

Copyright is owned by the Author of the thesis. Permission is given for a copy to be downloaded by an individual for the purpose of research and private study only. The thesis may not be reproduced elsewhere without the permission of the Author.

A Study of the Growth of Axillary Buds in Angiosperms

A Dissertation Presented in Partial Fulfilment of the Requirements for the
Degree of Master of Science in Botany at Massey University

David Frank Jowett

1991

MASSEY UNIVERSITY

Instructions:

- (1) Please complete two of these forms, by providing title details and striking out one option from each of the sections 1-3.
- (2) If you select option b. of any section you must include a specific time period. The maximum permitted period is 24 months.
- (3) Include the two forms with the copies of your thesis submitted to your supervisor.
- (4) The Library must receive the original of your thesis.
- (5) We strongly recommend that you provide the Library with two copies of your thesis if it has colour plates.

Massey University Library. Thesis Copyright Form

Title of thesis:

A Study of the growth of axillary buds in angiosperms.

- (1) (a) I give permission for my thesis to be made available to readers in the Massey University Library under conditions determined by the Librarian.
(b) I do not wish my thesis to be made available to readers without my written consent for _____ months.
- (2) (a) I agree that my thesis, or a copy, may be sent to another institution under conditions determined by the Librarian.
(b) I do not wish my thesis, or a copy, to be sent to another institution without my written consent for _____ months.
- (3) (a) I agree that my thesis may be copied for Library use.
(b) I do not wish my thesis to be copied for Library use for _____ months.

Signed

D.F. Jowett
D.F. Jowett

Date

3 May 1991

The copyright of this thesis belongs to the author. Readers must sign their name in the space below to show that they recognise this. They are asked to add their permanent address.

Abstract

A description of the growth of axillary buds in the period before bud break was made in a number of angiosperms. This entailed a study of the growth of buds at representative locations in a plant as well as at different stages in the plant's growth. A number of different patterns of axillary bud development were found to exist. A way of assessing the significance of the differences between patterns was found. This involved comparing the observations with the theoretical possibilities which existed. A loose classification of the patterns was then constructed using the theoretical possibilities as a basis. An analysis of the data for each species was carried out to see if a cause for the **cessation** of bud growth could be determined. This analysis pointed towards the existence, in a large number of species, of a correlation between growth in an axillary bud and growth in surrounding tissues, particularly the expanding subtending leaf. One species - *Salix fragilis* - was chosen as the subject for a particularly detailed analysis. A clear correlation was established between growth in an axillary bud and growth in the stem in the immediate vicinity of the bud as well as in its subtending leaf. A number of experiments aimed at finding out the nature of a correlation between growth in an axillary bud and its subtending leaf were carried out with this species. These demonstrated that removal of a subtending leaf at an early stage in its growth had a significant depressing effect on axillary bud growth. This depressing effect was most pronounced during the period of most rapid growth in the axillary bud and its subtending leaf.

The data from the general survey of over thirty plant species and the experiments with *Salix fragilis* seem to support the notion that the process of axillary bud growth - as opposed to that of lateral shoot outgrowth **from** axillary buds - is affected more by conditions within the growing stem than by influences exerted by the stem apex.

The author gratefully acknowledges the guidance and support of Professor R.G.Thomas. Appreciation is also expressed to Ed Minot for his guidance with statistical analysis, Dr R.E. Rowland for his help with histoautoradiography and the other members of staff and fellow students in the Department of Botany and Zoology who have assisted with this study.

Contents

	Page
Acknowledgements	iii
List of Figures	v
Chapter 1: Introduction	1
Chapter 2: A Survey of the Different Patterns of Axillary Bud Growth in Angiosperms	25
Chapter 3: Rate of Leaf Primordium Initiation in Axillary Buds Relative to the Rate of Initiation of Leaf Primordia in the Shoot Apex	34
Chapter 4: Axillary Bud Growth Patterns	39
Chapter 5: Correlations	60
Chapter 6: Investigation of the Effect of Removal of Subtending Leaf Primordia on Axillary Bud Growth in <i>Salix fragilis</i>	69
Chapter 7: An Analysis of the Distribution of Photosynthate in a Shoot Apex of <i>Salix fragilis</i>	89
Chapter 8: Discussion	101
Appendix: Section 1	106
Section 2	194
Bibliography	199

List of Figures and Plates

		Page
FIG. 1.1	Drawings of a stem apex of <i>Salix fragilis</i> .	11
FIG. 1.2	Axillary bud initiation within the apical bud of <i>Salix fragilis</i> .	12
FIG. 1.3	Axillary bud growth in <i>Salix fragilis</i> .	13
FIG. 1.4	Two sets of graphs of the number of leaf primordia per axillary bud plotted against node number in <i>Salix fragilis</i> .	16
FIG. 1.5	<i>Stachys sylvatica</i> . Drawings showing the structure of a shoot and the sylleptically developing axillary bud or shoot.	17
FIG. 1.6	Drawings of an axillary bud in <i>Ulmus procera</i> ; bud development in this species is proleptic.	20
FIG. 1.7	Comparison of leaf position with total leaf length and prophyll length for a single plant of <i>Eichhornia crassipes</i> .	24
FIG. 2.1	Documentation for a dissection of a shoot of <i>Lolium perenne</i> .	30
FIG. 2.2	Graph of number of leaf primordia per axillary bud, length of longest axillary bud leaf primordium, and subtending leaf length against node number in a shoot of <i>Lolium perenne</i> .	31
FIG. 2.3	Graphs showing the relationship between internode length below a node, and the length of the leaf at that node, in single shoots in four species.	32

FIG. 2.4	Graphs of internode length below a node, and leaf length, against node number in four species.	33
FIG. 3.1	Simplified diagrams based on the growth curves of <i>Salix fragilis</i> , <i>Melicytus ramiflorus</i> and <i>Lolium perenne</i> .	37
FIG. 3.2	Relative rate of leaf primordium initiation for a number of plant species.	38
FIG. 4.1	Growth curves for <i>Helianthus annuus</i> .	48
FIG. 4.2	Growth curves for <i>Stachys sylvatica</i> .	49
FIG. 4.3	Growth curves for <i>Hebe speciosa</i> .	50
FIG. 4.4	Growth curves for <i>Trifolium repens</i> .	51
FIG. 4.5	Growth curves for <i>Salix fragilis</i> .	52
FIG. 4.6	Growth curves for <i>Ulmus procera</i> .	53
FIG. 4.7	Growth curves for <i>Aristotelia fruticosa</i> .	54
FIG. 4.8	Growth curves for <i>Melicytus ramiflorus</i> .	55
FIG. 4.9	Growth curves for <i>Muehlenbeckia australis</i> .	56
FIG. 4.10	Growth curves for <i>Pittosporum crassifolium</i> .	57
FIG. 4.11	Growth curves for <i>Lonicera x americana</i> .	58
FIG. 4.12	Growth curves for <i>Sambucus nigra</i> .	59

FIG. 5.1	<i>Salix fragilis</i> . Graphs of the number of leaf primordia per axillary bud, and the length of subtending leaves plotted against node number in four shoots.	64
FIG. 5.2	<i>Hebe speciosa</i> . Graphs of the number of leaf primordia per axillary bud, and the length of subtending leaves plotted against node number in four shoots.	66
FIG. 5.3	<i>Passiflora mollissima</i> . Graphs of the number of leaf primordia per axillary bud, and the length of subtending leaves plotted against node number in two shoots.	67
FIG. 5.4	<i>Lycopersicon esculentum</i> . Graphs of the number of leaf primordia per axillary bud, and the length of subtending leaves plotted against node number in five shoots.	68
FIG. 6.1 to 6.4	Graphs of the number of leaf primordia per axillary bud against node number for the calculation of growth depression in the leaf removal experiments.	74
FIG. 6.5	Data from the leaf removal experiment.	79
FIG. 6.6	Three dimensional graph for the leaf removal experiment.	83
FIG. 6.7	Drawings of distorted axillary buds.	84
PLATES 7.1 to 7.5	Photomicrographs of sections through an axillary bud of <i>Salix fragilis</i> .	94

PLATES 7.6 to 7.9 Histoautoradiography experiment - photomicrographs of longitudinal sections through the apical region of a shoot in *Salix fragilis* into which radioactive carbon had been fed.

CHAPTER 1

Introduction

Growth in all but the simplest of plants depends on their ability to form branching structures. Branches can originate when the stem apex itself divides, as it does in lower vascular plants such as *Psilotum*, *Lycopodium* and *Selaginella* (Esau 1965), or from the outgrowth of lateral buds, laid down on the main shoot distal to the apex. These lateral buds are most frequently subtended by a leaf. In some ferns with dorsiventral rhizomes they seem to arise without reference to leaves, but it is more common for them to originate from or near to the adaxial side of a leaf base or rhachis (Esau 1965). The bulbils of *Lycopodium selago* occupy the sites where leaves are normally found (Cutter 1966).

In seed plants lateral buds - when present - are usually found in an axillary position, in other words on the stem just above the point of insertion of the leaf. Lateral buds are generally present in the axils of most leaves except those in the lower regions of annual shoots of some gymnosperms (Foster and Gifford 1974). In a few instances they are found in other than axillary positions - in species of *Nymphaea* and *Nuphar* occasional buds occur in what are normally leaf sites (Cutter 1965). Lateral buds in a number of species are associated more closely with the leaf above than the leaf below - the early slow growth of a tiller bud in the Gramineae involves the making of vascular connections with the leaf immediately above the bud. The later, exponential growth phase starts some time after the establishment of the vascular connection (Fletcher and Dale 1973; Sharman 1945).

In angiosperms, lateral buds are usually formed slightly later than subtending leaf primordia, commonly when such leaves are in their second or third plastochrone (Esau 1965). But in some species buds form much later by dedifferentiation of already vacuolated cells or from small pockets of meristematic cells - called **detached meristems** - which have become isolated from the apical meristem by differentiation of intervening tissues (Cutter 1971). Bud primordia may also arise adventitiously from various organs and tissues in the plant. Such a pattern is found in *Musa*: the earliest vascular connection of the lateral bud in this species is made, as in the grasses, with the trace of the next leaf above (Barker and Steward 1962). However, the lateral buds in the aforementioned cases are at least located in axillary positions. Indeed, lateral buds in angiosperms are usually referred to as **axillary buds**.

The growth and development of axillary buds is one facet of plant growth to have received relatively little attention. Bud initiation has been explored extensively (Cutter 1965) and bud break - or lateral shoot outgrowth - has provided a fertile ground for numerous researchers, especially in relation to grasses. But it is the period in between which remains relatively enigmatic. Axillary buds are the major source of new vegetative shoots and frequently act as primordia for flowers or inflorescences, and when one considers the large range of growth patterns found in seed plants it seems likely that a similar number of different behavioural patterns might exist in this group of plants. However, the pattern found in *Salix fragilis* exemplifies most of the important features of axillary bud growth.

The following description is aimed at clarifying the experimental data presented in the thesis. The description draws on experimental data obtained in this study, since, to my knowledge, these stages of axillary bud growth have not been described before.

Leaf primordia are initiated at the stem apex (FIG. 1.1). An axillary bud then forms in the axil of an expanding leaf primordium; it becomes visible on the surface of the stem when the subtending leaf is about 7 mm. long (FIG. 1.2). The first primordial structure to become visible is a sheathing prophyll. The axillary bud apex inside it (FIG. 1.3a) initiates foliage leaf primordia (FIG. 1.3b). Later in the growing season - late December to early January in New Zealand - secondary axillary buds are then initiated in the axils of the first formed bud leaf primordia in these primary axillary buds. In other words the older primary axillary buds on a shoot contain a number of secondary axillary buds. The sheathing prophyll does **not** subtend a secondary bud. Secondary axillary buds are laid down at the first-formed three or four nodes of the primary buds. Hence, when bud break ensues, the basal nodes of the developing shoot arising from the primary bud already bear sizable axillary buds. The more apical nodes contain no such buds at this stage, the leaf primordia at these nodes being smaller than the apparent minimum size for a subtending leaf. However, the rate of leaf primordium initiation in the axillary buds in the basal nodes of the new shoot is slower than in the more distal axillary buds. The latter are subtended by full or nearly full sized foliage leaves whilst the former remain small. Hence, while axillary buds in the most basal nodes are the **largest** on the shoot just after it has commenced growing out as a shoot, they are overtaken by the faster growing, more distal axillary buds. This effect will be noticed in the graphs in FIG. 1.4 which illustrate the growth of a single shoot of *Salix fragilis* from its

parent axillary bud through to maturity. Two major features are illustrated: firstly, the growth rate in a particular axillary bud relative to the rate of growth in the stem apex does not remain constant. This rate can be estimated from the vertical distance between successive graphs. (The assumption is made that the shoots sampled were all behaving in a similar fashion. Experience with all the species sampled showed that this assumption is acceptable.) Hence, the bud at node 10 had 1.3 leaf primordia on 2 October, 8.2 leaf primordia on 17 October, 12.3 leaf primordia on 23 November, 14.9 leaf primordia on 24 January and 15.4 leaf primordia on 25 March; secondly, buds initiated at the three or four most basal nodes of the growing shoots increase in size by only 5 to 6 leaf primordia in a whole season. Those initiated higher up the shoot grow more rapidly and to a greater final size - buds laid down at nodes 20 to 30 in mid summer initiate about 17 primordia in only 3 months.

The terms **bud break**, **bud growth** and **bud outgrowth** should be clarified at this point. In *Salix fragilis*, most axillary buds contain only small leaf primordia and grow as compact buds with short axes and short internodes. Growth in such buds is termed **bud growth**. In the spring most axillary buds grow out to form lateral shoots. The onset of this process is termed **bud break**, and elongation growth in the shoot that forms from them is termed **outgrowth**.

In 1975 Phillips identified the need for information regarding the phase of bud growth between initiation and outgrowth in his review article on apical dominance and although this appeared fifteen years ago its salient points remain essentially valid today. He suggested that the apical meristem is commonly dominant to some degree over the lateral meristems. Investigations of this apical dominance have stressed the role of a diffusible signal, apparently arising in the stem apical bud, its effects being expressed in several ways, particularly in the correlative inhibition of axillary buds. In general "it is reasonable to conclude," wrote Phillips, "that interacting nutritional and hormonal conditions must be appropriate to allow bud outgrowth." Phillips also stated that "in all cases it appears that the development of each lateral bud is arrested at some stage...and apical dominance is clearly imposed." It is clear that he considered the events in the growing axillary bud eventually come under the inhibitory influence of the stem apex. He claims that "lateral buds of species with complete apical dominance cease cell division activity very soon after initiation" but concedes that "regrettably few studies have been conducted of the changes in lateral buds which occur during the imposition of correlative inhibition." It would appear that conventional wisdom - Phillips' review has not been questioned as far as I

can tell - is that the same features are responsible for the inhibitory control of both bud outgrowth and bud growth.

One or two facets of axillary bud behaviour should be clarified at this point. Firstly a distinction should be drawn between axillary buds and axillary or lateral shoots. The most noticeable differences are as follows:

a) leaf primordia on apical buds in shoots grow into leaves without a period of rest; growth becomes exponential at an early stage of leaf primordium development - it may be exponential from the time of initiation onwards. By contrast, leaf primordia in axillary buds do not undergo expansion growth, although the present study has found that, in *Salix*, their cells remain essentially meristematic.

b) internode extension is present in shoots derived from active apical buds but absent in axillary buds.

Phillips talked of plants with weak apical dominance - he cited *Coleus* (Thimann and others 1971) - in which developmental processes move at less than maximal rates, and those with complete apical dominance such as *Tradescantia* where apical cell activity is apparently blocked at a certain point and growth ceases (Yun and Naylor 1973). It is necessary to define two terms which will be used in descriptions of these and other patterns of bud behaviour. As defined by Halle (1978), **Syllepsis** is the continuous development of an axillary bud into a shoot without an evident period of rest between bud initiation and outgrowth. *Coleus* and *Stachys* are essentially sylleptic (FIG. 1.5). **Prolepsis** is the discontinuous development of a lateral shoot, there being a distinct period of inactivity between the time of bud inception and bud outgrowth. A sylleptic branch is at least partly synchronous in its development with its parent axis while a proleptic one is not. Halle (1978) suggests that these developmental definitions can be reinforced by morphological differences. He says that sylleptic branches lack basal bud scales and have an extended basal internode (hypopodium) generally below the first leaf or leaf pair. This leaf (or leaf pair) is of a normal size and shape for adult foliage. Proleptic branches such as those of *Ulmus* have one or more basal bud scales and leaf shape and size undergo a transition towards the adult leaf (FIG. 1.6). However, Halle writes: "shoots with sylleptic form and proleptic growth are known, though examples of proleptic form and sylleptic behaviour are rare." (Interestingly the present study finds that *Salix* is apparently an example of the latter type; one wonders if Halle's statement is based on limited data regarding axillary bud growth.) He also states: "Syllepsis is much the more common form of branching in herbaceous plants."

Phillips' review covered the work relevant to the topic of apical dominance produced up to 1975, most of it relating to bud outgrowth. Information regarding growing buds - as opposed to outgrowing buds - was presented, but most has not been found to be relevant to the present study. The nature of the correlative signal was discussed by Phillips. Early investigators, as well as those working in the 1970s, have emphasised the importance of the nutrient supply in regulating bud development. Much more research has been concentrated on the other possibility that the signal from the apical bud is of a hormonal nature. Phillips noted that, though considerable evidence argues against the view that nutrient availability and supply comprise the basic correlative mechanism regulating bud growth, and that apical dominance is effected through hormonal controls, this does not mean that nutrient and water status are unimportant. Soon after it was demonstrated in 1933 (Thimann and Skoog) that auxin (probably indole-3-acetic acid; IAA) was synthesised in growing apical buds it was reported that exogenous IAA would substitute for the apical bud in maintaining inhibition of the axillary buds in bean plants (Thimann and Skoog 1934). This observation has been confirmed innumerable times in succeeding years for many species. There are also numerous data indicating that cytokinins are essential for bud outgrowth (Ali and Fletcher 1971, Sachs and Thimann 1967, for example). However, there is little evidence that cytokinins operate as correlative signals. Abscisic acid (ABA), though present at high levels in axillary buds (Tucker and Mansfield 1973) is also not regarded as a likely participant in the correlative signal. Gibberellins (GA) do appear to be implicated in some instances, perhaps interacting with auxins (Phillips 1975). The mechanism of action of a correlative signal was also discussed extensively, there being essentially four main ideas:

1. **Lack of essential factors** - there is little concrete evidence to show that bud outgrowth - or the lack of it - is related to a lack of essential factors in that bud.

2. **Inhibitory factors are directly involved** - levels of the growth inhibitor ABA have been found to decline in buds of *Pisum sativum* shoots, *Acer pseudoplatanus* shoots and *Solanum tuberosum* tubers following their release from apical dominance (Dorfling 1974, Goodwin and Cansfield 1967). Levels of ABA in inhibited buds of *Xanthium strumarium* were found to be higher than in other parts of the plant (Tucker and Mansfield 1973) and fall after decapitation of the main shoot.

3. Hormonal factors affect the supply of nutrients - Went (1939)

offered the nutrient diversion theory which proposed that metabolites move towards regions of highest auxin concentration. Dominant buds and shoots are known to be the principal sites of auxin synthesis (Sheldrake 1973) and the theory holds that metabolites move to these organs in response to stimuli provided by auxin rather than as a result of their sink activity.

4. An adequate supply of nutritive and hormonal factors to a growing lateral can be maintained only if the bud is suitably served with a continuous vascular connection with the vascular tissues of the main stem.

The theory that vascular supply constrains buds against break is not held up by the evidence. Furthermore, bud growth clearly continues in the absence of any vascular connection (this study).

There have been several developments since 1975. Also, there is information obtained before this date and not presented in Phillips' review which is of relevance to bud growth. Firstly, a link between apical dominance and axillary bud growth has been proposed. The absence of buds from one or more nodes on the main shoot in *Pisum* and their presence at later formed nodes has prompted some researchers (Gould and others 1987) to suggest that apical dominance not only inhibits outgrowth of lateral shoots but can also suppress the initiation and early development of axillary buds. However, one could provide numerous alternative explanations for this observation. For instance, McIntyre (1968) notes that bud growth in *Phaseolus vulgaris* is very responsive to nitrogen supply up to a certain level. Water supply is also critical: water stress causes inhibition. (In the present study it was found that in *Vicia faba*, a plant closely related to *Phaseolus vulgaris* and sharing that plant's tendency of having nodes at which all axillary bud development is apparently suppressed, cases were found where **all** nodes bore axillary buds. In addition, Moreland (1973) found that the inhibiting effect of growing leaves on the cotyledonary buds in *Phaseolus* was much greater than that of the apical bud itself. As the growth rate declined, the leaves ceased to inhibit. And Wardlaw and Mortimer (1970) provide evidence which shows that the slow rate of movement of carbohydrate into lateral buds in pea might limit their growth. Tamas and Schlossberg (1982) grew stem segments of *Phaseolus* bearing axillary buds in a number of different growth media containing various growth substances and concluded that axillary bud growth is under the control of several hormones. IAA and ABA tend to inhibit growth. GA and cytokinin have the opposite effect. Such data suggest, at least, that factors other than apical dominance may be involved in the control of

axillary bud growth. The present study contains information which suggests that bud growth and bud outgrowth are, in some instances, two separate phenomena. By contrast, it would seem that, in other instances, typified by *Coleus*, axillary buds are essentially outgrowing from the earliest stages of their development. Apical dominance is hence likely to be a significant factor in the control of all phases of growth in the so-called axillary buds in this species. It may well be that in *Phaseolus*, axillary buds are similarly essentially outgrowing from their inception.

Tucker's work on apical dominance in "Rogue" tomato (1976) prompted the comment that lateral shoot growth is controlled by a delicate interaction between all the major growth hormones. The primary correlative signal appears to be auxin derived from young growing leaves. The same issue arises in the present study with three solanaceous species, their bud development being sylleptic for the most part.

A number of investigators have examined the morphology and cytology of lateral buds at the stage where bud growth ceases - or, as Phillips stated, during the imposition of correlative inhibition. Several reports demonstrate that no mitoses occur in the apical meristem of a lateral bud on a plant showing complete apical dominance (Booker and Dwivedi 1972, Cutter 1972, Naylor 1958, for example). Sawhney and Naylor (1982) have found that isolated axillary buds of *Tradescantia paludosa* can remain in a quiescent state for extended periods when grown on a medium containing only salts and water; it appears that tissue contact with the rest of the plant is not required for the maintenance of quiescence. This suggests a certain degree of autonomy exists within the axillary bud; and Yun and Naylor (1973) demonstrated that, whereas cell division occurs, albeit infrequently, in the major part of the meristem of inhibited axillary buds in this species, divisions are absent from a group of cells located in the summit of the apex. These cells were found to be particularly sensitive to the imposition of nutritional stress.

A number of investigations reveal an apparently complex control mechanism for growth in axillary buds:

a) in looking at the developmental potential of axillary buds of water hyacinth - *Eichhornia crassipes* - Richards (1982) has found that axillary buds - which stop growing at the same time as their subtending leaf stops expanding - undergo cell vacuolation which, starting in the outer regions of the bud eventually extends, as the bud ages, to its apical region. Apices of oldest buds senesce. (The graphical representation of Richards' results is shown in FIG. 1.7.

This is the conventional way of presenting information of this type. The reader will note that, in the present study, data are graphed in the reverse sense, the youngest node being to the far right on the horizontal axis rather than to the left. This enables comparisons to be made between different stages of growth in one axillary bud or one region of a shoot.)

b) Zamski and others (1985) have found that the pattern of axillary bud development in *Rosa* depends on their location on the shoot. When the bud begins to grow out as a lateral shoot, the first formed axillary buds on it grow proleptically; that is to say they undergo a period of inhibition prior to sprouting. As the lateral shoot continues to grow, the later formed axillary buds grow without interruption immediately on formation. The former proleptic buds are initiated in the parent bud before it grows out as a lateral shoot. The latter sylleptic buds are initiated on the outgrowing lateral shoot;

c) Phillips (1975) cites evidence for mature leaves being the principal sites of ABA synthesis from whence it is evidently transported acropetally into the apical buds. For this reason it is possible that ABA is involved in examples of correlative inhibition of axillary buds by their subtending leaves commented on by Goebel in 1880. Though this research may have been aimed at elucidating the bud break phenomenon, it may provide insight into the changes identified in the present study that occur in bud growth as the subtending leaf grows;

d) Snow and Snow (1942) showed that in several species of herbaceous angiosperms some factor from the subtending leaf primordium was necessary for the initiation of an axillary bud since it failed to arise if the leaf primordium was excised at an early stage of development. However, in *Cucurbita pepo* this did not occur (Sheldrake 1973). In *Ipomoea*, Kuse (1961) reported that growth of axillary buds is inhibited by a young subtending leaf while it is promoted by a fully expanded one. And Neville (1961) found that if leaf primordia in *Gleditschia* are destroyed, buds become abortive or parenchymatous. Cutter (1965) has commented that axillary bud inception and development are dependent on some activity of the subtending leaf primordium - she cites the previous three or four pieces of research - but Wardlaw (1943) suggests that one should bear in mind that the axillary bud is part of an integrated developing system in which any contiguous organ may act as a controlling factor;

e) the influence of other parts of the plant on axillary bud growth has been investigated most completely for *Nicotiana tabacum* (McDaniel 1978), in which it was concluded that axillary bud meristems respond to signals from such parts. It was also found that distance, measured in nodes, between the axillary

bud apex and the root system appeared to be important in regulating its apical meristem function (McDaniel and others 1989);

f) Champagnat (1954) found that the behaviour of axillary buds on horizontal stems depended on whether they were on the top or the bottom surface of the stem. If such a stem was inverted in the summer, extension growth in the following spring was most rapid in the uppermost buds. If the inversion was carried out in the spring - up until March - the lowermost buds expanded more rapidly. Champagnat postulated induction of fixed properties by gravity which would determine subsequent growth rates on bud break - the work certainly suggests that correlative influences of many forms from outside the bud can affect its growth and development;

g) in studies of *Helianthus* (Wetmore and Garrison 1966), it was found that removal of a pair of leaves at a particular node had a marked depressing effect on elongation of the subjacent internode so long as the leaves were excised before they were half grown; removal of leaves above or below had little effect; the effect was limited to a single internode. Leaf removal did not completely suppress internodal elongation on the subjacent internode, suggesting the process is not completely dependent on the associated leaves for the stimuli required for development. Such a response would suggest the operation of a hormonal mechanism. (This last piece of research may be of significance to the experimental work carried out in the present study.)

In the research work mentioned above there is a tendency to concentrate on bud break. Many authors have preferred to use the term "bud growth" in their descriptions of phenomena which actually occur after bud break. The adoption of such a policy would suggest that the development of an axillary bud into a lateral shoot is regarded as a continuous process which may or may not be temporarily interrupted. However, bud growth as I have defined it has been almost completely ignored. This is a situation which needs rectifying if we are to gain a clearer understanding of the apical dominance phenomenon. In the present study an attempt is made to determine when, or indeed if, axillary buds do stop growing after their initiation and early growth. Without such information, theories about the effect of the stem apex on axillary bud growth could only be tentative, and a major aim of the study is to determine whether or not dominance by the stem apex over axillary buds occurs during the earliest stages of bud growth (before bud break). Obviously a large number of "different" species needed examination. This was essential if more than one

pattern of behaviour exists and all patterns were to be identified. It was, in fact, only after a number of arbitrarily chosen species had been studied that further selection of species could be made effectively. Hopefully most different patterns of axillary bud growth were eventually surveyed.

A clear description of axillary bud growth was needed in each case. This entailed a study of the growth of buds at representative locations in a plant as well as at different stages in the plant's growth. When the dynamics of axillary bud growth had been determined it became clear that a number of different patterns did, in fact, exist. One way of assessing the significance of the differences between patterns was to compare the observations with the theoretical possibilities which existed. A loose classification of the patterns was then constructed using the theoretical possibilities as a basis.

Finally, an analysis of the data for each species was carried out to see if a cause for cessation of bud growth could be determined. This analysis pointed towards the existence, in a large number of species, of a correlation between growth in an axillary bud and growth in surrounding tissues. One species - *Salix fragilis* - was chosen as the subject for a particularly detailed analysis. A clear correlation was established between growth in an axillary bud and growth in the stem in the immediate vicinity of the bud as well as in its subtending leaf; a number of experiments aimed at finding out the nature of a correlation between growth in an axillary bud and its subtending leaf were carried out with this species. These demonstrated that removal of a subtending leaf at an early stage in its growth had a significant depressing effect on axillary bud growth. This depressing effect was most pronounced during the period of most rapid growth in the axillary bud and its subtending leaf.

The data from the general survey of over thirty plant species and the experiments with *Salix fragilis* seem to support the notion that axillary bud growth is affected more by conditions within the growing stem than by influences exerted by the stem apex.

FIG 1.1 Drawings of a stem apex of *Salix fragilis*

FIG. 1.1a Apical region of a growing shoot showing expanding foliage leaves and the unfolding apical bud. The compact bud contains 12 leaf primordia.

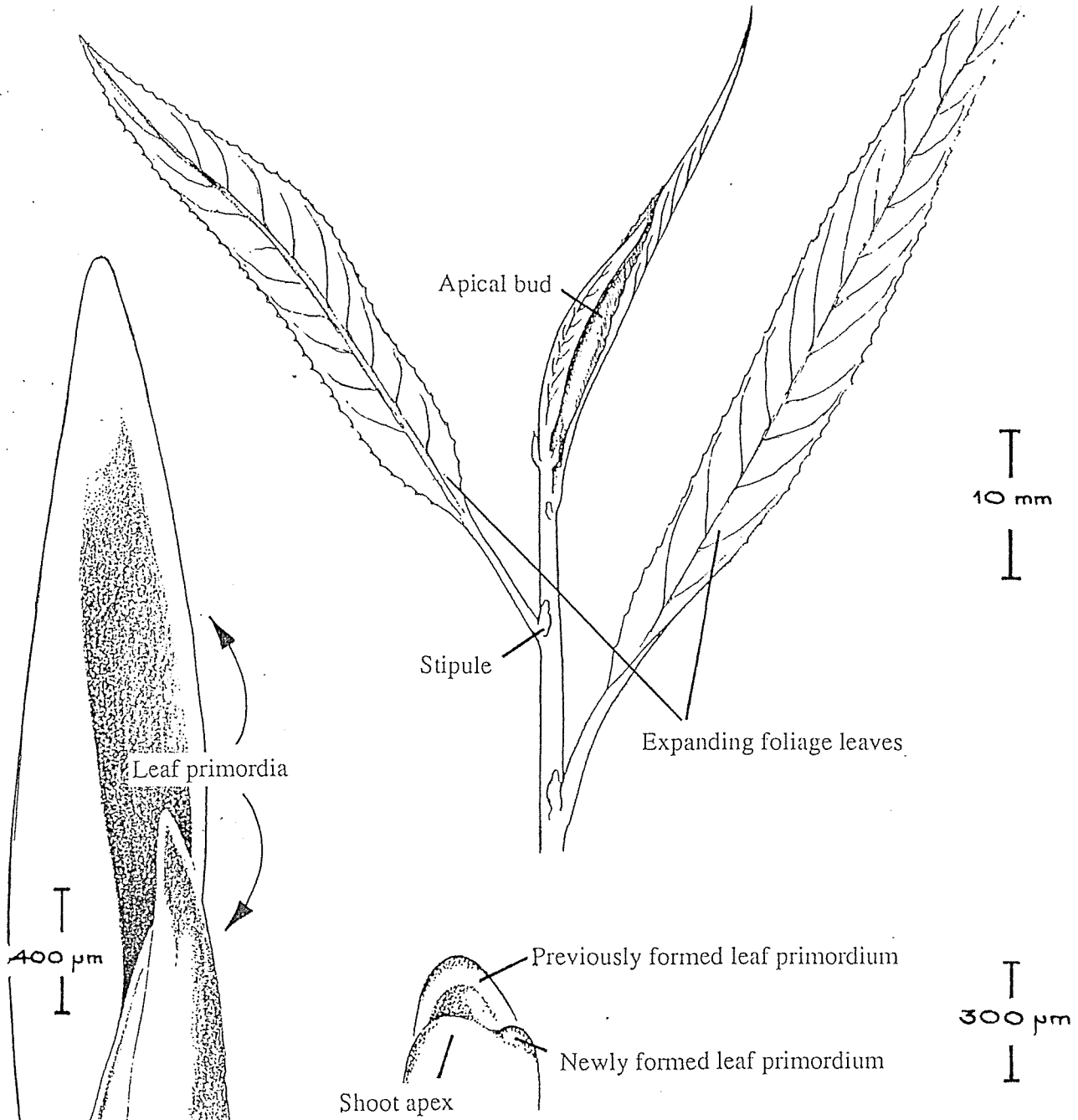


FIG. 1.1c The stem apex and youngest leaf primordia, all other leaf primordia having been removed.

FIG. 1.1b Inner region of the stem apex. 8 leaf primordia have been removed; two primordia and the apex are still enclosed.

FIG. 1.1a Apical region of a growing shoot showing expanding foliage leaves and the unfolding apical bud. The compact bud contains 12 leaf primordia.

FIG. 1.2 Axillary bud initiation within the apical bud of *Salix fragilis*. Internodes between successive leaf primordia in the apical bud are very short; primordia are very close together. The axillary bud has become visible in the axil of a leaf primordium which is 7 mm long.

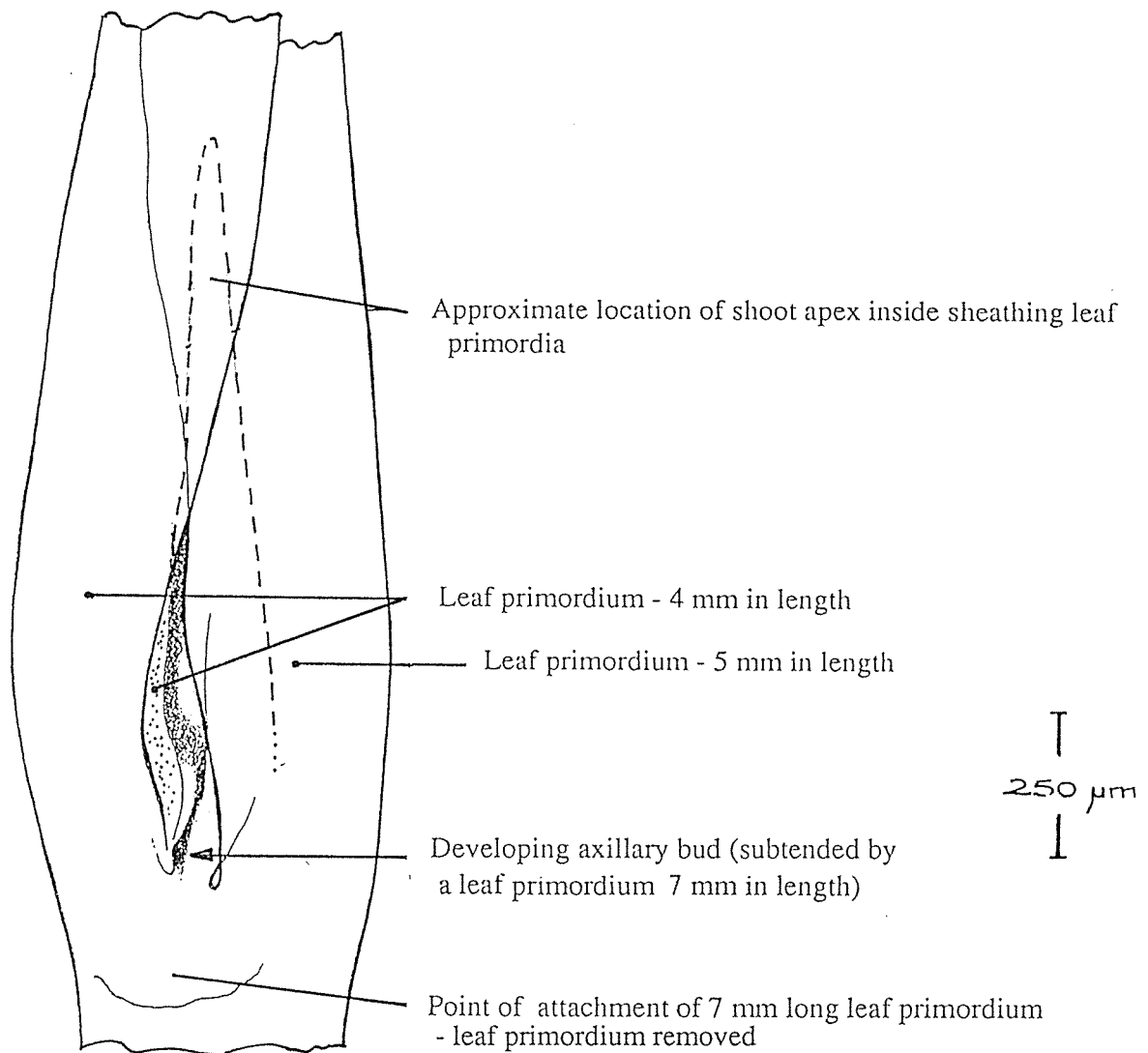


FIG. 1.3 Drawings of axillary buds in *Salix fragilis* at various stages of development.

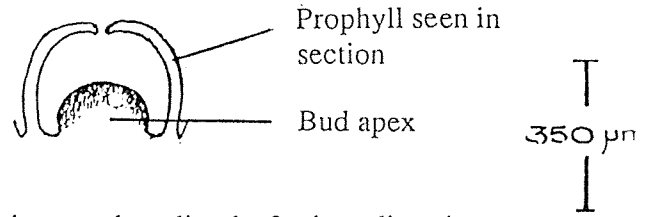


FIG. 1.3a By the time a subtending leaf primordium is 13 mm long the apex of the axillary bud is visible within the sheathing prophyll.

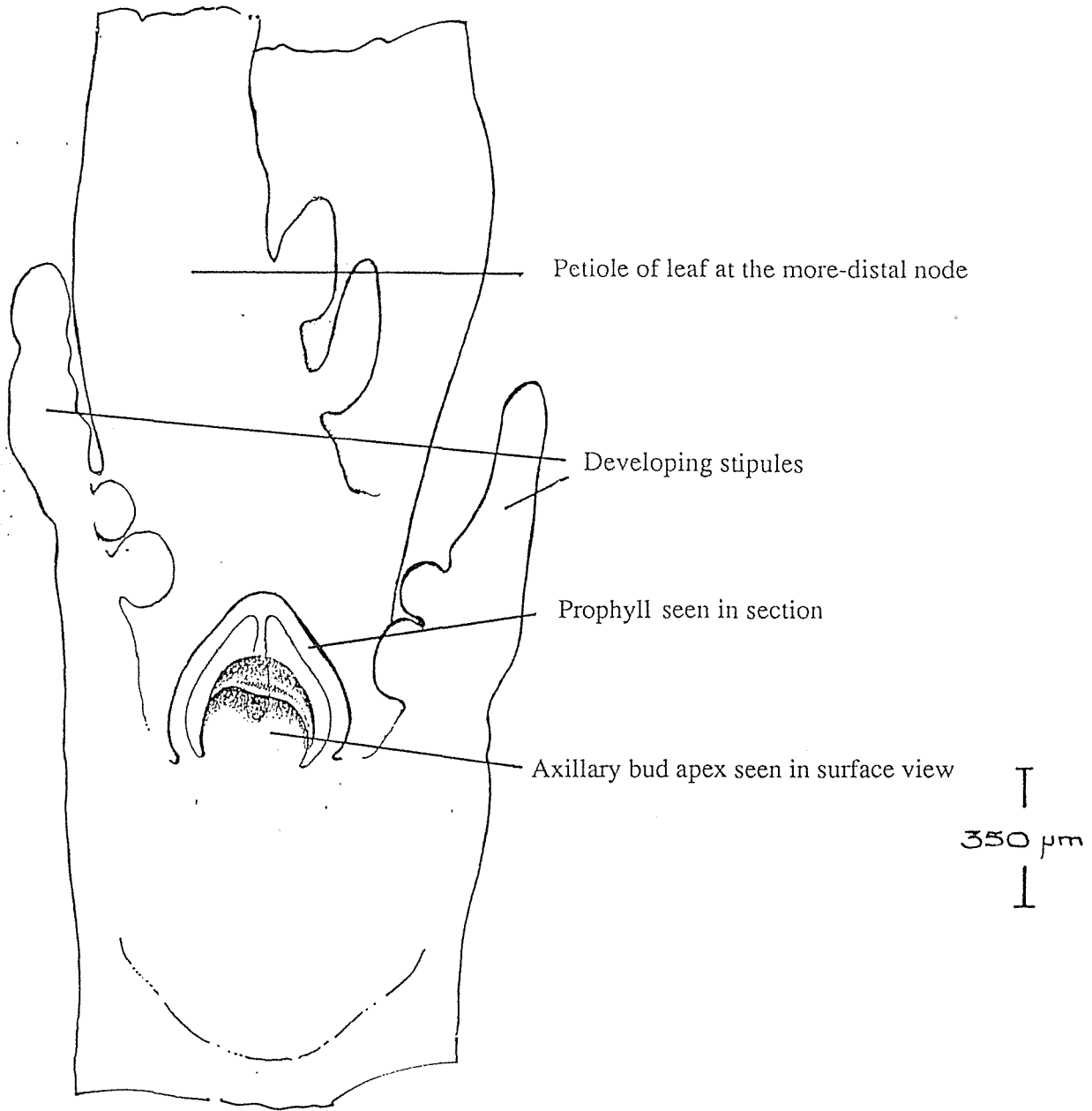


FIG. 1.3b Leaf primordium initiation within the axillary bud is now obvious. The bud's subtending leaf is 18 mm long.

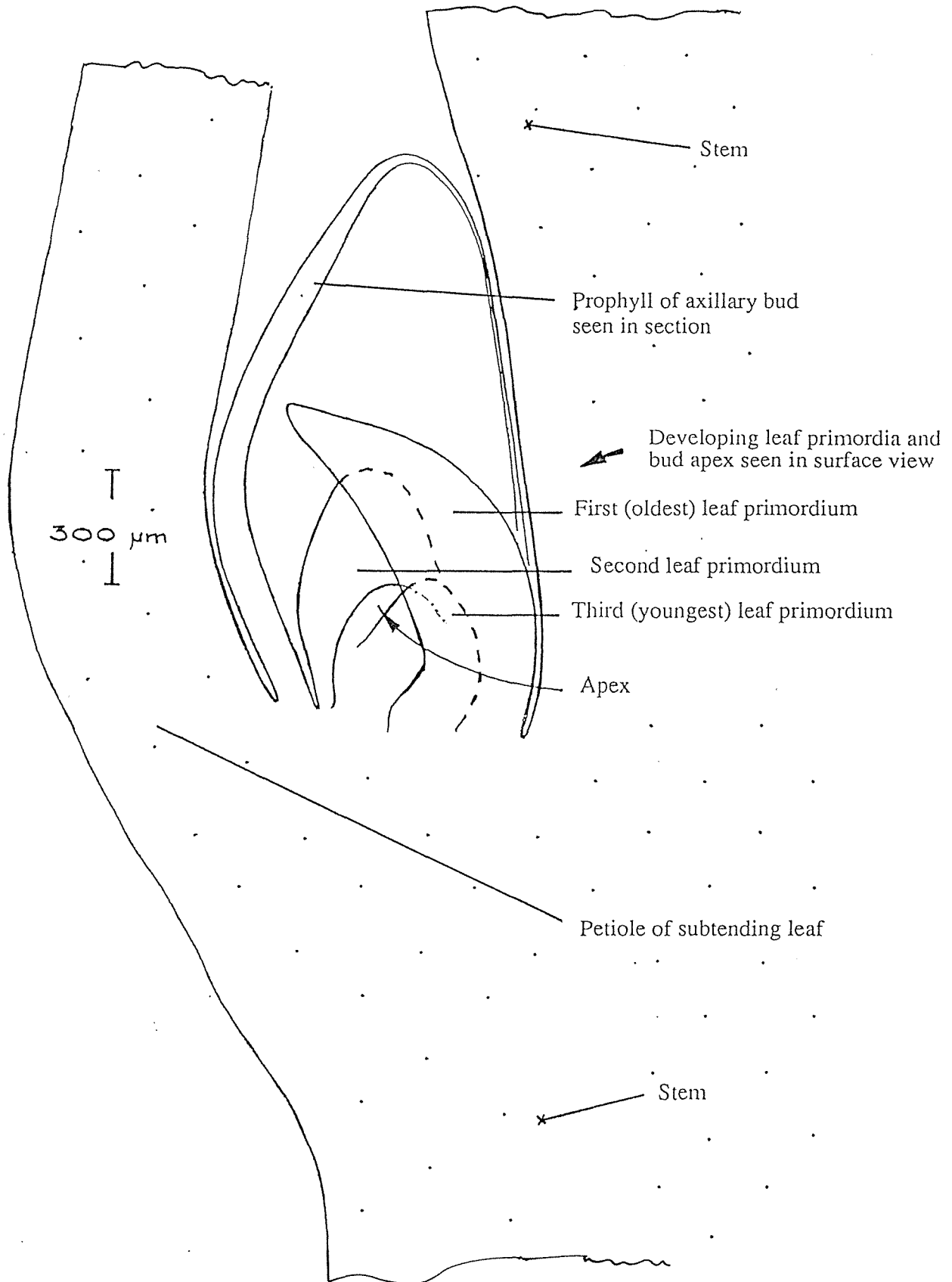


FIG. 1.3c The axillary bud now contains 3 leaf primordia at various stages of development. The bud's subtending leaf is 35 mm long. The primordia have been initiated in an anticlockwise direction looking down the shoot. This direction would have remained constant within this bud, but varies randomly between buds on a shoot.

FIG. 1.4 Two identical sets of graphs of the number of leaf primordia per axillary bud plotted against node number in *Salix fragilis*. The five shoots were studied at different times of year - the date of each dissection is shown on the second set of graphs. Nodes are numbered from the base of the shoot upwards - the most apical node has the highest node number. The numbers on the vertical line in the second set of graphs indicate the number of leaf primordia in the axillary buds at node 10 on each shoot. The shaded area in the first set of graphs denotes maximum axillary bud primordium initiation rates.

