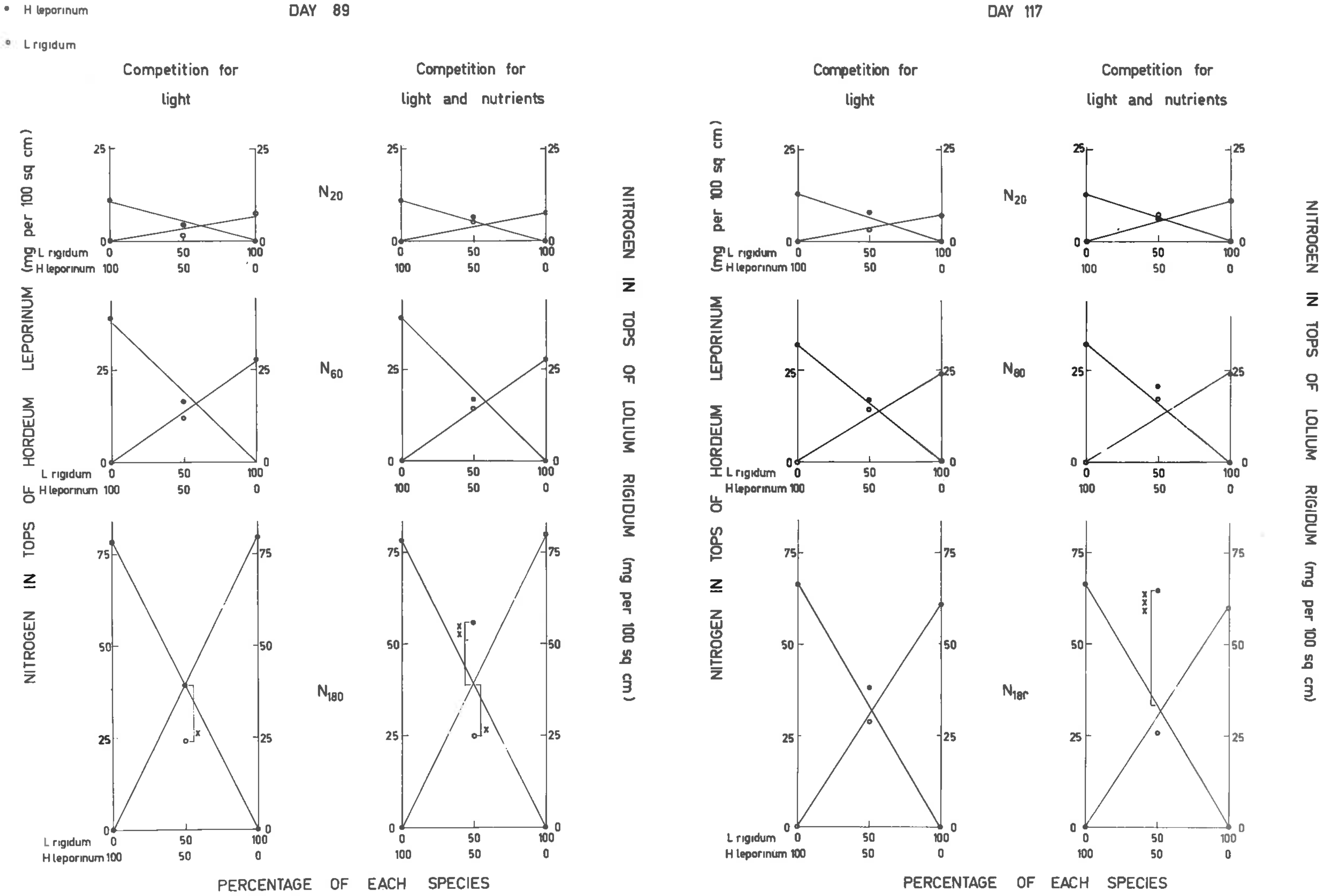
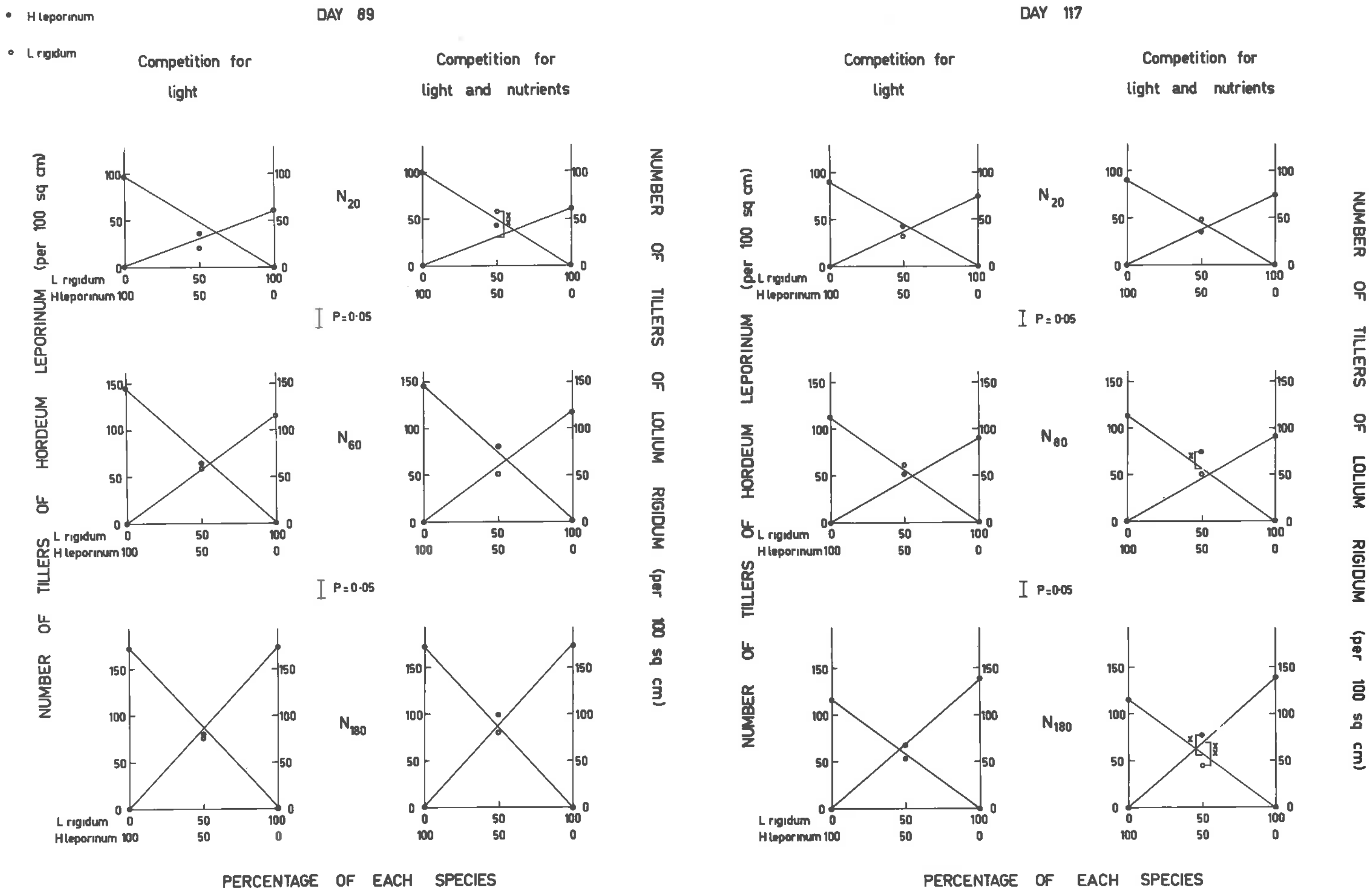

