PRIMARY BUD-AXIS NECROSIS
OF GRAPEVINES

by

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Primary bud-axis necrosis (PBN) is an abnormality of Vitis vinifera wherein the primary bud-axis of the compound bud aborts and becomes necrotic; the secondary bud-axes remain healthy and develop more than those in unaffected buds. Natural levels of PBN were found to be positively correlated with main shoot length and diameter, and the number and length of lateral shoots ("shoot vigour") and with butt circumference and pruning weight per vine ("vine vigour"). 'Shiraz' had the highest natural levels of all cultivars studied with up to 30 percent of nodes on vigorous vines showing PBN; in addition, nodes with lateral shoots had up to four-fold greater incidence of PBN than nodes without lateral shoots.

Anatomical studies revealed that under natural conditions necrosis commenced soon after flowering and was largely completed by mid-summer.

PBN was induced or increased by various shoot treatments (shoot thinning, topping, defoliation), or by treatment with gibberellic acid (GA$_3$). Besides increasing PBN the treatments increased main shoot length and/or lateral shoot number and length. The level of induced PBN was directly proportional to the severity of shoot treatments (thinning, topping, defoliation) or the concentration of exogenous GA$_3$. In both cases, highest levels of PBN were induced by treatments applied near flowering time with response diminishing with later treatment; shoot treatment and GA$_3$ application induced up to 80 and 100 percent PBN respectively on treated shoots.

The degree of susceptibility to both shoot treatment-induced and GA$_3$-induced PBN appeared to be primarily determined by the stage of bud development and to a lesser extent by the stage of shoot development: young, still differentiating buds were more susceptible than mature buds. Vigorous and/or seeded cultivars were most susceptible to both natural and induced PBN.

These results led to the hypothesis that induction of PBN is associated with high levels of gibberellins in the shoot and bud leading to premature elongation of the primary bud-axis; this development subsequently leads to abortion and necrosis of this axis possibly because it is subject to inhibition.
This hypothesis was tested by measuring the changes in endogenous levels of gibberellins in primary bud-axes following shoot treatment (thinning, topping, defoliation) using the barley endosperm biossay. Shoot treatment was found to increase both the concentration of gibberellin-like substances and bud tissue D.Wt. to three times that of control 21 days after treatment. Furthermore, there was a strong positive correlation between endogenous concentration of gibberellins in primary bud tissue and i) shoot vigour, ii) vine vigour and iii) subsequent development of PBN.

Shoot thinning, topping and defoliation of whole vines resulted in reduced yield per vine (topping plus defoliation of single shoots reduced yield per node) in the following growing season due to fewer and smaller bunches even though shoot number per vine and per node was generally increased. The reduction in yield was strongly correlated with increase in both PBN level and ratio of secondary to primary shoots. It is proposed that the significant decreases in grapevine productivity which may follow the use of viticultural techniques designed to increase shoot vigour on the one hand, or to reduce the number of leaves on the other, may be due in part to increased PBN.
I hereby declare that the thesis here presented is my own work, that it contains no material previously published, except where due reference is made in the text, and that no part of it has been submitted for any other degree.

I consent to this thesis being made available for photocopying and loan if accepted for the award of M. Ag. Sc.

Peter R. Dry
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CHAPTER I

LITERATURE REVIEW
1.1 BUD DEVELOPMENT AND STRUCTURE IN THE GRAPEVINE

There have been a number of reviews concerning the development and structure of buds of the grapevine (May 1964; Bessis 1965; Bugnon and Bessis 1968; Carolus 1971; Pratt 1974; Srinivasan and Mullins 1981; Fournioux and Bessis 1982). When these reviews are compared, there are some differences in interpretation arising from differences in terminology. The aim of this review is to clarify this situation and to provide a basis for the research on the development of a particular bud abnormality, i.e. primary bud-axis necrosis (PBN) in the grapevine.

All buds of *Vitis* begin development as a meristem axillary to a leaf, i.e. every leaf primordium formed at a shoot apex has a primordial bud (meristem) in its axil. The subsequent development of a bud will depend on whether it is in the axil of a "true" or "foliage" leaf or in the axil of leaf developed in the form of a bract (= phyll, scale). If the former case, the bud will remain in a primordial state while it is subject to correlative inhibition; once this inhibition is removed, the bud develops rapidly. Such buds usually develop into a shoot in the same season as their subtending leaf expands.

If the latter case, the bud develops a limited number of nodes, with no expansion of internode or leaf cells, before entering into a state of organic dormancy; bud burst will only occur after organic dormancy has been relieved. Such buds usually develop into a shoot in the growing season after the one in which their subtending bract "expands" (May 1964).

1.1.a The "prompt" bud and lateral shoot

The first bud arising in the axil of the leaf subtended by a current season's shoot (of the order N, after Bugnon and Bessis 1968) is known variously as the "prompt" bud (Srinivasan and Mullins 1981), prompt bourgeon, bourgeon anticipe (Bugnon and Bessis 1968), and axillary bud (May 1964, Pratt 1974). This bud typically grows out, i.e. "bursts", into a shoot in the same season as its formation. This shoot, of the order N+1, is known as a lateral shoot (Srinivasan and Mullins 1981), a summer lateral (Pratt 1974), entre coeur, rameau anticipe (Bugnon & Bessis 1968), and first order lateral (May 1964).

The development of the "prompt" bud into a lateral shoot is inhibited by the presence of the apex or growing point of the main shoot. If this source of correlative inhibition is removed, the lateral shoot develops rapidly, in a similar fashion to the main shoot (May 1964).
The lateral shoot differs morphologically from the main shoot in that it has one basal prophyll and a long internode between this and the first foliage leaf. The lateral shoot may abscise above the prophyll early in its development (so-called "non-persistent lateral" by Antcliff et al. 1958); this typically is the case for main shoots of low vigour. Alternatively, and particularly on vigorous main shoots, lateral shoots may grow several metres long with many leaves. Such laterals may themselves have lateral shoots (N+2), arising, of course, from prompt buds.

In between these extremes, other lateral shoots may develop to varying degrees, largely dependent on the vigour of the main shoot, the presence or absence of an inflorescence or tendril at the same node, and the orientation of the main shoot. Laterals at nodes without inflorescence or tendril (N0) are usually the longest and those at the next distal node (N1) are the shortest. Those at node N2 are intermediate in length (Bouard 1966). Laterals are longer on shoots at 45 degrees from the vertical compared with upright, horizontal or downpointing shoots (Basler and Koblet 1972).

If the main shoot is topped or pinched (tipped) the growth of laterals is greatly stimulated, with the magnitude of the response decreasing as distance from the point of topping increases. Laterals which develop several leaves or more and lignify and survive into the winter have been termed "persistent laterals" by Antcliff et al. (1958). Lateral shoots may bear bunches ("second crop"), a characteristic more common to some cultivars than others. It has been demonstrated that anlagen and young tendrils on lateral shoots have the potential to form inflorescences but this potential is seldom expressed due to correlative inhibition by the lateral shoot apex (Srinivasan and Mullins 1981). The phyllotaxic plane of the lateral shoot (N+1) is at right angles to the main shoot (N) (Bessis 1965). Typically, for most cultivars of Vitis vinifera, lateral shoots are less frequent on the basal nodes of the main shoot.

1.1.b. Latent buds

The first leaf of the lateral shoot is reduced to a bract or prophyll (Pratt 1974). The bud which develops in the axil of this bract is known variously as the "primary bud" (Pratt 1974), the "primary latent bud" or "latent bud" (Srinivasan and Mullins 1981), the "dormant bud" (May 1964), "bourgeois principal" (Carolus 1971), and "bourgeon latent principal" (Fournioux and Bessis 1982). This latent bud (henceforth called "primary latent bud", PLB for reasons outlined below) develops slowly within the
bract and, before entering organic dormancy later in the growing season, will typically have 6 to 10 leaf primordia and up to 3 inflorescence primordia, depending on the cultivar (Srinivasan and Mullins 1981).

Prilleux (1856) was the first to establish that the PLB does not arise directly on the main shoot but rather arises as the axillary bud of the first bract-like leaf of the lateral shoot. This relationship was later confirmed by Muller-Thurgau (1883) and Bugnon (1953). Although this has subsequently been discussed in the English language (May 1964, Pratt 1974, Srinivasan and Mullins 1981), it is not described in English-language viticultural texts presently available, e.g. Winkler et al. 1974, Weaver 1976. The PLB is often wrongly assumed to be axillary to the foliage leaf on the main shoot in some texts.

Since the PLB and the shoot subsequently arising from it (normally in the following growing season) are branches of the second order (N+2), their phyllotaxic plane is parallel to that of the main shoot (N) (Bessis 1965).

The PLB typically has two (Bugnon 1953), two or more (Pratt 1974), three to four (May 1964) basal prophylls before foliage leaf primordia are formed. The fourth prophyll usually carries a small leaf lamina which mostly abscisses with it; sometimes it remains as the first leaf (May 1964). There is little or no internodal elongation between these bracts (Pratt 1974).

Additional buds develop in the axils of the basal bracts of the PLB. Although such authors as Pratt (1974), Srinivasan and Mullins (1981), only mention buds formed in the axils of the two most-basal bracts, others such as May (1964), Carolus (1971), Fournioux and Bessis (1982) emphasize that buds form in the axil of every bract or scale of the PLB. However, it is usually only the axillary buds of the two most-basal bracts which are obvious. These two buds are most commonly known as the "secondary and tertiary latent buds" (Pratt 1974; Srinivasan and Mullins 1981); however, May (1964) and Carolus (1971) refer to all buds axillary to the bracts of the primary latent bud as "secondary".

The secondary and tertiary latent buds (SLB) (TLB) develop nodes and leaf primordia later, but in the same season as the PLB. Typically, the PLB develops more nodes than the SLB which in turn develops more than the TLB. The SLB may form inflorescence primordia in some cultivars but the TLB is usually barren ("vegetative", "unfruitful") (Srinivasan and Mullins 1981).

The PLB, SLB and TLB, enclosed by the basal bract of the lateral shoot and the two basal bracts of the PLB, constitute the "winter bud", or "eye" (l'oeil) of the mature shoot (viticulturally termed "cane") (Fig. 1.1).
The SLB and TLB, and therefore the shoots that can potentially arise from them, are branches of the third order (N+3) with a phyllotaxic plane at right angles to that of the PLB (N+2).

The other "secondary" buds, so described in the terminology of May 1964, i.e. those buds in the axils of bracts of the PLB, additional to the SLB and TLB, are usually quite small and may not be very apparent if an "eye" is sectioned in winter. However, in some varieties, e.g. 'Rauschling', 'Elbling', and 'Muller-Thurgau', the quaternary bud is well developed (May 1964; referred to as "K3" in his review). In others, it is very small, e.g. 'Pinot Noir'. This quaternary bud is also, of course, a branch of the third order (N+3) (Fig. 1.2).

Therefore, the "eye" is a compound or mixed bud which consists of several buds, the one located in the axil of the other (Srinivasan and Mullins 1981). Occasionally, what appears to be two "eyes", side by side at the same node, can occur. According to May (1964), this situation only arises if the second leaf of the lateral shoot is reduced to a bract.

1.1.c. Formation of primordia in the primary latent bud

This subject has been most recently reviewed by Srinivasan and Mullins (1981).

i) Leaf primordia: Leaf primordia form on the flanks of the primordial shoot apex, arising in acropetal succession from the apical meristem and with distichous phyllotaxy (Carolus 1971). "... Associated with each leaf primordium are two ovoid, stipular scales, located one on either side of the leaf primordium. Initially, the scales are as big as leaf primordia but their growth soon ceases and they become sclerified. The leaf primordia are pointed structures which become lobed at their bases and rapidly assume a leaf-like appearance. The first two or three leaf primordia grow rapidly and envelop the subsequent primordia. The later-formed leaf primordia are relatively slow growing and they remain small. Hairs develop from the upper epidermal cells of leaf and scale primordia and produce a tomentum (hair or wool) which encases each whorl of leaves" (Srinivasan and Mullins 1981).

Therefore the apical meristem of the PLB is protected by the basal scale (bract) of the lateral shoot, the basal scales (bracts) of the PLB (which subtend the SLB, TLB, etc. buds), the stipular scales, the basal leaf primordia and the tomentum (May 1964; Srinivasan and Mullins 1981). The SLB and TLB, as a result of their location, are protected in a similar but
Fig. 1.1 (a) Diagrammatic transverse section through a compound bud of 'Concord'.

(b) Diagrammatic longitudinal section in the plane of the cane axis. Lat. lateral shoot; LS, leaf scar; 1, primary bud in axil of prophyll (solid black) of lateral shoot; 2, secondary bud in axil of basal prophyll (horizontally hatched) of primary bud; 3, tertiary bud in axil of next higher prophyll (vertically hatched) of primary bud (from Pratt 1974).
Fig. 1.2 Shadow tracings of the scales, leaves and axillary buds of a 'dormant bud' (compound bud) sampled in winter (cv. Freisamer). Only the three most basal leaves are shown. NB = scale belonging to the lateral shoot; NB to NB = scales belonging to the 'dormant shoot' formed within the 'dormant bud'; B to B = leaves of the 'dormant shoot', each with their appended two scales; K to K = axillary buds (the axillary buds of B and B are too small to be shown at this magnification (from May 1964).
not identical fashion.

The number of leaf primordia, formed by the primary latent bud before dormancy, varies with cultivar. For example, 12 to 13 leaf primordia are formed in 'Sultana' but 'Gutedel' (syn. 'Chasselas'), 'Riesling', 'Auxerrois' and 'Freisamer' produce fewer than 12 (May 1964).

ii) Anlagen: Anlagen are club-shaped, meristematic protruberances which arise from the apices of latent buds; they are "uncommitted primordia" which may be directed to form inflorescence primordia, tendril primordia or shoot primordia (Srinivasan and Mullins 1981). Depending on the cultivar, the PLB apex produces 3 to 8 leaf primordia before dividing into two almost equal parts; the part opposite the youngest leaf primordium is the Anlage, the other part continuing to function as the apex of the primordial shoot. The formation of Anlagen from the apex is regarded as the stage of initiation of the inflorescence axis.

Anlagen develop as broad, blunt, obovate structures, lacking stipular scales. Further development of Anlagen starts with the formation of a bract, which is followed by division of the Anlage into two unequal parts called "arms". The larger adaxial part (nearer to the apex) is the "inner arm", and the smaller abaxial part adjoining the bract is the "outer arm" (Srinivasan and Mullins 1981).

iii) Inflorescence primordia: Anlagen which develop as inflorescences undergo branching to form a conical structure composed of many rounded branch primordia. Branching of the inner arm is much greater than that of the outer arm and gives rise to the main body of the inflorescence primordium. The primary branch primordia of both arms give rise to branch primordia of the second and third order, each of which is subtended by a bract. The degree of branching of the inner arm gradually decreases in an acropetal direction, giving the inflorescence primordium a conical shape. Depending on the cultivar, one to three inflorescence primordia will usually be formed before the PLB enters into dormancy (Srinivasan and Mullins 1981).

iv) Tendril primordia: Although most Anlagen initiated in latent buds give rise to inflorescences, there are some which give rise to tendrils. A mature latent bud which contains one or more inflorescence primordia is called a "fruitful bud", whereas one which contains tendril primordia in
the place of inflorescence primordia is called "unfruitful, vegetative, or barren" (Srinivasan and Mullins 1981). (Note that these terms are usually applied to the "eye" as a whole rather than just the PLB. However, it is only a minor distinction because if the PLB is not fruitful, the "eye" as whole is unlikely to be fruitful.)

The external morphology of "fruitful eyes" is indistinguishable from that of "unfruitful" (May 1964).

v) Bud "primordia": In addition to the previously described N+3 buds in the axils of the basal bracts of the PLB, i.e. SLB, TLB, etc., there are also buds in the axils of the leaf primordia. Some of these buds are not true primordia because the most developed of these buds, in the axils of the basal leaf primordia, may have two or three leaf primordia by the time the PLB becomes dormant. The buds of younger (more distal) leaf primordia are preformed only as swellings in the tissue (May 1964) and are thus properly termed "primordia". These buds are of the same order as the SLB, TLB, etc., i.e. N+3. However, there is one important difference: they are subtended by primordia of foliage leaves. Therefore, these buds have the potential to develop into shoots at the same time (in the same season) as their subtending leaf expands. In fact, the "rule" previously outlined is obeyed because these buds are the "prompt" buds for the next growing season. Fournioux and Bessis (1982) distinguish between the two types of axillary buds of the PLB by referring to them as "bourgeons N+3 prefoliaires", i.e. SLB, TLB, on the one hand, and "bourgeons N+3 foliaires", i.e. the bud primordia, precursors of "prompt" buds, on the other (Figs 1.3, 1.4).

The SLB and TLB may also contain bud primordia in the axils of their basal bracts in a similar fashion to the PLB (May 1964). Such buds, are, of course, branches of the fourth order - "bourgeons N+4 prefoliaires" in the terminology of Fournioux and Bessis (1982) and are termed "bourgeon tertiaire A1" by Carolus (1971) (Fig. 1.5).

1.1.d. Base buds: There is still some confusion in recent literature concerning the origin of "base buds", even though this subject has been recently reviewed by Pool et al. (1978). Winkler (1926) was the first to call the buds at the base of the cane "base buds" according to Pool et al. (1978), in order to distinguish them from the buds (eyes) counted at pruning. Grapegrowers in Australia refer to the latter as "clear buds"
Fig. 1.3 Diagrammatic representation of the complex of axillary buds of the grapevine (from Fournioux and Bessis 1982).

$F = \text{leaf at node on main shoot } N$

$PF, PF_1, PF_2 = \text{prophylls}$

$F_2, F_3, F_3', F_4, F_4' = \text{leaf primordia}$
Fig. 1.4 The different types of buds present on a vine (pruned to a single cane and spur) in early summer and capable of developing into shoots if released from correlative inhibition. Prompt buds on main shoot (▲); primary latent buds (●); prompt buds on lateral shoot (○); base buds (●); unburst primary latent buds (●); latent buds on old wood (●) (from Fournioux and Bessis 1982).
Fig. 1.5 (a) Longitudinal and (b) transverse sections of a compound bud. e1, e2, e3: basal prophylls of primary latent bud ("bourgeon principal P") subtending secondary ("bourgeon secondaire A₁"), tertiary ("bourgeon secondaire A₂") and quaternary ("bourgeon secondaire A₃") latent buds respectively (from Carolus 1970).
The French use the term "oeil franc" to distinguish those buds (eyes) separated from the base buds by a definite internode. Buds at nodes more than 2 cm above the base of the cane have been termed "count nodes" (Pool et al. 1978). This, in turn, has led to the concept of components of yield per vine comprising "count crop" (= crop from count nodes on canes and renewal spurs) plus "non-count crop" (= crop from bases of canes and renewal spurs, i.e. base buds plus "water shoots").

The O.I.V. (Anon 1963) defines base bud (contre-bourgeon) as the "... dormant bud at the base of a cane which may develop when the other buds are destroyed" in English. This definition provides no information as to the possible origin of base buds. However, the French definition for "contre-bourgeon" is "... bourgeon secondaire ou prompt bourgeon latent qui peut evoluer lorsque le bourgeon principal est detruit". The use of the terms "secondaire", "prompt" and "principal" for buds corresponds to the terminology of Carolus (1971) and does give some hint as to the possible origin of base buds.

Base buds have two possible sources:

i) Commonly, of all the latent buds contained within the "eye", it is usually only the PLB which bursts in spring to produce the main or primary shoot. In such cases, the SLB and TLB (and quaternary, etc. if present) will remain enclosed by the bracts of the PLB and will not burst unless the primary shoot is destroyed by frost, etc. (If a vine is severely pruned, the SLB and TLB may burst at the same time as, or soon after, the PLB, resulting in two or three shoots per node.) The SLB and TLB thus constitute the lowest-two (most proximal) base buds.

ii) The uppermost buds (the term "upper" here is relative because the physical distance is very small) of the crown of base buds ("yeux de la couronne"; Fournioux and Bessis 1982) have a different origin. Pool et al. (1978) state that these buds "... develop in the axil of a bud scale or bract at the base of a green shoot. At such a node, the axillary bud (central bud) does not immediately grow into a shoot, but develops bud scales, a few leaves, and sometimes inflorescence primordia. Internodal elongation is minimal. The buds axillary to the first two bracts of the central base bud usually develop into buds with bud scales (side buds)."
These three buds become dormant. On the cane, they appear in a row parallel to the bud scale scar. Bud scale scars occur on opposite sides of the cane in the same alternating sequence as leaf scars, but the internode elongation is minimal." And also "... The lateral shoot and the primary bud are equivalent in origin to the central and first side buds respectively." (Fig. 1.6)

Therefore, put in another way, the "central" bud is derived from a "prompt" bud (N+1) which became dormant instead of growing into a lateral shoot. However, before going into dormancy, a limited amount of development results in the formation of two "side" buds in each of the axils of two basal bracts; one of these "side buds" is equivalent to the PLB (N+2) and the other side bud must also be a branch of the second order (N+2), not a SLB (N+3). The only problem with the description of the origin of the "uppermost base buds" by Pool et al. (1978) is that they describe the "central" bud as being in the axil of a bract, whereas "prompt" buds must, by definition, be subtended by a foliage leaf (May 1964).

Therefore, it is possible that the description of the origin of the "uppermost base buds" by Pool et al. (1978) is correct in all but their assumption that the "central bud" is equivalent to the lateral shoot (and thus "prompt" bud"). An alternative hypothesis might be that the "central" bud is derived from the "bourgeon N+3 prefoliaire" immediately distal to the TLB, i.e. the "quaternary bud". The "side" buds are equivalent to N+4 buds in the axils of the two basal bracts of this bud.

Pool et al. (1978) found the average number of base buds to be 3.3 on 'White Riesling' (the only Vitis vinifera cultivar examined) and 2.4 to 4.2 on French and American hybrids. Therefore, in the case of V. vinifera at least, the question of the source of the uppermost base buds is somewhat academic because the SLB and TLB make up approximately two-thirds of the base bud "population".

In practice, it is not always possible to classify readily the buds on the basal portion of a cane. Between the "base buds" and the first obvious count node, there may be one or more nodes which had small leaf blades and separated by short (1 to 2 cm) internodes. Such buds are transitional in structure between base buds and buds at count nodes, and may be difficult to classify when pruning a vine (Pool et al. 1978). This is certainly the case for 'Shiraz' (Dry, unpubl. data).
Fig. 1.6 'Concord' buds on a 1-node spur, A. Arm showing cane with 3 base buds and 1 count node (May 1, Northern hemisphere). B. Base bud 3 cut transversely showing cane bract, central bud and its first bract (stippled), side bud 1 and second central bud bract (hatching), and side bud 2 (no hatching). C. Same, cut longitudinally along dashed line of B, and across the longitudinal axis of the cane. D. Bud at count node cut transversely, showing leaf scar, scar of deciduous lateral and its bract (stippled), the primary bud and its first bract (hatching), secondary bud and second primary bud bract, tertiary bud (no hatching). E. Same, cut longitudinally along dashed line of D, and along the longitudinal axis of the cane (from Pool et al. 1978).
Base buds of *V. vinifera* cultivars do not burst under normal circumstances. Consequently, they may be left behind on the vine framework as a result of pruning practice and become embedded in the wood. Such buds may exist in a latent state for many years and, if stimulated to burst by severe pruning, etc., the shoots arising from these buds are commonly termed water shoots ("gourmands").

1.1.e. Bud dormancy

A large number of terms have been used to describe plant dormancy phenomena. For grapevines, the three phases of dormancy first defined by Kondo (1955) viz. "conditional", "organic" and "environmental", appear to have been widely used, e.g. Antcliff and May (1961). More recently, Lang et al. (1985) have chosen the term "dormancy" to describe the condition whereby there is no visible growth of any structure containing a meristem (e.g. a vegetative bud) and propose the following terminology:

**Ecto-dormancy**: Regulated by factors which are within the plant but which are external to the dormant structure.

**Endo-dormancy**: Regulated by factors within the dormant structure itself.

**Eco-dormancy**: Regulated by factors external to the plant, environmental in nature.

These terms are analogous with the "conditional", "organic" and "environmental" phases of Kondo (1955) respectively.

i) **Ecto-dormancy** is due to an inhibiting effect (usually termed "correlative inhibition") exerted on the latent bud by other organs. The three main sources of correlative inhibition are the main shoot apex, the lateral shoot and the leaf. The inhibition exercised by lateral shoots on latent buds is polarised in a basipetal direction, i.e. a bud at a given node is not inhibited by lateral shoots that are proximal to that node (Fournioux and Bessis 1982). The combination of topping of the main shoot and removal of lateral shoots is the most effective treatment to release latent buds from ecto-dormancy (Nigond 1961). This phenomenon is utilised in the technique of "double pruning" (Dry and Smart unpubl.) and arises naturally if a vineyard is damaged by hail, at or soon after flowering (Fournioux and Bessis 1982).

*Since changed to "paradormancy" (Lang 1986)*
ii) Endo-dormancy is due to a state of inhibition within the bud itself. Kondo (1955) stated that this was the phase in which cuttings would not burst in 20 days at favourable temperature. Endo-dormancy develops first in the basal buds of the shoot during January in Australia, and moves in a wave up the shoot. The onset coincides with cessation of shoot growth, start of periderm development, lignification of bud scales and veraison. The onset of endo-dormancy is favoured by an early decrease in shoot growth rate and by the presence of mature leaves; it is inhibited by young leaves, active shoot tips and clusters (Nigond 1961).

The "depth" of endo-dormancy is greatest at the beginning of autumn, i.e. the majority of buds on a vine are in deep dormancy before the vine as a whole shows the other signs normally associated with dormancy such as leaf fall, and the intensity of dormancy decreases gradually during autumn and winter. The need for a chilling requirement in order to release V. vinifera buds from endo-dormancy is not well proven; if it does exist, the requirement is small and easily satisfied under southern Australian conditions (Antcliff and May 1961).

At the onset of endo-dormancy, the weight of the bud ceases to increase and remains constant until late autumn, when very slow growth may recommence under mild climatic conditions (May 1964). Therefore, endo-dormancy lasts in each grape bud for only a few months and is largely broken by the start of winter. Thereafter, dormancy is maintained by low temperatures and is therefore environmental.

iii) Eco-dormancy is the result of unfavourable environmental conditions; if buds are placed under suitable temperature conditions, they will usually burst. There is an inverse relationship between the time to budburst and temperature (Antcliff and May 1961).

1.1.f. Summary

Fig. 1.7 and Table 1.1 describe the origin of the different buds likely to be found on a grapevine shoot. The structure on a dormant grape shoot (cane) which is commonly called a bud ("eye" in French) is actually a multitude of buds of different orders. For convenience, the word "bud" will be used for the compound structure and the primary latent bud will be referred to as the "primary axis" or PLB and the secondary and tertiary latent buds will be referred to as "secondary axes" or SLB and TLB.
Fig. 1.7 Diagrammatic representation of grapevine main shoot (N), lateral shoots of first (N+1), second (N+2) and third (N+3) order and compound buds (stippled).
Table 1.1 Summary of grapevine bud origin.

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<thead>
<tr>
<th>Order&lt;sup&gt;1&lt;/sup&gt;</th>
<th>Type of leaf subtending bud&lt;sup&gt;2&lt;/sup&gt;</th>
<th>Origin</th>
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<td>N</td>
<td>(S)</td>
<td>Main shoot</td>
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<tr>
<td>N + 1</td>
<td>F</td>
<td>Prompt bud and lateral shoot</td>
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<td>N + 2</td>
<td>S</td>
<td>Primary latent bud</td>
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<td>F</td>
<td>Prompt bud on N + 1 lateral shoot</td>
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<td>N + 3</td>
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<td>(i) Secondary, tertiary latent bud</td>
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<td>S</td>
<td>(ii) Primary latent bud on N + 1 lateral shoot</td>
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<td>F</td>
<td>(i) Prompt bud primordia in axils of leaf primordia of N + 2 primary latent bud</td>
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<tr>
<td></td>
<td>F</td>
<td>(ii) Prompt bud on N + 2 lateral shoot</td>
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<td>N + 4</td>
<td>S</td>
<td>(i) &quot;Bud primordia&quot; in axils of basal bracts of N + 3 secondary latent bud</td>
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<tr>
<td></td>
<td>S</td>
<td>(ii) Secondary, tertiary latent bud on N + 1 lateral shoot</td>
</tr>
</tbody>
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1 Terminology of Bugnon and Bessis (1968)
2 S = scale (bract, prophyll); F = foliage leaf

All buds of the grapevine are axillary, subtended by either a foliage leaf or a bract. The subsequent development of each type of bud is largely determined by the nature of the subtending leaf and the effect of correlative inhibition. A bud in the axil of a foliage leaf, e.g. a "prompt" bud, in the axil of a foliage leaf on a main shoot, can usually overcome the inhibiting effect of the main shoot apex. However, a bud in the axil of a bract, e.g. the PLB in the axil of the basal bract of a lateral shoot, is inhibited by the growing points of both the main shoot and lateral shoot and remains dormant, as a bud. If both sources of correlative inhibition at a particular node are removed, e.g. by topping the main shoot and/or removal of the lateral shoot at that node, then the PLB is able to burst to produce a shoot (Huglin 1958; Dry, unpubl.)
1.2 SHOOT DEVELOPMENT AND MORPHOLOGY

1.2.a. Budburst

The initial growth of dormant buds into a shoot is a result of the expansion of preformed nodes, internodes, leaves and anlagen. Subsequently, the shoot apex recommences meristematic activity to produce new nodes. Therefore, the basal 6 to 10 or so nodes on a shoot were initiated in the bud in the previous growing season (together with the organs at those nodes), with distal nodes initiated after budburst. The division between the two parts of each shoot is called the "point of discontinuity" and is sometimes indicated by a distinctly short internode (Bouard and Pouget 1971). For 'Shiraz', this point occurs, on average, between the 8th and the 9th nodes (Dry unpubl.).

The timing and rate of budburst is affected by winter and spring temperatures (May 1964; Lavee 1977), cultivar, pruning date and the position of a bud in relation to a pruning cut (Antcliff et al. 1956, 1957). Distal nodes usually burst first.

The presence of growing shoots on a cane inhibits the burst of more proximal buds (Bessis 1965). This phenomenon is particularly apparent in non-pruned vines. Also, bud fertility has a significant effect on budburst. Fruitful buds burst in preference to non-fruitful (Antcliff and Webster 1955; Antcliff et al. 1957). Bessis (1965) claimed that if there are more than 2 shoots per node, it is only because the secondary buds at that node are fruitful; however, Antcliff and Webster (1955) and others, have shown this is often, but not always, the case. Percentage budburst decreases as pruning severity decreases (Antcliff et al. 1956).

During winter the bud centre (excluding bud scales) has a dry matter content of about 50 percent and as budburst approaches and the bud weight increases, the percentage dry matter declines to about 25 percent at 3 weeks before budburst (Pouget 1963; May 1964).

1.1.b. Shoot growth

The growth of the whole shoot approximately follows a sigmoid curve. The fastest rate of shoot growth occurs just before or at flowering, up to 5 cm per day or more (Bouard 1971). The position of a shoot on a vine or bearing unit may have an influence on its rate of growth; for example, shoots adjacent to pruning cuts, or in apical positions, tend to grow more vigorously than others. Not all shoots
on a single vine grow at the same rate, however, a "vigorous" vine will have a majority of shoots growing at a greater rate than a "less vigorous" vine. Shoot length is the product of internode length and node number; on vigorous shoots internode length is initially the greatest cause of difference. Vigorous vines have longer shoots at the end of the growing season due to both longer internodes and more nodes.

Node formation usually stops soon after flowering, by which time the shoot will usually have 30 or more nodes (Bouard and Pouget 1971). The interval between formation of successive nodes (the plastochron) is about 7 days during early shoot growth, increasing gradually to (1 or 2 days) per flowering (Coombe, pers. comm.).

For traditionally-pruned vines, there is a constant number of nodes per shoot at the time of flowering. Using the "number of visible internodes" (the number of internodes >10mm long) as an index, Pratt and Coombe (1978) found the majority of shoots on Vitis vinifera cultivars to have 16 to 18 visible internodes at 70 per cent capfall (ignoring the small number of shoots on each vine with internodes <10mm). The authors suggested that the rate of development of flowers and production of nodes by the shoot tip are closely synchronised. However, this generalisation was developed on normally-pruned vines; shoots on lightly-pruned vines, e.g. mechanically hedged or "minimally-pruned", usually have fewer than 16 to 18 visible internodes at flowering (Table 1.2; Clingeleffer 1983a).

The growth of internodes continues for 12 to 32 days for 'Ugni blanc' (Bouard and Pouget 1971). Internode growth is initially by cell division, followed by cell expansion. Those internodes formed in the bud are slow to elongate whereas those formed during the period of rapid shoot growth, elongate the fastest.

Short internodes occur at basal nodes where they can be less than 1 cm. The longest internodes are usually found on shoots of vigorous vines, and, in particular on "shade" shoots or watershoots. Internode length increases from the base of the shoot until the "point of discontinuity", where there is a small decrease for one or more internodes. Bouard (1971) found an increase from the first internode (3cm) to the sixth (12.5cm) - internodes 9 to 20 fluctuated about a mean of 12cm.

1.2.c. Shoot morphology

The average internode length for any shoot is said to be set at an early stage; the length of the internode above the first bunch can therefore be used as an indication of subsequent shoot growth (Pratt and Coombe 1978).
Table 1.2 Shoot length, nodes per shoot and node length of 4 wine grape varieties at flowering 1982, when pruned to 2-bud spurs or minimal pruned (from Clingeleffer 1983a).

<table>
<thead>
<tr>
<th>Variety</th>
<th>Shoot length (cm)</th>
<th>Nodes per shoot</th>
<th>Internode length (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cabernet Sauvignon</td>
<td>2-bud spurs 57</td>
<td>15.1</td>
<td>3.8</td>
</tr>
<tr>
<td></td>
<td>Minimal</td>
<td>12</td>
<td>6.7</td>
</tr>
<tr>
<td>Shiraz</td>
<td>2-bud spurs 100</td>
<td>17.6</td>
<td>5.7</td>
</tr>
<tr>
<td></td>
<td>Minimal</td>
<td>20</td>
<td>8.7</td>
</tr>
<tr>
<td>Grenache</td>
<td>2-bud spurs 57</td>
<td>16.3</td>
<td>3.5</td>
</tr>
<tr>
<td></td>
<td>Minimal</td>
<td>11</td>
<td>8.0</td>
</tr>
<tr>
<td>Semillon</td>
<td>2-bud spurs 62</td>
<td>16.0</td>
<td>3.9</td>
</tr>
<tr>
<td></td>
<td>Minimal</td>
<td>17</td>
<td>8.5</td>
</tr>
</tbody>
</table>

In *Vitis vinifera*, the pattern of bunch or tendril distribution along a shoot is discontinuous; typically, a bunch or tendril is absent at every third node. The internode between two nodes with bunch or tendril for every triplet of nodes is longer than the adjacent internodes (Fig. 1.8), i.e. N1N2 > N2N0 or N0N1 (Bouard 1971). For *Vitis vinifera* N1N2 > N2N0 > N0N1 in 70 to 95 per cent of cases (depending on the cultivar) compared to N1N2 > N0N1 > N2N0. However, for other species of *Vitis*, this may be reversed (Bernard 1980). This pattern is repeated every three internodes along a shoot, unless there are two successive nodes without a bunch or tendril (Bouard 1971). In addition to internode length, length of lateral shoots and thickness of the diaphragm also show this rhythmic pattern (see Fig. 1.8). Persistent laterals are most likely to be found at nodes without bunch or tendril.

There is no rhythmic pattern for internode diameter; the diameter is greatest for basal internodes and gradually decreases along the shoot; for example, 12mm at the first, decreasing to 7mm at the fifteenth for 'Ugni blanc' (Bouard 1971).
Fig. 1.8 Diagrammatic representation of pattern of internode length, tendril distribution and lateral shoot length on a shoot of 'Ugni blanc' (syn. 'Trebbiano') (adapted from Bouard 1971).
1.2.d. Shoot vigour

Winkler et al. (1974) define "vigour" as "... the quality or condition that is expressed in rapid growth of the parts of the vine. It refers essentially to the rate of growth." "Capacity" by contrast, is defined as "... the quantity of action with respect to the total growth and total crop of which the vine or part of it is capable. The term refers to ability for total production rather than to rate of activity."

On a single shoot basis, vigour and capacity are linked, i.e. a vigorous shoot has a large capacity. Therefore, it is legitimate to describe a long, thick shoot as a vigorous shoot. Consequently, the terms "vigour" and "capacity" are often used interchangeably in viticultural literature or, more frequently, the term "vigour" is used exclusively. This is particularly the case when whole vines are discussed and "vigour" is often used when "capacity" would be more appropriate.

A "vigorous vine" may be defined as one on which most of the shoots were "vigorous". If such a vine was pruned lightly (i.e. increasing the number of nodes retained at pruning) its vigour would probably decline (i.e. the average rate of growth of most of its shoots will decline) but its capacity will increase.

1.3 FLORAL INITIATION AND BUD FERTILITY

1.3.a. Inflorescence primordia development

This subject was recently reviewed by Srinivasan and Mullins (1981). They recommended a developmental or phenological code for "flowering" (floral initiation) in the grapevine using stages 0 to 11 related to changes in the shape of organs or to the addition of new structures.

The early stages of floral initiation have been previously described in 1.1.a. from Stage 0 when the latent bud is in a vegetative stage with three to eight leaf primordia to Stage 1, formation of the first Anlage, to Stage 7, when the inflorescence primordium has branched into a conical shape. At this stage, when the latent bud enters endo-dormancy, the appearance of the fully-developed inflorescence primordium is "... rather like a bunch of grapes in which each berry-like branch primordium is a protruberance of undifferentiated meristematic tissue" (Srinivasan and Mullins 1981).
It is generally agreed that Stage 1 coincides with the time of flowering of the main shoot, commencing with buds of basal nodes and progressing acropetally along the shoot (May 1964; Carolus 1971). Pratt (1979) found that Stage 1 took place 6 and 12 days before flowering, when the main shoot had about 13 expanded leaves and 6 to 7 nodes in the primary latent bud for V. labruscana ('Concord') and V. vinifera ('Riesling') respectively. Similarly, Srinivasan and Mullins (1976) reported 5 leaf primordia in the primary bud when Stage 1 was reached in 'Shiraz'.

1.3.b. Initiation of floral primordia

Differentiation of flowers from inflorescence primordia is said to begin after the dormant latent buds are activated in spring (Scholefield and Ward 1975; Srinivasan and Mullins 1981). Initially, each branch primordium divides many times, ultimately forming the flower initials (Stage 8). The sequence of events in flower development is terminated with the mature flower at anthesis (Stage 11).

1.3.c. Effect of node position on bud fertility

This topic was well reviewed by Khanduja and Balasubrahmanyam (1972). Buds at the most basal 2 or 3 count nodes are usually less fruitful than the next 10 or so distal count nodes; however, there are marked differences between cultivars. For example, 'Sultana' has fruitful buds located more distally than 'Riesling'.

The fruitfulness of 'Sultana' canes has been studied in detail (Antcliff and Webster 1955a, b; Antcliff et al. 1956, 1957); the typical trend in fruitfulness along a cane for this cultivar is shown in Table 1.3.

<table>
<thead>
<tr>
<th>Node position</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>11</th>
<th>12</th>
<th>13</th>
<th>14</th>
</tr>
</thead>
<tbody>
<tr>
<td>Percentage of nodes with fruitful shoots</td>
<td>22</td>
<td>27</td>
<td>38</td>
<td>48</td>
<td>57</td>
<td>57</td>
<td>58</td>
<td>59</td>
<td>57</td>
<td>53</td>
<td>54</td>
<td>50</td>
<td>50</td>
<td>45</td>
</tr>
</tbody>
</table>

May and Cellier (1973) studied the fruitfulness of ten grapevine
cultivars over four seasons by forcing dormant single-node cuttings and measuring the number and weight of inflorescences after budburst. They concluded that two factors control the number of inflorescences per node (strictly speaking, on "primary" shoots only) and, to a lesser extent, the weight of inflorescences per node. Firstly, the quadratic trend, i.e. the increase in fruitfulness from the proximal part of the cane to its middle portion, and the subsequent decrease from the middle to the distal portion, is constant from year to year and is most likely a genetically-fixed characteristic. Secondly, the linear trend, i.e. the increase in inflorescence number from the basal buds towards the tip of the cane, is influenced by seasonal conditions.

1.3.d. Fertility of "secondary shoots"

Shoots arising from secondary and tertiary latent buds are termed "secondary shoots". Shoots arising from secondary latent buds are occasionally fruitful (depending on cultivar) but shoots arising from tertiary latent buds are rarely fruitful for any cultivar (Winkler et al. 1974).

The fertility of "primary" and "secondary" shoots has usually been compared by using nodes with more than one shoot per node. In such cases, unless the phyllotaxic plane of the shoots has been taken into consideration, it is usually assumed that the most fruitful shoot, of the two or three shoots at that node, is the "primary" shoot. As a result, from such studies, the "primary" shoot is always found to be more fruitful than the "secondary" shoots (Bessis 1965). Antcliff and Webster (1955b) collected data from 'Sultana' nodes with two shoots (the frequency of 2-shoted nodes varied from seven to 11 percent over the four years of their study) and found that 18 percent of such nodes had both shoots fruitful, 52 percent had one shoot fruitful (which they assumed was always the "primary" shoot) and 30 percent had both shoots not fruitful. The primary latent bud did not burst at 3.3 percent of nodes (the authors did not explain how they identified unburst buds as primary latent buds) and two percent of the assumed "secondary" shoots were fruitful.

An alternative method of determining the fertility of "secondary" shoots, employed by Huglin (1958) and Bessis (1965), is to remove all shoots from canes four weeks after budburst and thus "force out" "secondary" (the assumption here is that the majority of buds initially bursting are primary latent buds and relatively few "primary" shoots will make up the shoot population resulting from the "forced" burst). Both
authors found that the fertility of the "primary" shoots was greater using this technique. The ratio of "secondary" shoots to "primary" shoots for bunches per shoot at nodes one to eight was 0.35, 0.40, and 0.50 for 'Chardonnay', 'Aligote' and 'Pinot noir' respectively (Bessis 1965).

Compared to "primary" shoots, the fertility of "secondary" shoots was irregular with regard to node position but "secondary" shoots at nodes one and two were always less fruitful than more distal nodes (Bessis 1965).

Kornechuk and Plakida 1950, 1959 (cited in Khanduja and Balasubrahmanyam 1972) found "secondary" shoots (termed "replacement buds" by these authors) to be 33 percent as fruitful as "primary" shoots in 'Chasselas', 20 percent in 'Riesling', 15 percent in 'Aligote', 6 percent in 'Muscat blanc' and 46 percent in 'Cabernet' (franc or sauvignon?).

Carbonneau and Casteran (1979) identified "primary" and "secondary" shoots by considering their different phyllotaxies. The primary latent bud, and consequently the primary shoot, has a phyllotaxic plane parallel to that of the cane whereas "secondary" shoots have one perpendicular to the cane. (Because the shoots arising from secondary and tertiary latent buds have the same phyllotaxic plane, it is not possible to distinguish one from the other, unless it is assumed that, in the situation where there are 3 shoots at a node, the "secondary" is always more fruitful than the "tertiary").

Fournioux and Bessis (1982) also used phyllotaxy to distinguish between "primary" and "secondary" shoots.

Carbonneau and Casteran (1979) found "primary" shoots were more fertile (with more and larger bunches) than "secondary" shoots in irrigated and non-irrigated 'Cabernet Sauvignon' vines (Table 1.4). In addition, irrigation significantly increased the ratio of "secondary" to "primary" shoots.