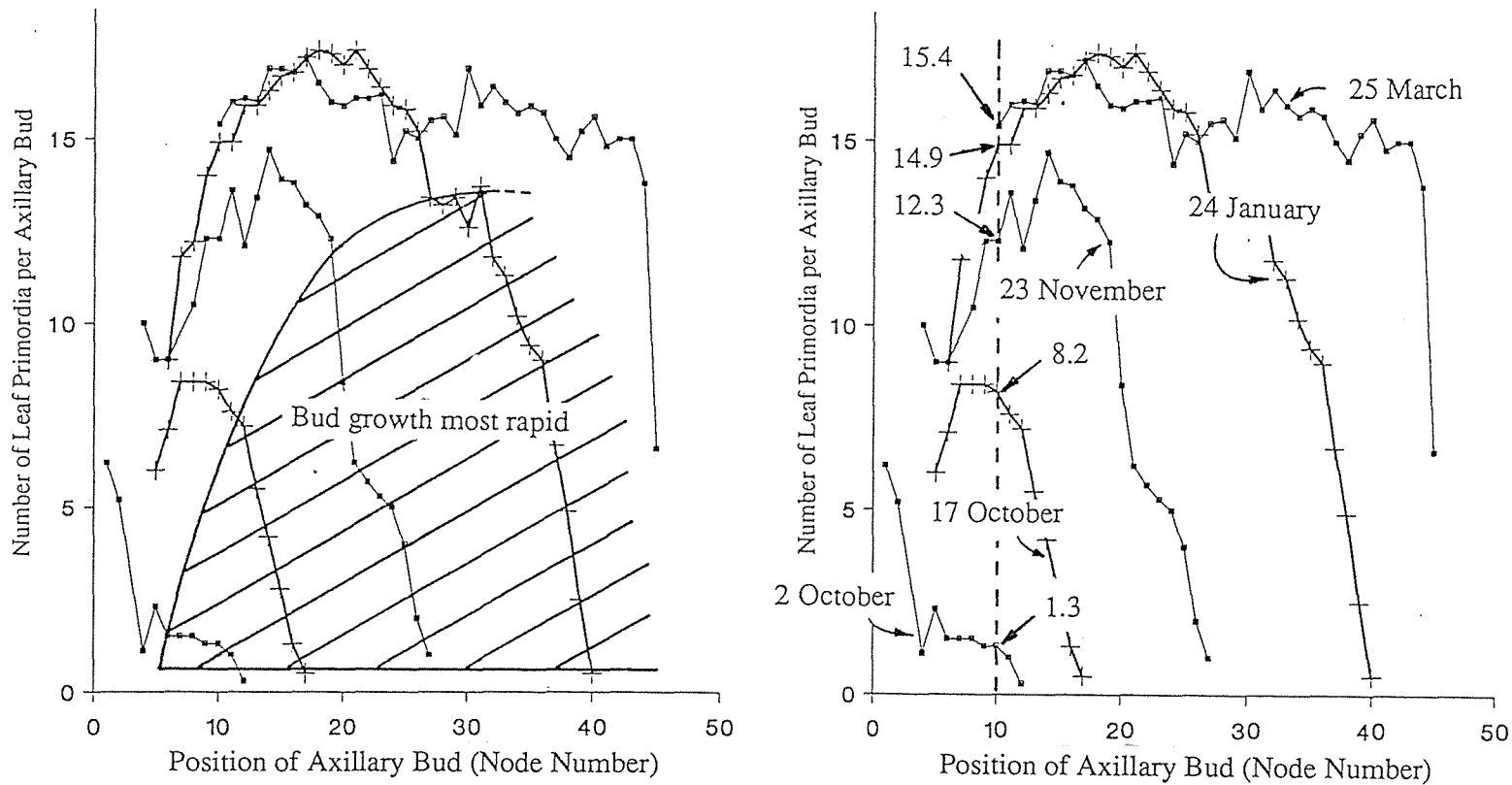


FIG. 1.5 *Stachys sylvatica*. Drawings showing the structure of a shoot and the sylleptically developing axillary bud or lateral shoot.

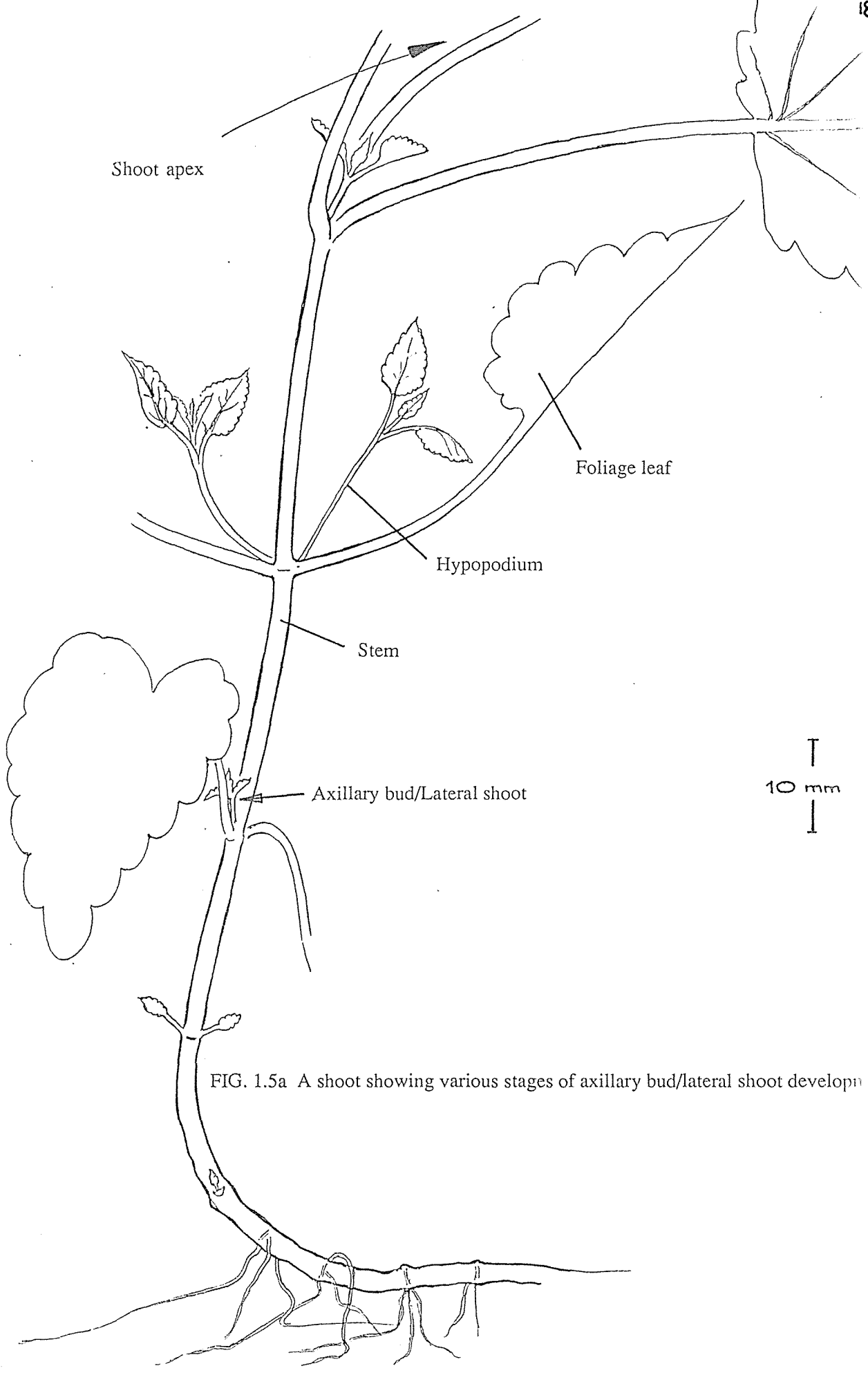


FIG. 1.5a A shoot showing various stages of axillary bud/lateral shoot development

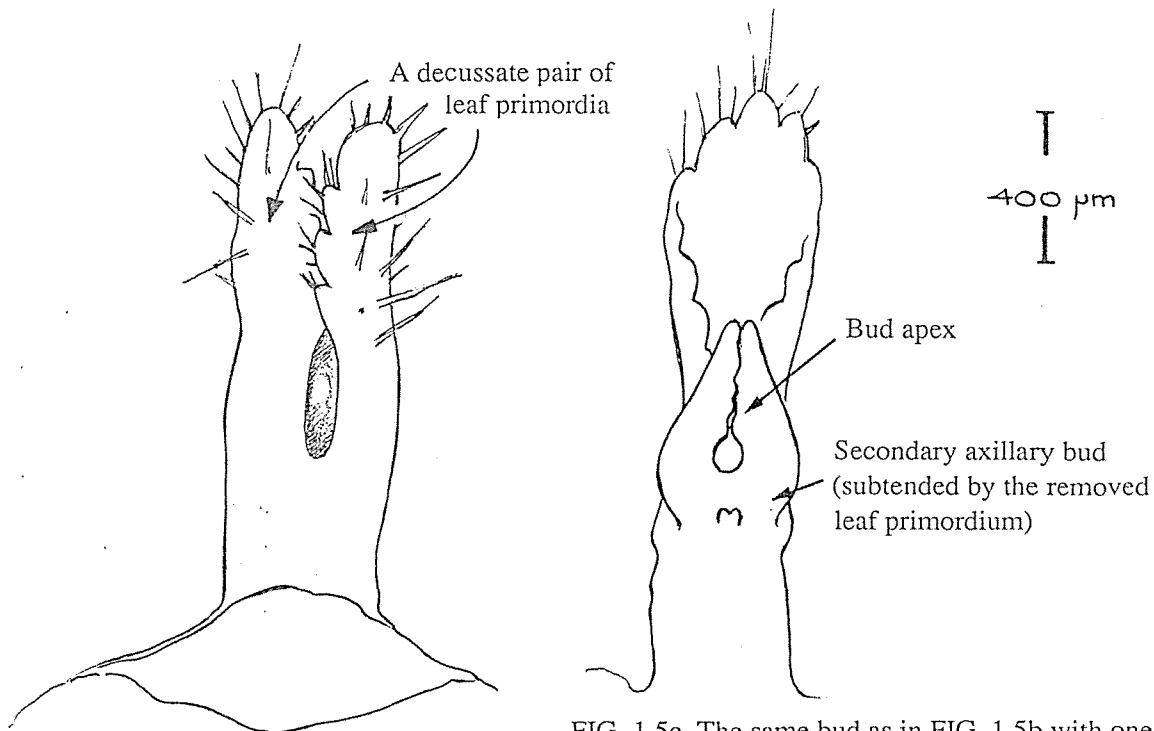


FIG. 1.5b A small axillary bud/lateral shoot viewed from below.

FIG. 1.5c The same bud as in FIG. 1.5b with one primordium removed, viewed from the side.

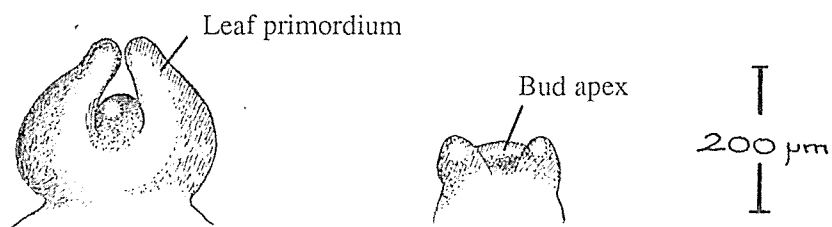


FIG. 1.5d,e The apical region of axillary buds at different stages of development.

FIG. 1.6 Drawings of an axillary bud in *Ulmus procera*; bud development in this species is proleptic.

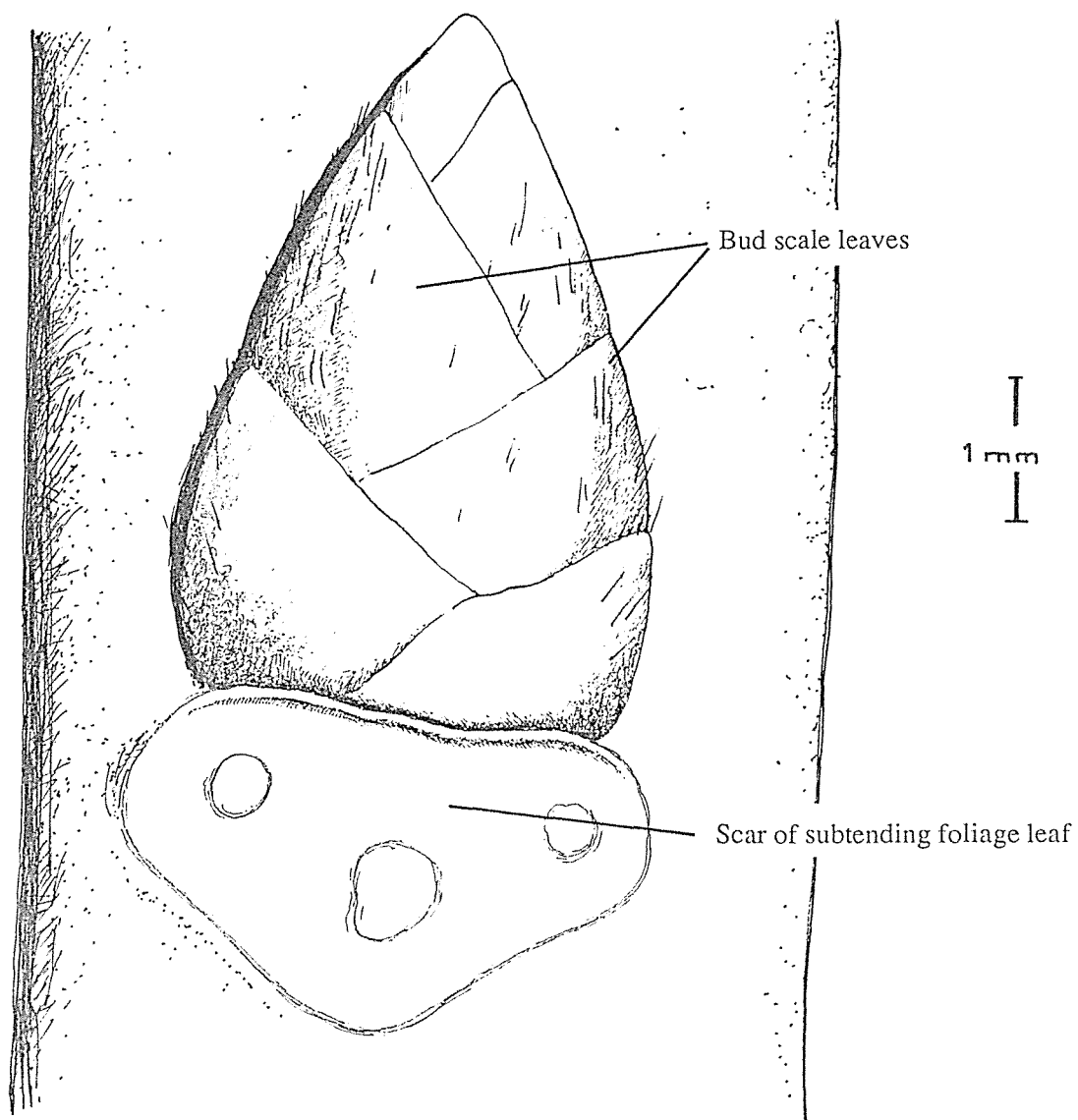


FIG. 1.6a An intact bud - only scale leaves are visible.

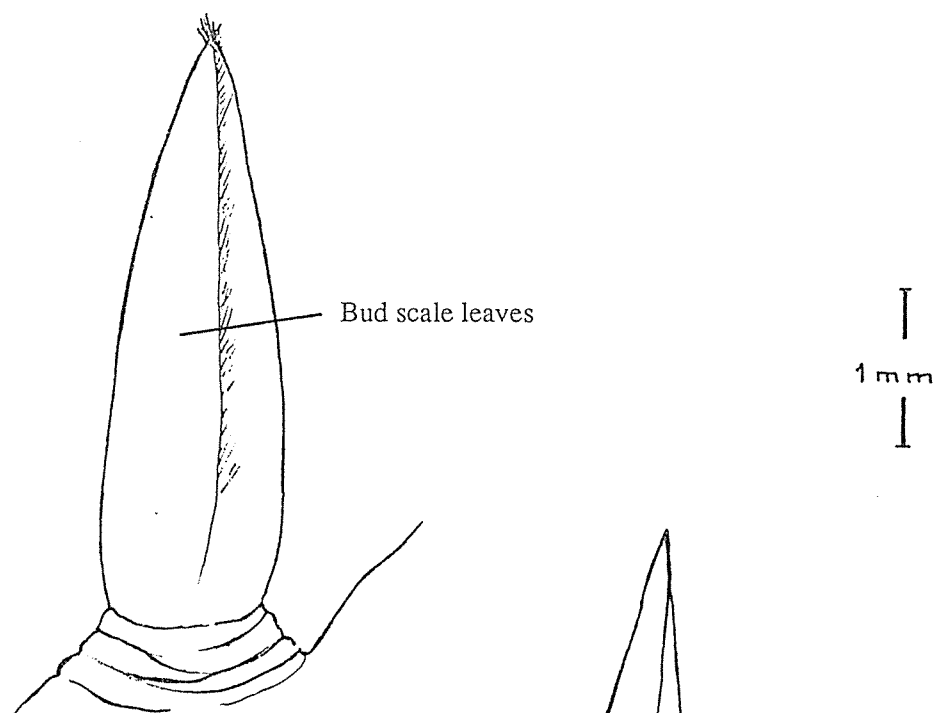


FIG. 1.6b Nine scale leaves have been removed.

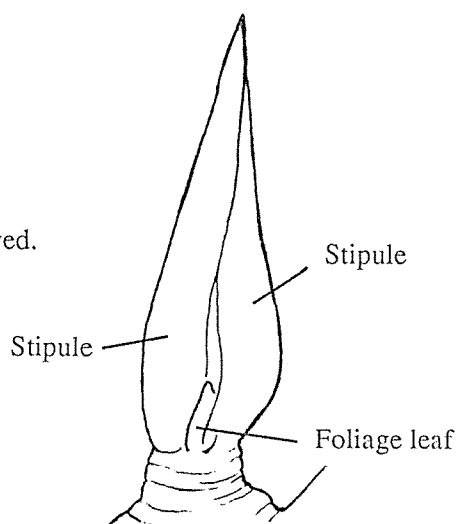


FIG. 1.6c Twelve scale leaves have been removed. The thirteenth structure is a foliage leaf enclosed within a pair of stipules.

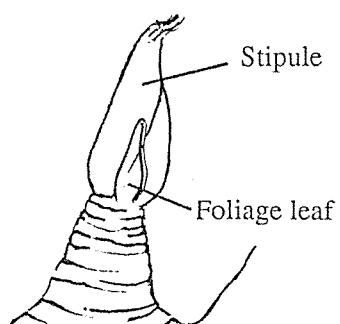


FIG. 1.6d In this bud the fourteenth primordial structure is a foliage leaf which is larger than the previous one both in absolute terms and relative to its enclosing stipules. After the twelfth structure (a scale leaf) all primordia initiated are foliage leaf primordia. The number of scale leaves in fully grown axillary buds can vary between nine and twelve.

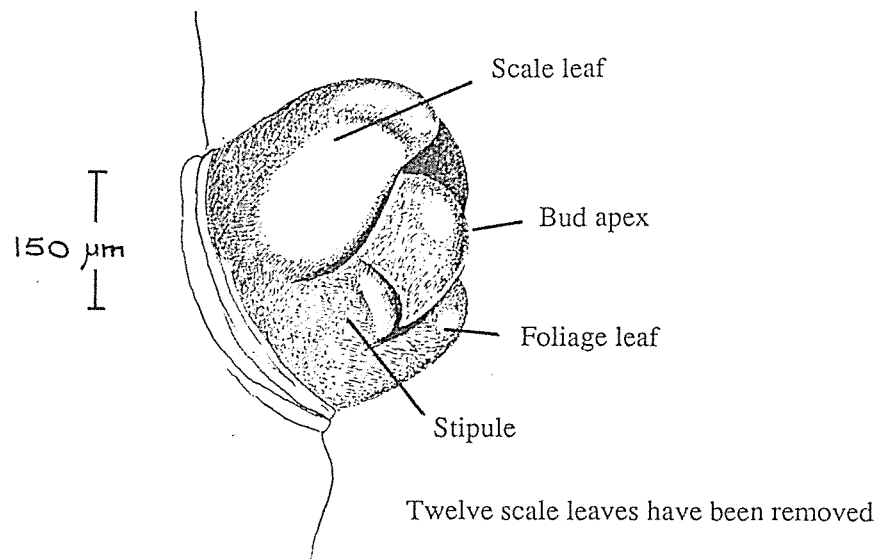
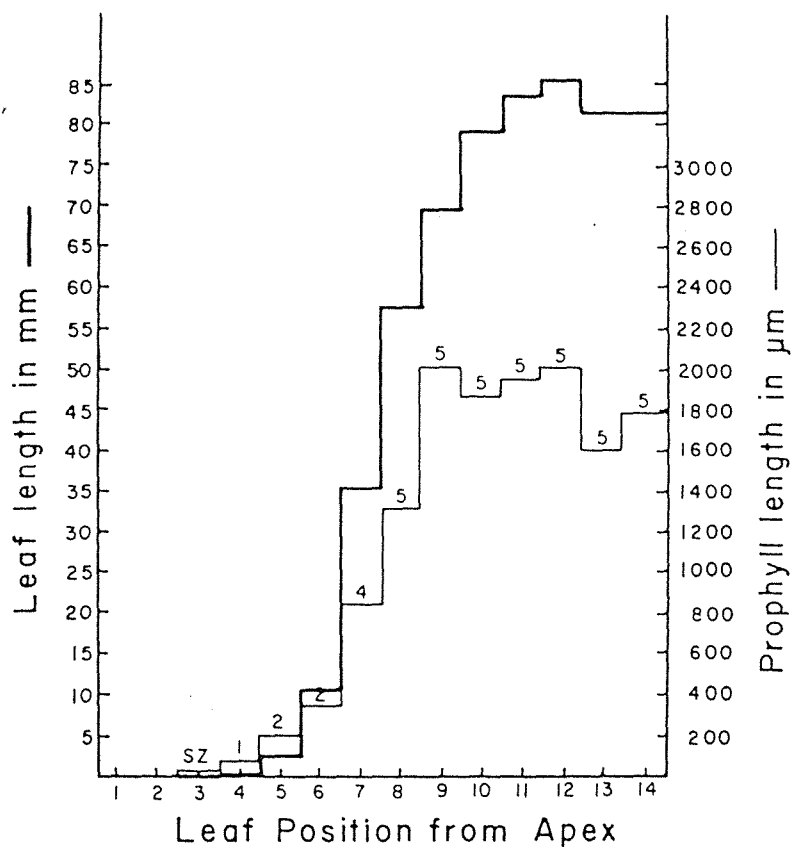


FIG. 1.6e An axillary bud apex at the time of transition from scale leaf initiation to foliage leaf initiation.

FIG. 1.7 *Eichhornia crassipes*. —

Comparison of leaf position numbered from the apex with both total leaf length (thick line) and prophyll length (thin line) for a single plant. Prophyll length measures bud length during early development since the prophyll encases the rest of the bud. Numbers associated with the graph of prophyll length are the number of leaves inside the tubular prophyll. The axillary bud shell zone (SZ) is visible in the axil of the third leaf from the apex. The axillary bud increases in length and produces leaves as the subtending leaf expands (leaves 4–9), but as that leaf matures, the bud stops growing in length and stops producing new leaves (leaves 9–14).



Reproduced from: Richards, J.H. Developmental potential of axillary buds of water hyacinth. *American Journal of Botany* 69(4), 1982. Page 616

CHAPTER 2

A Survey of the Different Patterns of Axillary Bud Growth in Angiosperms.**Materials and Methods****Materials**

The major objective of this study was to describe the growth pattern of axillary buds in a wide range of angiosperm plants with different growth forms. The following species were studied:

<i>Acer platanoides</i>	<i>Aristotelia fruticosa</i>
<i>Aucuba japonica</i>	<i>Bromus wildenowii</i>
<i>Clematis montana</i> cv.	<i>Cordyline australis</i>
<i>Crocasmia x crocosmiifolia</i>	<i>Hebe speciosa</i> .
<i>Helianthus annuus</i>	<i>Hydrangea macrophylla</i>
<i>Ilex aquifolium</i>	<i>Lolium perenne</i>
<i>Lonicera x americana</i>	<i>Lupinus angustifolius</i>
<i>Lycopersicon esculentum</i>	<i>Melicytus ramiflorus</i>
<i>Muehlenbeckia australis</i>	<i>Myoporum laetum</i>
<i>Passiflora mollissima</i>	<i>Phormium tenax</i>
<i>Pittosporum crassifolium</i>	<i>Salix fragilis</i>
<i>Sambucus nigra</i>	<i>Solanum aviculare</i>
<i>Solanum tuberosum</i>	<i>Stachys sylvatica</i>
<i>Tradescantia fluminensis</i>	<i>Trifolium repens</i>
<i>Tropaeolum majus</i>	<i>Ulmus procera</i> cv. <i>Van Houlte</i>
<i>Viburnum japonicum</i>	<i>Vicia faba</i>
<i>Vitis arnurensis</i>	<i>Zea mays</i>

Plants growing on the Massey University Campus, in my garden, or *en route* between these two locations, acted as the major source of experimental material. Other plants were grown from seed in the botany department greenhouse. A great deal of consideration was given to the selection of plants so that examples of woody, herbaceous, monocarpic, polycarpic, annual and perennial plants were studied. In general a single plant, or a uniform population of plants, was sampled throughout the survey in order to obviate the need for a

large amount of replication - preliminary studies on a large number of shoots from different *Salix fragilis* plants indicated that growth was very uniform within a species; a number of shoots from at least six different trees were examined and in all cases the same basic pattern was found to exist.

It was found that certain features made examination of bud development difficult or impossible. Pubescent leaf primordia were difficult to identify as discrete structures; latex secretions obscured bud primordia as dissection proceeded; buds which did not protrude far from the stem, but instead were located close to or below the level of the stem's surface were inaccessible. However, it was found that most dicotyledonous plants and many monocotyledonous ones were amenable to the methods used.

Method

Shoots and seedlings were observed under an Olympus binocular dissecting microscope at magnifications of up to 40 times. The procedure for dissecting a shoot was as follows: the subtending leaf at the proximal node - node number one - was removed, care being taken so as not to damage the axillary bud; the leaf's length was measured; the axillary bud at node one was examined, and if a sheathing structure was present it was removed; the length of the outermost foliage or scale leaf primordium was measured (in one or two instances the outermost primordium was exceeded in length at an early stage of bud growth by the leaf primordium immediately inside it. In such instances the longest visible leaf primordium was measured); successive leaf primordia were carefully removed with a fine scalpel until the apex of the axillary bud was reached; the total number of leaf primordia in the axillary bud was noted; the procedure was repeated at successive nodes until the shoot apex was reached, a scalpel and the dissecting microscope having to be used for the last stages. Distances were measured between successive nodes on shoots in many instances. FIG. 2.1 shows documentation for the dissection of a shoot of *Lolium perenne*.

Lengths were measured in three ways:

1. Eyepiece Micrometer
2. Ruler
3. Specially Constructed Stage Micrometer

Large length measurements such as some internode lengths and most subtending leaf lengths were made with a standard metric ruler. Smallest measurements were made with an eyepiece micrometer. However, a need was found for a more

flexible system of measurement for some structures within axillary buds which could not be dealt with by these two means. A micrometer was constructed by scribing eight equal divisions into one single millimetre on a 300 millimetre ruler. The divisions were checked for accuracy with the eyepiece micrometer and, when possible, the measurements being made with this micrometer were checked for accuracy against an eyepiece micrometer. This micrometer was found to be invaluable for making measurements where, for instance, structures were not lying flat or were not within reach of the eyepiece micrometer scale. A conventional stage micrometer was found to be unsuitable for making measurements in any of the situations encountered - it may be very accurate but it is clearly designed for such jobs as calibration of the eyepiece micrometer and is clumsy in the extreme when used to make direct measurements.

It became clear that an accurate assessment of primordium initiation needed some account to be taken of the dynamic nature of the process. In each species a survey was made of the different stages of development in the bud apex to determine at what stage of growth in one primordium - say primordium number 5 - the next primordium - in this case number 6 - first became visible. At this point primordium number 5 was regarded as being "completely initiated." The "degree of completion" of the next primordium was calculated by dividing its length by the length of the previously "completed" primordium. Hence all counts contain fractions of a primordium. The reader should refer to FIG. 2.3, which illustrates axillary bud apices from *Salix fragilis* and clarifies the calculation of the total number of primordia in a bud, as well as referring again to FIG. 2.1.

Treatment of Results

Preliminary assessment of the importance of each parameter indicated that the internode length correlated quite well with subtending leaf length. (See FIG. 2.4.) Hence it was decided to omit internode length from the list of parameters being analysed. Two further reasons for this omission were:

a) In a number of instances, more especially amongst the monocotyledonous species, the exact measurement of the length of internodes was made impossible because the point of insertion of leaves on the stem is not clearly defined.

b) Inconsistent leaf arrangement in a number of species would have caused very significant difficulties. For instance, in *Lupinus angustifolius*,

opposite and alternate leaf arrangements were often found on the same shoot, with a transitional region in which an internode was difficult to identify clearly. Hence, it would have been important to measure the internode distance between two leaves forming a decussate pair in some locations but impossible in others. In *Feijoa sellowiana* both decussate and whorled leaf arrangements were found, sometimes on the same shoot, making for similar difficulties.

For each species the data from only four or five representative dissections only have been included. These dissections were made at different stages in the plant's life in an attempt to show something of the dynamics of axillary bud growth. In a number of species, plants were grown from seed. Seedlings were grown under identical conditions in order to minimise development of different morphological patterns. Care was taken to choose samples which were truly representative of the majority of seedlings. Where samples were taken from saplings, bushes or trees, a similar approach of looking for representative shoots was taken. In the case of *Salix fragilis*, a small group of trees growing in one location was chosen, and water shoots growing out approximately horizontally were sampled; the terminal shoots from *Aristolelia fruticosa* saplings growing in one location were sampled; in the case of *Myoporum laetum*, shoots were taken from the outside of the approximately spherically shaped canopies of bushes of similar age and size growing in one plantation. In most cases measurements were made throughout the year (or the growing season in the case of deciduous species). Exact dates are given in the appendix.

It was assumed that any one stage would have developed into the next stage had it not been destroyed by dissection. This would seem to be a fair assumption, bearing in mind the uniform nature of the sampled material and the stability and predictability of developmental processes within any particular species. MacDaniel's work with tobacco (MacDaniel, 1989) is of relevance here.

Results were tabulated. For each shoot or seedling examined a graph was plotted of the following three parameters against the number of the node at which axillary buds and their subtending leaves were found:

- a) the number of leaf primordia in each axillary bud
- b) the length in millimetres of the first-formed (oldest) or longest primordium in each bud
- c) the length in centimetres of the leaf subtending that bud.

The base of a shoot was either the point of insertion on the main axis or, in the case of seedlings, the point of attachment to the embryonic root. The first-formed node was labelled number 1. In the case of seedlings this was the

cotyledonary node (in dicotyledons) or the coleoptile node (in monocotyledons). The data from the rye grass shoot illustrated in FIG. 2.1 are graphed in FIG. 2.2.

Data for all species examined are given in the appendix. Selected examples have been used in the text to illustrate particular points. The graphs illustrate axillary bud growth **relative to growth in the apex of the shoot that bears them**. An **absolute** value for axillary bud growth can not be measured using such destructive techniques, but may be inferred from comparisons between successive dissections.

Axillary bud growth, in terms of the rate of initiation of leaf primordia, often occurs in a limited number of apparently distinct stages; I have defined them as follows:

Phase 1 - Bud Initiation

Phase 2 - High Bud Growth Rate

Phase 3 - Low Bud Growth Rate

In *Salix fragilis*, axillary bud growth was found to follow this typical pattern. Axillary buds first become visible about ten or eleven nodes below the shoot apex. At the stage when leaf primordia can be detected in the axillary bud, measurement of the rate of leaf primordium initiation on them can start. This rate has been found initially to lie between 1 and 1.25 times the rate of leaf primordium initiation in the shoot apex. After a period of rapid growth, initiation of primordia slows down. (This slowing seems to coincide with the cessation of expansion growth in the subtending leaf.) In some axillary buds, notably those close to the base of the shoot, axillary bud growth remains slow throughout shoot growth.

However, many of the examples described later did not follow this pattern. In such cases one or more of these phases were absent.

It would seem that the most significant feature of an axillary bud - which is essentially a **primordial** vegetative or reproductive lateral shoot - is its **potential** for rapid expansion. The size of the individual primordial structures within the bud would seem to be of less significance in this respect than the **number** of structures formed. Leaf primordium initiation is also more directly dependent on the activity of the bud apex. Hence it was decided to concentrate on the data relating to the number of primordia per bud - the graph of this function against node number was defined as the **Growth Curve**. Graphs of data for each particular species are located immediately after the relevant tables of data in the appendix.

FIG. 2.1 Documentation for the dissection of a shoot of *Lolium perenne*. The stem is represented by the long vertical line. Short horizontal lines drawn across this vertical represent nodes, and the dots above them represent axillary buds. Node numbers (enclosed in circles) are written below each node and leaf length in centimeters is written by the side. Tie lines are drawn to boxes at the side which contain data relating to each axillary bud. Within this, numbers in the top left corner indicate lengths of successive leaf primordia in millimeters or micrometers. Numbers followed by the letter P indicate the number of leaf primordia present in the axillary bud. Diagrams of the apical region of each bud are included. The leaf primordia are numbered in the same way as on the shoot, with the distal primordia (the first formed) being number one. The diameter of the axillary bud apex in micrometers is also shown. The shoot apex is also illustrated; leaf primordia are numbered in the same way as leaves on the rest of the shoot.

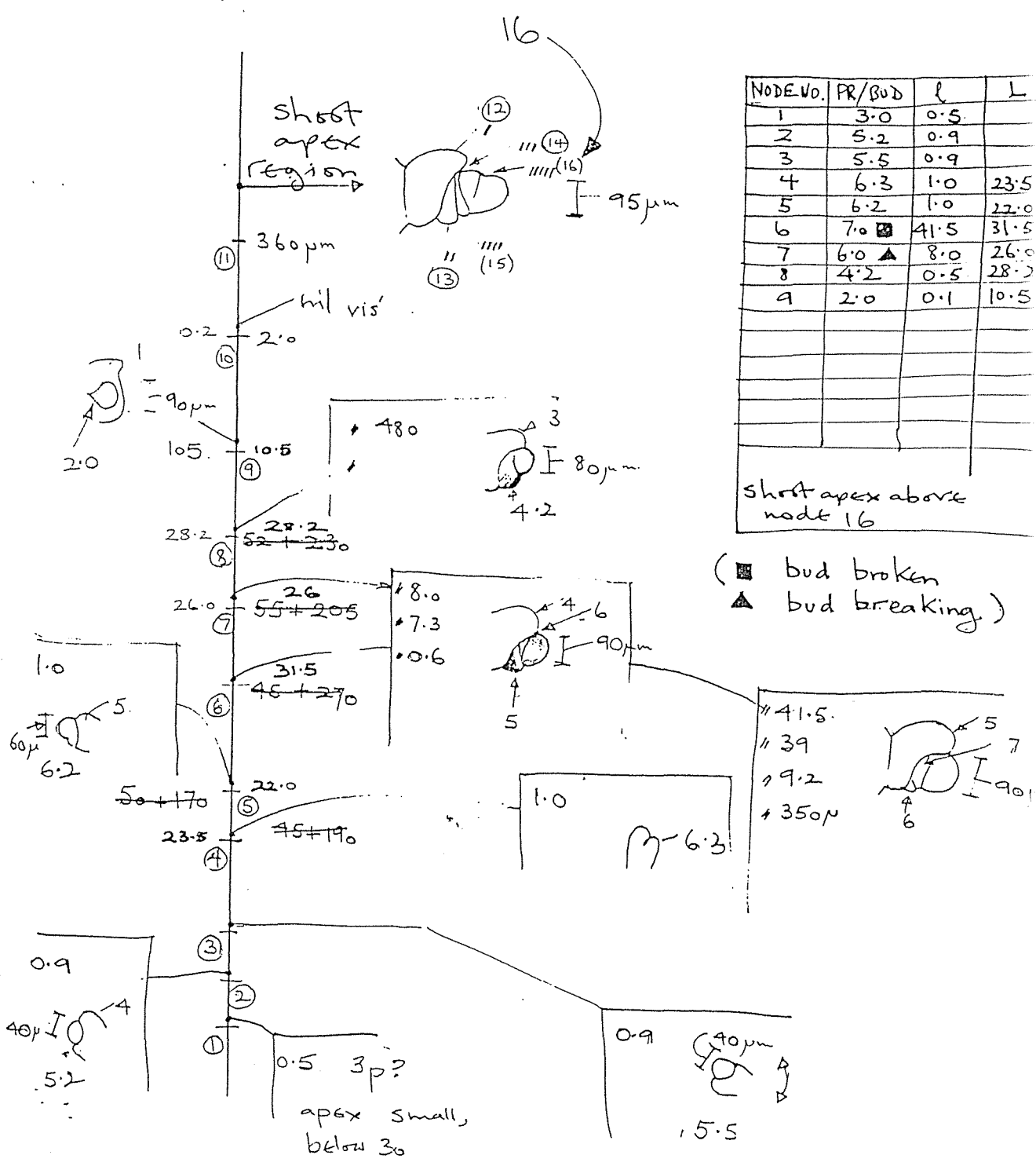


FIG. 2.2 Graph of number of leaf primordia per axillary bud - A, length of longest axillary bud leaf primordium - B, and subtending leaf length - C, against position on the shoot (node number) at which the axillary bud and its subtending leaf are found, in the shoot of *Lolium perenne*. Documentation for the dissection is presented in FIG. 2.1

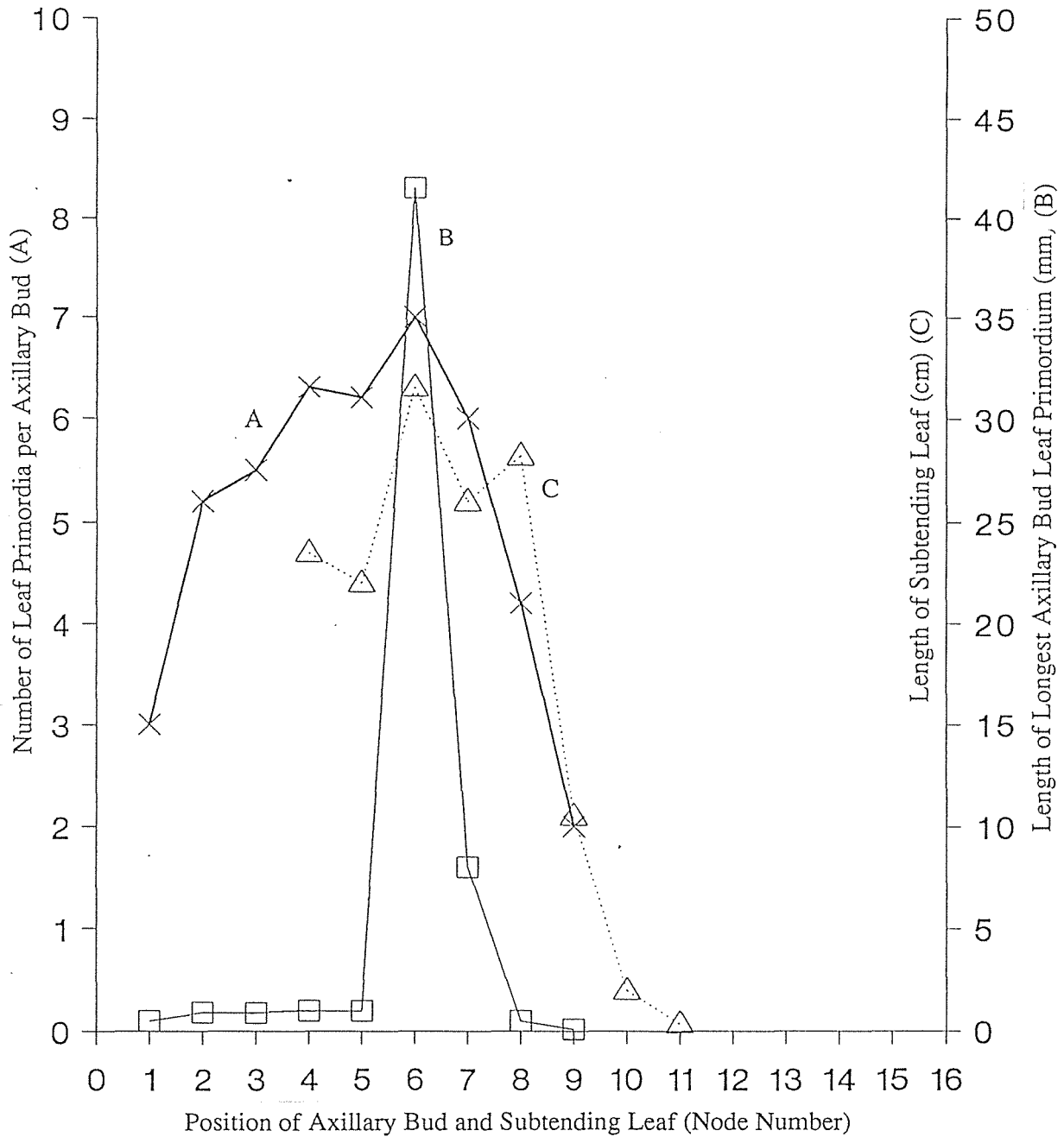


FIG. 2.3 Front and side views of axillary bud apices in *Salix fragilis* to illustrate the method of calculating the total number of leaf primordia in an axillary bud. It was found that initiation of a leaf primordium on the axillary bud apex occurred when the previously formed leaf primordium had grown to about $110\mu\text{m}$ above the apex. At this point the growing primordium was regarded as fully formed. A primordium which was less than $110\mu\text{m}$ long was regarded as partially formed. Its length above the apex was measured and expressed as a fraction of $110\mu\text{m}$ to give a measure of its stage of growth. For instance, the primordium in apex e extends $50\mu\text{m}$ above the bud apex, and therefore comprises $50/110$ primordia, or 0.45 primordia. If this was, say, the tenth primordium to be initiated, the total number of primordia in this axillary bud would have been recorded as 10.5, as this measure was expressed in the data to an accuracy of one decimal place.

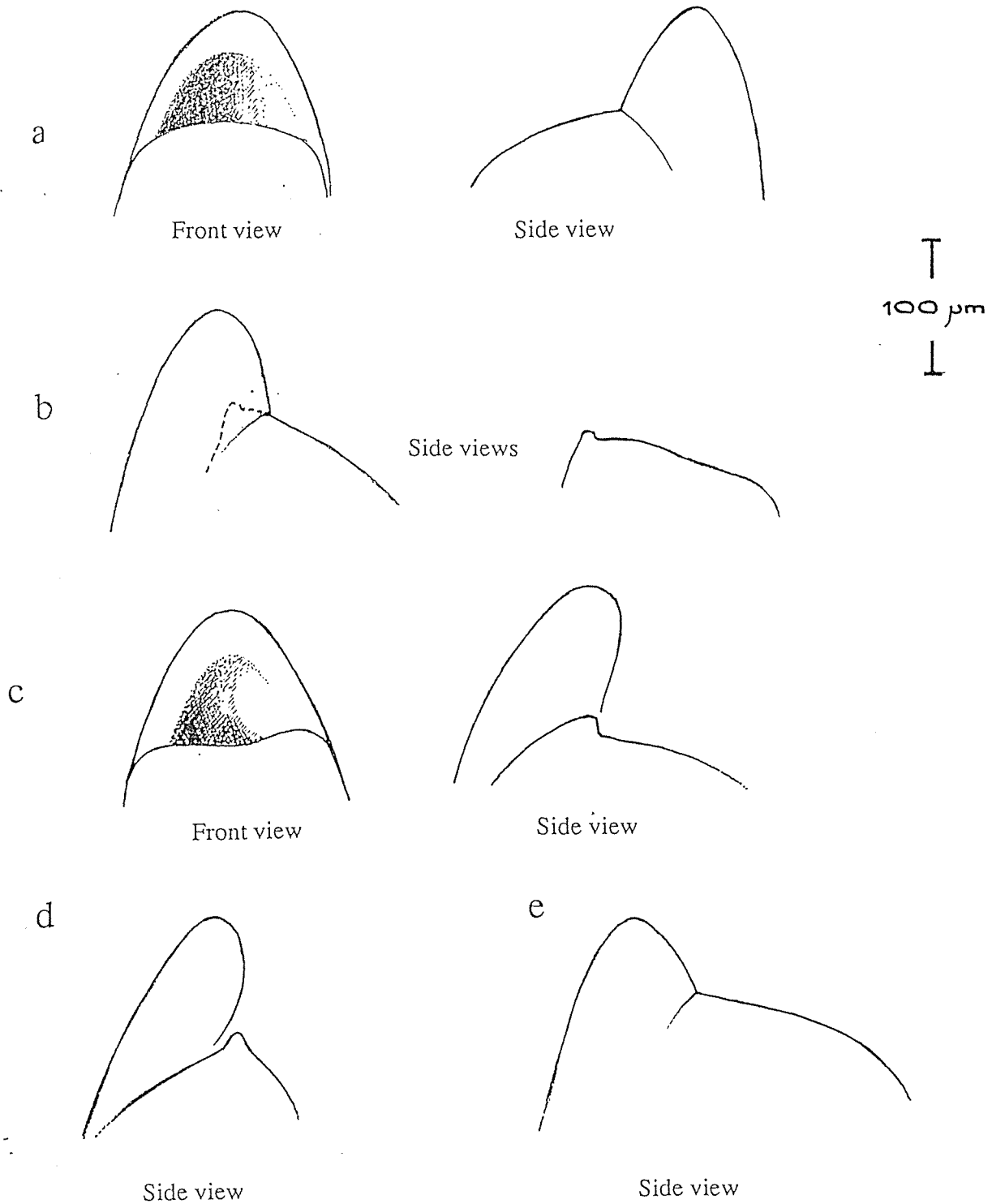
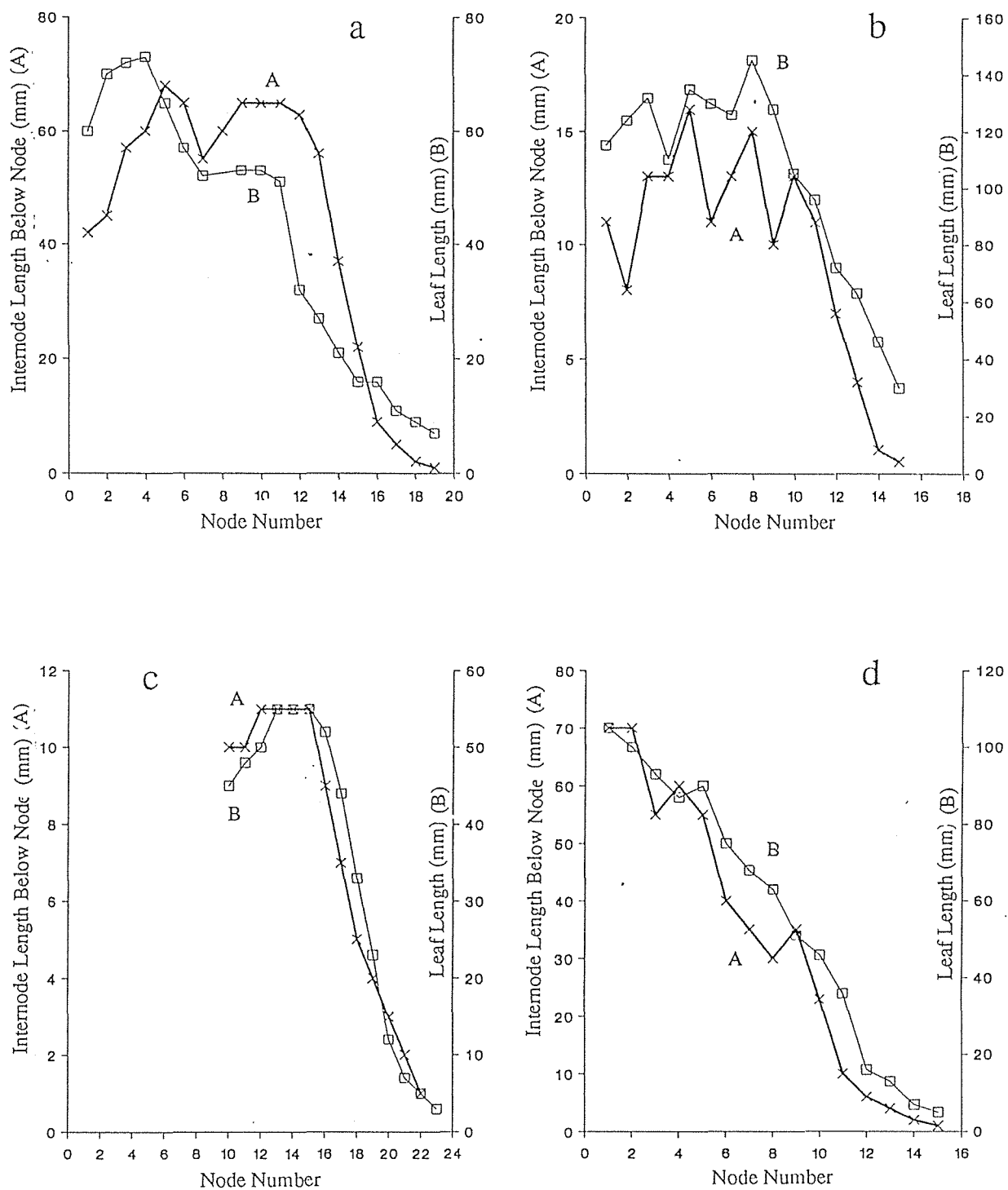


FIG. 2.4 Graphs of internode length below a node - A, and leaf length - B, against node number in a): *Muehlenbeckia australis*, b): *Meliccyus ramiflorus*, c): *Hebe speciosa* and d): *Passiflora mollissima* indicating a correlation between leaf length and internode length.