● H leporinum
○ L rigidum
DAY 89
DAY 117
Competition for light
Competition for light and nutrients
Competition for light
Competition for light and nutrients
N20
N60
N180
N20
N60
N180
NITROGEN IN TOPS OF HORDEUM LEPORINUM (mg per 100 sq cm)
NITROGEN IN TOPS OF LOLIUM RIGIDUM (mg per 100 sq cm)
0
25
50
75
L rigidum 0 50 100
H leporinum 100 50 0
x
xx
xxx
PERCENTAGE OF EACH SPECIES
PERCENTAGE OF EACH SPECIES

Figure 49 Effect of kind of competition on tiller numbers of *H.leporinum* and *L.rigidum* in mixtures at three nitrogen levels. Significance of deviation from linearity, where it exists, appears as crosses thus :

x represents P = 0.05

xx represents P = 0.01

Bars represent least significant differences (P = 0.05) between any two points on the figure.

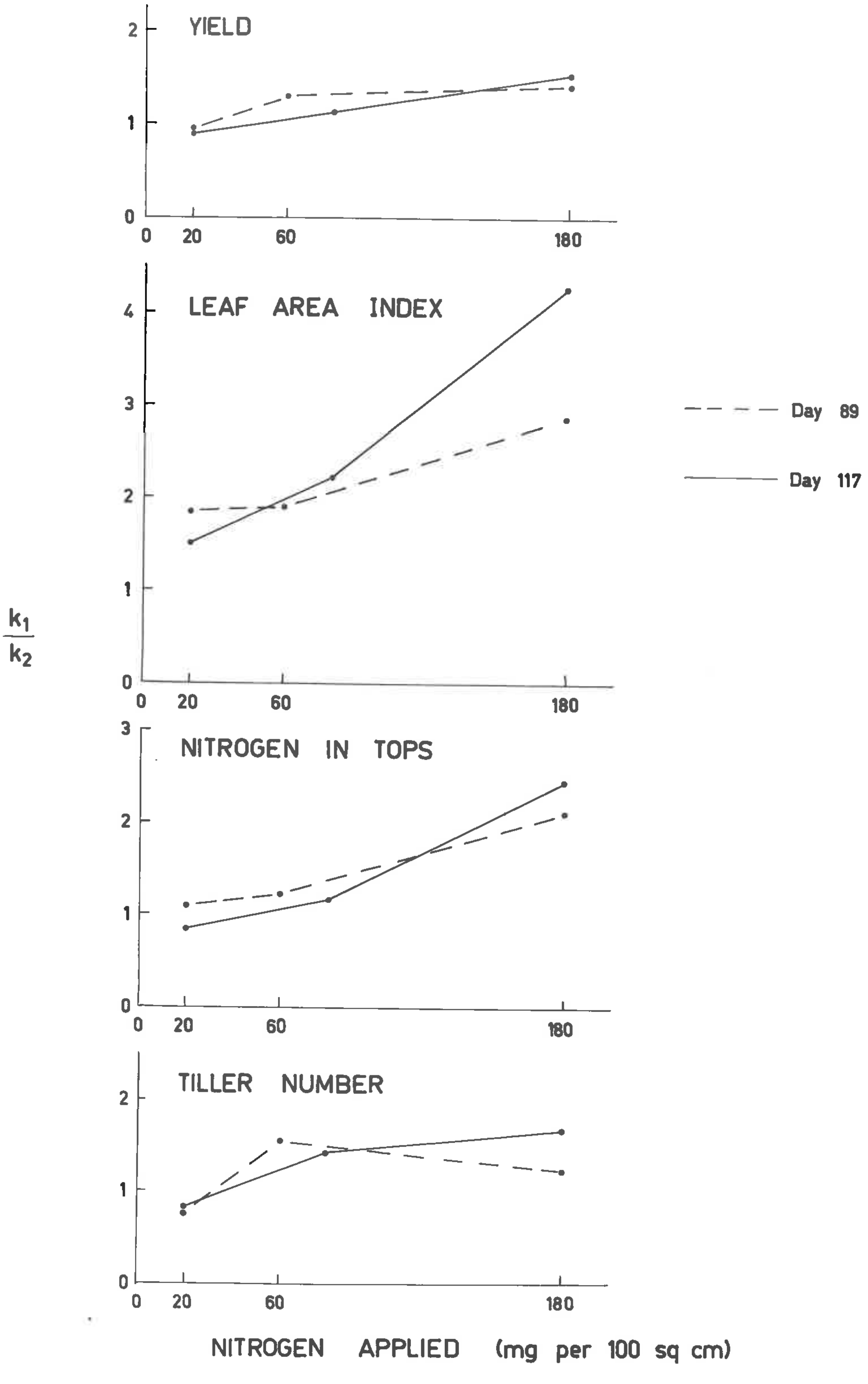

● H leporinum
○ L rigidum
DAY 89
DAY 117
Competition for light
Competition for light and nutrients
N20
N60
N180
P = 0·05
NUMBER OF TILLERS OF HORDEUM LEPORINUM (per 100 sq cm)
NUMBER OF TILLERS OF LOLIUM RIGIDUM (per 100 sq cm)
L rigidum 0 50 100
H leporinum 100 50 0
0
50
100
150
PERCENTAGE OF EACH SPECIES