Table 1.4 Fertility of "primary" and "secondary" shoots of 'Cabernet Sauvignon' (adapted from Carbonneau and Casteran 1979).

<table>
<thead>
<tr>
<th></th>
<th>Inflorescences per shoot</th>
<th>Flowers/Inflorescence</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Irrigated</td>
<td>Non-irrigated</td>
</tr>
<tr>
<td>Primary shoots</td>
<td>1.84</td>
<td>1.94</td>
</tr>
<tr>
<td>Secondary shoots</td>
<td>1.23</td>
<td>1.32</td>
</tr>
</tbody>
</table>

Bessis (1965) also found "secondary" shoots had smaller inflorescences than "primary" shoots. The average weight of inflorescences on "secondary"
shoots was half that on "primary" shoots for 'Chasselas' and 'Rkatztiteli' (Koval and Nikiforova 1962; cited in Khanduja and Balasubrahmanyam 1972).

1.4 BUD ABNORMALITIES IN GRAPEVINES AND OTHER WOODY PLANTS

A large number of different bud abnormalities have been described in grapevines and other woody plants. These can be divided into two categories. In the first category, lack of budburst is the main symptom, either at a single node or at several node positions, e.g. "blind buds", "bud failure", "bud death" or abscission of whole buds ("bud drop"). In the second category, observed by bud dissection, there is death of part or of whole buds, or of one or more buds within a compound bud, e.g. "bud necrosis" or "bud death"; budburst may take place if one bud at a node is unaffected.

1.4.a. "Blind buds", "bud failure", "bud death"

i) Grapevines: Reviewing the literature on this topic presents some difficulties because it is not always easy to separate those cases where the lack of budburst is a result of a bud abnormality (due to one of a number of possible causes), from those where the buds are "normal" but inhibited from bursting for physiological reasons. An example of the latter type is poor budburst at nodes on the mid-section of horizontally-trained canes (these are often termed "blind buds"). When such canes are trained in an arch so that the mid-section is higher than the basal or apical sections, budburst at the mid-section is significantly improved (Clingleffer 1983). In such a case, poor budburst is due to correlative inhibition. A similar situation can arise when the number of nodes per cane is increased; Rosner and Cook (1983) found an inverse relationship between cane length and percentage of "blind buds" at nodes one to four.

Smit (pers. comm.) has microscopically examined buds of various winegrape cultivars in South Africa, during the course of studies on bud fertility. He reports "dead buds", without obvious mite damage on spur-pruned vines of all winegrape cultivars, including "Chenin blanc", 'Semillon', "Muscat Gordo Blanco", 'Cinsaut', 'Palomino' and 'Crouchen'. Usually, the percentage of "dead buds" on spurs was less than 10, and less often 20 to 40, particularly for 'Crouchen', 'Chenin blanc' and 'Muscat Gordo Blanco'. He does not state if the whole compound bud was dead or just one or more of the axes.

Smit (pers. comm.) also reports "dead buds" on 'Sultana' grown in the
Orange River region of South Africa. In 1978, the mean percentage for all vineyards was 25, with variation between vineyards of 7 to 58 percent; there was variation between seasons. He describes the symptoms as follows:

"... Dying of buds starts in the central apical bud meristem and gradually proceeds outwards. During bud analysis in May, all degrees of bud dying may be present from browning of the central meristem top to the greater part of the bud core being dead. Erinose bud mites were definitely not the problem." One could possibly interpret this description as not only death of the whole bud but also death of just the primary axis.

In India, "bud mortality" has been described by a number of authors. Bindra (1977), Chundawat et al. (1977), Dabas (1979) have observed a high incidence of "dead buds" in 'Banquabad' and 'Anab-e-Shahi' (both seeded cultivars) but not in 'Beauty Seedless'. These reports refer only to "buds" but Bindra and Chohan (1975) state that usually "... one or two of the three buds in the compound bud" are found dead and very occasionally "... all three".

There are other Indian reports of "bud mortality" but in these cases, the authors are referring to abscission of flowers from inflorescences ("flower bud drop" or "flower bud shedding") before flowering, e.g. Bindra and Brar 1977. (Unfortunately, the term "flower bud drop" is also used in Indian literature where the authors are obviously referring to mortality of compound buds, partly or as a whole, when they presumably mean "fruitful bud drop").

Pool et al. (1978) have found a high mortality for "base buds" in New York State grapevines. Base buds of V.labruscana ('Concord') had 46 and 61 percent mortality for "sun" and "shade" canes respectively whereas the values for V.vinifera ('Riesling') were 19 and 36 percent.

ii) "Bud failure", "bud drop" in other plants: In almonds, a genetic factor has been blamed for "bud failure" (Kester 1976). Bud drop in peach and other stone fruits in California has been found to be associated with above-average temperatures in late September and early October (Brown 1958).

Shoot tip abortion is known in some species which do not form the terminal buds (Shulman 1982), e.g. Ulmus (Millington 1963), Syringa (Garrison and Wetmore 1961), Citrus (Kozlowski 1973).

In pistachio, abscission of flower buds is induced by seeded fruits (Porlingis 1974).

1.4.b. "Bud necrosis", "bud death" in grapevines
In this category those reports are reviewed where the abortion or the partial or complete necrosis of the primary axis of the compound bud has been (or appears to have been) confirmed microscopically, as distinct from those previously reviewed where it appeared that the whole compound bud was affected.

Bindra and Chohan (1975) reported "death" of part of the bud (the primary axis alone?) in the seeded cultivar Anab-e-Shahi in India. Necrotic tissue extended downward from the bud apex to varying degrees, necrosis commenced soon after flowering (Bindra 1980). The description by Smit (pers. comm.) mentioned above could be interpreted as partial or complete nerosis of the primary axis of 'Sultana' buds in South Africa.

Bernstein (1969, 1973) reported bud necrosis for a range of cultivars in Israel. He described a partial or complete necrosis of the primary axis - the secondary axes or the bud as a whole were rarely affected. Externally, those buds with a necrotic primary axis appear identical to normal buds. 'Dattier de Beirouth' (syn. 'Waltham Cross') and 'Queen of the Vineyard' were found to be the most "susceptible" cultivars. The percentage of buds with partially or completely necrotic primary axes was greatest on the basal part of the cane (nodes one to six approximately) and varied from one year to the next.

Lavee et al. (1981a) further reported on this condition in Israel. The induction of necrosis was found to take place during flowering in 'Queen of the Vineyard' and the incidence was highest in vigorous vineyards.

1.5 POSSIBLE CAUSES OF BUD ABNORMALITIES

1.5.a. Poor budburst, bud abscission, death of whole buds

This section includes those abnormalities where the manifestation is poor or nil budburst, bud abscission or death of whole buds and is confined to grapevines unless otherwise indicated.

i) Poor maturity of winter canes: Winkler et al. (1974) stated that "bud failure" follows poor bud development caused by incomplete wood maturation (lignification) during the previous season. The basal parts of such winter canes used for spur or cane pruning appear to be well lignified but distal parts may have a typical red colour in winter. Failure of wood to lignify often results from vigorous late-season growth following overuse of
nitrogenous fertilizers, defoliation, virus diseases or potassium deficiency. Similarly, Antcliff et al. (1957) noted that 'Sultana' canes should be "well-ripened" and have good wood maturity for good budburst.

ii) Bud mites: The grape erineum mite, Colomerus vitis (Eriophyes vitis) is widespread on grapevines throughout the world. According to Flaherty et al. (1981) this mite exists in three morphologically identical but physiologically different strains, recognised by the characteristic injury each causes. The symptoms of the "erineum" or "leaf blister" strain are most commonly observed in vineyards but have little economic significance. In California, the "bud mite" strain is reported to live within grape buds, (not producing leaf blister symptoms) feeding at the base of the outer bud scales and causing a distinctive blister-like growth on the inner surfaces. Generally, the mites are confined to the outer bud scales but they may penetrate deeper into the bud. Most commonly, bud break is still able to take place but the young shoots are characterised by short basal internodes, scarification, flattened shoots, "witches broom" growth or "zigzagged" shoots. Leaves are usually stunted and wrinkled and the veins are prominent and drawn together. In severe cases, whole buds may be killed in winter and early spring (Flaherty et al. 1981). Within the vineyard, outbreaks are sporadic and localised (Winkler et al. 1974). Infestation of buds on a cane is not uniform but generally is more prevalent in basal buds. For definite diagnosis (usually carried out after shoot symptoms appear) infested bud scales should show blisters and scars on the inner surface; in addition, mites and/or their remains will often be seen (Flaherty et al. 1981).

In Australia, the leaf-blister strain is present in most vineyards but rarely causes an economic problem. Loder (1971) suggested that bud-mites (Eriophyes vitis) were the cause of "spur failure", i.e. lack of budburst and/or stunted shoot growth on 2-node spurs in South Australian vineyards on the basis of a higher mite count in buds at basal nodes than apical nodes of winter canes. On the other hand, Goodwin (1977) concluded, after six years research, that there was no conclusive evidence in favour of bud mite damage in Australia; furthermore, he also stated that "... in California, extensive studies showed that their "bud mite injury" was caused by early-season boron deficiency".

The grape leaf rust mite Calepitrimerus viti, has been reported as causing bud damage in Portugal but not in Australia (Goodwin 1977) or California (Flaherty et al. 1981). This species is rarely seen in Australian vineyards. Typical symptoms include a bronzed or rust-like
appearance of both leaf surfaces. The leaf curl strain causes few abnormal plant hairs on colonised spots.

iii) Winter injury: The degree of cold that a grapevine can withstand depends on cultivar, degree of lignification of canes and the weather pattern preceding the freeze (Winkler et al. 1974). All vinifera cultivars, if fully dormant, can withstand temperatures as low as -12°C. However, if not well-matured, canes and buds can be killed by less severe temperatures. Pool et al. (1978) assumed that "death" of "base" buds was due to winter cold, "base" buds being more susceptible than buds at count nodes.

iv) Application of growth regulators: This subject has been most recently reviewed by Considine (1982) who reported that BOA, CCC, CEPA, auxins and especially gibberellins (GA3) are capable of reducing the proportion of buds that are able to burst in grapevines. In general, those chemicals that reduce budburst also delay budburst: compounds which both reduce and delay include CEPA, GA3, CCC, SADH (at high concentrations), MH and IT3456. On the other hand, NAA and ABA have been shown to delay budburst but not interfere with the proportion of buds which burst.

Although CCC (Weaver et al. 1968) and CEPA (Clore and Fay 1970) reduced budburst in the year following treatment, in general, with the notable exception of GA3, application of growth regulators to grapevines rarely has a carry-over effect (Considine 1982).

Whole-vine sprays of GA3, applied before or during flowering, resulted in reduced budburst in the following season with 'Waltham Cross' (Stannard et al. 1974), 'Sylvaner' (Julliard and Balthazard 1965) and 'Barlinka' (Uys and Blommaert 1974). The effect of GA3 on budburst is only pronounced for seeded cultivars (Weaver 1960; Weaver and McCune 1961).

Reduced budburst following GA3 application can result in significant yield reductions, largely a consequence of reduced bunch numbers per vine (Stoler and Bernstein 1963a; Uys and Blommaert 1974; Weaver and McCune 1961), e.g. a decrease in 'Waltham Cross' bunch number of up to 80 percent was recorded (Stannard et al. 1974). Immersion of the base of single bud cuttings in GA3 solution also results in reduced budburst (Antcliff and May 1961).

Application of GA3 to several Prunus species at various times during the growing season, including floral initiation, inhibits the development of
both floral and vegetative buds (Bradley and Crane 1960). Such inhibited
buds usually fail to survive the winter. Similarly, Stembridge and Larue
(1969) found that GA₃ applied before leaf fall induced bud mortality and
retarded bud development in peach. (Inhibition of flower bud development,
i.e. floral initiation, by GA₃, without any detrimental effect to the buds,
is a widely observed phenomenon in many plants, including grapevines
(Srinivasan and Mullins 1981), and should not be confused with the GA₃-
induced inhibition of bud development and bud mortality).
Lin et al. (1984) found application of GA₃ to inflorescence buds of
pistachio, when cell division in the sub-apical meristem of the rachis had
essentially terminated, induced cell division in the bases of the buds with
subsequent bud abscission. Further, a direct correlation has been found
between "bud failure" in almonds and the amount of gibberellin in the tree
(Kester 1976).

1.5.b. Primary bud necrosis of grapevines

i) Winter injury: Zabadal (1981) reports that where buds have been injured
by extreme cold, it is possible for the primary axis alone to be killed but
for the secondary axes to remain alive.

ii) Vigour: Bud mortality of "Anab-e-Shahi" and "Sultana" in India was
found to be closely related to vine vigour (Bindra 1977; Jindal and Dabas
1982) and attributed to the excessive vegetative growth resulting from
over-use of nitrogenous fertilizers (Bain et al. 1981). A reduction in
irrigation and nitrogen addition (Bindra and Chohan 1975), root exposure
and pruning or shoot pinching or CCC application (Bindra et al. 1975) were
found to decrease both vine vigour and bud mortality.

Bernstein (1969, 1973) and Lavee et al. (1981a), working with 'Queen of the
Vineyard' in Israel, found a higher incidence of bud necrosis on thick
canes compared to thin canes and in higher vigour vineyards compared to low
vigour vineyards.

Irrigation of 'Cabernet Sauvignon' in the Bordeaux region of France
increased the ratio of "secondary shoots" (those derived from the secondary
axes) to "primary shoots" (those derived from primary axes) from 0.20 to
0.35 (Carbonneau and Casteran 1979). Irrigation also significantly
increased vine vigour. The authors hypothesized that the increased water
content of the bud tissues depressed cellular differentiation and normal
anatomic development of the primary axis. As a result, "... the primary bud (axis) is strongly depressed during the floral-initiation period and disappears before bud-burst time, or, at least, is not induced in the latent (compound) bud." It is possible that the authors are referring to abortion of the primary axis, i.e. the same condition described by Bernstein (1969, 1973) and Lavee et al. (1981a); however, they do not cite any references to support their hypothesis nor give details of any anatomical study.

In contrast, Meriaux et al. (1981), working with 'Grenache' in the south of France, found that irrigation resulted in poorer budburst (Carbonneaux and Casteran 1979 found no effect of irrigation on budburst), particularly at the base of canes, but with no effect on the ratio of "secondary" to "primary" shoots.

iii) Application of gibberellins: The first reports of gibberellin injury to grapevines as a whole, and to buds in particular, appear to have emanated from the work of Weaver and others in California and is summarised in Weaver and McCune (1961). Foliar sprays at concentrations of 5ppm GA₃ or higher were found to decrease shoot and bunch numbers in the following season on seeded cultivars, one reason being that "... the primary buds on sprayed vines were often dead, but the two lateral buds [the authors presumably mean secondary and tertiary buds here] had often developed." By comparison, very high concentrations of GA₃ (up to 1 000 ppm) to seedless cultivars such as 'Thompson Seedless' (syn. 'Sultana') did not cause any noticeable bud injury.

The next reports of this bud injury phenomenon came from Israel, where application of GA₃ to the seeded cultivars Queen of Vineyard, Alphonse Lavalee and Panse Precoce also resulted in necrosis of the primary axis and elongation of the secondary axes, giving the appearance of a "split bud" in winter (Stoler and Bernstein 1963a,b - cited in Lavee et al. 1981b). GA₃ application to leaves is more effective than to the buds themselves and only young and developing buds are particularly sensitive. GA₃ results in elongation of the primary axis, development of a necrotic layer at the base of and usually eventual necrosis of the primary axis. Naturally-occurring necrosis in the primary axis of 'Queen of the Vineyard' buds is similar to that induced by exogenous treatments of GA₃ (Lavee et al. 1981b). The seedless cultivars, Sultana and Perlette, were not sensitive to exogenous application of GA₃ and levels of bud necrosis were the same in control and
sprayed vines (Bernstein 1969, 1973).

iv) Defoliation and shoot topping caused by hail damage (see 1.6.e).

1.6 SUMMER PRUNING OF GRAPEVINES

Early during the investigations, it was apparent that summer pruning of grapevines had a large effect on the development of bud necrosis. Therefore the topic is reviewed in this section.

"Summer pruning" of grapevines is defined by Winkler et al. (1974) as "... removal of buds, shoots or leaves while they are green or herbaceous." There are a number of summer pruning operations carried out in vineyards, not all of which will be reviewed here (for example, those involved with the training of young and mature vines).

1.6.a Types of summer pruning operations.

i) Tipping (pinching): This is the removal by hand of the distal end (8 to 12 cm) of growing shoots. No expanded leaves are removed. The immediate effect is to stop shoot elongation — however, the effect is only temporary because growth will be usually continued by the most distal lateral. Tipping is carried out on shoots less than 60 cm long to increase resistance to wind damage (Winkler et al. 1974). Tipping is also used at the start of flowering to induce better fruit set (Coombe 1970).

ii) Topping (slashing, hedging, "rognage"): This practice consists of removal of 20 cm or more from the end of shoots; it may be carried out several times from late spring when shoots are actively growing or just before harvest, when shoot growth has usually ceased to facilitate harvesting operations. At present, topping is usually mechanised.

Topping is practised on young shoots to increase resistance to wind damage and at the start of flowering to increase fruit set (Winkler et al. 1974). It is also carried out in vigorous vineyards, both in Australia and overseas (a) to decrease canopy shading and fungal disease incidence (Lavee 1982), and (b) to facilitate cultural operations such as chemical spray application and weed control.

The increased adoption of this practice in Australian vineyards has coincided with an increase in vine vigour which has followed the use of
irrigation, better clones and rootstocks, and better nutrition. Also increased awareness of the detrimental effects of dense canopies to fruit quality (Smart 1984) has resulted in an increase in the incidence of hedging operations, and not just in vigorous vineyards. In some cases, the first hedging operation may be carried out soon after flowering and repeated 3 or 4 times, e.g. the Margaret River area of Western Australia.

Repeated topping is practised in many European vineyards ("rognage" in France); although topping has a weakening effect, this may be offset by improved exposure of the basal leaves to radiation. These leaves are normally shaded and senesce prematurely - topping exposes these leaves and it is thought their renewed photosynthetic activity offsets to a considerable degree the loss of the uppermost leaves (Winkler et al. 1974).

Although topping may be aimed at reducing canopy shading, it may be counter-productive because in some cases, topping can in fact increase shading. For example, a single topping of vigorous vines before or soon after flowering may significantly increase the number of shoot apices within a smaller volume, as a result of lateral shoot development - this leads to an increase in leaf density (Winkler et al. 1974; Lavee 1982)

iii) Removal of mature leaves ("effeuillage"): This practice of removal of basal leaves, often together with lateral shoots at basal nodes, is used in table grape culture to improve fruit quality, i.e. to improve colouration, to decrease wind damage and bunch rot (Andris 1982). In Europe, it is carried out to decrease bunch rot in wine grapes particularly in regions with a high incidence of rainfall during the growing season. Also, the increased berry temperature resulting from improved bunch exposure, will increase respiration of malic acid and thus decrease titratable acidity of the must (Casteran 1971).

iv) Shoot thinning: Shoot thinning, also called "crown suckering", "suckering" or "deshooting", is a procedure performed early in the growing season prior to flowering. This practice is mainly carried out in table grape vineyards, particularly in California, to facilitate bunch thinning and to reduce harvest damage. Most cultivars are shoot thinned when shoots are 10 to 15cm long (Andris 1982). This practice is distinct from the springtime removal of suckers from trunks in most vineyards.
1.6.b. Effect of topping and defoliation on lateral shoot growth.

The stimulation of lateral shoot growth is a commonly-observed response to topping or defoliation. This is an expected phenomenon since both the main shoot apex and leaves have been shown to be a source of correlative inhibition. Hirschfeld 1979 (cited in Lavee 1982) found the growth rate of lateral shoots of grapevines to be dependent on distance from the point of topping and the severity of topping (Fig. 1.9).

All levels of defoliation (0 to 75 per cent) of potted vines at set significantly increased lateral number but defoliation at later times did not (Kliwerer and Fuller 1973). Removal of young leaves and shoot topping in apple (Mika 1971, 1983), walnut (Maugut 1976) and other deciduous fruit trees (Giesberger 1975) also promotes development of lateral shoots.

1.6.c. Effects on budburst, fruitfulness, yield and vigour in the season following summer pruning of grapevines.

Most studies of the effects of defoliation and topping on grapevines have been confined to effects in the same season (Kliwerer and Fuller 1973). Those which have been extended to following seasons are mentioned below:

i) Budburst: May et al. (1969) examined the effects of shoot thinning (removal of all non-fruiting shoots) and defoliation (various levels of defoliation of remaining fruiting shoots), applied 4 weeks after flowering (start of lag phase of berry development) with 'Sultana'. Newly-produced leaves were removed on two subsequent occasions. (The authors give no indication as to the relative numbers of fruitful and non-fruitful shoots, only that shoot thinning, with no defoliation, resulted in a 16 percent reduction in leaf area per vine relative to the control.) Shoot thinning had no effect on percent budburst. Defoliated shoots had lower percent budburst than foliated on the same vine; also, leaf area per vine and percent budburst were negatively correlated.

By comparison, Peterson and Smart (1975) found no effect on percent budburst in 'Shiraz' from the topping of all shoots to either 6 or 10 nodes per shoot at the same growth stage. In addition, earlier times of topping had no effect on percent budburst.

ii) Fruitfulness: Khanduja and Balasubrahmanyam (1972) cite a number of reports in which tipping increased fruitfulness of "primary" and
Fig. 1.9 The growth rate of lateral shoots on control (o) and topped (●) shoots of 'Perlette'. Node 1 is most distal node on topped shoot and comparable node on control shoot (from Lavee 1982)
"secondary" buds. The increase may be located at proximal or median nodes of the cane. Tipping "De Chaunac" vines several times in mid-summer had no effect on fruitfulness (Wiebe 1975). Topping just before flowering increased fruitfulness of vigorous varieties but decreased it with those which are moderately-vigorous (Sapozhnikova 1964 - cited in Khanduja and Balasubrahmanyam 1972). Topping 'Shiraz' to 6 or 10 nodes during bunch elongation or fruit set had either no effect or caused a small increase in bunch number per shoot or per vine in the following season (Peterson and Smart 1975).

Defoliation 4 weeks after flowering resulted in decreased percentages of fruitful shoots, bunches per node and berries per bunch with 'Sultana' (May et al. 1969), for both defoliated vines compared to controls, and defoliated compared to foliated shoots on the same vine. Similarly, Wagner et al. (1978) found that 50 percent defoliation (removal of basal leaves, i.e. "effeuillage") at the start of flowering reduced fruitfulness for a range of varieties in Alsace, the largest decreases being for 'Muscat Ottonel' (47 percent decrease relative to control) and 'Chasselas' (37 percent).

iii) Yield: Removal of non-fruiting shoots of 'Sultana' at the end of flowering decreased yield in the following season (Thomas and Barnard 1937) but, when carried out 4 weeks later, had no effect on yield (May et al. 1969); however, defoliation at that time reduced yield per vine. Yield per node was positively correlated with leaf area per vine in the previous season, with the most severe defoliation treatment resulting in an 80 percent reduction relative to the control.

Twenty, 40 or 50 percent defoliation of whole vines after set reduced yields in the next season by 15, 46 and 70 percent respectively, due to fewer and smaller bunches (Winkler et al. 1974).

Peterson and Smart (1975) found topping to 6 or 10 nodes close to flowering resulted in either no effect or a small increase in yield in the following season. However, Le Roux and Malan 1945 (cited in Winkler et al. 1974) found that, although topping at flowering increased yield in that season, yield in subsequent years was reduced.

iv) Vigour: Both tipping and topping, when carried out several times, have been found to reduce vine vigour, particularly when practised each season.
(Wiebe 1975; Thomas and Barnard 1937; Khanduja and Balasubramanyam 1972; Winkler et al. 1974). The last reference cites several reports where these practices are said to have caused "severe weakening and injury".

Although not the following season, Casteran (1971) and Kliwer and Fuller (1973) found reduced pruning weights in the winter following summer pruning treatments. Topping ("rognage") 3 times after flowering reduced pruning weights in all cultivars in each of 3 years; 'Cabernet Sauvignon' was the most severely affected with a 50 percent reduction (Casteran 1971).

1.6.d. Effects of tipping, topping or defoliation on growth regulator activity.

i) Grapevines: There are few reports on this subject. Matsui et al. (1979) topped shoots to 10 nodes (plus removal of subsequent lateral shoot growth) at 4 times, commencing just before flowering and at subsequent 3 week intervals. The earliest treatment resulted in highest cytokinin (CK) activity and lowest growth inhibitor activity in latent buds (no comparison was made with untreated controls). Also, the earliest treatment resulted in the highest percentage burst of latent buds.

Acropetal movement of exogenously-applied gibberellic acid (GA₃) took place after tipping (Alleweldt 1961).

ii) Other plants: By comparison, there are a number of reports where activity of GA and CK increased in subtending buds or proximal buds and leaves following defoliation or removal of the shoot tip. Removal of the leaves subtending the terminal bud of apple stimulates budburst in tropical areas. Increased GA (3 times that of control), CK and decreased abscisic acid (ABA) activity was found in the apical tissues of closed buds following defoliation and prior to burst (Notodimedjo et al. 1981; Taylor et al. 1984). Exogenous GA₃ stimulated budburst in both defoliated and control shoots (Taylor et al. 1984). Dormant pruning increased GA activity (3 times that of control) in shoots (Grochowska et al. 1984).

Defoliation resulted in increased CK activity in cocoa buds prior to budburst (Taylor et al. 1984) and increased GA activity in sap of Douglas fir seedlings (Sweet 1974). Coppicing of Eucalyptus obliqua increased GA activity in the remaining stump, when one shoot was left attached (Taylor et al. 1982).
Shoot top removal has been shown to increase GA activity in lateral buds of *Brassica oleracea* after 7 days (Thomas 1972) and in proximal leaves of *Phaseolus* (Goodwin et al. 1983), to increase CK activity in stem and roots of *Phaseolus* in 2 days (Van Staden and Carmi 1982) and in bleeding sap of debudded tobacco and tomato plants (Colbert and Beever 1981), and to decrease ABA activity in axillary buds of *Xanthium strumarium* (Tucker and Mansfield 1973).

Buds on defoliated *Xanthium* plants showed a rapid rise in CK content, reaching 4 to 5 times that of control 3 days after defoliation (Henson and Wareing 1977).

Several hypotheses have been advanced to explain the above observations:

1. Young leaves and shoot apices are strong sinks for root-produced CK and GA; partial defoliation or removal of the shoot apex increases their availability to other sinks such as axillary buds (Grochowska et al. 1984; Sweet 1974; Kinet 1977; van Staden and Carmi 1982). A modification of this hypothesis envisages a cytokinin-mediated release from correlative inhibition preceding an increase in GA activity (Tucker 1976; Grochowska et al. 1984).

2. Apically-produced auxin moves basipetally and induces accumulation of ABA in axillary buds. Removal of the shoot apex decreases ABA activity; CK and GA are involved in budburst and extension following release from inhibition (Tucker and Mansfield 1973). GAs are not involved in apical dominance directly - when apical dominance is removed or weakened, GAs enhance axillary bud and shoot growth (Phillips 1969, 1975).

3. Mature leaves are a source of ABA and other inhibitors of budburst; removal of this source allows the GA content of the bud apex to increase and budburst follows. CK activity (not necessarily limiting before budburst) is then utilized in expansion of new leaves (Taylor et al. 1984).

1.6.e Effects of hail damage

Hailstorms occurring after shoot growth has commenced can result in defoliation, topping of main and lateral shoots, destruction of lateral shoots and inflorescences or young bunches, destruction of buds and shoot lesions.

May (1961) found damage caused by hailstorms just before and just after
flowering in different years reduced fruitfulness of 'Sultana' in the following seasons; bud dissections showed this to be due mainly to death of the primary axis of buds. Similarly, fruitfulness of 'Sylvaner' (Huglin 1958) and 'Pinot noir' (Bessis et al. 1981) was significantly reduced following severe damage due to hail close to flowering. In the latter case, bunches per shoot and flowers per shoot were reduced by 30 percent, compared to a neighbouring undamaged vineyard. In all three cases, the buds whose fertility was studied were found not to be damaged directly by the hail but the canes carrying those buds had been topped (to 4 to 8 nodes, Bessis et al. 1981) defoliated and scarred.

Fournioux and Bessis (1982) studied the effects of a hailstorm just before flowering on subsequent regrowth in the same season and, also, on the fate of primary latent buds. They observed that after the hailstorm, the buds most likely to burst were those judged in a state of least correlative inhibition, i.e. referring to the N+1 prompt buds that had not yet burst and the N+2 prompt buds (those on the already developed N+1 lateral shoots). Also, some base buds of shoots N and watershoots were found to have burst. The N+2 PLBs, being subjected to high correlative inhibition, were least likely to burst; however, when N+2 PLBs were 1 or 2 nodes below the point of topping of shoots N, and the lateral shoots at the same node had been destroyed, they were able to burst, with resultant shoot growth, because the sources of inhibition had been completely removed.

In most cases, where the source of correlative inhibition had not been removed entirely, N+2 PLBs started the budburst process; some bud expansion took place and the bud scales partially separated. The authors called these buds "debourre" (Bessis et al. 1981 referred to them as "bourgeons dans le coton"; in English, "woolly bud"). However, because inhibition had not been completely lifted, these "debourre" buds did not develop any further (also, it is likely that the simultaneous development of distal N+1 and N+2 prompt buds would have provided additional sources of correlative inhibition).

In winter, although most of the compound buds with the primary axis in the "debourre" state were morphologically distinguishable from normal buds by virtue of the wool, they still appeared to be quite healthy. However, when dissection was carried out, the primary axis was found to be dead. Subsequent shoot growth from such nodes was found to be a result of burst of N+3 secondary and tertiary latent buds.
1.6.f. Other effects of defoliation

Continuous defoliation of all shoots on 'Pinot noir' from just after budburst and maintained until cessation of shoot growth (all lateral shoots plus water shoots removed as well) reduced final shoot length (60 percent of control) and slightly increased node number per shoot. By comparison, the same treatment to only half the shoots on a vine, reduced final shoot length (20 percent of control) and node number per shoot (50 percent of control). In addition, this latter treatment caused death of the shoot tip of defoliated shoots whereas defoliation of all shoots did not. For example, where defoliation of half of the shoots commenced just after budburst, death of all shoot tips of defoliated shoots had occurred 73 days later (Fournioux and Bessis 1981a). Furthermore, where the foliated shoots were topped to 3 nodes, so that 3 mature leaves were retained, death of the shoot tips of the defoliated shoots also occurred. As a result, the authors suggest that mature leaves produce a translocatable inhibitory factor (Fournioux and Bessis 1981b).

1.7 GIBBERELLINS

During the course of the investigations, it became apparent that endogenous application of GA$_3$ could induce bud necrosis in grapevines. Therefore, the role of endogenous GAs and the effect of exogenous application of GAs is reviewed in this section.

At the latest count, there are 71 different chemically characterised, naturally-occurring GAs (Sponsel 1985). At least 38 have been found in higher plants, including GA$_3$, the main GA in commercial use (Graebe and Ropers 1978). The most conspicuous characteristic of the GAs is their ability to cause stem elongation, especially in dwarf plants, including many genetic dwarfs. Both cell elongation and division are stimulated by GAs.

1.7.a. Endogenous gibberellins

GAs have been found in leaves and root and stem xylem sap in many different species, including woolly plants. GAs can be transferred from xylem to phloem sap and have been found in phloem sap of a number of species (Goodwin 1978; Treharne 1982). There are many examples of correlations between endogenous GA content and both stem elongation and leaf expansion (Goodwin 1978).
There is very little information on endogenous GA of buds (Saunders 1978). Non-polar GA activity predominates in buds of Picea sitchensis during the growing season (Lorenzi et al. 1975; cited in Goodwin 1978). A peak in endogenous GA-like substances occurs during bud swelling in Acer (Eagles and Wareing 1964), Douglas fir (Lavender et al. 1973), Populus (Bachelard and Wightman 1973) and pecan (Wood 1983), and is thought to be a result of translocation from roots.

The endogenous levels of hormones, including GA, can fluctuate diurnally. Also, there may be large gradients in concentration over small distances within the plant (Saunders 1978).

i) Endogenous levels in grapevines: Gibberellins have been detected in xylem sap of grapevines (Skene 1967; Niimi and Torikata 1978) and tentatively identified as GA₁, GA₃, GA₅ and GA₉ (Skene 1967; Golinka 1973, cited in Srinivasan and Mullins 1981). The level of activity increases from the start of active shoot growth, reaching a peak after flowering, then decreasing when shoot growth ceases (Niimi and Torikata 1978).

For 'Sultana' and 'Corinth', xylem sap contained 0.14-0.33 and 0.07 ug GA₃ equivalents per litre respectively (Skene 1967). In the latter case, it was estimated that 7 ng GA would pass from the roots to the top of the plant each day, and this correlated with the concentration in the expanded leaves of 10 ng GA₃ equivalents per gram D.Wt.

Berries of seedless varieties contain lower levels of GA-like substances than seeded (Weaver and Pool 1965a,b) and Sidahmed (1976) suggests that seeds are the main source of GA in seeded cultivars whereas the leaves are the main source in seedless.

GAs have been found in inflorescences and tendrils (Lilov and Christov 1977; Monakov 1976, cited in Srinivasan and Mullins 1981) and tendrils are said to contain a higher GA content than any other organ (Monakov loc cit).

Hagiwara et al. (1980) found low levels of GA in bursting buds (15 - 20mm long) of 'Sultana' (seeded and seedless) and 'Emperor' (seeded) grapes. However, Mannini and Ryugo (1982) found GA activity in extracts of dormant buds and young shoots of three seeded varieties with the greatest activity in the latter case. Removal of fruit from potted cuttings of 'Cabernet Sauvignon' decreased the level of GA-like substances (Hoad et al. 1977). When translocation is restricted by girdling, the GA status of 'Corinth'
berries is markedly increased in both basic and acid fractions of the extract (Weaver and Pool 1965a).

1.7.b. Sites of gibberellin synthesis

The main sites of GA synthesis appear to be root and shoot tips, young leaves, floral parts, immature seeds and germinating embryos; however, it is possible that more or less all tissues have the ability to produce some GA (Graebe and Ropers 1978). As evidence for roots as a site of synthesis of GAs, Jones and Phillips (1966) found GA activity to diffuse from detached root tips of sunflower without loss of endogenous activity. However, for the same species, they found that the apical bud, young leaves and internodes appeared to be the main source for shoots. Goodwin et al. (1978), in reviewing the evidence for root production of GA, concluded that although the roots are certainly a major site of GA synthesis, there is no convincing evidence that a high proportion of the GAs in the plant as a whole are produced in the roots (unlike cytokinins for which there is considerable evidence for the roots as the major site of synthesis). The roots may be a site of interconversion of one GA to another (Crozier and Reid 1971; cited in Wright 1978).

GAs form in young developing seeds in large quantities in cherry (Feucht and Khan 1973) and almond (Ryugo 1976). The concentration of GA in developing seeds of apple is 15 to 500 times greater than in the leaves and shoots (Luckwill 1974); activity appears 4 to 5 weeks after bloom with the greatest concentration after 9 weeks. GA translocated from the seed after bloom counteracts the favourable effect of auxin and flower bud formation in apple (Buban and Faust 1982).

GAs may be involved in exerting an influence more at the site of synthesis (or application) rather than being transported (Treharne 1982).

1.7.c. Response to applied gibberellins

i) All species: Application of GAs promotes stem elongation in a large number of different species. In cases where young leaves are a major site of synthesis for stem elongation, removal of such leaves can be partially or completely replaceable by exogenous GAs application. Cell division and elongation are both affected in the response. Applied GA increases the rate of leaf primordia production and also increases the volume of the apical dome (Goodwin 1978).
Also, leaf enlargement and elongation are promoted by GAs application; in young leaves, cell division is affected whereas in more mature leaves, it is mainly cell enlargement (op cit). GAs application increases the total leaf area in hops (Williams 1961; cited in Goodwin 1978).

Response to application of GAs to dormant buds varies considerably among woody species (Brian et al. 1959, cited in Saunders 1978). Budbreak may be stimulated in Acer (Leike 1967, cited in Saunders 1978), Citrus (Guardiola et al. 1982), apple and pear (Walker and Donoho 1959), delayed (Brian et al. 1959) in apple and pear (Walser et al. 1981) or affected little or not at all in apple and pear (Walker and Donaho 1959; Brown et al. 1960).

Yotsuya et al. (1984) stimulated shoot elongation of summer dormant buds of pear in in vitro culture with GA_{4+7}.

ii) Grapevines: Some grapevine cultivars are sensitive to exogenous GA (Srinivasan and Mullins 1981). GA has a pronounced promoting effect on shoot growth (Weaver and McCune 1961; Weaver et al. 1966; Julliard and Balthazard 1965; Lavee 1980) but not all cultivars respond equally (Allweleldt 1964). For example, application of 40 ppm GA_{3} resulted in a 24 percent increase in shoot length (over that of control) of 'Thompson Seedless' (syn. 'Sultana') after 3 weeks but only a 5 percent increase when applied to a seeded form of this cultivar (Hagiwara et al. 1980). By comparison, application of 10 ppm GA_{3} to 'Tokay' (seeded), when shoots were up to 50 cm long, resulted in a 40 percent increase in shoot length over control after 2 weeks (Weaver et al. 1966).

GA_{3} application reduces "fruitfulness" in the following season, by delaying the onset of initiation as well as reducing both the number and size of inflorescence primordia (Julliard and Balthazard 1965; Antcliff 1967). Although GA_{3} inhibits the formation of inflorescence primordia from Anlagen, GA_{3} enhances the initiation of Anlagen (Srinivasan and Mullins 1981). Anlagen were formed precociously at normal node positions and at nodes more proximally situated than is normal. These GA_{3}-induced Anlagen developed into tendrils (Srinivasan and Mullins 1981). Cultivars vary in their response to GA-induced decrease in fruitfulness. Most seedless cultivars, e.g. 'Sultana' and a few seeded cultivars, e.g. 'Zinfandel' (Weaver and McCune 1961), 'Pinot blanc', 'Pinot gris', 'Auxerrois' and 'Riesling' (Julliard and Balthazard 1965), are relatively tolerant whereas most seeded cultivars are sensitive, e.g. 'Carignan', 'Red Malaga',
'Ribier', 'Flame Tokay' (Weaver and McCune 1961), 'Chasselas', 'Traminer' and 'Sylvaner' (Julliard and Balthazard 1965). \( \text{GA}_3 \) (20 ppm) applied to 'Waltham Cross' just after flowering reduced bunch number by 80 per cent in the following season but had no effect on bunch weight (Stannard et al. 1974). Sensitivity to \( \text{GA}_3 \) is greatest during early shoot growth (Weaver and McCune 1961).

Exogenous \( \text{GA}_3 \) promotes tendril growth and can transform young inflorescences into tendrils (Srinivasan and Mullins 1981). \( \text{GA}_3 \) application causes bud internode elongation (Bernstein and Fahn 1960).

In seeded cultivars, high concentrations of \( \text{GA}_3 \) may be injurious to vegetative growth as well as to the fruit. For example, shoots and canes may split and crack and become excessively lignified (Weaver and McCune 1961), leaves may become chlorotic (Julliard and Balthazard 1965) and shoot growth may be abnormal in the following season (Stannard et al. 1974).

Also, budburst in the following season is both delayed and decreased, and death of the primary axis of the bud may also occur. By contrast, no injury to seedless cultivars has been observed, even with concentrations as high as 1,000 ppm. Pruning weight may be increased by \( \text{GA}_3 \) sprays (Weaver and McCune 1961), presumably as a result of increased shoot growth.

1.7.d. Movement of gibberellins after application

The subject of GA translocation was reviewed in detail by Graebe and Ropers (1978). \( \text{GA}_3 \), applied to mature leaves, is translocated to the growing region including the immature expanding leaves but not to other mature leaves, with movement occurring primarily in the phloem. However, considerable amounts may also reach the xylem. Chailakhyan et al. (1974) showed that \( \text{GA}_3 \) applied to a basal leaf of an otherwise defoliated shoot of Perilla nankinensis reached the top of the plant even after girdling of the stem. This may be explained by radial translocation from phloem to xylem, demonstrated for \( [^{14}\text{C}] \) \( \text{GA}_3 \) in stems of young willow. The opposite process was also shown (Bowen and Wareing 1969).

i) Response to different methods of application and subsequent translocation of GA in grapevines: The rapid response of shoot elongation to \( \text{GA}_3 \) applied to foliage suggests that \( \text{GA}_3 \) is rapidly absorbed by leaves and readily translocated to growing tips and young internodes, resulting in
cell expansion; however, evidence suggests that very little of the GA₃ applied is actually absorbed into the plant (Weaver et al. 1966). These authors found that application to young leaves and internodes was more effective than application to older, particularly the first leaf above the first mature leaf. However, overall, intact internodes and leaves were found to be poor avenues for entry; if the internode was scratched, much GA entered and moved upwards in the xylem. Leaves about four-fifths full size and light green in colour afforded some penetration of C¹⁴ labelled GA₃ but older leaves did not. No visible movement occurred out of the leaf after one day and most movement took place after 7 days. Lavee et al. (1981b) found cut petioles to be better entry sites than intact blades.

Labelled GA₃ entering through leaf blades or internodes moves mainly towards the shoot tip in field vines (Weaver et al. 1966) but upwards, downwards and transitional movement in potted vines (Alliwedt 1961, 1962). Hale and Weaver (1962) found GA₃ moved downwards with leaf metabolites. When applied through cut petioles, labelled GA₃ was found in higher levels in buds above the treated petiole compared with those below (Lavee et al. 1981b).

1.7.e. Commercial uses of GA₃ in viticulture

i) To increase berry size: Most seedless table grape cultivars throughout the world are treated with GA₃ to increase berry size. The main cultivar treated is 'Sultana' (syn. 'Thompson Seedless') for which increases in berry size of up to 40 per cent have been reported (Jensen and Lynn 1976). The normal practice with this cultivar is to apply two sprays; the first (5 to 20 ppm GA₃) at full bloom (30 to 80 percent capfall) reduces set and causes some increase in berry size; the second (20 to 40 ppm) approximately 2 weeks later when berry size is 4 to 5 mm diameter further increases berry size and also results in longer and stronger bunch stems (Weaver 1982). The spray when applied is directed at bunches and surrounding foliage.

The response of other seedless cultivars such as 'Black Monukka', 'Delight', 'Beauty Seedless', 'Flame Seedless' and 'Perlette' is generally similar to that of 'Sultana'; however, proper timing of sprays is critical for 'Perlette' (Weaver 1976).

GA₃ application to seeded table grapes usually only results in a very small increase in size, if at all. However, an exception is 'Waltham Cross'
(syn. 'Rosaki', 'Dattier') for which an increase of 50 to 70 percent in berry size is obtained in South Africa by dipping bunches into 10 to 20 ppm GA₃ at fruit set (Weaver 1976).

ii) To thin compact bunches of seeded cultivars: To decrease the incidence of bunch rot in winegrape cultivars with compact bunches, GA₃ at 1 to 10 ppm (depending on cultivar) has been applied 3 weeks before flowering. Bunch loosening is a result of reduced set, bunch elongation and/or production of shot berries. This practice, no longer recommended in California due to the injurious effects of GA₃ foliar sprays on seeded cultivars (Weaver 1982), has not been widely used in Australian vineyards.