CHAPTER 3

**Rate of Leaf Primordium Initiation in Axillary Buds
Relative to the Rate of Initiation of Leaf Primordia
in the Shoot Apex**

In most species, leaf primordium initiation occurs at a fairly constant rate in the axillary buds close to the shoot apex. Leaf primordium initiation in these buds can be usefully expressed as a rate **relative to the rate of initiation of leaf primordia in the shoot apex**. This rate, referred to from now on as the **Relative Rate of Primordium Initiation**, can be inferred from the slope of a single growth curve. However, there is an important reservation about such a procedure - the form of successive growth curves must remain the same. If the slope of the growth curve changes with time, or if the shoot apex changes behaviour, one must resort to comparing successive growth curves to find the relative rate. Three examples will illustrate the problem. In FIG. 3.1, simplified growth curves have been drawn representing shoot growth in *Salix fragilis*, *Melicytus ramiflorus* and *Lolium perenne*. They cover a period of six to nine months. The locations of the shoot apex are indicated by a solid square on the horizontal axis. In *Salix*, the slope of the growth curve changes radically during the early phases of growth. Only when growth has become well established does the slope of the steep portion of the curve (representing buds close to the apex) accurately relate the rate of primordium initiation in all the buds on that part of the curve to the rate of initiation in the apex. Comparison between successive graphs shows that the slope of the growth curve decreases at a particular point, indicating that primordium initiation is slowing down - this point is indicated by arrows on the diagram.

Growth of shoots in *Melicytus* was followed from the start of the spring flush in September through to mid summer, with a final dissection being made in mid winter. The slope of the growth curve in phase 2 - the rapid growth phase - was found to remain the same throughout. The change from phase 2 to phase 3 - indicated by the slope reduction - occurred at a progressively later stage in axillary bud development: in September, growth slowed when buds at about node 12 contained 14 primordia; in early October growth was slowing when buds contained about 20 primordia (these were found at about node 20); in mid October growth slowed in buds at about node 30 containing 22 primordia; and in late November growth slowed at about node 41 in buds containing 26 primordia.

(By mid July the situation in the shoot had changed in that axillary buds along its whole length had apparently recommenced growing. This particular sample was therefore not considered as having the same growth pattern as the previous four and is not included in this argument.) The regions of the growth curves which relate to phase 2 of bud growth are fairly obvious in this species.

In *Lolium*, the shoot apex develops into a progressively larger, more complex structure as it grows. In the first shoot dissected, the apical region contained only four leaf primordia less than 3mm long. In the second, dissected 45 days later, it still contained four primordia less than 3mm long. Then, 45 days later still, it contained 6 such primordia, and 30 days after that it contained 8 primordia less than 3mm in length. The final dissection, made 53 days after the previous one, revealed the apical region of the shoot still contained 8 leaf primordia shorter than 3mm in length. (It would appear that the shoot's apical region builds from a rudimentary structure into a large, relatively stable form, before the onset of flowering, which involves a far more radical change in form.) This gradual change in structure in the apical region provides a confusing factor. If the rate of leaf primordium initiation in the axillary buds relative to that in the apex is to be determined one must calculate the growth in a bud at a specific node over a period and compare that with the growth in the shoot apex over the same period. This actually gives a different result from that obtained by simply reading the slope of the growth curve. For instance, the slopes of the growth curve in plants dissected on June 1st and July 17th were 2.17 and 1.70 respectively, but comparison of the two graphs shows that the rate of initiation of primordia at node 7 was only 0.53 times that at the shoot apex over this period. (This phenomenon was only detected in the grasses. In all of the other species studied the form of the shoot apex remained basically stable throughout the period studied.)

Not all the species studied were amenable to this form of analysis - FIG. 3.2 shows the values for all that were. In all cases data represent the slopes of the early, straight portions of the growth curves representing phase 2 growth. The minimum and maximum rates are given for each species. One or two points are of interest:

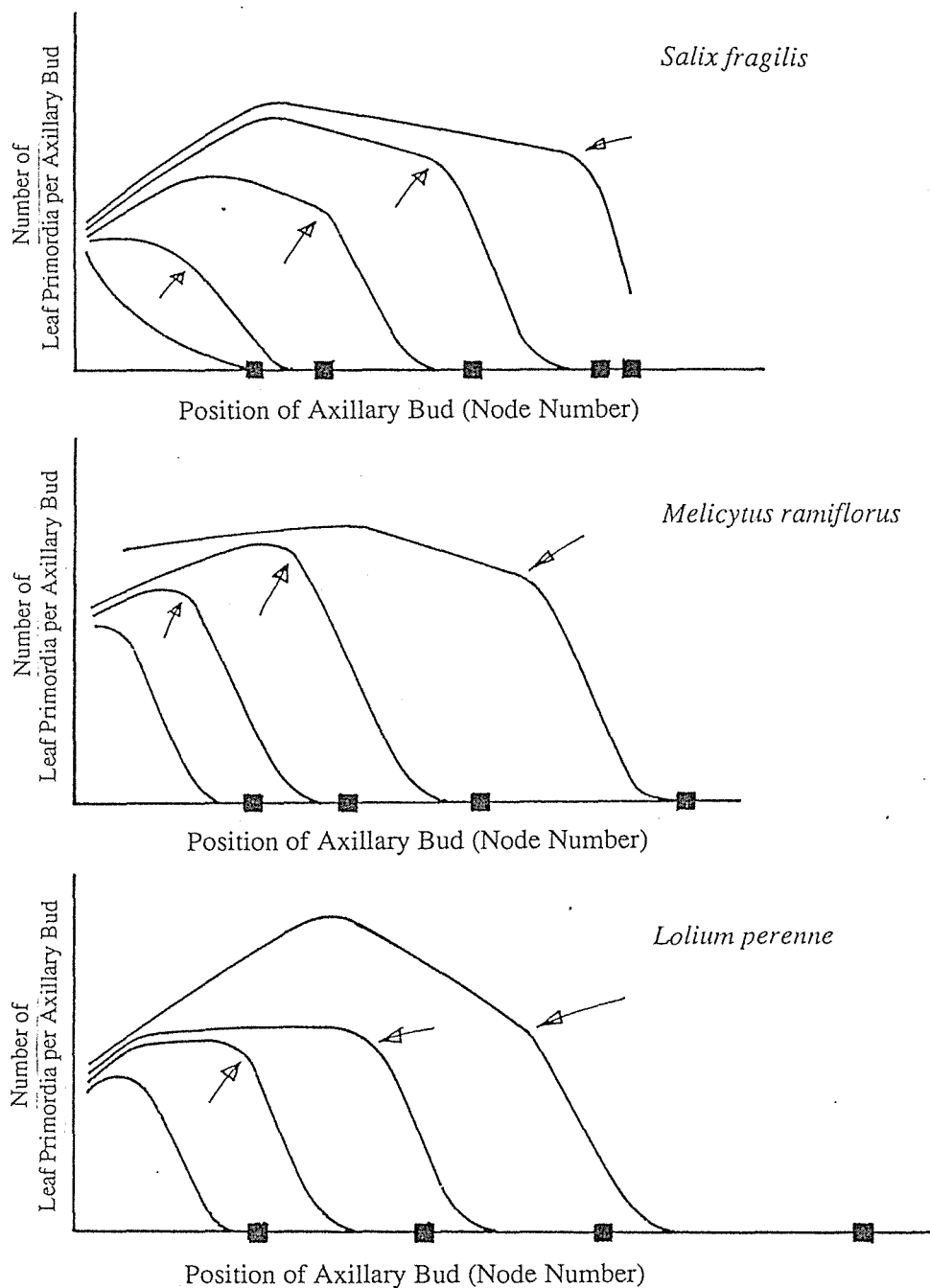
1. *Ulmus*, *Salix*, *Aristotelia* and *Melicytus* - the large trees contained in the survey for which calculations of growth curve slope could be carried out - have relative rate maxima greater than unity.

2. In sylleptic species - *Tropaeolum*, *Vitis* and *Stachys* - relative rates are less than unity, even in the region where buds are youngest and growing most rapidly.
3. In *Bromus*, there was a large range of slopes (0.93 to 2.68) with a very high maximum. When the rate of axillary bud primordium initiation relative to shoot apex primordium initiation was calculated by comparison between successive graphs a greater range of values was obtained (0.85 to 3.1). A similar situation was found in *Lolium*, though the range between minimum and maximum slopes was less (1.8 to 2.17), and direct calculation by comparison between graphs yielded generally lower values (0.53 to 1.66).
4. This small number of randomly selected species displays a large range of relative rates, only a few having average relative rates close to unity.

Discussion

It is of interest from a viewpoint different from that of calculating relative rates of initiation, that the slope of the growth curve in the two grasses studied remains constant while the apex is undergoing changes in form. It indicates that the axillary buds are growing at a constant rate **relative to each other**. In other words they appear to have a developmental program which is not influenced by the apex. This in fact relates to the fundamental issue which this study is aimed at investigating - the relationship between the growth of axillary buds and the functioning of the stem apex. Conventional wisdom has it that bud break is controlled by activity in the stem apex, but no such link has been established for growth in axillary buds before bud break. The information presented in this chapter is not conclusive of any argument, but it does suggest that there is **no** general or universal pattern to be found in the figures of relative growth rates for the considerable range of species studied. However, the patterns **within** each species are relatively uniform.

FIG. 3.1 Simplified diagrams based on the growth curves of *Salix fragilis*, *Melicytus ramiflorus* and *Lolium perenne*. Arrows indicate points at which axillary bud growth slows down. The graphs cover most of the growing season (*Salix*) or the period between the onset of the spring growth flush and the onset of flowering (*Melicytus* and *Lolium*). Black squares on the horizontal axis indicate the locations of shoot apices.



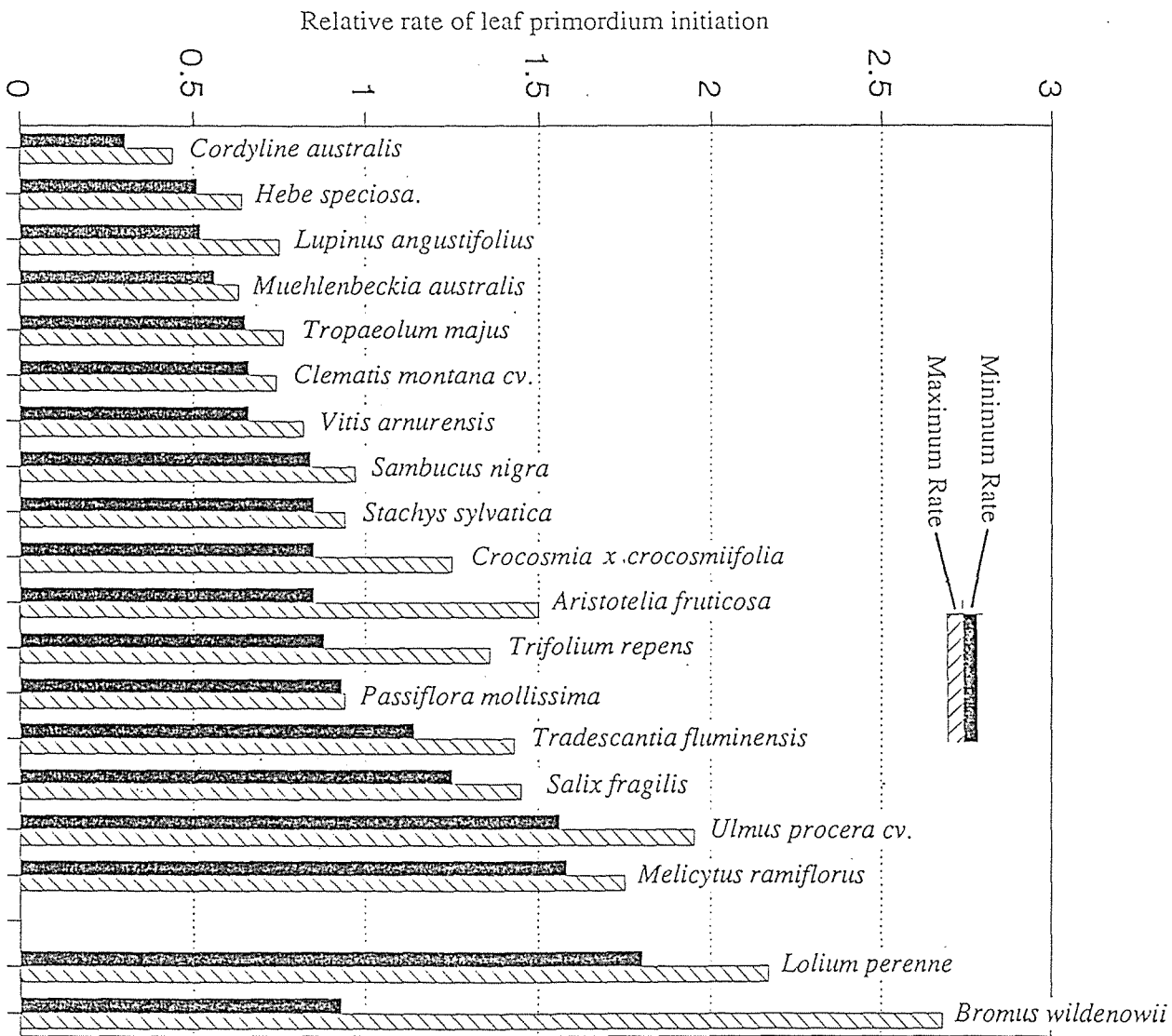


FIG. 3.2 Relative rate of leaf primordium initiation for a number of plant species. The values for *Lolium* and *Bromus* are those for the slope of their growth curves. All other values were obtained in a similar way.

CHAPTER 4

Axillary Bud Growth Patterns

As more and more plants were examined their patterns of axillary bud primordium initiation and growth were found to fall into a few clearly defined categories. A first separation into monocarpic and polycarpic plants led to further separations. Polycarpic plants were classified according to whether they were sylleptic or proleptic. (A sylleptic pattern is one in which axillary buds develop directly into a lateral shoot without a period of rest, whilst proleptic buds enter a period of rest at some time in their growth, before breaking to form a lateral shoot. These definitions refer only to growth in a general sense. In a sylleptically growing bud the leaf primordia themselves develop into expanding leaves in much the same way as leaf primordia in the shoot apex, while the leaf primordia in a proleptically growing bud enter a period of restricted growth - with no expansion growth - before becoming foliage leaves. Initiation of leaf primordia continues unabated in sylleptic buds, but is arrested at some time in proleptic buds.) The proleptic species then provided a further series of distinct groups. It is difficult to say how many more different patterns would have been detected in a larger sample of plants.

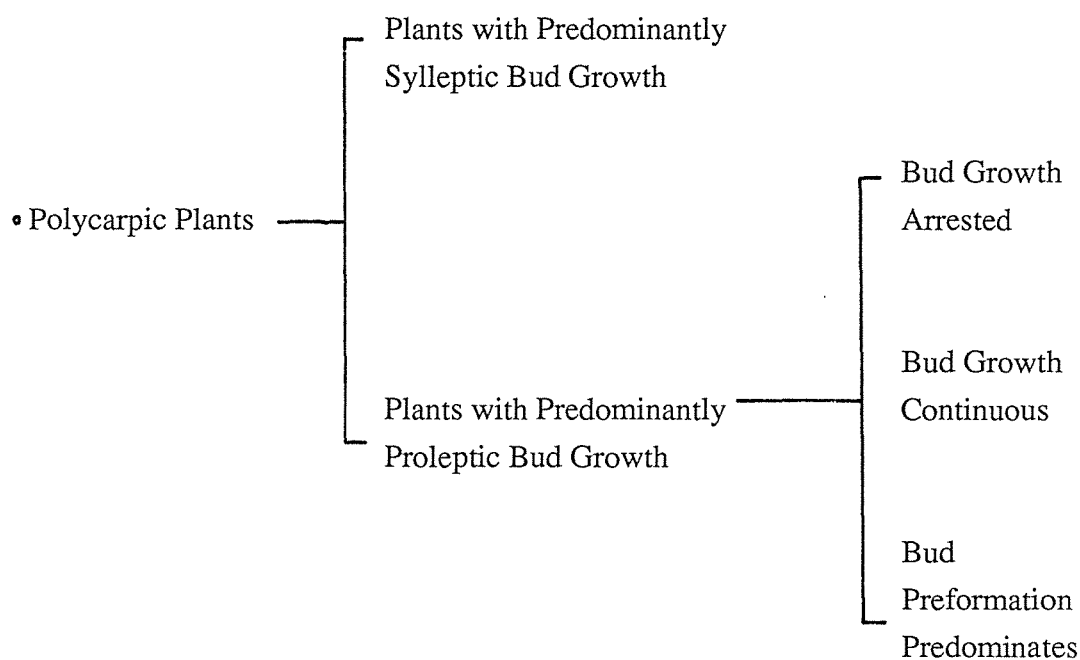
The theoretical possibilities for variation in bud behaviour would seem to be as follows: in the period of growth immediately following the initiation of an axillary bud the rate of initiation of bud leaf primordia may be greater than, the same as, or less than, the rate of initiation of leaf primordia in the shoot apex. Leaf primordium initiation may continue in the axillary bud at this rate relative to the shoot apex for a protracted period or it may change; primordium initiation in deciduous plants can be expected to cease at the end of the summer. The **form** of primordia initiated within one bud may remain constant, or may change gradually or abruptly, or may indeed change from foliar to floral. All bud leaf primordia can be expected to grow, but a clear distinction can be drawn between the restricted growth of a primordial structure and the kind of expansion growth which occurs in a growing leaf.

The following classification system, based on the plants surveyed in the present study, does seem to encompass the theoretical variations discussed above. The examples described will hopefully be representative of the groups as a whole, though variations in specific features will obviously occur within each group to a greater or lesser extent. Data concerning each plant are to be found in

the appendix. In the discussion of growth curves, reference is made to plant or shoot numbers. These are the numbers given to each plant or shoot in the appendix.

Classification Outline

- Monocarpic Plants



- Unique Bud Growth Types

Group Descriptions

MONOCARPIC PLANTS

Helianthus annuus; *Vicia faba*; *Lupinus angustifolius*; *Zea mays*

Group characteristics: flowering occurs only once during the plant's lifetime; the onset of flowering coincides with a change - in some, most or all axillary buds - from initiation of leaf primordia to initiation of primordial floral structures. Hence axillary buds capable of continuing vegetative growth are not present.

Discussion

In *Helianthus*, developments in the first formed buds reflected the pattern of growth in the stem apex: leaf primordia were initiated in a decussate pattern early on; a change in axillary buds to spiral phyllotaxis, with inflorescence formation correlated with stem apex flowering, occurred later in buds higher up the shoot; nodes in various locations often had no axillary buds, especially when growing conditions were adverse. In FIG. 4.1 four growth curves are presented. Curve (a) is for a young seedling in which all the nodes present on the main shoot had axillary buds. The shoot apex was just above node 14. Curve (b), plant 2, shows that, at the nodes above node 3, no axillary buds were present. The shoot apex, which was by now flowering, was just above node 30. Plant 3, curve (c), had a region between nodes 5 and 9 in which axillary buds were not present, but buds were initiated on the shoot above this region. On plant 4, curve (d), only one vegetative bud was found. Additional data are located in the appendix.

In *Vicia*, most plants had a number of nodes without axillary buds; primary bud complexes - groups of axillary buds in the same axil, usually at different stages of development - were found in the lower nodes, and many axillary bud apices flowered after the shoot apex bearing them had flowered. Similarly, many axillary buds in *Lupinus* had been induced to flower by the time the shoot apex flowered. In *Zea*, flowering occurred in axillary buds at three or four nodes below the shoot apex following flowering in the shoot apex.

POLYCARPIC PLANTS

Plants Exhibiting Sylleptic Bud Development

Stachys sylvatica; *Vitis arnurensis*; *Tropaeolum majus*; *Solanum tuberosum*;
Solanum aviculare; *Lycopersicon esculentum*.

Group Characteristics: axillary buds do not pass through a rest period after their initiation before their outgrowth as a lateral shoot; the pattern of leaf primordium expansion in axillary buds is similar to that in the shoot apex, though it apparently occurs at a lower rate. It could be said that such structures are buds only at their initiation, becoming developing lateral shoots very soon afterwards.

Discussion

In *Stachys*, leaf primordium initiation in axillary buds close to the shoot apex occurred at a similar rate to that found in the shoot apex itself. After about five nodes had been laid down between the bud and the shoot apex, primordium initiation slowed significantly. The slope of the growth curve in the linear, phase 2 region was between 0.85 and 0.94. (FIG. 4.2)

Rates of initiation in buds of both *Vitis* and *Tropaeolum* in the region of the shoot close to the shoot apex were less than in the shoot apex itself. It is difficult to determine whether or not a slowing in initiation occurred later, since bud break, senescence or flowering occurred in older regions of the shoot. Not all buds in *Vitis* are sylleptic. Second order buds laid down at the base of axillary shoots remain unbroken throughout the summer, autumn and winter, breaking the following spring to form new laterals.

Syllepsis was found to occur widely in the three solanaceous species studied. However, these species were characterised by a distinctive pattern of flower initiation: the shoot apex flowers after a number of leaf primordia - characteristic for each species - has been initiated. In *Solanum aviculare*, the transition occurs after initiation of about 21 leaf primordia; in *Lycopersicon* it occurs after 10 or 11 leaf primordia have been initiated on the initial shoot developing from the plumule, but in subsequently formed laterals it occurs after initiation of 4 or 5 leaf primordia. *Solanum tuberosum* differs from the other two species in that a subsidiary axillary bud does not take over as the main shoot apex after the apical bud has flowered. It also seems to have more flexibility in terms of the time of floral initiation, which occurred after 16 nodes had been initiated in two cases and after 21 nodes had been initiated in two other cases.

Plants Exhibiting Proleptic Bud Development

1. Bud Growth Arrested

Tradescantia fluminensis; *Trifolium repens*; *Bromus willdenowii*; *Lolium perenne*; *Passiflora mollissima*; *Cordyline australis*; *Phormium tenax*; *Hebe speciosa*;

Group Characteristics: each axillary bud stops growing completely after having developed for a particular time or after it has grown to a particular size.

Discussion

It is difficult to conceive of a plant in which axillary buds initiate primordia unceasingly. Not only would such a plant be wasting resources on a structure with little gain, but sheer size would eventually become limiting. However, contained in this group are species in which axillary bud growth ceased at a relatively early stage. In *Tradescantia*, buds stopped growing when they had attained 4 or 5 leaf primordia. A very similar pattern is found in *Trifolium*, growth ceasing at between 5.0 and 5.2 primordia per bud. In the two grasses studied, *Bromus* and *Lolium*, the cessation of growth at between 4 and 5 primordia per bud in the former and between 5 and 5.2 primordia per bud in the latter was detected in seedlings which were growing crowded together. One can see the most significant example of this pattern in the graphs relating to *Lolium*, especially plant 3, found in the appendix. After the seedlings were separated the majority of axillary buds broke within a fairly short space of time.

It has been apparent that bud growth ceases when buds have initiated a certain number of primordia. But another consideration is the distance between the shoot apex and the bud at the time the latter ceases growth. In *Trifolium* this distance was about 5 nodes. However, in *Tradescantia*, *Bromus* and *Lolium* this distance is highly variable. Hence the data obtained in this limited survey suggest that number of primordia per bud rather than the location of the bud on the shoot was the more significant factor. Maximum bud size in *Passiflora* appeared to be approximately 16 primordia. In *Cordyline*, 4.5 primordia per bud was the largest size attained in the relatively young plants examined - this size may of course be exceeded as the plant grows. *Phormium* is closely related to *Cordyline* and shares many features with it, especially the tendency to grow continuously along one major axis. Bud growth apparently slows rather than arrests, if the dissection of a mature plant is representative.

The developmental pattern in *Hebe* warrants a far more detailed study than has been possible here. However, it is clear that buds formed early in shoot expansion remained smaller than those formed later - it is difficult to say whether they would continue growing at all in fact - whilst some of the largest buds, which did not grow (as buds) larger than 4 primordia, were apparently destined to break eventually to form lateral shoots. Four growth curves for *Hebe* are presented in FIG. 4.3. Virtually no growth occurred in the buds at nodes 4 to 6; buds below nodes 13 or 14 attained their own characteristic size before their growth slowed; buds above nodes 15 to 18 - depending on the shoot - flowered. Buds between nodes 5 and 12 on shoot 2 were larger than those in comparable positions on shoot 3. This was probably due to variations in the sample material.

Growth curves for *Trifolium* are shown in FIG. 4.4. Plants 1 to 4 were seedlings of increasing age.

In a number of other species the number of primordia initiated per axillary bud was significantly larger. Growth curves for *Aristotelia* are shown in FIG. 4.7. Scale leaves were laid down in the shoot apex during autumn. Foliage leaves were then initiated within the compact apical bud. Axillary bud growth appeared to cease either when a maximum size had been reached - between 6 and 8 leaf primordia - or the buds were a particular distance from the apex - 8 to 10 nodes.

Melicytus is a woody perennial which had shoots which were continuously expanding and in which no interruption in the growth of the shoot apex could be seen. Larger and larger buds were found on the shoot until flowering and bud break were followed by initiation of new laterals. FIG. 4.8 shows growth curves for *Melicytus*. The first four graphs have a form which partly echoes that of *Hebe* in that a different bud size maximum was reached in each bud, this size being characteristic for a particular node number. Additional growth past this maximum in the buds between nodes 20 and 30 in shoot 5 may have been due to the commencement of spring flush activity.

2. Bud Growth Continuous.

Ulmus procera cv. Van Houlte; *Salix fragilis*; *Clematis montana* cv.; *Aristotelia fruticosa*; *Melicytus ramiflorus*; *Pittosporum crassifolium*; *Muehlenbeckia australis*; *Sambucus nigra*

Group Characteristics: axillary buds grow as long as the shoot apex continues to initiate leaf primordia.

Discussion

Almost half of the plants studied fell into this group. There are major differences in growth strategy: in a number of species the bud growth rate is apparently inversely related to the distance between a bud and the shoot apex. Superimposed on this basic pattern is a number of different strategic features - hence the exact pattern of axillary bud growth differs significantly from species to species. In *Ulmus* and *Salix*, the condition in the youngest shoots - the more basal axillary buds are largest - is rapidly superseded as the more apical buds grow at a greater rate. The end result is a shoot bearing axillary buds all of

similar size. In both cases it may appear as if bud growth ceases while activity at the shoot apex continues. In fact, by late January or early February most shoot apices had become senescent. Activity may have continued in the axillary buds in the distal region of the shoot, but this group of plants is defined on the basis of activity at the shoot apex so these two species do fulfill the stated criteria. FIG. 4.5 shows five growth curves for *Salix*. Some aspects are discussed in the introductory chapter. Growth curves for *Ulmus* are shown in FIG. 4.6. Axillary buds grew to a maximum size of about 20 leaf primordia. The apical region of all shoots died back during autumn, leaving the most apical surviving axillary bud to develop as the new shoot apex. By July (shoot 4) this bud has grown to a greater size than all the buds below it. Such was not the case in *Salix* - see FIG. 4.5.

Axillary bud growth in *Sambucus* (FIG. 4.12) is of a similar form to that in *Salix* or *Ulmus* in that regions of high and low growth rate can be identified, but differs in that the more basal axillary buds initiate leaf primordia at a rate only marginally less than in the most apical axillary buds. Hence the slope of the growth curve is relatively constant throughout its length. Coincidence between a reduction in rate of axillary bud leaf primordium initiation and the reduction in subtending leaf expansion rate is shared with *Salix* and a number of other species. The reader can check this by referring to the relevant graphs in the appendix.

Muehlenbeckia has continuously expanding shoots; FIG. 4.9 shows growth curves for *Muehlenbeckia*.

The organisation of a breaking axillary bud in *Pittosporum* - a plant in which a flush of axillary and apical bud break occurs four or five times per year - differs from that in all other plants examined. The largest leaf primordia and axillary buds subtended by them were found towards the apical end of the predominantly preformed bud. (Preformation is the process in which all the leaf primordia on any one shoot are laid down within the shoot's parent bud. This phenomenon is discussed at greater length in the next section. The growth rate is greatest in those buds which eventually become lateral shoots in the next growth flush - these were found at node 25 or thereabouts. The minimum growth rate was found in the most basal buds. *Clematis* followed a similar pattern to that found in *Salix* or *Ulmus*. FIG. 4.10 shows growth curves for *Pittosporum*. Shoot 1 was a terminal shoot dissected about 4 weeks after breaking. Axillary buds were not yet detected in its more basal nodes. As the lower leaves on the shoot expanded - shoots 2,3 and 4 - buds became visible in their axils. The discrepancy

between the total number of nodes on the four shoots may stem from either the different times of year that dissections were carried out - sampling was not carried out during one single growth flush - or from the use of non-uniform plant material.

3. Bud Preformation Predominates

Aucuba japonica; *Lonicera x americana*; *Hydrangea macrophylla*; *Viburnum japonicum*; *Ilex aquifolium*; *Acer platanoides*

Group characteristics: two different patterns of bud preformation are discernible. Either, after bud break, the apex forms no new leaf primordia, giving rise exclusively to floral structures, or else, as in the case of *Ilex*, the apex continues to initiate leaf or bract primordia, but the leaves are not destined to expand until the following season.

Discussion

In *Hydrangea*, *Aucuba*, *Lonicera* and *Viburnum*, the shoot apex flowers after a certain number of nodes has been laid down on the main shoot. Some or all of the axillary bud apices may flower as well. In *Acer*, shoot apex and axillary buds develop a compact organisation comprising scale and foliage leaf primordia. In *Ilex*, a compact apical bud is formed of foliage leaf primordia only - axillary buds similarly are comprised of foliage leaf primordia. The final size of buds is related closely to the number of fully grown foliage leaves eventually formed on the shoot which the bud gives rise to. FIG. 4.11 has four growth curves for *Lonicera*. Only those axillary buds which were initially vegetative were represented on the graphs. Nodes above node 13 on three of the shoots and above node 15 on the youngest one were flowering - no foliage leaves were initiated in these buds. The discrepancy between this point of transition from vegetative to flowering was not attributable to any particular cause. All shoots were taken from one plant, all had developed at a similar time of year, and all were taken from similar positions on the plant.

Unique Bud Growth Types

Crocoshmia x crocosmiifolia; *Myoporum laetum*;

Discussion

In *Myoporum*, buds initiated a maximum of 10 or 11 primordia, but the occurrence of growing buds, breaking buds, and buds in transition to flowering - all in close proximity on the same shoot - provided a rather confusing picture. Similarly, *Crocoshmia* has a unique pattern of development, no doubt shared by plants of similar type having a corm as a perennating organ. The initial pattern of growth resembled that found in many seedlings, but bud break occurred at some of the proximal nodes to form lateral, aerial shoots. Buds which did not break continued to initiate leaf primordia, reaching a maximum size of about 10 primordia before growth apparently ceased. The main shoot, incorporating nodes above node 13, had become an inflorescence by early summer. Many of the axillary buds subsequently grew out as prostrate rhizomes. The reader is referred to the relevant pages in the appendix for the data regarding these species.

FIG. 4.1 Growth curves for *Helianthus annuus*:

- a) - stem length 3 cm; b) - stem length 13 cm;
 c) - stem length 30 cm; d) - stem length 60 cm.

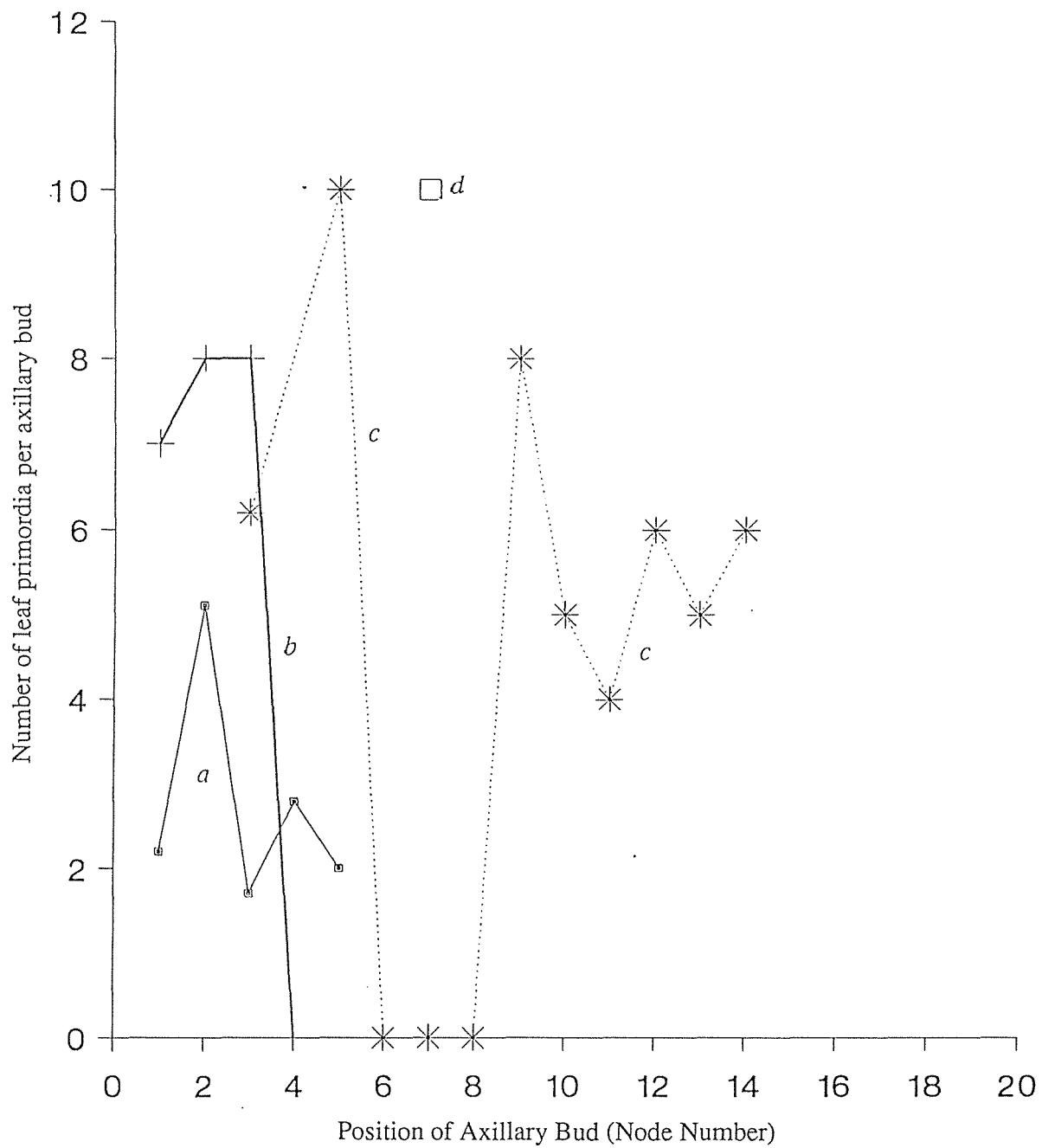


FIG. 4.2 Growth curves for *Stachys sylvatica*. The location of the shoot apices is indicated on the horizontal axis as follows:

- ▲ shoot apex, plant 1;
- shoot apex, plant 2;
- shoot apex, plant 3;
- shoot apex, plant 4.

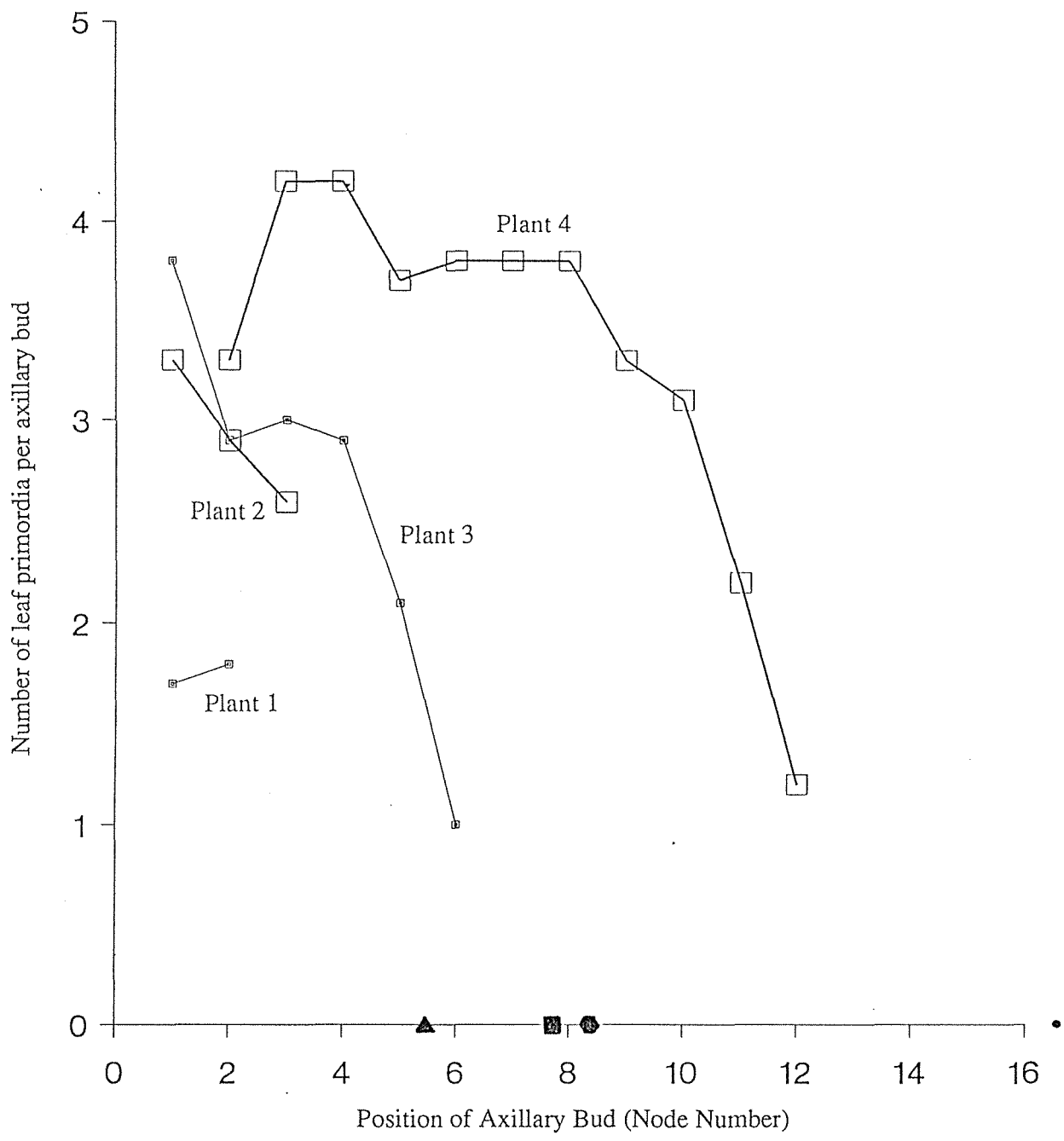


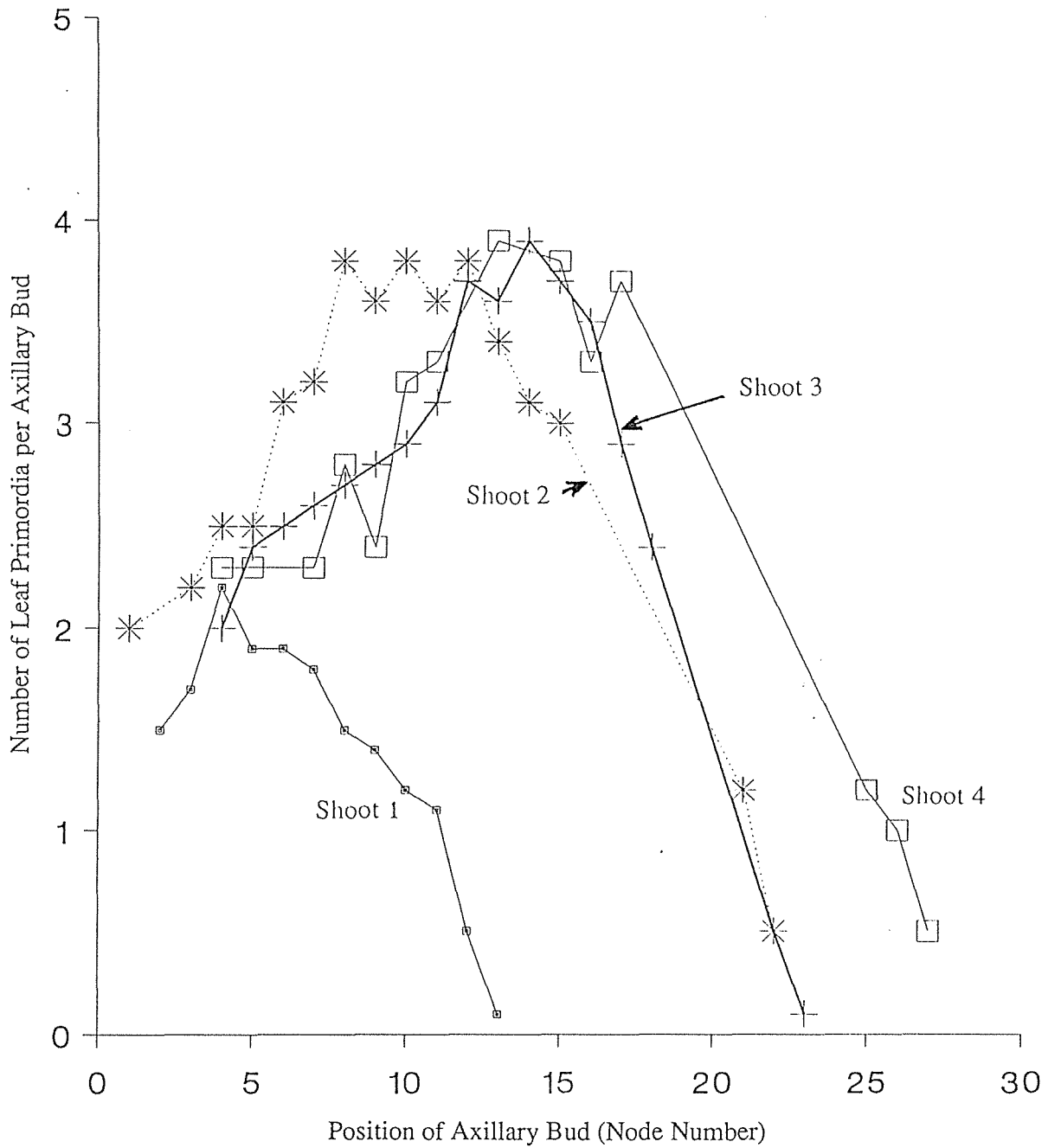
FIG. 4.3 Growth curves for *Hebe speciosa*.

FIG. 4.4 Growth curves for *Trifolium repens*. The location of the shoot apices is indicated on the horizontal axis as follows:

- ▲ shoot apex, plant 1;
- shoot apex, plant 2;
- shoot apex, plant 3;
- shoot apex, plant 4.

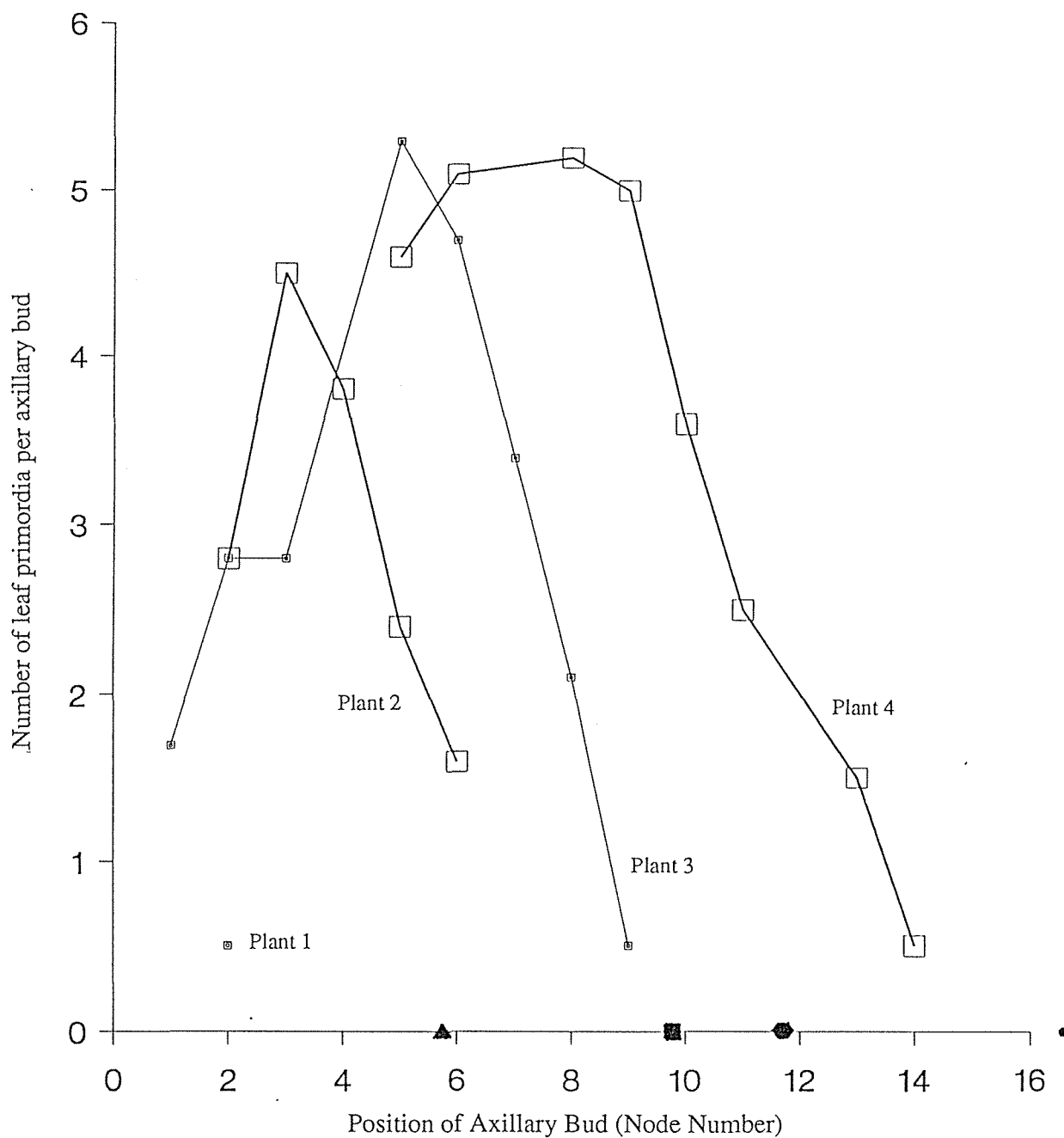


FIG. 4.5 Growth curves for *Salix fragilis*. The date of each dissection is shown on the relevant curve.