earlier maturation of *H.leporinum* allowed growth of *L.rigidum* to increase at the end of the season. Aspinall and Milthorpe (1959) noticed that this occurred when the late maturing white persicaria (*Polygonum lapathifolium*) was competing with barley.

The value of K_1/K_2 (see section 5.3.3) which de Wit terms the relative growing coefficient of the first species relative to the second, has been calculated for *H.leporinum* relative to *L.rigidum*. The results, when competition was for light and nutients, are shown in Figure 50. The coefficients tended to rise with increased nitrogen supply, and at high nitrogen, increased with time. The character most sensitive to competition was apparently leaf area index; this character was also most sensitive to nitrogen application (Figure 43). The results, when competition was for light only, have not been presented because K_1/K_2 varied little from unity either between nitrogen treatments or harvests.

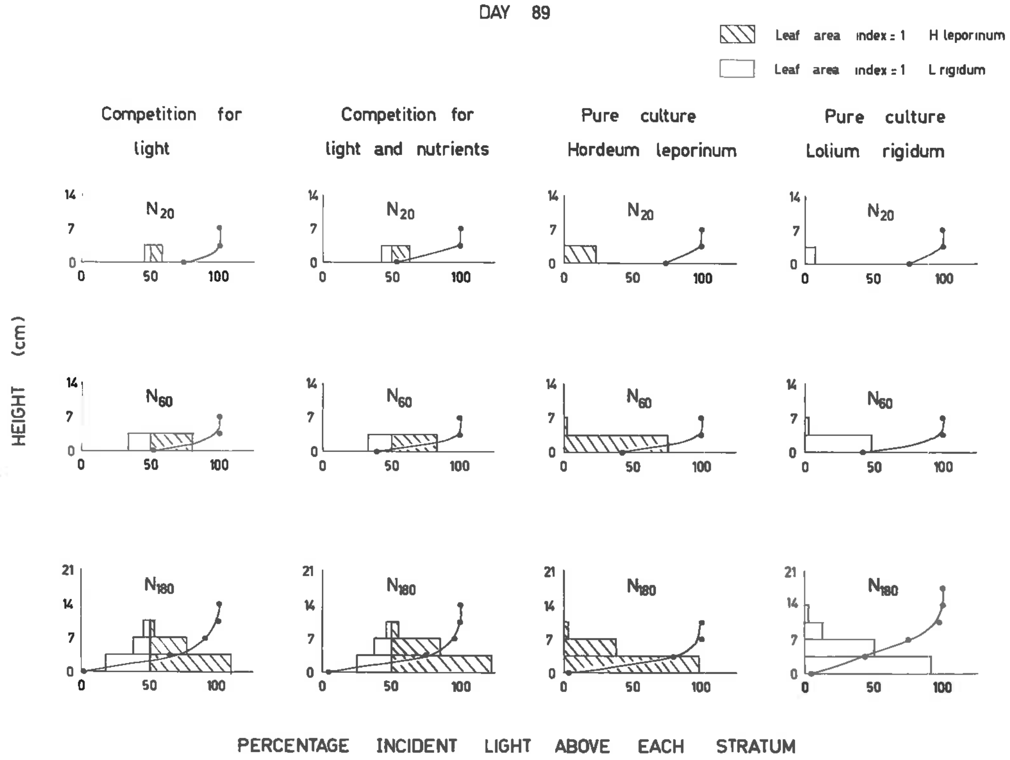
Figure 51 shows profiles of leaf area and light penetration for every treatment at the last two harvests. Only at high nitrogen levels did light interception become complete.

Figure 50 The relative crowding coefficient ($^{k1}/k_2$) of *H.leporinum* in relation to *L.rigidum* when competition was for light and nutrients.