GA₃ is not normally applied to seeded table grapes because the production of shot berries detracts from the appearance of the bunch; however, in India, bunches of 'Anab-e-Shahi' are dipped in low concentrations of GA₃ at flowering to reduce set and increase berry size (Weaver 1976).

iii) To thin compact bunches of seedless table grapes: The use of a spray at flowering for this purpose on 'Sultana' was discussed in (i). 'Perlette', a cultivar with very compact bunches, has been thinned by a 10 to 15 ppm GA₃ spray at flowering; however, the response has been variable (Weaver 1982).

iv) To increase fruit set: Spray applications of 100 ppm GA₃ to 'Concord' (Vitis labruscana) increases set by approximately 16 percent if applied 11 days or so after flowering (Weaver 1976). Although GA₃ either has no effect or decreases set of 'Zante Currant' (syn. 'Corinth', 'Black Corinth'), a mixture of 1 ppm GA₃ and 100 ppm CCC is used to increase set of this cultivar; CCC has the effect on set while GA maintains berry size (El-Zeftawi and Weste 1970).

v) Induction of seedlessness; GA₃ treatment can induce seedlessness and advanced maturity in seeded 'Delaware' (V. labruscana). This practice is used in Japan where bunches are dipped in 100 ppm GA₃, 10 days before flowering and again 2 weeks after flowering. The first dip results in seedlessness, the second in berry enlargement. Almost 100 percent seedlessness can be obtained (Weaver 1976).

Dipping bunches in 100 ppm GA₃ 8 days after full bloom induced 75 percent seedlessness with glasshouse-grown 'Italia' in New Zealand without any
change in berry size or shape (Jordan 1984). Also, GA$_3$ has been successfully used with the following cvs. grown outdoors in New Zealand: 'Pearl of Csaba', 'Chasselas Rose Royale', 'Pirovana', 'Schuyler' and 'Cardinal' (Hanh and Jackson 1984).

1.8 GENERAL RESEARCH AIM

The general aim of this study has been to examine the incidence of bud abnormalities in _Vitis vinifera_ to determine the effect of such abnormalities on productivity, particularly expressed as yield per node and to determine the cause of the abnormalities.

The observation of an association between hailstorm damage and the development of a particular abnormality, i.e. primary bud necrosis (PBN), led to the preliminary experiments described in Chapter 2. In turn, this led to an interest in the relationship between summer pruning operations and PBN, and the causal nature of that relationship.

A review of the literature on bud abnormalities also revealed the existence of an association between exogenous application of gibberellic acid (GA$_3$) and PBN. Consequently, an hypothesis was tested that shoot topping or thinning or defoliation leads to an increase in endogenous levels of GA in developing buds, thus inducing PBN.

The detailed research aims engendered after the preliminary experimentation are outlined in 2.5.
A hailstorm at the time of flowering in 1979 resulted in severe damage to shoots of 'Shiraz', 'Sultana' and 'Pedro Ximenez' grapesvines. Dissections of externally-normal compound buds on damaged shoots during the following winter revealed a large proportion of buds in which the primary bud-axis was completely necrotic whereas the "secondary" bud-axes were normal. Experiments subsequently conducted on these cultivars during the 1980/81 season confirmed that (a) topping and defoliation of single shoots and (b) shoot thinning together with topping plus defoliation of remaining shoots on whole vines, induced primary bud-axis necrosis (PBN) and increased the secondary/primary shoot ratio, particularly at distal nodes. Highest levels of PBN on untreated vines were found at proximal nodes.
A hailstorm, accompanied by very strong winds on November 14, 1979, caused severe damage to vineyards at Virginia, Angle Vale, Roseworthy and much of the Barossa. At Roseworthy, the major plantings of 'Shiraz', 'Pedro Ximenez' and 'Sultana' had just started flowering.

Damage consisted of severe defoliation, all main shoots were topped to some degree with most to 4 to 10 nodes, most lateral shoots were either topped or destroyed, inflorescences were partly damaged or destroyed and most main shoots had large lesions (Fig 2.1).

Although rapid regrowth took place, mainly from (a) previously unburst prompt buds on main shoots and lateral shoots, (b) the most distal primary latent buds (PLB) on main shoots and (c) base buds, yields were considerably lower than normal, approximately 20 to 30% of that expected, depending on the cultivar.

During the course of routine bud dissections (for the purpose of student practicals on bud fruitfulness) in the following winter (1980), it became apparent that, for a large proportion of compound buds on 'Shiraz', and to a lesser extent 'Sultana', the primary axis was dead whereas the two secondary (i.e. secondary and tertiary) axes were quite normal. In such cases, the compound bud as a whole, appeared normal, i.e. externally those buds with a dead primary axis were identical to those with a normal primary axis. The only exceptions were those cases in which the secondary axes had developed the appearance of a "split bud" and only a small amount of necrotic tissue from the primary axis remained between them; however, there were relatively few examples of these.

Initially, this phenomenon was thought to be a result of a direct impact by a hailstone on the bud, or alternatively, an injury to the part of the stem adjacent to the node. However further examination of damaged canes revealed that, where direct hits had occurred, the buds had been destroyed at the time of the hailstorm or the whole bud had died soon afterwards. Some buds with dead primary axes were located at nodes without an injury for one or two internodes above and below. Therefore, direct injury was discarded as a possible cause.

Because this bud abnormality had not previously been observed on material from the same vineyard it was assumed that the hailstorm must be the cause. Bud material had been examined for the previous five years, mainly 'Sultana' and 'Shiraz' cultivars, and, in the case of 'Sultana', only at nodes five to ten to ensure that students had a reasonable chance of finding inflorescence primordia. In the case of 'Shiraz', most material
Fig. 2.1 Damage to 'Sultana' vines in the Roseworthy College 'Home vineyard' resulting from a severe hail-storm on Nov. 14, 1979.
examined would have been from node three or distally because a 2-node spur would have been left on the vine when the cane was removed.

In order to quantify this phenomenon, 72 'Sultana' and 50 'Shiraz' buds, from obviously damaged canes, were dissected in late June, 1980 and examined under a low-power microscope (Table 2.1). In both cases, and in particular for 'Shiraz', the percentage of buds with just the primary axis dead with normal secondary axes is much greater than those with more extensive death.

For 'Sultana' only, the presence of a third, well-developed secondary axis, i.e. "quaternary bud", was recorded. For 40 per cent of buds, this axis was obvious and three-quarters of these buds had a dead primary axis. Therefore, it was concluded that, in cases where the primary axis had died at an early stage, the secondary axes developed more than normal.

Table 2.1. Condition of "externally normal" 'Sultana' and 'Shiraz' buds examined in June, 1980.

<table>
<thead>
<tr>
<th>Condition of Buds</th>
<th>'Sultana'</th>
<th>'Shiraz'</th>
</tr>
</thead>
<tbody>
<tr>
<td>Primary axis only dead</td>
<td>47</td>
<td>62</td>
</tr>
<tr>
<td>Primary and one secondary axis dead</td>
<td>6</td>
<td>8</td>
</tr>
<tr>
<td>Primary and two secondary axes deada</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>No death of any axis</td>
<td>47</td>
<td>26</td>
</tr>
<tr>
<td><strong>100</strong></td>
<td><strong>100</strong></td>
<td></td>
</tr>
</tbody>
</table>

a Whole bud dead.

At the time, I was not aware of any reports in the literature which described the death of the primary, but not the secondary axes, of the compound bud of the grapevine. "Blind buds" were mentioned briefly in texts such as Winkler et al. (1974) and there were occasional references to "bud death", (e.g. Pool et al. 1978, Bindra 1977), with an implication that the compound bud as a whole was dead. Bud mites and winter freeze were also known to be possible causes of "whole" bud death (Winkler et al. 1974).

May (1961) had observed a decrease in "fruit bearing potential" of cv. 'Sultana' in seasons following severe hailstorms - he attributed this principally to an "... actual killing of primary buds" and also to mechanical damage to shoots and a removal of correlative inhibition resulting in the premature burst of primary buds. In 1959, 37.5 percent of
buds were found to be dead on canes present at the time of the hailstorm on November 19, 1958. However, it is not clear if the author was referring to buds killed by actual impact of hailstones. Indeed, the high percentage of dead primary buds incorrectly attributed to direct hail damage when, in fact, it may have been a result of abortion of the primary axis.

In order to determine if the hailstorm had any causal effect on this bud condition, a series of preliminary experiments was carried out in the 1980/81 season in an attempt to reproduce the condition by artificial means, i.e. defoliation, shoot topping and lateral removal, and injury.

In this thesis, the condition shall be referred to as primary bud-axis necrosis and abbreviated to PBN.
2.2 MATERIALS AND METHODS

2.2a Experimental design

(i) Experiment 80/1: The aim of this experiment was to determine if shoot topping, defoliation or injury, separately or in combination, would induce PBN. Twenty cv. Shiraz vines in the Roseworthy College "South" vineyard, having about 75 shoots each, were reduced to the 12 most vigorous shoots per vine on 11 November, 1980 (50 per cent flowering, 16 visible internodes). Eight treatments were allocated at random to each of 8 shoots per vine (leaving 4 shoots per vine unused in the experiment). Each treatment had 20 single shoot replicates (Table 2.2).

Topping: The shoot was topped to 10 nodes by cutting through the middle of the internode above the 10th node. (In this and all other experiments, nodes are numbered from the base, with node 1 defined as the first "clear" node separated from the base of the shoot by at least the thickness of a pencil, i.e. 7mm).

Defoliation: At every node (100 per cent) or at half the nodes (50 per cent), the leaf and lateral shoot were removed by cutting through the petiole and the base of the internode. In the latter case of 50 per cent defoliation, nodes 2, 3, 6, 7 and 10 were defoliated.

Injury: At every internode (100 per cent) or at half the internodes (50 per cent), the stem was injured by hitting the mid-portion of the internode two or three times with a hammer to which a piece of quartz (15-20mm diameter) had been glued. The shoot was held in one hand with the hammer in the other in order to provide some resistance to the blows. By trial and error, this method of injury was found to best duplicate the effects of hail impact. The aim was to cause as much damage as possible without actual shoot breakage. For the 50 per cent level, internodes between the following nodes were injured: N1-2, N2-3, N5-6, N6-7, N9-10.

The described format was used so that some nodes, i.e. 4 and 8, which were not defoliated nor had injury to an adjacent internode, could be compared with nodes 2 and 6 with defoliation plus adjacent injury. No bunches were removed on Nov. 11.

(ii) Experiment 80/2: The aim of this experiment was to determine the
effect of timing of shoot treatment on the incidence of PBN. Twelve cv. Shiraz vines in the Roseworthy College "South" vineyard were reduced to the 12 most vigorous shoots on Nov. 6, 1980. The experiment employed a split-plot design in which single vines were used as the main plots (4 blocks of 3 vines, block groups being selected with uniform butt circumference, measured at 30cm above ground level) and 6 shoots per vine used as sub-plots (shoots allocated to each sub-plot at random). "Shoot treatment" (sub-plot) was applied to half the shoots on each vine (i.e. 6) at one of three times (main plot). The "shoot treatment" comprised topping to 10 nodes, 50 per cent defoliation and 50 per cent injury (identical to treatment A in Experiment 80/1).

(iii) Experiment 80/3: The aim of this experiment was to examine the effect of shoot thinning, shoot topping, defoliation and injury, applied on a whole vine basis, on the incidence of PBN. Also, to determine if there were any differences in cultivar susceptibility. Eight vines each of cultivars Shiraz, Pedro Ximenez (Roseworthy College "South" vineyard) and Sultana ("Home" vineyard) were used in separate randomised block designs (4 blocks on the basis of butt circumference, single vine plots) for each cultivar.

"Control" vines were neither shoot-thinned nor had any shoot treatments. "Treated" vines for each cultivar were reduced to 20 vigorous shoots per vine and all shoots were topped to 10 nodes, and also given 50 per cent defoliation and 50 per cent injury (identical to treatment A, Expt. 80/1) on November 13.

Flowering of all three cultivars was well advanced on this date.

2.2.b Collection and examination of buds.

(i) Experiment 80/1: All treated shoots were cut off at their base in July, 1981, bundled and taken to the laboratory where the buds were examined over a period of two days. Initially, all buds were dissected by removing the outer bud scales and the secondary axes; however, this was time-consuming and an alternative method was developed and used in these and in subsequent experiments in this thesis: a transverse cut was made with a scalpel across the compound bud at about half the height of the bud. With practice, it was found that this enabled the state of the primary axis to be readily determined and, at the same time, the other bud axes could be
seen. If necessary, an additional cut was made at greater "depth" if there was any doubt regarding the state of the primary axis. This method enabled large numbers of buds to be processed relatively quickly. The bud at node 1 (the most proximal node) was not examined because it has been found that the bud at this node often possessed some of the characteristics described for "base buds" (Pool et al. 1978) and it was difficult to determine, using the method employed, which of the "buds" within the bud scales was the primary axis.

(ii) Experiment 80/2: Three shoots from each sub-plot were removed from each vine in July, 1981 and the buds examined. The remaining 3 shoots of each sub-plot were retained on the vine such that each vine was pruned to six, 10-node canes (i.e. 3 "shoot-treated" and 3 "control"). All remaining lateral shoots were removed at pruning plus any primary latent bud which had burst in the previous season (these usually occurred only at node 10). The retained canes were used for measurement of shoot index, budburst and fruitfulness in the spring of 1981.

(iii) Experiment 80/3: On "treated" vines, 10 shoots were removed for bud examination in July and August, 1981 and 8 shoots retained as canes (all lateral shoots, etc. removed as in Expt. 80/2). On "control" vines, 10 of the most vigorous shoots were removed for bud examination and 8 "good" shoots retained as 10-node canes. The latter were examined in spring as in Expt. 80/2.

2.2.c. The Bud Index

When dormant (compound) buds were examined, they were "scored" as follows:

N  No visible necrosis of the primary axis, i.e. normal bud.
P  Primary axis necrotic (PBN); no necrosis in secondary axes.
X  Unknown (either the bud at that node had been damaged physically or was absent or the state of the primary axis was undetermined).
B  Burst of the primary latent bud in the previous season.
D  Whole compound bud dead.

The formula for the Bud Index is 100P/N+P i.e. the percentage of buds with PBN within the population of buds which excludes "unknown", "completely dead" and "burst" buds. (In the 1980 experiments, this latter component was relatively high; however, in subsequent years, even though
the percentage of such buds was relatively low, as a result of changes in experimental technique, the original formula was still retained.)

The Bud Index was determined using nodes 2 to 9 inclusively; node 10 was excluded due to the large proportion of primary latent buds which burst at this node.

For statistical analysis, all Bud Index data was transformed to degrees, and all tests for significant differences between means carried out on the transformed data. However, results are presented as percentages.

2.2.d. The Shoot Index

Approximately one month after budburst, or later, the number of shoots at each node was counted. At the same time, each shoot was scored as either a "primary shoot", i.e. derived from a primary axis or a "secondary shoot", i.e. derived from a secondary axis, based on the phyllotaxic plane of the shoot relative to the cane (a primary shoot being oriented parallel to the cane (Fig. 2.2.a,c) whereas secondary shoots are at right angles to the cane (Fig. 2.2.b,d); Carbonneau and Casteran 1979; Carbonneau, pers. comm.; Fournioux and Bessis 1982).

Theoretically, the greater fruitfulness of primary shoots could be used to distinguish them from secondary shoots; however, this characteristic was never used in this study and shoot angle alone was employed. In fact, there were several cases where shoots identified as primary had fewer inflorescences per shoot than secondary shoots at the same node.

In practice, when scoring shoots, relatively few were found with their phyllotaxic plane exactly at 0° (parallel to the cane) or 90° (right angles) and most fall somewhere in between, 0 to 30° and 60 to 90°. Those shoots at angles of 30 to 60° approximately were designated as unknowns.

The formula for the Shoot Index is: 100y/y+z where

y = number of nodes with primary shoot absent
z = number of nodes with primary shoot present.

For statistical analysis, the Shoot Index percent data were transformed in the same way as were Bud Index data.

2.2.e Budburst and fruitfulness measurements

In Expt. 80/2 and 80/3, yield components were measured but the results are not presented in this chapter, but in Ch. 8; the following yield components were determined in spring 1981 on nodes 2 to 9 inclusively:

(i) Shoot number per node
Fig. 2.2 Phyllotaxic plane relative to the winter cane: (a) primary shoot oriented parallel to cane, one shoot per node; (b) "secondary" shoot oriented at right angles to cane, one shoot per node; (c) primary shoot parallel to cane (right) and "secondary" shoot at right angles to cane (left), two shoots per node; (d) two "secondary" shoots per node, both at right angles to cane; unburst primary bud not visible. 

* "secondary shoot" includes secondary, tertiary or quaternary shoots.
(ii) Inflorescence number on primary and/or secondary shoots
(iii) Inflorescence number per node
(iv) Mean number of flowers per inflorescence (see Appendix for details of method)

Using the above data, the following components were derived:

(v) Percent nodes burst
(vi) Percent of nodes burst with > 2 shoots per node
(vii) Flower number per node

In addition for Expt. 80/3 Shiraz only; the following were measured at harvest in 1982:

(viii) Fruit weight (gms) per node
(ix) Mean berry weight
and the following derived:

(x) Mean bunch weight
(xi) Mean berry number per bunch

Note that data on yield components, although presented on a "whole vine" basis, really refer to measures on designated nodes, i.e. nodes 2 to 9, on the "treatment" shoots retained as canes at pruning (data was not collected for replacement spurs).

2.2.f. Statistical analysis

(i) Experiment 80/1: The data was analysed by 2-way ANOVAR (means of 20 single cane replicates for each treatment) and by Duncan's multiple range test (Little and Hills 1978). To examine the effects of individual factors, data were pooled and analysed by one-way ANOVAR (data from treatments 'C' and 'G' was excluded due to excessive burst of primary latent buds).

(ii) Experiment 80/2: The data were analysed by split-plot ANOVAR (Little and Hills 1978) (means of 12 single shoot replicates for each treatment). Bud Index on a per node basis (results in Fig. 2.4) was derived using 9 nodes for each node position and two-way ANOVAR carried out on the resulting data (means of 4, 3-vine replicates per treatment). Correlations of Bud Index and Shoot Index was tested by pooling all treatments (n = 24). Fertility and yield component data for (a) primary and secondary shoots individually and (b) all shoots, were analysed by 2-way ANOVAR (means of four 3-cane replicates for each treatment; means of twelve 3-cane replicates for shoot treatment and control when pooled over time).
(iii) Experiment 80/3: Data were analysed by 2-way ANOVAR comparing 4 means of 19 shoot replicates (Bud Index) or 8 shoot replicates (Shoot Index) for each treatment. Bud and Shoot Index on a per node basis were derived using 10 and 8 nodes respectively for each node position and analysed by 2-way ANOVAR (means of four single-vine replicates per treatment). Correlation of Bud Index and Shoot Index was tested by pooling treated and control data from all varieties (n = 24). Data on fertility and yield components were analysed as for Expt. 80/2 (means of four 8-shoot replicates per treatment).
2.3 RESULTS

2.3.a Experiment 80/1

(i) Burst of primary latent buds: As expected, burst of primary latent buds occurred in all treatments except H (control) soon after the removal of the sources of correlative inhibition, i.e. the main shoot tip and/or lateral shoots (Table 2.2). The combination of 100 per cent defoliation and lateral shoot removal plus topping (treatments C and G) resulted in high percent burst of primary latent buds. As a result, the Bud Index data from these treatments was not included in the analysis.

(ii) Bud Index: Treatments which included topping produced the highest levels of PBN (Table 2.1, Fig. 2.3). The effect of topping alone combined with 50 per cent defoliation (F, G, H) produced significantly more PBN than treatments with no topping with (E) or without (F) defoliation (Table 2.2; Fig. 2.3). Burst of the primary latent bud (Table 2.2) and should therefore be regarded as unreliable. No consistent response could be discerned from the removal of injury or partial defoliation. When the pooled data are considered, it is apparent that topping and 50 per cent defoliation were effective in inducing PBN; however, "injury" did not differ significantly from control (Table 2.3).

2.3.b. Experiment 80/2

(i) Bud Index: Earlier shoot treatment (topping to 10 nodes, 50 per cent defoliation and lateral shoot removal and 50 per cent injury) resulted in more PBN than later treatment (Fig 2.4). Although shoot treatment was effective in inducing PBN, there was a significant interaction between timing and shoot treatment since shoot treatment was significantly greater than control only for the first date, Nov. 7 (Table 2.4). Although statistical analysis of Bud Index by node position data was not possible, it is nevertheless apparent that the earlier times of shoot treatment had most effect at the distal nodes (Fig. 2.5). Also, analysis of the pooled data shows that shoot treatment had most effect at the distal nodes (Fig. 2.6). The graphs of Bud Index at different times of shoot treatment (Fig. 2.4) suggests a more linear relationship with stage of shoot development (number of visible internodes) than with calendar date.

(ii) Shoot Index: The same trends found with Bud Index are apparent for the Shoot Index (Table 2.4). Shoot Index and Bud Index are well correlated (r = 0.65, significant at 1 per cent level); although as is clear from their formulae, they measure different things: the Bud Index determines the state of the primary axis at all nodes whereas the Shoot Index determines
the percentage of nodes with primary shoot absent only for those nodes where shoots are positively identified as primary and/or secondary. Therefore, the percentage of nodes burst and the ability to "identify" the shoots are the causes of the differences between these two indices.

(iii) Fertility of primary and secondary shoots: Primary shoots have more inflorescences per shoot and more flowers per inflorescence and per shoot than secondary shoots on both treated and control canes (Table 2.5).

2.3.c Experiment 80/3

(i) Burst of primary latent buds: Primary latent buds burst soon after shoot treatment, mainly at node 10. The percentage burst, for nodes 2 to 10 inclusively, was 7, 10 and 21 for 'Pedro Ximenez', 'Sultana' and 'Shiraz' respectively.

(ii) Bud Index: Shoot thinning, shoot topping, defoliation and injury to whole vines induced significantly more PBN than untreated vines, in all three cultivars; the greatest difference was for 'Shiraz' (Table 2.6). It is obvious that the difference between treated and control vines was chiefly attributable to differences in the distal nodes for all three cultivars (Figs. 2.7a, 2.8a,b). Furthermore, the distal nodes on treated vines had significantly more PBN than proximal nodes whereas the reverse was true for untreated vines, i.e. the natural level of PBN was highest at the proximal nodes.

Bud Index and vine vigour (as measured by butt circumference at 30cm) were positively correlated as shown in the cases below.

Shiraz: Treated \( r = .96 \) (sig. at 1%)

Control \( r = .88 \) (sig. at 5%)

Pedro Ximenez: Treated \( r = .98 \) (sig. at 1%)

The correlation coefficients were not significant in other sets probably due to low values of 'n' (i.e. \( n = 4 \)). The percentage of nodes where the whole compound bud was found to be dead was less than 2 for all cultivars.

(iii) Shoot Index: The effects on Shoot Index paralleled the effects on Bud Index (Table 2.6) and they are well correlated \( (r = 0.84, \text{significant at } 0.1\% ) \). The data for each node position are presented for 'Sultana' only in
Fig. 2.7b; nodes 5, 8 and 9 on treated vines had more PBN than corresponding nodes on untreated.

There were no significant differences between treated and control vines for percentage of nodes burst (= percentage of nodes with one or more shoots) of 'Sultana' and 'Shiraz' (Pedro X. not analysed) but treated vines had a significantly higher percentage of nodes with 2 or more shoots (Table 2.6); these effects were greater at distal nodes. In some instances, all shoots at nodes with 2 or more shoots were scored as "secondary" shoots (e.g. Fig. 2.2d) and, for a small proportion of cases, what appeared to be necrotic primary bud tissue was visible in the gap between "secondary" shoots (Fig. 2.9a,b,c,d); verification as primary bud tissue was achieved by removal and dissection under a low-power microscope.

The number of shoots designated as "unknowns", i.e. they could not be said to be either primary or secondary based on their phyllotaxic plane, was relatively high, e.g. 40 percent of all scored shoots for 'Sultana', 32 for 'Pedro X.' and 25 for 'Shiraz'. This is much higher than the corresponding figure for "unknowns" in bud dissection, i.e. 4, 2 and 3 per cent of buds examined for 'Sultana', 'Pedro X.' and 'Shiraz' respectively.

The proportion of primary shoots (for those scored as either primary or secondary) was greater for control vines than treated vines for all three cultivars (Table 2.7). This resembles the trends found with Shoot Index.

(iv) Fertility of primary and secondary shoots: Primary shoots had more inflorescences per shoot than secondary shoots on both treated and control vines, for all three cultivars, with the exception of 'Sultana' control (Table 2.8). Also, there was no significant difference between treated and control for either primary or secondary shoots, with one exception: primary shoots on 'Shiraz' control vines had more inflorescences per shoot than on treated vines.
Table 2.2 Effect of shoot topping, defoliation and injury on Bud Index and percentage of nodes which had burst primary latent buds (Expt. 80/1, 'Shiraz')

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Shoot topping</th>
<th>Defoliation</th>
<th>Injury</th>
<th>Bud Index</th>
<th>Nodes with PLB burst</th>
</tr>
</thead>
<tbody>
<tr>
<td>Code</td>
<td>%</td>
<td>%</td>
<td>%</td>
<td>%</td>
<td>%</td>
</tr>
<tr>
<td>A</td>
<td>+</td>
<td>50</td>
<td>50</td>
<td>70 a</td>
<td>14</td>
</tr>
<tr>
<td>B</td>
<td>+</td>
<td>50</td>
<td>100</td>
<td>67 a</td>
<td>16</td>
</tr>
<tr>
<td>C</td>
<td>+</td>
<td>100</td>
<td>50</td>
<td>57 *</td>
<td>57</td>
</tr>
<tr>
<td>D</td>
<td>+</td>
<td>50</td>
<td>0</td>
<td>64 ab</td>
<td>14</td>
</tr>
<tr>
<td>E</td>
<td>+</td>
<td>0</td>
<td>50</td>
<td>75 a</td>
<td>6</td>
</tr>
<tr>
<td>F</td>
<td>-</td>
<td>50</td>
<td>50</td>
<td>44 bc</td>
<td>4</td>
</tr>
<tr>
<td>G</td>
<td>+</td>
<td>100</td>
<td>100</td>
<td>35 *</td>
<td>70</td>
</tr>
<tr>
<td>H</td>
<td>-</td>
<td>0</td>
<td>0</td>
<td>34 c</td>
<td>0</td>
</tr>
</tbody>
</table>

1 Topping to 10 nodes
2,3 Nodes 2 to 9, 2 to 10 respectively
* Not included in analysis

Means followed by same letter are not significantly different at 5% level

Table 2.3 Bud Index; pooled data for topping, defoliation and "injury" (Expt. 80/1, 'Shiraz')

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Control&lt;sup&gt;c&lt;/sup&gt;</th>
<th>Treatment</th>
<th>LSD .05</th>
</tr>
</thead>
<tbody>
<tr>
<td>Topping&lt;sup&gt;a&lt;/sup&gt;</td>
<td>38</td>
<td>68</td>
<td>23</td>
</tr>
<tr>
<td>Defoliation&lt;sup&gt;b&lt;/sup&gt;</td>
<td>26</td>
<td>64</td>
<td>29</td>
</tr>
<tr>
<td>&quot;Injury&quot;&lt;sup&gt;b&lt;/sup&gt;</td>
<td>45</td>
<td>69</td>
<td>27</td>
</tr>
</tbody>
</table>

<sup>a,b,c</sup> Means of 120, 80 and 40 canes respectively

These data could also be presented as follows:

- Defoliation + Defoliation Sum
- Topping 34 (b) 44 (c) 78
+ Topping 75 (6) 64 (D) 139
Sum 109 108
Table 2.4 Effect of timing of shoot treatment\(^1\) on Bud Index and Shoot Index (Expt. 80/2, 'Shiraz')

<table>
<thead>
<tr>
<th>Time of shoot(^2) treatment</th>
<th>Bud Index *</th>
<th>Shoot Index *</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Control</td>
<td>Treated</td>
</tr>
<tr>
<td>Nov. 7</td>
<td>13</td>
<td>70 ***</td>
</tr>
<tr>
<td>Nov. 19</td>
<td>29</td>
<td>51 ns</td>
</tr>
<tr>
<td>Dec. 15</td>
<td>27</td>
<td>32 ns</td>
</tr>
<tr>
<td>Sub-plot means</td>
<td>22</td>
<td>51 ***</td>
</tr>
</tbody>
</table>

\(^1\) Topping to 10 nodes, 50\% defoliation, 50\% injury.
\(^2\) No. of visible internodes ws 16, 22, and 29 on Nov. 7, 19 and Dec. 15 respectively.
\*,** indicates means in same row are significantly different at 5 and 1\% level respectively; ns, not significant at 5\% level.
Means in same column followed by same letter are not significantly different at 5\% level.

Table 2.5 Numbers of inflorescences and flowers per shoot and per inflorescence in the spring of 1981 of shoots treated and untreated from the previous season (Expt. 80/2, 'Shiraz')

<table>
<thead>
<tr>
<th>Treatment in 1980</th>
<th>Inflorescences(^1) per shoot</th>
<th>Inflorescences(^2) per shoot</th>
<th>Flowers(^2) per inflorescence</th>
<th>Flowers(^2) per shoot</th>
</tr>
</thead>
<tbody>
<tr>
<td>CONTROL UNTREATED</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Primary shoots</td>
<td>2.7</td>
<td>2.7</td>
<td>580</td>
<td>1566</td>
</tr>
<tr>
<td>Secondary shoots</td>
<td>2.1</td>
<td>1.9</td>
<td>488</td>
<td>927</td>
</tr>
<tr>
<td></td>
<td>**</td>
<td>*</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>SHOOT TREATMENT(^3)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Primary shoots</td>
<td>2.5</td>
<td>2.4</td>
<td>571</td>
<td>1370</td>
</tr>
<tr>
<td>Secondary shoots</td>
<td>1.6</td>
<td>1.9</td>
<td>407</td>
<td>773</td>
</tr>
<tr>
<td></td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
</tr>
</tbody>
</table>

\(^1\) Pooled over all times
\(^2\) Nov. 7 treatment only
\(^3\) Topped to 10 nodes, 50\% defoliation, 50\% injury
\*,**, indicates means significantly different at 5 and 1\% level respectively.
Table 2.6 Effect of shoot thinning, shoot topping, defoliation and injury to whole vines on Bud Index, Shoot Index, and budburst in 'Shiraz', 'Pedro Ximenez' and 'Sultana' (Expt. 80/3)

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Bud Index %</th>
<th>Shoot Index %</th>
<th>Nodes burst %</th>
<th>Nodes burst with &gt; 2 shoots %</th>
</tr>
</thead>
<tbody>
<tr>
<td>'SHIRAZ'</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>10</td>
<td>3</td>
<td>-</td>
<td>11</td>
</tr>
<tr>
<td>Treated</td>
<td>66</td>
<td>58</td>
<td>-</td>
<td>44</td>
</tr>
<tr>
<td></td>
<td>***</td>
<td>***</td>
<td></td>
<td></td>
</tr>
<tr>
<td>'PEDRO X.'</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>6</td>
<td>2</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Treated</td>
<td>17</td>
<td>19</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>*</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>'SULTANA'</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>1</td>
<td>11</td>
<td>70</td>
<td>10</td>
</tr>
<tr>
<td>Treated</td>
<td>33</td>
<td>44</td>
<td>77</td>
<td>24</td>
</tr>
<tr>
<td></td>
<td>***</td>
<td>***</td>
<td>ns</td>
<td>**</td>
</tr>
</tbody>
</table>

1 Treatment on Nov. 13; 16, 15 and 18 visible internodes for 'Shiraz', 'Pedro X.' and 'Sultana' respectively
*,**,*** indicates means significantly different at 5, 1 and 0.1% level respectively; ns, not significant at 5% level.

Table 2.7 Effect of shoot thinning, shoot topping, defoliation and injury to whole vines on proportion of shoots designated primary or secondary in spring 1981 in 'Shiraz', 'Pedro Ximenez' and 'Sultana' (Expt. 80/3)

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Primary %</th>
<th>Secondary %</th>
</tr>
</thead>
<tbody>
<tr>
<td>'SHIRAZ'</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>83</td>
<td>17</td>
</tr>
<tr>
<td>Treated</td>
<td>27</td>
<td>73</td>
</tr>
<tr>
<td>'PEDRO X.'</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>60</td>
<td>40</td>
</tr>
<tr>
<td>Treated</td>
<td>39</td>
<td>61</td>
</tr>
<tr>
<td>'SULTANA'</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>75</td>
<td>25</td>
</tr>
<tr>
<td>Treated</td>
<td>48</td>
<td>52</td>
</tr>
</tbody>
</table>

1 Treatment applied in spring 1980.
Table 2.8 Effect of shoot thinning, shoot topping, defoliation and injury to whole vines on inflorescences per shoot on primary and secondary shoots in spring 1981 on 'Shiraz', 'Pedro Ximenez' and 'Sultana' (Expt. 80/3)

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Primary</th>
<th>Secondary</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2.45</td>
<td>1.86 *</td>
</tr>
<tr>
<td>Control</td>
<td>2.03</td>
<td>1.65 *</td>
</tr>
<tr>
<td>Treated</td>
<td>**</td>
<td>ns</td>
</tr>
<tr>
<td>'PEDRO X.'</td>
<td>0.68</td>
<td>0.48 ***</td>
</tr>
<tr>
<td>Control</td>
<td>1.57</td>
<td>0.78 **</td>
</tr>
<tr>
<td>Treated</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>'SULTANA'</td>
<td>0.64</td>
<td>0.28 ns</td>
</tr>
<tr>
<td>Control</td>
<td>0.62</td>
<td>0.25 *</td>
</tr>
<tr>
<td>Treated</td>
<td>ns</td>
<td>ns</td>
</tr>
</tbody>
</table>

1 Treatment applied in spring 1980
*,**, *** indicates means significantly different at 5, 1 and 0.1% level respectively; ns, not significant at 5% level
Fig. 2.3 Effect of shoot treatment on Bud Index by node position (Expt. 80/1, 'Shiraz'). Shoots topped to 10 nodes (---); no topping (---); 50% defoliation (+,x); no defoliation (o,•). Each point represents percentage of 20 nodes.

Fig. 2.4 Effect of timing of shoot treatment on Bud Index (mean of nodes 2 to 9); Expt. 80/2, 'Shiraz'. Calendar date (o); # visible internodes (•).
Fig. 2.5 Effect of timing of shoot treatment on Bud Index by node position (Expt. 80/2, 'Shiraz'). Shoot treatment (tapped to 10 nodes, 50% defoliation and injury) on Nov. 7 (x), Nov. 19 (+), Dec. 15 (o); untreated control shoots, pooled (●).

Fig. 2.6 Effect of shoot treatment on Bud Index by node position (Expt. 80/2, 'Shiraz'; pooled over time). Shoot treatment (o); untreated control (●).
* indicates means at same node significantly different at 5% level.
Fig. 2.7 Effect of shoot treatment to whole vines on (a) Bud Index, (b) Shoot Index (Expt. 80/3, 'Sultana'). Shoot treatment - thinned to 20 shoots, shoots topped to 10 nodes, 50% defoliation and injury (o); control (s). Vertical bar represents LSD (.05) for separation of shoot treatment means at different nodes.

*, **, indicates means at same node significantly different at 5 and 1% level respectively.
Fig. 2.8 Effect of shoot treatment to whole vines on Bud Index of (a) 'Shiraz', (b) 'Pedro Ximenez' (Expt. 80/3). Shoot treatment, as for Fig. 2.6 (○); control (■).
Fig. 2.9. a,b,c,d Necrotic primary bud tissue (1) remaining in the gap between two "secondary"* shoots (2).

* "secondary" shoot includes secondary, tertiary or quaternary shoots.
Fig. 2.10 Comparison of Bud Index of untreated shoots on partially-defoliated vines (Expt. 80/1 (x); Expt. 80/2 (o)) with untreated shoots on control vines (Expt. 80/3 (●)). Cv. Shiraz.
2.4 DISCUSSION

The preliminary experiments carried out during the 1980/81 season confirmed that (a) topping and defoliation of single shoots and (b) shoot thinning together with topping plus defoliation of remaining shoots on whole vines, induced primary bud axis necrosis (PBN). This condition appeared identical to that induced by the hailstorm.

As previously mentioned, when these experiments were commenced I was not aware of any reports in which the necrosis of the primary axis alone is described for grapevines. One possible exception was the apparent reference to death of part of the bud (the primary axis alone?) in the cultivar Anab-e-Shahi by Bindra and Chohan (1975) in India; the description in this case is vague and it has not been possible to clear up this point by correspondence.

During May 1980, Professor Shimon Lavee visited Roseworthy and examined buds from the 1980 experiments. He was able to confirm that the necrosis of the primary axis observed in buds from the Roseworthy vineyard was identical to that observed in Israel under natural conditions, and subsequently reported in Lavee et al. (1981a). However, neither they nor any other workers have reported PBN caused by shoot topping or defoliation up to the present time (1985).

The burst of primary latent buds was expected following the removal of shoot tip and lateral shoots; however, the levels (up to 70 per cent of nodes with primary latent bud-burst) were much higher than those reported by Huglin (1958) and Fournioux and Bessis (1982). To decrease the incidence of this phenomenon in subsequent years of this study, lateral shoots were retained at all nodes, and leaves only were removed in "defoliation" treatments.

Although injury resulted in increased (but not significant) PBN (Expt. 80/1), it was not considered to be a major factor in inducing this condition and therefore was not studied further.

In all experiments, topping and defoliation induced most PBN at distal nodes. However, in untreated whole vines (Expt. 80/3), the proximal nodes had the highest incidence of PBN and in this respect, agreeing with the observations of Lavee et al. (1981a).

The effect of defoliation appears to be associated with a factor translocated between shoots since control shoots on partially defoliated vines (shoot thinning plus partial defoliation of half or more of the remaining shoots) had more PBN at distal nodes than shoots on untreated vines (Fig. 2.10).

Lavee et al. (1981a) found that induction of bud necrosis took place
during flowering. Therefore, the decrease in PBN with later time of shoot treatment is perhaps not unexpected (Expt. 80/2). Again, the decrease is most marked for the distal nodes (Fig. 2.5). The positive correlation between PBN and vigour was also noted by Lavee et al. (1981a).

The strong positive correlation between Bud Index and Shoot Index is considered to be significant because it demonstrates that any change in the level of PBN, observed in bud dissection, will express itself as a change in (a) the proportion of primary and secondary shoots and (b) the proportion of nodes with and without primary shoots. This, in turn, has consequences for yield because primary shoots have more and larger inflorescences than secondary shoots, as shown by the results of Expts. 80/2 and 80/3 and also noted by Antcliff and Webster (1955b) and Bessis (1965), amongst others.

Topping, defoliation and shoot thinning to whole vines induces much higher levels of PBN on 'Shiraz' than either 'Sultana' or 'Pedro Ximenez'. Also, the natural levels of PBN on 'Shiraz' are higher. For these reasons, most of the subsequent work in this study has concentrated on 'Shiraz'.

2.5 RESEARCH AIMS (1981 AND SUBSEQUENT YEARS)

From the results of the 1980 experiments it was apparent that shoot topping and/or defoliation was able to induce a bud abnormality previously undescribed in Australia, i.e. primary bud-axis necrosis (PBN). Although the initial observation of this phenomenon resulted from damage caused by a hailstorm, and hailstorms do not occur frequently in most grapegrowing regions in Australia, the practice of summer pruning, i.e. hedging, slashing, has been increasingly used in this country for several reasons: one factor of major significance which has necessitated its use is the increased vine vigour resulting from irrigation (the proportion of vineyards irrigated in Australia has increased significantly in the past decade). Another cause has been the use of invigorating rootstocks, increased fertiliser use, improved soil management, etc. In addition, there has been an increase in the proportion of vineyards planted in cooler regions and/or with high summer rainfall and deep, fertile soils. Very often, a poor choice of vine spacing and trellis type has led to major problems with the management of excess vigour.

A documented response to defoliation of grapevines, particularly if carried out close to flowering, is a decrease in yield. The main yield components usually affected in such cases are bunches per shoot and bunches per vine, i.e. a decrease in fertility. An increase in vine vigour may
also be accompanied by a decrease in bunches per shoot (but not usually yield per vine as a result of compensation by other components).

The decrease in fertility in these instances is usually attributed to a decrease in photosynthetic capacity in the case of defoliation, and to excessive shading within the canopy when associated with increased vine vigour. In both cases, it would normally be assumed that it is the fertility of the primary latent bud which has been decreased. However, above findings provide an alternative explanation for the decrease in fertility, (one which has been previously not recognised nor suspected in grapevines) namely the induction of primary bud-axis necrosis by defoliation, topping or shoot thinning, compounded by a general increase in vine vigour. It is likely, however, that this hypothesis could only account in part for a decrease in fertility.

This foregoing explanation, plus the reports in 1981 by Lavee et al. (1981a,b) of (a) a relationship between vine vigour and PBN, and (b) the artificial induction of PBN in grapevines by exogenous application of gibberellic acid (GA$_3$) led to the following research aims:

1. To define and quantify the response of grapevines to the induction of PBN by shoot thinning, shoot topping and defoliation.

2. To examine the response in different cultivars, both seeded and seedless.

3. To study the natural levels of PBN and to examine the relationship with vine vigour.

4. To study the anatomical development of PBN.

5. To examine the effects of exogenous application of gibberellic acid (GA$_3$) and other growth regulators on induction of PBN.

6. To investigate the effect of shoot topping and defoliation on endogenous levels of GAs in grapevine buds.

7. To determine the effect of shoot thinning, topping, defoliation and growth regulator application on yield components.

Most of this work was carried out on cv. Shiraz for two reasons: (a) because this cv. has a high natural and inducable level of PBN, and (b) because it is Australia's most important red wine-grape.
CHAPTER 3

NATURAL LEVELS OF PRIMARY BUD-AXIS NECROSIS

ABSTRACT

Natural levels of PBN are positively correlated with shoot vigour (as measured by shoot diameter and length, and number of lateral shoots) and vine vigour (as measured by butt circumference). Natural levels may vary from one season to another within the same vineyard and, of all cultivars examined in Australia, are highest with 'Shiras'. A decrease in shoot vigour, achieved by lighter pruning, brought about a decrease in PBN level.
3.1 INTRODUCTION

The preliminary experiments in 1981 (Chapter 2) showed a strong correlation between vine vigour (measured as butt circumference) and natural level of PBN, i.e. levels measured in control vines. This relationship between vigour and various bud conditions was also shown by Lavee et al. (1981a) who found "bud necrosis" (for nodes 1 to 10) averaged 40 per cent in vigorous and 10 per cent in moderately vigorous vineyards of cv. Queen of the Vineyard in Israel. Also, there was a higher incidence of bud necrosis on thick (>10mm diameter) than thin (<10mm) canes, particularly at nodes 1 to 4 (Fig. 3.1). "Bud mortality" of 'Anab-e-Shahi' and 'Sultana' in India was found to be closely related to vine vigour (Bindra 1977; Jindal and Dabas 1982).

An increase in vigour, as a result of irrigation, was associated with an increased "ratio of secondary shoots to primary shoots" (and possible mortality of the primary axis) with 'Cabernet Sauvignon' (Carbonneau and Casteran 1978) and decreased bud burst with 'Grenache' (Meriaux et al. 1981).

In South Africa, the percentage of "dead buds" may be as high as 58 per cent in 'Sultana' vineyards, and up to 20 to 40 per cent for 'Crouchen', 'Chenin blanc' and 'Muscat gordo blanco' (Smit, pers. comm).

"Bud necrosis" in Israel (confirmed as PBN) is highest at the proximal nodes of the cane and is very low after node 7 (Fig. 3.1).