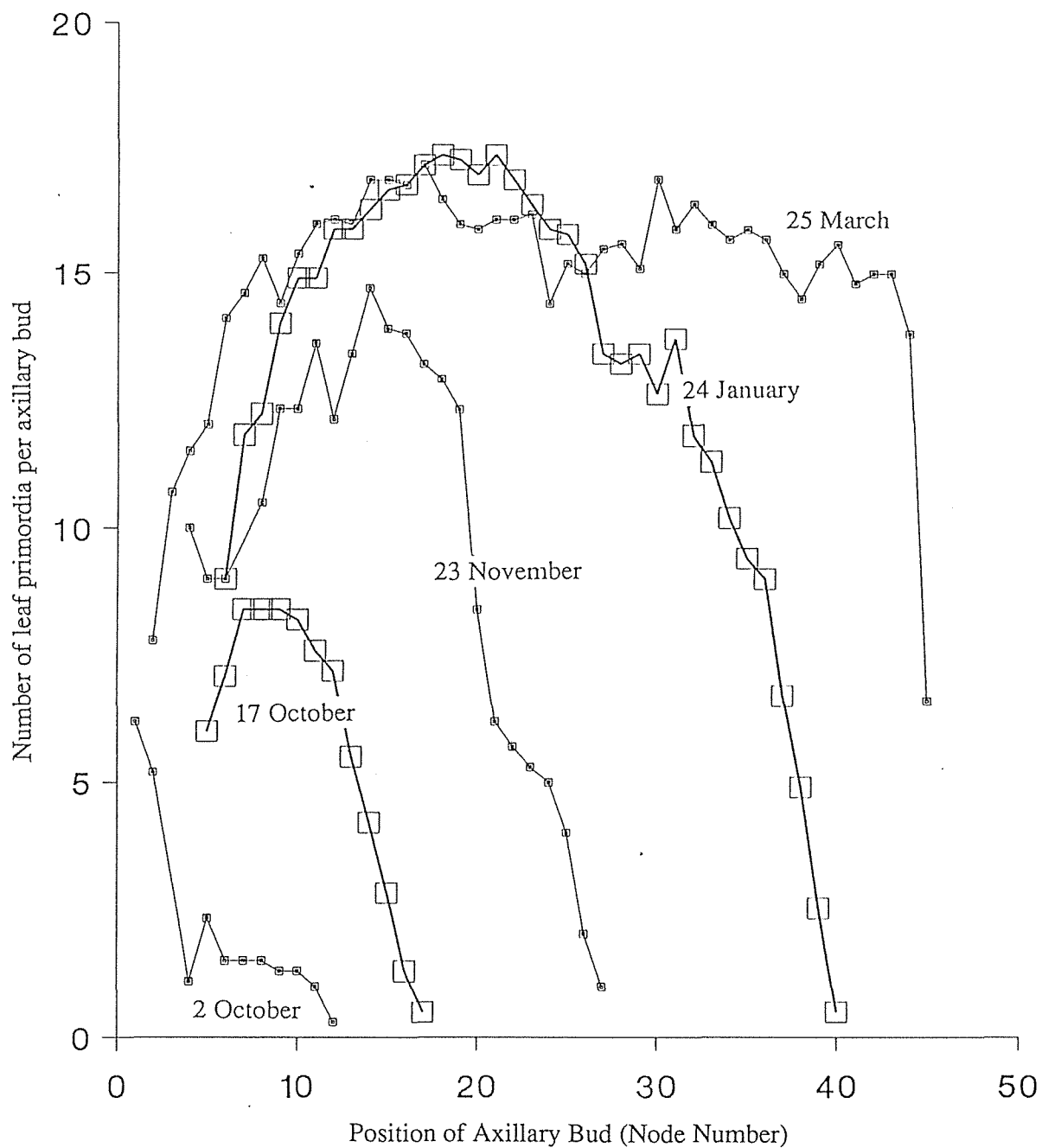


FIG. 4.6 Growth curves for *Ulmus procera* cv. Van Houlte. The date of each dissection is shown on the relevant curve.

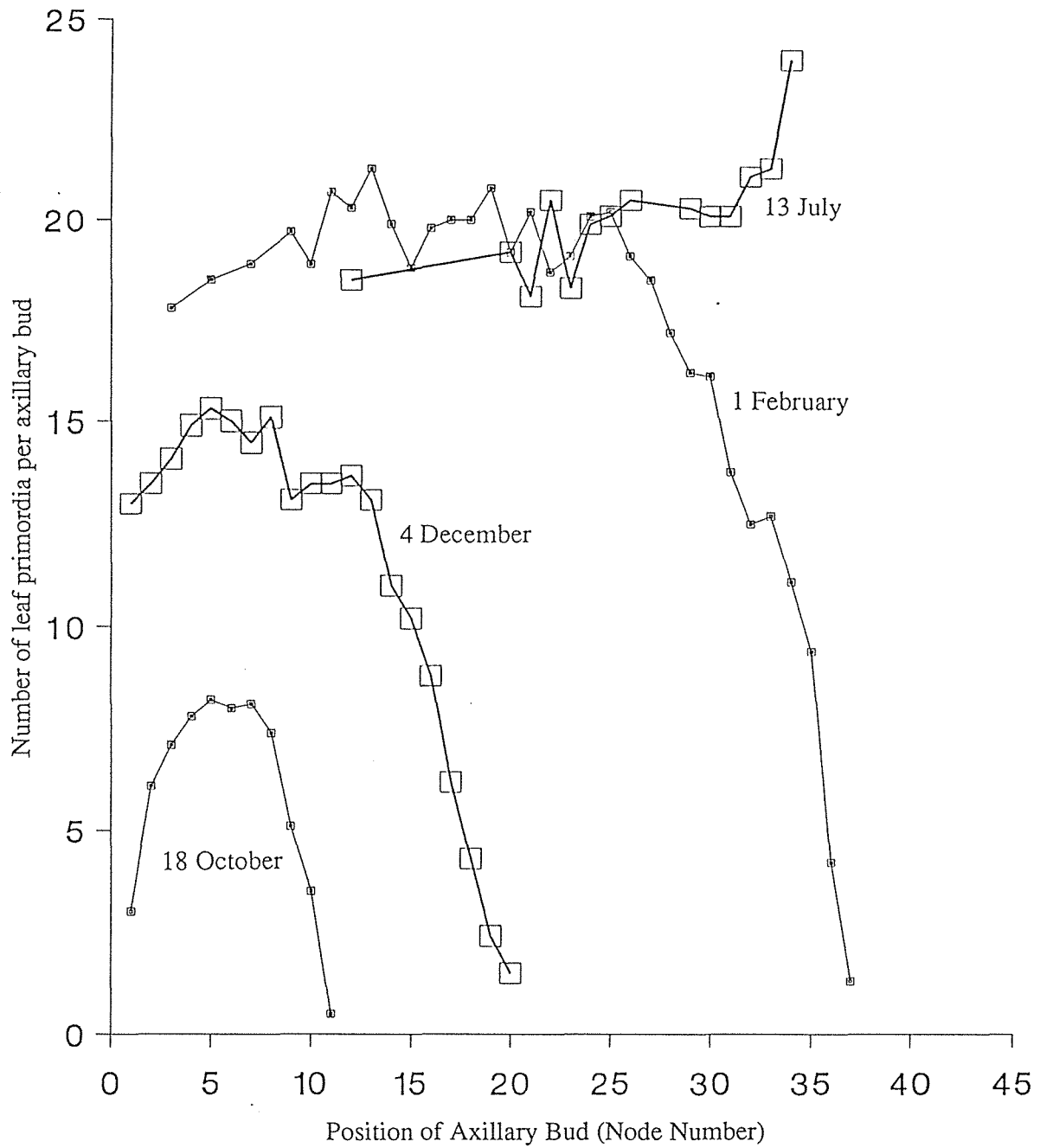


FIG. 4.7 Growth curves for *Aristotelia fruticosa*. The date of each dissection is shown on the relevant curve.

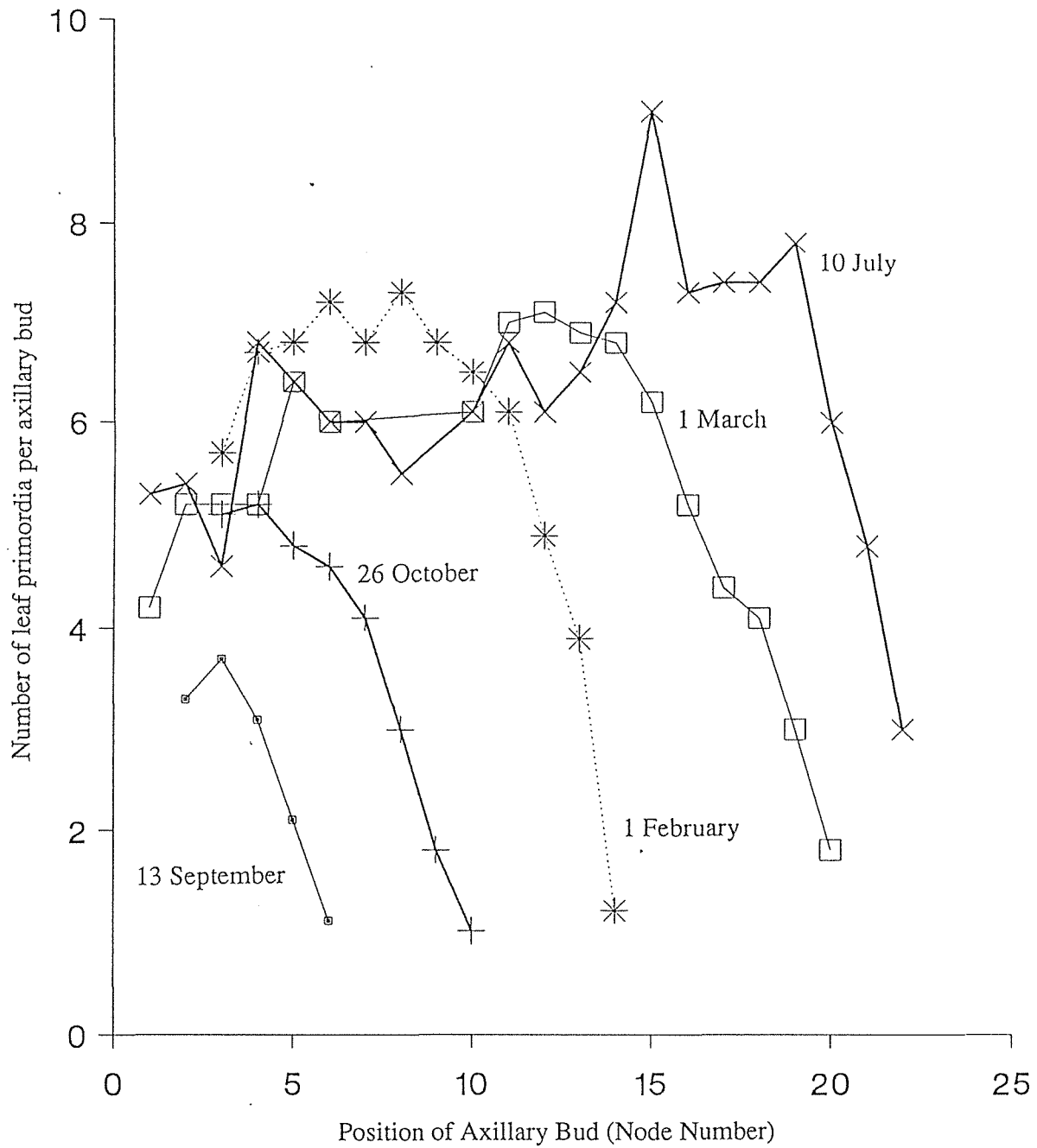


FIG. 4.8 Growth curves for *Melicetyus ramiflorus*. The date of each dissection is shown on the relevant curve.

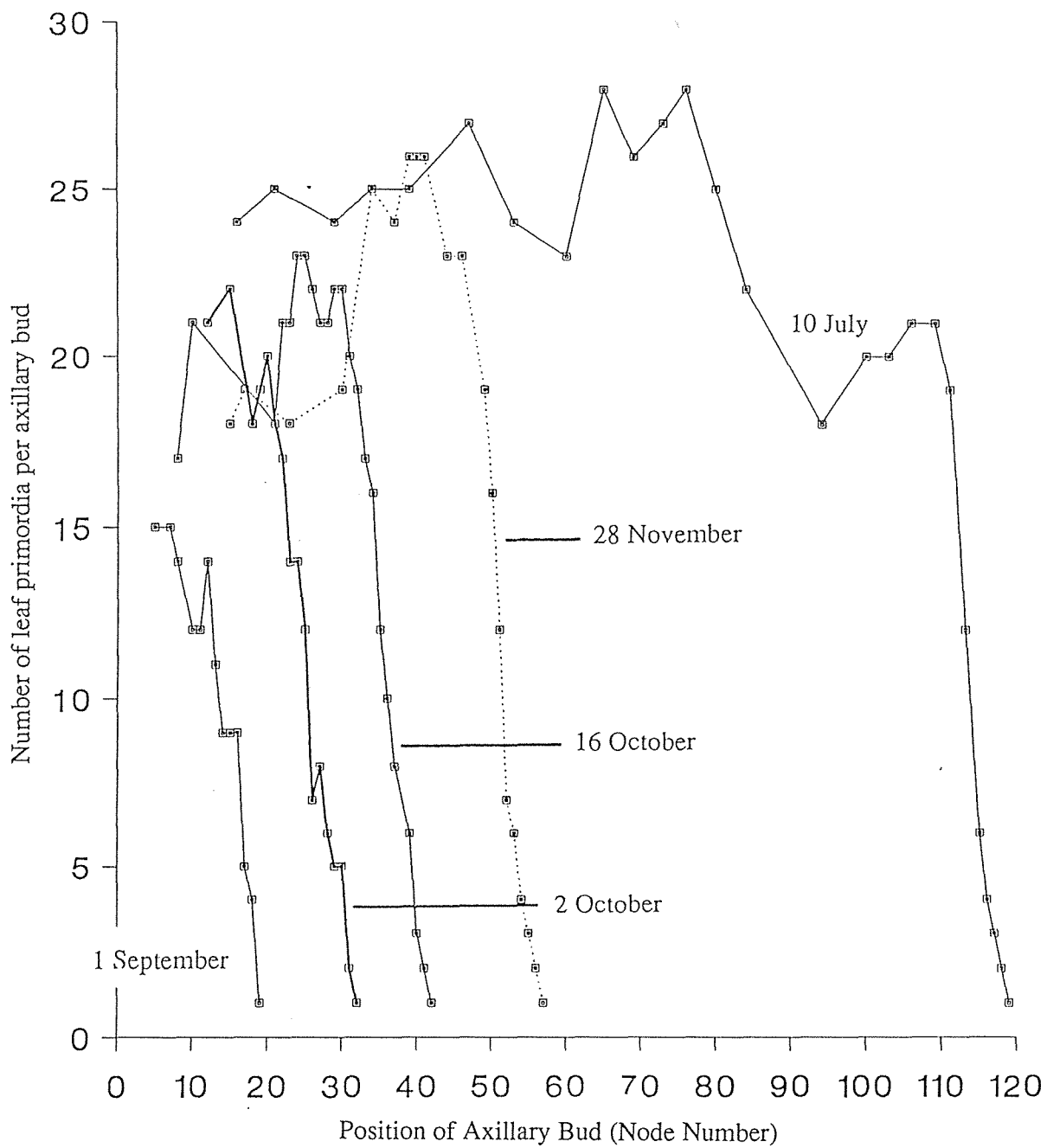


FIG. 4.9 Growth curves for *Muehlenbeckia australis*. The date of each dissection is shown on the relevant curve.

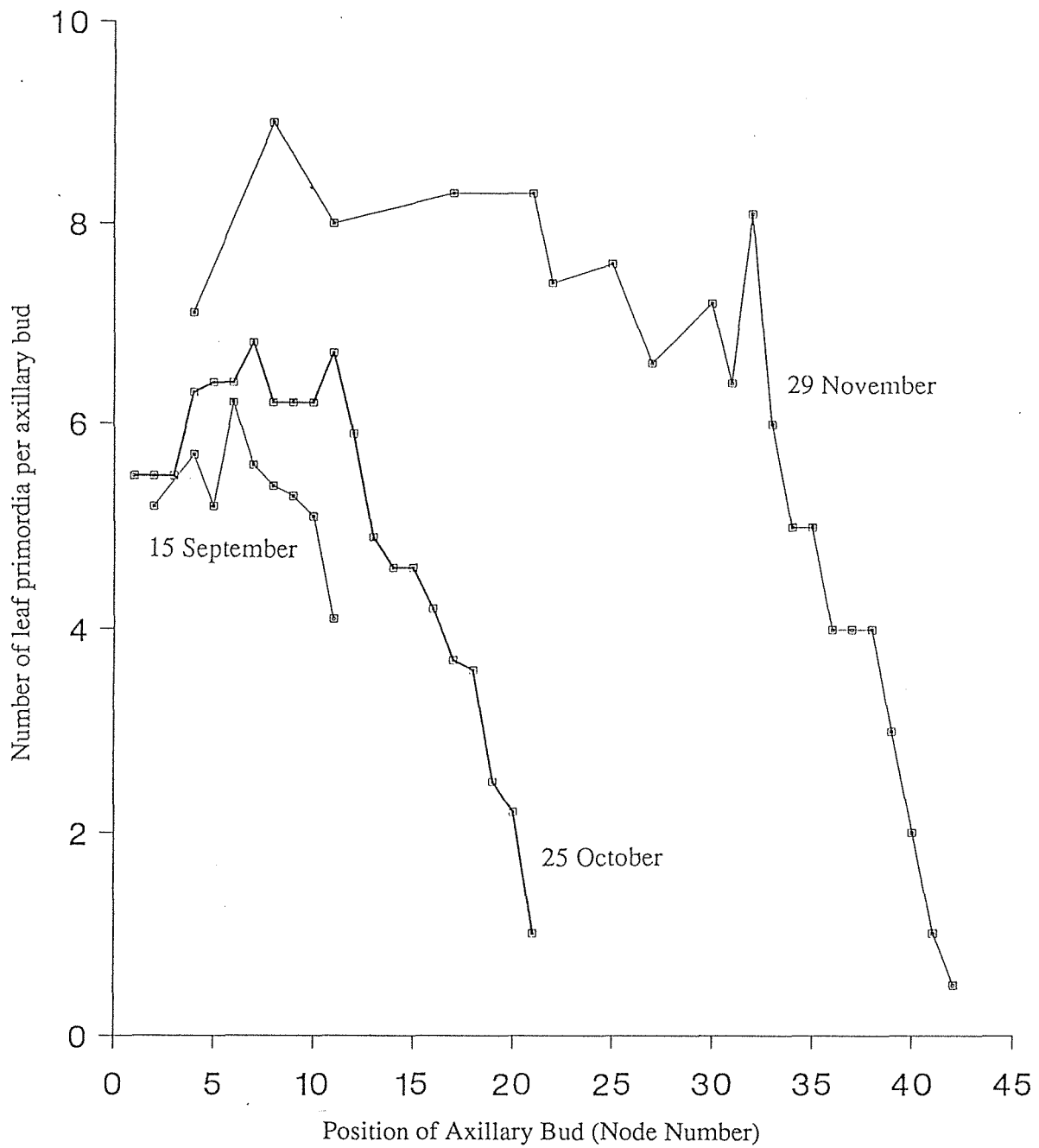


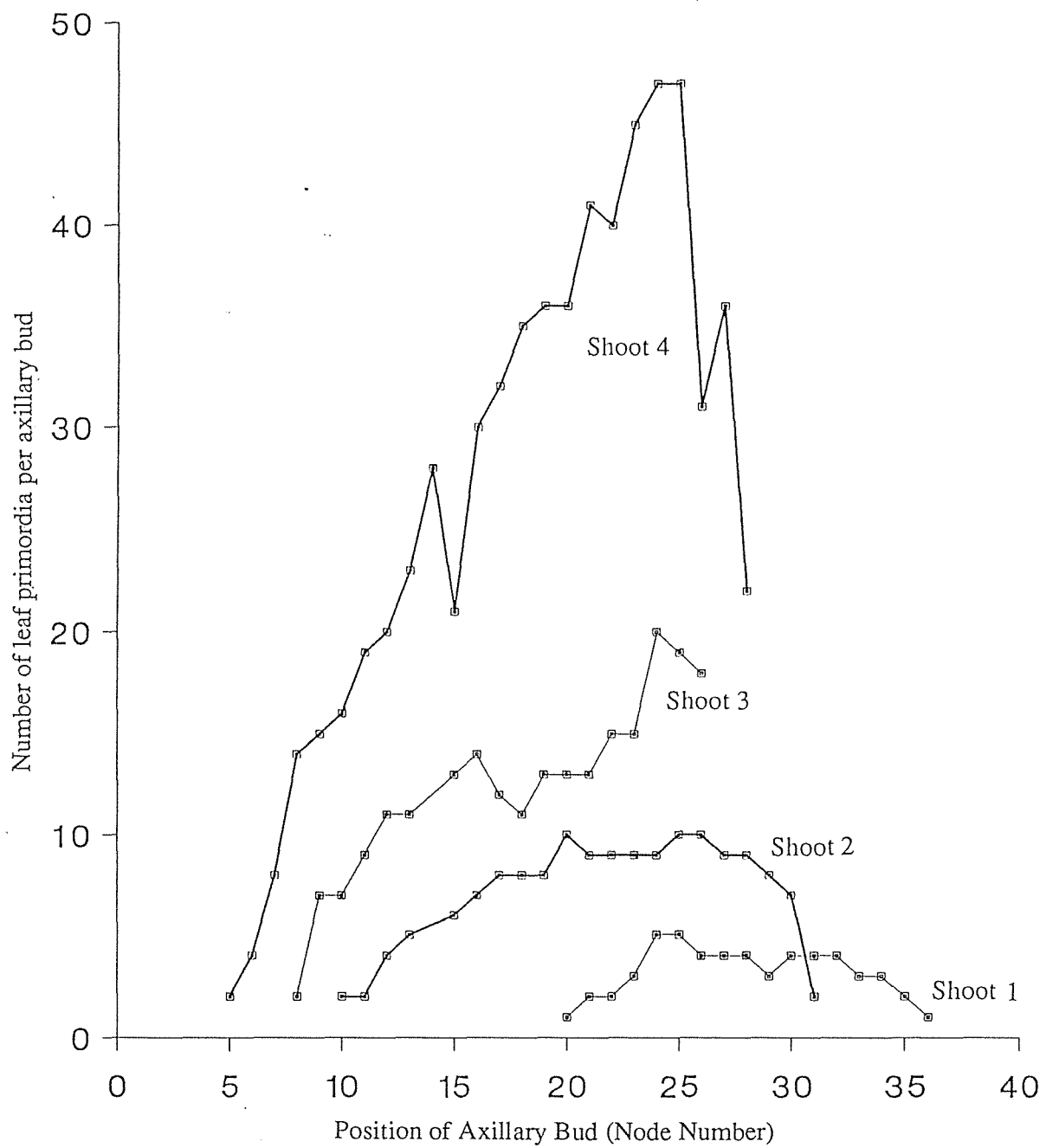
FIG. 4.10 Growth curves for *Pittosporum crassifolium*.

FIG. 4.11 Growth curves for *Lonicera x americana*. The date of each dissection is shown on the relevant curve.

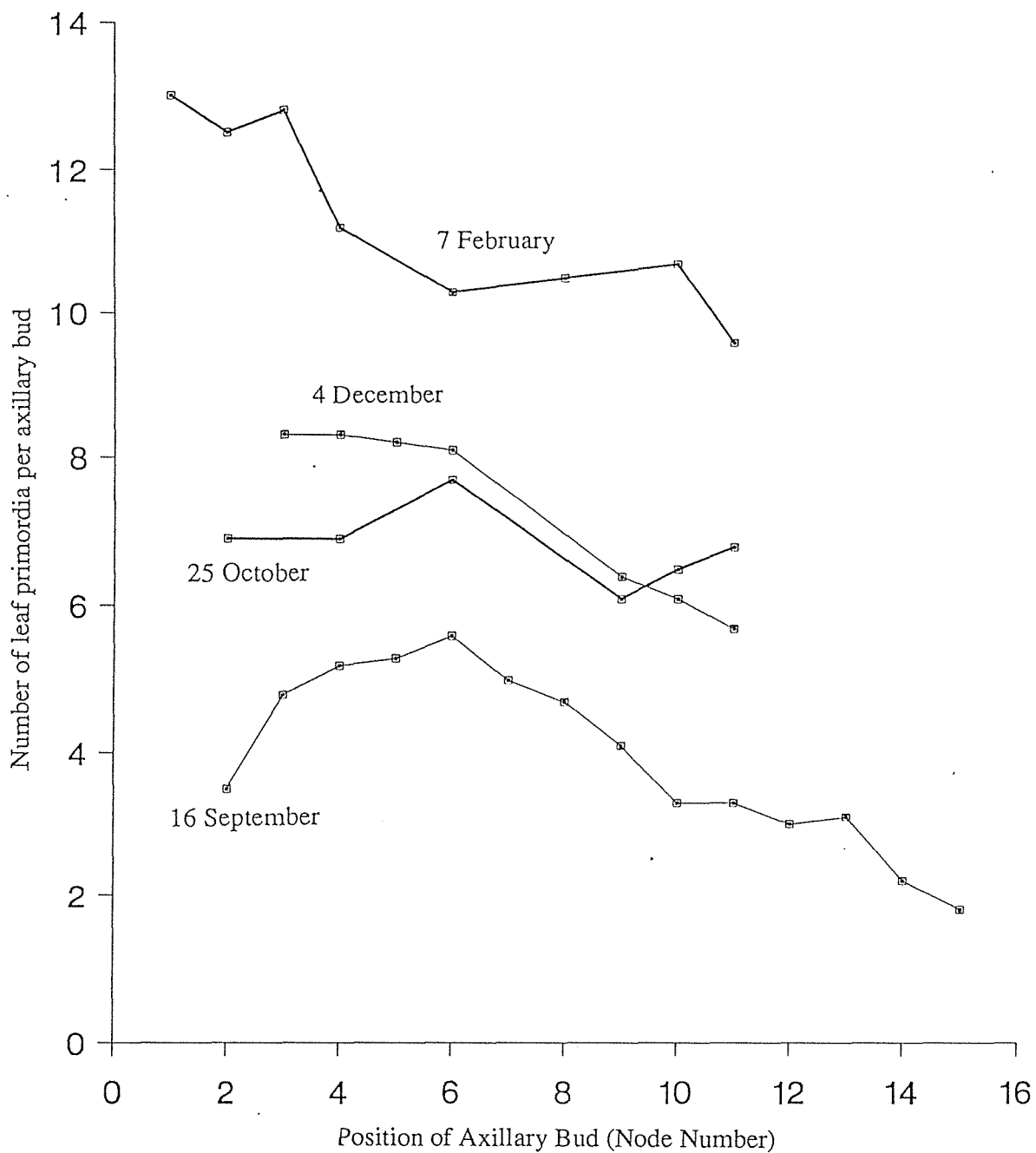
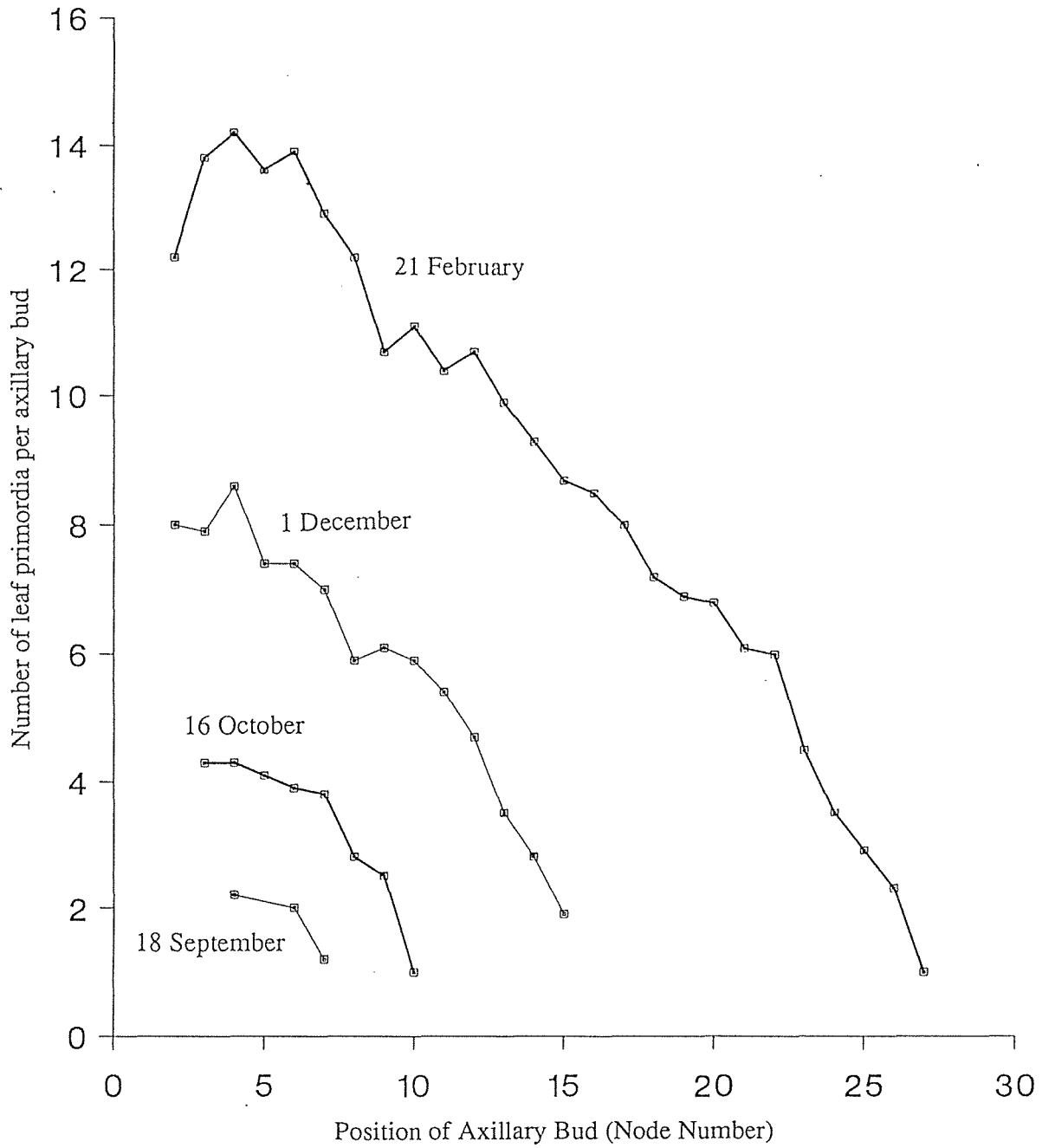


FIG. 4.12 Growth curves for *Sambucus nigra*. The date of each dissection is shown on the relevant curve.



CHAPTER 5

Correlations

a) Correlations Between Axillary Bud Growth and Subtending Leaf Growth Throughout The Shoot

A correlation between the relative rate of initiation of leaf primordia in axillary buds and the growth of their subtending leaves became apparent during a more extensive examination of *Salix fragilis*. In a large number of shoots it was noticed that the maximum slope of the growth curve always coincided with the slope maximum in the graph of subtending leaf length against node number. This discovery prompted an examination of the other plants being studied.

The graphs of data for each plant were assessed according to whether there was:

1. a close correlation
2. a general correspondence
3. an unclear correlation

between growth in an axillary bud and its subtending leaf. A close correlation was regarded as existing when the slopes of the graphs of subtending leaf length and number of leaf primordia per axillary bud against node number change simultaneously in the same sense, or the two graphs closely resemble each other. The species are grouped accordingly below.

1. Close Correlation

Aucuba japonica
Bromus wildenowii
Clematis montana cv.
Hydrangea macrophylla
Ilex aquifolium
Lolium perenne
Melicytus ramiflorus
Muehlenbeckia australis
Salix fragilis
Sambucus nigra
Tradescantia fluminensis
Trifolium repens
Ulmus procera
Zea mays

2. General Correspondence

Aristotelia fruticosa
Crococsmia x crocosmiiflora
Hebe speciosa
Lonicera x americana
Lupinus angustifolius
Myoporum laetum
Viburnum japonicum
Vitis arnurensis

3.Unclear Correlation

Acer platanoides

Cordyline australis

Helianthus annuus

Passiflora mollissima

Phormium tenax

Tropaeolum majus

Graphs illustrating examples from each group are reproduced in FIG. 5.1 to 5.3.

Species with sylleptic bud development have not been included. I would argue that throughout their structure they possess growing lateral shoots rather than developing axillary buds. However, the correlation between leaf primordium initiation in axillary buds and growth of their subtending leaves is close. FIG. 5.4 shows graphs for shoots of *Lycopersicon esculentum* at progressively later stages of development.

b) Correlations between Axillary Bud Growth and Growth in their Subtending Leaves, at the Base of Shoots

In a number of species a tendency for the buds lowest down on a shoot to be smaller than those higher up correlates with the leaves being smaller at the lower nodes. Hence in *Aristotelia* the buds at nodes 1 to 3 were significantly smaller than the largest buds found higher up, and the leaves found at these nodes were often only half the length of the largest leaves. However, in *Sambucus*, the buds at nodes 2 and 3 were only marginally smaller than the largest buds, found at nodes 4 to 6; the leaves at nodes 2 and 3 were marginally smaller than those above them. In all species studied - *Sambucus*-like and *Aristotelia*-like - there does appear to be a correlation between bud growth and subtending leaf growth in this particular region of the shoot. In a third group of species there was clearly no such correlation. These were all, apart from *Ulmus*, plants with proleptic bud growth in which bud preformation predominated. *Ulmus* actually shares another major feature with these species: at maturity all axillary buds contained clearly predictable numbers of two different forms of leaf primordium: scale leaves and foliage leaves. The three sets of plants discussed are listed below:

<i>Sambucus</i> Group	<i>Aristotelia</i> Group	<i>Ulmus</i> Group
<i>Aucuba japonica</i>	<i>Crocasmia</i>	<i>Ilex aquifolium</i>
<i>Clematis montana</i>	<i>Hebe speciosa</i>	<i>Lonicera x americana</i>
<i>Hydrangea macrophylla</i>	<i>Lolium perene</i>	<i>Viburnum japonicum</i>
	<i>Lupinus angustifolius</i>	
	<i>Muehlenbeckia australis</i>	
	<i>Melicytus ramiflorus</i>	
	<i>Pittosporum crassifolium</i>	
	<i>Salix fragilis</i>	
	<i>Trifolium repens</i>	
	<i>Vitis arnurensis</i>	
	<i>Zea mays</i>	

The reader should refer to the graphs in the appendix for further clarification.

c) Correlation between the size of the first-formed axillary bud leaf primordium and the size of the axillary bud.

Measurements of the size of leaf primordia were often not carried out, usually because such measurements were difficult or impossible to make. Consideration was given to making measurements - where possible - of a number of primordia in each axillary bud, but doubts were held as to the usefulness of such information. As has been discussed earlier, the rate of primordium initiation was identified as a more significant feature of bud growth. Leaf primordium size was, however, identified as being significant in relation to bud break. It has become apparent, during the course of this study, that bud growth and bud break are probably two separate processes, each with their own distinct features. Since the expansion of leaf primordia is one of the first signs of bud break, the measurements of the length of the first primordia enabled those buds which were breaking to be disregarded as growing buds - instead they were considered to be outgrowing shoots.

Since axillary bud leaf primordia continue to grow while the axillary bud apex is initiating them, the existence of a correlation between the size of the first-formed axillary bud leaf primordium and the size of the axillary bud would seem to be quite probable.

The reader is referred to the data and graphs in the appendix for further clarification.

Discussion

A number of different issues are discussed in this chapter. All relate to the interrelationship between distinct morphological features, but a common thread running through virtually all the observations is discernible - the axillary bud grows as part of the shoot apex in its early life, and its growth patterns reflect the activity within the apex. Hence, where the first formed leaves on a shoot are small when fully grown, the axillary buds they subtend are generally smaller than average, both in terms of the number and size of leaf primordia. Where environmental factors affect growth in the shoot apex they affect both leaf growth and axillary bud growth - this is especially visible in *Salix* and *Ulmus*. It would be my contention that the slowing in growth in the axillary buds is related to their movement away from the apical region, in which expansion growth is largest, to the region in which general plant growth is restricted and shoot elongation is not occurring. There would seem to be two alternative explanations for such a scenario. Either expansion growth in the apical region directly or indirectly stimulates enhanced growth in the axillary bud, or the axillary bud is responding to enhanced growing conditions within the apical region.

FIG. 5.1 *Salix fragilis*. Graphs of the number of leaf primordia per axillary bud, and the length of subtending leaves plotted against node number in four mature shoots. The major consideration is whether or not an inflexion in one graph coincides with an inflexion in the other. If one is following the growth of a shoot the graphs need to be read from right to left. In graph 1 the reductions in slope are closely coincidental, but while there is a plateau in the graph of number of primordia per bud, the subtending leaf length graph has a sharp peak. This can be explained by the fact that leaves at the lowest nodes were small even when fully expanded while the axillary buds subtended by these leaves continued to grow throughout the season. In graphs 2,3 and 4 the inflexions are remarkably coincidental. Leaves at many proximal nodes were no longer present. However, axillary buds were present at all nodes. Those not represented on the graph were not dissected.

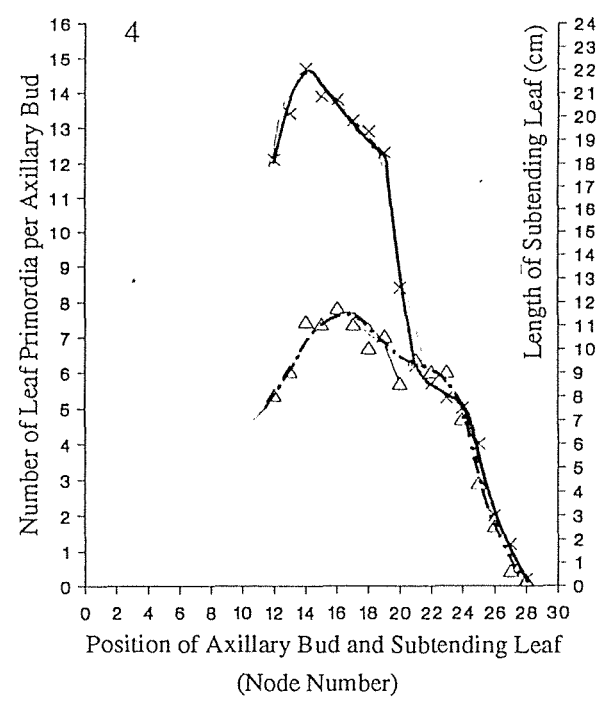
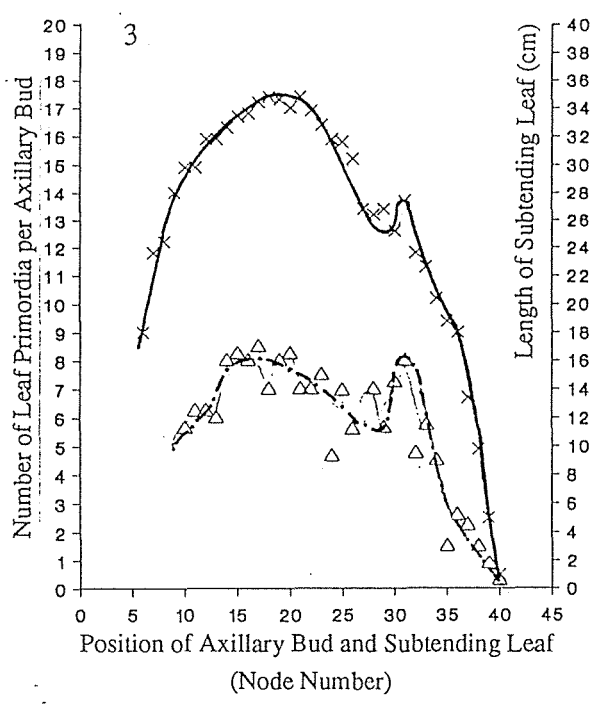
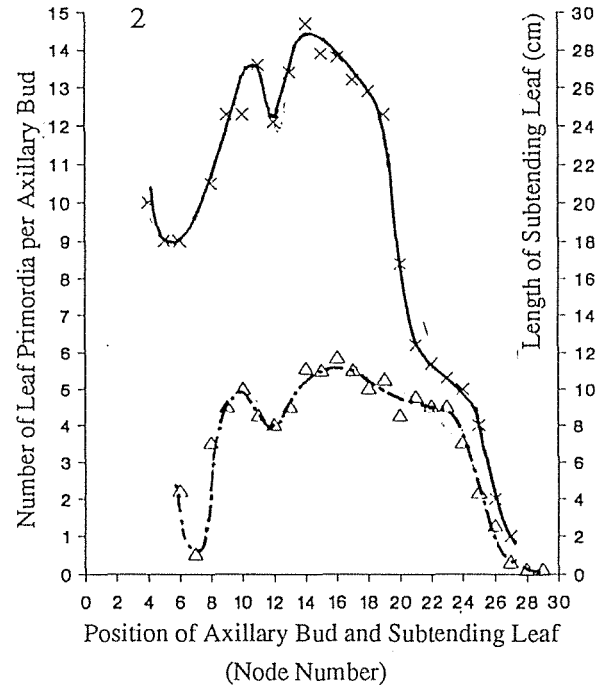
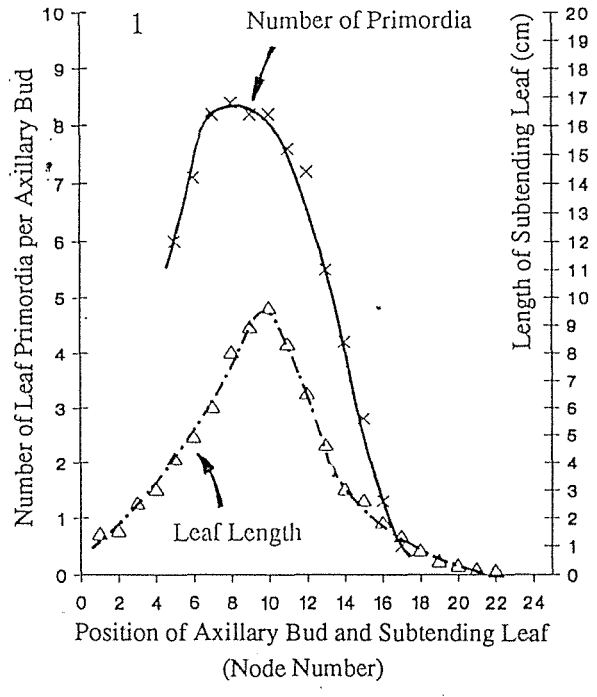


FIG. 5.2 *Hebe speciosa*. Graphs of the number of leaf primordia per axillary bud, and the length of subtending leaves, plotted against node number, in four shoots. Data are taken from the relevant section in the appendix. Leaves were not present at proximal nodes in graphs 3 and 4 due to senescence.

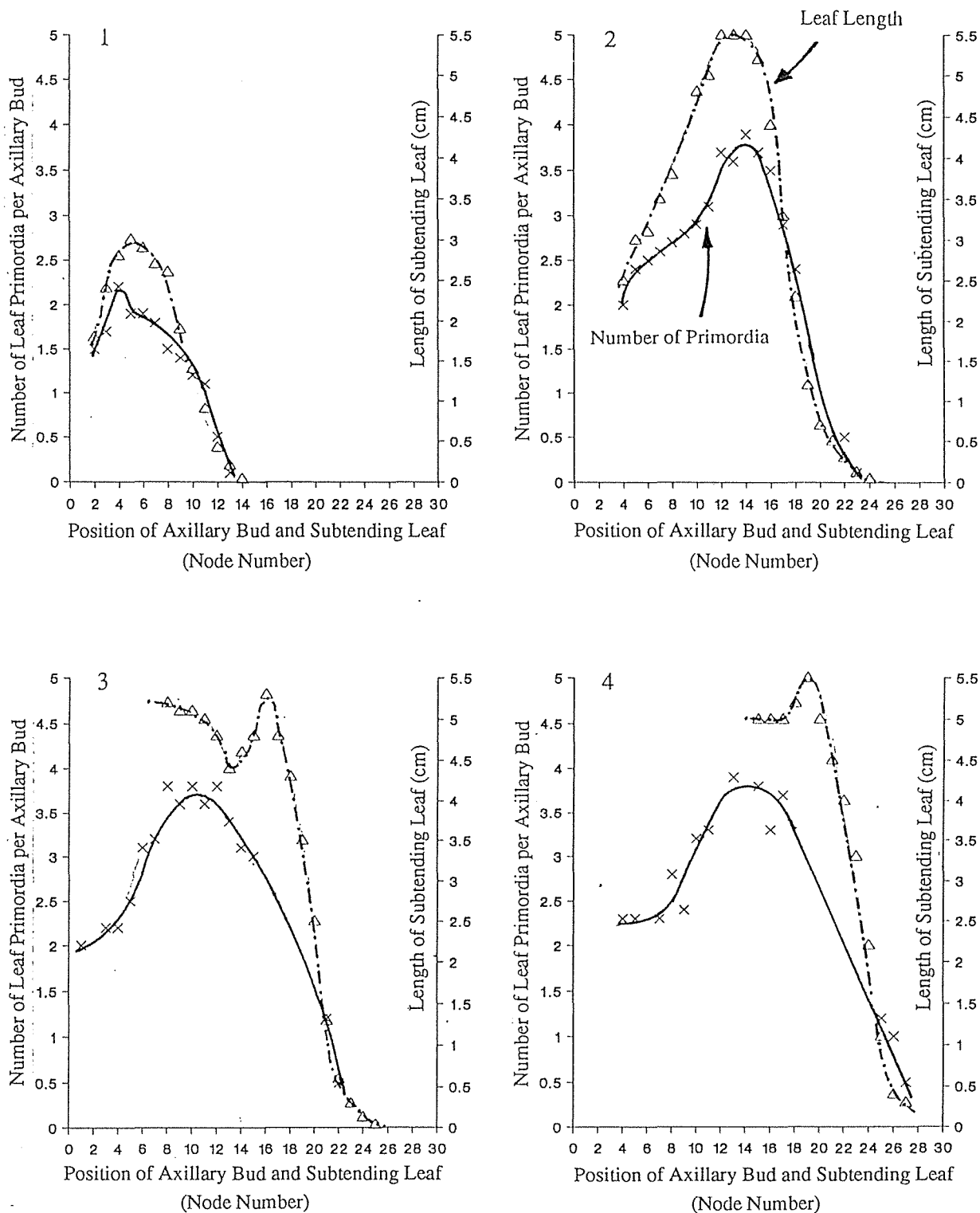


FIG. 5.3 *Passiflora mollissima*. Graphs of the number of primordia per axillary bud, and the length of subtending leaves, plotted against node number, in two shoots at different stages of development. Data are taken from the relevant section in the appendix.