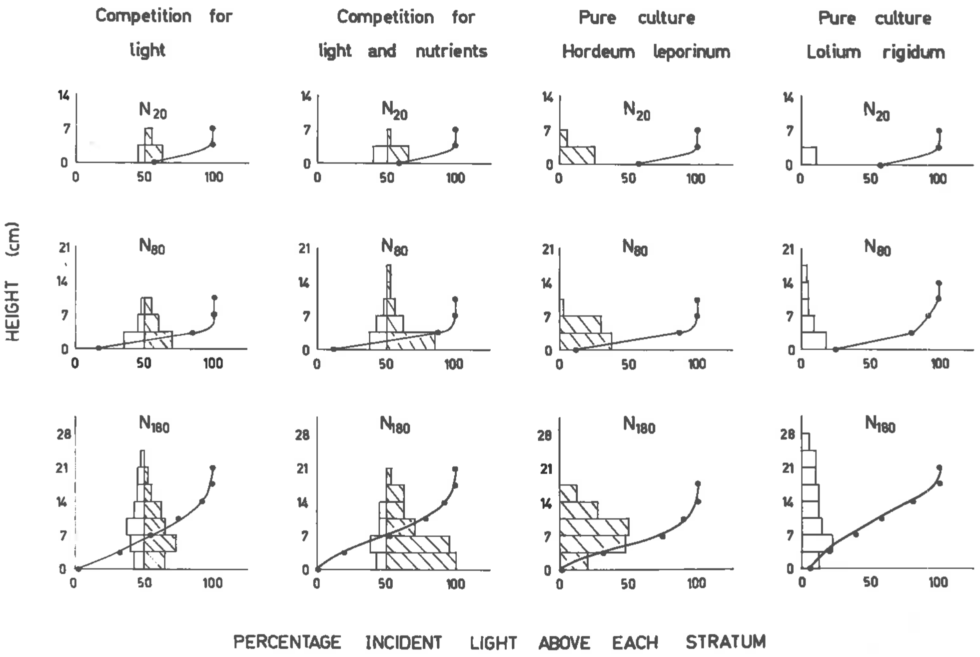

YIELD
LEAF AREA INDEX
NITROGEN IN TOPS
TILLER NUMBER
$\frac{k_1}{k_2}$
Day 89
Day 117
0
1
2
3
4
0
20
60
180
NITROGEN APPLIED (mg per 100 sq cm)

<u>Figure 51</u> Leaf area index at 3.5 cm intervals, and light penetrating to each 3.5 cm interval, in all mixtures.

DAY 89



DAY 117



6.4.0 Discussion

6.4.1. Growth of pure cultures

Growth of the 2 species in pure culture was similar. *H.leporinum* had slightly larger seedlings and could perhaps grow better at extremely low levels of nitrogen (Table 25). This was probably because of its larger seed giving it larger nitrogen reserves. Its larger seed would also result in a larger root system, which would lead to better exploitation of the soil environment and hence more complete use of the little nitrogen which was available.

It was unfortunate that nitrogen levels used here were not high enough to enable a complete description of the nitrogen response curve of each grass. At day 89 there was perhaps a suggestion that the response of *H.leporinum* was tending to be non linear (Figures 42, 43 and 44). If this was so, then higher applications of nitrogen may favour *L.rigidum*, and the yield of this species when nitrogen is non limiting may be considerably greater than the yield of *H.leporinum* under such conditions.

6.4.2. Behaviour of the species in mixtures

I will first discuss competition for light alone and begin by discussing development of leaf area and ability of the two species to intercept light.

In mixtures where competition was for light only, *H.leporinum* tended to intercept more of the total light than did *L.rigidum*. In Table 31, the proportion of all the incident light which was intercepted by *L.rigidum* is shown for the high nitrogen treatments at the last two harvests. This was calculated (Black 1958) using stratified cuts and light interception data in the following way. Let us take a hypothetical example of a sward 21 cm high; in the 17.5 to 21 cm layer, 75% of the leaf area is attributable to *H.leporinum* and 25 % to *L.rigidum*. If the amount of light incident at the top of the layer is 100 % and at the bottom (that is, at 17.5 cm) is 20 %, then of the 80 % light intercepted, 60 % was intercepted by *H.leporinum* $(\frac{75}{100} \times 80)$ and 20 % by L.rigidum $(\frac{25}{100} \times 80)$. This calculation can be repeated for each layer, and the total for each species is the percentage of all incident light intercepted by each species.

The fact that *L.rigidum* intercepted less than half the total incident light, yet contributed about half the dryweight at both harvests (Table 31) probably indicates that its nett assimilation rate was higher than that of *H.leporinum*. This was acutally measured in section 4.00. (Figure 24), where the reader will remember that nett assimilation rate of *L.rigidum* was in fact considerably higher than that of *H.leporinum*. Thus while the two species did not equally share the light environment, *L.rigidum* obtained sufficient light to maintain itself in the sward at parity with *H.leporinum*. To do this *L.rigidum* apparently had to intercept only 35 % of incident light.

The results in Figures 46 – 49 confirm that neither species was gaining through competition for light. In

TABLE 31

The percentage of total yield attribuable to *L.rigidum* and the percentage of incident light intercepted by *L.rigidum* in the mixtures.

	Competition for light		Competition for light and nutrients	
	% of yield of mixture	% of light intercepted	% of yield of mixture	% of light intercepted
Day 89	49	34	41	25
Day 117	54	38	40	17

almost all cases of competition for light only, the performance of a species in a mixture was half its performance in pure culture.

I turn now to consider those mixtures where competition was for nutrients as well as for light. Figure 51 shows that in this circumstance, and at high nitrogen, H.leporinum grew taller than L.rigidum. At the final harvest, above a depth in the sward to which 50 % of incident light penetrated, L.rigidum and H.leporinum had LAI's of 0.4 and 1.9 respectively where competition was for light and nutrients, compared with 1.2 and 1.4 respectively where competition was for light only. Table 31 shows that L.rigidum was intercepting less than a quarter of the light and was only about 40 % of the total dry weight. It is apparent that in this treatment L.rigidum was suffering from competition for light.

There are two possible explanations for the success of H.leporinum when competition is complete. This grass may be able to compete successfully with L.rigidum for nutrients, or there may be an interaction between competition for light and for nutrients. Remember that it has been shown that competition for light alone does not lead to dominance of either species in the circumstances of this experiment.

If competition for nutrients is the sole reason for the dominance of one species over the other, then when nitrogen level is reduced, competition effects should become greater, leading to a higher degree of suppression of the less aggressive species. Figures 46 - 49 show that suppression was least where nitrogen was lowest and most where nitrogen was highest. It seems that the effect was other than simply an effect of competition for nitrogen.

Consideration must now be given to an interaction effect. This could happen in two ways. First, there could be a small effect of both competition for light and of competition for nutrients, with neither sufficiently large to measure; and yet the interaction, if one species is aggressive for both, may be positive and sufficiently large for a measurable effect. Considering the high proportion of light intercepted by *H.leporinum* when competition was for light only, this must be considered a possibility. However, the fact that greater light interception of *H.leporinum* did not lead to dominance when unaccompanied by competition for nutrients, and that if anything, the sward was becoming *L.rigidum* dominant (*L.rigidum* 54%, at N180 in the final harvest, where competition was for light), suggests that this kind of interaction is unlikely. In view of the results at day 89 however, where *H.leporinum* gained and *L.rigidum* lost in competition for light only, the possibility that the results can be explained in this way must not be dismissed.