The relationship between vine vigour and PBN is discussed in this chapter together with the effect of both cultivar and site on the natural levels of PBN.
3.2 MATERIALS AND METHODS

Much of the data used in this Chapter has been derived from "control" vines in experiments described in other chapters. Similarly, the methods of measurement of the various "vigour indices" used in this chapter have been described elsewhere, especially Chapter 2.

In addition to the above, data has also been collected from the following sites, details of the first four of which are given in Appendix A.

3.2.a Virginia, South Australia, cv. Shiraz.
During July 1984, 42 shoots were collected from approximately 30 adjacent vines. Shoots were collected over as wide a range of diameters as possible and divided into 3 approximately equal groups, based on shoot diameter, i.e. 12, 14 and 16 shoots per class.

Bud Index by node position was determined for each diameter class. Also, both shoot diameter and mean Bud Index (nodes 2 to 11) were determined for each of the 42 shoots.

3.2.b Waikerie, South Australia, cv. Shiraz.
During winter 1981, the 10 most "vigorous" shoots from a vigorous, irrigated vineyard were collected from each of 4 representative vines and used for determination of Bud Index by node position.

3.2.c Barossa (Williamstown), South Australia, cv. Shiraz.
Two nearby vineyards, one classed as "vigorous", the other classed as "low vigour" were used in this study.

In June 1983, the 10 most vigorous shoots were selected from each of 4 vines (in the case of the "vigorous" vineyard, 4 control vines in Expt. 82/15; in the case of the "low vigour" vineyard, 4 representative vines) and used for determination of Bud Index.

3.2.d Swan Valley, Western Australia, cv. Shiraz.
Bud index and shoot diameter were determined for twenty shoots collected from this vineyard, classed as "vigorous", in May 1985.

3.2.e Roseworthy "South Vineyard", Mechanical pruning experiment, cv. Shiraz.
The twenty most vigorous shoots were selected at random from each of mechanically-pruned and normal hand spur-pruned vines in June 1985. Bud
index, shoot diameter and shoot length were determined for each shoot. Mechanically-pruned and hand-pruned vines were pruned to a mean of 256 and 62 nodes per vine respectively in winter 1984 and these pruning levels remained relatively constant over the 6 years of this experiment.
3.3 Results

3.3.a Relationship between PBN and vine vigour in 'Shiraz'.

(i) Butt circumference: A significant positive correlation was found between Bud Index and butt circumference (except for control vines in Expt. 81/5). The correlations for treated vines (whole vines thinned to 20 shoots per vine, all shoots topped to 10 nodes plus some defoliation) were better than those for control vines (Table 3.1).

(ii) Shoot diameter: A strong positive correlation was found between the diameter of a shoot and the mean Bud Index (for nodes 2 to 10) for that shoot in both treated and control vines (Table 3.2). The greatest difference in Bud Index between thick and thin shoots was found at the proximal nodes (Table 3.3; Figs. 3.2, 3.3).

Shoot thinning to several levels (where shoots themselves were not treated) had a significant effect on the diameter of the remaining shoots (Table 3.4) shown by the negative correlation between number of shoots retained per vine and shoot diameter ($r = -0.94$, significant at 6 per cent level). On the other hand, shoot thinning plus shoot topping and defoliation had no significant effect on shoot diameter ('Shiraz', Expt. 81/5; 'Sultana', Expt. 83/7). Similarly, there was no significant difference in shoot diameter between treated (topped and defoliated) and untreated shoots on a vine thinned to 20 shoots ('Shiraz', Expt. 81/1B).

(iii) Shoot weight: Although this variable was measured in only one year (as an alternative index of shoot vigour to shoot diameter), the results show that shoot weight was also positively correlated with Bud Index, in both "treated" and "control" vines (Table 3.5).

(iv) Percentage of nodes with lateral shoots: A positive correlation existed between this variable and Bud Index (Table 3.5). For any node at which the primary bud was necrotic, there was a 1.5 to 3 times greater chance of that node having a lateral shoot than not. Expressed another way, nodes with lateral shoots had 200 to 400 per cent greater incidence of PBN than nodes without lateral shoots on both treated shoots and vines, and control shoots and vines (Tables 5.8, 5.20). This index, as expected, was also positively correlated with shoot diameter, another index of shoot vigour (Table 3.6).
(v) **Number of lateral shoots per shoot**: This index is similar to "per cent nodes with lateral shoot". Therefore, as expected, it was also positively correlated with Bud Index (Table 3.6). Whole vine treatment, i.e. thinning to 20 shoots per vine, topping to 10 nodes and 50 to 100% defoliation, significantly increased the number of lateral shoots per cane, compared to control vines, e.g. 3.4 times (Expt. 83/2) 3.9 times (Expt. 83/4) and 5.3 times (Expt. 81/5) for ' Shiraz' and 4.4 times for 'Sultana' (Expt. 83/7).

(vi) **Mean length of lateral shoots**: The results were conflicting: whole vine treatment decreased mean lateral shoot length while at the same time increasing lateral number per cane whereas in Expt. 83/4 both number and length increased. Also, there was no significant correlation between lateral length and Bud Index in Expt. 81/5 (Table 3.6).

**3.3.b. Natural levels of PBN**

(i) **Shiraz**: In a range of vineyard sites there is a tendency for higher levels of PBN to be found in the more vigorous vineyards (Table 3.7): however, the results are variable and clearly other factors than vigour influence the development of PBN.

(ii) **Other cultivars**: ' Shiraz' appears to have the highest natural levels of PBN in the cultivars examined. The level in other seeded cultivars is generally low, and of these, it is highest in the more vigorous cultivars (Table 5.7). In seedless cultivars the levels are generally low or undetectable; 'Sultana' had the highest levels in the seedless cultivars examined.

(iii) **The distribution of PBN along the shoot**: The pattern of PBN distribution along the shoot is very consistent in all cultivars. Whenever PBN has been determined by node position, the curves are always the same as those shown in Figs. 5.3, 3.2, 3.3 and elsewhere, i.e. the proximal nodes have significantly higher levels of PBN than the distal nodes. The level of PBN, as measured by bud index, usually drops to nil beyond the 6th node in untreated vines.

**3.3.c Effect of mechanical pruning on PBN.**

One of the consequences of mechanical pruning is a large increase in node number retained per vine relative to hand spur-pruned vines, which in turn leads to a significant increase in shoots per vine, even after 6 years of mechanical pruning. Such shoots were shorter and thinner shoots and had a low level of PBN (Table 3.8) agreeing with the tendency mentioned in
(i) above. Bud size was also observed to be appreciably smaller on shoots from mechanically-pruned vines (not measured).
### Table 3.1 Summary of correlations between Bud Index and butt circumference (cm) for cv. Shiraz

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Control vines</th>
<th>Correlation coefficient (r)</th>
<th>Level of significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>80/3</td>
<td>.88</td>
<td>.96</td>
<td>5%</td>
</tr>
<tr>
<td></td>
<td>Treated vines</td>
<td></td>
<td>1%</td>
</tr>
<tr>
<td>81/5</td>
<td>.30</td>
<td>ns</td>
<td>5%</td>
</tr>
<tr>
<td></td>
<td>.79</td>
<td></td>
<td>5%</td>
</tr>
<tr>
<td>83/1</td>
<td>.55</td>
<td>.58</td>
<td>5%</td>
</tr>
</tbody>
</table>

a Mean per vine as percentage for 80/3, degrees for 81/5, 83/1

### Table 3.2 Summary of correlations between Bud Index and shoot diameter (mm) for cv. Shiraz

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Correlation coefficient (r)</th>
<th>Level of significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>81/1B&lt;sup&gt;c&lt;/sup&gt;</td>
<td>.73</td>
<td>1%</td>
</tr>
<tr>
<td>81/5&lt;sup&gt;d&lt;/sup&gt; (i)&lt;sup&gt;e&lt;/sup&gt;</td>
<td>.46</td>
<td>1%</td>
</tr>
<tr>
<td></td>
<td>(ii)&lt;sup&gt;f&lt;/sup&gt;</td>
<td>.49</td>
</tr>
<tr>
<td></td>
<td>(iii)&lt;sup&gt;g&lt;/sup&gt;</td>
<td>.47</td>
</tr>
<tr>
<td></td>
<td>(iv)&lt;sup&gt;g&lt;/sup&gt;</td>
<td>.32</td>
</tr>
<tr>
<td>82/2&lt;sup&gt;h&lt;/sup&gt; Virginia&lt;sup&gt;i&lt;/sup&gt;</td>
<td>.58</td>
<td>5%</td>
</tr>
<tr>
<td></td>
<td>.73</td>
<td>0.1%</td>
</tr>
</tbody>
</table>

a As degrees
b Mean values per shoot
c Treated and control shoots pooled
d, e Shoot treatment; f, g no shoot treatment
d, f 500 ppm ccc; e, g 0 ppm ccc
h All shoot thinning treatments pooled with control
i Control vines
Table 3.3 Relationship between Bud Index and shoot diameter; 'Shiraz', Virginia, South Australia

<table>
<thead>
<tr>
<th>Shoot diameter class (mm)</th>
<th># shoots per class</th>
<th>Bud Index (%) at nodes:</th>
<th>2 to 4</th>
<th>5 to 7</th>
<th>8 to 11</th>
<th>2 to 11</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt;10</td>
<td>12</td>
<td>45 a</td>
<td>42 a</td>
<td>13 a</td>
<td>31 a</td>
<td></td>
</tr>
<tr>
<td>10 to 12</td>
<td>16</td>
<td>19 ab</td>
<td>17 b</td>
<td>2 b</td>
<td>11 b</td>
<td></td>
</tr>
<tr>
<td>&gt;12</td>
<td>14</td>
<td>6 b</td>
<td>0 c</td>
<td>0 b</td>
<td>2 c</td>
<td></td>
</tr>
</tbody>
</table>

Means in columns followed by the same letter are not significantly different at the 5% level.

Table 3.4 Effect of severity of shoot thinning per vine on mean shoot diameter (mm) (Expt. 82/2, 'Shiraz')

<table>
<thead>
<tr>
<th>Number of shoots retained per vine</th>
<th>Shoot diameter (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>75a</td>
<td>11.4 c</td>
</tr>
<tr>
<td>20</td>
<td>12.7 b</td>
</tr>
<tr>
<td>10</td>
<td>12.9 b</td>
</tr>
<tr>
<td>5</td>
<td>13.8 a</td>
</tr>
</tbody>
</table>

a Unthinned control
Means followed by same letter are not significant at 5% level.
### Table 3.5 Summary of correlations between Bud Index per vine\(a\) and shoot weight per vine (g) from nodes 1 to 10 of cv. 'Shiraz'.

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Correlation coefficient (r)</th>
<th>Level of significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>83/1</td>
<td>Control vines</td>
<td>.73</td>
</tr>
<tr>
<td>83/2</td>
<td>Treated vines</td>
<td>.86</td>
</tr>
<tr>
<td>83/2</td>
<td>Control vines</td>
<td>.37</td>
</tr>
<tr>
<td>83/4</td>
<td>Treated and control vines pooled</td>
<td>.4</td>
</tr>
</tbody>
</table>

\(a\) As degrees

### Table 3.6 Summary of correlations between lateral shoot measurements and Bud Index or shoot diameter, cvs. 'Shiraz' and 'Sultana'.

<table>
<thead>
<tr>
<th>Experiment*</th>
<th>Variable</th>
<th>Correlation coefficient (r)</th>
<th>Level of significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>81/1A,1B(^1)</td>
<td>Bud Index, (a,b) % nodes with lateral shoot</td>
<td>.81</td>
<td>0.1%</td>
</tr>
<tr>
<td>81/1B(^1)</td>
<td>Shoot diameter, (c) % nodes with lateral shoot(c)</td>
<td>.72</td>
<td>5%</td>
</tr>
<tr>
<td>81/5(^1)</td>
<td>Bud Index, (a,d) lateral shoot number per main shoot</td>
<td>.75</td>
<td>0.1%</td>
</tr>
<tr>
<td>81/5(^1)</td>
<td>Bud Index, (a,d) Mean length per lateral shoot</td>
<td>-.36</td>
<td>ns</td>
</tr>
<tr>
<td>81/5(^1)</td>
<td>Bud Index, (a,d) % nodes with lateral shoot(d)</td>
<td>.57</td>
<td>5%</td>
</tr>
<tr>
<td>83/7(^2)</td>
<td>Bud Index, (a,d) lateral shoot number per main shoot</td>
<td>.33</td>
<td>5%</td>
</tr>
</tbody>
</table>

\(a\) As degrees
\(b,c,d\) Mean per vine, per 10 shoots, per shoot respectively
\(1,2\) 'Shiraz' and 'Sultana' respectively
* All treatments pooled except in case of 83/7 (treated vines only)
Table 3.7 Summary of natural levels of PBN measured as Bud Index for cv. Shiraz.

<table>
<thead>
<tr>
<th>Vineyard site</th>
<th>Vigour&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Bud Index %</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>SOUTH AUSTRALIA</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Roseworthy College</td>
<td></td>
<td></td>
</tr>
<tr>
<td>&quot;South Vineyard&quot;</td>
<td>M to H&lt;sup&gt;b&lt;/sup&gt;</td>
<td>12</td>
</tr>
<tr>
<td>&quot;Variety Vineyard&quot;</td>
<td>H</td>
<td>16</td>
</tr>
<tr>
<td>Waikerie</td>
<td>H</td>
<td>16</td>
</tr>
<tr>
<td>Virginia</td>
<td>H</td>
<td>14</td>
</tr>
<tr>
<td>Williamstown</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(a)</td>
<td>H&lt;sup&gt;d&lt;/sup&gt;</td>
<td>8</td>
</tr>
<tr>
<td>(b)</td>
<td>L</td>
<td>5</td>
</tr>
<tr>
<td>Waite</td>
<td></td>
<td></td>
</tr>
<tr>
<td>&quot;Alverstoke&quot;</td>
<td>M&lt;sup&gt;d&lt;/sup&gt;</td>
<td>7</td>
</tr>
<tr>
<td>&quot;Claremont&quot;</td>
<td>M&lt;sup&gt;e&lt;/sup&gt;</td>
<td>23</td>
</tr>
<tr>
<td><strong>WESTERN AUSTRALIA</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Swan Valley</td>
<td>H</td>
<td>27</td>
</tr>
</tbody>
</table>

<sup>a</sup> L = low vigour; M = moderate; H = high
<sup>b</sup> Average for all years
<sup>c,d,e</sup> Expts. 82/8, 82/15, 82/10 respectively.
Table 3.8 Effect of mechanical pruning on shoot number per vine, Bud Index, shoot diameter and length (cv. Shiraz)

<table>
<thead>
<tr>
<th></th>
<th>Mechanical pruning</th>
<th>Hand spur pruning</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shoots per vine (1985-85 season)</td>
<td>236</td>
<td>140</td>
</tr>
<tr>
<td>Bud Index a,b</td>
<td>1</td>
<td>11</td>
</tr>
<tr>
<td>Shoot diameter (mm) a</td>
<td>7.7</td>
<td>1.1</td>
</tr>
<tr>
<td>Shoot length (cm) a</td>
<td>69</td>
<td>185</td>
</tr>
</tbody>
</table>

a Mean of 20 canes, measured in June, 1985
b Nodes 2 to 10 inclusively
Fig. 3.1 Distribution of necrotic buds along thin (<10mm diameter) and thick (>10mm diameter) shoots of 'Queen of the Vineyard' and number of inflorescence primordia per bud (PF) in a vigorous vineyard. (from Lavee et al. 1981a)
Fig. 3.2 Effect of shoot diameter on Bud Index by node position (Expt. 81/5, 'Shiraz'; untreated vines). Shoot diameter <9mm (o); >9mm (o).
Each point represents mean of 35 to 45 shoots.

Fig. 3.3 Effect of shoot diameter on Bud Index by node position ('Shiraz', Swan Valley, WA). Shoot diameter <11mm (o); >11mm (o).
Each point represents mean of 9 to 11 shoots.
3.4 DISCUSSION

The positive correlation between the level of PBN and vine vigour with 'Shiraz' was also shown for 'Queen of the Vineyard' by Lavee et al. (1981a); the authors found a relationship between both vineyard vigour and shoot diameter, and incidence of PBN. In the case of shoot diameter, there is a close similarity between the data in Figs. 3.2 and 3.3 and Table 3.3, and that of Lavee et al. 1981a; (Fig. 3.1).

Not only was the natural level of PBN related to vine vigour but also the degree of response to whole vine treatment (shoot thinning/topping/defoliation) and shoot treatment (topping/defoliation) was greater with increasing vigour (Chapter 5).

Even though the assessment of vineyard vigour as a whole was subjective in this study, there does appear to be a correlation between vineyard vigour and incidence of PBN, as distinct from vine vigour. Within the same vineyard, butt circumference was a reliable indicator of between-vine variation in vigour and is positively correlated with PBN level per vine. Likewise, shoot diameter and weight which are both good indices of shoot vigour were positively correlated with PBN level per cane. Shoot thinning increased the growth rate of the remaining untreated shoots and thus the shoot diameter and weight, relative to shoots and untreated vines. However, shoot thinning in combination with topping of all remaining shoots had no effect on shoot diameter relative to shoots on control vines; presumably the growth potential derived from thinning was diverted into lateral shoot development on topped shoots.

Lighter pruning (which in the examples cited was achieved by mechanical pruning) resulted in an increase in shoots per vine with a concomitant decrease in individual shoot vigour; as expected, this was associated with a lower level of PBN.

Increase in the number of lateral shoots per shoot (cane), or the percentage of nodes with a lateral shoot, mainly occurs in response to shoot topping, and to a lesser extent, shoot thinning. Both measures of lateral shoots per shoot are correlated with PBN per shoot. Thus, it is no coincidence that topping results in a significant increase in both numbers of laterals and PBN at the distal nodes.

This is the first report of a positive correlation between PBN at a node and the presence of a lateral shoot at the same node. It should therefore follow that, at least for 'Shiraz', nodes with lateral shoots will have lower fertility, due to loss of the primary axis. Whether this is in fact the situation will be examined in Chapter 8. By comparison, in 'Sultana', the presence of strong lateral shoots on canes has been used as an indicator of fruitful canes (Antcliff et al. 1958).
The question also needs to be asked: is there a causal relationship between lateral shoot development and PBN at the same node or are they merely associated, i.e. both "induced" by the same causal agent? This will be further discussed in Chapter 8.

The levels of PBN in 'Shiraz' are not as high as those cited for 'Queen of the Vineyard' by Lavee et al. (1981a); this may be due to differences in the methods of calculation of Bud Index and per cent necrotic buds, or to relative vigour or location. Whatever the reason, it appears that some cultivars are more susceptible than others; differences in susceptibility can only be partly explained by differences in vigour, because cultivars more vigorous than 'Shiraz' at Roseworthy, eg. 'Farana', 'Gros Colman', and 'Mantuo', have lower levels of PBN. Certainly, whether a cultivar is seeded or not has a large bearing on degree of susceptibility.

The natural level of PBN can fluctuate from season to season in the same vineyard; this has been observed both for 'Shiraz' at Roseworthy and for 'Queen of the Vineyard' in Israel. It is interesting that there has been no significant decrease in natural PBN level in the "South" vineyard at Roseworthy even though there has been a significant decrease in the response to whole vine treatment (attributed to a decrease in vine vigour associated with a decrease in the amount of irrigation: see Chapter 5). Perhaps the differences in PBN due to differences in vigour between vines are greater than those between seasons within the same vineyard. In this case, unless the same vines are measured each season, it may not be possible to detect significant changes from season to season.
CHAPTER 4

ANATOMICAL DEVELOPMENT OF PRIMARY BUD-AXIS NECROSIS (PBN)

ABSTRACT

Study of the anatomy of grapevine buds with primary bud-axis necrosis (PBN) confirmed that necrosis commenced soon after flowering and was largely completed by mid-summer; at the same time, the "secondary" bud-axes remained healthy and showed greater development than normal. "Natural" PBN was anatomically identical to that induced by shoot treatment (thinning/topping/defoliation) or exogenous application of GA$_3$ and appeared the same as the "bud necrosis" previously reported in Israel. Development of PBN followed a period of active bud growth which was accelerated by shoot treatment.
There have been a few reports of partial or complete necrosis of the primary bud-axis (PBN) of grapevines (Bindra and Chohan 1975; Bernstein 1969, 1973; Lavee et al 1981a,b; Smit pers.comm.). In these reports the primary bud-axis tissue was completely necrotic when observed microscopically in winter whereas the secondary bud-axes (i.e. secondary, tertiary and quaternary buds) had a green, apparently normal appearance; similarly there was no external difference in the appearance of compound buds with either necrotic or normal primary bud-axes.

There are differences in the published descriptions of the development of this condition; for example, Bindra (1980) describes the necrotic tissue as "... extending downwards from the bud apex" whereas Lavee et al. (1981a) observed that "... the deterioration of the central (primary) bud started with the appearance of a necrotic layer at its third or fourth node and developed upwards" and "... a necrotic pattern develops without inducing a defined abscission layer".

In winter, compound buds with a necrotic primary bud-axis differ anatomically from those with normal primary bud-axis in that the secondary bud-axes are larger than normal and fill the space within the bud scales created by the drying and shrinking of the primary bud-axis; basal tissues of the primary bud-axis and of the compound bud as a whole usually remained green and undamaged (Lavee et al. 1981a,b; Figs. 4.1, 4.2, 4.3).

Exogenous application of GA₃ may also induce PBN but, unlike "natural" PBN, is usually associated with an elongation of the primary and secondary bud-axes (Fig. 4.2) which may manifest itself as a "split bud" in which the secondary bud-axes push apart the bud scales and the necrotic tissue disintegrates forming a gap (Lavee et al. 1981b; Fig. 4.3.c).

Necrosis commences at flowering (Bindra 1980; Lavee et al. 1981a). The final number of buds with PBN is usually reached within 3 weeks of full bloom according to Lavee et al. (1981a); however, Bernstein (1969, 1973) states that many buds develop necrosis during mid- to late summer.

This chapter describes: a) the anatomical appearance of PBN under "natural" conditions and "induced" by shoot treatment (thinning/topping/dedefoliation) or application of exogenous GA₃; b) the seasonal development of PBN; and c) the changes in primary bud dry weight and size preceding the development of PBN induced by shoot treatment.
4.2 MATERIALS AND METHODS

4.2.a. Examination of 'Shiraz' buds.

i) **Summer**: Shoot pieces including nodes 7, 8 and 9 were collected from "treated" (thinning/topping/defoliation) and "control" vines at Roseworthy in January 1983 and buds were examined immediately. Whole buds were cut transversely or longitudinally while still attached to the stem and photographed at low magnification with a combination macro-lens/bellows system under reflected incandescent light.

ii) **Winter ("fresh" buds)**: Cuttings were collected in winter from "treated" (as above or exogenous application of GA$_3$) and "control" vines from the 1981/82 season at Roseworthy. They were soaked in "Chinosol" (0.5 per cent) overnight and stored in heat-sealed plastic bags at 2°C. Buds were treated and photographed as in i) above in October 1982.

iii) **Winter (fixed buds)**: Single buds, with some woody stem tissue attached, were collected from "treated" and "control" vines (as for ii above) and fixed in FAA (ethanol 95% : acetic acid (glacial) : formalin (37 to 40% formaldehyde) : water = 50 : 5 : 10 : 30 v/v/v/v). The procedures for preparation of sections for microscopic examination are described in O'Brien and McCully (1981): buds were dehydrated in an alcohol/water series and embedded in Spurr's epoxy resin. Sections (2 um) were prepared with a microtome fitted with a glass knife, directly stained with Azure B or Toluidine Blue and mounted in DPX. Photomicrographs of longitudinal and transverse sections are presented as a collage because the field of view of the microscope/camera system was not sufficiently large to include whole bud sections.

4.2.b. Seasonal development of PBN in 'Shiraz' vines.

i) **Experiments 82/14, 83/8**: Identical experiments were carried out on 'Shiraz' grapevines at Roseworthy College in the 1982/83 and 1983/84 seasons: ten vines were thinned to the 20 most vigorous shoots per vine, all shoots topped to 10 nodes and all main leaves removed (no lateral leaf or inflorescence removal) at full bloom (November 8 in 1982, November 10 in 1983); 10 non-treated vines were used as controls. Replicates were chosen using measurements of butt circumference. One shoot per vine (chosen at random on "treated" vines and from vigorous shoots on "control" vines) was
sampled at 0, 2, 4, 6 and 10 weeks after full bloom and buds examined at nodes 2 to 10 in longitudinal section; buds with any signs of necrosis of the primary axis were recorded as "necrotic". In winter, five shoots were collected from each vine and used to determine winter level of necrosis. Results at each sampling time were expressed as a percentage of the winter level of necrosis.

ii) Experiment 82/9: This experiment is described in 6.2.a.iv; GA$_3$ was applied to 'Shiraz' leaf blades at nodes 5 to 10 inclusively on November 9. Five GA$_3$-treated shoots were sampled on December 16 and January 17 (approximately 5 and 9 weeks after treatment respectively) and examined for the presence of necrosis at nodes 2 to 12 as in 4.2.b.i. Results were expressed as "Bud Index" and compared with winter observations.

4.2.c. Observations on primary buds after shoot treatment (thinning/topping/defoliation) of 'Shiraz' vines.

i) Bud weight measurements: The changes in dry weight (D.Wt) of primary bud tissue on "treated" (thinning/topping/defoliation) and "control" 'Shiraz' vines was followed in both 1983/4 (Experiment 83/1; see 5.2.viii) and 1984/5 seasons. In the 1984/5 season 10 "treated" vines were thinned to 12 shoots per vine on November 15, all shoots topped to 10 nodes with 100 per cent defoliation (no lateral leaf removal); 10 non-treated vines were used as controls with replicates chosen on the basis of butt circumference. Shoot sections (nodes 7 to 10 inclusively) were removed at 0, 1, 2 and 4 weeks after treatment from one shoot per vine.

In both seasons, the primary bud was removed as follows: using a low-power microscope the outermost small bract of the compound bud (sometimes missing) was first removed with fine-pointed forceps, then the bract enclosing the secondary bud and the secondary bud itself (cut off at base with scalpel), followed by the tertiary bud and enclosing bract (cut off at base). Buds in which the primary bud had burst (less than 15 per cent of buds at node 10 only) were excluded; however, where the primary bud had obviously elongated, these were included as long as the bud had not passed the "woolly bud" stage. After removal, buds were freeze-dried (1983/4) or oven-dried at 40°C for 48 hours (1984/5) and then weighed.

ii) Bud length and node number: In the 1984/85 season, bud length and node number were determined at the final sampling, i.e. 4 weeks after
"treatment". Whole compound buds (10 each from "treated" and "control" vines), from which the outermost bract and secondary bud had been removed, were excised from nodes by cutting through the base of the bud at the point of attachment of the second bract; buds from nodes 7 to 9 inclusively were used. Bud sections were hand-cut with a razor blade, mounted in water and examined at low magnification. Length (measured with a graduated eye piece) and node number were determined for each bud.

iii) **Photomicrography of bud sections**: Samples of buds from ii) above were also prepared for sectioning and photomicrography. Whole buds were excised, the outermost bract and secondary bud removed and the specimen immediately fixed in formalin (37 to 40 per cent formaldehyde) : proprionic acid : ethanol (70 per cent), 5 : 5 : 90 v/v/v. The procedures for preparation of sections for photomicrography were as described in O'Brien and McCully (1981). Buds were dehydrated in a tertiary butyl alcohol (TBA) series, culminating with TBA/liquid paraffin, infiltrated with molten (58°C) paraffin wax (7 transfers over 3 days) and embedded in molten paraffin wax in plastic moulds. Sections (10 μm) were cut with a metal knife on a rotary microtome, transferred to slides and incubated at 30 to 40°C, dewaxed by passage through two baths of xylene followed by two baths of absolute alcohol (one minute per step) and prepared for staining by washing in 70 per cent ethanol. Sections were stained with safranin (one per cent in 70 per cent ethanol) followed by fast green (two per cent in pure clove oil) with dehydration in ethanol series between stains, washed in clove oil, xylene (twice) and mounted in DPX. Photomicrographs of primary buds in LS (as a collage in the case of buds from "treated" vines) were taken at low magnification using a camera/microscope system.
4.3 RESULTS

4.3.a. Examination of 'Shiraz' buds.

i) Summer: Figs. 4.4.a,b show a bud in early January, before and after longitudinal section respectively. Sectioning reveals complete necrosis of the primary bud-axis (PBN) and the healthy, green tissue of the secondary and tertiary bud-axes; at the same time, the bud has a normal external appearance. Comparison of longitudinal sections of a normal bud with healthy primary bud-axis (Fig. 4.4.c) and a bud with PBN (Fig. 4.4.d) shows the greater development of the secondary and tertiary bud-axes of the latter. Fig. 4.4.e (and also 4.6.a) shows a bud with PBN in transverse section; in this case, the bud has been cut relatively close to the base in order to show that loss of the primary bud-axis by necrosis has been partly compensated by better development of the secondary, tertiary and quaternary bud-axes (the quaternary bud is a branch of the third-order (N+3) as are the secondary and tertiary buds).

ii) Winter ("fresh" buds): Buds sectioned in winter (Fig. 4.5.a-d) had a similar appearance to those in summer; however, the necrotic tissue of the winter buds was darker. Necrosis of the primary bud-axis did not extend into the supporting tissue (Fig. 4.5.b). Buds with PBN induced in response to exogenous application of GA₃ had greater extension of all bud-axes (Fig. 4.6.a) compared to buds with PBN induced by "shoot treatment" or occurring naturally (Figs. 4.4, 4.5). For some buds with PBN the space normally occupied by the primary bud became almost filled by greater development of the secondary, tertiary (and quaternary) buds (Fig. 4.6.b); in other cases, the necrotic tissue disintegrated leaving a cavity (Fig. 4.6.c).

iii) Winter (fixed buds): Figs. 4.7.a-c and 4.8.a-c show photomicrographic collages of longitudinal and transverse bud sections respectively; because of its disorganisation the necrotic primary bud-axis tissue was completely (Fig. 4.7.b) or partially (Fig. 4.7.c) lost during sectioning. In Fig. 4.7.b,c, the margin between the necrotic primary bud-axis tissue and the healthy supporting tissue can be clearly seen as well as well-developed secondary, tertiary and quaternary (for Fig. 4.7.b) bud-axes. The secondary bud in Fig. 4.7.b has been displaced. Similarly, secondary (partially lost in 4.8.b) and tertiary (completely lost in 4.8.c) bud-axes are better developed in buds with PBN (4.8.b,c) than in normal buds (Fig. 4.8.a). External dimensions of normal buds and buds with PBN were similar.
4.3.b. Seasonal development of PBN.

i) Shoot treatment (thinning/topping/defoliation): The largest increase in PBN (as a percentage of the winter level) took place between 2 and 6 weeks after full bloom for buds on "control" vines and four to ten weeks after full bloom for buds on "treated" vines; similar trends were apparent in both seasons (Fig. 4.9). Two weeks after full bloom, primary buds at nodes 2 to 3 on both treatments showed partial necrosis; in addition, primary buds at nodes 9 to 10 on "treated" vines showed some elongation.

Four weeks after full-bloom, more extensive necrosis was showing in buds at nodes 2 to 3, with a lesser amount at nodes 4 to 5, for both treatments; in addition, some buds at nodes 8 to 10 on "treated" vines had a slight degree of tissue browning plus elongation. Six weeks after full-bloom, some primary buds at nodes 2 to 5 were completely necrotic for both treatments; buds at nodes 8 to 10 on "treated" vines had elongated further but showed only partial necrosis.

By ten weeks, a large proportion of primary buds at nodes 2 to 5 for both treatments had well-developed PBN, resembling the winter condition; the remaining buds had no or partial necrosis. In the case of "treated" vines, necrosis at nodes 8 to 10 was well developed and resembled the winter condition in many cases; some buds were only partly necrotic and buds at nodes 5 to 7 showed the least signs of necrosis.

In most cases, the first sign of PBN was the appearance of a necrotic layer at nodes 1 to 2 with subsequent development of necrosis distally. In fewer than 20 per cent of cases, PBN appeared to start as a browning of the apical meristem tissue of the primary bud which extended, in time, in a proximal direction towards the base of the bud. In both cases, the end result was complete necrosis of the primary bud.

ii) Exogenous GA₃ application: Necrosis of primary bud tissue was observed only in buds at nodes 5 to 8 at the first sampling (5 weeks after GA₃ application); in addition, elongation of the primary axis was apparent at nodes 7 to 12. Four weeks later, PBN was more extensive with Bud Index values being 73, 40 and 0 percent for nodes 2 to 4, 5 to 10 and 11 to 12 respectively (compared with winter values of 68, 44 and 16 respectively for the same node positions; Table 6.17).
In most cases, the first sign of PBN induced by GA₃ treatment appeared to be the development of a necrotic layer at nodes 1 to 2 of the primary bud which subsequently extended distally until the whole bud was affected; however, there was no abscission of the primary bud.

4.3.c. Observations on primary buds after shoot treatment (thinning/topping/defoliation) of 'Shiraz'.

i) Bud weight measurements: There was a rapid response to shoot treatment: primary buds on treated vines had dry wts. 40 percent more than those on control vines after 4 days and 60 to 80 percent more after 14 days in 1983 (Table 8.2) and 1984 (Fig. 4.10). During the 28-day sampling period in 1984, control buds had a 130 percent increase in D.Wt.

ii) Bud length and node number: Twenty-eight days after treatment, primary buds on shoot-treated vines not only weighed more but were also approximately twice as long as those on control vines; this difference was a result of longer internodes and not more nodes (Table 4.1; Fig. 4.11). The primary bud-axes of "treated and "control" in Fig. 4.11 are 3.2 and 1.5mm in length respectively; the node number of the "treated" bud was difficult to determine whereas the "control" appears to have 11 nodes.

Table 4.1 Effect of shoot treatment (thinning/topping/defoliation) of 'Shiraz' on length and node number of primary bud-axes.

<table>
<thead>
<tr>
<th></th>
<th>Length (mm)ᵃ</th>
<th>Node numberᵃ</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>1.33</td>
<td>9.2</td>
</tr>
<tr>
<td>Treated</td>
<td>2.55</td>
<td>9.7</td>
</tr>
</tbody>
</table>

ᵃ Indicates means significantly different at 5% level; ns = not significant
Means of 10 buds.
Fig. 4.1 Longitudinal section through a mature winter bud, cv. Queen of the Vineyard. A: Normal, B: Central bud dry ("necrotic"). a = Central ("primary") bud, b = axillary ("secondary") bud, c = bud base (from Lavee et al. 1981a).
Fig. 4.2 Necrosis development in untreated and GA$_3$-treated 'Queen of the Vineyard' buds. A: Control with necrotic central ("primary") bud. B: GA$_3$-treated with elongating active central bud. C: GA$_3$-treated with elongated necrotic central bud. a = scales, b = hairs, c = central bud-axis, d = axillary ("secondary") bud-axis, e - necrotic layer, f = bud base (from Lavee et al. 1981b).
Fig. 4.3 (A) Longitudinal cut through a GA$_3$-treated bud with necrotic centre ("primary") and developing axillary ("secondary") bud. General view of a normal bud (B) and a "split" bud (C) induced by GA$_3$ treatments of 'Queen of Vineyard' grapevine (from Lavee et al. 1981b).
Fig. 4.4 Development of PBN in 'Shiraz' buds in mid-summer. General view of same bud before (a) and after (b) longitudinal section showing necrotic primary axis and normal "secondary" axes. (c) Longitudinal section of normal bud. Longitudinal (d) and transverse (e) sections of a bud with PBN showing necrotic primary axis and normal "secondary" axes, 1, 2, 3, 4 = primary, secondary, tertiary and quaternary axes respectively; 5 = margin between necrotic primary axis tissue and healthy bud base tissue.
Fig. 4.5 Examination of 'Shiraz' buds in mid-winter. Longitudinal and transverse sections respectively of a normal bud (a, c) and a bud with PBN (b, d), the latter showing a necrotic primary axis and normal "secondary" axes. 1, 2, 3 = primary, secondary and tertiary axes respectively; 4 = margin between necrotic primary axis tissue and healthy bud base tissue.
Fig. 4.6  a. Longitudinal section through a 'Shiraz' bud with PBN induced in response to GA₃ treatment showing elongated necrotic primary axis and normal "secondary" axes, b,c. Transverse sections of 'Shiraz' buds with PBN showing better-than-normal development of "secondary" axes. In the case of (c), the necrotic primary axis tissue has completely disintegrated. 1, 2, 3, 4 = primary, secondary, tertiary and quaternary axes respectively.
Fig. 4.7 Photomicrographic collages of longitudinal sections of 'Shiraz' buds. a: Normal bud, b, c: Buds with PBN showing remains of necrotic primary axis tissue and normal "secondary" axes. In the case of (b), the primary axis has completely disintegrated and been lost during sectioning; the secondary axis has been partly lost. 1, 2, 3, 4 = primary, secondary, tertiary and quaternary axes respectively (1 = normal position of primary for (b); 5 = margin between necrotic primary axis tissue and healthy bud base tissue.)
Fig. 4.8 Photomicrographic collages of transverse sections of 'Shiraz' buds. a: Normal bud. b, c: Buds with PBN showing necrotic primary axes and normal "secondary" axes. Secondary axes partially (b) or completely (c) lost during sectioning. 1, 2, 3, 4 = primary, secondary, tertiary and quaternary axes respectively.
Fig. 4.9 Pattern of PBN development at nodes 2 to 10 on shoots of 'Shiraz' vines in 1982/83 (open circles) and 1983/84 (solid circles). Treated vines (shoot thinning/topping/defoliation at full bloom), solid lines; untreated vines, dashed lines. Each point represents a mean of 90 buds.
Fig. 4.10 Change in primary bud-axis D.Wt. over time for shoot-treated (o) and control (●) 'Shiraz' vines. Shoot treatment applied at Day 0. Buds from nodes 7 to 10. Shoot treatment values are significantly different (0.001% level) from controls at all sampling dates after Day 0.
Fig. 4.11 Effect of shoot treatment (thinning/topping/defoliation) on development of primary bud-axes of 'Shiraz'. Longitudinal sections of primary bud-axes from (a) untreated control vines and (b) shoot-treated vines. Buds sampled 28 days after shoot treatment applied on 15/11/84. (Photomicrographic collage used for (b)).
4.3 DISCUSSION

Primary bud-axis necrosis of grapevines (PBN) described in this study appears to be identical to the bud necrosis described by Lavee et al. (1981a,b) and may be the same as the bud abnormalities reported by Bindra and Chohan (1975) and Smit (pers.comm.). Similarities between PBN and bud necrosis reported by Lavee et al. (1981a,b) include:

- Complete necrosis of the primary bud-axis while the other bud-axes remain unaffected.
- The external appearance of normal buds and buds with PBN is almost identical; however the latter are slightly elongated in some cases.
- The basal, supporting tissue proximal to the primary bud is unaffected.
- The secondary, tertiary and quaternary bud-axes are usually more developed than normal to compensate for loss of the primary bud-axis.
- Exogenous application of GA$_3$ can induce both conditions.
- The first anatomical signs of PBN and bud necrosis are observed soon after flowering.

The significant elongation of the whole compound bud associated with the GA$_3$-induced bud necrosis of Lavee et al. (1981b) was not observed with PBN induced by shoot treatment (thinning/topping/defoliation); however, elongation of young buds on shoots treated with GA$_3$ was observed in this study.

Whereas Lavee et al. (1981a,b) found that the final number of necrotic buds was reached within three weeks of full-bloom, this study showed that PBN took longer to develop, in fact, up to 10 weeks after full-bloom before winter levels of natural or shoot treatment-induced PBN were approached. There is no satisfactory explanation for this difference except that it may be a result of different climatic conditions and cultivars.

Lavee et al. (1981a,b) suggested that necrosis started at primordial node 3 to 4 of the central (primary) bud and developed distally; however, examination of Figs. 4.1, 4.2, 4.3 shows: i) complete necrosis of the primary bud from primordial node 1 to the apex and ii) the "necrotic layer" (representing the point at which necrosis started) in Fig. 4.2A at primordial node 1. Therefore, it is possible that bud necrosis described by Lavee et al. (1981a,b), like PBN, started with development of a necrotic layer at primordial nodes 1 or 2.

Anatomical examination of buds on shoot-treated or GA$_3$-treated vines suggests that development of PBN is associated with a growth surge of the primary bud (and possibly the whole compound bud): for example, (i)
elongation of the primary bud precedes the appearance of necrosis; (ii) some necrotic primary buds are elongated; and (iii) secondary and tertiary buds are generally larger and have more extension than normal. Lavee et al. (1981a,b) also observed such elongation. These observations have been confirmed by measurements of primary bud weight and length on shoot-treated vines, particularly from buds at distal nodes where the incidence of PBN is greatest; an increase in primary bud D.Wt. of 60 to 80 percent was accompanied by an approximate doubling in length compared with control. The response to shoot treatment was very rapid; by interpolation, it is estimated that primary buds on shoot-treated vines weighed up to 20 percent more than controls just two days after treatment. The growth surge appeared to continue for up to 14 days after treatment; subsequently the growth rate of "treated" and "control" primary buds was the same. Taylor et al. (1984) measured a 50 percent increase in the D.Wt. of apex tissue of closed terminal apple buds in the 14 day period following defoliation.

The onset of "natural" PBN at flowering is also associated with a period of rapid development of the primary bud; during the 28 day period following full-bloom, the D.Wt. of primary buds on untreated vines more than doubled.

The greater degree of development of secondary, tertiary and quaternary buds associated with PBN may either take place in response to the death of the primary bud as a compensating mechanism or may be part of the general "growth" response by the compound bud to shoot treatment or other stimuli.

Mites have occasionally been suggested as a possible cause of whole or part bud death of grapevines in Australia (Loder 1971); however, that PBN is not caused by mites is indicated by the following evidence:

i) There were few signs of mites (eggs or bodies) observed during bud dissection nor the distinctive signs of blisters on the inner surfaces of the bud scales (1.5.a.ii).

ii) The first signs of PBN appeared well before the time at which mite damage to buds is evident.

iii) Shoot symptoms (1.5.a.ii) indicative of bud mite damage were not seen.

iv) The general mite population within vineyards at Roseworthy (where much of this study was carried out) is low, largely because insecticides are not used and the mite predator population is probably high.
v) Outbreaks of bud mite damage are sporadic and localised whereas "natural" PBN occurs every season and is widespread throughout a vineyard.

vi) There is no logical reason why shoot treatment or GA₃ application should increase the incidence of bud mite damage.

This appears to be the first report of PBN in Australia; although the condition seems to be widespread, particularly in vigorous vineyards (Chapter 3), there are a number of possible explanations why it has not been previously reported:

i) The external morphology of normal buds and buds with PBN is almost the same.

ii) Most of the research on bud anatomy in Australia has been confined to the cultivar 'Sultana' which, like all seedless cultivars, has a low incidence of PBN (Chapter 3).

iii) A high incidence of PBN is not expressed as "blind buds", poor bud-burst or a reduction in shoot number per vine but rather as an increase in the secondary/primary shoot ratio and a reduction in bunch number per vine (Chapter 8); the latter would most often be attributed to causes other than bud abnormality (Chapter 8).

iv) The proportion of vigorous vines appears to have increased in recent years due to the greater use of irrigation and nitrogenous fertilisers, especially during establishment, rootstocks and virus-free clones.
CHAPTER 5

EFFECTS OF SUMMER PRUNING TREATMENTS ON PRIMARY BUD-AXIS NECROSIS

ABSTRACT

The level of induced primary bud-axis necrosis (PBN), on a per shoot or per vine basis, was directly proportional to the severity of shoot topping, shoot thinning or defoliation, applied singly or in combination. Shoot topping or thinning induced more PBN than defoliation. Whereas shoot topping resulted in increased levels of PBN at distal nodes on topped shoots, thinning had an effect at all nodes on remaining shoots. The highest levels of PBN are induced just before flowering with the response subsequently diminishing with later time of treatment. The response to treatment was greatest for seeded cultivars and for vigorous vines.
5.1 INTRODUCTION

Preliminary experiments carried out in the 1980/81 season revealed that (a) topping and defoliation of single shoots and (b) shoot thinning plus shoot topping and defoliation of whole vines induced primary bud necrosis (PBN) of several grapevine cultivars of Vitis vinifera L., on a per shoot and per vine basis respectively (Chapter 2).