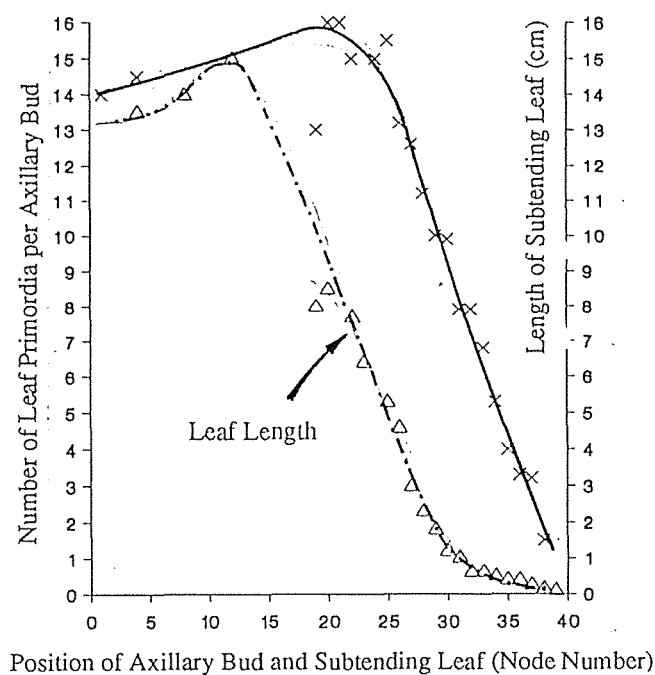
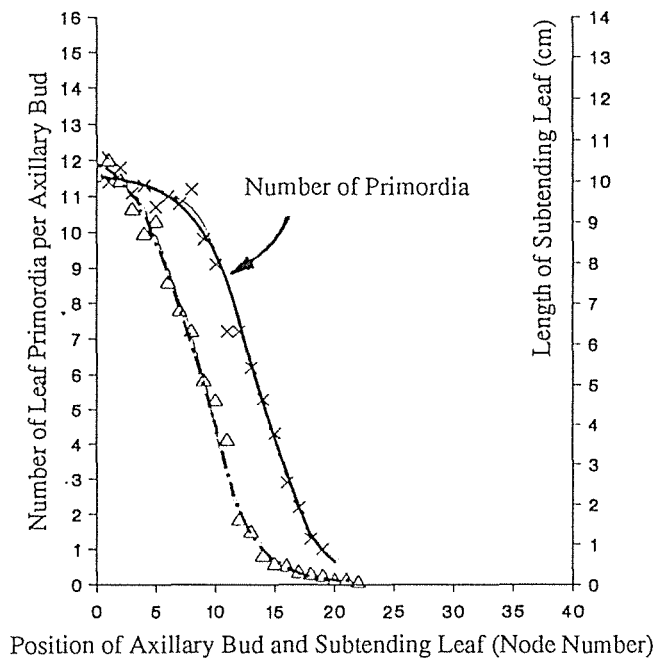
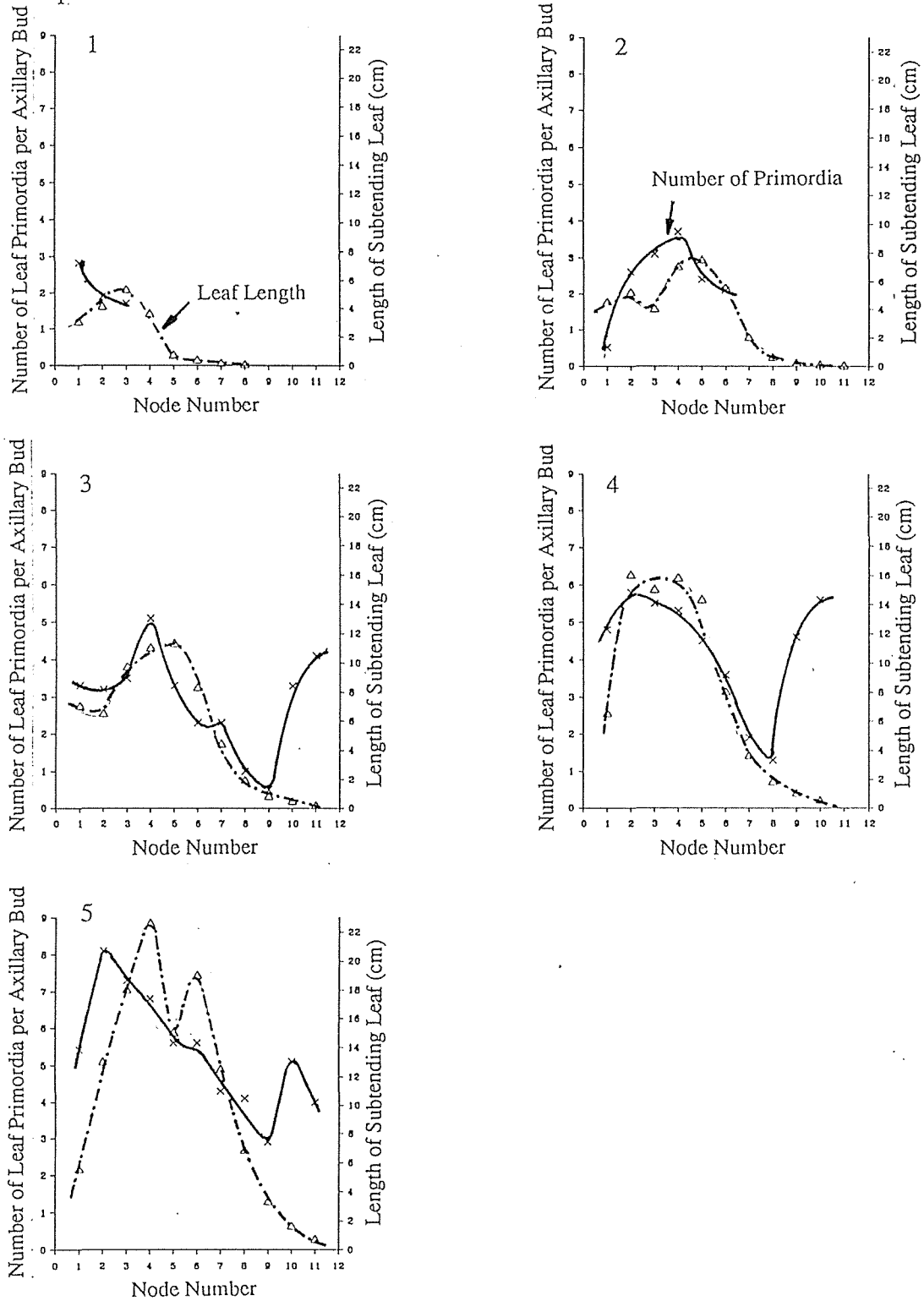


FIG. 5.4 *Lycopersicon esculentum*. Graphs of the number of primordia per axillary bud, and the length of subtending leaves, plotted against node number, arranged in order of increasing age. In graphs 3 and 4 one can see that once growth was well established in the main shoot the correlation between the two graphs over most of their lengths is very close. However, it will be noted that primordium initiation in the "axillary buds" at nodes 10 and 11 in graph 3 and 9, 10 and 11 in graph 4 does not correlate with subtending leaf growth. This is because the axillary buds immediately below the main shoot apex had grown out as main shoots after the previous main shoot apex had flowered.



CHAPTER 6

Investigation of The Effect of Removal of Subtending Leaf Primordia on Axillary Bud Growth in *Salix fragilis*

Introduction

Previously mentioned data in this study indicate that the growth of an axillary bud may correlate with growth in the tissues surrounding it, especially the leaf which subtends it. Ways in which this correlation could be examined were sought and special consideration was given to experiments which could determine if there was a causal link between axillary bud growth and growth in its surrounding tissues. The author had been impressed by the experiments carried out by, amongst others, Ball, Wardlaw and Sussex, (Steeves and Sussex 1971) and proceeded to design an experiment in which a determination of the effect of removal of a subtending leaf, at various stages in its development, on the growth of the axillary bud which it subtends, would be made. This type of experiment has the advantage that it is relatively simple to perform but suffers from the major drawback that the effects of general tissue damage are difficult to compensate for. Considerable thought was given to the design of controls but it was found that an unambiguous experimental control could not be provided, at least within the restricted time available. Instead the experiments were designed with as large a number of experimental parameters as possible. The range of values of these parameters was also expanded as much as possible. It was hoped that the results obtained could then be usefully interpreted without controls. However, ultimately it had to be accepted that the effects of general tissue damage could not be discounted.

Method

Willow plants were grown from cuttings. The cuttings were taken in early December and grown initially in sand in the propagating greenhouse on a warm bed held at 22 °C and provided with an automatic sprinkler system. When well rooted they were transferred to a standard potting mixture and grown outside under an automatic sprinkler system.

The recipe for the potting mixture was as follows:

50% peat

50% pumice

to 30 litres was added:

500ml dolomite lime

300ml Three Month Osmocote Controlled Release Fertiliser (Sierra

Chemicals): total Nitrogen 14%

Phosphorus 6.1%

Potassium 11.6%

Sulphur 3.0%

250ml superphosphate

Plants with shoots bearing at least 8 or 10 fully grown foliage leaves were selected. A plant was positioned under a dissecting microscope, the shoot tip was irrigated with water and the apical bud was carefully teased open to expose the innermost leaf primordia. One or more primordia were dissected from the apical region and the remaining primordia were smoothed back together. Initially, complete removal of the primordia was attempted. Subsequent examination indicated that in some instances sufficient primordial tissue remained after the dissection to provide for a viable, if drastically restricted, leaf structure. As a result, in further experiments the proportion of the leaf primordia which was removed was deliberately varied. The top 10 centimetres of shoot was enclosed in a polythene bag to give the exposed region as much protection as possible and the plant was returned to the greenhouse. Consideration was given to the establishment of controls. However, the dissection experiment was aimed at **comparing** activity in one bud with activity in the surrounding buds. Hence a treatment such as enclosing the whole apical region in a large (about 15 cm across) polythene bag would be expected to affect regions several nodes away from the node from which the leaf primordium was excised as well as that region itself. The polythene bag was removed after one week. After periods of time varying between 15 and 108 days the shoots were dissected and measurements of subtending leaf length, number of leaf primordia in each axillary bud, and length of the first leaf primordium in each bud were made. Care was taken to identify buds which were in the process of breaking or were

growing out into shoots. Such buds were to be treated differently from the rest in the analysis of results. The procedure was repeated a number of times.

Measurement of the extent of leaf primordium removal provided a number of problems. Firstly, the dissection had to be carried out quickly and carefully so as to minimise damage to the remainder of the apical region, and measurements of the original length of the leaf primordium and the proportion of the primordium which was removed were difficult under these conditions. Secondly, some senescence occurred in partially excised leaf primordia. Observations to find out **when** senescence occurred were not made. Hence the length of time the partially excised leaf primordium was active was not determined. However, in many instances the "detipped" leaf continued to grow. Its ultimate length was measured and expressed as a percentage of the lengths of the leaves on the shoot on either side of it - in other words as a percentage of its projected final length had it remained entire.

A second method of dealing with plants before and after dissections was developed after the first series of experiments had been completed in early January. A small shade house was constructed and regular irrigation inside it was established. Cuttings were grown under these conditions for six weeks before dissections were carried out. They were returned immediately after initial dissections - no further precautions were needed to protect the opened buds at stem apices. Three further series of experiments were carried out during the year.

Results

STEP 1.

The results were tabulated and a graph of node number against number of primordia per axillary bud was prepared for each shoot. The best smooth curve was plotted through all points except those representing two types of bud:

1. buds which were breaking or had broken
2. buds whose subtending leaves had been removed by dissection

Those of the first type were excluded because it had been noticed that the growth rate in axillary buds changed significantly when bud break occurred. The second type were those in which depression of growth was to be estimated. The vertical distance between these points and the curve was measured. This was taken as the **bud growth depression**. The procedure is demonstrated in FIG. 6.1 to 6.4.

STEP 2.

The following data were collected:

1. Initial length of the leaf primordium at time of dissection (**Primordium Length**)
 2. Ultimate length of the partially or fully excised leaf as a percentage of the lengths of the leaves on either side of it. (**Leaf Length**)
 3. Length of time between initial dissection and taking of measurements. (**Growth Period**)
 4. Bud growth depression (**Depression**)
- (These are tabulated in FIG. 6.5 below.)

A multiple regression analysis of the data was carried out. This showed that a significant correlation existed between axillary bud growth depression and **both** the length of the subtending primordium or leaf at the time of its removal **and** the percentage of the primordium or leaf removed. These three sets of data were plotted on a three dimensional graph. This is presented in FIG. 6.6.

Discussion

The experimental results show that axillary bud growth, as represented by the rate of initiation of leaf primordia in the buds, was depressed by the excision of some or all of the growing buds' subtending leaves. The maximum depression was apparently obtained when a subtending leaf primordium was excised when about 5 mm in length, but significant degrees of depression also occurred when subtending leaves as long as 25 or 30 mm - about 20% of their potential final length - were excised. The maximum depression of growth was about 4 leaf primordia. Under normal conditions the buds would have grown to a size of between 12 and 16 leaf primordia, so the maximum growth depression was as much as 25 - 30%. When the subtending leaf primordium was only partly excised, less depression resulted in the axillary bud. Unfortunately, insufficient data were collected to enable a complete picture to be drawn, but it does look as if the depressing effect was still significant when as much as 20% of the subtending leaf remained intact. In the introduction to this chapter the problem of accounting for the effects of general tissue damage was discussed. Such effects are inevitable, but one has to assess their likely significance. When appreciable proportions of the subtending leaf primordium remained intact one would not expect general tissue damage to have affected the growth of the

axillary bud; the bud would have been some distance from the damaged area. But depression of bud growth did occur under these circumstances. It is more difficult to discount the effects of general tissue damage where complete excision was carried out.

However, it is the author's contention that all of the growth depressions encountered were a result of a specific feature of the tissue damage imposed. The developing axillary bud does not have a vascular connection with the rest of the plant (see chapter 7). All nutrients must pass into it from the surrounding tissue. A major proportion of the surrounding tissue is leaf base. This tissue will contain high levels of nutrient when the leaf is expanding rapidly. Removal of the leaf, even partly, will reduce its sink effect, nutrient levels in the leaf base will be reduced and hence less nutrient will be available to diffuse into the axillary bud. Support for this theory is provided by the evidence of growth distortion in axillary buds where tissue was removed from the immediate vicinity of the axillary bud. Drawings of such buds are shown in FIG. 6.7. Growth in these buds was greatest on the adaxial side and as a result the tip of the bud has grown away from the stem. This explanation would tie in with the author's contention that axillary bud growth is provided for and stimulated by the same factors that effect tissue growth in the regions surrounding the axillary bud, including the expanding leaves.

FIG. 6.1 to 6.4 Graphs of the number of leaf primordia per axillary bud against their nodal position on the shoot for the calculation of growth depression in the leaf primordium removal experiments.

FIG. 6.1

Node number of excised leaf primordium ————— 17
 Length of leaf primordium before excision (mm) ————— 8
 Final relative length of remains of excised leaf primordium (%) ————— 0
 Axillary bud growth depression (number of leaf primordia) ————— 2.12
 Growth period (days) ————— 16

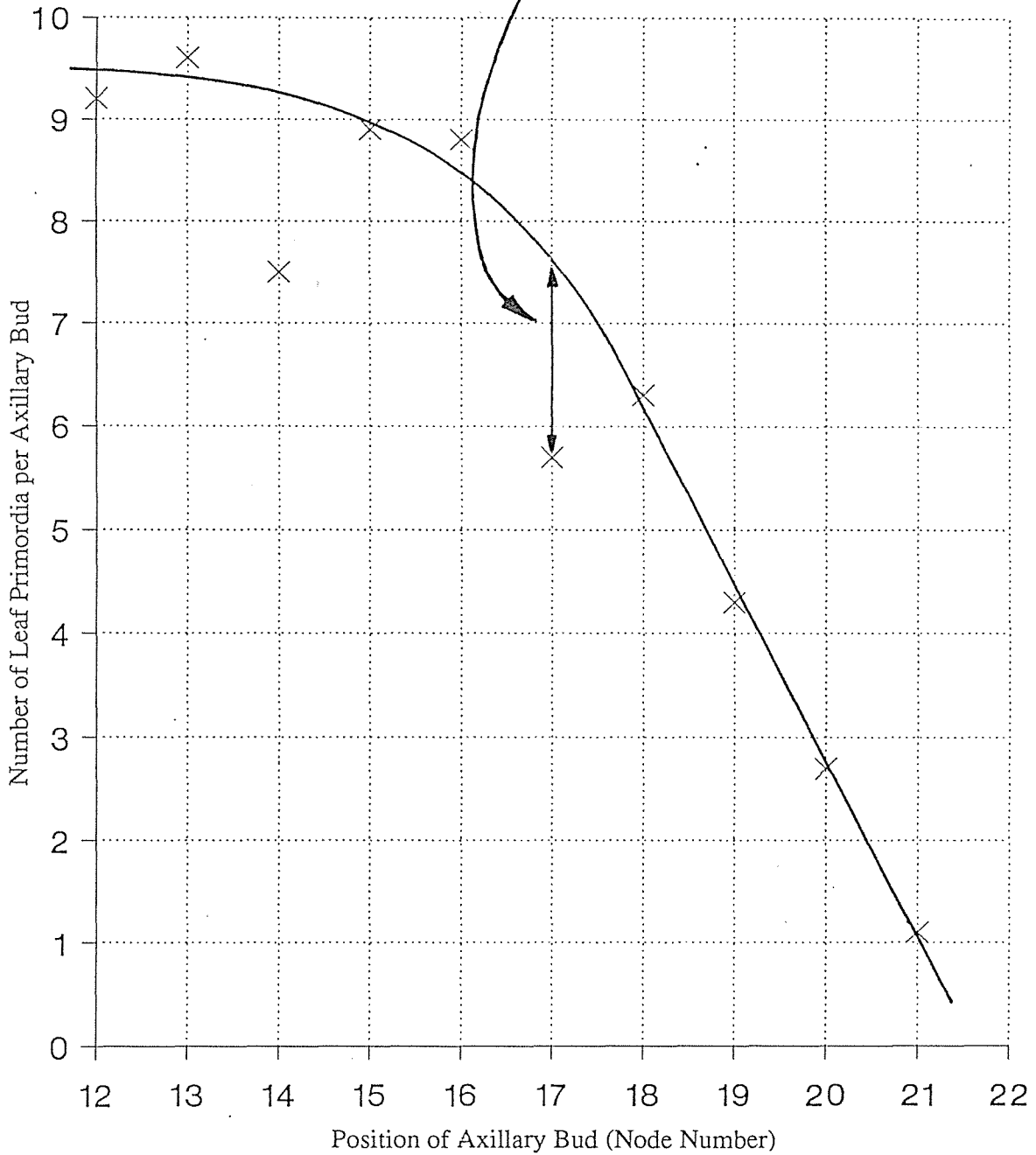


FIG. 6.2

Node number of excised leaf primordium	22	23	24
Length of leaf primordium before excision (mm)	10	8	4
Final relative length of remains of excised leaf primordium (%)	0	0	8
Axillary bud growth depression (number of leaf primordia)	0.64	1.64	0.82
Growth period (days)	18	-----	-----

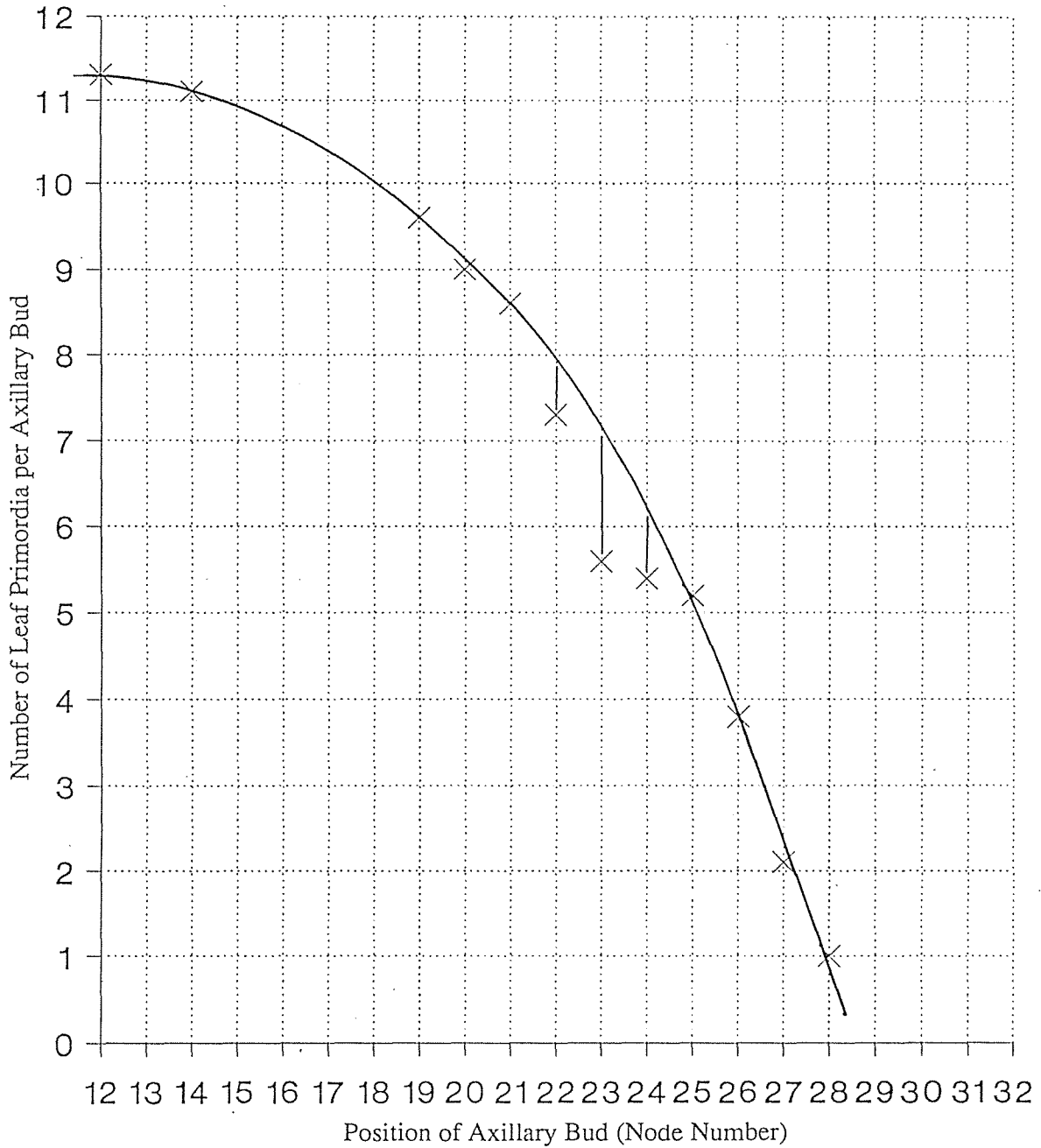


FIG. 6.3

Node number of excised leaf primordium	13	16
Length of leaf primordium before excision (mm)	17	5
Final relative length of remains of excised leaf primordium (%)	0	0
Axillary bud growth depression (number of leaf primordia)	1.3	2.8
Growth period (days)	64	-----

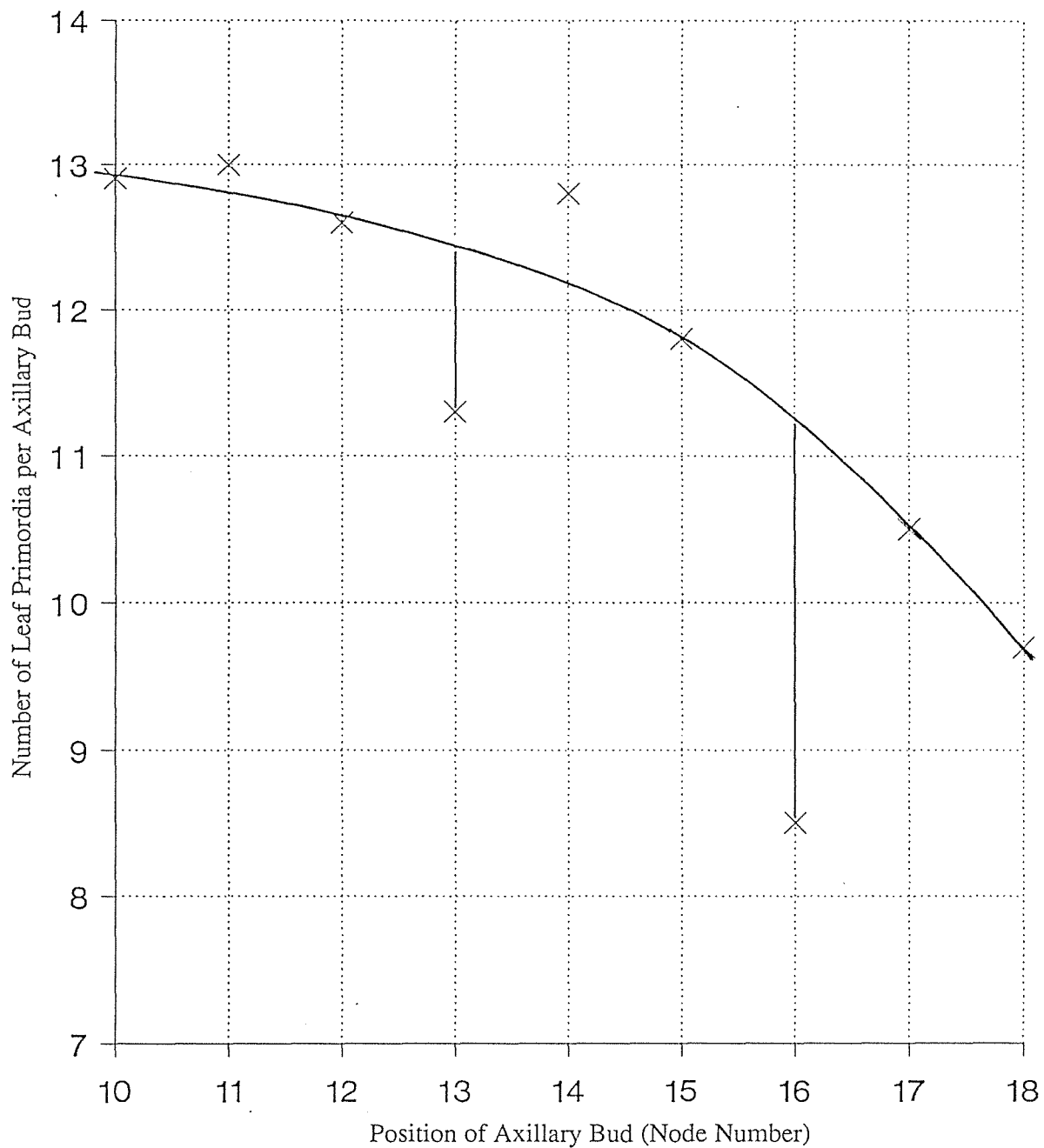


FIG. 6.4

Node number of excised leaf primordium	5
Length of leaf primordium before excision (mm)	25
Final relative length of remains of excised leaf primordium (%)	36
Axillary bud growth depression (number of leaf primordia)	0.55
Growth period (days)	21

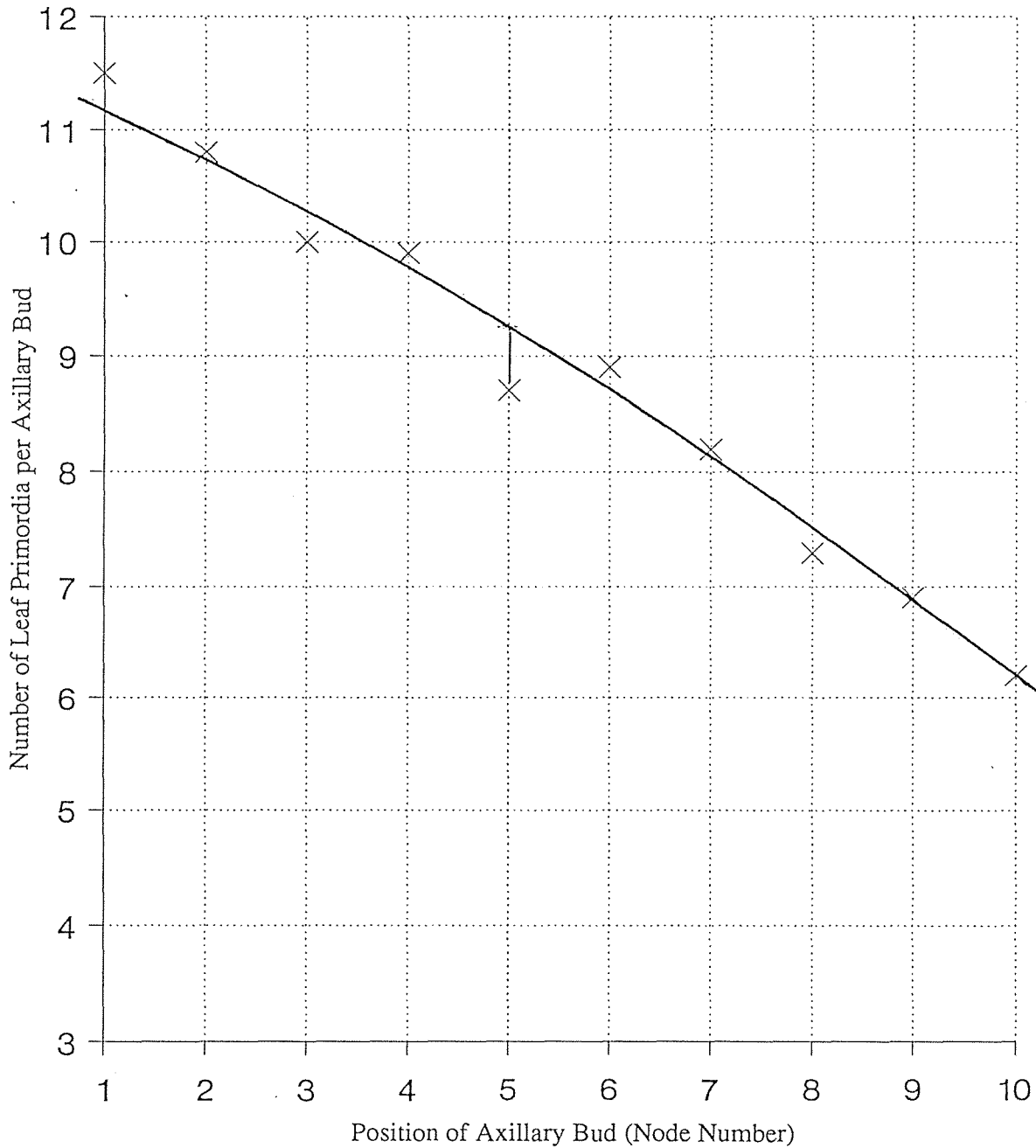


FIG 6.5 Data from the experiment to determine the effect of removal of a subtending leaf primordium on axillary bud growth.

The following data are listed below:

1. The length in mm of the leaf primordium at the time it was partially or fully excised. (**Primordium Length**)
2. Where the excised leaf primordium grew into a mature structure its length was expressed as a percentage of its expected final length. The expected final length was estimated from the lengths of the fully expanded leaves immediately above and below. (**Leaf Length**)
3. The period of growth between excision of leaf primordia from the shoot apex and the taking of measurements of axillary bud size. (**Growth Period**)
4. Growth depression. The calculation of this value is explained in STEP 1 at the start of the Results section of chapter 6. (**Growth Depression**)

Primordium Length (mm)	Leaf Length (%)	Growth Period (days)	Depression (no. of primordia)
3	0	15	3.48
12	7	15	0.7
9	0	15	1.52
4	0	15	0.82
3	30	15	0.4
3	20	16	0.1
3	20	16	0.5
1	20	16	0.5
0.5	0	16	1.6
14	0	16	0.76
9	0	16	1.52
23	0	16	0.53
14	5	16	0.74
5	10	16	1.0
8	0	16	2.12

Primordium Length (mm)	Leaf Length (%)	Growth Period (days)	Depression (no. of primordia)
10	0	18	0.64
8	0	18	1.64
4	8	18	0.82
1.5	0	17	2.0
4	20	42	0.37
68	0	37	0
83	0	37	0.3
20	0	37	1.88
17	0	64	1.3
5	0	64	2.8
110	0	37	-2.5
78	0	37	0.25
9	10	64	0
3	0	64	0.6
3	0	60	0.88
4	15	60	0.12
2.5	12.5	38	2.2
53	0	65	0.35
50	0	65	-0.1
49	0	65	0
115	0	65	-0.25
85	0	65	0.25
70	0	65	0
11	0	108	0.74
8	0	108	0.74
5	0	108	2.3
70	0	108	0.2
50	0	108	0.63
45	0	108	0.94
10	0	108	1.2
8	0	108	0.13
5	0	108	1.0
4	0	108	3.04
8	0	26	0

Primordium Length (mm)	Leaf Length (%)	Growth Period (days)	Depression (no. of primordia)
6	0	26	0.9
4	0	26	4.45
20	0	23	0.66
31	35	21	-0.25
25	36	21	0.55
132	36	21	-0.1
60	14	21	0
68	40	21	0.8
140	20	21	0.3
30	30	25	0
45	50	25	0
32	20	25	0
38	25	25	0
95	30	24	0.3
31	40	24	0.1
28	30	24	0.2
40	60	26	0
28	50	26	0.2
46	25	26	0.7
110	12	26	0.2
52	5	22	0.9
24	0	22	1.1
14	5	22	0.7
26	5	22	0.9
30	5	22	1.4
30	5	23	0
22	5	23	1.0
17	0	23	0.65
26	0	23	1.1
13	0	23	0.2
17	5	23	0.8
13	0	23	0.6
33	5	23	0.65
32	5	23	1.0

Primordium Length (mm)	Leaf Length (%)	Growth Period (days)	Depression (no. of primordia)
46	5	23	0.6
21	5	22	0.55
22	5	22	0.7
20	5	22	0.85
16	5	22	0.2
41	5	20	0.1
80	5	20	0.55
40	5	20	1.0
40	5	20	0.5
37	5	20	0.7

FIG. 6.6 Leaf removal experiment. Three dimensional graph relating axillary bud growth depression to the proportion of the subtending leaf/primordium which was excised, and the length of the subtending leaf/primordium at the time of excision.

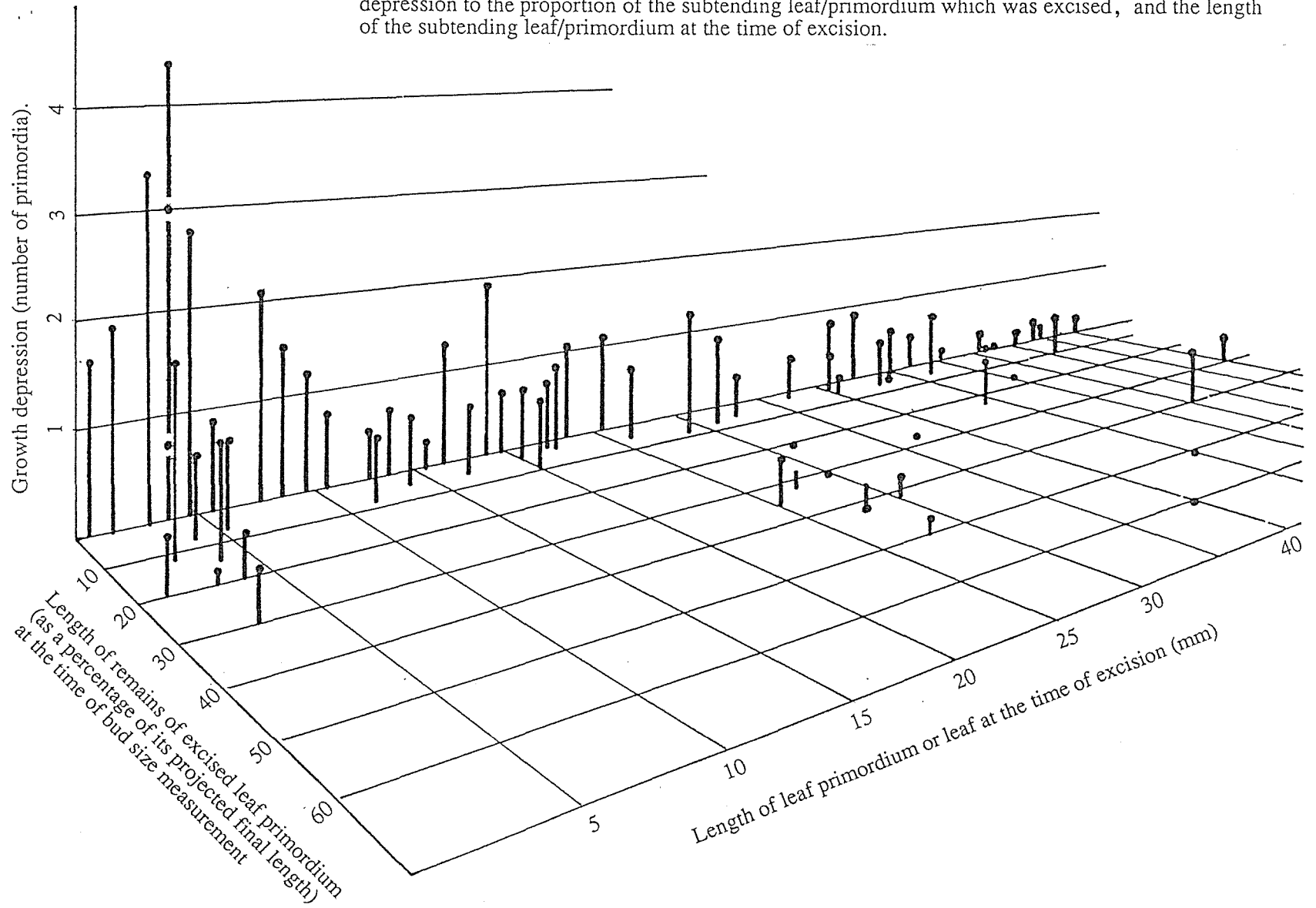


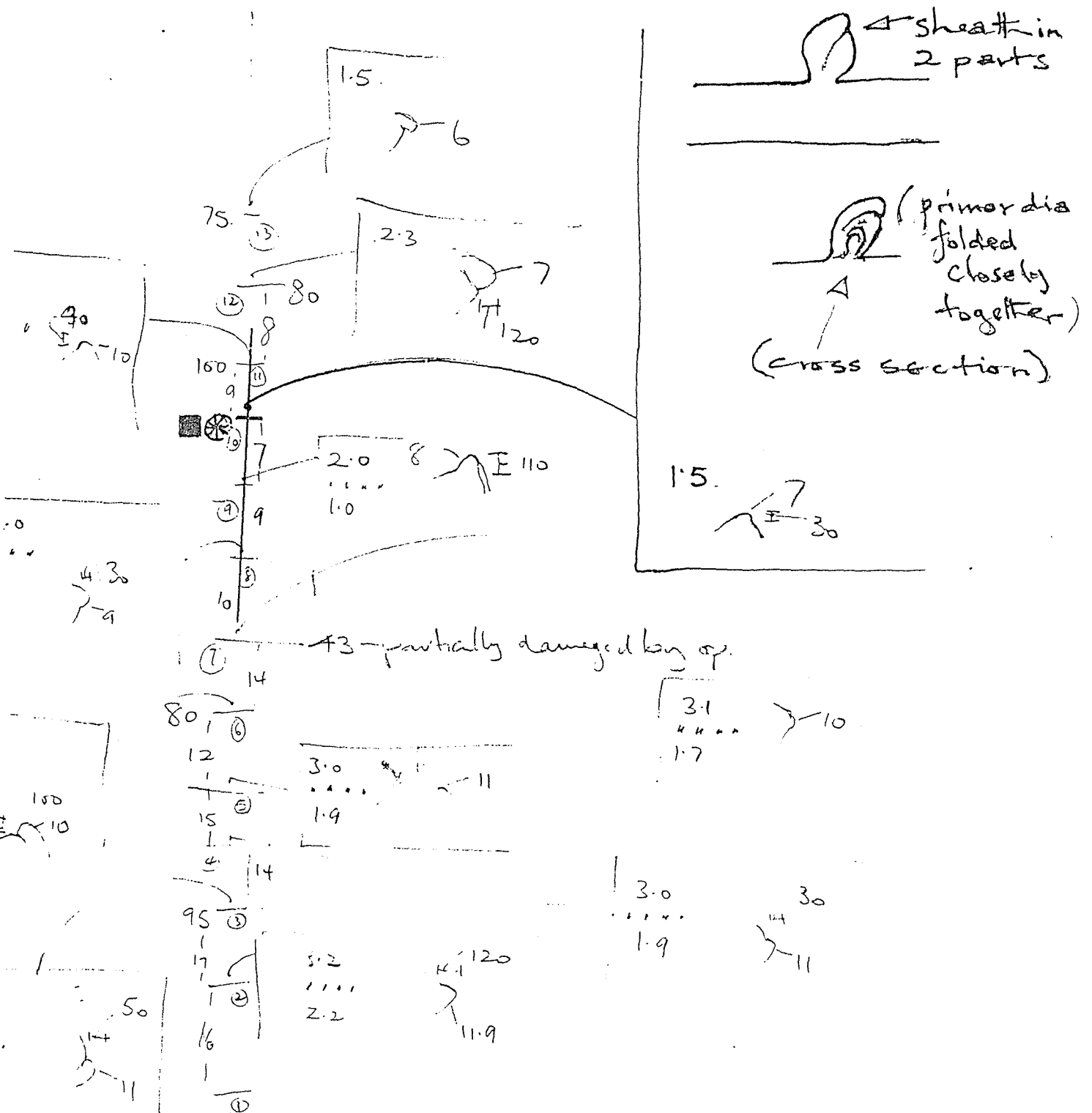
FIG. 6.7 Drawings of distorted axillary buds. The drawings were made in pencil at the time of dissection and the relevant parts have been reinforced with ink.

lengths. 5, 8, 11 mm on 7/4

July 47
~~85~~

(32)

■ ○ leaf excised when 5 mm long.

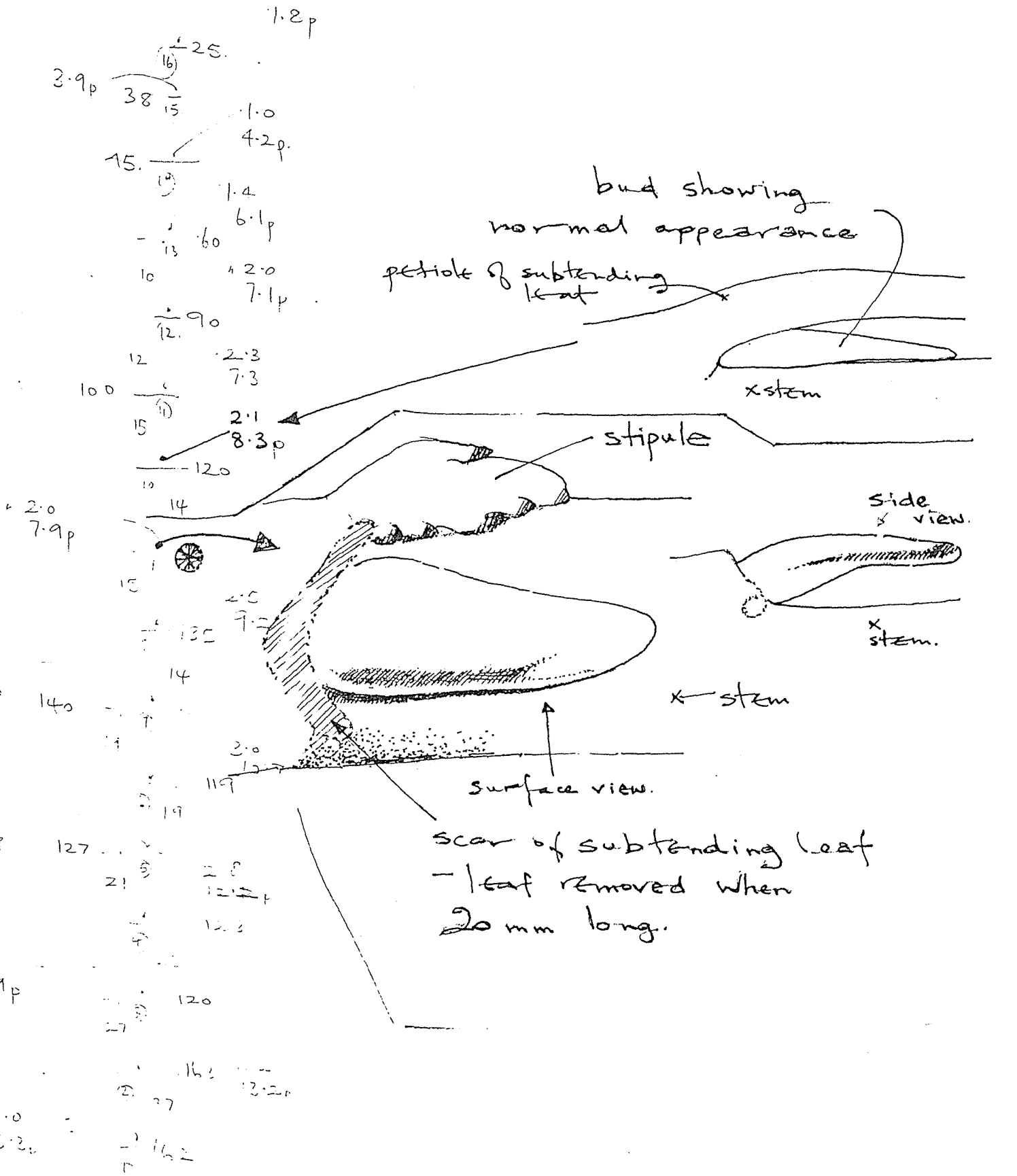


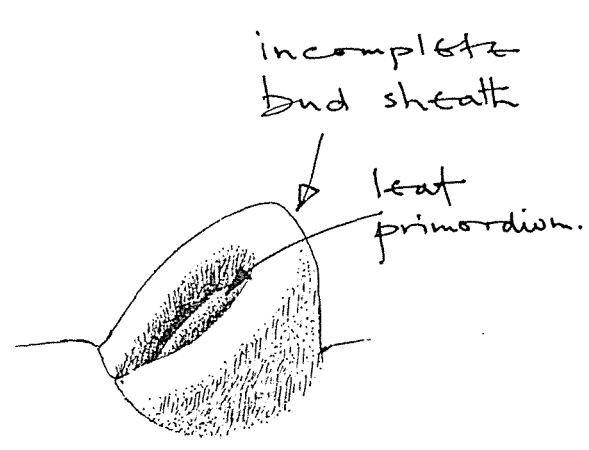
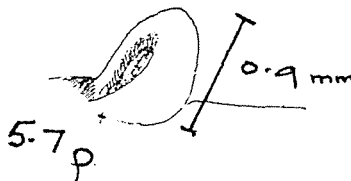
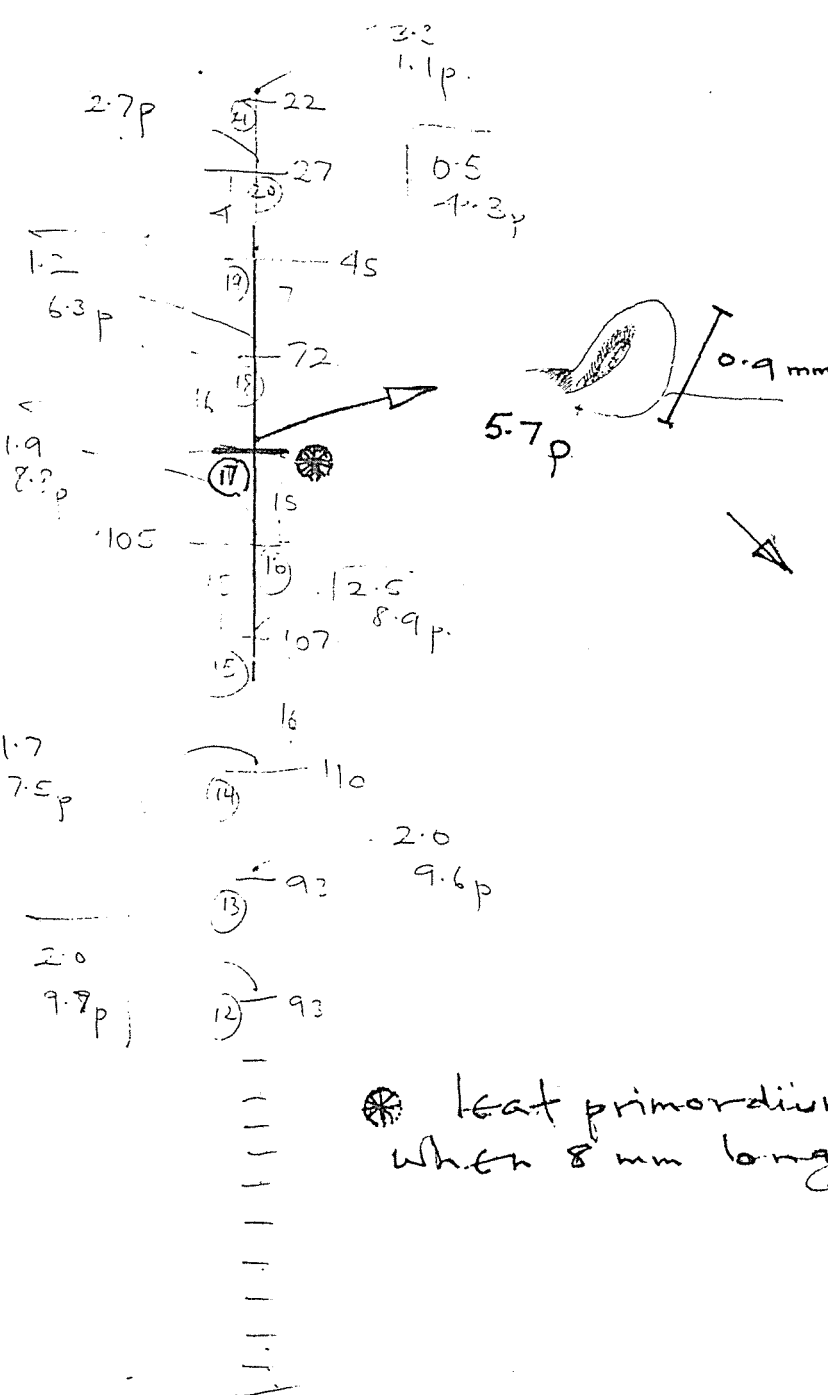
20 → 2

11 Dec - 3 Jan

7C - no useful evidence, 86 (55)

apex failed to grow on after the dissection but no bud break occurred in the shoot



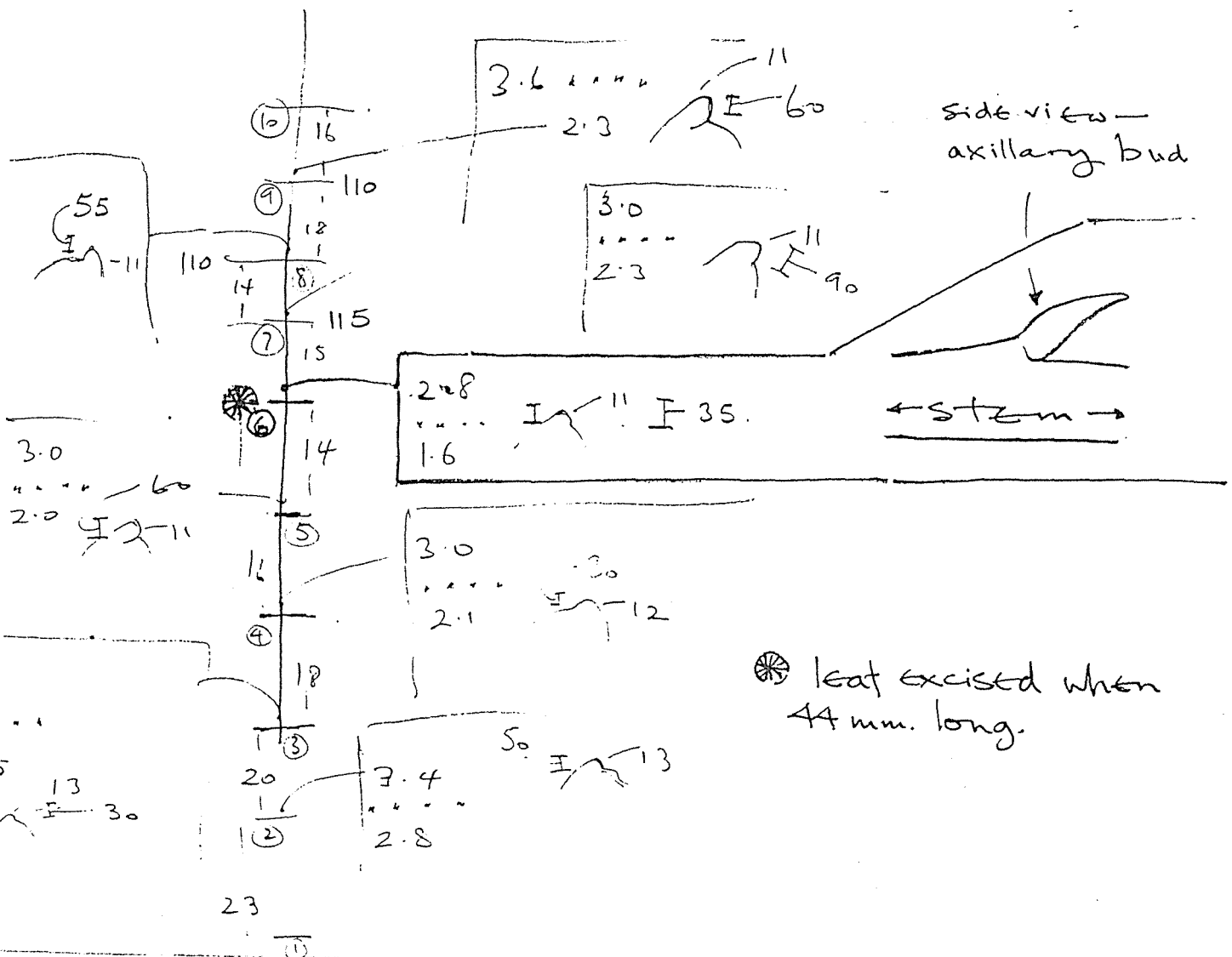


⊗ leaf primordium excised when 8 mm long.