A second way in which an interaction could occur, is if an advantage in competition for one factor led to an advantage for the other. Thus if there were a small effect of competition for nitrogen, resulting in a slightly lower growth rate for *L.rigidum*, *H.leporinum* may be able to grow taller. From this point the fact that *L.rigidum* received less light may affect its ability to compete for nitrogen, thus intensifying the original nitrogen effect. A large positive interaction could thus result from a small initial advantage in competition for one of the factors (in this case either light or nutrient, but more likely nutrients). It is proposed that this is what happened here.

H.leporinum germinated faster, had a larger seed, and hence produced a larger root system quicker than *L.rigidum*. This was probably the mechanism which set the interaction described above in motion. Its roots could explore the soil first, leaving less nutrient for its competitor. When a soluble nutrient such as nitrogen is involved, it may even be more important for the nutrient to be rapidly used by plants, because the nutrient may be leached before roots are produced in the soil zone in which the nutrient was originally present. This may be especially important in the field.

Experiments separating above and below ground competition have not been widely reported. However, Donald (1958) achieved a full separation of competition for light and for nutrients in mixtures of *Phalaris tuberosa* and *Lolium perenne*. The aggressive species, *L.perenne*, gained whether there was competition for light alone or nutrients alone, but the interaction between light and nutrients was strongly positive. Donald's explanation of the interaction was essentially the same as that in this text. The main modification of Donald's interpretation here offered is the sequential nature of events. Donald rightly points out the extreme complexity which can occur, and that even where roots (or tops) are not competing an interaction can be set in motion, which leads to reduced exploitation of the environment by the roots (or tops).

The explanation I have offered leads to the logical conclusion that it is the species which is aggressive when competition begins which leads to subsequent greater aggressiveness, no matter what the mechanism which first gives aggression, nor which mechanism subsequently gives aggression. This is similar to the conclusion drawn after consideration of the results of the experiment described in section 5 (Experiment 3).

Aspinall (1960) grew barley and white persicaria (*Polygonum lapathifolium*) together using a similar technique to that of Donald (1958). He found that, for the conditions of his experiment, competition for nutrients affected the balance in mixtures more than did competition for light, though the interaction factor was virtually absent. Nevertheless he explained his results in terms of an interaction when he said that 'depression of growth by a reduced supply of nutrients soon leads to the shoots of the suppressed species being shaded by the aggressor'. His results do not suggest that this process was going on, but suggest only that success depended on ability to compete for nutrients. Even where what he calls an interaction was present, depression of the suppressed species was only that amount of depression obtained by adding the effects of competition for light and nutrients alone, that is, there was no interaction.

I turn now to a consideration of the results of my experiment on density (Experiment 8) in terms of the results of this experiment. The explanation for the success of *H.leporinum* in both experiments has been its earlier exploitation of the environment, in an unspecified way in the density experiment, probably by the roots in this experiment. There is every reason to suppose that competition between roots ultimately led to success or failure in the density experiment. Soil nitrogen level was probably superior (this is assumed because growth was superior) so that at the low density, adequate nitrogen was available to allow the roots of *L.rigidum* to permeate as much or more of the soil as did those of *H.leporinum*. Success of *L.rigidum* could have followed either because it was taller, or because its roots had access to more nutrient, but eventually through interaction. At high densities, superior early root growth by *H.leporinum* could have reduced available nitrogen to a level which adversely affected growth of *L.rigidum*, causing a typical light x nutrient interaction and leading to the success of the former species.

7.0.0. GENERAL DISCUSSION

In this section I intend to discuss firstly, the establishment of annual grass species, secondly the temperature factor in relation to seedling growth, thirdly post-germination competition, and finally, in the light of my results and discussion, review management practices which may influence the outcome of competition.

7.1.8. The Establishment of the Annual Grass Species.

The first point I shall consider is the effect of rate of germination on the success or failure of an annual grass germinating from the surface of the soil. Factors of the environment at the time of the first seasonal rains which may influence the ability of seeds to germinate from the soil surface are air temperature, duration and intensity of rain, strength of wind, and cloud cover following rain. Any condition which tends to dry out the seed will, relatively, favour those seeds which germinate most rapidly.

The results clearly indicate that *H.leporinum* is able to germinate more rapidly than *L.rigidum* under laboratory conditions. Under conditions more closely approximating those in the field, establishment follows a similar pattern. Further, germination as slow as that of *L.rigidum* may completely inhibit its establishment from the soil surface under less favourable conditions.

The slow germination of *L.rigidum* in comparison to *H.leporinum* can possibly be extended to comparison with other Mediterranean annual species. For example, Trumble (1937b) found that *L.rigidum* germinates at least one day slower than *Vulpia myuros*, *Brachypodium distachyon*, and the weedy herb *Echium plantagineum*. Smith (1968a) found that *L.rigidum* germinates slower than *H.leporinum*, but a little faster than subterranean clover. I have found that *Bromus rigidus*, *Bromus mollis*, and *Vulpia myuros* all germinate much more promptly than L.rigidum (Table 32). The property of rapid germination may be characteristic of the successful annual pasture species, except perhaps those, such as subterranean clover, which bury their seeds.

The climate of southern Australia was discussed in the literature review. The most important points were that, firstly, there is considerable variation in the amount and timing of the first seasonal rains, and secondly, that there are often summer and 'pre-opening' autumn rains, subsequently followed by drought. The effect of summer and pre-opening autumn rains on the survival of seeds of H.leporinum and L.rigidum is the next point to be discussed.