There have been no previous reports of "summer pruning" treatments, i.e. shoot thinning, topping or defoliation, inducing PBN in grapevines, although such treatments have been found to cause a reduction in budburst and yield in the following season (May et al. 1969; Winkler et al. 1974). In the long-term, such treatments may reduce vine vigour (Khanduja and Balasubrahmanyam 1972; Wiebe 1975; Winkler et al., 1974); however, the short-term response to shoot thinning and/or shoot topping will usually be an increase in the vigour of remaining main shoots and lateral shoots (Lavee 1982). A positive correlation of PBN with shoot vigour was noted by Lavee et al. (1981a).

Defoliation by natural causes, e.g. frost, hail (May 1961), and downy mildew (Dry 1976), has been shown to reduce grapevine yield in the season following defoliation.

Exogenous application of gibberellic acid (GA) induces PBN in grapevines (Lavee et al. 1981b) and shoot topping and defoliation of other plants has been shown to increase endogenous levels of GA (1.6.d).

This chapter describes the results of experiments carried out to examine the effects of shoot thinning alone, shoot topping alone and defoliation alone, plus combinations of all three, on induced PBN, as measured by "Bud Index". (This index is described in Chapter 2.) In addition, experiments were carried out on both single shoots and whole vines, on a number of cultivars and at several sites. The effect of timing of summer pruning on development of PBN is also examined.
5.2 MATERIALS AND METHODS

Unless otherwise specified, all experiments were carried out on 'Shiraz'. Details of experiments are found in Table 5.1.

5.2.a Experimental design

(i) Experiment 81/1A: Aim: To test the effect of timing of "whole vine" treatment. All vines (except untreated controls) were thinned to the 20 most vigorous shoots per vine, all remaining shoots being topped to 10 nodes and 50 per cent of main leaves removed (no lateral shoot or inflorescence removal) on one of three dates. In winter 1982, 10 shoots per vine were chosen at random to be removed for determination of Bud Index, per cent nodes with lateral shoots and shoot diameter.

(ii) Experiment 81/1B: Aim: To test the effect of treating half the shoots with untreated vines; i.e. three different levels of defoliation. Treated shoots were topped to 10 nodes and all main leaves removed; all lateral shoots and inflorescences were retained. Shoot thinning and shoot treatment was carried out on November 11, 1981 (18 visible internodes). In winter 1982, 10 shoots per plot were used for determination of Bud Index, per cent nodes with lateral shoots and shoot diameter.

(iii) Experiment 82/1A: Aim: To test the effect of timing of whole vine treatment. This was similar to Expt. 81/1A in that vines were reduced to 20 shoots per vine and all shoots were topped; however, half of the shoots were topped to 5 nodes, the other half to 10 nodes. Also, the timing was slightly different to Expt. 81/1A. In winter 1983, 10 shoots per vine were chosen at random for determination of Bud Index.

(iv) Experiment 82/1B: Aim: To compare shoots topped to 6 nodes with shoots topped to 10 nodes on the same vine, at three times. Vines were reduced to the 20 most vigorous shoots, half of the shoots (shoots chosen at random) were topped to 6 or 10 nodes with 50 per cent defoliation (no lateral shoot or inflorescence removal). In winter 1983, all 6 node and 10 node shoots from each vine were used for determination of Bud Index (based on 4 nodes).

(v) Experiment 82/2: Aim: To compare (a) different levels of summer pruning severity (whole vines), (b) different levels of shoot thinning (all shoots
untreated, whole vines), (c) treated shoots (topped to 10 nodes plus 50 per cent defoliation) with non-treated shoots on the same vine and (d) shoots (topped to 10 nodes) with 50 and 100 per cent defoliation on the same vine.

All treatments were carried out on November 28th, 1982 (13 visible internodes). No lateral shoots or inflorescences were removed for any treatment. Fig. 5.1. a to f shows the appearance of vines after treatment. The most vigorous shoots were retained in all shoot thinning treatments.

For determination of Bud Index in winter 1983, 20, 10 or 5 shoots were removed depending on original degree of shoot thinning. In the case of the untreated control, the 10 most vigorous shoots were removed from each vine.

(vi) Experiment 82/8: Aim: To test the effect of shoot thinning plus shoot topping and defoliation on induced PBN in a range of cultivars, chosen to include high and low vigour, and seeded and seedless. One vine each of the cultivars listed in Table 5.7 was thinned to the 20 most vigorous shoots per vine, all shoots were topped to 10 nodes and 100 per cent defoliated (all lateral shoots and inflorescences retained). Also, one adjacent vine of the same cultivar was left as an untreated control. The vines, in the Roseworthy College Variety Vineyard were all spur-pruned except Perlette which was cane-pruned. In winter 1983, 20 topped shoots on the treated vine and 20 vigorous shoots on the control vine were removed for determination of Bud Index (nodes 2 to 9).

(vii) Experiment 82/15: Aim: To test the effect of shoot thinning, shoot topping and defoliation on 'Shiraz' at sites other than Roseworthy College. Eight vines were each used at (a) Alverstoke vineyard, Waite Agricultural Research Institute, Glen Osmond, S.A. and (b) the vineyard of Mr A. Wilson, Williamstown, S.A. (See Appendix A for details of vineyard sites.) Four vines were untreated and four were thinned to the 20 most vigorous shoots, each shoot topped to 10 nodes and 50 per cent defoliated (all lateral shoots and inflorescences retained); see Table 5.2 for further details of experimental design. The vines at Glen Osmond were treated on November 8, 1982 (end of flowering, 18 visible internodes) and at Williamstown on November 14, 1982 (50 per cent flowering, 17 visible internodes). In winter 1983, the 10 most vigorous shoots each on treated and control vines were used for determination of Bud Index.

(viii) Experiment 83/1: Aim: To test the effect of shoot thinning, plus shoot topping and defoliation on induced PBN. Treated vines were thinned to 10 most vigorous shoots, all shoots topped to 10 nodes and 100 per cent
defoliated (all lateral shoots and inflorescences retained) on November 3, 1983 (start of flowering, 15 to 16 visible internodes). Control vines were completely untreated. On November 11 and November 24, i.e. 8 and 21 days after shoot treatment, on each of 2 shoots per vine (most vigorous shoots used on control vines), the distal 4-node shoot segments, i.e. nodes 7 to 10, were removed for determination of endogenous GA levels. In winter 1984, on treated vines, 4, 10 node shoots were retained as canes at pruning for budburst and yield component determinations in the following season (all lateral shoots removed), and two, 10 node shoots were removed for determination of Bud Index. The remaining 4 shoots with 6 nodes, which had been used as the source of buds for GA determination, were discarded. On control vines, 4 vigorous shoots were pruned to 10 nodes and retained as canes; 10 shoots were removed for Bud Index determination. On control vines each 10 node shoot used for Bud Index determination was weighed to examine the relationship between shoot weight and Bud Index. Spring measurements are described in Materials and Methods, Chapter 8.

(ix) Experiment 83/2: This experiment was similar to Experiment 83/1 except the level of shoot thinning was less severe (20 shoots per vine) and the thinning plus shoot treatment was carried out 2 weeks later (November 18, end of flowering, 17 visible internodes).

(x) Experiment 83/3: Aim: To test the effect of defoliation of whole vines at a single time on induced PBN. All main leaves, separated from the shoot tip, were removed on November 18, 1983 (end of flowering, 17 visible internodes). No lateral shoot defoliation (in order to lessen the severity of defoliation) or removal, nor shoot thinning and topping was carried out. During March, 1984, the yield of treated and control vines was measured. In winter 1984, 10 vigorous shoots were removed from treated and control vines for determination of Bud Index (nodes 2 to 10).

(xi) Experiment 83/5: Aim: To test the effect of topping alone, without shoot thinning or defoliation. The ten most vigorous shoots were selected on treated vines on November 17, 1983 (17 visible internodes, end of flowering); 5 shoots, chosen at random were topped to 10 nodes on that date (Treatment A), the remaining 5 were left untreated (Treatment B). The topped shoots were not defoliated. In winter 1984, each of the 2 lots of 5 shoots were removed for determination of Bud Index, together with 5 vigorous shoots from paired control vines.
(xii) **Experiment 83/7:** Aim: To test the effect of whole vine treatment (thinning to 20 shoots per vine, topping to 10 nodes, 100 per cent defoliation; no lateral shoot or inflorescence removal) on 'Sultana'. Four vines were treated on November 8, 1983 (17 visible internodes, 50 per cent flowering). Control vines were left untreated. In winter 1984, 10 shoots picked at random from treated vines, and the 10 most-vigorous shoots from control vines, were removed for determination of Bud Index and number of lateral shoots per main shoot.

5.2.b Measurements

(i) **Bud Index** and **Shoot Index** were determined as for Chapter 2 and unless otherwise specified, nodes 2 to 9 were used in all experiments.

(ii) **Shoot diameter** was measured at the midpoint of the internode between nodes 1 and 2 at the time of bud dissection.

(iii) **Butt (trunk) circumference** was measured at 30 to 60 cm above soil level.

(iv) **Shoot weight** was measured at the time of bud dissection.

(v) **Percent nodes with lateral shoots** was determined by noting the presence or absence of a persistent lateral at each node position at the time of bud dissection. In this way, the degree of association between presence or absence of a lateral shoot and presence of PBN at the same node could be determined. For the purposes of this study, a persistent lateral was defined as a woody lateral shoot longer than 25mm.

(vi) **Percent nodes with primary latent budburst** (in the season of shoot treatment) was determined at the time of bud dissection. However, no data is given in the "Results" section because the percentage was always less than 5 and often 1 or 2. This low figure, compared to 1980 experiments, resulted from the retention of lateral shoots.

(vii) **Unknowns in bud dissection** were less than 10 per cent for all treatments in all experiments.

5.2.c Statistical analysis
One way-, two way- or split plot analysis of variance (Little and Hills 1978) were used as appropriate.
5.3 RESULTS

5.3.a The effect of combinations of shoot thinning, shoot topping and defoliation.

(i) On a per shoot basis: Comparison of treated (topped and defoliated) and control shoots on the same vine reveals that treated shoots had a higher mean Bud Index over all nodes (significant in 1982, Table 5.3; not significant in 1981, Table 5.2); however, in both years, it was only the distal nodes (nodes 8 to 10) where the difference was significant [Fig. 5.1, Table 5.6]. The same results were achieved in 1980, over all nodes for both the earliest time of shoot treatment and pooled data (Tables 2.7, 2.8) and for the distal nodes (Fig. 2.6). Distal nodes had significantly more PBN than proximal nodes for treated but not control shoots on the same vine (Fig. 5.2). Control shoots on a treated vine, (i.e. whole vine thinned to 20 shoots, half shoots topped and defoliated, remaining half untreated), had significantly more PBN than shoots on a non-treated vine, over all nodes (Table 5.2) and at distal nodes (Fig. 5.2). This result was also found in 1980/81 (Fig. 2.10). There was no difference between treated and control shoots for per cent nodes with lateral shoots (Table 5.2).

(ii) On a per vine basis: Table 5.9 summarises the effect of shoot thinning to 20 shoots per vine plus shoot topping and defoliation on induced PBN, on a per vine basis, over 4 seasons. The response to the treatment varied considerably, even though the same vineyard (South vineyard, Roseworthy College) was used in each year; however, the level of PBN in control vines did not change significantly.

An increase in the severity of whole vine treatment resulted in an increase in the incidence of PBN, e.g. in Expt. 81/1B. Similar results can be seen in Table 5.4. The combination of shoot thinning, topping and defoliation had most effect on the level of PBN at the distal nodes; this was observed consistently in all years (Tables 5.4, 5.8; Fig. 5.3). Similarly, an increase in the severity of treatment to whole vines resulted in an increase in PBN only at the distal nodes (Table 5.4) or, put another way, the response was most pronounced at the distal nodes (Table 5.8). The distribution of PBN incidence by node position was very similar in each year of this study, for both treated and control vines (Fig. 5.4). The percentage of nodes with lateral shoots was significantly higher on treated vines than control vines (Table 5.2).
5.3.b. The effects of shoot thinning, topping and defoliation.

(i) **Shoot thinning:** Increased severity of shoot thinning resulted in increased incidence of PBN. In Expt. 82/2, vines were thinned but all shoots were left untreated; the effect of shoot thinning was significant at proximal as well as distal nodes but most pronounced for the latter (Table 5.5). The relationship between the number of shoots per vine \(x\) and Bud Index \(y\) for nodes 2 to 10 in Expt. 82/2 can be expressed by the formula \(y = 2.30x^{-0.71}\) (\(r = -0.964\), significant at 5% level). Although not in the same experiment (but with the same cultivar and site), comparison of Experiments 2 and 3 in 1983 shows that the Bud Index (nodes 2 to 10) on treated vines in Expt. 2 (thinned to 10 shoots/vine, all shoots topped to 10 nodes, 100 per cent defoliation) was 78 per cent whereas that on treated vines in Expt. 3 (thinned to 20 shoots/vine, shoots treated as in Expt. 2) was much lower at 28 per cent. The magnitude of this difference cannot be explained by differences in time of treatment nor vine vigour, and must therefore be attributed to differences in thinning levels.

(ii) **Topping:** Comparison of topped (to 10 nodes) shoots with non topped shoots, on vines neither thinned nor defoliated, shows that topping alone induced PBN, but only at distal nodes (Table 5.11). This response was also observed in Expt. 80/1 (Table 2.4). Control shoots on a treated vine had a higher Bud Index value at all nodes (but significant at nodes 2 to 4 only) compared to shoots on a control vine, suggesting a whole vine effect induced by topping of just 5 shoots out of 70 or so shoots on a single vine. In Expt. 82/1B, shoots were topped to 6 nodes and 10 nodes on the same vine (and defoliated to 50 per cent). Nodes 2 to 5 on 6-node shoots had significantly more PBN than corresponding nodes on 10 node shoots for November 7 and December 1 treatments but not for October 17 treatment; however, there was no significant difference between these nodes and nodes 6 to 9 on 10-node shoots at any time (Table 5.3).

(iii) **Defoliation:** There was no significant difference between shoots on which all main leaves had been removed (100 per cent defoliation) and on the same vine, shoots which had half of the main leaves removed (50 per cent defoliation), e.g. Bud Index values of 39 and 37 per cent respectively for Expt. 82/2. The effect of defoliation alone, without the complicating effects of topping and shoot thinning was examined in several different experiments in 1981/82 and 82/83 (experimental details are not given in Materials and Methods). For example:
(a) Removal of the 6 youngest separated leaves from shoots at two different stages of development (17 and 24 separated leaves per shoot).
(b) Removal of main leaves at single node positions (one node position per shoot) at several times and in both seasons.
(c) Removal of main leaves at nodes specified as N0, N1 or N2 (Bouard, 1971), either at different N0 + N1 + N2 combinations along the shoot or comparison of defoliation at all N0 nodes with all N1 nodes with all N2 nodes.

In all cases, the Bud Index was determined at treated nodes and at nodes proximal and distal to treated nodes. In none of these experiments was it possible to find any significant differences from controls. The only difference of any magnitude (but not significant) occurred as a result of removal of the 6 youngest separated leaves; treated nodes had more PBN than control nodes at the first time of treatment. Complete removal of all main leaves from a vine at one time (no shoot removal or topping) resulted in a small but significant increase in PBN level over control (Expt. 83/3: Treated = 19 per cent, Control = 8 per cent). This treatment resulted in a 61 per cent decrease in yield per vine in that season, mainly due to decreases in berries per bunch (50 per cent decrease relative to control) and berry weight (19 per cent decrease relative to control); there was no effect on bunch number per vine.

5.3.c The effect of timing of shoot thinning, topping and defoliation.

(i) On a per shoot basis: Earlier time of shoot treatment (topping and defoliation) resulted in higher levels of induced PBN for nodes 2 to 5 on 6-node shoots and 10-node shoots, nodes 6 to 9 on 10-node shoots, and over all nodes (Table 5.3).

(ii) On a per vine basis: As with per shoot treatment, earlier time of treatment (shoot thinning, topping plus defoliation) of whole vines resulted in higher levels of PBN in both 1981/82 and 82/83 seasons (Table 5.10). That the response to treatment decreased with time is best seen in Fig. 5.5; the slopes of the curves for Bud Index versus number of visible internodes are similar in both years; however, the response to treatment overall was greatest in 1981. The response to treatment at different times on a per node basis is seen in Figs. 5.6 a, b. The general trend in both years was for the difference between early and later treatments to be greatest at the distal nodes, i.e. the response was greatest at those nodes. For example, in 1981 (Fig.
5.6a), treatment at the 14 visible internode stage resulted in significantly more PBN than (a) the 18 visible internode stage at nodes 8 and 9 only, and (b) the 25 visible internode stage at nodes 6 to 9 only. The response at 18 and 25 visible internodes over all nodes was very similar and both times had significantly more PBN than the control at all nodes except node 2.

However, in 1982 (Fig. 5.6b), treatment at 16 and 25 visible internodes did not result in more PBN than the control at any node (although 16 visible internode treatment overall was significantly greater than control, Table 5.10). But the response to treatment at 10 visible internode stage was very marked, such that it had more PBN than treatment at 16 visible internodes for most nodes, and, in particular, the distal nodes. The greater response at the distal nodes for the earliest time of treatment in both years can also be seen if node positions within treatments are compared. For example, in both years, the distal nodes of the earliest treatments had more PBN than proximal nodes (Fig. 5.6 a, b); however, for the two later treatments in both years have relatively flat curves, i.e. no significant difference between proximal and distal nodes. If similar (but not identical) treatments from different experiments in 1983 are compared (same vineyard with the same cultivar) a similar response is noted (Fig. 5.7). The percentage of nodes with lateral shoots was determined in Expt. 81/1A. All times of whole vine treatment had a higher percentage than control but there was no significant difference between times. For all treatment times and for control vines, nodes with PBN had significantly more nodes with laterals than nodes with normal buds.

5.3.4 Response to treatment in cultivars other than 'Shiraz'.

Shoot thinning, topping and defoliation was not able to induce PBN in the seedless cultivars tested, i.e. 'Perlette', 'Canner', 'Zante Currant' and 'Tunn Currant' (Table 5.7) with the exception of 'Sultana', which was tested in a neighbouring but different vineyard (Table 5.12). For 'Sultana', there was a small but significant response to treatment but only at the distal node positions. Amongst the seeded cultivars a response was induced only in the vigorous ones such as 'Mantuo' and 'Farana'. Compared to 'Shiraz', all other cultivars tested had both a lower natural level of PBN and a lesser response to treatment.
Table 5.1 Details of experiments with the cultivar Shiraz.

<table>
<thead>
<tr>
<th>Expt. No.</th>
<th>Location 1</th>
<th>Expt. 2 design</th>
<th>Block size (vines)</th>
<th>Plot size</th>
<th>No. replicates</th>
</tr>
</thead>
<tbody>
<tr>
<td>81/1A 1B</td>
<td>RAC-S</td>
<td>RB</td>
<td>6</td>
<td>1 vine</td>
<td>4 or 6</td>
</tr>
<tr>
<td></td>
<td>RAC-S</td>
<td>RB</td>
<td>6</td>
<td>1 shoot (10)</td>
<td>6 or 1 vine</td>
</tr>
<tr>
<td>82/1A 1B</td>
<td>RAC-S</td>
<td>RB</td>
<td>4</td>
<td>1 vine</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>RAC-S</td>
<td>SP</td>
<td>4</td>
<td>1 vine</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>x 1 shoot (10)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>RAC-S</td>
<td>RB</td>
<td>4</td>
<td>1 vine</td>
<td>4</td>
</tr>
<tr>
<td>8</td>
<td>RAC-V</td>
<td>CR</td>
<td>-</td>
<td>1 shoot</td>
<td>20</td>
</tr>
<tr>
<td>15</td>
<td>WA, WI</td>
<td>RB</td>
<td>4</td>
<td>1 vine</td>
<td>4</td>
</tr>
<tr>
<td>83/1 2</td>
<td>RAC-S</td>
<td>RB</td>
<td>4</td>
<td>4 vines</td>
<td>4</td>
</tr>
<tr>
<td>3</td>
<td>RAC-S</td>
<td>RB</td>
<td>4</td>
<td>1 vine</td>
<td>7</td>
</tr>
<tr>
<td>5</td>
<td>RAC-S</td>
<td>RB</td>
<td>6</td>
<td>1 vine</td>
<td>6</td>
</tr>
</tbody>
</table>

1 RAC-S and RAC-V = South and Variety vineyards respectively, Roseworthy College (RAC); WA = Alverstoke Vineyard, Waite Agric. Res. Inst., Glen Osmond; WI = Vineyard of A. Wilson, Williamstown.
2 RB = randomised block; SP = split-plot; CR = completely randomised.
3 Replicates were selected on the basis of butt circumference in expt. 8/1A, 81/1B, 82/1A, 82/1B, 82/2, 82/15, 83/1, 83/2, 83/3, 83/5.

Table 5.2 Effect of shoot thinning, topping and defoliation on Bud Index and percent nodes with lateral shoots (Expt. 81/1B).

| Treatment 1 | Shoot topping/defoliation 2 | Bud Index Shoot % | % nodes with lateral shoots Nodes with normal buds 5 All nodes |
|-------------|------------------------------|-------------------|----------------|-----------------------|----------------|-----------------|
| -           | -                            | 13 c              | 32             | 7                      | 8 c             |
| +           | +                            | 57 a              | 59             | 34                     | 45 a            |
|             |                              | 32 bc             | 64             | 26                     | 40 ab           |
|             |                              | 40 b              | 46             | 19                     | 38 b            |

1 On November 11
2 Thinned to 20 shoots per vine
3 Topped to 10 nodes, 100% defoliation
4 Non-treated and treated shoots on same vine
5 All row means in comparison of PBN vs. normal nodes are significantly different at 1% level.

Means in same column followed by same letter are not significantly different at 5% level.
Table 5.3. Comparison of Bud Index (%) at different node positions on shoots topped to 6 and 10 nodes at different times (Expt. 82/1B).

<table>
<thead>
<tr>
<th>Date</th>
<th>6 node Nodes 2-5</th>
<th>10 node Nodes 2-5</th>
<th>Nodes 6-9</th>
<th>All nodes 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oct. 17</td>
<td>62 a</td>
<td>51 b</td>
<td>71 a</td>
<td>61</td>
</tr>
<tr>
<td>Nov. 7</td>
<td>44 a</td>
<td>29 b</td>
<td>44 a</td>
<td>39</td>
</tr>
<tr>
<td>Dec. 1</td>
<td>37 a</td>
<td>8 b</td>
<td>23 a</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>LSD (5%) 3</td>
<td>20</td>
<td>16</td>
<td>14</td>
</tr>
</tbody>
</table>

1 Number of visible internodes was 10, 17 and 25 on Oct. 17, Nov. 7 and Dec. 1 respectively.
2 Main plot means.
3 For comparison of date means.
Means in same row followed by same letter are not significantly different at 5% level.

Table 5.4 Effect of shoot treatment (thinning/topping/defoliation) on Bud Index (Expt. 82/2).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Shoot # per vine topping</th>
<th>Shoot Defoliation %</th>
<th>Bud Index % at nodes</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>2 to 4</td>
<td>5 to 7</td>
</tr>
<tr>
<td>75 1</td>
<td>-</td>
<td>0</td>
<td>26 b</td>
</tr>
<tr>
<td>20</td>
<td>-</td>
<td>0</td>
<td>30 ab</td>
</tr>
<tr>
<td>20</td>
<td>+,- 3</td>
<td>0,50</td>
<td>43 ab</td>
</tr>
<tr>
<td>20</td>
<td>+</td>
<td>50,100</td>
<td>36 ab</td>
</tr>
<tr>
<td>10</td>
<td>-</td>
<td>0</td>
<td>47 a</td>
</tr>
</tbody>
</table>

1 Unthinned control.
2 To 10 nodes.
3 Ten shoots untreated plus 10 shoots topped to 10 nodes with 50% defoliation.
4 Ten shoots 50% defoliation, plus 10 shoots 100% defoliation.
Means in same column followed by same letter are not significantly different at 5% level.
Table 5.5 Effect of severity of shoot thinning (all shoots untreated) on Bud Index (Expt. 82/2).

<table>
<thead>
<tr>
<th>Shoot # per vine</th>
<th>Bud Index % at nodes</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2 to 4</td>
</tr>
<tr>
<td>75¹</td>
<td>26 c</td>
</tr>
<tr>
<td>20</td>
<td>30 bc</td>
</tr>
<tr>
<td>10</td>
<td>47 b</td>
</tr>
<tr>
<td>5</td>
<td>69 a</td>
</tr>
</tbody>
</table>

¹ Unthinned control.
Means in same columns followed by same letter are not significantly different at 5% level.

Table 5.6 Comparison of Bud Index on treated (topped to 10 nodes, 50% defoliation) and non-treated shoots on the same vine¹ (Expt. 82/2).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Bud Index % at nodes</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2 to 4</td>
</tr>
<tr>
<td>Topping</td>
<td></td>
</tr>
<tr>
<td>-</td>
<td>0</td>
</tr>
<tr>
<td>+</td>
<td>50</td>
</tr>
<tr>
<td></td>
<td>ns</td>
</tr>
</tbody>
</table>

1 Thinned to 20 shoots per vine.
* Indicates means significantly different at 5% level; ns, not significant.
Table 5.7 Effect of cultivar on PBN (as Bud Index %), induced by shoot treatment (Expt. 82/8).

<table>
<thead>
<tr>
<th>Cultivar</th>
<th># vis. internodes</th>
<th>Control</th>
<th>Treated</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seedless</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Perlette</td>
<td>13</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Canner</td>
<td>16</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Zante Currant</td>
<td>15</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Tunn Currant</td>
<td>12</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Seeded</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shiraz</td>
<td>14</td>
<td>16</td>
<td>42</td>
</tr>
<tr>
<td>Mantuo</td>
<td>14</td>
<td>3</td>
<td>15</td>
</tr>
<tr>
<td>Farana</td>
<td>12</td>
<td>1</td>
<td>7</td>
</tr>
<tr>
<td>Gros Colman</td>
<td>16</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td>Gordo</td>
<td>10</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Red Frontignac</td>
<td>17</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

1 Thinned to 20 shoots per vine, all shoots topped to 10 nodes plus 100% defoliation.
2 Percent flowering was 5 for Shiraz and Farana; 20 to 40 for Canner, Zante Currant, Mantuo and Gordo; 50 to 70 for Gros Colman, Red Frontignac and Tunn Currant; 100 for Perlette.
* Indicates means significantly different at 5% level; ns, not significant.

Table 5.8 Effect of shoot treatment on Bud Index (Expts. 83/1, 83/2).

<table>
<thead>
<tr>
<th>Expt.</th>
<th>Bud Index % at nodes</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2 to 4</td>
</tr>
<tr>
<td>83/1</td>
<td>Control</td>
</tr>
<tr>
<td></td>
<td>Treated 1</td>
</tr>
<tr>
<td></td>
<td>**</td>
</tr>
<tr>
<td>83/2</td>
<td>Control</td>
</tr>
<tr>
<td></td>
<td>Treated 2</td>
</tr>
<tr>
<td></td>
<td>ns</td>
</tr>
</tbody>
</table>

1 Thinned to 10 shoots per vine, shoots topped to 10 nodes plus 100% defoliation.
2 Thinned to 20 shoots per vine, shoots topped to 10 nodes plus 100% defoliation.
**,**,**:* indicates means significantly different at 1% and 0.1% levels respectively; ns, not significant at 5% level.
Table 5.9 Summary of the effect of shoot treatment\(^1\) over 4 years\(^2\) on Bud Index (% ('Shiraz', RAC South Vineyard))

<table>
<thead>
<tr>
<th>Year</th>
<th>Expt.</th>
<th>Control Vines</th>
<th>Treated Vines</th>
</tr>
</thead>
<tbody>
<tr>
<td>80</td>
<td>80/3</td>
<td>10</td>
<td>60 ***</td>
</tr>
<tr>
<td>81</td>
<td>81/1B</td>
<td>13</td>
<td>57 **</td>
</tr>
<tr>
<td>82</td>
<td>82/2</td>
<td>13</td>
<td>38 *</td>
</tr>
<tr>
<td>83</td>
<td>83/2</td>
<td>10</td>
<td>28 **</td>
</tr>
</tbody>
</table>

1 Thinning to 20 shoots per vine, topping to 10 nodes per shoot plus 50 to 100\% defoliation.
2 Different vines treated each year.
*, **, ***: indicates means significantly different at 5, 1 and 0.1\% level respectively.

Table 5.10 Effect of timing of shoot treatment\(^1\) on Bud Index and % nodes with lateral shoots (Expts. 81/1A, 82/1A).

<table>
<thead>
<tr>
<th>Expt.</th>
<th>Date</th>
<th>Bud Index %</th>
<th>Nodes with PBN(^3)</th>
<th>Nodes with normal buds(^3)</th>
<th>All nodes</th>
</tr>
</thead>
<tbody>
<tr>
<td>81/1A</td>
<td>Untreated</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td></td>
<td>13 c</td>
<td>32</td>
<td>7</td>
<td>8 b</td>
</tr>
<tr>
<td>Oct. 29</td>
<td></td>
<td>77 a</td>
<td>65</td>
<td>24</td>
<td>48 a</td>
</tr>
<tr>
<td>Nov. 6</td>
<td></td>
<td>57 b</td>
<td>59</td>
<td>34</td>
<td>45 a</td>
</tr>
<tr>
<td>Dec. 1</td>
<td></td>
<td>51 b</td>
<td>57</td>
<td>25</td>
<td>38 ab</td>
</tr>
<tr>
<td>82/1A</td>
<td>Untreated</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td></td>
<td>16 c</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oct. 17</td>
<td></td>
<td>61 a</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nov. 7</td>
<td></td>
<td>39 b</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dec. 1</td>
<td></td>
<td>23 c</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1 Thinned to 20 shoots per vine, topping to 10 nodes (81/1A) or 5 and 10 nodes (10 shoots each, 82/1A) plus 50\% defoliation.
2 Number of vis. internodes was 14, 18 and 25 on Oct. 29, Nov. 6 and Dec. 1 respectively (81/1A) and 10, 16 and 25 on Oct. 17, Nov. 7 and Dec. 1 respectively (82/1A).
3 All row means in comparison of PBN vs. normal nodes are significantly different at 1\% level.
Means in columns followed by same letter are not significantly different at 5\% level.
Table 5.11 Effect of shoot topping\(^1\) on Bud Index (Expt. 83/5)

<table>
<thead>
<tr>
<th>Treatments</th>
<th>Shoot topped per vine</th>
<th>Shoot topping</th>
<th>Bud Index % at nodes</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>2 to 4</td>
</tr>
<tr>
<td>0</td>
<td>-2</td>
<td></td>
<td>20 b</td>
</tr>
<tr>
<td>5</td>
<td>-3</td>
<td></td>
<td>31 a</td>
</tr>
<tr>
<td>5</td>
<td>+3</td>
<td></td>
<td>26 ab</td>
</tr>
</tbody>
</table>

1 To 10 nodes.
2 Untreated control.
3 Shoots on same vine.

Means in columns followed by same letter are not significantly different at 5\% level.

Table 5.12 Effect of shoot treatment\(^1\) of 'Sultana' on Bud Index and number of lateral shoots per main shoot (Expt. 83/7).

<table>
<thead>
<tr>
<th>Bud Index % at nodes:</th>
<th># lateral shoots per main shoot</th>
</tr>
</thead>
<tbody>
<tr>
<td>2 to 4</td>
<td>5 to 7</td>
</tr>
<tr>
<td>Untreated control</td>
<td>3</td>
</tr>
<tr>
<td>Treated</td>
<td>2</td>
</tr>
<tr>
<td>ns</td>
<td>*</td>
</tr>
</tbody>
</table>

1 Thinned to 20 shoots per vine, shoots topped to 10 nodes plus 100% defoliation
*, **, *** : indicates means significantly different at 5, 1 and 0.1\% level respectively; ns, not significant at 5\% level.
Fig. 5.1 Appearance of 'Shiraz' vines after "summer pruning" on 28/11/82 (South vineyard, Roseworthy College, Expt. 82/2).
Thinned to 20 (a,b,c,) 10 (d) or 5 (e) shoots per vine; no shoot thinning (f). All shoots (a) or 50% of shoots (b) topped to 10 nodes and defoliated; no shoot topping or defoliation (c,d,e,f). No lateral shoot or bunch removal in any treatments.
Fig. 5.2 Effect of shoot treatment on Bud Index by node position (Expt. 81/1B, 'Shiraz'). Thinned to 20 shoots per vine (---); no shoot thinning (—-); shoots topped to 10 nodes plus 50% defoliation (+,x); shoots not topped or defoliated (o,•). Each point represents mean of 6, 10 node replicates. For comparison of treatment means at each node position, vertical bars represent LSD.05. For comparison of node positions within treatments, means followed by the same letter are not significantly different at 5% level (no significant difference between any node position where letters absent).
Fig. 5.3 Effect of shoot treatment on Bud Index by node position (Expt. 82/15, 'Shiraz'; (a) Waite, (b) Williamstown). Vines thinned to 20 shoots, shoots topped to 10 nodes plus 50% defoliation (o); control vines (●).

*, ** indicates means at same node are significantly different at 5 and 1% level respectively.
Fig. 5.4 Summary of the effect of shoot treatment on Bud Index by node position over four seasons. Treatments (---) with highest Bud Index levels for that season compared to controls (-----) from the same experiment. Expt. 80/3 (○); 81/1 (x); 82/1 (●); 83/1 (+). Shoot treatment = thinning to 10 or 20 shoots per vine, all shoots topped to 10 nodes plus 50 or 100% defoliation.

Fig. 5.5 Effect of timing (measured as number of visible internodes) of shoot treatment on Bud Index. Expt. 81/1A (●); 82/1A (○). Shoot treatment = thinning to 20 shoots per vine, all shoots topped to 5 or 10 nodes plus 50% defoliation.
Fig. 5.6 Effect of timing of shoot treatment on Bud Index by node position; (a) 1981, (b) 1982. Shoot treatment (thinning to 20 shoots per vine; shoots topped to 10 nodes plus 50% defoliation) on Oct. 29, 1981 and Oct. 17, 1982 (+); Nov. 6, 1981 and Nov. 7, 1982 (a); Dec. 1, 1981 and 1982 (b); untreated controls (o). Each point represents mean of 6, 10 node replicates.
For comparison of treatment means at each node position, vertical bars represent LSD.05. For comparison of node positions within treatments, means followed by the same letter are not significantly different at 5% level (no significant difference between any node position where letters absent).
Fig. 5.7 Effect of timing of shoot treatment on Bud Index by node position. Shoot treatment (thinning to 10 (x) or 20 (o, •) shoots per vine plus 50 or 100% defoliation) on Nov. 3 (x) Expt. 83/1; Nov. 18 (•) Expt. 83/2; Dec. 3 (o) Expt. 83/4.

Fig. 5.8 Diagrammatic representation of the effect of node position on response to (a) shoot thinning alone, (b) shoot topping alone, (c) shoot thinning plus shoot topping. The hatched area represents the natural level of PBN.
5.4 DISCUSSION

The series of experiments carried out over the period 1981/82 to 1983/84, in which the effects of shoot thinning, shoot topping and defoliation have been examined, singly and in combination, have confirmed the initial observations made in 1980/81, i.e. increased severity of treatment both on a per shoot and a per vine basis, results in increased levels of PBN.

Of the three treatment factors, i.e. shoot thinning, shoot topping and defoliation, the first two appear to have the greatest effect. Shoot thinning exerts the greatest influence on a per vine basis whereas shoot topping has the greatest effect at the single shoot level. Defoliation appears to have little effect unless it is a severe whole-vine or whole-shoot defoliation, or unless it is combined with one of the other factors, in particular, shoot topping (when, of course, it then resembles severe hail damage).

A consistent feature in each year was the pronounced response at the distal, rather than the proximal nodes (in this instance nodes 6 to 10 versus nodes 2 to 5); this was seen at the single shoot level in response to topping and, at the whole vine level, in response to combinations of all three factors. This response is shown in two ways, (a) the difference in PBN level between treated and control shoots (or vines) was greater at distal nodes than proximal nodes and (b) distal nodes had significantly more PBN than proximal nodes on treated shoots (or vines). Differences between proximal and distal nodes were greatest for shoot topping alone; on the other hand, Table 5.5 shows a significant response to shoot thinning alone, at proximal as well as distal nodes. The whole vine response to these two factors in this regard, and the interaction between them when in combination, can possibly be summarized in Fig. 5.8.

The greatest response to topping occurred at distal nodes; this is not surprising when one considers that the release of correlative inhibition is most pronounced at distal nodes, and, as a consequence, lateral shoot development and burst of primary latent buds are promoted (Fournioux and Bessis 1982). Topping and defoliation of individual shoots and whole vines significantly increased the proportion of nodes with lateral shoots (Tables 5.2, 5.10). On the other hand, the response to shoot thinning, where the shoots themselves are neither topped nor defoliated, occurred at all nodes (nodes 2 to 10) because there is a general stimulation to growth of those remaining shoots as a whole. Put in another way, there is a decrease in correlative inhibition at all nodes. Untreated shoots on shoot-thinned vines have a significantly higher proportion of nodes with lateral shoots.
than shoots on untreated vines (Table 5.2). The greater the severity of shoot thinning, the greater the growth stimulation of the remaining shoots and the greater the incidence of PBN. (Table 5.5).

Thinning to 10 untreated shoots per vine induced the same mean level of PBN over all nodes (nodes 2 to 10) as thinning to 20 shoots, all topped to 10 nodes and with 50 per cent or more defoliation (Table 5.4); however, comparison of each of the 3-node segments of the shoot reveals that the former treatment had more (but not significant) PBN at proximal nodes (nodes 2 to 4, 5 to 7) whereas the latter treatment had significantly more PBN at distal nodes (nodes 8 to 10). Also, the former treatment had significantly more PBN at all node positions than control vines whereas the latter treatment was significant only at the distal nodes (nodes 8 to 10). This response is expected on the basis of the preceding discussion.

A possible explanation for the difference in response to defoliation alone on the one hand, and shoot thinning alone and shoot topping alone on the other, is that the main effect of defoliation is the reduction in photosynthetic area and the potential reduction in assimilate production; if only a proportion of shoots on a vine are defoliated, they will not be greatly affected because assimilate will be translocated to them from other foliated shoots (May et al. 1969).

If all shoots, or the majority of shoots, on a vine are defoliated, the decrease in assimilate production will usually be of a relatively temporary nature, dependent on the severity of defoliation, because the remaining leaves are able to increase their rate of photosynthesis (Hofacker 1978). Defoliation has only a relatively small effect on the lifting of correlative inhibition at any particular node (Fournioux and Bessis 1982).

On the other hand, the effects of shoot topping and thinning are similar in that they both result in a reduction in the number of main shoot growing points per vine, albeit by different means. Therefore, any topping or thinning can potentially affect all of the shoots on a vine (as distinct from the effect of topping on the actual shoot treated) and this is why control shoots on treated vines consistently have higher levels of PBN than control shoots on non-treated vines, in the same experiment. In fact, topping of only 5 shoots out of 70 or so appears to have increased the level of PBN above the natural level in the remaining shoots (Table 5.10). This is the explanation for the translocated effect described in Chapter 2.

The decline in response to the same whole-vine treatment over the 4 years of experimentation on Shiraz vines in the Roseworthy College South vineyard (shown in Table 5.9) can possibly be attributed to a decrease in vine vigour over that period. In this vineyard, the amount of irrigation
decreased after 1981, both by a delay in the onset of irrigation and by a
decrease in the actual amount of water applied each week. This change in
irrigation practice is reflected in the pruning weights of Pedro Ximenez
vines in the same vineyard (Table 5.13).

<table>
<thead>
<tr>
<th>Year</th>
<th>Pruning weight (kg.vine(^{-1}))(^a)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1981</td>
<td>3.1</td>
</tr>
<tr>
<td>1982</td>
<td>2.4</td>
</tr>
<tr>
<td>1983</td>
<td>1.2</td>
</tr>
<tr>
<td>1984</td>
<td>1.8</td>
</tr>
<tr>
<td>1985</td>
<td>1.5</td>
</tr>
</tbody>
</table>

\(^a\) Mean of 30 vines, all pruned to 30 + 10x nodes per vine each year, where
x = pruning weight in kg.

The highest levels of PBN were induced in response to treatments
(topping/defoliation of single shoots or thinning/topping/defoliation of
whole vines) applied before flowering. Treatments applied later had less
effect and eventually a stage was reached when treatment had no significant
effect, i.e. it did not induce additional PBN above that of the natural
level of the control (Tables 5.3, 5.10). The nature of the relationship
between Bud Index and time of whole vine treatment (using number of visible
internodes as an index of stage of shoot development) was similar in 1980
(Fig. 2.4), 1981 and 1982 (Fig. 5.5). The difference in level of response
between 1981 and 1982, over all stages of shoot development, can possibly
be explained in terms of the decrease in vineyard vigour previously
mentioned.

It is at the distal nodes (nodes 6 to 10) that the greatest difference
in response to treatment between early and late treatments was found. This
suggests that the susceptibility to induced PBN decreases with time,
particularly for those nodes at which the natural level is low, i.e. nodes
6 to 10. However, susceptibility was also related to the distance of a
node from the point of topping; the 4 nodes proximal to point of topping
had the same mean Bud Index value on shoots topped to 6 nodes (i.e. nodes 2
to 5) as on shoots topped to 10 nodes (i.e. nodes 6 to 9) at all times and
significantly greater than that for the same nodes (i.e. nodes 2 to 5) on
10-node shoots at all times (Table 5.3).
The response to whole vine treatment of 'Shiraz' at other sites was similar to that at Roseworthy (Fig. 5.3), confirming that this phenomenon is not unique to the Roseworthy vineyard. The natural levels of PBN are highest in vigorous vineyards (Lavee et al. 1981a) and the results from the 3 sites studied not only confirmed this but also suggest that response to thinning/topping/defoliation of whole vines is greatest in vigorous vineyards.