50 x 44 mm from apex on 7/4.

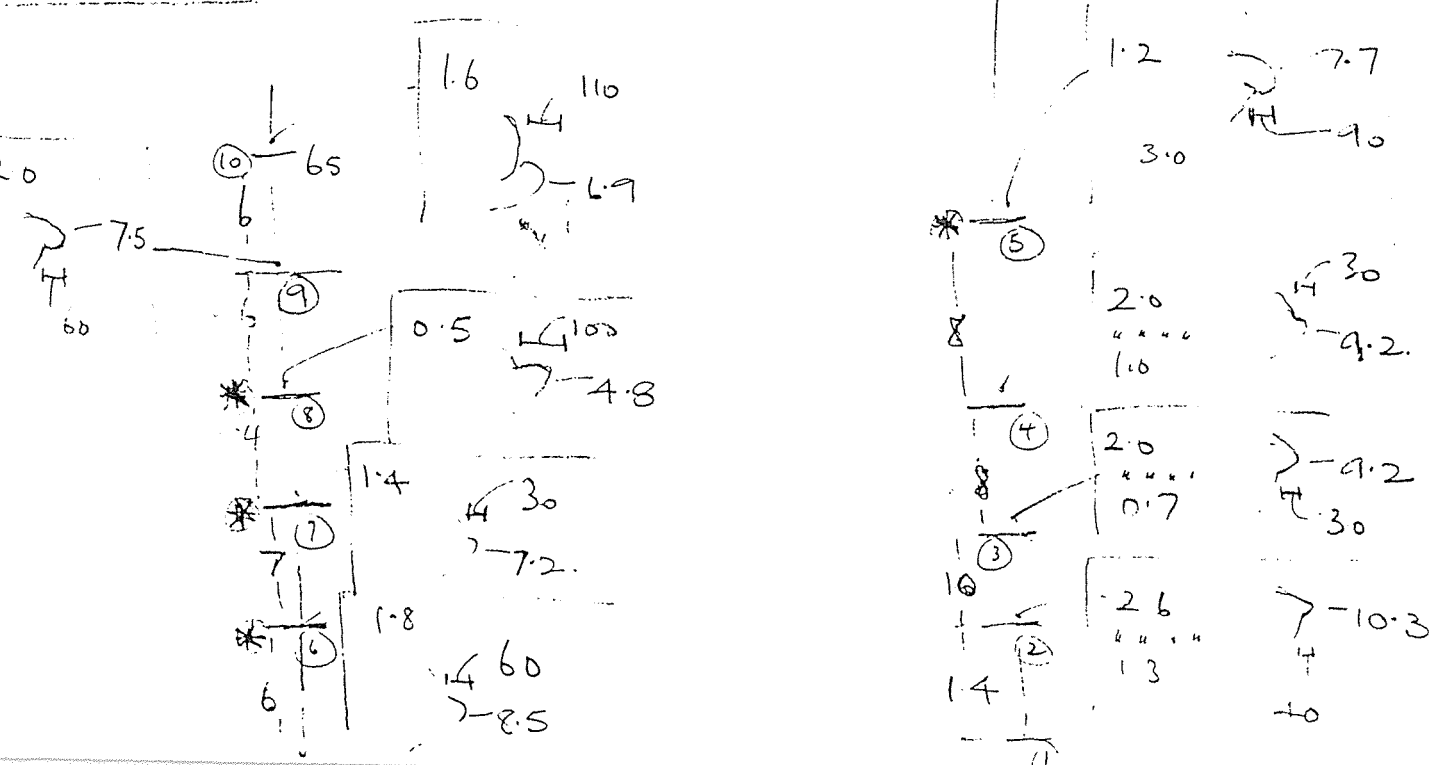
1088

(3)



primordia removed at 4, 5, 8, 10 mm on 7/4

July 2



CHAPTER 7

An Analysis of the Distribution of Photosynthate in a Shoot Apex of *Salix fragilis*.

Introduction

The data from experiments in which young leaf primordia were removed from willow shoots (chapter 6) demonstrate a clear correlation between leaf expansion and axillary bud growth. This suggests that initiation of leaf primordia in the axillary bud may be influenced by some factor or factors which cause or are involved in leaf expansion in the shoot. It was decided to investigate one feature which could provide information about such a hypothetical link, namely photosynthate distribution. Firstly, a survey of the anatomical structure of the bud region was carried out. Secondly, a few preliminary experiments were carried out in which radioactive ^{14}C in the form of carbon dioxide was "fed" to a leaf in various locations on the shoot and for various times; analyses of the radioactive content were made of the soluble fractions extracted from leaves, internodes and axillary buds. These experiments were carried out in order to determine the most suitable conditions to use for feeding radioactive carbon to regions of the shoot in which axillary growth was rapid as well as those in which growth was declining. When these results had been assessed a single histoautoradiographical experiment was performed in which radioactive carbon was fed to a shoot. Resulting nodal tissues were sectioned and stained, covered with a thin film of photographic emulsion and left in total darkness for several weeks. The photographic emulsion was then developed.

Anatomical survey

Materials and Method

A shoot which had a number of fully expanded leaves as well as an actively growing apex was removed from a plant. Leaf lengths and internode distances were measured. The nodal regions were removed from the stem. In the youngest regions the whole stem was taken from below the leaf insertion to just above the axillary bud. In older regions the stem was cut longitudinally to remove the part of the stem opposite the axillary bud - this was to allow rapid penetration of fixative, dehydration agents etc. into the tissues. In general the portions of tissue were no more than 1.5 millimetres thick, 2 millimetres wide and 7 millimetres long. The following protocol was then followed:

Process	Reagent	Time
Fixing	Chrom-acetic	18 - 24 hours
Washing	Distilled Water	24 hours
	Running Water	24 hours
Dehydration	20% Ethanol	1 hour
	30% Ethanol	1 hour
	40% Ethanol	1 hour
	50% Ethanol	1 hour
	60% Ethanol	1 hour
	70% Ethanol	1 hour
	80% Ethanol	1 hour
	90% Ethanol	6 hours
	90% Ethanol	6 hours
	100% Ethanol	6 hours
Clearing	Chloroform	1 hour
	Xylene	2 hours
Wax Embedding	50:50 Xylene: Molten Paraffin Wax	
	Paraffin Wax	1 hour
	Molten Paraffin Wax	1 hour

The embedded tissue was then microtomed into 8 micrometer-thick serial transverse or longitudinal sections which were mounted on slides. The following staining protocol was then followed:

Process	Reagent	Time
Wax Removal and Rehydration	Xylene	5 minutes
	50:50 Xylene:Absolute Alcohol	5 minutes
	Absolute Alcohol	5 minutes
	95% Ethanol	5 minutes
	85% Ethanol	5 minutes
Staining and Dehydration	Safranin (1% w/v)	24 hours
	85% Ethanol	10 seconds
	Anilin Blue (1% w/v)	2 minutes
	Acid Alcohol	a few seconds
	95% Ethanol	a few seconds
	Absolute Alcohol	a few seconds
	Xylene	2 minutes

Stained sections were then mounted in DPX.

Serial sections of a number of buds were examined, and morphological features of interest in the nodal regions were identified. A number of photomicrographs have been used to illustrate these features - PLATES 7.1 to 7.5.

Histoautoradiography

Materials and Method

A single pot-grown plant similar to those used in the leaf removal experiments with shoots bearing several fully expanded leaves and with an actively growing apex was chosen. It had been growing in the open air. All leaf lengths and internode lengths on one shoot were measured. A recently fully expanded leaf on this shoot was exposed for three hours to air containing 50 microcuries of ^{14}C as carbon dioxide in a perspex chamber in the laboratory. The chamber was illuminated from above with two 150 watt GEC Photoflood lights, a perspex-walled water bath containing circulating cold tap water being placed between the lights and the chamber. After exposure the leaf was removed from the chamber and nodal regions were removed and prepared for sectioning. Transverse and longitudinal sections were made. These were taken through the staining regime previously described except that the safranin stage was omitted.

After clearing in xylene the sections were allowed to air dry. They were then covered with a thin film of Ilford L4 Nuclear Emulsion in a dark room and left in absolute darkness for six weeks. Subsequent development followed this protocol:

Process	Reagent	Time
Development	Kodac Microdol X	5 minutes
Wash	Distilled Water	a few seconds
Fixing	Ilford Ilfofix	10 minutes
Wash	Distilled Water	15 minutes
	Distilled Water	15 minutes

The slides were allowed to air dry for two hours, then mounted in DPX.

Results

Photomicrographs of various sections are shown in PLATES 7.6 to 7.9.

Discussion

The original intention of these experiments was to find out if there was some obvious physical constraint on nutrient supply to the axillary buds. If so one would have been able to further examine the nature of such a constraint to see if it tied in with the reduction in axillary bud growth rate described in chapter 5. If not, perhaps suggestions for further exploration would emerge.

The presence of ^{14}C atoms fixed into structural tissues is indicated by the black silver grains located immediately on top of that tissue. All cell walls are lightly stained with aniline blue. The axillary bud sheath contains a higher concentration of ^{14}C than the bud apex and bud leaf primordia (PLATE 7.6). In this respect it resembles the leaf and stem tissue. The anatomical survey dealt with earlier in this chapter also suggests this conclusion. The transition between the apical region with its low concentrations of ^{14}C and the sub-apical region with higher concentrations is quite distinct (PLATE 7.8).

The provascular tissue seen in section on either side of the sub-apical tissue shows very little sign of ^{14}C accumulation (PLATES 7.6, 7.8). This

contrasts with the situation in tissues in and around the stipules (PLATE 7.9) - these tissues contained the highest concentrations of deposited ^{14}C in the whole plant.

It appears that there is no general constraint on photosynthate availability - radioactive tracer is spread throughout the plant's tissues. Where cell wall deposition is greatest, for instance in expanding leaves and stipules, very high levels of ^{14}C have accumulated. However, a good vascular supply is available to these regions. But the bud sheath has noticeably higher levels of ^{14}C than the other regions of the axillary bud, no functional vascular tissue being present in the bud itself. The variations in activity within the axillary bud, which these different patterns of ^{14}C accumulation imply, tie in with contemporary ideas (Nelson and Langdale 1989) about the way that individual cells forming discrete regions of tissue behave in an independent fashion, responding to signals derived from their surroundings.

PLATES 7.1 to 7.5 Photomicrographs of transverse sections through a small axillary bud in *Salix fragilis*. The bud has one leaf primordium and was subtended by a leaf 10 mm in length.

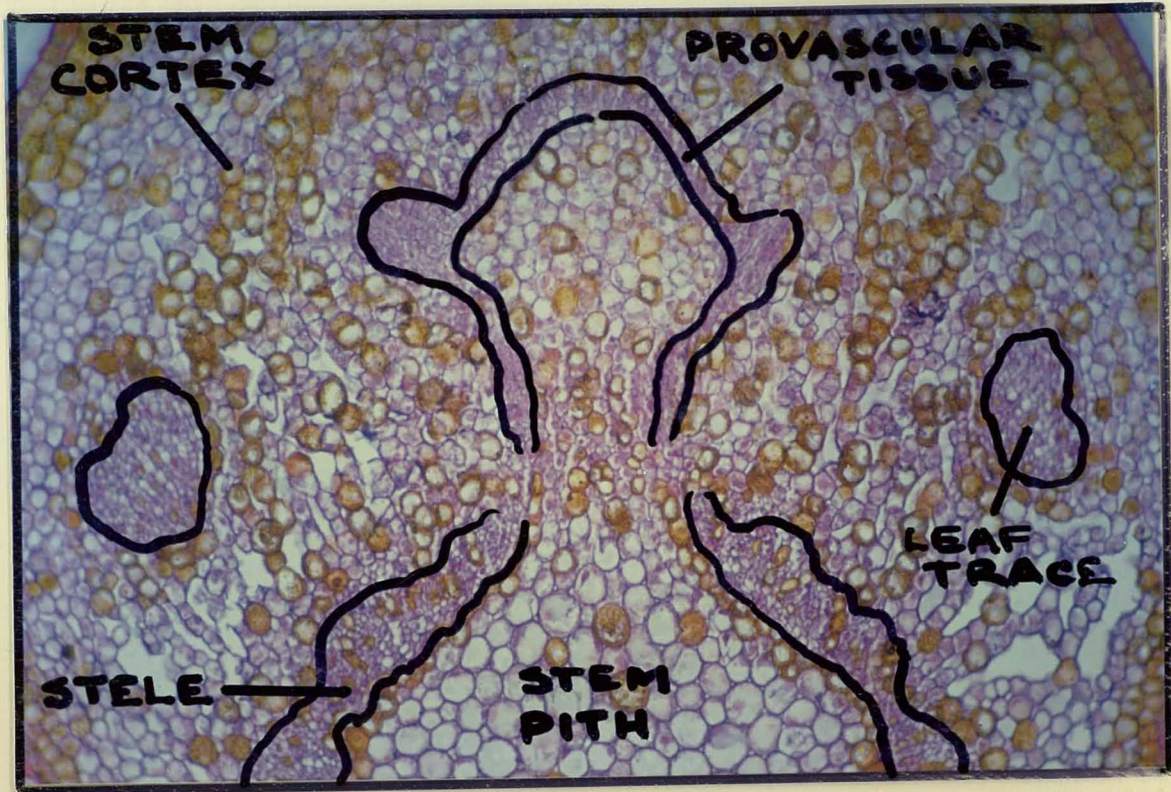


PLATE 7.1 Section through a region below the bud showing the vascular tissue of the leaf traces, provascular tissue, stem pith, and stem and petiole cortical tissues. The pith consists of large, vacuolated cells. It is surrounded by a stele of vascular tissue except in the branch or bud gap region where it is continuous with the sub-apical parenchyma tissue of the axillary bud. Provascular tissue surrounds the sub-apical parenchyma. Most of the provascular tissue is destined to form vascular tissue supplying the lateral shoots, but the two enlarged regions on either side are associated with accessory buds; they will probably remain provascular until such time as the accessory buds break. Cortical tissue consisting of vacuolated cells and containing air spaces is located outside the vascular and provascular tissue. The nature of the yellow-brown deposit in the cells forming two or three layers in the epidermal region of the stem and distributed throughout the stem and leaf tissues was not ascertained. It tested negatively for tannins and suberin.

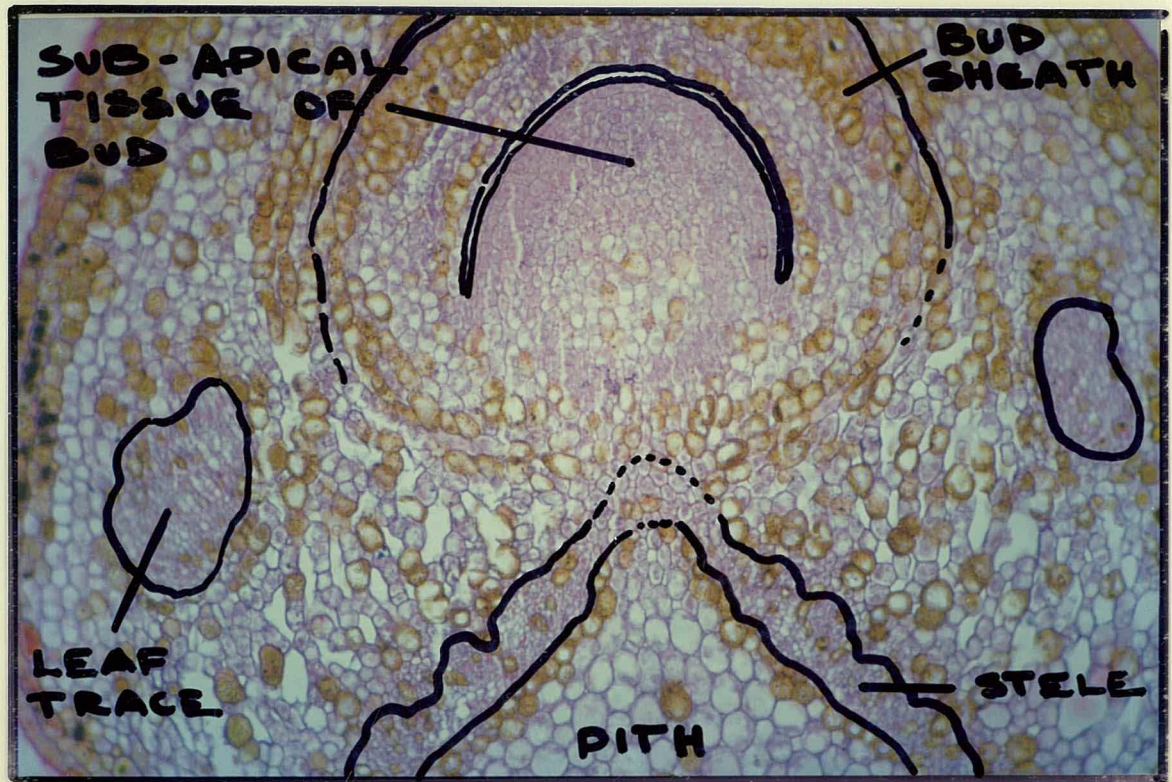


PLATE 7.2 Section through the proximal region of the bud showing the sub-apical tissue of the bud and the proximal region of the sheath. Some vacuolation is visible in the bud tissue, but most consists of non-vacuolated cells. The outer two or three layers of the bud sheath are predominantly deposit-filled cells, as are the outer layers of the stem and petiole.



PLATE 7.3 Section through the bud in the vicinity of its apex, showing the bud sheath, the proximal region of the bud leaf primordium, stem, and petiole of the subtending leaf. The deposit-filled cells form coherent layers in the leaf petiole epidermis (abaxial and adaxial surfaces) and in the sub-epidermal region of the bud sheath (inside and outside layers) as well as being present in the axillary bud apical region itself.

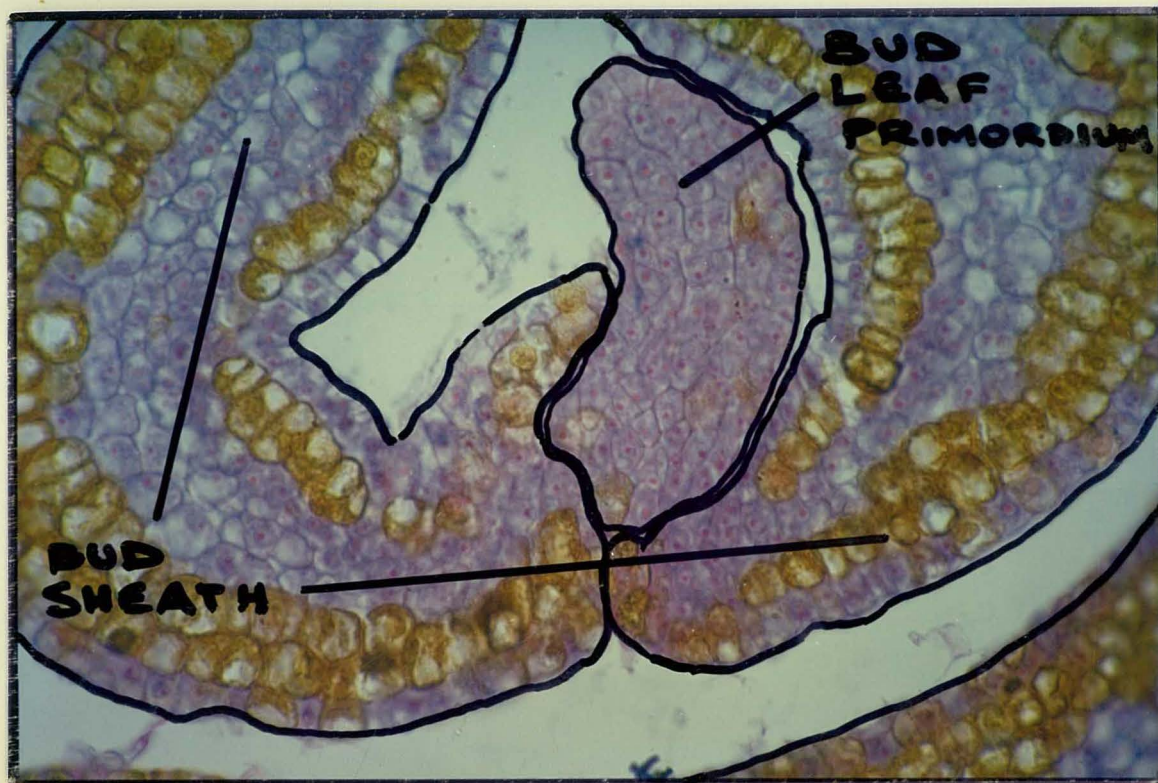


PLATE 7.4 Section through the distal region of the bud, showing the bud sheath, the gap between the separate sides of the sheath, and the distal region of a bud leaf primordium. The deposit-filled cells are located sub-epidermally. The leaf primordium tissue consists of non-vacuolated cells (nucleoli are stained red) while the bud sheath cells are predominantly vacuolated. It would appear that the axillary bud contains meristematic tissues (leaf primordia, bud apex and some of the bud sub-apical tissue) and non-meristematic tissues (the proximal region of bud sub-apical tissue, and bud sheath).

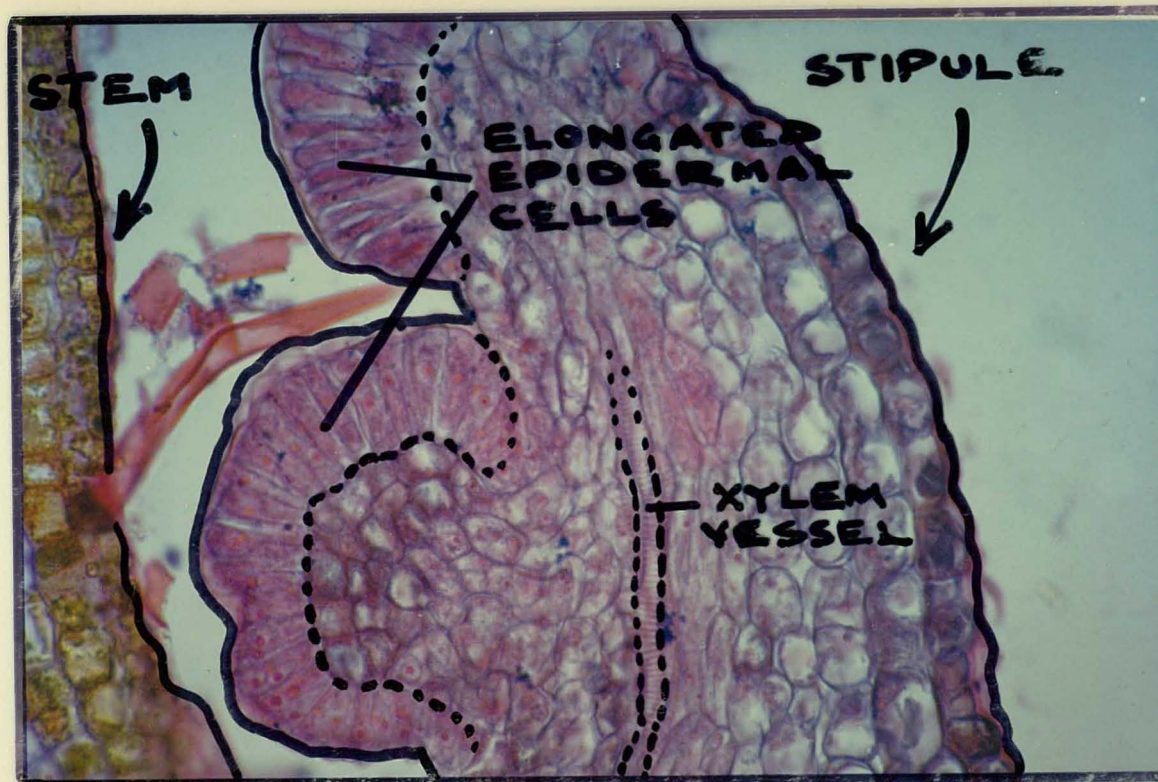


PLATE 7.5 Longitudinal section through a stipule. The stipule is free of deposit filled cells. It has a vascular supply (xylem lignification is stained red) and is lined on the adaxial surface with nodules having elongated, non-vacuolated epidermal cells.

PLATES 7.6 to 7.9 Histoautoradiography experiment - photomicrographs of longitudinal sections through the apical region of a shoot in *Salix fragilis* into which radioactive carbon had been fed.

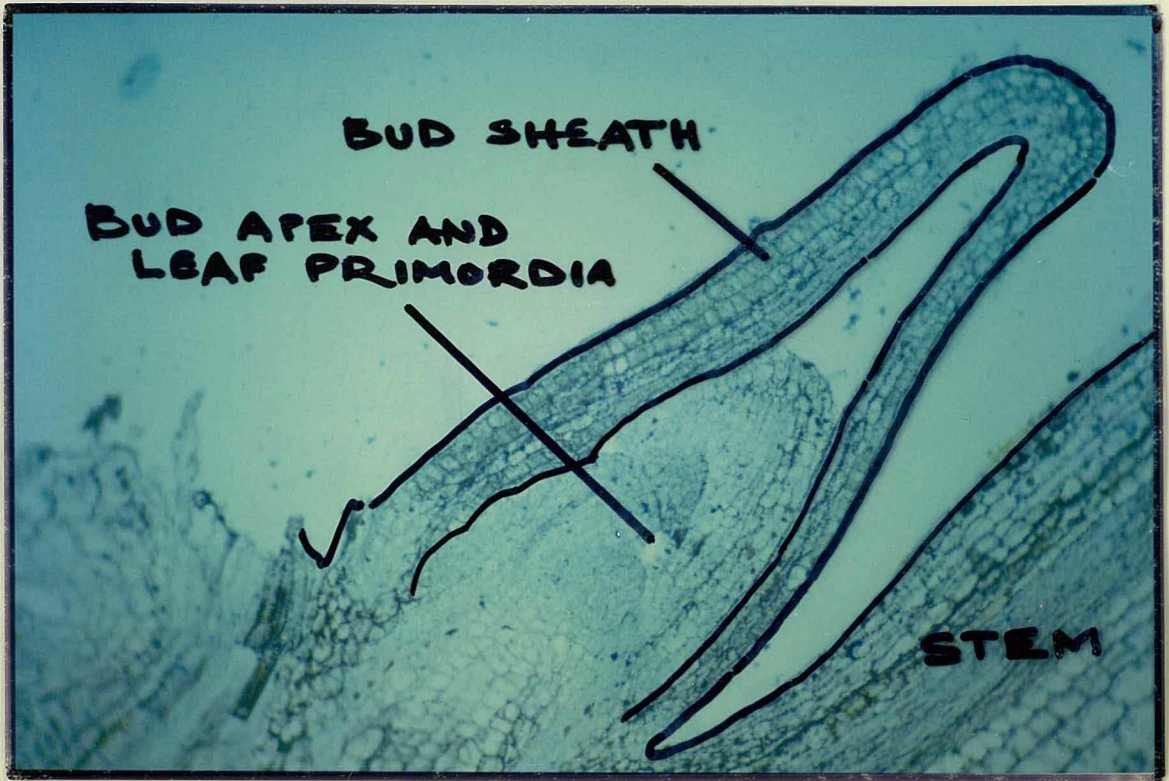


PLATE 7.6 Longitudinal section through an axillary bud containing three developing leaf primordia. Cell walls are stained very light blue; black silver grains indicate the presence of ^{14}C atoms in the underlying structure.

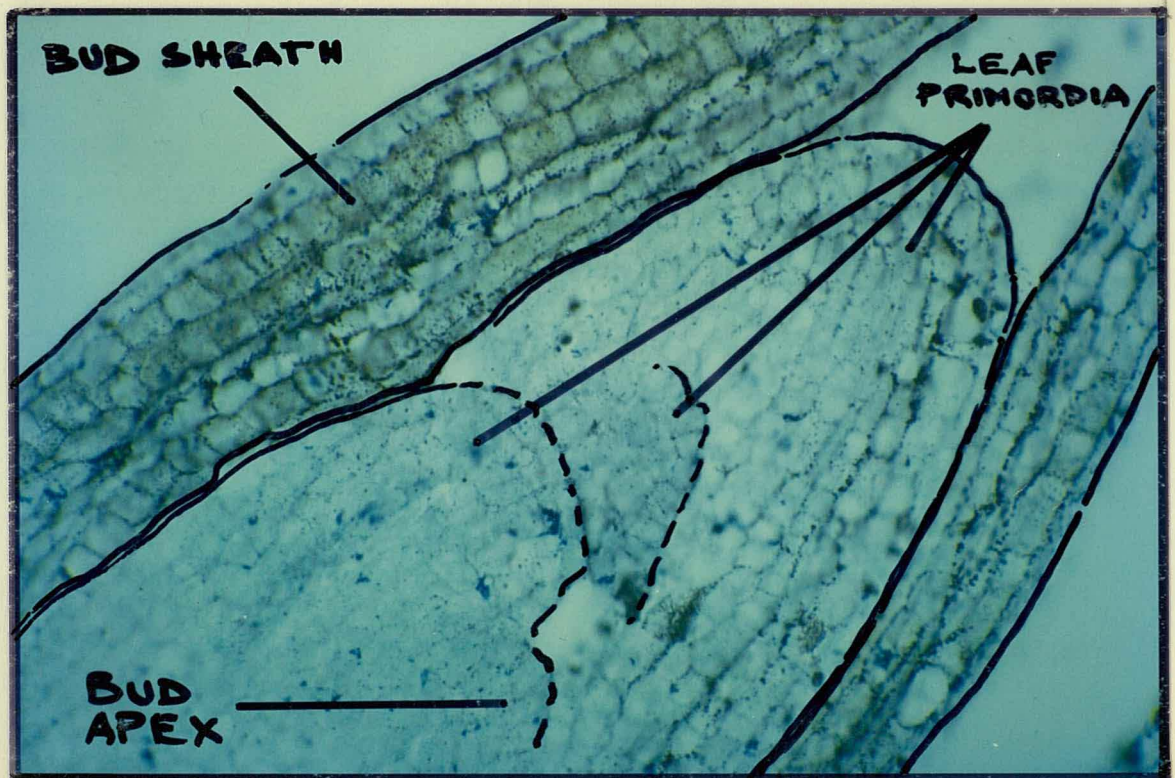


PLATE 7.7 Longitudinal section through the apical region of the axillary bud pictured in PLATE 7.6.

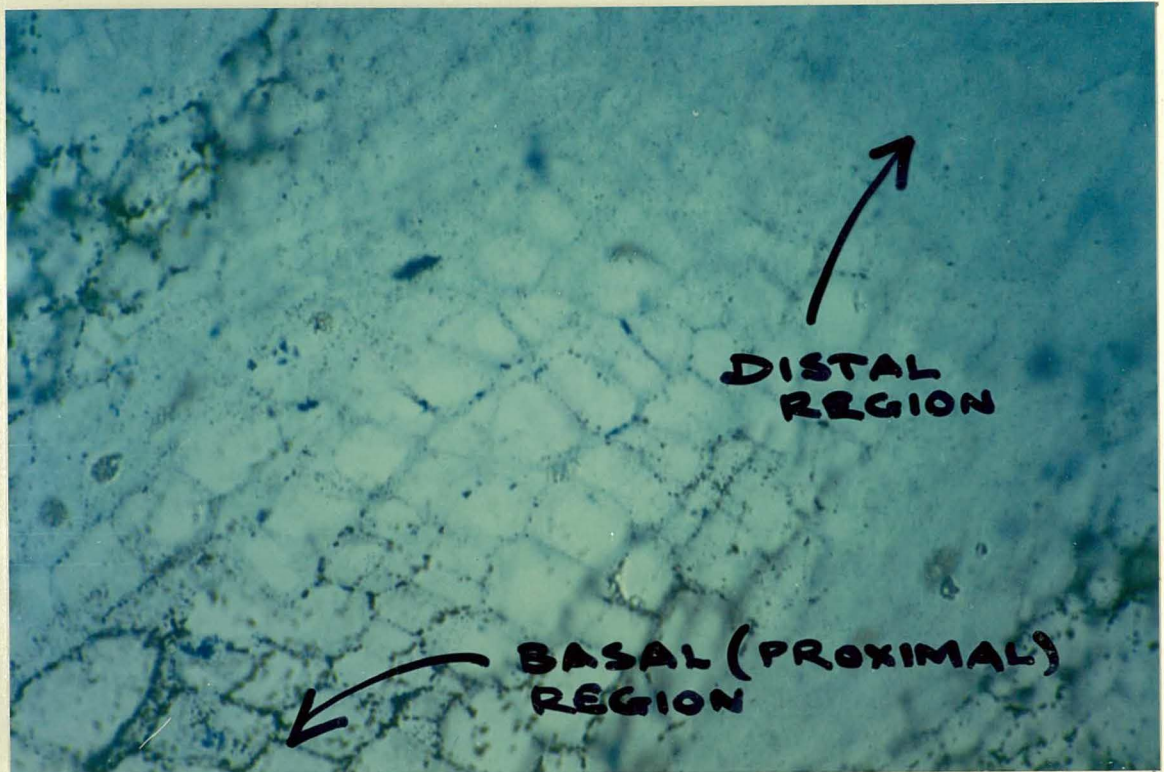


PLATE 7.8 Longitudinal section through the basal region of the axillary bud pictured in PLATE 7.6.

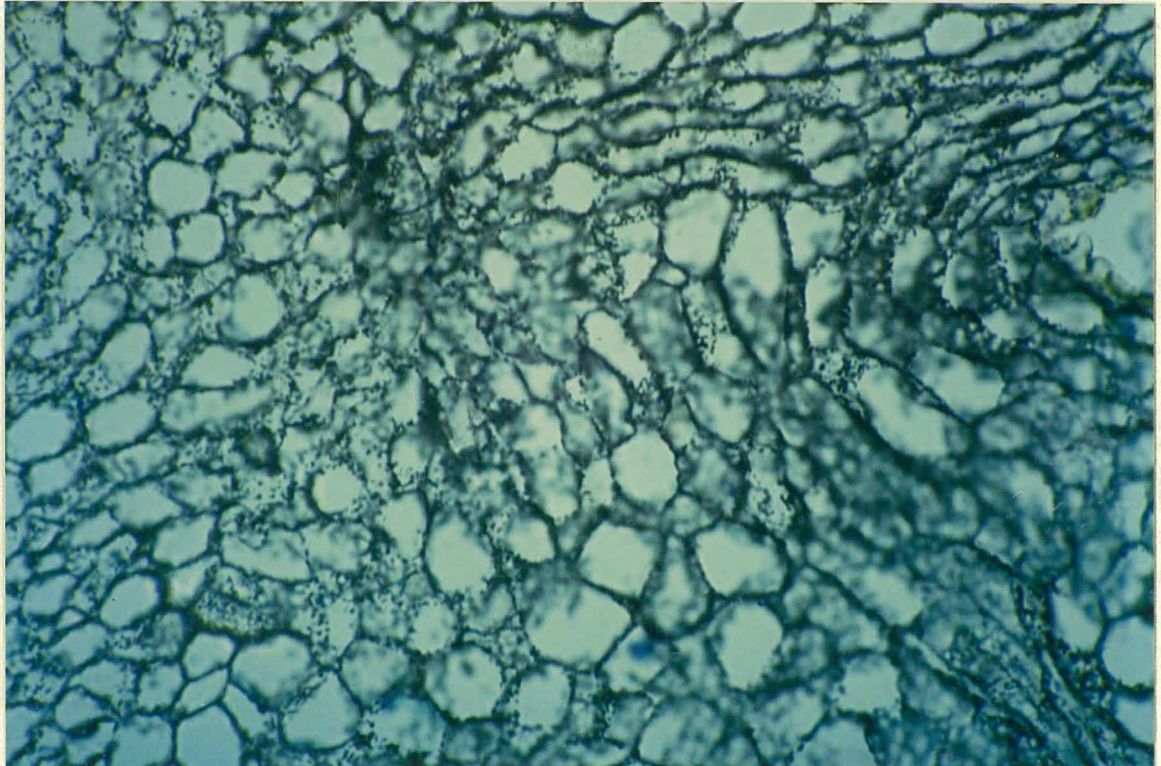


PLATE 7.9 Longitudinal section through tissues in the region of the leaf stipules adjacent to the axillary bud pictured in PLATE 7.6.

CHAPTER 8

Discussion

This study was aimed at elucidating features of the growth of axillary buds in angiosperms. One of the first ideas to emerge from an initial morphological survey was that the process of axillary bud growth in different species varied. The survey - described in chapter 4 - has shown that a large number of apparently different patterns of axillary bud development exists. When one considers the range of lateral growth strategies amongst the angiosperm plant species this is not an unexpected conclusion. An attempt has been made to classify the species studied according to the distinct differences in growth patterns. This approach has enabled the whole topic to be analysed more easily. However, it could also have led to the idea that hard and fast distinctions exist between different patterns when in fact they probably do not. For instance, the division into monocarpic and polycarpic species is based on one aspect of bud behaviour - the permanent retention of viable axillary buds in some part of the plant other than the seed. But the type of behaviour identified, particularly in monocarpic species where patterns of axillary bud growth are closely linked to floral development in the shoot apex, is present in shoots in many polycarpic species.

The distinction between proleptic and sylleptic behaviour is also somewhat blurred. Of the species classified as exhibiting sylleptic bud development, one - *Vitis arnurensis* - possesses resting buds which enable the plant to overwinter; these buds hence grow in a proleptic fashion. Several of the proleptic species have axillary buds whose structure is typical of sylleptic species. For instance, axillary buds in *Passiflora* have a hypopodium and no specialised sheathing structures. And under certain conditions axillary buds on rooted cuttings of *Salix fragilis* were found in this study to break almost immediately after initiation. It could be argued that, since bud break in sylleptic species occurs effectively at the time of their initiation, one should consider the extreme step of excluding them from consideration **at all** within the topic of pre-break axillary bud growth. However, in view of the statements made at the start of this paragraph this would not be a sensible move.

Passiflora also illustrates another issue, that of the existence of several axillary structures at each node. In *Vicia faba*, axillary buds are initiated one after another in each of the proximal nodes. Hence four or five buds can exist at

different stages of development in each of these lowest nodes. Most form lateral shoots. In *Passiflora*, each leaf subtends three different axillary structures - one forms a tendril, one is an axillary bud which forms the lateral shoot and one is an accessory axillary bud. In *Myoporum*, bud complexes develop in nodes in specific regions of the shoot. In some cases all buds at one node flower, but combinations of flowering and vegetative buds at a single node can occur. It is difficult to resolve the behaviour of the axillary structures in these kinds of patterns with the idea that the apex in some way dominates the behaviour of other parts of the plant. This type of behaviour often occurs while the the shoot apex continues to grow vegetatively so that the argument that apical dominance can be temporarily suspended under certain conditions can not be used to explain all such phenomena. A better model would seem to be one in which each axillary structure responds to the existing local conditions, these conditions being set by influences from all parts of the plant, including the stem apex.

In truly sylleptic species such as *Coleus*, the presence of an actively growing shoot apex correlates with a reduced rate of growth in lateral shoots. In truly proleptic species such as *Salix*, removal of the shoot apex tends to initiate axillary bud outgrowth. A single, unified theory for apical dominance needs to explain how, on the one hand, the functioning of the shoot apex can effect a particular growth rate in another part of the plant whilst in another species it can cause complete suppression of outgrowth. Furthermore it would need to explain how outgrowth of the axillary bud can occur while accessory buds remain suppressed. A model which has buds or shoots responding to local conditions provides the best explanation for such anomalies.

The determination of relative rates of leaf primordium initiation in axillary buds was carried out because it was reasoned that if apical dominance affected the earliest phases of growth in the axillary bud, one would expect rates of leaf primordium initiation in the axillary buds (or lateral shoots in sylleptic species) to be lower than rates of leaf primordium initiation in the apex, especially since the axillary buds are closer to the apex in this early phase of their growth. This was found not to be the case - relative rates varied from about 0.5 to 2.5. Upon reflection it has become clear that this reasoning is false. In general, plants which are taller than they are wide can be expected to make less provision for lateral nodes than for nodes on the main axis. In *Ulmus* the terminal bud eventually becomes larger than the buds immediately below it even though it started life similarly as an axillary bud. On average axillary buds can be expected to initiate nodes more slowly than the shoot apex. And even where

relative rates of primordium initiation are greater than unity, primordium initiation in axillary buds can slow down while the shoot apex continues to grow, leading to the same condition of the axillary bud containing a smaller number of nodes than the shoot that supports it. Hence this section of the study serves only to dispel the notion that suppression of growth activity in axillary buds occurs as a matter of course.

The initiation of axillary buds was not explored in detail in this study. The main emphasis was placed on the later stages of bud growth. In most species the distinct parts of the apical region of shoots were found to behave in a similar fashion, internode extension and leaf expansion occurring at the same time as the axillary buds were initiating primordia at their maximum rate. At the same time that internode extension ceases and leaf expansion is completed, primordium initiation in the axillary bud slows. Apparent exceptions to this pattern were found, but a connection between high levels of activity in the apical regions of a shoot as a whole and those in the axillary bud may still exist in these cases. Also, patterns of behaviour in some monocotyledonous species, for example in *Musa*, differ greatly from those encountered in the dicotyledonous ones. These species really need separate consideration. It still remains that the vast majority of the data in the plant survey point to the existence of a link between the rate of growth of an axillary bud and the rate of growth in the surrounding tissues. Further evidence for such a link was obtained in experiments with *Salix fragilis*. These involved the excision of leaves and leaf primordia from shoots and shoot apices. The existence of a correlation between leaf removal and depressed growth in the subtended axillary bud was quite clear. Failure to discount the effects of general damage in these experiments discounts their value to a certain extent, but they should be regarded as complementary to the other information presented.

The existence of patterns of development in which axillary buds appear to be autonomous to a large extent - *Ulmus* and *Nicotiana tabacum* are obvious examples - seems to be at odds with any model in which the activities within the shoot apex are said to affect the growth in the shoot's axillary buds. The axillary buds in these species at least must have intrinsic controls which largely determine their pre-bud break growth.

Many of the data collected in this study lead to the conclusion that bud growth and bud break may well be separate processes. In *Salix fragilis*, the growth pattern and structure of leaf primordia in the axillary bud were different from those in the shoot apex in that vacuolation and expansion growth were

absent in the latter but present in the former. In some species the axillary buds only initiated a limited number of leaf primordia. If it is the case that the processes are separate there is **no reason to suppose** that apical dominance, which has been demonstrated repeatedly to apply to the bud break phenomenon, should in any way affect pre-break bud growth.

The one major conclusion to be made is that the early phases of axillary bud growth in non-sylleptic angiosperm species before bud break ensues are more likely to be affected by local and/or intrinsic factors rather than by influences originating in the stem apex itself. I will return to the review article which prompted this study (Phillips 1975). "In all cases it appears that the development of each lateral bud is arrested at some stage and apical dominance is clearly imposed." It is clear that bud growth is arrested in some species but not by any means in all. And the arrest of bud growth is not, as far as I can see, anything to do with the imposition of apical dominance - apical dominance is a fact of life which applies to all buds at any stage of their growth and relates solely to the phenomenon of bud break and shoot outgrowth.