Both H.leporinum and L.rigidum are able to resist germination following wetting at high temperatures, yet both species (especially L.rigidum) are able to germinate if the temperature is subsequently reduced. The results indicate that germination of both species following rain in summer will be poor, though not completely inhibited, if the temperature is above 32°C (90°F). Daily variation in temperature, if the higher temperature is above 32°C also inhibits germination. For example, seeds of L.rigidum experiencing 38°C for 12 hours fail to germinate even if this temperature is followed by 12 hours at 12°C, 20°C or 26°C. Thus, if summer rains are followed by high temperatures, the risk of germination at this unfavourable time of the year by both these annual grasses will be low, even if the rain is heavy enough to keep the seed wet for more than one day.

The seeds of both species remain undamaged by light summer rains even when the rains are followed by cool

TABLE 32

Percentage germination of viable seed of several annual pasture grasses illustrating rate of their germination compared to Hordeum leporinum and Lolium rigidum (germinated at 20°C in Petri dishes).

Species	Day 1	2	3	4	5
Bromus rigidus	0	90	100	100	100
Bromus mollis	0	97	100	100	100
Vulpia myuros	0	0	100	100	100
Hordeum leporinum	20	77	87	95	96 *
Lolium rigidum	0	4	45	76	90 **

* Final germination (100 %) after 6 days

** Final germination (100 %) after 11 days weather. If the seed is kept wet for longer periods, some damage results, but H.leporinum can be kept wet for up to 20 hours, and dried, with very little effect on subsequent germination, while L.rigidum can be kept wet for 25 hours, and perhaps longer, with very little effect on subsequent total germination after drying (a longer period because it germinates more slowly than H.leporinum)

The combination of rain and temperature in summer most likely to cause germination is heavy rain followed by low temperature. In these circumstances, non-dormant seeds are likely to germinate. The risk of a return to normal summer drought conditions and the ability of the species to resist drought is thus of potential ecological importance. The results of experiments where seedling growth was studied, indicate that H.leporinum is far better able to survive than L.rigidum because of its deeper and more rapid root penetration following its more rapid germination. On the other hand, its more rapid germination means that it is more likely to have to survive such conditions : that is, the slower the potential rate of germination, the more unlikely it is that germination will actually occur.

The above discussion applies to non-dormant seeds, and reveals that they have considerable resistance to germination during the summer. If however, seeds are dormant in summer, resistance to summer rains may be complete. Results of dormancy studies with H.leporinum showed that most seeds are dormant during the summer, at least of the line tested. At the times when germination tests were conducted (9th April and 12th June in the year following seed collection) the seeds are not completely dormant : that is, dormant in the sense that germination is completely inhibited. However, if seeds dry out before germination commences - far more likely if germination is slower than normal - then the seeds will in fact be effectively dormant.

Dormancy of *H.leporinum* is relieved (that is, germination becomes more rapid) by leaching the seed dispersal units (the fertile floret and the two sterile florets) for a short period before the commencement of the germination test, or by removing the outer, sterile florets from the seed dispersal units. These treatments simulate leaching by heavy rainfall, of the kind which may be experienced at the opening of the season. Also it was found that dormancy is relieved with the passing of time - seeds germinated more slowly on the 9th April than they did on the 12th June. Further work is needed to determine the amount of leaching necessary, that is the amount of rainfall necessary, to relieve dormancy completely in the middle of the summer. However, it seems possible that dormancy, together with the other protective mechanisms described, ensures almost complete protection against out of season germination.

7.2.C. The Temperature Factor in Relation to Seedling Growth.

I turn now to a consideration of the response of the seedling growth rate of the two species to temperature, in relation to temperatures recorded at different times of the year at Adelaide. The quite different response curves are surprising, considering that both species occur 'naturally' in the same environment. The comparison between 10°C and 17°C is of particular interest as these temperatures are similar to the mean July (11.5°C) and the mean April (17.5°C) temperatures at Adelaide.

There is no variation in the relative growth rate of H.leporinum at 10°C and 17°C. Considering mean temperatures this species can apparently grow as well in mid-winter as in mid-autumn, at Adelaide. Actual growth rates, of course, will depend on day to day variations in temperature. For example, the chance of any day recording a temperature of 24°C, a temperature at which the relative growth rate of H.leporinum is considerably higher than at 17°C or less, is far greater in the autumn when the mean temperature is 17.5°C than in winter, when the mean temperature is 11.5°C. Mean maximum temperatures, which will be more closely correlated to day temperatures, indicate that autumn temperatures may be such that the relative growth rate of H.leporinum is in fact greater in autumn than in winter. The mean maximum temperature in April is 23°C and in July is 16°C, while the mean minimum temperature in April is 12°C and in July is 7°C.

The relative growth rate of L. rigidum, on the other hand, responds markedly to an increase in temperature from 10° to 17°C, yet remains almost constant at 17°C and 24°C. Thus, if mean maximum temperatures are considered, there will be little variation in relative growth rate in the autumn and winter months, but if mean temperatures, or mean minimum temperatures are considered, the variation in relative growth rate will be quite important. The whole question of growth rates at different times of the year will depend also on the light environment, the response of swards rather than isolated plants to temperature, and the effect, if any, of diurnal variation of light and temperature.

The difference in response to temperature of the two species leads to the conclusion that the temperature regimes following opening rains at different times of the year will affect botanical composition, though the manner in which this effect operates remains obscure. This conclusion is in contrast to that drawn in the literature review where it appeared, on the basis of several studies, that the response of relative growth rate to temperature varied little between species.

7.3.0. Interspecific Competition Between *Hordeum leporinum* and *Lolium rigidum*.

The growth of isolated seedlings of *H.leporinum* and *L.rigidum* was studied in a controlled environment. It was found that both the seed and the embryo of *H.leporinum* are considerably larger than those of *L.rigidum*, but that the relative growth rate of *L.rigidum* is superior at all temperatures measured. The result of this combination of circumstances is that seedlings of *H.leporinum* are larger than those of *L.rigidum* at emergence and for some time after emergence, but seedlings of *L.rigidum*, because of their superior relative growth rate, eventually become equal in size to those of *H.leporinum*.