Natural levels of PBN were found to be low in all seedless cultivars tested, and low in most seeded cultivars except 'Shiraz', 'Mantuo' and 'Pedro Ximenez'. Similarly, PBN could not be induced by whole vine shoot treatment in any seedless cultivars in 1982 (Table 5.7) although it was possible with 'Sultana' in 1980 (Table 2.6) and 1983 (Table 5.12) even though natural levels in 'Sultana' appear to be low. For the seeded cultivars, it was only the vigorous ones in which PBN could be induced, confirming the relationship between vigour and PBN. The general lack of response in seedless cultivars may be significant because application of gibberellic acid can induce PBN in seeded but not seedless cultivars (Weaver and McCune 1961, Lavee et al. 1981b). In addition, there are other correlated differences in responsiveness of seedless and seeded cultivars to applied GAs; for example, only seedless cultivars are sensitive to GA-induced barrenness (lack of bud fruitfulness). Also, seedless cultivars are more responsive to GA-induced increases in berry set and berry growth (Considine 1982).
CHAPTER 6

EFFECT OF EXOGENOUS APPLICATION OF GROWTH REGULATORS ON PRIMARY BUD-AXIS NECROSIS

ABSTRACT

Exogenous application of gibberellic acid (GA$_3$) resulted in significantly increased levels of PBN in 'Shiraz', but not 'Sultana', grapevines when applied to leaf blades, petioles or as a whole-vine spray. The greatest response followed treatment at flowering or soon after. GA$_3$ application also increased number and length of lateral shoots and delayed and decreased budburst in the following year. "Shoot treatment" (shoot thinning/topping/defoliation) and GA$_3$ application at the same stage of shoot development induced the same PBN response and, when combined, their effects were additive. Exogenous application of ABA or CCC had no effect on the level of GA$_3$—or "shoot treatment"—induced PBN, whereas ethephon increased the level of PBN on otherwise non-treated vines.
6.1 INTRODUCTION

Exogenous application of gibberellic acid (GA$_3$) inhibits bud development in stone fruit and may cause bud death or abscission in stone fruit and pistachio; in grapevines, particularly for seeded cultivars, poor budburst in the following season may result (1.5.a.iv). There are relatively few reports of GA$_3$-induced necrosis of the primary axis of the compound bud in grapevines (Weaver and McCune 1961; Bernstein 1969, 1973; Lavee et al. 1981b); in the most recent of these reports this phenomenon has been described in detail.

Increase in the concentration of GA$_3$ solution applied to leaf blades or petioles results in an increase in the level of bud necrosis (Lavee et al. 1981b). Also, petiole application was found to be more effective than blade application. The highest levels of bud necrosis (80 to 90 per cent) occurred in response to GA$_3$ (20ppm) application just before or at flowering and thereafter the levels declined such that even high concentrations (100ppm) were ineffective 3 weeks after flowering. Young leaves are more effective avenues of entry to GA$_3$ than mature leaves (Weaver et al. 1966) and young, still differentiating buds in the axils of young leaves, on shoots of various stages of development, are susceptible if GA$_3$ is applied to young leaves (Lavee et al. 1981b).

Both acropetal and basipetal movement of GA$_3$ within the shoot have been observed in grapevines after application (1.7.d). In most plants, GA$_3$ applied to mature leaves moves acropetally, primarily in the phloem; however, significant amounts may also reach the xylem, as shown by shoot girdling experiments (Graebe and Ropers 1978).

Applied abscisic acid (ABA) is known to reduce GA$_3$ activity (Goodwin 1978; Graebe and Ropers 1978; Walton 1980).

Not only does GA$_3$ application induce PBN in grapevines but also shoot treatment (thinning/topping/defoliation), singly or in combination (Chapter 3). One could hypothesize that the response to these summer pruning treatments occurs as a result of increased endogenous levels of GA$_3$; although there have been no reports for grapevines, shoot topping and defoliation have been found to increase endogenous levels of GAs in other woody plants (1.6.d.ii). Therefore, by exogenous application of inhibitors of GA$_3$ activity such as ABA and 2-chloroethyltrimethyl ammonium chloride (CCC) (Goodwin 1978), it may be possible to modify the response to shoot treatment, i.e. to decrease the level of induced PBN.

The relationship between shoot vigour, lateral shoot development and PBN was discussed in Chapter 3. Both CCC and chloroethylphosphoric acid (ethephon) are known to inhibit vegetative growth when applied to
grapevines (Lavee et al. 1977). Also, ABA can inhibit bud outgrowth when applied to decapitated plants (Walton 1980). Therefore, inhibition of main shoot growth or suppression of lateral shoot development by application of CCC, ethephon or ABA may reduce the level of PBN in shoot-treated and non-shoot treated vines. Also, the use of summer pruning in the form of canopy hedging has become more common in recent times in Australian vineyards, as a method of canopy management. In some cases, this has been combined with foliar sprays of ethephon to prevent subsequent lateral shoot development.

In this chapter, the effects of i) concentration, timing, and method and site of application of GA₃; ii) shoot girdling in combination with GA₃ application and iii) ABA, CCC and ethephon application, on the development of "natural" and shoot-treatment induced PBN were examined.
6.2 MATERIALS AND METHODS

Details of experiments are summarised in Table 6.1.

6.2a Application of GA$_3$ to leaf blades.

(i) Experiment 81/3: This experiment examined the effect of GA$_3$ application at two concentrations and at three different times on the level of induced PBN in 'Shiraz'. On each of 10 vines, the 9 most vigorous shoots were selected and treatments applied at random to single shoots. Leaf blades at nodes 5 to 10 inclusively were sprayed with a hand-held atomiser. It was intended to apply 1 ml of solution to each blade had Lavee et al. (1981b); but this caused too much run-off. Therefore, 2 squeezes of the atomiser were applied to each blade and all to the lower surface. The GA$_3$ solutions were made from 'Gibrel' (4227 ppm potassium gibberellate) and the controls were distilled water plus Tween 20 (0.1 per cent). No shoot thinning nor any other shoot treatments were carried out on the treatment vines. In winter 1982, all treated shoots were removed for determination of the Bud Index for nodes 2 to 15.

(ii) Experiment 81/4: This experiment compared the effect of GA$_3$ application to the youngest 6 leaves on 'Shiraz' shoots on two different dates. Eight vigorous shoots on each of five vines were used on each date, 4 shoots (allocated at random) were sprayed with 100 ppm GA$_3$, the blades of the distal 6 separated leaves treated as in Expt. 81/3. The other 4 shoots were untreated. No shoot thinning or other shoot treatments were applied. In winter 1982, all treated shoots were removed for determination of the Bud Index at the 6 treated nodes plus the 5 nodes proximal and distal to the treated nodes. In order to be able to exactly specify the treated nodes, the number of separated leaves was recorded for each treated shoot at the time of treatment.

(iii) Experiment 82/3: The effect of GA$_3$ application at two concentrations (30, 100 ppm) on the level of induced PBN in 'Sultana'. For each treatment, the 10 most vigorous shoots per vine were used on each of 4 vines, with no shoot thinning or shoot treatment. GA$_3$ was applied on November 5 (17 visible internodes, 50% flowering) and the method is the same as that described in Expt. 81/3. In winter 1983, all treated shoots were removed and used for determination of the Bud Index (nodes 2 to 15), total shoot length, number of lateral shoots per shoot and shoot diameter.
(iv) **Experiment 82/9**: The effect of \( \text{GA}_3 \) application at three different times on the level of induced PBN in 'Shiraz'. This experiment was similar to Expt. 81/3; however, in this case, only one \( \text{GA}_3 \) concentration (30 ppm) was used and different treatments were applied to different vines. (In Expt. 81/3, PBN levels in untreated control shoots were higher than expected and it is possible that untreated shoots were affected by \( \text{GA}_3 \) translocation from treated shoots on the same vine.) For each treatment, the 10 most-vigorous shoots on each of 4 vines were used, with no shoot thinning or other shoot treatments. The method of application is the same as that described in Expt. 81/3. In winter 1983, all treated shoots were removed and used for determination of the Bud Index (nodes 2 to 15).

### 6.2.b Application of gibberellic acid (\( \text{GA}_3 \)) to petioles

(i) **Experiment 81/6**: The effect of \( \text{GA}_3 \) application via the petiole on induced PBN in 'Shiraz', compared with shoot treatment (topping to 14 nodes, 100 per cent defoliation, lateral shoot removal up to and including node 5) at the same time. Also, abscisic acid (ABA) was applied via petiole in an attempt to counteract the effect of \( \text{GA}_3 \) and/or shoot treatment. On each of 6 vines, the 16 most-vigorous shoots were selected and treatments allocated at random (2 shoots/treatment/vine). All treatments were applied on November 11, 1981 (just after set, 19 visible internodes). No shoot thinning was carried out. Petiole application was carried out in a similar fashion to that described in Lavee *et al.* (1981b). The leaf blade at node 5 was removed immediately prior to attachment of a plastic tube (3 mm internal diameter) connected to an open plastic syringe cylinder (2 ml capacity) (Fig. 6.1). The petiole was cut, at an angle, at a point at which the diameter of the petiole was similar to the internal diameter of the plastic tube. The petiole was smeared with petroleum jelly ('Vaseline') before the tube was fitted, taking care not to cover the cut with 'Vaseline'. This treatment prevented most leakages; moreover, leakages were detectable very early and in all cases, petioles were recut and the tubes refitted. One ml of solution (1 ml \( \text{NaH}_2\text{PO}_4/\text{K}_2\text{HPO}_4 \) buffer for control; 0.5 ml buffer + 0.5 ml 20 ppm \( \text{GA}_3 \) or 0.5 ml 200 ppm ABA; 0.5 ml 20 ppm \( \text{GA}_3 \) + 0.5 ml 200 ppm ABA) was introduced to the syringe cylinder immediately after attachment and the top of the cylinder was covered with 'Parafilm'. The cylinder was kept in a close-to-vertical position by means of wire ties. Air bubbles in the plastic tubing were removed by lightly tapping with the index finger. Each tube was rechecked several times to eliminate bubbles. The tubes remained on the petioles for 24 hours and
solutions were taken up by that time under all conditions (under hot
conditions in other experiments, high transpiration rates ensured that most
solutions were taken up within a few hours). In winter 1982, all treated
shoots were removed for determination of the Bud Index at nodes 2 to 14.

(ii) Experiment 81/7: This experiment was identical to Expt. 81/6 except
for the additional factor of timing of treatments, i.e. treatments were
applied on November 18 and November 25, 1981 (21 and 23 visible internodes
respectively). Four vines were used in this experiment, 2 for each time of
treatment, and 1 vine of each pair for shoot treatments; all four vines
were reduced to 24 vigorous shoots per vine. Growth regulator treatments
were applied at random to 6 shoots per treatment per vine at each
time. Measurement of diameter and count of number of visible internodes on each
shoot at time of treatment showed no significant differences between
treatments at either time. Shoot thinning, shoot treatment (as for Expt.
81/6) and petiole application (as for Expt. 81/6) were all carried out on
the same day at each time. In all cases, petioles at node 5 were used
(with the exception of 3 shoots where node 6 was used due to defoliation at
node 5). The procedure of petiole application was identical to that of
Expt. 81/6. Leaking tubes were retreated on the same day and syringes were
removed after 24 hours. Unlike Expt. 81/6, 4 shoots at time 1 and 2 shoots
at time 2 had incomplete or no uptake after 24 hours, (5 out of these 6
were treatments including ABA) and these shoots were labelled and
subsequently not used in further analysis. In winter 1982, 4 shoots per
treatment were removed and used for determination of the Bud Index (nodes 2
to 13), lateral shoot number and length. The remaining 2 shoots per
treatment were retained on the vines as canes (14 nodes), and all lateral
shoots were removed, for Time 2 treatments only. In spring 1982, these
canes were used for determination of the Shoot Index (described in Chapter
2) and shoots per node, bunches per shoot and bunches per node. Also, the
phenology on GA$_3$ treated and control shoots was compared, i.e. per cent of
nodes burst over time, number of visible internodes and date of flowering.
Initially, the data from this experiment was analysed as for a randomised
block design with 16 treatments. Subsequently, where interactions were
suspected, the data was pooled and analysed as for split-plot design
(Little and Hills 1978); otherwise, data were pooled and standard 2 way AOV
employed.

(iii) Experiment 82/10: The effects of girdling (2 mm width) on response
to GA$_3$ application via the petiole at node 6. Girdling above or below node
6 should prevent translocation of GA₃ in the phloem to distal or proximal nodes respectively; however, there should be no effect on movement within the xylem. The 12 most vigorous shoots on each of 6 vines were used for the experiment; GA₃ was applied to all 12 shoots on 3 vines. There was no shoot thinning or shoot treatment (other than girdling) on any vine. On the same day (Nov. 16; 21 visible internodes) but prior to GA₃ application 4 shoots on each vine were selected at random and either girdled above or below node 6, or not at all. One ml of 10 ppm GA₃ in buffer was applied as in Expt. 81/6. In winter 1983, treated shoots were removed for determination of the Bud Index.

6.2.c. Application of abscisic acid (ABA) to petioles

(i) Experiment 81/6, 81/7: These experiments were previously described in 6.2.b. The aims in these experiments with regard to ABA application were: (a) to determine if ABA applied simultaneously with GA₃ would counteract the GA₃-induced response and (b) to determine if ABA had any effect on levels of PBN induced by shoot treatment (topping and defoliation) or on natural levels of PBN in non-treated shoots.

(ii) Experiment 82/11: This experiment was carried out in 1982 because there was no response to ABA application to a single node per shoot in the 1981 experiments. Therefore, in this experiment ABA (100 ppm in PO₄ buffer) was applied via petioles to 2 or 4 nodes per shoot to determine if ABA could counteract the PBN-inducing effect of shoot thinning, shoot topping and defoliation. Eight 'Shiraz' vines were used of which 4 were thinned to the 20 most vigorous shoots per vine, all shoots topped to 10 nodes and 100 per cent defoliated (no lateral shoot or inflorescence removal) on November 16, 1982 (21 visible internodes). The four ABA treatments were each applied at random to 5 shoots per vine (on the 4 control vines, the 20 most-vigorous shoots were used) immediately after shoot treatment, on the same day. The method of application of ABA to petioles was the same as that described in Expt. 81/6. In winter 1983, all treated shoots were removed for determination of the Bud Index.

6.2.d. Application of growth regulators to whole vines

(i) Experiment 81/5: The effects of a whole vine foliage spray of (2-chlorethyl) trimethylammonium chloride (Chlormequat, CCC) on the response to shoot thinning plus shoot topping and defoliation. Sixteen
'Shiraz' vines were used in this experiment, 8 of which were thinned to the 20 most-vigorous shoots, all shoots topped to 10 nodes plus 100% defoliation and removal of lateral shoots up to and including node 4 (no inflorescence removal) on Nov. 13, 1981 (18 visible internodes). CCC* at 500ppm plus wetting agent was thoroughly applied to all foliage on shoot-treated and non-treated vines with a knapsack sprayer. Control vines were similarly sprayed with tap water plus wetting agent. Both CCC and water sprays were applied on Nov. 14, 1981. In winter 1982, 10 treated shoots were selected at random from shoot treated vines and 10 of the most vigorous shoots selected from non-shoot-treated vines for determination of the Bud Index. Also, shoot diameter, lateral number and length (by node position) were measured.

(ii) Experiment 82/4: The effect of a whole vine foliar spray of chlorecthyl phosphonic acid (ethephon) on the response to shoot thinning plus shoot topping and defoliation. Twelve 'Shiraz' vines were used in this experiment, 6 of which were thinned to the 20 most-vigorous shoots, all shoots topped to 10 nodes and 50% defoliated (no lateral shoot or inflorescence removal) on November 20, 1982 (21 visible internodes). Ethephon ('Ethrel') at 300 ppm plus wetting agent was thoroughly applied to all foliage with a knapsack sprayer on the following day. Control vines were sprayed with rainwater plus wetting agent. In winter 1983, 10 treated shoots were selected at random from shoot treated vines and 10 of the most vigorous shoots selected from non-shoot-treated vines for determination of the Bud Index.

(iii) Experiment 83/4: The aim of this experiment was identical to that of Expt. 82/4, i.e. it is a repeat of that experiment except an additional ethephon concentration (900 ppm) was included. The procedure was the same as Expt. 82/4; shoot treatment and foliar sprays were applied on December 3, 1983 (24 visible internodes). During application of foliar sprays, particular care was taken to ensure that the ends of topped shoots (and comparable areas on control vines) were thoroughly treated. In winter 1984, 10 shoots per vine were removed (as for Expt. 82/4) for determination of the Bud Index, lateral number and lateral shoot length (nodes 2 to 10).

(iv) Experiment 83/6: This experiment examined the effects of whole vine foliar sprays of gibberellic acid (GA₃, 100 ppm) and ethephon (500 ppm) in

* Cycocel 100A (100g/L chlormequat)
combination with a light hedging to both sides of the canopy. Eighteen
'Shiraz' vines were used in this experiment, of which 9 were lightly hedged
on Dec 1, 1983 by hand, using a long bladed knife, such that approximately
30 cm was removed on both sides of the canopy. On the same day, vines were
thoroughly sprayed with either tap water, GA$_3$ or ethephon (plus wetting
agent) using a knapsack sprayer. In winter 1984, the pruning weight of all
vines was measured. After pruning, 20 of the most vigorous shoots were
selected for measurement of shoot length (on hedged vines, the length to
the hedging cut, if present, and the length of the most distal lateral
shoot were both measured and combined to give "shoot length") and of these,
10 were then selected at random for determination of the Bud Index (nodes 2
to 10).
6.3 RESULTS

6.3.a. Application of \( \text{GA}_{3} \) to leaf blades

Application of \( \text{GA}_{3} \) to leaf blades induced necrosis of the primary bud axis in 'Shiraz' (Table 6.2) but not in 'Sultana'. In the latter case, Bud Index values for 0, 30 and 100 ppm \( \text{GA}_{3} \) were 1, 2 and 1 respectively; 100 ppm application increased shoot length by 22 per cent relative to control but 30 ppm did not result in any significant increase. Neither concentration had any effect on cane diameter nor number of lateral shoots per cane. The following results are derived from experiments with 'Shiraz':

(i) **Effect of \( \text{GA}_{3} \) concentration**: This was examined in 1981 only. When applied to blades at nodes 5 to 10, increased \( \text{GA}_{3} \) concentration resulted in increased PBN for each date of application (Fig. 6.2.a) and for each node position i.e. nodes 2 to 4, 5 to 10 and 11 to 15 (Fig. 6.2.b). However, for all times pooled, 100 ppm resulted in significantly more PBN than 30 ppm at treated nodes only, with no difference at nodes above, below or for all nodes (Table 6.2).

(ii) **Effect of timing of \( \text{GA}_{3} \) application**: This was examined for application to blades at nodes 5 to 10 in both 1981 and 1982; the first two times on which \( \text{GA}_{3} \) was applied were almost identical with respect to number of visible internodes but the third time was significantly later in 1982 than 1981. However, in spite of these similarities, there were differences in response between the two years. For all nodes (i.e. 2 to 15), Times 1 and 2 had significantly more PBN than Time 3 in both years; however, in 1982 only, Time 1 application was more effective than Time 2. In general, in both years, Times 1 and 2 were more inductive than Time 3 at all node positions; exceptions were nodes 5 to 10 in 1981 (no difference between any time) and nodes 2 to 4 in 1982 (Time 2 equal to Time 3) (Tables 6.2, 6.3). There was no significant difference between PBN values for \( \text{GA}_{3} \) application at Time 3 and control for any node position. Similarly, treatment at Time 1 (17 visible internodes) resulted in more PBN than at Time 2 (24 visible internodes) when \( \text{GA}_{3} \) was applied to the youngest 6 separated leaves, for all node positions, i.e. treated nodes and 5 nodes "above" and "below" (Table 6.4). The inverse relationship between time of \( \text{GA}_{3} \) treatment (stage of shoot development as visible internodes) and level of PBN at treated nodes (5 to 10) is shown in Fig. 6.4 (\( r = -.998 \), significant at 1 per cent
level).

(iii) Interactions between GA₃ concentration and timing of application:
There was no difference in response between 30 and 100 ppm GA₃ over all node positions and over all times in Expt. 81/3. However, for time 1 only, 100 ppm was more effective than 30 ppm over all nodes; the largest difference for any node position was at nodes 11 to 15 (Table 6.2). The slopes of the response curves indicate an interaction between time of application and concentration, e.g. compare the slopes for Nov. 17 and Nov. 28 application dates (Fig. 6.2.a).

(iv) Comparison of treated nodes with nodes distal (above) and proximal (below) to treated nodes: For GA₃ applied to nodes 5 to 10, the results in 1981 and 1982 are not conclusive. In 1981, the greatest response over and above the natural, i.e. control, levels of PBN, occurred at the "treated" nodes, with less effect at nodes "above" and "below"; for the first 2 times of GA₃ application, there was no difference between nodes "above" and nodes "below" (Table 6.2). However, in 1982, there was generally no difference between "treated" nodes and either nodes "above" or "below": however, at the first 2 times, the response to GA₃ application was greater at nodes "below" than nodes "above" (Table 6.3).

By comparison, when GA₃ was applied to the 6 youngest separated leaves, the response at nodes "above" was the same as "treated" nodes at both times of application; nodes "above" and "treated" were each greater than nodes "below" at both times of application (Table 6.4, Fig. 6.4). Nevertheless, nodes below had significantly more PBN in response to GA₃ application at both times, and for times pooled (Table 6.4, Fig. 6.4); for controls, there were no significant differences between times for any node position (data not presented).

6.3.b Application of GA₃ via leaf petiole.

(i) General response: Application of 10 ppm GA₃ to a single petiole per shoot (either at node 5 or 6) resulted in significantly greater levels of PBN than controls in 1981 and 1982 (Tables 6.5; 6.6; 6.7), at the treated node and at nodes proximal and distal to the treated node; however, in both years, the GA₃ induced response was greatest at the treated and distal nodes (Tables 6.7, 6.8).
(ii) **Timing of application**: This was only examined in 1981 (Expt. 81/7); Nov. 18 application resulted in more PBN than Nov. 25 (Table 6.6). There was no interaction between GA₃ concentration and time of application; however, shoot treatment was only effective on Nov. 18. (Table 6.6).

(iii) **GA₃ application and shoot treatment**: GA₃ application induced more PBN than shoot treatment (when pooled over other factors) but there was no synergistic interaction. In Expt. 81/6, there was an additive effect when the two factors were combined (Table 6.5) but this was not observed in Expt. 81/7 over all nodes but did occur at nodes 2 to 4 (Table 6.8).

(iv) **Comparison of treated node and nodes proximal and distal to the treated node**: Without the interfering effect of shoot treatment (topping plus defoliation), the response to GA₃ application alone (after control Bud Index values are deducted) was greater at the treated node and distal nodes than proximal nodes; in 1981, there was no significant difference between levels of PBN at treated and distal nodes (Table 6.8) but in 1982, treated node levels were higher (Table 6.7). When GA₃ application was combined with shoot treatment, the response to GA₃ at treated and distal nodes (5 to 13) was less than that at proximal nodes (2 to 4) because the shoot treatment itself increased the level of PBN at nodes 5 to 13; therefore the additional response to GA₃ was less at those nodes (Table 6.8).

(v) **Effect of GA₃ application on lateral shoot development**: An increase in the number of lateral shoots per main shoot (measured as percentage of nodes with lateral shoot or mean number of lateral shoots per node) and the mean length per lateral shoot occurred in response to GA₃ application to non-treated shoots, i.e. not topped or defoliated (Table 6.9); the lateral shoot number was about doubled and the lateral shoot length was about quadrupled.

(vi) **Effect of GA₃ application on phenological development in the following season**: GA₃ application delayed:-
- budburst (as percentage of nodes burst; Table 6.9).
- rate of shoot development (as number of separated leaves per shoot; Fig. 6.5).

and - flowering (on Nov. 4, shoots on control canes were at the stage of 30 to 50 per cent flowering whereas shoots on GA₃-treated canes were just starting to flower).
There were fewer shoots per node on GA₃- treated vines (see Chapter 8).
although there was no significant difference in final budburst (measured as per cent nodes burst). Also, shoots on GA$_3$-treated canes had the same leaf number as shoots on controls by November 4.

(vii) Effect of shoot girdling on response to GA$_3$ application: Girdling at the internode immediately above or below the treated node, just prior to GA$_3$ application, had no effect on the levels of PBN induced in response to GA$_3$ at nodes proximal or distal to the treated node (Table 6.7). However, girdling above or below significantly increased the level of PBN at both the treated node, and treated node plus distal nodes pooled. As a result, when the control levels are deducted, the effect due to GA$_3$ application alone at the treated node was greatest in the absence of girdling.

(viii) Correlation between Bud Index and Shoot Index: The relationship between these indices was examined for Nov. 25 treatments in Expt. 81/7. On a per cane basis, i.e. pooled over all treatments (n = 8), the indices were found to be positively correlated (r = .762, significant at 5 per cent level).

6.3.c. Application of ABA to petioles.

(i) Effect of ABA on GA$_3$-induced response: ABA (100 ppm) applied to the petiole simultaneously with GA$_3$ had no effect on the GA$_3$-induced response, measured as Bud Index (Tables 6.5, 6.6) or any other variable, e.g. lateral shoot development, budburst in the following season, etc.

(ii) Effect of ABA on natural levels of PBN in non-treated shoots: ABA application had no effect on levels of PBN in non-treated shoots in 1981 (Tables 6.5, 6.6) or 1982 (data not presented).

(iii) Effect of ABA on shoot treatment-induced response: Similarly, ABA application to a single node in 1981 (Tables 6.5, 6.6) or up to 4 nodes per shoot in 1982 (data not presented) had no effect on the levels of PBN induced in response to shoot treatment (thinning, topping, defoliation). In the latter case, the typical response to shoot treatment occurred, with or without ABA.

6.3.d. Application of growth regulators to whole vines

(i) CCC application combined with shoot thinning plus topping and
defoliation: CCC had no effect on the level of PBN induced in response to shoot treatment, over all nodes or at any node position (Table 6.10). However, CCC application to otherwise non-treated vines resulted in an increase in level of PBN over all nodes and particularly for distal nodes (but the increase for distal nodes was not significant at the 5 per cent level). The response to shoot thinning, topping and defoliation was the same as that described in Chapter 5, i.e. an increase in PBN over all nodes, and at distal nodes in particular, relative to control. The overall effect of CCC application (pooled over shoot treatments) was a decrease in lateral shoot length with no effect on lateral shoot number; total lateral shoot length per main shoot was less (significant at 6 per cent level) on CCC-treated vines. By comparison, shoot treatment (pooled over CCC) significantly increased lateral shoot number but decreased mean lateral shoot length. Due to the over-riding effect of the lateral shoot number component, shoot treatment significantly increased total lateral shoot length per main shoot (Table 6.11). The interaction between CCC and shoot treatment resulted from shorter laterals on shoot treatment plus CCC compared with no shoot treatment plus CCC (Table 6.11).

(ii) Etahephon application combined with shoot thinning, topping and defoliation: The results obtained in two almost identical experiments in two consecutive years were very similar. In both years, application of 300 ppm ethephon induced increased levels of PBN, when pooled over shoot treatment, and nodes 2 to 10 (Tables 6.12, 6.13); this was a result of response at nodes 2 to 4 and 5 to 7 only, in both years. When the response to application of 300 ppm ethephon to shoot treated (ST) and non-shoot treated vines (NST) is examined separately, it is found that a response occurred with NST but not ST vines in both years; this response was significant at all node positions, i.e. 2-4, 5-7, 8-10, in both years (Tables 6.12, 6.13). Application of 300 ppm ethephon increased levels of PBN in NST vines over that on ST in both years, the response being at nodes 2-4 and 5-7 only. Shoot treatment produced the expected response in both years, in the absence of ethephon, with the main effect at distal nodes (Tables 6.12, 6.13).

The inclusion of an additional level of ethephon (900 ppm) in 1983 introduced further complications because, although not significantly different to 300 ppm at any node position when pooled over shoot treatment, 900 ppm had the opposite effect to 300 ppm on ST and NST vines, i.e. 900 ppm significantly increased the level of PBN on ST vines at all nodes.
(greatest response at nodes 8-10) but not on NST vines (Tables 6.12, 6.13). Ethephon, at either concentration, had no effect on number of lateral shoots per main shoot but did decrease mean lateral shoot length significantly on ST vines (particularly at the distal nodes) the magnitude of the decrease (up to 30 per cent) being related to ethephon concentration. On the other hand, shoot treatment significantly increased number of lateral shoots (by four times) at all ethephon concentrations and mean lateral shoot length (by about 180 per cent overall). As a result, the effect of shoot treatment was by far the major factor determining total length of lateral shoots per main shoot (Table 6.14).

Lightly hedging both sides of the canopy was found to have no significant effect on shoot length, pruning weight or level of PBN. Therefore, data for the effect of whole vine sprays of GA₃ and ethephon was pooled over hedging (Table 6.15). In this experiment, ethephon (500 ppm) increased level of PBN and decreased shoot length and pruning weight (but not significant at 5 per cent for any variable whereas GA₃ (100 ppm) increased level of PBN (significant at 5 per cent), and increased pruning weight and shoot length (neither significant at 5 per cent level).
Table 6.1 Details of experiments with the cultivar Shiraz

<table>
<thead>
<tr>
<th>Expt. No.</th>
<th>Location 1</th>
<th>Expt. 2 design</th>
<th>Block Size (No. vines)</th>
<th>Plot size</th>
<th>No. replicates</th>
</tr>
</thead>
<tbody>
<tr>
<td>81/3</td>
<td>RAC-S</td>
<td>RB</td>
<td>1</td>
<td>1 shoot</td>
<td>9</td>
</tr>
<tr>
<td>4</td>
<td>RAC-S</td>
<td>SP</td>
<td>5</td>
<td>1 vine</td>
<td>5 or 10</td>
</tr>
<tr>
<td>5</td>
<td>RAC-S</td>
<td>RB</td>
<td>4</td>
<td>1 shoot (4)</td>
<td>4</td>
</tr>
<tr>
<td>6</td>
<td>RAC-S</td>
<td>RB</td>
<td>6</td>
<td>2 shoots</td>
<td>6</td>
</tr>
<tr>
<td>7</td>
<td>RAC-S</td>
<td>SSP</td>
<td>2</td>
<td>1 vine</td>
<td>4 or 8</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>82/4</td>
<td>RAC-S</td>
<td>RB</td>
<td>3</td>
<td>1 vine</td>
<td>3</td>
</tr>
<tr>
<td>9</td>
<td>RAC-S</td>
<td>RB</td>
<td>4</td>
<td>1 vine</td>
<td>4</td>
</tr>
<tr>
<td>10</td>
<td>Waite</td>
<td>SP</td>
<td>3</td>
<td>1 vine</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>11</td>
<td>Waite</td>
<td>SP</td>
<td>2</td>
<td>1 shoot (4)</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>83/4</td>
<td>RAC-S</td>
<td>RB</td>
<td>4</td>
<td>1 vine</td>
<td>4</td>
</tr>
<tr>
<td>6</td>
<td>RAC-S</td>
<td>RB</td>
<td>3</td>
<td>1 vine</td>
<td>6</td>
</tr>
</tbody>
</table>

1 RAC-S = South vineyard, Roseworthy College (RAC); Waite = Claremont vineyard, Waite Agric. Res. Ins., Glen Osmond.
2 RB = randomised block; SP = split-plot; SSP = split-split-plot.
   Factorial combination of treatments used in expts 81/5 (2 x 2), 81/6 (2 x 4), 82/4 (2 x 2), 83/4 (2 x 3).
3 Replicates blocks were selected for uniformity on the basis of butt circumference in expts. 81/4, 81/5, 82/4, 82/9, 82/10, 82/11, 83/4, 83/6.
Table 6.2 Effect of GA₃ on PBN; GA₃ was applied to leaf blades (nodes 5 to 10) at two concentrations and three times of application (Expt. 81/3).

<table>
<thead>
<tr>
<th>GA₃ concn. ppm</th>
<th>November date*</th>
<th>2 to 4</th>
<th>5 to 10</th>
<th>11 to 15</th>
<th>2 to 15</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>7</td>
<td>57 cd</td>
<td>17 c</td>
<td>0 b</td>
<td>15 d</td>
</tr>
<tr>
<td>0</td>
<td>17</td>
<td>40 de</td>
<td>8 c</td>
<td>1 b</td>
<td>13 d</td>
</tr>
<tr>
<td>0</td>
<td>28</td>
<td>7 e</td>
<td>15 c</td>
<td>0 b</td>
<td>8 d</td>
</tr>
<tr>
<td>30</td>
<td>7</td>
<td>94 b</td>
<td>83 b</td>
<td>29 ab</td>
<td>59 bc</td>
</tr>
<tr>
<td>30</td>
<td>17</td>
<td>91 b</td>
<td>98 b</td>
<td>63 a</td>
<td>83 ab</td>
</tr>
<tr>
<td>30</td>
<td>28</td>
<td>79 bcd</td>
<td>78 b</td>
<td>2 b</td>
<td>51 c</td>
</tr>
<tr>
<td>100</td>
<td>7</td>
<td>99 ab</td>
<td>97 ab</td>
<td>64 a</td>
<td>88 a</td>
</tr>
<tr>
<td>100</td>
<td>17</td>
<td>100 a</td>
<td>100 a</td>
<td>69 a</td>
<td>96 a</td>
</tr>
<tr>
<td>100</td>
<td>28</td>
<td>85 bc</td>
<td>100 a</td>
<td>7 b</td>
<td>49 c</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>GA₃ (a)</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>Pooled over</td>
<td>35 b</td>
<td>13 c</td>
<td>0 b</td>
<td>12 b</td>
</tr>
<tr>
<td>30</td>
<td>time</td>
<td>88 a</td>
<td>86 b</td>
<td>31 a</td>
<td>64 a</td>
</tr>
<tr>
<td>100</td>
<td></td>
<td>94 a</td>
<td>99 a</td>
<td>47 a</td>
<td>78 a</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>GA₃ (b)</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Pooled over</td>
<td>7</td>
<td>83 a</td>
<td>66 a</td>
<td>31 a</td>
<td>54 a</td>
</tr>
<tr>
<td>GA₃ (a)</td>
<td>17</td>
<td>77 a</td>
<td>69 a</td>
<td>44 a</td>
<td>64 a</td>
</tr>
<tr>
<td>Pooled over</td>
<td>28</td>
<td>57 b</td>
<td>64 a</td>
<td>3 b</td>
<td>36 b</td>
</tr>
</tbody>
</table>

| GA₃ (b)        | 17             | 55 ab  | 91 a    | 65 a     | (24)    |
|                | 28             | 75 a   | 74 b    | 5 b      | (31)    |

Mean all times: 57 79 39 (21)

Numbers in parentheses are LDS .05 values for comparison of means within node groups 2-4, 5-10, 11-15.

* Numbers of visible internodes were 17, 21 and 25 on Nov. 7, 17 and 28 respectively and 60 per cent flowering occurred on Nov. 17. Means in the same column followed by the same letter are not significantly different at 5 per cent level.

(b) Less control values.
Table 6.3 Effect of GA$_3$ on PBN; GA$_3$ was applied at 30 ppm to leaf blades (nodes 5 to 10) on three dates (Expt. 82/9).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Bud Index % at nodes:--</th>
</tr>
</thead>
<tbody>
<tr>
<td>GA$_3$ concn.</td>
<td># visible internodes</td>
</tr>
<tr>
<td>Date</td>
<td>ppm</td>
</tr>
<tr>
<td>(a)</td>
<td></td>
</tr>
<tr>
<td>Nov. 9</td>
<td>30</td>
</tr>
<tr>
<td>Nov. 19</td>
<td>30</td>
</tr>
<tr>
<td>Dec. 14</td>
<td>30</td>
</tr>
<tr>
<td>(b)</td>
<td></td>
</tr>
<tr>
<td>Nov. 9</td>
<td>30</td>
</tr>
<tr>
<td>Nov. 19</td>
<td>30</td>
</tr>
<tr>
<td>Dec. 14</td>
<td>30</td>
</tr>
<tr>
<td>Mean all dates</td>
<td>30</td>
</tr>
</tbody>
</table>

Numbers in parentheses are LSD .05 values for comparison of means for nodes 2-4, 5-10 and 11-15.
(a) Timing of GA$_3$ application compared with untreated control; (b) less control values.
* 50% flowering
Means in the same column followed by the same letter are significantly different at 5% level.

Table 6.4 Effect of treating blades of six youngest separated leaves with 100 ppm GA$_3$ at two times on PBN (Expt. 81/4).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Bud Index % at nodes numbered:--</th>
</tr>
</thead>
<tbody>
<tr>
<td>GA$_3$ concn.</td>
<td># visible internodes</td>
</tr>
<tr>
<td>Date</td>
<td>ppm</td>
</tr>
<tr>
<td>Nov. 13</td>
<td>100</td>
</tr>
<tr>
<td>Dec. 3</td>
<td>100</td>
</tr>
<tr>
<td>Pooled over times</td>
<td></td>
</tr>
<tr>
<td>Nov. 13</td>
<td>100</td>
</tr>
<tr>
<td>Dec. 3</td>
<td>100</td>
</tr>
</tbody>
</table>

a, proximal to treated nodes; b, six treated nodes [nodes 12 to 17 (Nov. 13), 19 to 24 (Dec. 3)]; c, distal to treated nodes.
*,**,*** indicates that means were significantly different at 5%, 1% and 0.1% level respectively.
Means in the same row followed by the same letter are not significantly different at 5% level.
Table 6.5  Effects of GA$_3$, ABA, GA$_3$ + ABA application via petiole at node 5, with and without shoot treatment on Bud Index, nodes 2 to 14 (Expt. 81/6).

<table>
<thead>
<tr>
<th>Shoot treatment</th>
<th>Growth regulator</th>
<th>Mean $^1$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Nil</td>
<td>GA$_3$</td>
</tr>
<tr>
<td>No</td>
<td>18 b</td>
<td>72 a</td>
</tr>
<tr>
<td>Yes</td>
<td>29 b</td>
<td>86 a</td>
</tr>
<tr>
<td>Mean $^2$</td>
<td>24 y</td>
<td>79 x</td>
</tr>
</tbody>
</table>

1,2 Pooled over GA$_3$ and ABA, and shoot treatment respectively.  
$^*$ Indicates means significantly different at 5% level.  
Means followed by same letter are not significantly different at 5% level.

Table 6.6  Effects of GA$_3$, ABA, GA$_3$ + ABA application via petiole at node 5, with and without shoot treatment, at two different times on Bud Index, nodes 2 to 13 (Expt. 81/7)

<table>
<thead>
<tr>
<th>Date of PGR treatment</th>
<th>Shoot treatment</th>
<th>Growth regulator</th>
<th>Mean $^1$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Nil</td>
<td>GA$_3$</td>
</tr>
<tr>
<td>Nov. 18</td>
<td>No</td>
<td>16 c</td>
<td>90 a</td>
</tr>
<tr>
<td></td>
<td>Yes</td>
<td>60 b</td>
<td>100 a</td>
</tr>
<tr>
<td>Nov. 25</td>
<td>No</td>
<td>10 c</td>
<td>79 ab</td>
</tr>
<tr>
<td></td>
<td>Yes</td>
<td>26 c</td>
<td>79 ab</td>
</tr>
</tbody>
</table>

1 Pooled over GA$_3$ and ABA.  
$^*$ Indicates means significantly different at 5% level.  
Means followed by same letter are not significantly different at 5% level.
Table 6.7 Effect of GA₃ application via petiole at node 6, with and without girdling above or below node 6 on PBN (Expt. 82/10)

<table>
<thead>
<tr>
<th>Treatment</th>
<th>GA concn. ppm</th>
<th>2 to 5</th>
<th>6</th>
<th>7 to 10</th>
<th>2 to 10</th>
</tr>
</thead>
<tbody>
<tr>
<td>Girdle</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Above node 6 0</td>
<td>0</td>
<td>45 a</td>
<td>14 c</td>
<td>4 b</td>
<td></td>
</tr>
<tr>
<td>Below &quot; &quot; 0</td>
<td>0</td>
<td>56 a</td>
<td>50 b</td>
<td>16 b</td>
<td></td>
</tr>
<tr>
<td>-</td>
<td>10</td>
<td>52 a</td>
<td>50 b</td>
<td>18 b</td>
<td></td>
</tr>
<tr>
<td>Above node 6 10</td>
<td>10</td>
<td>59 a</td>
<td>100 a</td>
<td>42 a</td>
<td></td>
</tr>
<tr>
<td>Below &quot; &quot; 10</td>
<td>10</td>
<td>70 a</td>
<td>100 a</td>
<td>43 a</td>
<td></td>
</tr>
<tr>
<td>Pooled over girdling 10</td>
<td>0</td>
<td>51</td>
<td>36</td>
<td>12</td>
<td>(13) 32</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>62</td>
<td>100</td>
<td>43</td>
<td>(26) 58</td>
</tr>
<tr>
<td>Difference due to GA₃</td>
<td></td>
<td>11</td>
<td>64</td>
<td>31</td>
<td>(19)</td>
</tr>
</tbody>
</table>

*,**: significant at 5% and 1% level respectively.
Numbers in parentheses represent LSD 0.05 for comparison of nodes 2-5, 6, 7-10 means.
Means in the same column followed by the same letter are not significantly different at 5% level.

Table 6.8 Effect of GA₃ application via petiole at node 5 and shoot treatment on Bud Index (Expt. 81/7, Nov. 18 treatment only, pooled over ABA).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>GA₃ concn. ppm</th>
<th>2 to 4</th>
<th>5</th>
<th>6 to 13</th>
<th>LSD 0.05 X</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shoot treatment</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>-</td>
<td>0</td>
<td>25 c</td>
<td>17 c</td>
<td>13 c</td>
<td>ns</td>
</tr>
<tr>
<td>-</td>
<td>10</td>
<td>71 b</td>
<td>100 a</td>
<td>94 a</td>
<td>ns</td>
</tr>
<tr>
<td>+</td>
<td>0</td>
<td>55 bc</td>
<td>75 b</td>
<td>61 b</td>
<td>21</td>
</tr>
<tr>
<td>+</td>
<td>10</td>
<td>100 a</td>
<td>100 a</td>
<td>99 a</td>
<td>ns</td>
</tr>
<tr>
<td>Difference due to GA₃</td>
<td></td>
<td>46</td>
<td>83</td>
<td>81</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>+</td>
<td>45</td>
<td>25</td>
<td>38</td>
<td>27</td>
</tr>
</tbody>
</table>

x For comparison of means in same row
Means in the same column followed by the same letter are not significantly different at 5% level.
Table 6.9 Effect of GA₃ application via petiole at node 5 on lateral shoot number, length and budburst in the following season (Expt. 81/7, Nov. 18)

<table>
<thead>
<tr>
<th>Variable</th>
<th>GA₃ concn. ppm</th>
<th>2 to 4</th>
<th>5</th>
<th>6 to 13</th>
<th>2 to 13</th>
</tr>
</thead>
<tbody>
<tr>
<td>% nodes with lateral shoot</td>
<td>0</td>
<td>11</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of lateral shoots per node</td>
<td>0</td>
<td>0.25*</td>
<td>0</td>
<td>0.13*</td>
<td>0.15*</td>
</tr>
<tr>
<td>Mean lateral shoot length</td>
<td>0</td>
<td>385*</td>
<td>-</td>
<td>241</td>
<td>280</td>
</tr>
<tr>
<td>% nodes burst</td>
<td>0</td>
<td>88</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Indicates means significantly different at 5% level
a Shoots not topped or defoliated
b Pooled over shoot treatment and ABA

Table 6.10 Effect of CCC application and shoot treatment* to whole vines on Bud Index (Expt. 81/5)

<table>
<thead>
<tr>
<th>Treatment</th>
<th>CCC concn ppm</th>
<th>Bud Index % at nodes:</th>
<th>2 to 4</th>
<th>5 to 7</th>
<th>8 to 9</th>
<th>1 to 9</th>
</tr>
</thead>
<tbody>
<tr>
<td>-</td>
<td>0</td>
<td>34 a</td>
<td>8 b</td>
<td>8 b</td>
<td>18 b</td>
<td></td>
</tr>
<tr>
<td>-</td>
<td>500</td>
<td>41 a</td>
<td>26 ab</td>
<td>20 b</td>
<td>30 ab</td>
<td></td>
</tr>
<tr>
<td>+</td>
<td>0</td>
<td>34 a</td>
<td>48 a</td>
<td>68 a</td>
<td>48 a</td>
<td></td>
</tr>
<tr>
<td>+</td>
<td>500</td>
<td>40 a</td>
<td>38 a</td>
<td>71 a</td>
<td>47 a</td>
<td></td>
</tr>
</tbody>
</table>

* Shoot thinning, topping, defoliation.
Means in the same column followed by the same letter are not significantly different at 5% level.
Table 6.11 Effect of CCC application and shoot treatment\(^x\) to whole vines on number and length of lateral shoots\(^y\) (Expt. 81/5)

<table>
<thead>
<tr>
<th>Treatment</th>
<th>CCC concn. ppm</th>
<th>Number of lateral shoots per cane (1)</th>
<th>Mean length per lateral shoot mm (2)</th>
<th>Total length lateral shoots per cane mm (1) x (2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>-</td>
<td>0</td>
<td>0.38 b</td>
<td>400 a</td>
<td>159 b</td>
</tr>
<tr>
<td>-</td>
<td>500</td>
<td>0.50 b</td>
<td>265 b</td>
<td>122 b</td>
</tr>
<tr>
<td>+</td>
<td>0</td>
<td>2.50 a</td>
<td>220 bc</td>
<td>597 a</td>
</tr>
<tr>
<td>+</td>
<td>500</td>
<td>2.15 a</td>
<td>156 c</td>
<td>344 ab</td>
</tr>
<tr>
<td>-</td>
<td>Pooled over</td>
<td>0.44</td>
<td>333</td>
<td>140</td>
</tr>
<tr>
<td>+</td>
<td>CCC</td>
<td>2.33</td>
<td>*</td>
<td>**</td>
</tr>
<tr>
<td>Pooled over</td>
<td>0</td>
<td>1.44</td>
<td>310</td>
<td>378</td>
</tr>
<tr>
<td>shoot treatment</td>
<td>500</td>
<td>1.33</td>
<td>*</td>
<td>**</td>
</tr>
</tbody>
</table>

\(x\) Shoot thinning, topping, defoliation.
\(y\) For nodes 5 to 9 inclusively.