Appendix

SECTION 1

This contains the information obtained during the the survey of plant species described in chapter 4 - Axillary Bud Growth Patterns. The data are tabulated and graphs plotted according to the scheme laid out below. The abbreviated description of the particular data - which appears at the top of each column - is shown, with the full description and the ways the data are plotted on the graphs:

Abbreviation	Full description of data and mode of plotting
Node No.	Nodal position of axillary buds and subtending leaves on the shoot - plotted on the horizontal axis
Primordia/Bud	The number of leaf primordia in each axillary bud - plotted on the left vertical axis
Length 1st Pr.(mm)	The length in millimetres of the first-formed (oldest) or longest primordium in each bud - plotted on the right vertical axis
Length Sub. Leaf (cm)	The length in centimetres of the leaf subtending the axillary bud - also plotted on the right vertical axis.

Legend

The legend for all graphs is the same. It is shown below:

Primordia/Bud	×—×—×—×—×—
Length 1st Pr.(mm)	□—□—□—□—□—
Length Sub. Leaf (cm)	▽····▽····▽····▽····▽····

The horizontal axis in all cases is labelled "Node Number" - this is an abbreviation for: **nodal position of axillary buds and subtending leaves on the shoot.**

SECTION 2

This contains data concerning graphs in chapters 2 and 6.

SECTION 1

*Acer platanoides***Dissection Results**

Node No.	Primordia/Bud	Length 1st Pr.(cm)	Length Sub. Leaf (mm)
----------	---------------	--------------------	-----------------------

Shoot 1: dissected 18th October

1	1		13.0
2			0.2

shoot apex located above node 5

Shoot 2: dissected 27th November

1	6.2	3.0	26.0
2	6.3	4.5	18.0
3	5.1	2.4	9.5
4			0.4

shoot apex located above node 10

Shoot 3: dissected 5th February

1	5.5	2.3	33.0
2	6.2	2.8	30.0
3	7.5	4.5	22.0
4	5.8	2.0	10.5
5			3.5
6			5.7
7		scale leaves	5.0
8			4.0
9			3.5
10			1.7
11		foliage leaves	1.2
12			0.6

shoot apex located above node 12

Shoot 4: dissected 10th July

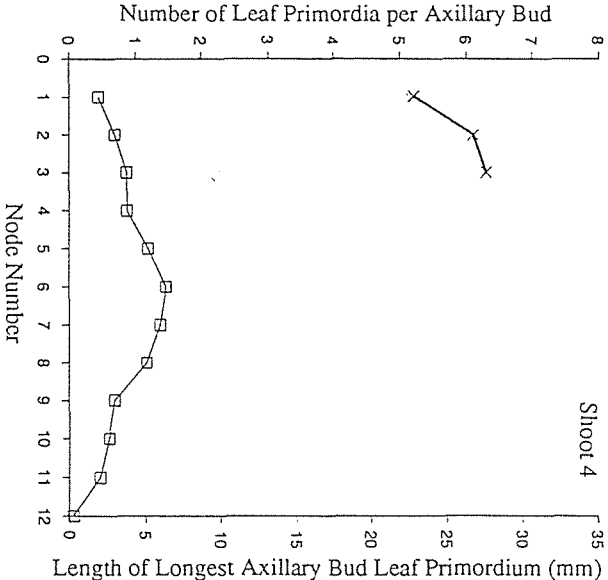
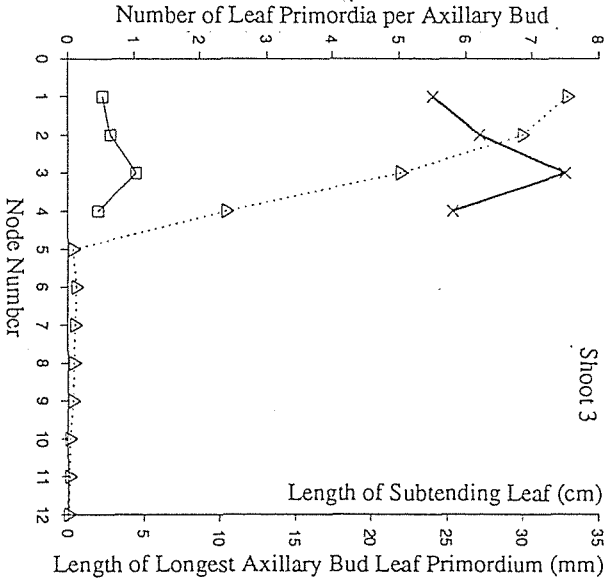
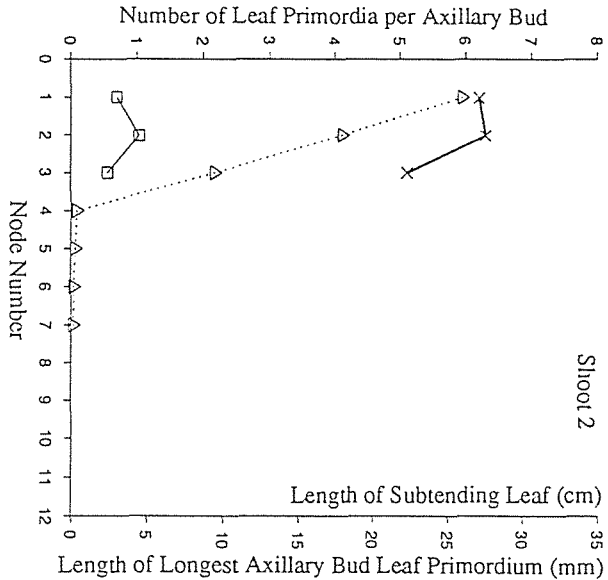
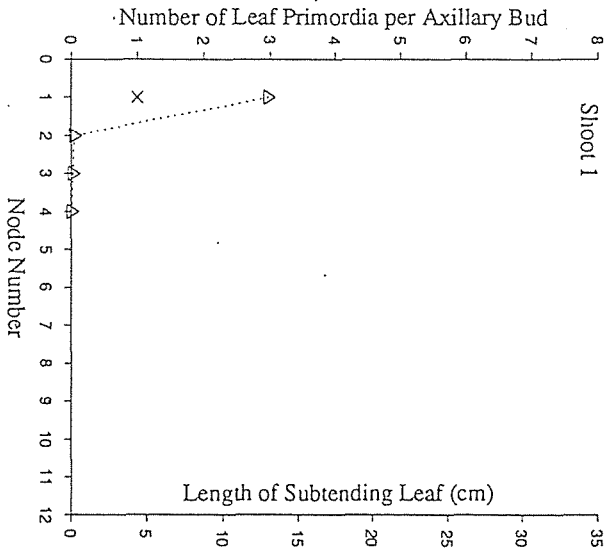
1	5.2	1.9	
2	6.1	3.0	
3	6.3	3.8	
4		3.8	

nodes 5 to 8: scale leaves

nodes 9 to 12: foliage leaves

shoot apex located above node 12

Aristotelia fruticosa



Dissection Results

Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf(cm)
----------	---------------	--------------------	----------------------

Shoot 1: dissected 13th September

2	3.3	1.5	7.5
3	3.7	1.7	7.4
4	3.1	1.3	4.1
5	2.1	0.4	1.5
6	1.1		0.6

shoot apex located above node 9

Shoot 2: dissected 26th October

3	5.1	2.3	7.5
4	5.2	2.3	7.5
5	4.8	2.3	13.3
6	4.6	2.0	12.5
7	4.1	1.7	4.6
8	3.0	1.0	0.7
9	1.8	0.15	0.68
10	1.0		0.3

shoot apex located above node 13

Shoot 3: dissected 1st February

3	5.7	2.5	14.0
4	6.7	2.8	19.0
5	6.8	2.4	10.5
6	7.2	2.9	16.5
7	6.8	2.7	15.0
8	7.3	3.0	11.8
9	6.8	2.9	11.5
10	6.5	2.7	9.0
11	6.1	2.5	12.0
12	4.9	1.8	7.8
13	3.9	0.9	2.3
14	1.2		1.0

shoot apex located above node 18

Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf(cm)
Shoot 4: dissected 1st March			
1	4.2	1.0	
2	5.2	0.5	
3	5.2	1.3	
4	5.2	1.2	
5	6.4	1.5	17.5
6	6.0	1.8	20.0
buds at nodes 7, 8 and 9: broken			
10	6.1	2.5	17.5
11	7.0	3.5	18.0
12	7.1	4.0	14.3
13	6.9	3.8	14.5
14	6.8	3.4	11.0
15	6.2	2.9	14.5
16	5.2	2.6	10.3
17	4.4	1.7	3.5
18	4.1	0.9	1.6
19	3.0	0.6	0.5
20	1.8		0.4
21			0.2
22			0.1
23			0.6
shoot apex located above node 24			
Shoot 5: dissected July 10th			
1	5.3		
2	5.4	3.0	
3	4.6	2.0	
4	6.8	4.0	
5	6.4	3.2	
6	6.0	3.5	
7	6.0	3.5	
8	5.5	4.0	
10	6.1	4.5	
11	6.8	5.0	16.8
12	6.1	4.5	15.5
13	6.5	4.2	17.0
14	7.2	6.0	16.0
15	9.1	5.0	12.3
16	7.3	4.8	16.0
17	7.4	5.5	12.8
18	7.4	5.0	11.8
19	7.8	5.0	10.6
20	6.0	4.5	9.8
21	4.8	2.0	7.7
22	3.0	1.0	
23			0.7
24			0.6 scale leaves
25			0.5
26			0.4 foliage
27			0.2 leaves
28			0.04
shoot apex located above node 28			

*Aucuba japonica***Dissection Results**

Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf (cm)
----------	---------------	--------------------	-----------------------

Shoot 1: dissected 12th September

1	1.3		4.4
2			3.2
3			2.0
4			0.32

shoot apex located above node 5

Shoot 2: dissected 24th October

1	1.2		14.3
2	2.0	0.3	19.0
3	1.0	0.12	12.7
4			6.5
5			0.3

shoot apex located above node 6

Shoot 3: dissected 27th November

1	3.1	1.2	20.0
2	3.2	1.7	21.0
3	3.0	0.8	21.5
4	1.4		4.0
5	1.3		0.47
6	1.0*		0.3
7	1.5**		0.15

shoot apex located above node 7

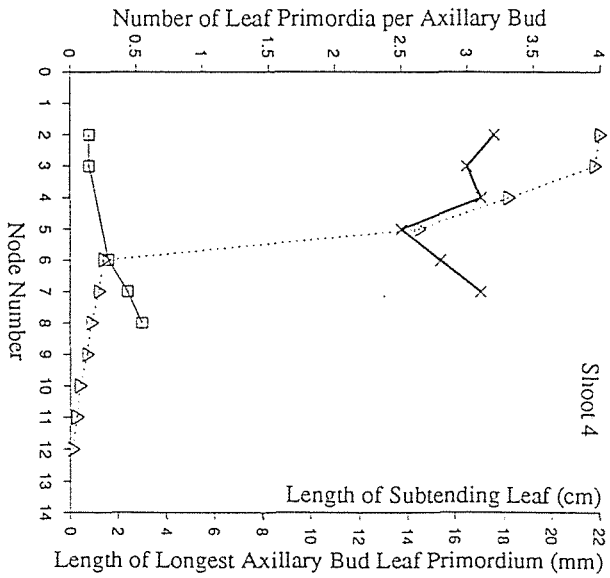
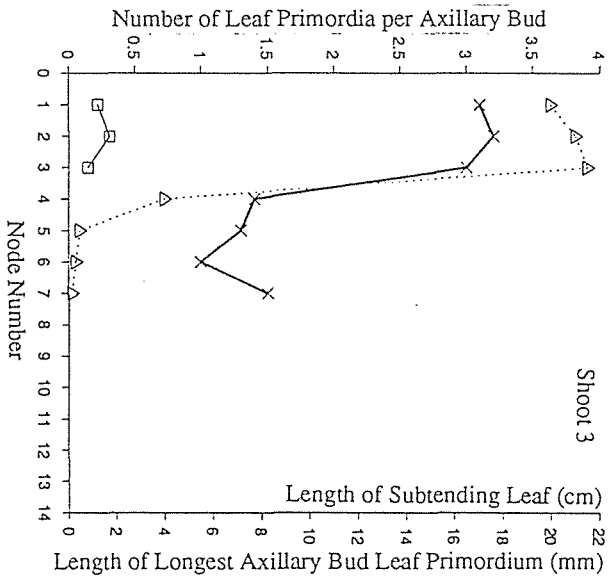
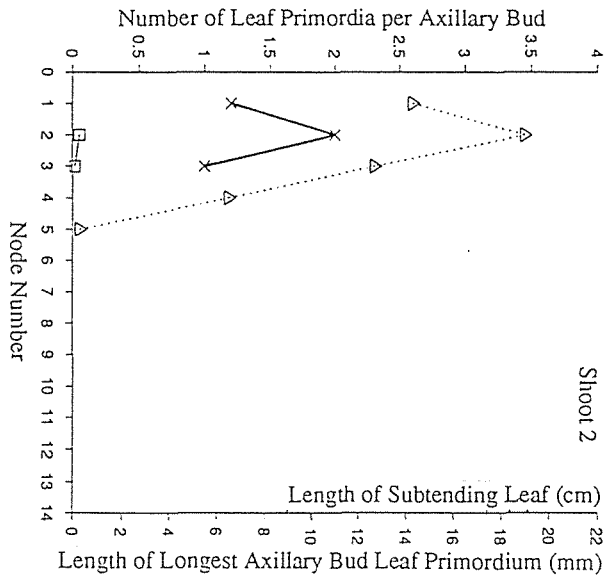
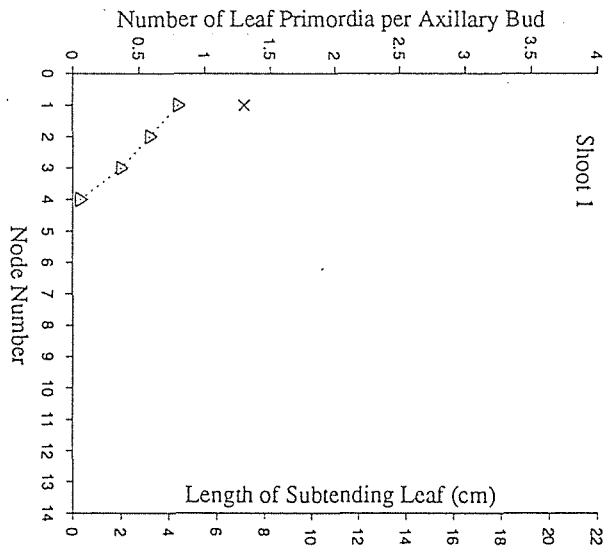
Shoot 4: dissected 5th February

2	3.2	0.8	22.0
3	3.0	0.8	21.8
4	3.1		18.2
5	2.5		14.5
6	2.8	1.6	1.4
7	3.1*	2.4	1.2

buds 8 to 12 flowering; shoot apex - located above node 12 - also flowering.

* axillary bud transitional between vegetative and floral

** axillary bud floral



*Bromus willdenowii***Dissection Results**

Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf(cm)
----------	---------------	--------------------	----------------------

Plant 1: dissected 11th May

1	bud not detected		3.0
2	2.0	0.12	14.0
3	1.0		13.0
4			0.33

shoot apex located above node 8

Plant 2: dissected 1st June

1	bud not detected		
2	4.2	0.25	9.0
3	4.5	0.36	34.0
4	4.3	0.5	38.5
5	1.5	0.2	28.0
6			9.5

shoot apex located above node 10

Plant 3: dissected 7 July

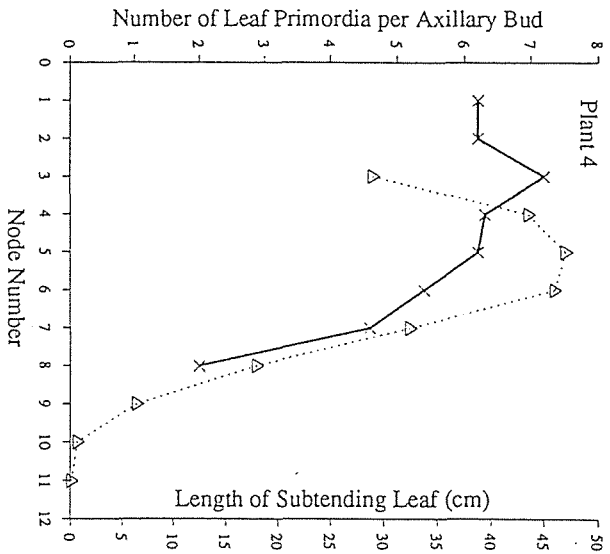
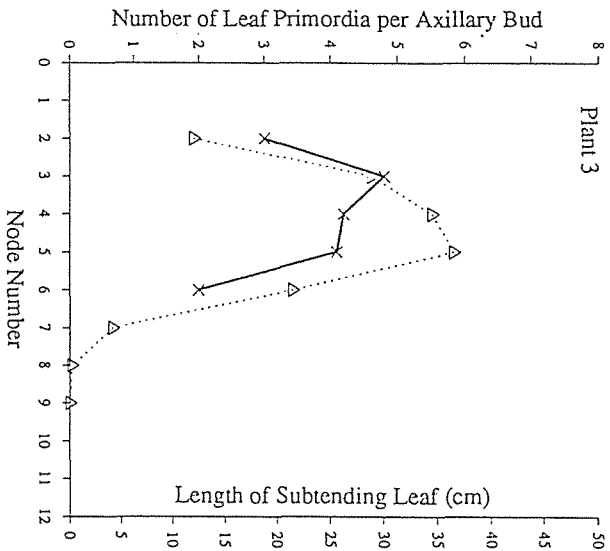
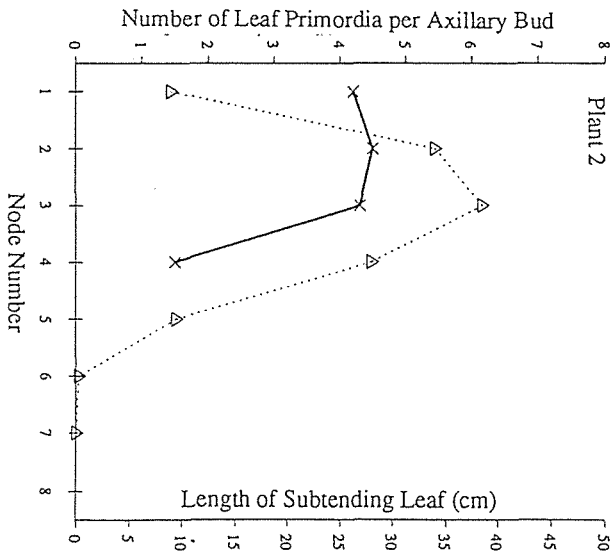
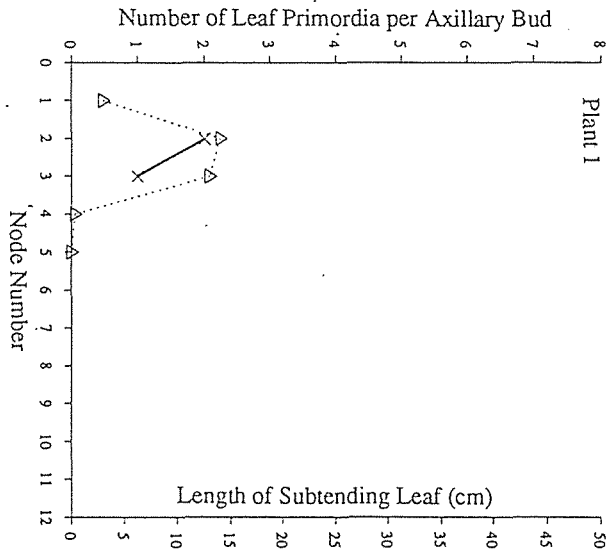
1	bud not detected		
2	3.0	0.5	12.0
3	4.8	1.0	28.9
4	4.2	0.6	34.5
5	4.1	0.25	36.5
6	2.0		21.5
7			4.2

shoot apex located above node 12

Plant 4: dissected 10th August

1	6.2	1.0	
2	6.2	1.0	
3	7.2	2.0	29.0
4	6.3	1.0	43.5
5	6.2	0.9	47.0
6	5.4	0.9	46.0
7	4.6	0.45	32.5
8	2.0	0.17	18.0
9			6.5
10			7.0

shoot apex located above node 16



*Clematis montana cv.***Dissection Results**

Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf (mm)
----------	---------------	--------------------	-----------------------

Shoot 1: dissected 4th October

1	5.3	4.0	18.5
2	5.1	2.5	15.5
3	4.0	3.0	13.5
4	4.8	2.0	12.0
5	4.6	1.8	8.4
6	4.0	1.5	5.0
7	3.5	0.9	2.4
8	3.1	0.5	1.4
9	2.1		0.8
10	1.0		0.4

shoot apex located above node 15

Shoot 2: dissected 7th Decemeber

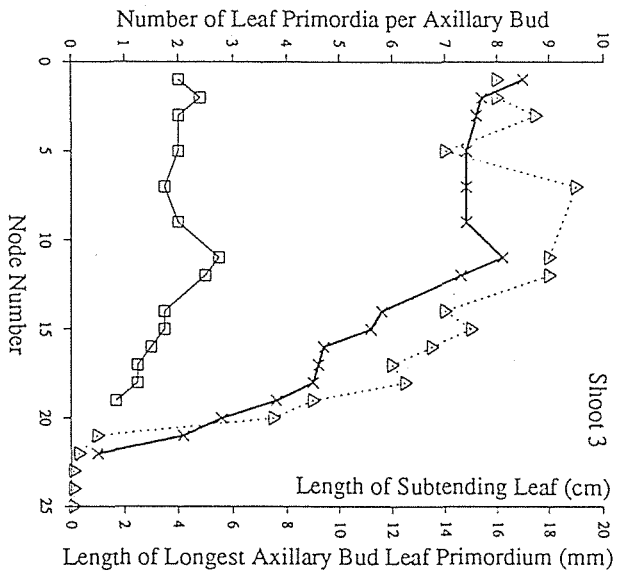
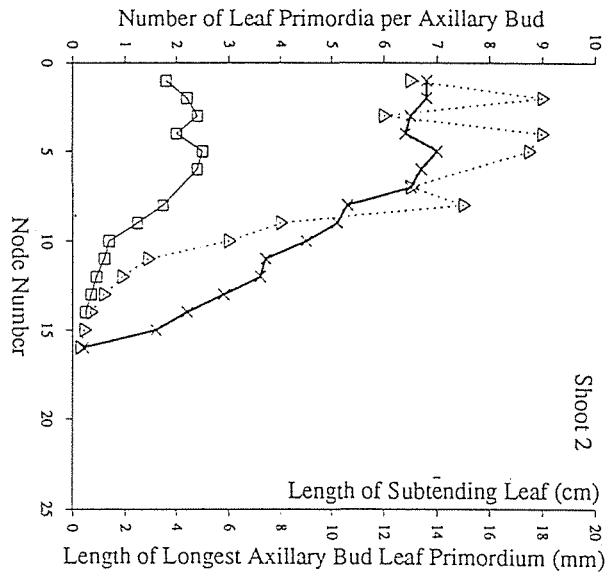
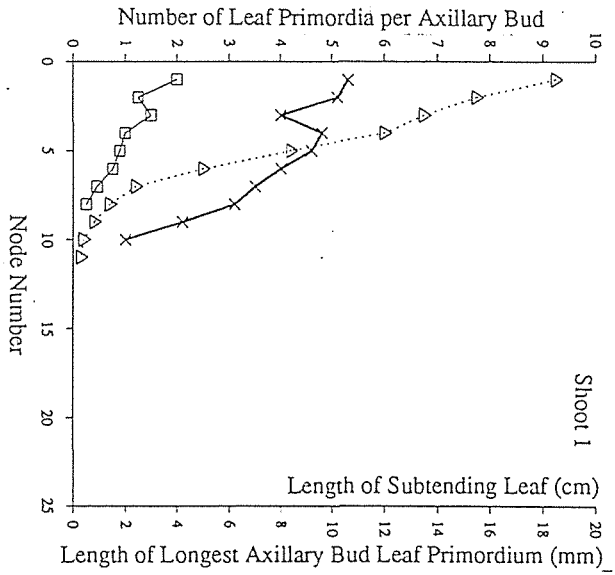
1	6.8	3.6	13.0
2	6.8	4.4	18.0
3	6.5	4.8	12.0
4	6.4	4.0	18.0
5	7.0	5.0	17.5
6	6.7	4.8	
7	6.5		13.0
8	5.3	3.5	15.0
9	5.1	2.5	8.0
10	4.5	1.4	6.0
11	3.7	1.2	2.9
12	3.6	0.9	1.9
13	2.9	0.7	1.2
14	2.2	0.5	0.7
15	1.6		0.45
16	0.2		0.3

shoot apex located above node 20

Shoot 3: dissected 7th February

1	8.5	4.0	16.0
2	7.7	4.8	16.0
3	7.6	4.0	17.5
5	7.4	4.0	14.0
7	7.4	3.5	19.0
9	7.4	4.0	
11	8.1 - breaking	5.5	18.0
12	7.3	5.0	18.0
14	5.8	3.5	14.0
15	5.6	3.5	15.0
16	4.7	3.0	13.5
17	4.6	2.5	12.0
18	4.5	2.5	12.5
19	3.8	1.7	9.0
20	2.8		7.5
21	2.1		1.0
22	0.5		0.3

Cordyline australis



Dissection Results

Node No. Primordia/Bud Length Sub. Leaf(cm)

Plant 1: dissected 12th October

1	bud present	3.3
2	bud present	9.0
3	bud present	14.8
4		15.9
5		3.5

shoot apex located above node 7

Plant 2: dissected 13th December

2	4.2	14.6
3	3.8	23.0
4	2.9	32.0
5	2.4	38.0
6	2.3	40.5
7	bud not dissected	44.9
8	1.5	52.0
9		50.0
10		40.0
11		16.5
12		6.5
13		2.8
14		1.1
15		0.6

shoot apex located above node 21

Plant 3: dissected 10th January

3	6.2*	23.0
4	bud not dissected	29.8
5	4.1*	33.5
6	3.8	39.5
7	4.8	44.0
8		50.0
9		48.0
10		50.0
11		52.0
12		51.0
13		37.0
14		23.0
15		11.5

shoot apex located above node 27

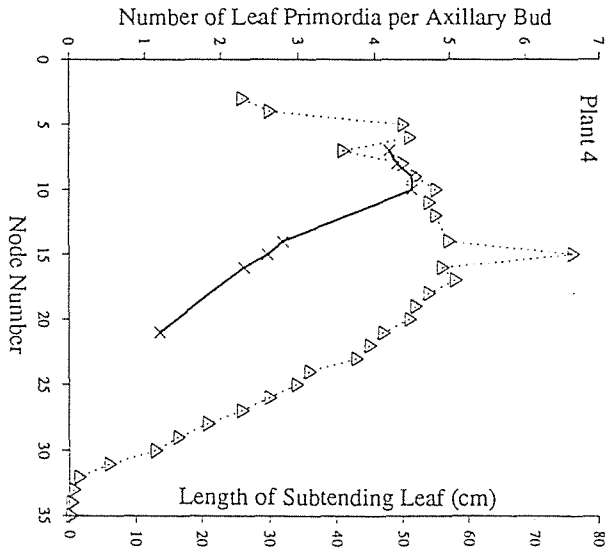
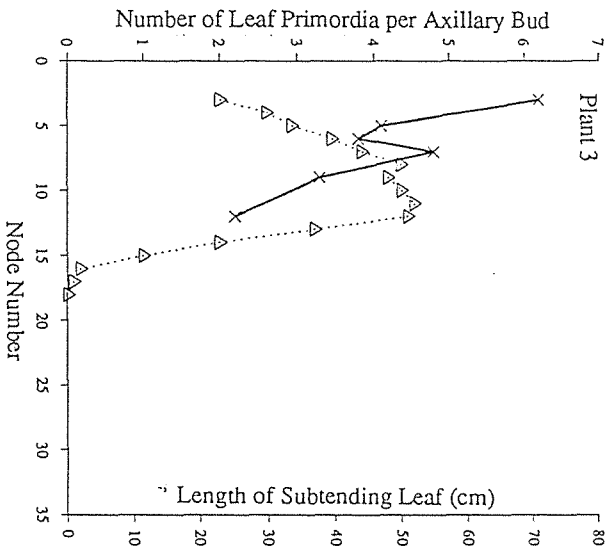
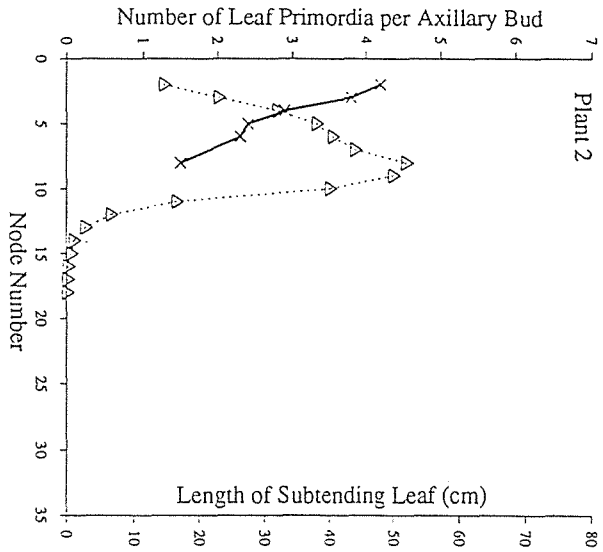
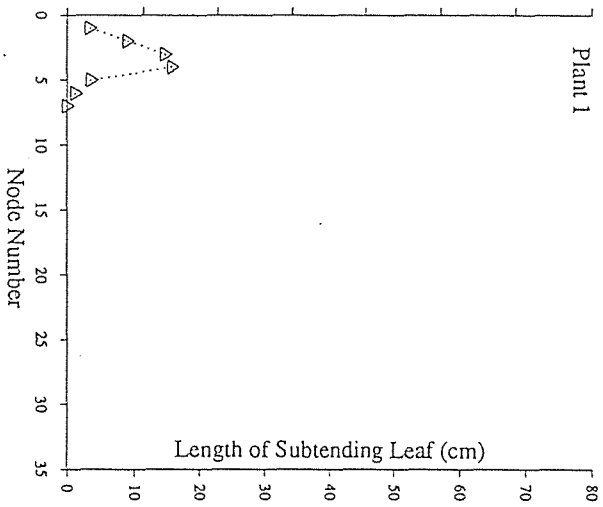
* chlorophyll visible in developing primordia

Node No. Primordia/Bud Length Sub. Leaf(cm)

Plant 4: dissected 22 February

3		26.0
4	buds not dissected	30.0
5		50.0
6		51.0
7	4.2	41.0
8	4.3	50.0
9	4.5	52.0
10	4.5	55.0
11	buds not dissected	54.0
12		55.0
14	2.8	57.0
15	2.6	76.0
16	2.3	56.0
17		58.0
18	buds not dissected	54.0
19		52.0
20		51.0
21	1.2	47.0
22		45.0
23		43.0
24		36.0
25		34.0
26		30.0
27		26.0
28		21.0
29		16.5
30		13.0
31		6.0
32		1.5
33		0.7

shoot apex located above node 38



Crocoshmia x crocosmiiflora

Node no.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf(cm)
----------	---------------	--------------------	----------------------

Plant 1

1			0.55
2	3.0		0.95
3	7.6	2.0	14.0
4	7.4	1.8	27.0
5	6.2	1.3	29.2
6	5.0	1.0	28.5
7	4.1	0.9	24.0
8	3.0	0.4	34.5
9	1.5	0.25	17.0
10			2.5
11			0.15

stem apex located above node 14

Plant 2: dissected 1st October

3	3	1.5	
5	9 - broken	4.0	
7	13 - broken	120.0	40.0
8	bud not dissected		40.0
9	8.1	2.0	40.0
10	9.2	2.7	47.0
11	8.1	1.7	45.0
12	8.2	2.0	53.0
13	7.1	1.6	52.0
14	6.0	1.2	50.0
15	5.0	1.2	48.0
16	4.2	0.8	40.0
17	3.0	0.4	38.5
18	2.0	0.25	17.8
19	0.5		2.5
20			0.5

stem apex located above node 24

Plant 3: dissected 2nd November

5	6.5	3.5	15.5
6	8.0	2.0	29.8
7	11.2	1.8	38.0
8	7.3	1.3	43.0
9	6.5	1.0	52.0
11	7.6	1.3	79.0
14	6.2		35.0
15	5.5	1.0	25.0
16	3.4	0.7	7.0
17	2.3		0.8
18	2.8		0.3
19	1 - flowering		0.28

nodes 20 to 29 contained in a terminal inflorescence

Node no.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf(cm)
----------	---------------	--------------------	----------------------

Plant 4: dissected 22nd December

3	8.0	2.0	17.0
4	9.2	2.5	32.0
5	8.0	2.0	43.0
6	9.1	2.4	48.0
7	8.5	2.0	60.0
8	9.0	3.0	74.0
9	10.0	2.6	93.0
10	8.5	2.7	110.0
11	9.0	3.0	117.0
13	5.6	1.4	59.0
14	5 - flowering	1.2	34.0
15	5 - flowering	3.5	15.0

nodes above node 15 contained in a terminal inflorescence

Plant 5: dissected 28th February

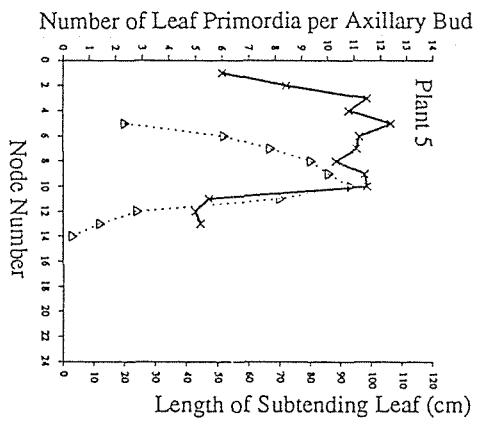
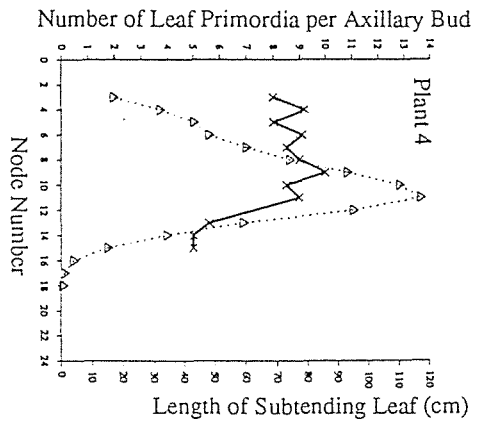
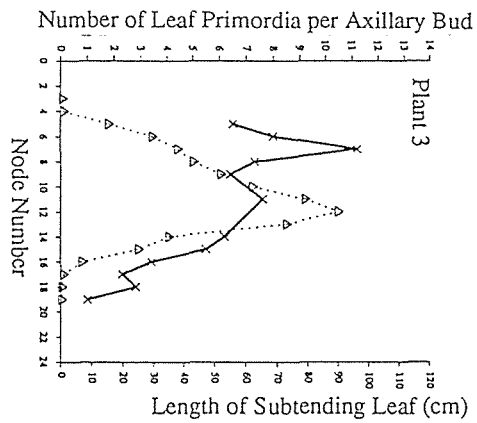
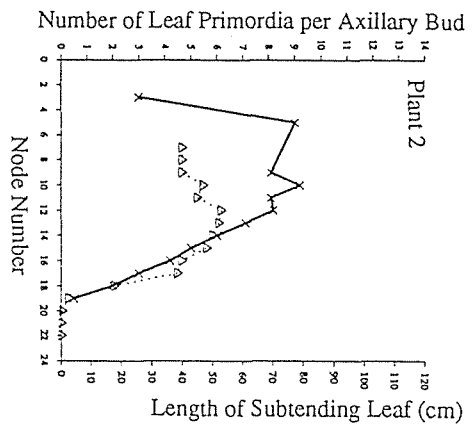
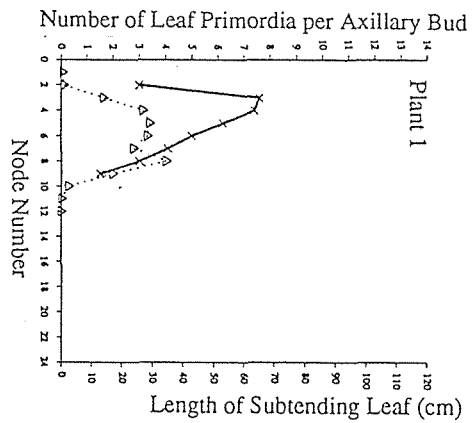
1	6.0		
2	8.4	3.8	
3	11.5	4.0	
4	10.8 - broken	4.0	
5	12.5	3.9	20.0
6	11.2	3.1	52.0
7	11.1	3.2	67.0
8	10.3	2.9	80.0
9	11.4	2.8	86.0
10	11.5	6.5	93.0
11	5.5	0.4	70.0
12	5.0	1.0	24.0
13	5.2	1.0	12.5
14	flowering	3.0	3.0

nodes above node 14 contained in a terminal inflorescence

Plant 6: dissected 13th July

7	12.0		
---	------	--	--

all other buds had grown out as rhizomes.
shoot apex located above node 26.



*Hebe speciosa***Dissection Results**

Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf (cm)
----------	---------------	--------------------	-----------------------

Shoot 1: dissected 22nd January

2	1.5	0.1	1.8
3	1.7	0.15	2.4
4	2.2	0.25	2.8
5	1.9	0.25	3.0
6	1.9	0.25	2.9
7	1.8	0.22	2.7
8	1.5	0.15	2.6
9	1.4	0.14	1.9
10	1.2	0.13	1.4
11	1.1	0.08	0.9
12	0.5		0.42
13	0.1		0.2
14			0.035

shoot apex located above node 15

Shoot 2: dissected 15th September

4	2		2.5
5	2.4		3.0
6	2.5	0.1	3.1
7	2.6		3.5
8	2.7		3.8
9	2.8		4.5
10	2.9		4.8
11	3.1	0.7	5.0
12	3.7	1.0	5.5
13	3.6	1.7	5.5
14	3.9	1.6	5.5
15	3.7	1.3	5.2
16	3.5	1.2	4.4
17	2.9	0.8	3.3
18	2.4	0.5	2.3

buds at nodes 19, 20 and 21: clearly flowering;

buds at nodes 22 and 23: too small to be identified as either vegetative or flowering.

22	0.5		0.3
23	0.1		0.12
24			0.04

shoot apex located above node 25

Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf (cm)
----------	---------------	--------------------	-----------------------

Shoot 3: Dissected 29th November

1	2.0	0.25	
3	2.2	0.25	
4	2.2	0.25	
5	2.5	0.35	
6	3.1	0.8	
7	3.2		
8	3.8	1.3	5.2
9	3.6	1.2	5.1
10	3.8	1.2	5.1
11	3.6	1.2	5.0
12	3.8	1.3	4.8
13	3.4	1.1	4.4
14	3.1	0.9	4.6
15	3.0	0.8	4.8
buds at nodes 16 to 20 clearly flowering			
21	1.2		1.3
22	0.5		0.6
23			0.3
shoot apex located above node 26			

Shoot 4: Dissected 22nd January

4	2.3		
5	2.3		
7	2.3		
8	2.8		
9	2.4		
10	3.2	0.1	
11	3.3	0.7	
12	4.9 - bud breaking	1.3	
13	3.9	1.0	
14	4.3 - bud breaking	1.3	
15	3.8	1.3	5.0
16	3.3	1.1	5.0
17	3.7	1.0	5.0
buds at nodes 18 and 24: intermediate between vegetative and flowering			
buds at nodes 19 to 23: clearly flowering			
25	1.2	0.25	1.1
26	1.0		0.4
27	0.5		0.3
shoot apex located above node 30			

*Helianthus annuus***Dissection Results**

Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf(cm)
----------	---------------	--------------------	----------------------

Plant 1

1	2.2	0.3	
2	5.1	0.9	9.5
3	1.7	0.3	8.8
4	2.8	0.2	4.8
5	2.0		1.8
6			1.0

stem apex located above node 14

Plant 2

1	7.0	1.6	
2	8.0		13.0
3	8.0	1.5	17.5
4			17.0
5			11.5
6	buds not detected		13.7
7			8.5
8			5.5

stem apex located above node 30 - flowering.

Plant 3

buds not detected at nodes 1 and 2

3	6.2		
4			
5	10.0	0.1	15.0
6			17.0
7	buds not detected		18.0
8			16.0
9	8.0	0.1	16.5
10	5.0	0.1	15.0
11	4.0	0.1	14.5
12	6.0	0.3	14.0
13	5.0		10.0
14	6.0		8.0
15			6.0
16			5.0

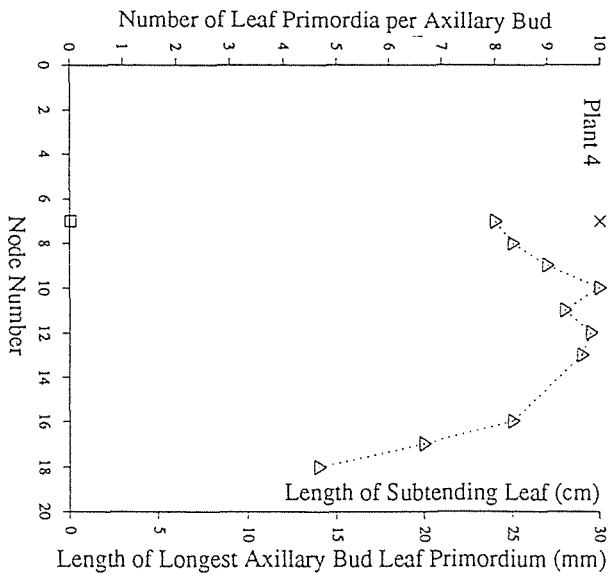
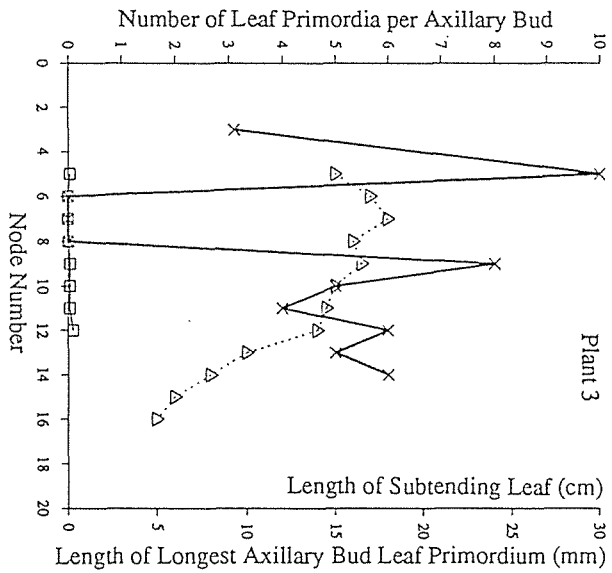
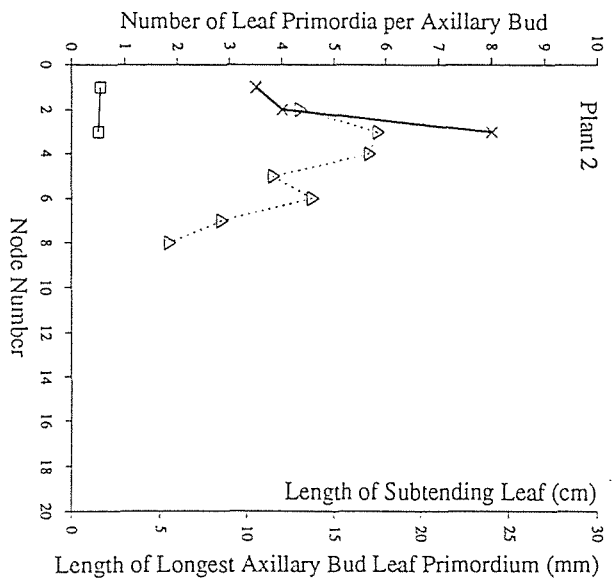
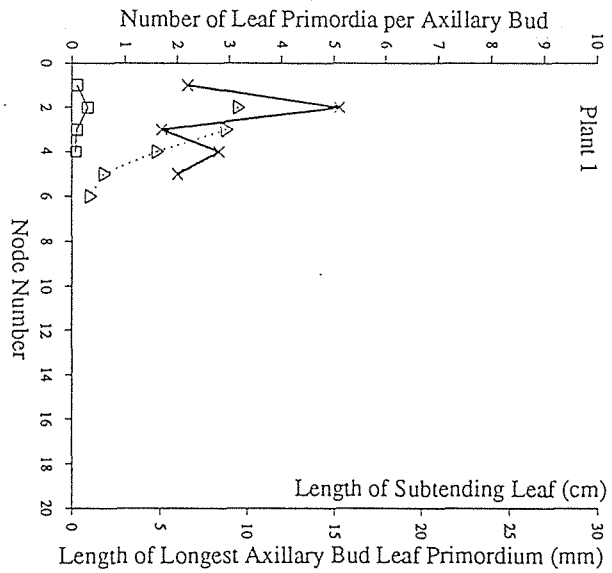
primordia above node 16 form a composite inflorescence.

Plant 4

Nodes 1 to 6: buds either senescent or not detected.

7	10.0	0.05	24.0
8			25.0
9			27.0
10			30.0
11			28.0
12	buds flowering		29.5
13			29.0
14			
15			
16	bud not detected		25.0
17	bud flowering		20.0
18	bud not detected		14.0

primordia above node 18 form a composite inflorescence.