The pattern of seedling sizes is confirmed when top weight, root weight, leaf area, or height of isolated plants are considered. In all these characters *H.leporinum* is initially superior, but loses its superiority as time proceeds. In the case of root length however, the evidence shows that the initial superiority of *H.leporinum* tends to increase with time.

On the basis of the above results with isolated plants, an hypothesis about the outcome of competition between the two species was formulated. It was postulated that if competition begins when *H.leporinum* plants are larger than *L.rigidum* plants, then *H.leporinum* will gain in competition between the species. If, however, competition begins after *L.rigidum* plants have become larger than *H.leporinum* plants, then *L.rigidum* will gain in competition between the two species. It was argued that the density affecting the outcome of competition will be the density of *H.leporinum*. This is because when the density of *H.leporinum* is high, plants of *L.rigidum*, regardless of the density of *L.rigidum*, will be shaded as soon as they emerge, or before they become as large as plants of *H.leporinum*. If the density of *H.leporinum* is low however, the superior relative growth of *L.rigidum* will lead to plants of that species being larger when competition between the species begins.

An experiment was conducted to test this hypothesis, and the results were found to be in agreement. It was found that above a density of 93 plants of *H.leporinum* per 100 sq cm, *H.leporinum* is the aggressor, and below this density (the critical density) *L.rigidum* is the aggressor. An index of aggression was formulated to analyse the results.

Factors of the environment which affect pre-competition growth will affect the critical density. For example, any factor which increases the size of *H.leporinum* seedlings relative to *L.rigidum* seedlings will reduce the critical density - that is, less *H.leporinum* seedlings will be required for aggression by that species, because seedlings of *L.rigidum* will potentially take longer to become greater in size. Thus at temperatures of 24°C, where relative growth rates are about equal, the critical density will be very low, and *L.rigidum* may never become the aggressor. Compared to 17°C, the critical density will be less at 10°C because at this temperature the relative growth rate of *H.leporinum* is comparatively closer to that of *L.rigidum*. Thus the critical density will depend on temperature.

Factors which affect the rate of germination will affect the critical density if they affect the rate of germination of the two species differentially. For example light rains which wet the seed of the two species for short periods, thus stimulating the rate of subsequent germination following drying and rewetting, will reduce the critical density if the first period of wetting is about 10 hours, and increase the critical density if the first period of wetting is about 20 hours. This is because maximum stimulation of rate of germination of *H.leporinum* occurs after 10 hours wetting, and of *L.rigidum* after 20 hours.

Nitrogen level may also affect the critical density. This conclusion can be drawn from a consideration of the results of Experiment 8 on the effect of density, and Experiment 9 on competition for light and nutrients (nitrogen). The results of Experiment 9 showed that neither species gained in competition for light, and that *H.leporinum* gained in competition for light and nutrients. The main difference in the results of the two experiments was that *H.leporinum* gained in competition with *L.rigidum* at a lower density in Experiment 9 (24 plants per 100 sq cm) than was predicted from the results of Experiment 8 (93 plants per 100 sq cm). The reason was probably that nitrogen levels were lower in Experiment 9. If this were so, the more rapid root growth of *H.leporinum* would mean that much of the limited amount of nitrogen would be absorbed by that species to the detriment of *L.rigidum* whose root system developed more slowly. If the nitrogen level had been higher, as it probably was in Experiment 8, a lesser proportion would be absorbed by H.leporinum before the root system of L.rigidum had developed. One can postulate a density by nutrient interaction, higher nutrient levels increasing the density necessary for the success of H.leporinum in competition with L.rigidum.

7.4.0. Management Practices which may Influence the Outcome of Competition between *H.leporinum* and *L.rigidum*.

In general, Australian farmers strongly prefer *L.rigidum* to *H.leporinum* in their pastures, and indeed sow only the former species. Smith (1966) conducted a survey amongst Australian farmers regarding their opinions of *H.leporinum* and found that these ranged from mild approval to strong condemnation. The most usual reason for approval of *H.leporinum* was its good early growth, and for condemnation was the injurious effect of its seeds on livestock.

The higher level of nitrogen in the tops of *H.leporinum* indicates that there is more protein in the leaves of *H.leporinum* than there is in the leaves of *L.rigidum*, a finding of some interest if livestock are deficient in protein in summer (Donald and Allden 1959). Whether these differences are maintained into summer has not been determined, although data from Shapter (1935) indicate that they may be.

7.4.1. The influence of rate of stocking.

Most experiments involving various stocking rates on annual pastures have recorded that at high stocking rates herbaceous plants (for example *Arctotheca calendula*, subterranean clover) are favoured, and that at low stocking rates annual grasses are favoured (Rossiter 1966). The reason that grasses succeed at low stocking rates is due to their ability to compete for light and perhaps their ability to compete for nutrients under these conditions.

The ability of grasses to compete for light is due to their superior height; thus the presence of a large number of grazing animals removing the tops will obviously reduce this height advantage. If grasses have an advantage in competition for nutrients, it will probably be due to their greater depth of rooting, or their greater surface area of root, enabling them to gain a greater share of a limited supply of nutrients. A higher density of grazing animals will probably reduce this advantage in two ways :

1) The bulk of the sward will be less and thus nutrients in the sward will be less, and perhaps sward requirements for nutrients will be less. In any case, competition for nutrients will be less intense.

2) There will be a rapid re-cycling of nutrients in the form of animal excreta, and nutrient availability will increase in the surface horizons of the soil, to the relative advantage of those species with shallower root systems.

The nett effect of the grazing animal on competition between annual pasture species will be to reduce the advantage of the winning species in the absence of the grazing animal. In fact, because of the lesser intensity of competition under heavy grazing, inherent ability for rapid growth may be of even greater importance than 'competitive ability'. Thus, the species with the greatest relative growth rate may be the most successful (as it will be also where there is no competition) though competition will not be absent under heavy grazing and will still affect the outcome.