*,”**: Indicates means are significantly different at 5% and 1% respectively.
Means in the same column followed by same letter are not significantly different at 5% level.

Table 6.12 Effect of ethephon application and shoot treatment\(^x\) on Bud Index (Expt. 82/4)

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Ethephon concn. ppm</th>
<th>Bud Index % at nodes:-</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>2 to 4</td>
</tr>
<tr>
<td>-</td>
<td>0</td>
<td>22 b</td>
</tr>
<tr>
<td>-</td>
<td>300</td>
<td>51 a</td>
</tr>
<tr>
<td>+</td>
<td>0</td>
<td>26 b</td>
</tr>
<tr>
<td>+</td>
<td>300</td>
<td>40 ab</td>
</tr>
<tr>
<td>-</td>
<td>Pooled over</td>
<td>37</td>
</tr>
<tr>
<td>+</td>
<td>ethephon</td>
<td>33</td>
</tr>
<tr>
<td>Pooled over</td>
<td>0</td>
<td>24</td>
</tr>
<tr>
<td>shoot treatment</td>
<td>300</td>
<td>46</td>
</tr>
</tbody>
</table>

\(x\) Shoot thinning, topping, defoliation.

* Indicates means significantly different at 5% level.
Means in same column followed by the same letter are not significantly different at 5% level.
Table 6.13 Effect of ethephon application and shoot treatment\(^X\) on Bud Index (Expt. 83/4)

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Ethephon concn. ppm</th>
<th>Bud Index % at nodes:</th>
<th>2 to 4</th>
<th>5 to 7</th>
<th>8 to 10</th>
<th>2 to 10</th>
</tr>
</thead>
<tbody>
<tr>
<td>-</td>
<td>0</td>
<td>35 b</td>
<td>10 c</td>
<td>0 c</td>
<td>15 b</td>
<td></td>
</tr>
<tr>
<td>-</td>
<td>300</td>
<td>80 a</td>
<td>80 a</td>
<td>14 bc</td>
<td>58 a</td>
<td></td>
</tr>
<tr>
<td>-</td>
<td>900</td>
<td>54 ab</td>
<td>37 b</td>
<td>14 bc</td>
<td>36 b</td>
<td></td>
</tr>
<tr>
<td>+</td>
<td>0</td>
<td>28 b</td>
<td>28 bc</td>
<td>23 b</td>
<td>29 b</td>
<td></td>
</tr>
<tr>
<td>+</td>
<td>300</td>
<td>34 b</td>
<td>32 bc</td>
<td>28 b</td>
<td>32 b</td>
<td></td>
</tr>
<tr>
<td>+</td>
<td>900</td>
<td>58 ab</td>
<td>55 b</td>
<td>64 a</td>
<td>59 a</td>
<td></td>
</tr>
<tr>
<td>-</td>
<td>Pooled over ethephon</td>
<td>56</td>
<td>42</td>
<td>9</td>
<td>36</td>
<td></td>
</tr>
<tr>
<td>+</td>
<td>ethephon</td>
<td>40</td>
<td>37</td>
<td>42</td>
<td>40</td>
<td></td>
</tr>
<tr>
<td>Pooled over shoot treatment</td>
<td>300</td>
<td>32 b</td>
<td>18 b</td>
<td>17 b</td>
<td>22 b</td>
<td></td>
</tr>
<tr>
<td>900</td>
<td></td>
<td>57 a</td>
<td>46 a</td>
<td>39 a</td>
<td>48 a</td>
<td></td>
</tr>
</tbody>
</table>

\(X\) Shoot thinning, topping, defoliation.
* Indicates means significantly different at 5% level.
Means in the same column followed by the same letters are not significantly different at 5% level.

Table 6.14 Effect of ethephon application and shoot treatment\(^X\) on lateral shoot number and mean lateral shoot length per cane (Expt. 83/4)

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Ethephon concn. ppm</th>
<th>Lateral number per cane (1)</th>
<th>Mean lateral shoot length per cane mm (2)</th>
<th>Total lateral shoot length per cane mm (1) x (2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>-</td>
<td>0</td>
<td>1.1 b</td>
<td>45 d</td>
<td>49 b</td>
</tr>
<tr>
<td>-</td>
<td>300</td>
<td>0.8 b</td>
<td>54 d</td>
<td>43 b</td>
</tr>
<tr>
<td>-</td>
<td>900</td>
<td>1.2 b</td>
<td>65 cd</td>
<td>78 b</td>
</tr>
<tr>
<td>+</td>
<td>0</td>
<td>4.3 a</td>
<td>118 a</td>
<td>509 a</td>
</tr>
<tr>
<td>+</td>
<td>300</td>
<td>3.6 a</td>
<td>93 b</td>
<td>336 a</td>
</tr>
<tr>
<td>+</td>
<td>900</td>
<td>4.3 a</td>
<td>83 bc</td>
<td>358 a</td>
</tr>
</tbody>
</table>

\(X\) Shoot thinning, topping, defoliation.
Means in the same column followed by the same letter are not significantly different at 5% level.
Table 6.15 Effect of whole vine sprays of GA$_3$ (100 ppm) and ethephon (500 ppm) on Bud Index$^x$, pruning weight$^2$ per vine and shoot length (Expt. 83/6, pooled over hedging)

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Bud Index %</th>
<th>Pruning weight kg</th>
<th>Shoot length mm</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>10 b</td>
<td>2.8 ab</td>
<td>899 a</td>
</tr>
<tr>
<td>GA$_3$</td>
<td>28 a</td>
<td>3.2 a</td>
<td>942 a</td>
</tr>
<tr>
<td>Ethephon</td>
<td>21 ab</td>
<td>2.1 b</td>
<td>843 a</td>
</tr>
</tbody>
</table>

$^x$ Nodes 2 to 10.
Means in the same column followed by the same letter are not significantly different at 5% level.
Fig. 6.1 Leaf petiole feeding from a 2 ml plastic syringe cylinder with a plastic tube to petiole.
Fig. 6.2 Relationship between GA$_3$ concentration (log x + 1 scale) and Bud Index (arc sine scale); Expt. 81/3, 'Shiraz':
(a) Effect of date of GA$_3$ application (pooled over nodes 2 to 15); (x) Nov. 7, (●) Nov. 17, (○) Nov. 28, (+) all times.
(b) Effect at different node positions (pooled over time); (x) Nodes 2 to 4, (●) 5 to 10, (○) 11 to 15, (+) all nodes.
Fig. 6.3 Relationship between stage of shoot development¹ at time of $\text{GA}_3$ application to leaf blades at nodes 5 to 10, and Bud Index at nodes 2 to 15, (Expt. 82/9, 'Shiraz').

¹ As no. visible internodes.

(-- --) control level.
Fig. 6.4 Effect of timing of GA₃ (100 ppm) application to six youngest separated leaves on Bud Index by node position (Expt. 81/4, 'Shiraz'). Control (——); treated (----); (●) Nov. 13, 17 leaves per shoot; (○) Dec. 12, 24 leaves per shoot.
1 Treated nodes = "I to V".
2 Node "-5" = Nodes 7 and 14 for Nov. 13 and Dec. 12 treatment respectively.
Nov. 13 and Dec. 12 GA₃ treatments are significantly different at all node positions except "-5 to -3" inclusively.
Fig. 6.5 Effect of GA₃ application (o) via petiole at node five on number of separated leaves per shoot in the following season; (●) = untreated control. (Expt. 81/7, pooled over shoot treatment and ABA).
* Indicates means are significantly different at 5% level.
6.4 DISCUSSION

The application of gibberellic acid (GA₃) to 'Shiraz' resulted in significantly increased levels of necrosis of the primary bud-axis (PBN), compared with control, when applied to leaf blades on petioles or as a whole vine foliage spray (Tables 6.2 to 6.9, 6.15). In general, the response to GA₃ applied to blades and petioles was similar to results reported by Lavee et al. (1981b) for the same concentrations of GA₃ on 'Queen of Vineyard' in Israel. These authors also found that petiole application was more inductive than blade application; in this study, application of 10 ug GA₃ to a single petiole per shoot could induce as much or more PBN at nodes proximal and distal to the treated node as 100 ug GA₃ applied to each of 5 leaf blades per shoot.

Although GA₃ is absorbed by leaf blades, uptake by mature leaves is said to be relatively poor (Weaver et al. 1966; mature leaves were defined by these authors as more than four-fifths final size and no longer light-green in colour). During and after flowering, leaves at nodes 5 to 10 would be regarded as mature by this definition. Since application of GA₃ to blades at flowering and up to 2 weeks later caused a significant increase in PBN in this study and Lavee et al. (op cit), one can assume that mature leaves may be better sites of entry for GA₃ than postulated by Weaver et al (1966), at least for 'Shiraz' and 'Queen of the Vineyard'.

The increase in level of PBN in response to increase in GA₃ concentration, for both blade and petiole application, was also shown by Lavee et al. (op cit), as was the decrease in PBN level with later time of application such that, in 1982, application to blades five weeks after 50 per cent flowering resulted in no significant increase in PBN above control levels.

What is the explanation for the decrease in response to applied GA₃ with time after flowering following blade and petiole application? Three ideas appear possible:

a) A decrease in the ability of leaf blades to take up GA₃ as leaf maturity increases. This is supported in part by the lack of response to GA₃ application to blades at nodes 5 to 10 at a time when application to blades at nodes 19 to 24 was effective in inducing PBN.

b) A decrease in shoot susceptibility as they mature; GA₃ application to the six youngest leaves was more inductive on Nov. 13 than Dec. 3.

c) A decrease in bud susceptibility with increasing degree of bud development. Young, still differentiating, upper buds on relatively mature shoots treated with GA₃ via leaf blades on December 12 were affected almost as much as those on less mature shoots treated one month before; in both
cases, proximal, more mature buds were affected less or not at all. Also, when GA$_3$ was applied via petioles, distal nodes were affected as were treated nodes but there was relatively little effect at proximal nodes. Lavee et al. (op cit) favour explanation (c) as they found similar results with GA$_3$ application via leaf blades and petioles.

The direction of translocation of GA$_3$ after blade or petiole application was not studied directly; rather, it was assumed that if GA$_3$ had a direct effect on the induction of PBN, then the pattern of PBN along a shoot might indicate possible direction of translocation. The results from blade application experiments suggest both basipetal and acropetal translocation (reported by Alleweldt 1961 and Hale and Weaver 1962) whereas those from petiole application experiments suggest translocation is primarily acropetal (reported by Lavee et al op cit). Therefore, it is difficult to draw any firm conclusions concerning the direction of translocation.

It is well-known that exogenous application of GA$_3$ to grapevines increases the rate of shoot growth (1.7.c.ii) and this has been confirmed here. However, most reports say little about the effect of GA$_3$ on lateral shoot development; in this study GA$_3$ application increased both lateral shoot number and length, e.g. GA$_3$ petiole application increased mean number of lateral shoots at nodes proximal and distal to the application node (both 1.6 times) and mean lateral shoot length (3.5 and 3.1 times respectively) on otherwise untreated shoots. It is significant, therefore, that high natural levels of PBN are associated with vigorous shoots and strong lateral shoot development (Chapter 3). Also, shoot topping increases both lateral shoot development (number and length) and level of PBN (Chapter 5).

The lack of effect of GA$_3$ on the PBN level of 'Sultana' is compatible with previous reports on the effect of GA$_3$ on 'Sultana' and other seedless cultivars (Weaver and McCune 1961); this is in spite of a significant increase in shoot length, also previously reported for 'Sultana' (Hagiwara et al. 1980).

The delay in budburst and reduction in budburst, i.e. fewer shoots per node in the season following GA$_3$ application, observed in this study, has also been reported by Weaver and McCune (1961) and others (1.7.c.ii).

The general lack of response to ABA, with both GA$_3$ and shoot treatment, is perhaps a result of a lack of mobility of ABA after exogenous application (Loveys 1984) and cannot necessarily be taken as evidence against involvement of endogenous GA$_3$ in induction of PBN in response to shoot thinning, topping and defoliation.
Application of CCC had no effect on levels of PBN in shoot-treated (thinning, topping, defoliation) vines. Although CCC acts in general as an inhibitor of shoot growth in grapevines and other plants, there have been reports of increases in shoot growth and endogenous GA$_3$ level in response to CCC application (Goodwin 1978); for example, CCC application increased GA$_3$ activity in *Vicia faba* and *Pisum*. However, it is unlikely that CCC application increased endogenous GA$_3$ activity in this case because there was no additive effect when CCC was combined with shoot treatment. Nevertheless, it is difficult to explain the increased PBN level in non-shoot treated vines sprayed with CCC.

In this experiment, CCC caused a significant reduction in mean lateral shoot length (also reported by Tezuka et al. 1980) but had no effect on lateral shoot number. By comparison, treatments which increase the level of PBN (i.e. shoot treatment and GA$_3$) increase both number and length of lateral shoots.

The increase in PBN level following ethephon application was unexpected and is difficult to explain. Ethephon (300 ppm) increased PBN level on non-shoot-treated vines (in two successive years) while shoot-treatment also increased PBN level. Therefore, the combination of ethephon and shoot-treatment might be expected to have, at least, an additive effect; in fact, ethephon at 900 ppm, but not at 300 ppm, did increase the level of PBN in shoot-treated vines. However, the complicating factor is that ethephon (at 300 ppm) on non-shoot-treated vines increased PBN to a significantly greater level than that on ethephon plus shoot-treated vines, and for this, there is no satisfactory explanation.

Nevertheless, the fact remains that ethephon (at 300 ppm but not at 500 or 900 ppm) on non-shoot-treated vines markedly increased the level of PBN at both proximal and distal nodes; by comparison, shoot treatment had its main effect on distal nodes. Although ethephon has been previously reported to cause abscission of terminal buds and shoot tips in a range of plants (Shulman 1982) this is the first report of ethephon-induced necrosis of the primary axis in grapevine buds. The only explanation for this effect of ethephon is that it induced an increased endogenous GA level; there is no precedent for such an event and the idea was not tested here.

The inhibition of shoot growth by ethephon is said to be accomplished by an inhibition of "lateral bud opening" (Szyjewicz et al. 1984). However, in this study, ethephon had no effect on burst of prompt buds (i.e. "lateral buds") following shoot topping; lateral shoot numbers were the same on ethephon-treated and control vines. By comparison, ethephon
significantly reduced lateral shoot length, particularly at the distal nodes of topped shoots. Brajkovich and Smart (1983) also reported no reduction of lateral shoot number following ethephon application to 'Shiraz'.

In conclusion, exogenous application of gibberellic acid to 'Shiraz' grapevines induced PBN, the response being almost identical to that reported on 'Queen of the Vineyard' by Lavee et al. (1981b). The degree of susceptibility to GA$_3$-induced PBN appears to be primarily determined by the stage of bud development and to a lesser extent by the stage of shoot development; young still differentiating buds are more susceptible than mature buds, irrespective of shoot age. Exogenous application of GA$_3$ also enhanced the rate of shoot growth and the number and length of lateral shoots.

Other shoot treatments, i.e. thinning, topping and defoliation, also increase shoot vigour and lateral shoot development with a concomitant increase in level of PBN (Chapter 5). In addition, natural PBN is induced during active shoot growth (Chapter 4) with the highest incidence on vigorous vines/shoots (Chapter 3). Therefore, induction of PBN appears to be regulated by the amount of gibberellin that reaches the bud and an increase in endogenous level of gibberellin is associated with an increase in shoot vigour.
Shoot thinning/shoot topping/defoliation of 'Shiraz' grapevines increased the concentration and amount per bud of GA-like substances in primary bud tissue to 3 and 5 times the control levels respectively, within 21 days of treatment. At the same time, mean dry weight of primary buds on treated vines increased to three times of those on control vines. This suggests that a systemic increase in GA activity in above ground parts of the grapevine follows the removal of whole shoots or shoot parts.
The results of investigations reported herein suggest an association between shoot treatment and increased endogenous activity of gibberellins (GAs) in grapevine buds. For example:

(a) Shoot treatment (thinning/topping/defoliation) and exogenous application of GA$_3$ results in extension of the primary bud-axis within two weeks of treatment (Chapter 4). Both treatments significantly increase the level of primary bud-axis necrosis (PBN) in seeded cultivars (Chapters 5 and 6) and decrease yield in the following season by increasing the ratio of secondary to primary shoots (Chapter 8).

(b) GA activity in xylem sap of grapevines increases to a peak at flowering and declines thereafter (Niimi and Torikata 1978); shoot treatment (thinning/topping/defoliation) induces more PBN at flowering than 3 weeks later (Chapter 5).

Increased activity of GAs in subtending buds and/or proximal buds and leaves following defoliation or removal of the shoot tip in both herbaceous and woody plants has been reported (see 1.6.d); however, there are no known reports for the grapevine. Nevertheless, GAs have been detected in both dormant and bursting buds of grapevines by bio-assay techniques (Hagiwara et al. 1980; Mannini and Ryugo 1982).

This chapter describes the results of experiments carried out to test the hypothesis that shoot treatment (thinning/topping/defoliation) of grapevines increases GA activity in the primary bud-axis.
7.2 MATERIALS AND METHODS

7.2.a Experimental design and sampling procedure

(i) Experiment 82/7: This experiment was carried out on 'Shiraz' vines in the Roseworthy College "South" vineyard. Eighteen vines (9, 2-vine plots) were thinned to 20 most vigorous shoots per vine, each shoot topped to 10 nodes and 50% defoliated (no lateral shoot removal) on November 12 (end of flowering). Control vines were untreated (randomised block design, blocked on the basis of butt circumference). Shoot samples were removed 4 and 18 days later: one complete shoot (chosen at random from all shoots on treated vines and from among vigorous shoots only on control vines) was taken from each vine at each time (thus 2 shoots per plot per time) between 7 and 8 am; control shoots were reduced to 10 nodes per shoot. Shoots were immediately placed in plastic bags into a container with ice and transported to the Waite Institute. Shoots were removed singly from the container for sampling of primary bud tissue. Primary bud axes were sampled by first removing the outermost bud scale, cutting off the secondary bud-axis at the base and discarding, removing the next bud scale, cutting off the tertiary bud-axis at the base and discarding, and cutting off the primary bud-axis at the base. The primary bud tissue was immediately dropped into Eppendorf tubes suspended over liquid nitrogen (N). Primary buds from nodes two to nine inclusively were sampled from each shoot giving up to 16 buds per plot per sampling in each tube; the few buds which showed obvious signs of burst were excluded. Tubes were immersed in liquid N for 5 to 10 seconds, then placed in the freezer of a domestic refrigerator. Bud tissue was weighed, and then freeze-dried.

(ii) Experiment 83/1: This experiment was described in 5.2.viii. Treated vines ('Shiraz') were thinned to the 10 most vigorous shoots per vine, each shoot topped to 10 nodes with 100% defoliation (no lateral shoot removal) on November 3 (start of flowering). Shoot samples were removed 8 and 21 days later; unlike 1982, only nodes 7 to 10 inclusively were taken from each of two shoots per vine (chosen as for expt. 82/7) giving 8 shoot segments per plot (4-vine plots) per time. In all other respects, the procedures were identical to Expt. 82/7.

7.2.b Extraction and purification of GAs from bud tissue.

The following procedure was used for both experiments (Coombe, pers.
Within 1 month of sampling:

(i) The tissue was ground with 4 ml distilled water/acetone (4:5) and washed sand until thoroughly macerated then washed with 4 ml of this mixture into a 50 ml centrifuge tube.

(ii) Titrated to pH 9.0 with 3N NH₄OH.

(iii) Centrifuged for 10 minutes at 2000 xg, supernatant removed, transferred to a second 50 ml centrifuge tube.

(iv) Pellet stirred vigorously with 4 ml 2 per cent NH₄HCO₃, centrifuged, and supernatant saved.

(v) Repeat of (iv).

(vi) 6 ml chloroform added to combined supernatants, mixed well, removed and top aqueous layer transferred to a third 50 ml centrifuge tube.

(vii) Chloroform remixed with 2 ml NH₄HCO₃, centrifuged at 2000 xg for 10 minutes, aqueous layer removed from top and added to previous batch.

(viii) pH adjusted to 3.0 with 10 per cent phosphoric acid.

(ix) Partitioned twice with ethyl acetate (10 ml then 5 ml), mixed by Ultra-Turrax and centrifuged for 10 minutes at 2000 xg.

(x) Ethyl acetate solution dried under warm nitrogen, redissolved in 1 ml ethyl acetate, 0.5 ml transferred to fresh tube for storage, remainder retained for paper chromatography.

(xi) Latter was streaked onto acid-washed 3 mm paper (Whatman), and run in descending isopropanol : NH₄OH:H₂O (10:1:1, v/v/v) for 4 hours.

(xii) Paper dried overnight, placed in plastic bag, purged with nitrogen and heat-sealed, then held in refrigerator until used for bio-assay.

7.2.c. Bio-assay

For Expt. 82/7, extracts were bio-assayed in 3 batches, i.e. on 4/2/83, 16/2/83 and 7/5/83 (3 replicates per treatment per sampling date in each batch). For Expt. 83/1, all extracts were bio-assayed on 22/3/84. All paper chromatograms were cut into 10 segments of equal width (Rf values 0-0.1, 0.1-0.2 ... 0.9-1.0) for bio-assay.

The barley endosperm bio-assay employed was as that described by Coombe (1971). Barley seed ('Clipper', W.I. 1980) were soaked in 50 per cent (by volume) H₂SO₄ for 4 hours at room temperature, then washed 10 to 15 times in distilled water, with vigorous shaking to dislodge husks. For the last few rinses, autoclaved (sterile) distilled water was used. Dehusked seed were soaked in sterile water for 20 to 24 hours in the refrigerator. After removal from the refrigerator and prior to cutting, seed were rinsed...
several times in sterile water. Endosperm pieces were prepared by cutting seed transversely 4 mm from the end away from the embryo, using a cutting block described in Coombe et al. (1967). Two pieces were added to each vial after the addition of paper strips and aqueous solution. The vials, 24 by 50 mm, were dry sterilised at 160°C. Portions of chromatography paper were added to vials (for the first bio-assay on 4/2/83, 2 mm and 20 mm strips were used separately to give 2 dilutions; for all subsequent bio-assays, including 1984, 3 mm and 30 mm strips were used). The following aqueous solutions were dispensed into vials: (i) 0.6 ml freshly prepared and autoclaved citrate-phosphate buffer (0.005 M, pH 4.5), (ii) 0.2 ml solution containing 25 ug each of chloramphenicol and streptomycin, (iii) 0.3 ml sterile water. Paper and water blanks were used plus GA₃ (10⁻¹₀, 10⁻⁹, 10⁻⁸ and 10⁻⁷ g per vial) standards (4 replicates of each). Vials were covered with plastic cling-wrap and incubated for 40 to 42 hours at 30°C. After incubation, 0.9 ml of water was added and the refraction of the diluted incubated material was measured with a Waters R4 differential refractometer set to read digitally at maximum sensitivity, and with water in the reference cell. The change in refractometer units was obtained by subtracting the readings obtained with a reagent blank, without endosperm.

7.2.d. Calculation of GA activity

GA activity (as GA₃ equivalents) was determined for each treatment X sampling date replicate by interpolation. Two or 3 mm (= x) and 20 or 30 (= 10x) wide strips were treated as replicates at each Rf value except where:

(i) the 10x value was less than 50 per cent of the x value, in which case inhibition was assumed and only the x value was used;
(ii) the x value was less than 10⁻¹⁰ g GA₃ equivalent value in which case only the 10x value was used.

All GA activity per replicate sample was totalled over all Rf values and expressed as amount of GA per bud and per D.Wt. of bud tissue.

7.2.e. Statistical analysis

GA activity data from Expt. 82/7 and 83/1 was analysed by two-way analysis of variance.
7.3 RESULTS

7.3.a Gibberellin activity

(i) Experiment 82/7: Significant activity of GA-like substances was detected in primary bud-axes of 'Shiraz' at both sampling times for the first bio-assay (Table 7.1). Buds from "treated" (shoot thinning/shoot topping/defoliation) vines had a significantly higher concentration of GA-like substances (1.6 times that of "control" buds per g D.Wt. bud tissue) when sampled 18 days after treatment; however, there was no significant difference when sampled 4 days after treatment (Table 7.1). Twenty-seven and 83 per cent recovery of a 0.2 mg GA₃ standard, with and without bud tissue respectively, was achieved in the first bio-assay. In the second and third bioassays less than 5 per cent recovery was achieved and negligible activity was found in the extracts; these results are therefore excluded.

"Treatment" significantly enhanced GA activity at Rf 0.4 to 0.6 for the second sampling (Fig. 7.1); the 0.2 mg GA₃ standard peaked at Rf 0.5 to 0.6.

(ii) Experiment 83/1: Results were similar to those of the first bio-assay of Expt. 82/7: "Whole-vine treatment" increased the concentration and amount per bud of GA-like substances to 3 and 5 times the "control" levels respectively, at the second sampling time. During the 13-day interval between samples, GA concentration and amount per bud increased 1.3 and 2.5 times respectively on "treated" vines; however, there was no significant increase for buds on "control" vines (Table 7.2).

"Treatment" mainly enhanced GA activity at Rf 0.4 to 0.6 for both sampling times (Fig. 7.2); the 0.2 mg GA₃ standard (without bud tissue) peaked at Rf 0.5 to 0.7.

7.3.b. Bud tissue dry weight

(i) Experiment 82/7: The total dry weight of bud tissue from "treated" vines was 31 per cent higher than that of controls, 18 days after treatment (Table 7.1); the mean weight per primary bud was not recorded but the numbers of buds per sample were about equal.
(ii) **Experiment 83/1**: The mean dry weight per primary bud was 45 and 85 per cent higher on "treated" than "control" vines, 8 and 21 days after treatment respectively (Table 7.2). "Treated" buds increased to three times the dry weight of "control" buds (determined by extrapolation) in the 21 day period after treatment.
Table 7.1 Effect of shoot thinning/shoot topping/defoliation ("Treated") on weight and gibberellin concentration (as GA$_3$ equivalents) of 'Shiraz' primary bud-axes at two sampling times (Expt. 82/7, Bio-assay No. 1)

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Time of Sampling (days after treatment)</th>
<th>Total weight of bud tissue* (mg D.Wt.)</th>
<th>Gibberellin concentration (ng GA$_3$ per g D.wt. bud tissue)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>4</td>
<td>32</td>
<td>221 a</td>
</tr>
<tr>
<td>Treated</td>
<td>4</td>
<td>48</td>
<td>67 a</td>
</tr>
<tr>
<td>Control</td>
<td>18</td>
<td>49</td>
<td>561 ab</td>
</tr>
<tr>
<td>Treated</td>
<td>18</td>
<td>64</td>
<td>1473 b</td>
</tr>
</tbody>
</table>

* Dry wt per bud was not measured but approximates that in Table 8.2. Means followed by the same letter are not significantly different at 5% level.

Table 7.2 Effect of shoot thinning/shoot topping/defoliation ("Treated") on weight and gibberellin activity (as GA$_3$ equivalents) of 'Shiraz' primary bud-axes at two sampling times (Expt. 83/1)

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Time of sampling (days after treatment)</th>
<th>Total weight of bud tissue (mg D.Wt.)</th>
<th>Mean weight per bud (mg D.Wt.)</th>
<th>GA concentration (ng GA$_3$ equiv. per g D.Wt. bud tissue)</th>
<th>GA amount per bud (ng GA$_3$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>8</td>
<td>61</td>
<td>2.0 a</td>
<td>270 a</td>
<td>0.5 a</td>
</tr>
<tr>
<td>Treated</td>
<td>8</td>
<td>84</td>
<td>2.9 b</td>
<td>499 ab</td>
<td>1.4 a</td>
</tr>
<tr>
<td>Control</td>
<td>21</td>
<td>75</td>
<td>2.7 b</td>
<td>245 a</td>
<td>0.7 a</td>
</tr>
<tr>
<td>Treated</td>
<td>21</td>
<td>106</td>
<td>5.0 c</td>
<td>669 b</td>
<td>3.3 b</td>
</tr>
</tbody>
</table>

Means in columns followed by the same letter are not significantly different at 5% level.
Figure 7.1 Histograms derived from extracts of 'Shiraz' primary bud-axes collected from "treated" (shoot thinning/shoot topping/defoliation; left) and control (right) vines 4 days ("first sample"; upper) and 18 days ("second sample"; lower) after treatment. Gibberellin-like substances were assayed by the barley endosperm test on paper chromatograms developed with isopropanol: \( \text{NH}_2\text{OH} : \text{H}_2\text{O} (10:1:1, \text{v/v/v}) \). Means of 2mm strips for each Rf value (0-0.1, 0.1-0.2 ... 0.9-1.0). Experiment 82/7.
Figure 7.2 Histograms derived from extracts of 'Shiraz' primary bud-axes collected from "treated" (shoot thinning/shoot topping/defoliation; left) and control (right) vines 8 days ("first sample"; upper) and 21 days ("second sample"; lower) after treatment. Gibberellin-like substances were assayed by the barley endosperm test on paper chromatograms developed with isopropanol: \( \text{NH}_4\text{OH} : \text{H}_2\text{O} (10:1:1, \text{v/v/v}) \). Means of 3mm strips for each Rf value (0.0, 0.1-0.2 … 0.9-1.0). Experiment 83/1.
In two successive seasons, shoot treatment (thinning/topping/defoliation) of 'Shiraz' grapevines increased the concentration of GA-like substances in the primary bud-axis. The response to treatment was relatively rapid with significant differences in GA concentration and amount per bud from control levels apparent after 18 to 21 days. Coincident with the increase in GA-like concentration was an increase in dry weight of treated buds to three times that of "controls".

One could hypothesize that shoot treatment caused the GA increase which in turn caused the bud growth. Similar results were obtained in response to defoliation of apple trees growing under tropical conditions: removal of subtending leaves resulted in a 3-fold increase in GA concentration (four-fold increase in amount per apex) in apex tissue of closed buds and preceded a marked increase in fresh and dry weight of apex tissue (Taylor et al. 1984). Increased activity of GAs in buds following defoliation or shoot tip removal has been reported for herbaceous and woody plants (see 1.6.d); however, this appears to be the first report for grapevines. The presence of GA activity has been previously reported for dormant and bursting grapevine buds (Hagiwara et al. 1980; Mannini and Ryugo 1982) but not for developing buds.

There are relatively few reports of actual concentrations of GA-like substances in grapevine tissues in general, and none at all known for buds (see 1.7.a.i). In this experiment, concentrations of GAs in primary bud tissue of 'Shiraz' are up to ten times higher than that reported for expanded leaves of 'Corinth' and 'Sultana' (Skene 1967); however, they are comparable with concentrations in apple buds (Taylor et al. 1984).

No major qualitative differences appear to exist between treated and control bud extracts with regard to types of GAs and inhibitors; zones of promotion and inhibition occurred at similar Rf values in each case.

The increase in GA activity in grapevine primary buds in response to shoot treatment (thinning/topping/defoliation) may be explained in terms of either a decrease in number of sinks for root-produced GAs or a decrease in number of mature-leaf sources of GA-inhibitors such as ABA (see 1.6.d.ii); the fact that increase in GA activity occurred concurrently with increase in bud D.Wt. would seem to lend more support for the former.

However, these results should only be taken as indicative and not definitive; the barley endosperm bioassay is responsive to only a small range of gibberellins whereas interpretation requires a more comprehensive understanding of the endogenous gibberellins both qualitatively and quantitatively (Pharis and King 1985).
CHAPTER 8

THE RELATIONSHIP BETWEEN PRIMARY BUD-AXIS NECROSIS AND GRAPE YIELD

ABSTRACT

Shoot thinning, topping and defoliation of whole vines and topping and defoliation of single shoots resulted in an increase in

- number of nodes with multiple shoots
- the ratio of secondary to primary shoots
- and the number of shoots per node,

and a decrease in

- bunch number per shoot
- flower and berry number per bunch
- and bunch weight and yield per node,

during the following season.

These correlated effects could be partly explained by an increased incidence of PBN following these treatments.

Number and size of inflorescences was strongly negatively correlated with presence of PBN at the same node on both treated and control shoots and vines.

Treatments with GA_3 had many of the above effects (increased PBN, decreased bunch number per shoot and per node) but had no effect on shoot number per node.
8.1 INTRODUCTION

The yield of a node retained at pruning can be expressed in terms of its components as follows:

\[
\text{Fruit weight per node (gms)} = \text{shoot number per node} \times \text{bunch number per shoot} \times \left[ (\text{flower number per bunch}) \times \text{berry number per flower number} \times \text{berry weight (gms)} \right] + \text{bunch stem weight (gms)}.
\]

- Bunch number per node (7) is the product of (1) and (2).
- Flower number per node is the product of (7) and (3).
- Berry number per bunch (8) is the product of (3) and (4).
- Bunch weight (gms) (9) is the product of (8) and (5) plus (6).

Of these components only (1), (2) and (3) are affected in the season of treatment and thus expressed in the following season, i.e. **shoot number per node** is potentially determined by the relative degree of development of the primary and secondary axes of the bud and the expression of this component is modified by pruning level; **bunch number per shoot** is potentially determined by the degree of inflorescence primordium initiation per axis and expression may be modified by physiological events during and after budburst; **flower number per bunch** is potentially determined by the extent to which branching of the inflorescence primordium occurs - the greater the amount of branching, the greater is the number of flower primordia that will be initiated just before and during budburst. Therefore, any mention of bud fruitfulness or fertility in this context refers to both number and size of inflorescence primordia. The actual bunch size is determined in the season following inflorescence primordium initiation by degree of fruit set, (i.e. number of berries per flowers), and berry development, (i.e. berry weight).

Relatively few reports have described the effects of shoot treatment (thinning, topping, defoliation) on yield components in the season following treatment. Shoot thinning, and defoliation (May et al. 1969) and GA application (1.7.c.ii) reduces shoot number per node whereas topping to 6 to 10 nodes per shoot has no effect (Peterson and Smart 1975). Topping can either increase or decrease bunch number per shoot or per node, shoot thinning has no effect and defoliation generally decreases bunch number per shoot or per node (1.6.c.ii). Bunch weight and number of berries per bunch are not affected by topping and decreased by shoot thinning or defoliation. Yield per node or per vine is generally decreased by defoliation, may be
decreased by shoot thinning and may be decreased, slightly increased or not affected by topping (1.6.c.iii). \( \text{GA}_3 \) application is known to decrease fruitfulness (bunch number and size) in grapevines and other woody plants (1.7.c.ii).

Until recently, it was thought that the defoliation-induced decrease in "fertility", i.e. inflorescence number and size, (a result of reduced inflorescence primordium initiation and size) was brought about by a decrease in assimilate availability to the developing bud (May et al. 1969); this hypothesis was supported by results from shading experiments (May and Antcliff 1963; Srinivasan and Mullins 1981). However, more recently, it has been suggested that fruitfulness in grapevines and other woody plants is not primarily limited by carbohydrate supply (Monselise and Goldschmidt 1982); in fact, "... the mechanism leading to inflorescence primordium initiation is not closely related to the mechanism of dry weight accumulation (i.e. photosynthesis) despite its requirements for high energy light." (Srinivasan and Mullins, 1981). Also, partial defoliation of grapevines (and other woody plants) does not necessarily result in a large reduction in total assimilate availability within the plant as a whole due to an increased rate of phytosynthesis in the remaining leaves (Buttrose 1966; Hofacker 1978) and mobilisation from starch reserves (May et al. 1969). Certainly, there is a minimum light requirement for inflorescence primordium initiation in grapevines and the improved bud fruitfulness on divided canopies, such as the Geneva Double Curtain, can be attributed to increased light interception by the canopy. Similarly, Peterson and Smart (1975) attributed the increase in bunch number in response to topping to an improved light and temperature environment of the remaining buds (in this case, the canopies of non-treated vines were excessively dense).

A combination of exposure to high temperature and high light intensity appears to be necessary for maximum bud fruitfulness in grapevines (Srinivasan and Mullins 1981). What then is the mechanism by which reduction of leaf area may result in a decrease in bud fruitfulness? In their review of flowering in the grapevine, Srinivasan and Mullins (1981) do not address this question; but, according to their hypothesis concerning the hormonal regulation of "flowering" ("flowering" here is used in its broadest context to include inflorescence primordium initiation), this question would need to be answered in terms of a reduced total cytokinin availability to the developing bud, or a reduction in the cytokinin/gibberellin ratio. Low light intensity has an inhibiting effect on endogenous cytokinin (CK) production; a reduction in leaf area may thus decrease CK levels because less light is intercepted. Alternatively, a
reduction in leaf area may result in a reduction in CK transported from the root system in the transpiration stream (root apices are the major source of CKs in plants and translocation of CKs occurs in the xylem; Skene 1972). However, defoliation and topping have generally been found to increase, rather than decrease, endogenous CK activity in shoots of a range of plants. Nevertheless, or perhaps partial defoliation improves the light environment of buds or subtending leaf at those nodes normally retained at pruning and this changes the hormone balance in the bud in favour of inflorescence primordium initiation. The contribution of leaves to bud fruitfulness is not well understood (Monselise and Goldschmidt 1982); likewise, the mechanism by which cytokinins control "flower" formation is unknown (Srinivasan and Mullins 1981).

A possible alternative to theories involving assimilate production or CKs to account for the decrease in yield following shoot treatment (thinning, topping, defoliation) is discussed in this chapter.
8.2 MATERIALS AND METHODS

Yield component data was derived from experiments for which the Materials and Methods have been described elsewhere, e.g. Expts. 80/2, 80/3, 81/7, 82/3, except for one experiment (82/17).

For Expt. 80/2, shoots per node, bunches per node and bunches per shoot were determined for treated and control shoots (means of nodes 2 to 9) on each vine, in spring 1981. The "bunches" were counted as "inflorescences" before flowering but will hereon be referred to as "bunches".

Similarly, for Expt. 30/3, these components were determined as means of nodes 2 to 9 for treated and control vines for each cultivar, i.e. 'Shiraz', 'Sultana' and 'Pedro Ximenez', in spring 1981. For 'Shiraz' only, flower number per bunch was determined about one week before flowering (see Appendix B for details of method). At harvest 1982, total weight of fruit per vine was measured using the 8 designated 10-node canes (nodes 2 to 9 only). Also, a 100-berry sample per vine (berries selected at random from harvested fruit) was used to determine mean berry weight. Fruit weight per node, bunch weight and berry number per bunch were derived for each vine using these measurements.

For Expt. 81/7, shoots per node, bunches per node and bunches per shoot were determined for each shoot (nodes 2 to 14) in spring 1982.

For Expt. 83/1, shoot number and bunch number per node were determined in spring 1984 at every node position on each of the 4, 10-node canes retained in winter 1984 and bunch number per shoot derived from these. Similarly, the weight of fruit was measured for every node at harvest (March 20, 1985). From the harvested fruit, a 200- berry sample was selected at random to determine mean berry weight per vine. Using these measurements, plus those made in spring 1984, bunch weight per node and berry number per bunch (per vine) were derived; for simplicity in deriving berry number per bunch, bunch stem weight was ignored in the calculation, i.e. it was assumed to be proportionally equal in treated and control vines.

In order to compare the fruitfulness of primary and secondary shoots on 'Shiraz', mean flower number per bunch (see Appendix B for details of method) and bunch number were determined using a random sample of 100 nodes for both treated and control vines in Expt. 80/3.

(i) Experiment 82/17: Aim: To examine the effects of (a) topping all shoots on a vine to 10 nodes with no shoot thinning or defoliation ("hedging") and (b) thinning to 20 most vigorous shoots per vine with no topping or
defoliation ("thinning") on yield in the following season. The eighteen 'Shiraz' vines in the "South" vineyard, Roseworthy College, used in this experiment (randomised block design, 6 blocks, single vine plots; blocking on the basis of butt circumference) had been pruned to 4,15-node canes and 4, 2-node spurs in the previous winter. Hedging (Treatment A) and thinning (Treatment B) were applied on November 15, 1982 (20 visible internodes). No yield component measurements were carried out in the 1982/83 season. In winter 1983, all vines were pruned to 6, 10-node canes and 6, 2-node spurs. Ten shoots (8 in the case of Treatment B), removed at pruning, were used for determination of Bud Index at nodes 2 to 10. Shoots per vine (on count nodes only) were counted at about one month after budburst. At harvest (March 11, 1984), bunch number and fruit weight per vine were measured (count nodes only). From these data and that collected earlier in spring, shoots per node, bunches per shoot, and mean bunch weight were calculated for each vine. Yield per vine and components were analysed by 2-way analysis of variance.
8.3 RESULTS

8.3.a Effect of shoot thinning plus topping and defoliation on yield

(i) 'Shiraz': Yield component results from several experiments (80/3, 81/7, 83/2) are summarised in Table 8.1; in these whole vines were thinned to 20 or 24 shoots per vine and all shoots topped to 10 or 14 nodes and 50 or 100 per cent defoliated. Also included are results from an experiment (80/2) in which treated (topped to 10 nodes plus 50 per cent defoliation) and control shoots were present on the same vine (the vine as a whole had been thinned to 20 shoots).

Relative to untreated controls, whole vine treatment increased shoots per node and decreased bunches per shoot, the end result being no effect on bunches per node. By comparison, shoot treatment decreased shoots per node, bunches per shoot and consequently bunches per node, relative to control shoots (80/2). This difference is not so much a result of differences between shoot treatment and whole vine treatment, but rather that untreated (control) shoots on shoot-thinned vines have more shoots per node than comparable shoots on non-thinned vines.

Whole vine and shoot treatment resulted in smaller bunches (fewer flowers per bunch) and consequently fewer flowers per node. With fewer flowers per bunch, the potential therefore existed for fewer berries per bunch, assuming no large differences in set between treated and control vines. In fact, whole vine treatment did result in smaller bunches, due to fewer berries per bunch, with no effect on berry weight. As a result, relative to control vines, whole vine treatment resulted in a reduction in fruit weight per node of 40 to 45 per cent.