Turning now to competition between *H.leporinum* and *L.rigidum* it seems probable that the advantages enjoyed by *H.leporinum* at high density will be substantially reduced by intense grazing pressure. Its advantages in competition with *L.rigidum* are due to its greater height, leaf area, and root depth and weight, all of which will be less significant when grazing pressure is high. Further, *H.leporinum* has an inferior relative growth rate to *L.rigidum*. Thus in competition between these species, the outcome is likely to be reversed when grazing intensity is high, compared to nograzing or light grazing, even though the density of *H.leporinum* is high. As there is a critical density, so will there be a critical grazing pressure, above which *L.rigidum* will be the more successful species, and below which *H.leporinum* will be the more successful species.

As well as being affected by total grazing pressure, competition between the two species will probably be affected by various other management practices involving livestock. For example there are two common management practices which may favour *H.leporinum* in competition with *L.rigidum* when the former is sown at high density, and may favour *L.rigidum* when it (*H.leporinum*)is sown at low density. These are deferred grazing and rotational grazing. They will affect the outcome of competition in this way because both systems involve periods when the pasture is left ungrazed.

7.4.3. The influence of fertiliser application

Consideration of the results of the experiment on competition for nutrients and of the argument that critical density will be increased at high nitrogen (page 250), suggests a management practice which may aid conservation of *L.rigidum*.

It seems likely that high nitrogen at the opening of the growing season will have a favourable influence on the success of *L.rigidum* if its main competitor is *H.leporinum*. It follows that artificial nitrogen applied at this time to such mixed pastures will favour *L.rigidum*. Whether other annual species with large seeds have lower relative growth rates than *L.rigidum* is not known, but if this is so, additions of nitrogen, together with manipulations of livestock numbers, may well be a way of maintaining *L.rigidum* (Table 33).

TABLE 33

Schematic account of the effects of high and low density of H.leporinum, heavy and light grazing pressure, and the application of nitrogenous fertilizers, on the outcome of competition between H.leporinum and L.rigidum.

	Light grazing		Heavy grazing	
	Low N	High N	Low N	High N
High density of H.leporinum	*HHH	HHL	HHL	HLL
Low density of H.leporinum	HHL	HLL	HLL	LLL

* HHH - very advantageous for H.leporinum
HHL - slightly advantageous for H.leporinum
HLL - slightly advantageous for L.rigidum
LLL - very advantageous for L.rigidum

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APPENDIX TABLE 1

Weight of tops (gm per 100 plants) and natural logarithm of weight of tops at successive harvests and for each species.

(a) 24°C

Day	H.leporinum	L.rigidum	$\log_e$ H.lep.	$\log_e$ l.rig.
2	.0369	.	-3.300	.
3	.	.0111	.	-4.501
4	.1263	.	-2.072	.
5	.2492	.0675	-1.390	-2.696
6	.3334	.1009	-1.110	-2.293
8	.5639	.2334	-0.573	-1.457
10	1.187	.4355	.166	-0.830
12	1.874	.5050	.626	-0.683
16	5.214	2.128	1.651	.756
20	14.74	5.771	2.688	1.753
24	34.67	16.31	3.547	2.791
28	86.91	48.67	4.465	3.886

(b) 17°C

Day				
5	.0573	.	-2.860	.
7	.2029	.0225	-1.595	-3.794
8	.2875	.0383	-1.245	-3.262
9	.3868	.0584	-0.949	-2.840
10	.6447	.1038	-0.439	-2.263
12	.9277	.2030	-0.075	-1.595
14	1.170	.3143	.157	-1.158
16	1.453	.5335	.372	-0.627
20	2.501	1.230	.916	.207
26	5.939	5.433	1.782	1.692

APPENDIX TABLE 1 (continued)

(c) 10° C

Day	H.leporinum	L.rigidum	$\log_e$ H.lep.	$\log_e$ L.rig.
9	.1058	.0328	-2.244	-3.417
13	.2856	.0800	-1.252	-2.526
17	.5863	.2444	-0.534	-1.411
21	1.099	.4975	.095	-0.697
25	2.083	.8744	.732	-0.135
29	3.714	1.829	1.311	.604
34	9.036	5.763	2.202	1.751
38	14.16	12.15	2.653	2.501

APPENDIX TABLE 2

Root weights (gm per 100 plants) and natural logarithms of root weights at successive harvests and each temperature.

(a) 24° C

Day	H.leporinum	L.rigidum	log$_e$ H.lep.	log$_e$ L.rig.
2	.0433	.	-3.140	.
3	.	.0070	.	-4.962
4	.1063	.	-2.242	.
5	.1600	.0404	-1.833	-3.211
6	.2451	.0750	-1.406	-2.590
8	.3934	.1392	-0933	-1.973
10	.8248	.2513	-0.181	-1.381
12	1.213	.2819	.191	-1.266
16	2.815	1.217	1.035	.196
20	7.002	3.087	1.946	1.127
24	13.50	7.266	2.603	1.983
28	43.50	20.45	3.773	3.020

(b) 17°C

Day	H.leporinum	L.rigidum	log$_e$ H.lep.	log$_e$ L.rig.
5	.0575	.	-2.856	.
7	.1275	.0145	-2.056	-4.234
8	.1646	.0329	-1.802	-3.414
9	.2092	.0400	-1.565	-3.219
10	.2942	.0838	-1.224	-2.479
12	.4397	.1555	-0.821	-1.858
14	.6902	.2521	-0.371	-1.378
16	.9590	.5993	-0.042	-0.513
20	.1911	1.2361	.647	.215
26	3.809	3.821	1.338	1.340

APPENDIX TABLE 2 (continued)

(e) 10° C

Day	H.leporinum	L.rigidum	$\log_e$ H.lep.	$\log_e$ L.rig.
9	.0848	.0205	-2.468	-3.887
13	.2381	.0675	-1.436	-2.696
17	.3275	.0975	-1.115	-2.328
21	.7838	.4456	-2.243	-0.807
25	1.576	.7556	. 457	-0.280
29	2.540	1.317	.932	.278
34	4.998	3.471	1.609	1.244
38	8.429	7.112	2.132	1.962