The results above refer to means of eight or more nodes per shoot, whereas the effect of whole vine shoot treatment was examined at different node positions in Expt. 83/1. Relative to control vines, shoot treatment significantly increased shoots per node, and decreased both bunches per shoot and bunch weight primarily at the distal node positions, i.e. nodes six to 10 (Figs. 8.1.a, b, c). The increase in shoots per node was not sufficient to compensate for the decrease in bunch number and size and, as a result, fruit weight per node was less on treated vines at all nodes (Table 8.1) but significantly only for nodes 8, 9 and 10 (Fig. 8.1.d).
(ii) 'Sultana' and 'Pedro Ximenez': For 'Sultana', whole vine treatment had the same effect as for 'Shiraz' (Table 8.2). However, in the case of 'Pedro Ximenez', although treatment also increased shoots per node, there was no corresponding significant decrease in bunches per shoot, with the result that treatment increased bunches per node.

8.3.b. Effect of time of shoot treatment (topping to 10 nodes plus 50 per cent defoliation) on yield components

Shoot treatment was applied at 3 different stages of shoot development in Expt. 80/2 i.e. 16, 22 and 29 visible internodes per shoot, with treated and non-treated (control) shoots on the same vines. The following yield components were measured for each of the six treatments (i.e. time x shoot treatment combinations): shoots per node, bunches per shoot and per node, flowers per bunch and per node. There was no significant difference between any time for any variable for either treatment or control. Likewise, when data were pooled over shoot treatment, there was no significant effect of timing; however, there was a tendency for a decrease in both bunches per shoot and number of flowers per bunch with later time of treatment (data pooled over time is presented in Table 8.1).

8.3.c. Effect of gibberellic acid (GA_3) application on shoots per node, bunches per shoot and bunches per node

Shoots treated with GA_3 (applied via petiole at node six) had fewer bunches per shoot and per node than un-treated shoots, independent of the effect of shoot treatment (topping to 14 nodes plus 100 per cent defoliation). While GA_3 and shoot treatments appear to have opposing effects on shoots per node, neither was significantly different from control. The effect of GA_3 treatment on bunch number per shoot was much greater than that of shoot treatment, and, in combination, there was no additive 'effect'. (Table 8.3)

8.3.d. Effect of shoot thinning plus topping and defoliation on fertility of primary and secondary* shoots

* Primary and secondary shoots are defined as originating from the primary bud-axis and secondary bud-axes respectively.
Primary shoots had more bunches per shoot than secondary shoots on both treated and control vines of 'Shiraz', 'Pedro Ximenez' and 'Sultana' (Tables 2.8, 8.4) and more flowers per bunch and thus more flowers per shoot on both treated and control vines of 'Shiraz' (Table 8.4).

Primary shoots on treated vines had fewer bunches per shoot and fewer flowers per bunch and per node than those on control vines, whereas there was no significant difference between secondary shoots on treated and control vines (Table 8.4).

8.3.e Relationship between primary bud necrosis (PBN) and fertility

The natural levels of PBN in control vines from Expt. 80/3 at proximal (2 to 5) and distal (6 to 9) nodes are compared with the mean bunches per shoot and mean bunch weight for nodes in Table 8.5. There was a tendency for high natural levels of PBN to be associated with low node fertility, and vice versa.

8.3.f. Effect of hedging and shoot thinning on yield per vine in the following season

Hedging (topping all shoots to 10 nodes, no shoot thinning or defoliation, topping carried out once only) reduced vine yield by 10 per cent relative to control in the following season (but not significant at 5 per cent level); hedged vines had more shoots per vine, due to more shoots per node (not significant) although there were fewer bunches per shoots (significant at 5 per cent level) and smaller bunches (not significant).

By comparison, thinning to 20 shoots per vine (no topping or defoliation), reduced vine yield by 23 percent relative to control. More shoots per node on thinned vines compensated for fewer bunches per shoot so that bunch number per vine was not affected, relative to control. However, bunches were significantly smaller, resulting in an overall reduction in yield per vine (Table 8.6).

Thinning and hedging both increased levels of PBN (Table 8.6).
Table 8.1 Summary of the effect of shoot treatment (thinning, topping, defoliation) on yield components in the following season of 'Shiraz'.

<table>
<thead>
<tr>
<th>Shoots per node</th>
<th>Control</th>
<th>Treated</th>
<th>Control</th>
<th>Treated</th>
<th>Control</th>
<th>Treated</th>
<th>Control</th>
<th>Treated</th>
<th>Control</th>
<th>Treated</th>
<th>Control</th>
<th>Treated</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1)</td>
<td>0.82</td>
<td>1.26</td>
<td>0.96</td>
<td>1.16</td>
<td>*</td>
<td>*</td>
<td>0.85</td>
<td>1.19</td>
<td>1.29</td>
<td>1.06</td>
<td></td>
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<tr>
<td>Bunches per shoot</td>
<td>Control</td>
<td>2.35</td>
<td>1.73</td>
<td>1.88</td>
<td>1.58</td>
<td>*</td>
<td>1.68</td>
<td>1.92</td>
<td>2.04</td>
<td>1.82</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(2)</td>
<td>Treated</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Bunches per node</td>
<td>Control</td>
<td>1.88</td>
<td>2.18</td>
<td>1.84</td>
<td>1.90</td>
<td>*</td>
<td>1.92</td>
<td>2.63</td>
<td>1.92</td>
<td>1.92</td>
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<tr>
<td>(1) x (2) = (3)</td>
<td>Treated</td>
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</tr>
<tr>
<td>Flowers per bunch</td>
<td>Control</td>
<td>610</td>
<td>424</td>
<td>610</td>
<td>424</td>
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<td></td>
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<tr>
<td>(4)</td>
<td>Treated</td>
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<td></td>
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<tr>
<td>Flowers per node</td>
<td>Control</td>
<td>1147</td>
<td>914</td>
<td>1147</td>
<td>914</td>
<td></td>
<td></td>
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<tr>
<td>(3) x (4) = (5)</td>
<td>Treated</td>
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<td></td>
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</tr>
<tr>
<td>Berries per bunch</td>
<td>Control</td>
<td>151</td>
<td>93</td>
<td>151</td>
<td>93</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>(6)</td>
<td>Treated</td>
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<tr>
<td>Berry weight (gms)</td>
<td>Control</td>
<td>1.02</td>
<td>1.05</td>
<td>1.05</td>
<td>1.05</td>
<td>*</td>
<td>1.18</td>
<td>1.19</td>
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</tr>
<tr>
<td>(7)</td>
<td>Treated</td>
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</tr>
<tr>
<td>Bunch weight (gms)</td>
<td>Control</td>
<td>154</td>
<td>98</td>
<td>154</td>
<td>98</td>
<td>*</td>
<td>163</td>
<td>107</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>(6) x (7) = (8)</td>
<td>Treated</td>
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</tr>
<tr>
<td>Fruit weight per node (gms)</td>
<td>Control</td>
<td>289</td>
<td>214</td>
<td>289</td>
<td>214</td>
<td>*</td>
<td>210</td>
<td>165</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(3) x (8) = (9)</td>
<td>Treated</td>
<td></td>
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</tbody>
</table>

a, c Treated = whole vine thinned to 20 shoots, topped to 10 nodes (a) 50% or (b) 100% defoliation; control = no treatments. Nodes 2 to 9 (a); 1 to 10 (c).

b Treated = whole vine thinned to 24 shoots, topped to 14 nodes, 100% defoliation; control = thinned to 24 shoots, no other shoot treatments. Nodes 2 to 14.

d Treated = thinned to 12 shoots, topped to 10 nodes, 50% defoliation; control = thinned to 12 shoots, no other shoot treatments. Control shoots on same vine; all times pooled. Nodes 2 to 9.

*, ** indicates means significantly different at 5 and 1% level respectively; ns, not significant at 5% level.
Table 8.2 Effect of shoot treatment (thinning, topping, defoliation) on shoots per node, bunches per shoot and bunches per node in the following season of 'Pedro Ximenez' and 'Sultana' (Expt. 80/3).

<table>
<thead>
<tr>
<th></th>
<th>Shoots per node</th>
<th>Bunches per shoot</th>
<th>Bunches per node</th>
</tr>
</thead>
<tbody>
<tr>
<td>'Pedro X'</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>0.95*</td>
<td>1.25</td>
<td>1.20**</td>
</tr>
<tr>
<td>Treated</td>
<td>1.43</td>
<td>1.10ns</td>
<td>1.58</td>
</tr>
<tr>
<td>'Sultana'</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>0.77*</td>
<td>0.48</td>
<td>0.38ns</td>
</tr>
<tr>
<td>Treated</td>
<td>0.94</td>
<td>0.40</td>
<td>0.38ns</td>
</tr>
</tbody>
</table>

a Nodes 2 to 9.
** indicates means significantly different at 5 and 1% level respectively; ns, not significant at 5% level.

Table 8.3 Effect of GA$_3$ application via petiole and shoot treatment (thinning, topping, defoliation) on shoots per node, bunches per shoot and bunches per node in the following season (Expt. 81/7, 'Shiraz').

<table>
<thead>
<tr>
<th>Treatment$^a$</th>
<th>GA$_3$ shoot treatment $^b$</th>
<th>Shoots per node</th>
<th>Bunches per shoot</th>
<th>Bunches per node</th>
</tr>
</thead>
<tbody>
<tr>
<td>-</td>
<td>0</td>
<td>1.04 ab</td>
<td>2.39 a</td>
<td>2.49 a</td>
</tr>
<tr>
<td>-</td>
<td>10</td>
<td>0.87 b</td>
<td>1.37 c</td>
<td>1.19 b</td>
</tr>
<tr>
<td>+</td>
<td>0</td>
<td>1.37 a</td>
<td>1.90 b</td>
<td>2.60 a</td>
</tr>
<tr>
<td>+</td>
<td>10</td>
<td>0.95 ab</td>
<td>1.86 bc</td>
<td>1.20 b</td>
</tr>
</tbody>
</table>

Pooled over

<table>
<thead>
<tr>
<th>GA$_3$ shoot treatment</th>
<th>Shoots per node</th>
<th>Bunches per shoot</th>
<th>Bunches per node</th>
</tr>
</thead>
<tbody>
<tr>
<td>- pooled over</td>
<td>0.96ns</td>
<td>1.88*</td>
<td>1.84ns</td>
</tr>
<tr>
<td>+ pooled over GA$_3$</td>
<td>1.16 ns</td>
<td>1.58</td>
<td>1.90</td>
</tr>
<tr>
<td>Pooled over shoot</td>
<td>0.91ns</td>
<td>2.14*</td>
<td>2.55*</td>
</tr>
</tbody>
</table>

a Pooled over ABA
b Nodes 2 to 14
** indicates means significantly different at 5 and 1% level respectively; ns, not significant at 5% level

Means in same column followed by same letter are not significantly different at 5% level.
Table 8.4  Flowers per bunch, bunches per shoot and flowers per shoot on primary (P) and secondary (S) shoots on shoot treated (thinning, topping, defoliation) and control vines of 'Shiraz' (Expt. 80/3). (i) Nodes where both primary and secondary shoot present together; (ii) Nodes where either primary or secondary shoot present, but not both together.

<table>
<thead>
<tr>
<th>Yield Component a</th>
<th>Shoot type</th>
<th>(i) Control</th>
<th>(i) Treated</th>
<th>(ii) Control</th>
<th>(ii) Treated</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flower number</td>
<td>P</td>
<td>660</td>
<td>450 *</td>
<td>590</td>
<td>530 ns</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>390</td>
<td>370 ns</td>
<td>380</td>
<td>410 ns</td>
</tr>
<tr>
<td>Bunch number</td>
<td>P</td>
<td>2.9</td>
<td>2.2 *</td>
<td>3.1</td>
<td>2.3 *</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>1.8</td>
<td>1.8 ns</td>
<td>2.0</td>
<td>2.0 ns</td>
</tr>
<tr>
<td>Flower number</td>
<td>P</td>
<td>1914</td>
<td>990 *</td>
<td>/%24q</td>
<td>1219 *</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>702</td>
<td>666 ns</td>
<td>760</td>
<td>820 ns</td>
</tr>
</tbody>
</table>

* Minimum of 40 shoots
** indicates means significantly different at 5 and 1% level respectively; ns, not significant at 5% level.

Table 8.5  Relationship between Bud Index and fertility (bunch number per shoot, bunch weight) at proximal (1 to 5) and distal (6 to 10) nodes on control vines of 'Shiraz' and 'Sultana' (Expts. 80/3, 83/1).

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Variable</th>
<th>Proximal nodes</th>
<th>Distal nodes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shiraz</td>
<td>Bud Index a</td>
<td>14</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Bunches per shoot (i) a</td>
<td>2.15</td>
<td>2.55</td>
</tr>
<tr>
<td></td>
<td>(ii) b</td>
<td>1.39</td>
<td>1.72</td>
</tr>
<tr>
<td></td>
<td>Bunch weight gms b</td>
<td>120</td>
<td>210</td>
</tr>
<tr>
<td>Sultana</td>
<td>Bud Index a</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Bunches per shoot a</td>
<td>0.31</td>
<td>0.66</td>
</tr>
</tbody>
</table>

a Means of nodes 2 to 5 (proximal) and 6 to 9 (distal) from Expt. 80/3.
b Means of nodes 1 to 5 (proximal) and 6 to 10 (distal) from Expt 83/1.
Table 8.6 Effect of (a) topping all shoots to 10 nodes (hedging) and (b) thinning to 20 shoots per vine (thinning) on Bud Index and yield per vine in the following season (Expt. 82/17, 'Shiraz').

<table>
<thead>
<tr>
<th>Variable</th>
<th>Hedging</th>
<th>Thinning</th>
<th>Control</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bud Index</td>
<td>17 ab</td>
<td>24 a</td>
<td>10 b</td>
</tr>
<tr>
<td>Nodes per vine</td>
<td>72</td>
<td>72</td>
<td>72</td>
</tr>
<tr>
<td>Shoots per node</td>
<td>0.96 ab</td>
<td>1.13 a</td>
<td>0.80 b</td>
</tr>
<tr>
<td>Bunches per shoot</td>
<td>1.31 b</td>
<td>1.17 b</td>
<td>1.58 a</td>
</tr>
<tr>
<td>Bunches per vine</td>
<td>90.7 a</td>
<td>95.0 a</td>
<td>90.7 a</td>
</tr>
<tr>
<td>Bunch weight (gms)</td>
<td>152.0 ab</td>
<td>124.1 b</td>
<td>168.2 a</td>
</tr>
<tr>
<td>Fruit weight per vine (kg)</td>
<td>13.8 ab</td>
<td>11.8 b</td>
<td>15.3 a</td>
</tr>
</tbody>
</table>

1 Means of 6 replicates; count node data only.
Means in same row followed by same letter are not significantly different at 5% level.
Fig. 8.1 Effect of shoot treatment to whole vines on yield components in the following season by node position (Expt. 83/1). Shoot treatment - thinned to 20 shoots per vine, topped to 10 nodes plus 100% defoliation (○); control vines (●). (a) Shoot number; (b) mean bunches per shoot; (c) mean bunch weight (gms); (d) fruit weight (gms).
* indicates means at same node are significantly different at 5% level.
8.4 DISCUSSION

Reducing shoot number per vine to around 20, with none, some or all of the shoots topped and defoliated, resulted in an increase in the number of shoots per node in the following season. Shoot topping alone also increased shoots per node, but to a much lesser extent.

The increase in shoots per node was neither a result of any differences in node number between treated and control vines, nor an increase in the number of nodes which burst (Chapter 2); rather, it was a consequence of an increase in the number of nodes with two or more shoots per node. For example, thinning and topping of 'Shiraz' resulted in a 4-fold increase in such nodes relative to the untreated control (Chapter 2). At the same time, there was also an increase in the proportion of secondary shoots, arising from the secondary bud axes, i.e. an increase in the secondary/primary shoot ratio (Chapter 3).

One or more secondary axes burst if the primary axis at that node had aborted. If it was simply a matter of sufficient secondary axes bursting to compensate for necrotic primary axes, then one would not expect any difference in shoots per node in response to treatment, i.e. at every node with a necrotic primary axis, a secondary axis would burst instead. However, that this does not happen is shown by the increase in shoots per node. Secondary axes are better developed on treated than control shoots (Chapter 4), and nodes where the primary axis is necrotic are most likely to have two or more shoots. Consequently, shoot topping increased the proportion of buds with PBN and of nodes with multiple shoots, most significantly at the distal nodes (Chapter 2).

The primary axis must abort quite early for the secondary axes to develop more than normal in the absence of the primary axis, i.e. before the development of the secondary axes is greatly advanced (Chapter 4), and the secondary axes thus have better development than normal to compensate for the aborted primary axis.

Shoot thinning and topping, alone or in combination, on a whole vine basis or shoot topping and defoliation on a per shoot basis, resulted in a decrease in bunch number per shoot. These treatments result in a reduction in leaf area per vine or per shoot. From previous reports, one would tend to conclude that the reduction in bunches per shoot was a direct result of the reduction in leaf area via effects on cytokinin and/or carbohydrate levels. Indeed, in Expt. 82/17, greater reduction in leaf area per vine resulted in greater reduction in bunch number per shoot. Also, May et al. (1969) found a positive correlation between leaf area per vine and bunch number per shoot.
However, there are a number of reasons why the results in this case cannot simply be explained in terms of cytokinin or carbohydrate level. The decrease in bunch number per shoot in response to thinning, topping and defoliation is a result of two factors:

(i) The secondary/primary shoot ratio is higher for treated vines and shoots. Also, secondary shoots have fewer bunches per shoot, irrespective of treatment; the lower fertility of secondary shoots has been previously reported (see 1.3.d).

When the primary axis aborts, the secondary shoots do not appear to become more fruitful on treated vines (Table 8.4) even though secondary axes appear to develop more than normal (Chapter 4). However, secondary axes may become more fruitful than normal on treated vines but this is not expressed; on control vines the only secondary axes likely to burst are the most fruitful whereas on treated vines secondary axes will have a whole range of fertilities, being forced to burst in the absence of a primary axis - therefore, the bunches per shoot figure for secondary shoots may be biased in favour of control vines.

(ii) The primary shoot component of the treated vine shoot population arises mainly from those nodes which are the least affected by treatment, i.e. the proximal nodes. For most cultivars, in particular for 'Sultana', and also, to a lesser extent, 'Shiraz', the proximal nodes, i.e. nodes 1 to 5 of a 10 node cane, are the least fruitful. Therefore, because "treatment" induces the highest levels of PBN at the normally most-fruitful nodes, the primary shoots of treated vines mainly arise from the proximal, least fruitful nodes compared to control vines, for which primary shoots arise from both proximal and distal nodes; in fact, if the natural level of PBN is high, more primary shoots will arise from distal (most fruitful) than proximal nodes in controls. Therefore, the net result is lower bunches per shoot for primary shoots on treated vines relative to control (Table 8.4).

If the reduction in bunches per shoot was simply a result of reduction in assimilate availability arising from partial defoliation, then one would not expect a major change in the secondary/primary shoot ratio. Also, one would not expect a decrease in bunches per shoot for just the distal nodes; at the time that treatment was carried out for most of the cases in Table 8.1, i.e. flowering, inflorescence primordium initiation would have still been in progress in buds at proximal nodes (Srinivasan and Mullins 1981).
and thus should also have been affected. Finally, if it is simply a question of assimilate availability, then why should treated shoots produce fewer bunches per shoot than non-treated shoots on the same vine? One might expect some compensatory translocation from foliated to defoliated shoots. Also, for the reasons outlined previously, it is difficult to explain the change in ratio of secondary to primary shoots, in terms of reduced cytokinin activity.

For the reasons outlined for bunch number per shoot, flower number and berry number per bunch and bunch weight are also reduced by shoot thinning and/or topping plus defoliation, i.e. inflorescence size, and consequent bunch size are smaller on secondary shoots compared to primary shoots. Bunch size is reduced only at distal nodes.

Overall, yield per node or per vine was mainly reduced by effects on bunch number per shoot and bunch size components. Shoot thinning reduced yield more than hedging, largely because of a greater increase in secondary to primary shoot ratio. By comparison, a similar hedging experiment, also with 'Shiraz', had either no effect on yield or caused a slight increase in yield in the following season (due to a slight increase in bunch number per shoot) when carried out at Griffith (Peterson and Smart 1975). The explanation for the difference in response may be that the vines at Griffith had higher vigour than those at Roseworthy; hedging, in the former case, resulted in an improved microclimate with better radiation interception by interior shoots, which probably offset any potential reduction in assimilate availability (or cytokinin level?). The vines at Roseworthy, with lower vigour, had a good canopy microclimate to begin with and thus did not respond in the same way.

GA\textsubscript{3} application also resulted in a reduced bunch number per shoot. Presumably, this is the result of two different effects; (a) a direct effect of GA\textsubscript{3} on inflorescence initiation, favouring the tendril development pathway (Srinivasan and Mullins 1981) and (b) an indirect effect via GA-induced PBN and a consequent increase in the secondary/primary shoot ratio. That GA\textsubscript{3} application should cause a greater reduction in bunch number per shoot than shoot treatment is thus to be expected. Although GA\textsubscript{3} application has been previously reported as causing reduced bunch number per shoot for a number of cultivars (1.7.c.ii), this appears to be the first report for 'Shiraz'.

The decrease in fertility, i.e. bunch number per shoot and bunch size, associated with an increase in PBN level on treated vines and shoots is paralleled by the negative correlation between PBN and bud fertility under natural conditions; nodes at which bud fertility is low tend to have the
highest incidence of PBN, i.e. the proximal 5 nodes or so. Lavee et al. (1981a) also noted this relationship and suggested that "... the endogenous conditions which lead to low inflorescence differentiation also initiate processes leading to necrosis of the central buds (i.e. primary axis) ...". They suggested that the balance of endogenous growth regulators, and particularly high gibberellin levels, might be responsible for both reduced inflorescence initiation and initiation of necrosis of the primary axis.

The decrease in bunch number and size, which often follows treatment of shoots is considered to be a result of a decrease in leaf area and also an increase in the secondary/primary shoot ratio. The former is a well-accepted phenomenon and may be mediated by a decrease in assimilate availability or cytokinin activity or both. The latter has not previously been appreciated as a contributory factor. However, Carbonneau and Casteran (1979) attributed an irrigation-depressing effect on fertility to an increase in the ratio of secondary to primary shoots, resulting from the irrigation-induced increase in vine vigour.

There may be a number of cases described in the literature where the decrease in fertility in the following season has been attributed solely to a decrease in leaf area and consequent effects on assimilate availability, whereas that decrease may have been contributed to by an increase in the incidence of PBN and thus secondary/primary shoot ratio. Similarly, there are many cases where a decrease in bud fertility resulting from an increase in vine vigour (due to the use of irrigation, rootstocks, etc.) has been attributed to an increase in canopy shading and consequent decrease in light interception by basal nodes; in these cases the increase in vine vigour may have been accompanied by an increase in PBN level (see Chapter 3) and the decrease in fertility may be due in part to this factor. Finally, the decrease in fertility resulting from GA3 application, particularly in seeded cultivars, may not be solely the result of a promotion of the tendril pathway of Anlagen development.

This work points to a significant detrimental reaction to grapevine productivity which may follow the use of viticultural techniques designed to increase shoot vigour on the one hand and to reduce the number of leaves for a variety of purposes on the other. Both groups of techniques are commonly used in modern viticulture, but need reassessment in the light of the negative effects caused by increased PBN.
CHAPTER 9

INTEGRATIVE DISCUSSION
CHAPTER 9

INTEGRATIVE DISCUSSION

This research investigated an abnormality of *Vitis vinifera* wherein the primary bud-axis of the compound bud aborts and becomes necrotic while the "secondary"* bud-axes remain healthy and develop more than those in unaffected buds. The abnormality has been termed Primary Bud-axis Necrosis (PBN) in this thesis.

The existence of PBN was first noted when buds were examined in the winter of 1980, following a severe hail-storm in the spring of 1979. Buds with PBN were found on hail-damaged shoots but the death of the primary bud could not be directly attributed to direct hail-damage because such buds were externally normal. Therefore, it appeared that a degree of physiological stress, caused by the hail-storm damage, resulted in induction of PBN. A series of experiments subsequently conducted during the 1980-81 season (described in Chapter 2) confirmed that artificial duplication of hail damage induced PBN; the treatments were: removal of approximately two-thirds of shoots, topping to ten nodes, and 50 to 100 per cent defoliation. In addition, these "shoot treatments" increased the secondary/primary shoot ratio in the following season. The cultivar Shiraz was found to be particularly responsive to induction of PBN by shoot treatment and the natural levels of PBN were found to be high in this cv. (Chapter 3). Therefore 'Shiraz' was used for most of the experiments described in this thesis.

Natural levels of PBN were found to be high in nodes one to six (from the base of the shoots) and positively correlated with shoot vigour (main shoot length and diameter, and number and length of lateral shoots) and vine vigour (butt circumference and pruning weight); nodes with lateral shoots had up to a four-fold greater incidence of PBN than nodes without lateral shoots (Chapter 3). 'Shiraz' had the highest natural levels of all cultivars studied with up to 30 per cent of nodes on vigorous vines with PBN. Lavee *et al.* (1981a) found a similar correlation between vine vigour and the incidence of a bud abnormality which they termed "bud necrosis".

"Bud necrosis", natural PBN and induced PBN appear anatomically identical as described in Chapter 4. Necrosis commences soon after flowering and is largely completed by mid-summer, for both natural and induced PBN.

* "Secondary" includes secondary, tertiary and quaternary bud-axes; also known as "accessory" buds.
The effects of summer pruning treatments, applied to individual shoots and to whole vines, on induction of PBN are described in Chapter 5. The level of induced PBN was directly proportional to the severity of shoot thinning, shoot topping or defoliation, applied singly or in combination. Shoot thinning and shoot topping induced more PBN than defoliation. Unlike defoliation, shoot thinning and topping both resulted in a reduction to the number of main growing points per vine; therefore, any degree of thinning or topping has the potential of affecting all shoots on a vine. For example, topping as few as five shoots out of about seventy increased the level of PBN on untreated shoots. Also, defoliation had less effect than either shoot thinning or shoot topping on the release of lateral shoots from correlative inhibition and the correlation between lateral shoot development and induction of PBN appears to be significant. For example, topping shoots to 10 nodes caused significantly more PBN and greater lateral development at distal nodes eight to ten whereas shoot thinning to 20 shoots per vine increased PBN level and lateral shoot development at all nodes tested (i.e. two to ten). Also, under natural conditions, nodes with lateral shoots had greater incidence of PBN than nodes without and levels of PBN were highest on vigorous shoots which have more lateral shoots (particularly at nodes one to six where natural levels of PBN are highest).

It is possible that the relationship between lateral shoot development and induction of PBN is a causal one, i.e. the lateral shoot competes with its axillary bud for assimilates or growth factors. However, there is more evidence in favour of an association between lateral development and induction of PBN. It is proposed that the node as a whole receives a growth stimulus with the lifting of apical dominance; this is expressed as an increase in development of the lateral shoot. At the same time, the primary bud-axis is forced into a degree of elongation growth; primary bud-axes on "shoot-treated" vines had 60 to 80 per cent greater D.Wt. and longer primordial internodes after 14 days compared to those on control vines (Chapter 4). However, the presence of the actively-growing lateral shoot provides a strong source of correlative inhibition which prevents continued development and burst of the primary bud, and hence it aborts. If the lateral shoot is removed, the subtended primary bud is able to continue development and burst, in the absence of this correlative inhibition (1.1.e.i). Primary buds are able to burst in the absence of correlative inhibition up to the time when the buds go into endo-dormancy (organic dormancy). Therefore, buds are presumably susceptible to induction of PBN up to this time as well.

Fournioux and Bessis (1982) offered a similar explanation to account
for their observation of so-called "debourre" buds following a hail-storm at flowering; they suggested that the primary buds started the bud-burst process with some bud expansion and partial separation of bud scales. However, sources of correlative inhibition (more distal lateral shoots in this case) prevented any further development of the primary buds. In the following winter, "debourre" buds were found to have a dead primary bud and healthy "secondary" buds. Shoots in the following spring were derived from "secondary" buds. Therefore, it seems likely that "debourre" buds are a form of PBN.

The greater the number of growing points removed, the greater the stimulus over the whole vine and thus the greater the number of buds with PBN. Buds most susceptible to PBN are found at those nodes most likely to undergo a growth stimulus, e.g. at distal nodes on topped shoots.

Lavee et al. (1981b) reported induction of "bud necrosis" by exogenous application of GA₃ in Israel. This led to a series of experiments described in Chapter 6 in which the effects of exogenous GA₃ and other growth regulators on the development of PBN were examined. Exogenous application of GA₃ induced PBN in the seeded cultivar Shiraz but not in the seedless cultivar Sultana. The anatomy of buds with PBN induced by "shoot treatment" and GA₃ was identical (with the exception of slightly more primary axis elongation in the latter case). The level of induced PBN was directly proportional to GA₃ concentration and severity of "shoot treatment". For both GA₃ application and "shoot treatment", highest levels of PBN were induced by treatment applied near flowering with the response diminishing with later treatment; GA₃ and "shoot treatment" induced up to 100 and 80 per cent PBN respectively on treated shoots.

It is proposed that induction of PBN is associated with high levels of gibberellin activity in the shoot and available to developing buds leading to premature elongation of the primary bud-axis and subsequent abortion. Exogenous GA₃ application is known to cause grapevine bud internode elongation (1.7.c.ii). The increased availability of GAs to the node also stimulates lateral shoot development. It is further proposed that shoot thinning, topping and defoliation decrease the number of potential sinks for root-produced GAs; young leaves and shoot apices are strong sinks for root-produced GAs and their removal increases the availability to other sinks such as axillary buds (1.6.d.ii). Roots are known to be a major site of GA synthesis (1.7.b); however, there is some doubt as to the actual proportion of total GAs in the plant that are produced by the roots (unlike cytokinins for which there is considerable evidence that the roots are a major synthetic site - 1.7.b). There are several alternative hypotheses to
account for the proposed increased availability of GAs in response to "shoot treatment":

(a) A cytokinin-mediated release from correlative inhibition preceding an increase in GA activity (1.6.d.ii).

(b) Mature leaves as a source of ABA and other inhibitors and hence their removal allows GA activity in the bud to increase (1.6.d.ii).

(c) Apically-produced auxin, moving basipetally, induces accumulation of ABA in axillary buds. Removal of the shoot apex decreases ABA activity indirectly allowing an increase in GA activity, resulting in lateral shoot development and extension of the primary bud-axis following release from inhibition (1.6.d.ii).

Additional evidence in favour of involvement of endogenous GAs in induction of PBN is:

(a) Vigorous vines show the greatest response to "shoot treatment"; such vines probably have higher levels of active GAs.

(b) Shoot thinning increases rate of growth of remaining shoots; increased endogenous GA activity is associated with increase in shoot growth rate;

(c) In seedless cultivars, there is no significant increase in PBN in response to either "shoot treatment" or GA_3 application. Endogenous levels of GAs may be lower in seedless cultivars than seeded and hence the above treatments do not increase endogenous GAs to supra-optimal and thus inductive levels, as is proposed for seeded cultivars.

(d) PBN is induced during the period of active shoot growth under natural conditions. The level of endogenous GA activity increases from the start of active shoot growth, reaching a peak after flowering, then decreasing when shoot growth ceases (1.7.a). Similarly, the highest levels of PBN are induced by treatments applied near flowering with the response diminishing with later treatment.

(e) Neither trunk nor shoot girdling had any significant effect on "shoot treatment"-induced PBN, perhaps because there was no effect on xylem-translocated GAs from the root system.

(f) Topping and/or defoliation of relatively few shoots on a vine induced the occurrence of increased levels of PBN on the other untreated shoots. The likely origin of this translocated effect is hormonal and, in this instance, GAs are proposed.

The number of lateral shoots per main shoot is more strongly correlated with level of PBN than mean lateral shoot length; both "shoot treatment" and GA_3 application affected lateral number proportionally more than lateral length. CCC and ethephon, exogenously-applied in an attempt to decrease endogenous GA activity in "shoot treated" vines, did not decrease
PBN level. It is perhaps significant that both CCC and ethephon decreased mean lateral shoot length but had no effect on lateral shoot number. Possibly the development of a lateral shoot beyond a critical stage is essential for induction of PBN at the same node and the final length of the lateral shoots is not important; the initial development of the lateral shoot may be essential to provide the source of correlative inhibition to suppress further primary bud development at that node.

The degree of susceptibility to induced PBN appears to be primarily determined by the stage of bud development and, to a lesser extent, by the stage of shoot development: young, still differentiating, primary buds are more susceptible than mature. On a vigorous shoot, the period of susceptibility may be more prolonged than the same node position on a less vigorous shoot.

Under natural conditions, nodes one to six have a higher incidence of PBN than more distal nodes; development of buds at these nodes is coincidental with active shoot growth and high endogenous levels of GAs. Furthermore, Lavee et al. (1981a) suggest that buds with a high potential for inflorescence differentiation, i.e. buds most likely to be fruitful, have a low tendency to become necrotic; buds at nodes one to six have a higher vigour potential and a lower "reproductive differentiation rate". They further suggest that "... the balance of endogenous growth regulators, and, particularly, high gibberellin levels, might be responsible for the smaller degree of inflorescence differentiation in the lower buds of grapevines and at the same time be involved in the initiation of necrosis in these buds". Similarly, number and size of inflorescences was strongly negatively correlated with presence of PBN at the same node on both treated and control 'Shiraz' vines (Chapter 8). There is considerable evidence in favour of high endogenous levels of GAs favouring the tendril development pathway (Srinivasan and Mullins 1981).

Assuming that the primary bud-axis does abort and becomes necrotic as a result of a gibberellin-induced growth stimulus, then why is it that the "secondary" bud-axes do not become subjected to the same growth stimulus with subsequent abortion? The most likely explanation is that the "secondary" bud-axes are correlative-inhibited by the "stimulated" primary axis (the "secondary" bud-axes are axillary to the basal prophylls of the primary bud-axis). The better-than-normal development of the "secondary" bud-axes in PBN-affected buds is a consequence of the abortion of the primary bud-axis and not a result of a growth stimulus induced by GAs.

The "gibberellin hypothesis" was tested by measuring the changes in
endogenous levels of gibberellins in primary bud-axes following shoot treatment (thinning/topping/defoliation) using the barley endosperm bioassay (Chapter 7). Shoot treatment increased both the concentration of gibberellin-like substances and bud tissue D.Wt. to three times that of controls, 21 days after treatment. These results lend support to the "gibberellin hypothesis"; however, the barley endosperm bioassay is responsive to only a small range of gibberellins and a more thorough qualitative and quantitative study of endogenous gibberellins is necessary for the testing of this hypothesis. Nevertheless, there is a strong positive correlation between endogenous concentration of GAs in primary bud tissue and i) shoot vigour, ii) vine vigour and iii) subsequent development of PBN (Table 9.1). Therefore, if the relationship between endogenous GAs and induction of PBN is not causal, then, there is certainly a strong association.

Shoot thinning, topping and defoliation of whole vines resulted in reduced yield per vine (topping and defoliation of single shoots reduced yield per node) in the following growing season due to fewer and smaller bunches even though shoot number per node and per vine were generally increased (Chapter 8). The increase in shoots per node is significant: at nodes with PBN, there is more than one "secondary" shoot to replace the absent primary shoot, a consequence of the better-than-normal development of "secondary" buds at nodes with PBN.

The reduction in yield per node and per vine is strongly correlated with an increase in both PBN level and the secondary/primary shoot ratio. It is proposed that the increased availability of GAs following "shoot treatment" reduces bunch number and size by: (a) a direct inhibitory effect of GAs on inflorescence initiation and development and (b) an indirect effect via GA-induced PBN and a consequent increase in the secondary/primary shoot ratio. Exogenous application of GA$_3$ reduces yield in the same way.

The reduction in yield which may follow the use of techniques designed to increase shoot vigour (e.g. irrigation, rootstocks) on the one hand, or to decrease the number of leaves and growing points (e.g. hedging, shoot thinning, leaf removal) on the other, may be due in part to increased PBN: this is the first report of this compensatory mechanism in grapevines. It is recommended that the proportion of nodes with multiple shoots and the secondary/primary shoot ratio be determined along with the usual measurements of yield components in situations where an increase in shoot vigour or a summer pruning operation results in a decrease in yield.
Table 9.1  Summary of positive correlations between concentration (ng GA$_3$ per g D.Wt. bud tissue) and amount (ng GA$_3$ per bud) of gibberellin-like substances in primary bud-axes of 'Shiraz' and i) PBN (Bud Index, nodes 7 to 10 ), ii) bud weight (mg D.Wt.), iii) butt circumference (cm), iv) shoot weight (g). Expt. 83/1; "treated" and "control" values pooled.

<table>
<thead>
<tr>
<th></th>
<th>Concentration (ng GA$_3$ per g)</th>
<th>Amount per bud (ng GA$_3$)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>i</strong> PBN (Bud Index)</td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td><strong>ii</strong> Bud weight (mg)</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td><strong>iii</strong> Butt circumference (cm)</td>
<td>ns</td>
<td>*</td>
</tr>
<tr>
<td><strong>iv</strong> Shoot weight (g)</td>
<td>**</td>
<td>**</td>
</tr>
</tbody>
</table>

1 Bud Index determined in following winter on same vines.

*,**,*** indicates r value is significant at 5, 1 and 0.1% level respectively; ns = not significant.


Antcliff, A.J., Webster, W.J. and May, P. (1956) Studies on the Sultana vine IV. A pruning experiment with number of canes per vine varied, number of buds per cane constant. Aust. J. Agric. Res. 7: 401-13


Weaver, R.J. (1960) Toxicity of gibberellic acid to seedless and seeded varieties of V. vinifera. Nature 187: 1135-6


Weaver, R.J., Alleweldt, G. and Pool, R.M. (1966) Absorption and translocation of gibberellic acid in the grapevine. Vitis 5: 446-54

Weaver, R.J., Kang, Y-D. and Pool, R.M. (1968) Relation of plant regulators to bud rest in Vitis vinifera grapes. Vitis 7: 206-12


Weaver, R.J. and Pool, R.M. (1965b) Relation of seedlessness and ringing to gibberellin-like activity in berries of Vitis vinifera. Plant Physiol. 40: 770-6


## APPENDIX A

Details of experimental sites

<table>
<thead>
<tr>
<th>LOCATION</th>
<th>OWNER/VINEYARD NAME</th>
<th>CULTIVAR</th>
<th>YEAR OF PLANTING</th>
<th>ROW X VINE SPACING (m)</th>
<th>TRELLIS TYPE</th>
<th>PRUNING METHOD</th>
<th>IRRIGATED</th>
<th>VIGOUR</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>SOUTH AUSTRALIA</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Roseworthy</td>
<td>RAC, &quot;South Vineyard&quot;</td>
<td>Shiraz</td>
<td>1951</td>
<td>3.9 x 3.0</td>
<td>0.45 m or</td>
<td>Spur or cane</td>
<td>Yes</td>
<td>M-H</td>
</tr>
<tr>
<td></td>
<td>&quot;</td>
<td></td>
<td></td>
<td></td>
<td>1.0 m tee</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>RAC, &quot;Home Vineyard&quot;</td>
<td>Sultana</td>
<td>1949</td>
<td>3.9 x 2.4</td>
<td>0.45 m tee</td>
<td>Cane</td>
<td>Yes</td>
<td>M</td>
</tr>
<tr>
<td></td>
<td>&quot;</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>RAC, &quot;Variety Vineyard&quot;</td>
<td>Various</td>
<td>1973</td>
<td>3.6 x 2.4</td>
<td>0.45 m tee</td>
<td>Spur or cane</td>
<td>Yes</td>
<td>M</td>
</tr>
<tr>
<td>Virginia</td>
<td>P. Grilli</td>
<td>Shiraz</td>
<td>1972</td>
<td>3.5 x 1.5</td>
<td>0.5 m tee</td>
<td>Cane</td>
<td>Yes</td>
<td>H</td>
</tr>
<tr>
<td>Williamstown</td>
<td>A. Wilson</td>
<td>Shiraz</td>
<td>~1965</td>
<td>3.6 x 1.8-2.1</td>
<td>0.45 m tee</td>
<td>Spur</td>
<td>Yes</td>
<td>H</td>
</tr>
<tr>
<td></td>
<td>&quot;</td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Waikerie</td>
<td>W. Schmitt</td>
<td>Shiraz</td>
<td>~1950</td>
<td>3.6 x 2.1</td>
<td>Single wire</td>
<td>Cane</td>
<td>No</td>
<td>L</td>
</tr>
<tr>
<td>Glen Osmond</td>
<td>R. Parish</td>
<td>Shiraz</td>
<td>1971</td>
<td>3.9 x 2.4</td>
<td>0.9 m tee</td>
<td>Spur</td>
<td>Yes</td>
<td>M</td>
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<tr>
<td></td>
<td>WARI, &quot;Alverstoke&quot;</td>
<td>Shiraz</td>
<td>1960</td>
<td>3.7 x 2.2</td>
<td>Single wire</td>
<td>Spur</td>
<td>Yes</td>
<td>M</td>
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<td></td>
<td>&quot;</td>
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<tr>
<td></td>
<td>WARI, &quot;Claremont&quot;</td>
<td>Shiraz</td>
<td>1967</td>
<td>2.7 x 1.8</td>
<td>Y trellis*</td>
<td>Spur</td>
<td>No</td>
<td>M</td>
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<tr>
<td><strong>WESTERN AUSTRALIA</strong></td>
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<td></td>
</tr>
<tr>
<td>Swan Valley</td>
<td>Evans and Tate</td>
<td>Shiraz</td>
<td>~1956</td>
<td>3.6 x 1.8</td>
<td>Narrow tee</td>
<td>Spur</td>
<td>No</td>
<td>H</td>
</tr>
</tbody>
</table>


L = low, M = moderate, H = high

*Claremont trellis (Coombe 1974)
APPENDIX B

Determination of flower number per inflorescence

Thirty-four 'Shiraz' inflorescences, representing the range of sizes normally encountered, were sampled just before flowering. The relationship between flower number per inflorescence ($y$) and inflorescence length in mm ($x$) was calculated as:

$$y = -478 + 5.55x \ (r = .91, \text{ significant at } 0.1\% \text{ level})$$
APPENDIX C

Measurements of 'Shiraz' shoots, "South Vineyard" (Roseworthy College)

Twenty moderately-vigorous to vigorous shoots were collected after active growth had ceased in January, 1982.

- Mean length (m) : 2.07
- No. visible internodes : 30.5
- No. of separated leaves : 30.0
- Diameter between nodes 1 and 2 (mm) : 9.7

<table>
<thead>
<tr>
<th>Variable</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
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</thead>
<tbody>
<tr>
<td>Frequency distribn. of bunches</td>
<td>0</td>
<td>9</td>
<td>37</td>
<td>24</td>
<td>12</td>
<td>18</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Frequency distribn. of bunches and tendrils</td>
<td>0</td>
<td>3</td>
<td>14</td>
<td>15</td>
<td>7</td>
<td>12</td>
<td>16</td>
<td>9</td>
<td>9</td>
<td>15</td>
</tr>
<tr>
<td>Mean lateral shoot length (mm)</td>
<td>7</td>
<td>75</td>
<td>200</td>
<td>143</td>
<td>143</td>
<td>163</td>
<td>89</td>
<td>116</td>
<td>121</td>
<td>112</td>
</tr>
<tr>
<td>Mean no. lateral shoots per node</td>
<td>0.3</td>
<td>0.7</td>
<td>0.7</td>
<td>0.9</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
<td>0.9</td>
<td>0.8</td>
</tr>
</tbody>
</table>
Rate of 'Shiraz' shoot development (as no. of visible internodes) and date of 50 percent flowering in "South vineyard", Roseworthy College during 1980/81, 81/82, 82/83 and 83/84 growing seasons.