*Hydrangea macrophylla***Dissection Results**

Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf(cm)
----------	---------------	--------------------	----------------------

Shoot 1: dissected 18th September

1	3.0	1.0	1.3
2	3.0	1.2	3.3
3	3.2	2.8	9.1
4	3.1	2.3	11.9
5	2.9	1.3	7.3
6	1.3	0.5	2.8
7	1.0	0.3	0.9
8	bud not detected		0.4
shoot apex located above node 8 - flowering			

Shoot 2: dissected 8th December

1	5.2		10.0
2	4.8		16.0
3	5.8		18.0
4	5.7		18.0
5	5.4		15.0
6	4.6		13.0
7	3.8		9.5
8	2.5		5.5
9	1.2		
shoot apex located above node 14			

Shoot 3: dissected 15th March

1	7.0	2.5	
2	6.2	1.5	
3	9.1	5.0	
4	8.0	1.0	
5	8.9	6.7	15.0
6	9.2	6.5	13.0
7	9.0 - flowering	7.3	14.0
8	8.1	5.0	13.0
9	6.1	2.5	13.2
10	5.0	1.5	11.0
11	4.2	1.2	9.5
12	2.9	0.9	1.5
13	2.1	0.25	1.2
14	1.8		0.8
15	0.5		0.7
16	0.1		0.5
shoot apex located above node 17 - flowering			

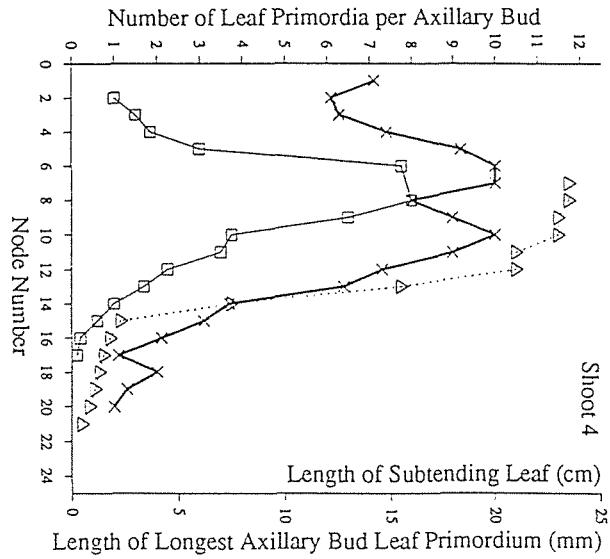
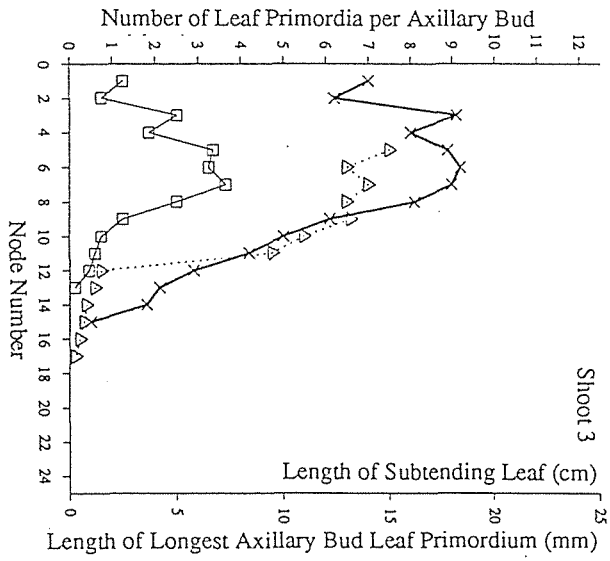
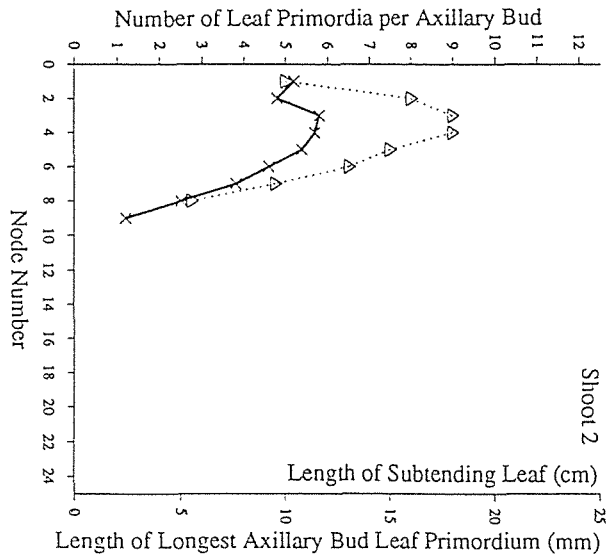
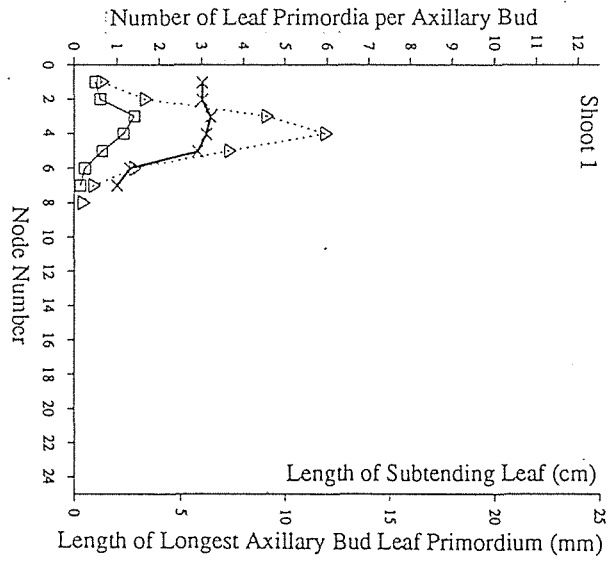
Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf(cm)
----------	---------------	--------------------	----------------------

Shoot 4: dissected 10th April

1	7.1		
2	6.1	2.0	
3	6.3	3.0	
4	7.4	3.7	
5	9.2	6.0	
6	10 - flowering	15.5	23.5
7	10 - flowering		23.5
8	8 - flowering	16.0	23.5
9	9 - flowering	13.0	23.0
10	10 - flowering	7.5	23.0
11	9 - flowering	7.0	21.0
12	7.3	4.5	20.0
13	6.4	3.4	15.5
14	3.7	2.0	7.5
15	3.1	1.2	2.3
16	2.1	0.4	1.8
17	1.1	0.25	1.5
18	2.0		1.3
19	1.3		1.1
20	1 - flowering		0.85
21	bud not detected		0.5
shoot apex located above node 21 - flowering			

Shoot 5: dissected 10th July

3		8.0	
4	10.8	8.0	
5	11 - flowering	10.0	
buds at nodes 6 to 14: flowering			
shoot apex located above node 14 - flowering			



*Ilex aquifolium***Dissection Data**

Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf (cm)
----------	---------------	--------------------	-----------------------

Shoot 1: dissected 5th October

1	5	0.8	0.8
2	6	1.3	0.9
3	4	0.7	1.0
4	4	0.5	1.0
5	4	0.25	1.2
6	4	0.25	1.3
7	4	0.25	1.35
8	4	0.36	1.3
9	4	0.3	1.2
10	4	0.5	1.0
11	2	0.25	0.8
12	2	0.15	0.7
13	1		0.5

shoot apex located above node 20

Shoot 2: dissected 5th December

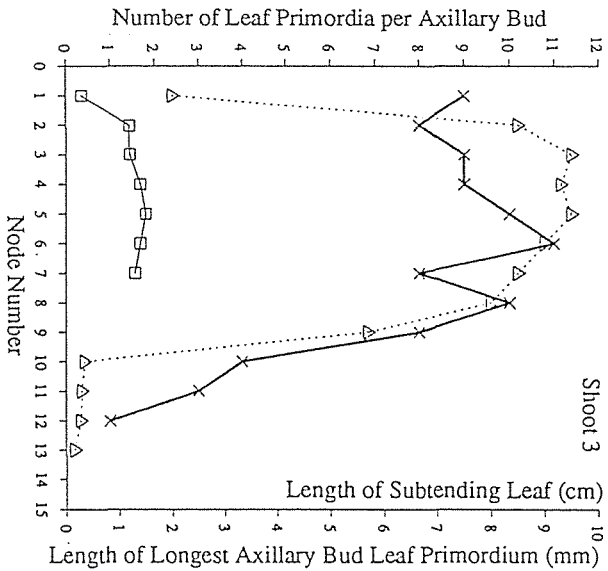
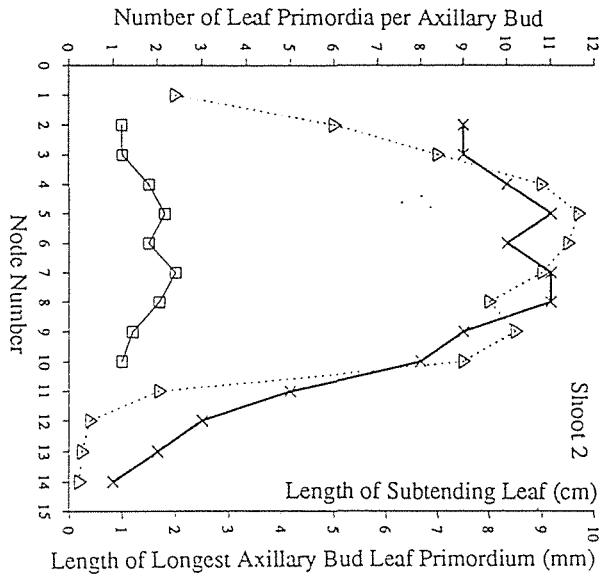
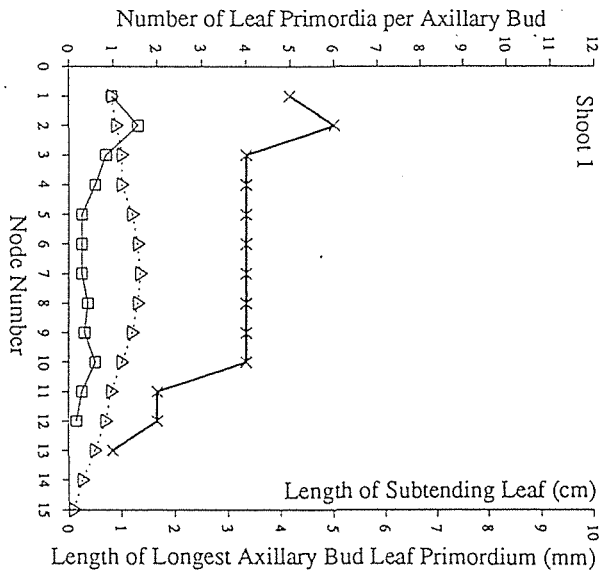
1			2.0
2	9	1.0	5.0
3	9	1.0	7.0
4	10	1.5	9.0
5	11	1.8	9.7
6	10	1.5	9.5
7	11	2.0	9.0
8	11	1.7	8.0
9	9	1.2	8.5
10	8	1.0	7.5
11	5		1.7
12	3		0.4
13	2		0.25
14	1		0.2

shoot apex located above node 24

Shoot 3: dissected 5th February

1	9	0.3	2.0
2	8	1.2	8.5
3	9	1.2	9.5
4	9	1.4	9.3
5	10	1.5	9.5
6	11	1.4	9.0
7	8	1.3	8.5
8	10		8.0
9	9		5.7
10	4		0.35
11	3		0.3
12	1		0.28

shoot apex located above node 25



*Lolium perenne***Dissection Results**

Node No.	Pirmordia/Bud	Length Lng.Pr.(mm)	Length Sub. Leaf(cm)
----------	---------------	--------------------	----------------------

Plant 1: dissected 10th April

1	1.5		1.1
2	4.3	1.0	8.5
3	3.4	0.3	16.0
4	1.5		13.0

shoot apex located above node 6

Plant 2: dissected 1st June

1	bud not detected		
2	3.0	0.5	1.8
3	5.2	1.2	28.0
4	5.4	1.3	34.0
5	5.0	1.0	32.0
6	4.2	0.6	32.0
7	2.0	0.3	23.0

shoot apex located above node 10

Plant 3: dissected 17th July

1	3.0	0.5	
2	5.3	0.8	4.5
3	5.2		17.5
4	5.2	0.9	25.0
5	5.1	1.0	20.0
6	5.3 - breaking	5.0	20.3
7	5.5	1.0	19.0
8	3.2	0.2	12.0

shoot apex located above node 14

Plant 4: dissected 10th August

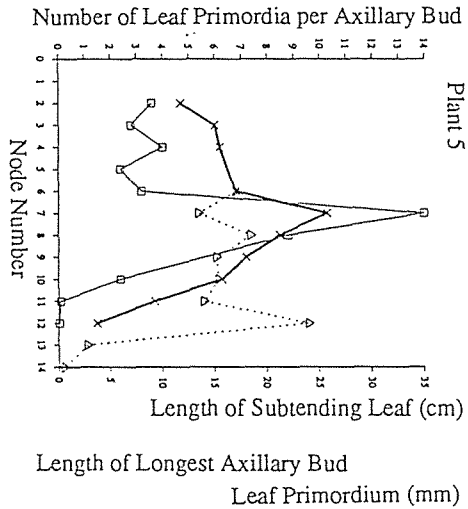
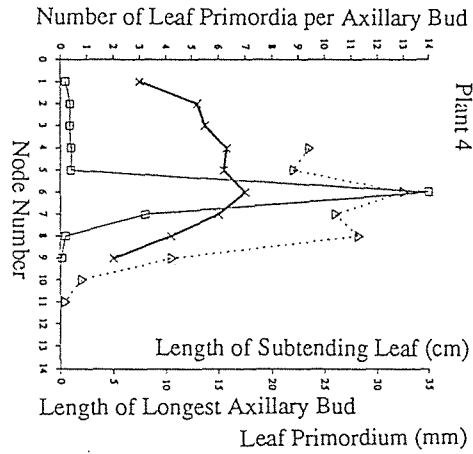
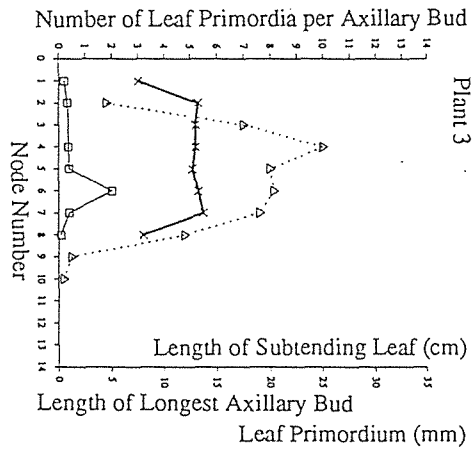
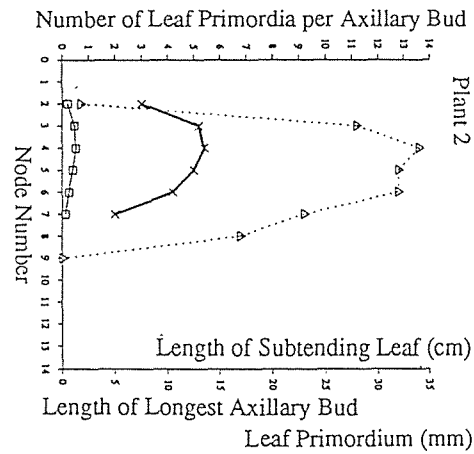
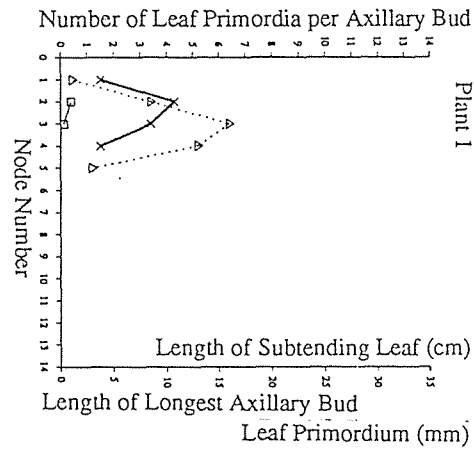
1	3.0	0.5	
2	5.2	0.9	
3	5.5	0.9	
4	6.3	1.0	23.5
5	6.2	1.0	22.0
6	7.0 - broken	41.5	31.5
7	6.0 - breaking	8.0	26.0
8	4.2	0.5	28.2
9	2.0	0.1	10.5

shoot apex located above node 16

Plant 5: dissected 3rd October; bud break occurring extensively.

2	4.7	9.0	
3	6.0	7.0	
4	6.2	10.0	
5		6.0	
6	6.8	8.0	17.0
7	10.3	90.0	13.5
8	8.5	22.0	18.5
9	7.2	7.0	15.2
10	6.3	6.0	15.4
11	3.7	0.25	14.0
12	1.5	0.14	24.0

shoot apex located above node 19



*Lonicera x americana***Dissection Results**

Node No. Primordia/Bud Length Sub. Leaf (cm)

Shoot 1: dissected 16th September

2	3.5	4.5
3	4.8	6.0
4	5.2	6.3
5	5.3	5.5
6	5.6	5.0
7	5.0	5.0
8	4.7	4.0
9	4.1	3.1
10	3.3	2.4
11	3.3	1.4
12	3.0	0.9
13	3.1	0.6
14	2.2	0.45
15	1.8	0.23
16		0.13

shoot apex located above node 19

Shoot 2: dissected 25th October

2	6.9	5.5
3		5.5
4	6.9	6.0
6	7.7	7.0
9	6.1	5.0
10	6.5	4.0
11	6.8	3.5
12	bud flowering	3.2
13	bud flowering	

shoot apex - located above node 13 - flowering

Shoot 3: dissected 4th December

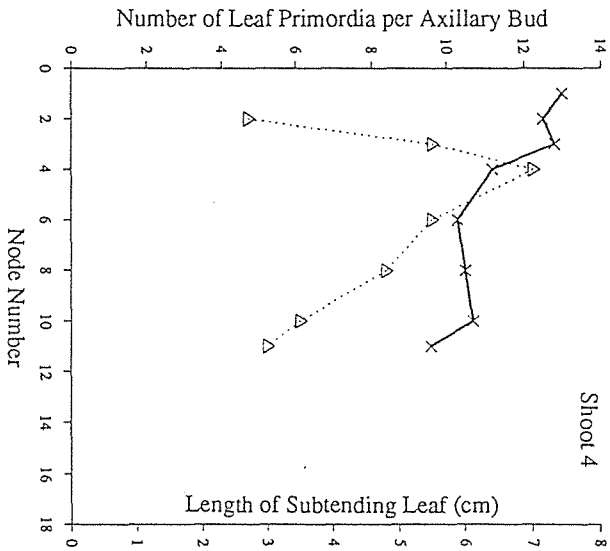
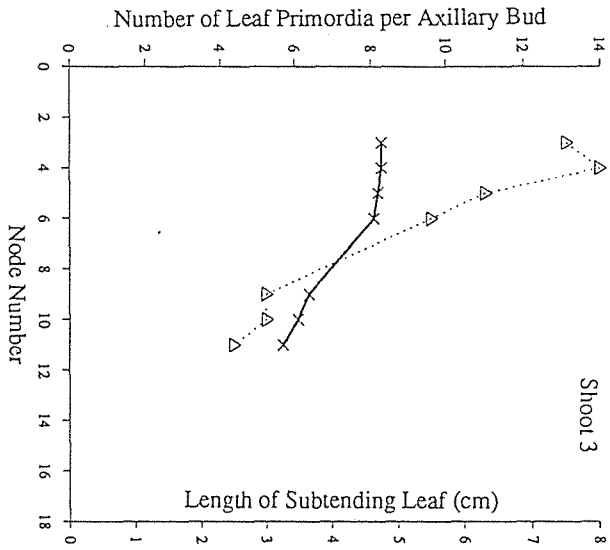
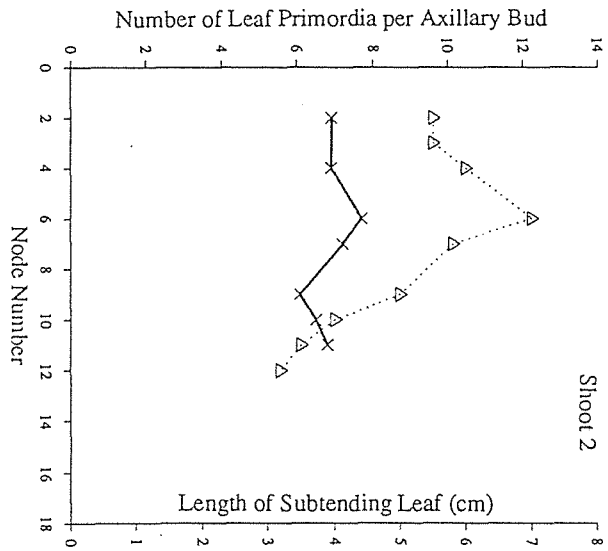
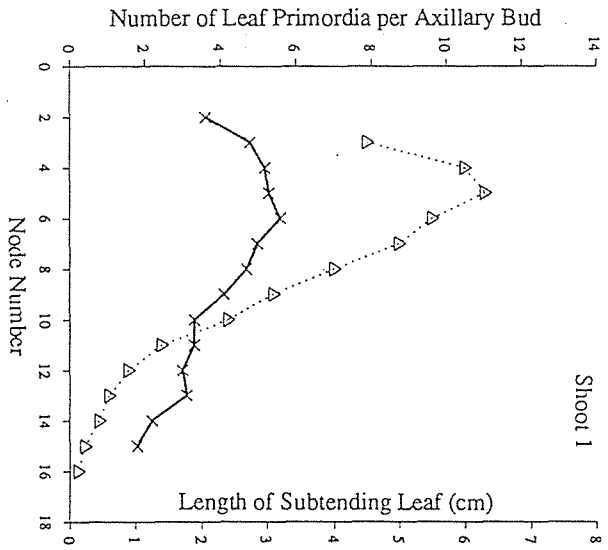
3	8.3	7.5
4	8.3	8.0
5	8.2	6.3
6	8.1	5.5
9	6.4	3.0
10	6.1	3.0
11	5.7	2.5
12	bud flowering	
13	bud flowering	

shoot apex - located above node 13 - flowering

Shoot 4: dissected 7th February

1	13.0	
2	12.5	2.7
3	12.8	5.5
4	11.2	7.0
6	10.3	5.5
8	10.5	4.8
10	10.7	3.5
11	9.6	3.0

buds at nodes 12, 13 and 14 and shoot apex - flowering.



*Lupinus angustifolius***Dissection Data**

Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf (cm)
----------	---------------	--------------------	-----------------------

Plant 1: dissected 8 days after seeds were sown

1	2.7	0.25	1.5
2	3.1	0.35	5.8
3	4.2	0.27	6.1
4	4.4	0.25	4.0
5	4.1	0.25	3.6
6	1.7		0.5
7	1.1		0.3

shoot apex located above node 15

Plant 2: dissected 18 days after seeds were sown

1	3.7	0.45	1.4
2	5.4	0.7	7.4
3	3.2	0.5	6.8
4	7.2	1.5	7.3
5	5.3	1.4	7.7
6	5.4	0.8	5.8
7	5.3	0.8	6.8
8	4.2	0.25	5.4
9	5.1	0.5	4.0
10	4.2	0.3	1.7
11	3.8	0.15	0.8
12	3.1		0.46
13	2.3		0.26
14	1.2		0.13
15	0.5		0.1

shoot apex located above node 23

Plant 3: dissected 40 days after seeds were sown

1	3.1	0.5	
2	6.1	0.7	6.7
3	7.3	0.7	6.7
4	7.6	1.3	6.5
5	7.5	1.7	6.2
6	8.2	1.3	6.3
7	7.6	1.0	6.2
8	6.8	0.9	6.0
9	7.4	1.3	5.4
10	6.2	1.0	
11	5.3	0.6	5.2
12	5.3	0.7	5.0
13	4.2	0.5	4.1
14	4.2		3.2
15	3.3		1.7
16	3.2		0.8
17	2.8		0.35
18	2.7		0.2
19	1.3		0.13
20	0.5		

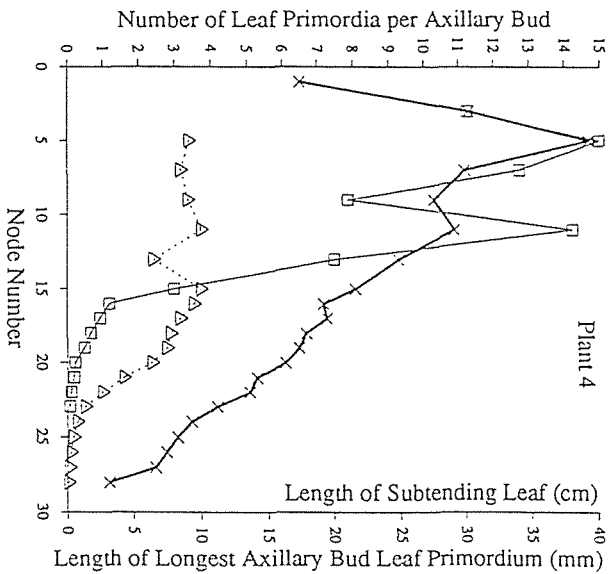
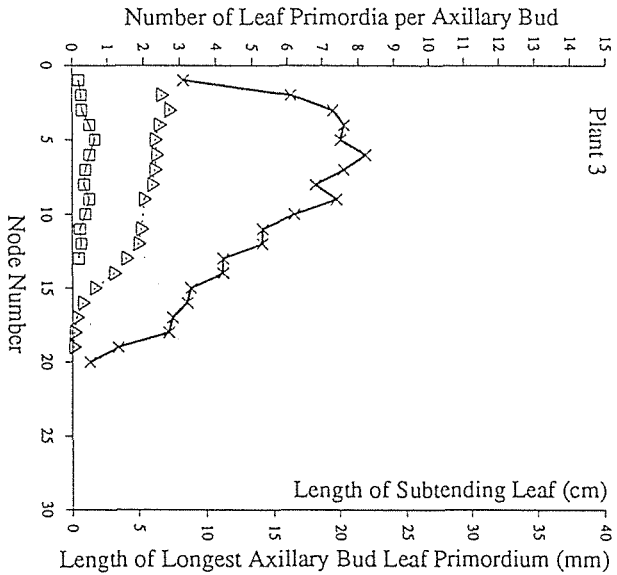
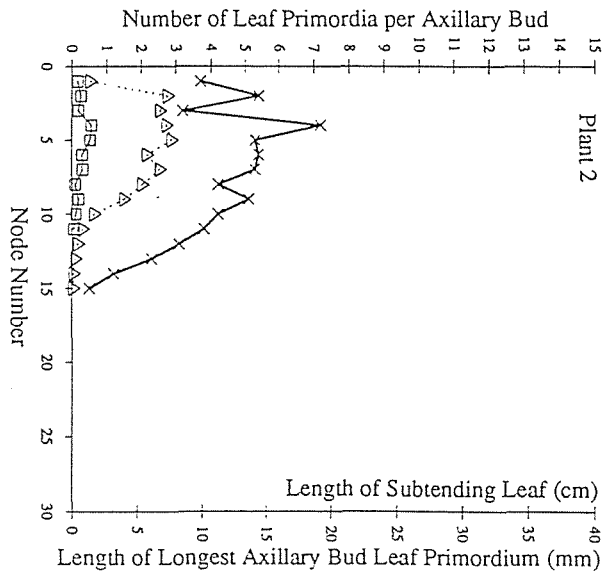
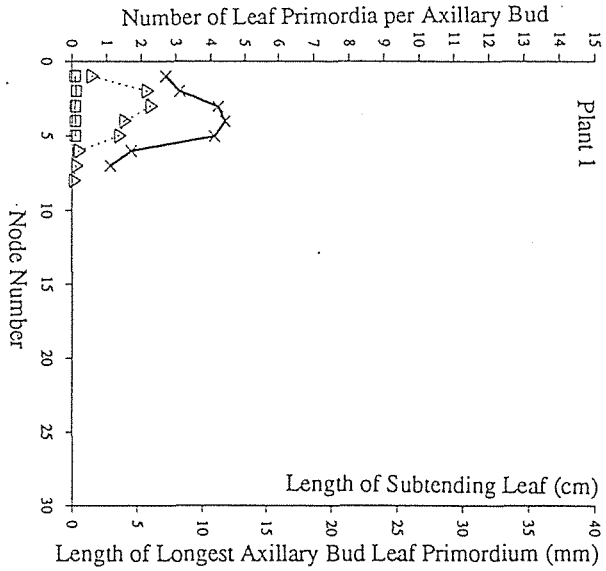
shoot apex located above node 29

Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf (cm)
----------	---------------	--------------------	-----------------------

Plant 4: dissected 50 days after seeds were sown

1	6.5		
3	11.3	30	
5	14.7	42	9.1
7	11.2	34	8.5
9	10.3	21	9.0
11	10.9	38	10.0
13	9.3	20	6.5
15	8.1	8.0	10.0
16	7.2	3.2	9.5
17	7.3	2.5	8.5
18	6.7	1.8	7.8
19	6.5	1.3	7.5
20	6.1	0.6	6.4
21	5.3	0.5	4.3
22	5.1	0.3	2.7
23	4.2	0.2	1.4
24	3.5		0.8
25	3.1		0.5
26	2.8		0.3
27	2.5		0.2
28	1.2		0.15

shoot apex located above node 36



*Lycopersicon esculentum***Dissection Results**

Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. leaf(cm)
----------	---------------	--------------------	----------------------

Plant 1

1	2.8	0.15	3.0
2	1.9	0.15	4.1
3	1.7	0.1	5.2
4	bud not detected		3.6
shoot apex located above node 10			

Plant 2

1	0.5		4.5
2	2.6	0.25	5.2
3	3.1	0.5	4.0
4	3.7	0.9	7.0
5	2.4	0.15	7.5
6	2.1	0.1	5.5
7	bud not detected		2.0
shoot apex located above node 13			

Plant 3

1	3.3	0.4	7.0
2	3.2	0.5	6.5
3	3.5	0.65	9.7
4	5.1	1.2	11.0
5	3.3	0.4	11.3
6	2.3	0.12	8.3
7	2.2	0.1	4.4
8	1.0		1.9
9	0.5		0.8
10	3.3	0.5	0.45
11	4.1	0.6	0.16
shoot apex located above node 11 - flowering			

Plant 4

1	4.8		6.5
2	5.8		16.0
3	5.5	1.5	15.0
4	5.3	1.5	15.8
6	3.6	0.7	8.0
7	1.9		3.6
8	1.3		1.8
9	4.6		1.0
10	5.6	1.5	0.5
shoot apex located above node 10 - flowering			

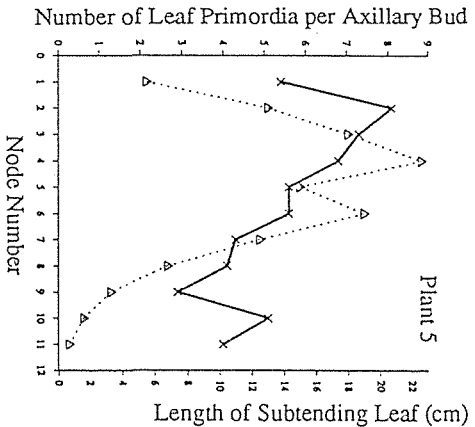
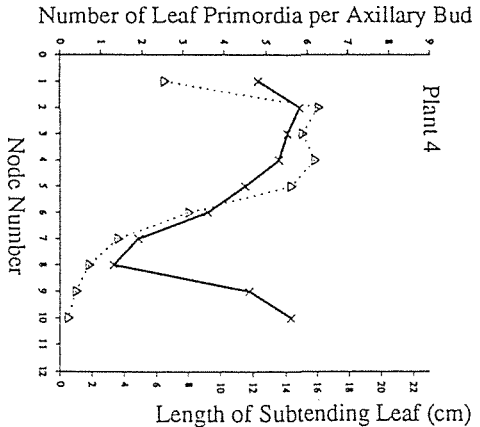
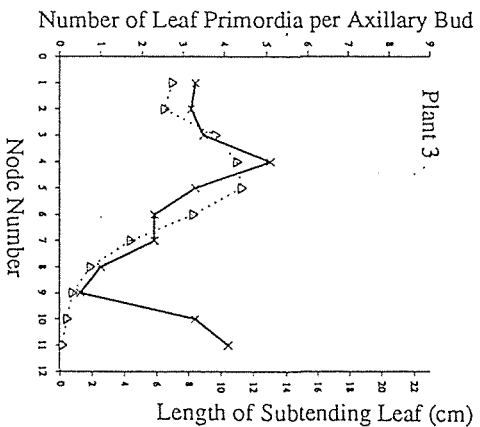
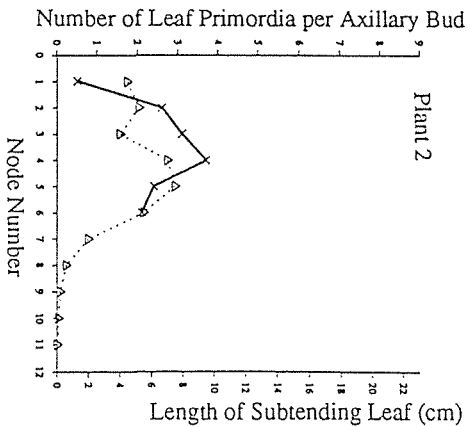
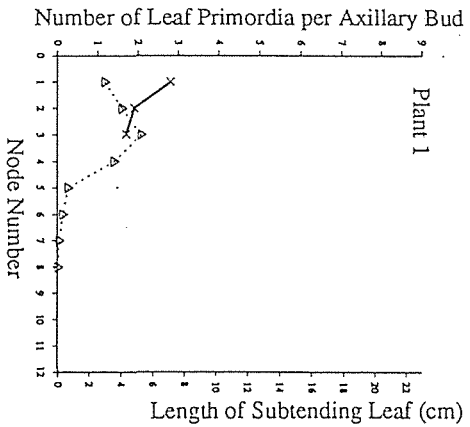
Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf(cm)
----------	---------------	--------------------	----------------------

Plant 5

1	5.4		5.5
2	8.1		13.0
3	7.3	14.0	18.0
4	6.8	4.0	22.6
5	5.6	3.0	15.0
6	5.6	3.0	15.0
7	4.3	1.0	12.5
8	4.1	0.5	6.8
9	2.9	0.12	3.3
10	5.1	1.2	1.6

inflorescence bearing 7 flowers and a shoot apex occupying the region between nodes 10 and 11 - main shoot growth taken over by the outgrowing bud axillary to node 11.

11	4.0 - flowering	7.0	0.7
----	-----------------	-----	-----



*Melicytus ramiflorus***Dissection Results**

Node No. Primordia/Bud Length Sub Leaf(cm)

Shoot 1: dissected 1st September

nodes 1 to 4: buds detected but not dissected

5	15	
7	15	2.0
8	14	
10	12	4.3
11	12	2.5
12	14	5.7
13	11	4.0
14	9	3.2
15	9	2.5
16	6	1.7
17	5	1.5
18	4	0.8
19	1	0.5

shoot apex located above node 31

Shoot 2: dissected 2nd October

nodes 1 to 11: buds detected but not dissected

12	21	6.1
15	22	8.9
18	18	9.1
19	19	8.5
20	20	8.5
21	18	7.1
22	17	6.8
23	14	5.5
24	14	4.4
25	12	3.6
26	7	2.4
27	8	1.8
28	6	1.5
29	5	1.1
30	5	0.7
31	2	0.5
32	1	0.4

shoot apex located above node 44

Node No. Primordia/Bud Length Sub. Leaf(cm)

Shoot 3: dissected 16th October

nodes 1 to 7: buds detected but not dissected

8	17	8.5
10	21	9.0
21	18	10.5
22	21	11.5
23	21	12.4
24	23	13.2
25	23	11.0
26	22	13.5
27	21	13.0
28	21	12.6
29	22	14.5
30	22	12.8
31	20	10.5
32	19	9.6
33	17	7.2
34	16	6.3
35	12	4.6
36	10	3.0
37	8	0.23
39	6	0.9
40	3	0.6
41	2	0.4
42	1	0.3

shoot apex located above node 55

Shoot 4: dissected 28th November

buds detected - but not dissected - up to node 15

15	18	12.0
17	19	10.0
23	18	12.5
30	19	14.8
34	25	16.0
37	24	17.5
39	26	
40	26	14.5
41	26	14.5
44	23	13.5
46	23	12.0
49	19	9.0
50	16	7.0
51	12	4.4
52	7	1.8
53	6	1.5
54	4	0.6
55	3	0.5
56	2	0.3
57	1	0.3

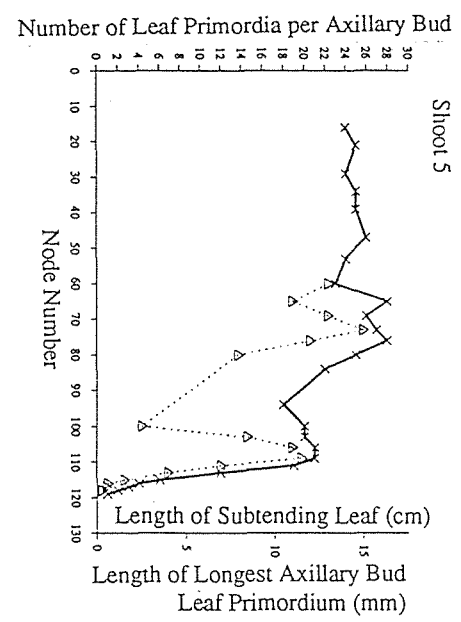
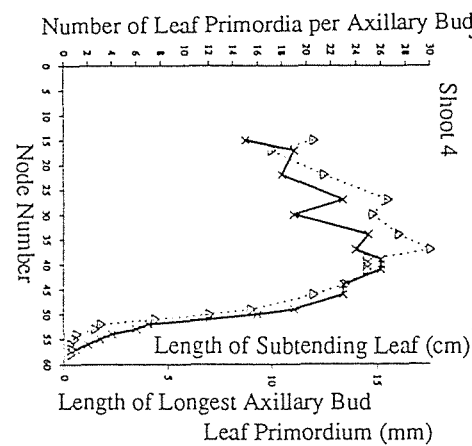
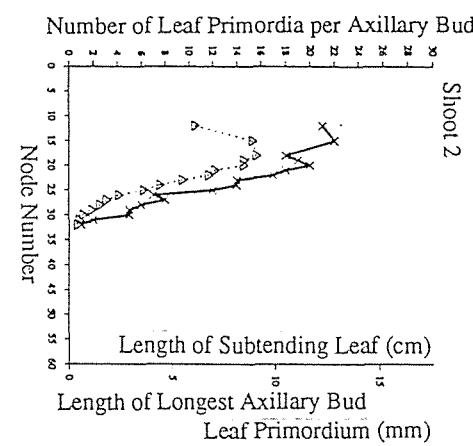
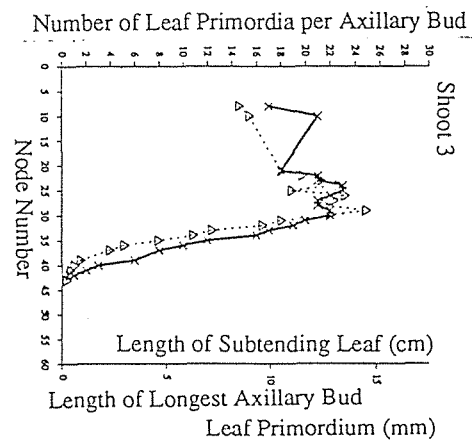
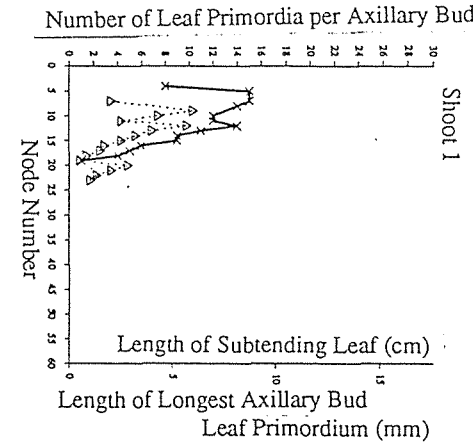
shoot apex located above node 71

Node No. Primordia/Bud Length Sub. Leaf(cm)

Shoot 5: dissected 10th July

16	24	
21	25	
29	24	
34	25	
39	25	
47	27	
53	24	
60	23	13.0
65	28	11.0
69	26	13.0
73	27	15.0
76	28	12.0
80	25	8.0
84	22	
94	18	
100	20	2.5
103	20	8.5
106	21	11.0
109	21	11.5
111	19	7.0
113	12	4.0
115	6	1.5
116	4	0.6
117	3	0.5
118	2	0.3
119	1	0.3

shoot apex located above node 132



*Muehlenbeckia australis***Dissection Results**

Node No. Primordia/Bud Length Sub. Leaf (cm)

Shoot 1: young vegetative shoot - dissected 15th September

1	5.5	5.7
2	5.5	6.0
3	5.5	7.0
4	6.3	7.2
5	6.4	7.3
6	6.4	6.5
7	6.8	5.7
8	6.2	5.2
9	6.2	
10	6.2	5.3
11	6.7	5.1
12	5.9	3.2
13	4.9	2.7
14	4.6	2.1
15	4.6	1.6
16	4.2	1.6
17	3.7	1.1
18	3.6	0.9
19	2.5	0.7
20	2.2	0.6
21	1.0	0.4

shoot apex located above node 28

Shoot 2: older shoot - dissected 25th October

4	7.1	6.5
8	9.0	7.0
11	8.0	6.5
17	8.3	5.7
21	8.3	5.8
22	7.4	4.6
25	7.6	3.8
27	6.6	3.5
30	7.2	2.8
31	6.4	2.4
32	8.1	1.8
33	6.0	2.0
34	5.0	1.8
35	5.0	1.3
36	4.0	1.3
37	4.0	1.1
38	4.0	0.9
39	3.0	0.8
40	2.0	0.7
41	1.0	0.4
42	0.5	0.3

shoot apex located above node 48

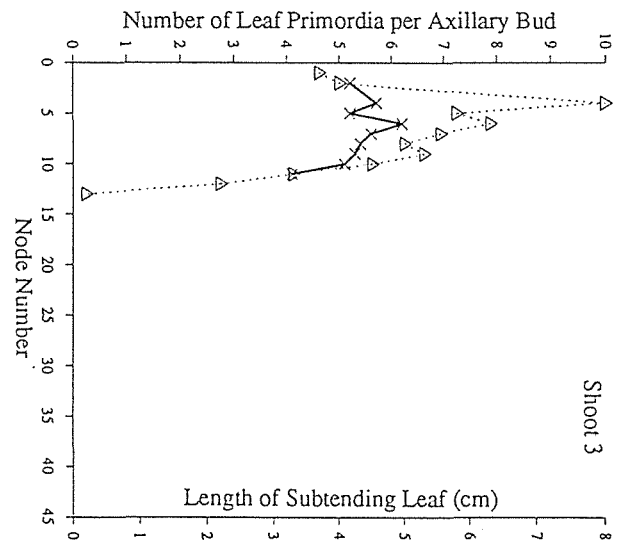
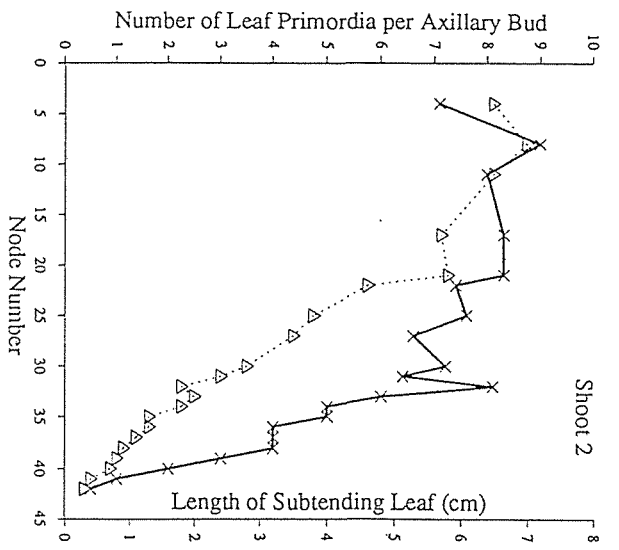
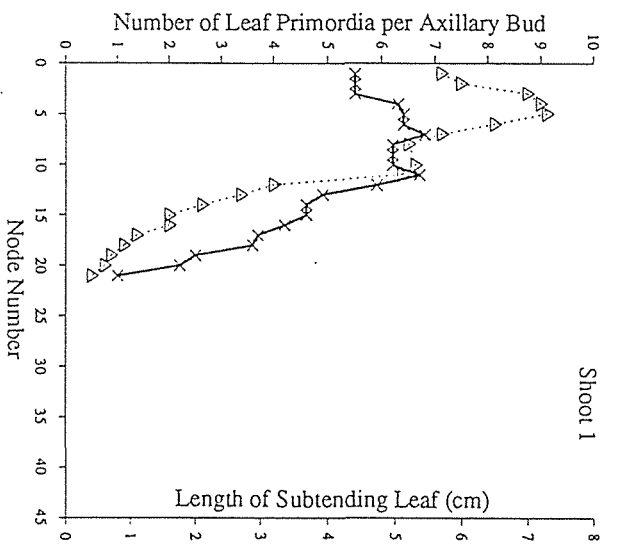
Node No. Primordia/Bud Length Sub. Leaf (cm)

Shoot 3: young lateral shoot - dissected 29th November

2	5.2	4.0
4	5.7	8.0
5	5.2	5.8
6	6.2	6.3
7	5.6	5.5
8	5.4	5.0
9	5.3	5.3
10	5.1	4.5
11	4.1	3.3

shoot apex located above node 13 - flowering

Muehlenbeckia australis



*Myoporum laetum***Dissection Results**

Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf (cm)
----------	---------------	--------------------	-----------------------

Shoot 1: dissected 20th September

1	6.1	1.2	6.3
2	6.1	1.0	6.3
3	7.8	1.0	9.0
4	5.3	0.5	4.5
5	6.8	1.5	8.5
6	6.5	1.9	10.9
7	4.2	0.7	6.6
8	5.2**	1.0	5.6
9	4.1	0.3	4.4
10	4.1	0.8	2.4
11	3.2	0.6	1.6
12	2.0**	0.2	1.1
13	2.0**	0.15	0.8
14	1.0**	0.12	0.6

shoot apex located above node 22

Shoot 2: dissected 26th October

8	8.7	4.0	7.0
9	7.1	2.7	6.5

nodes 13 to 22: all buds - axillary and accessory - flowering.

shoot apex located above node 26

Shoot 3: dissected 4th December

nodes 1 to 20: all buds flowering

21	12.0	7.0	8.0
23	14.0 - bud breaking		
26	10.1	4.0	
30	7.5	2.5	2.5
31	5.2	1.0	2.1
32	4.5	1.2	1.3
34	3.1	0.35	1.2
36	2.3		0.6

shoot apex located above node 46

Shoot 4: dissected 25th January

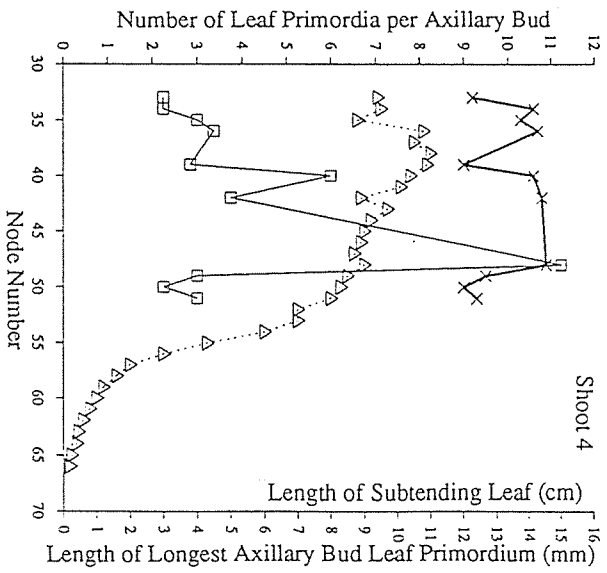
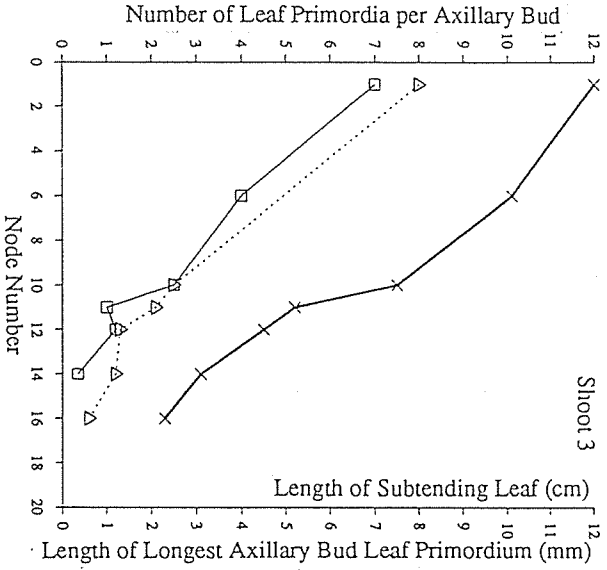
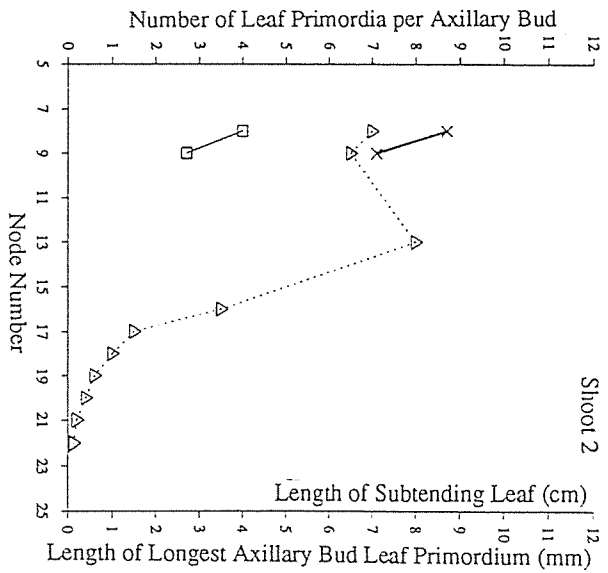
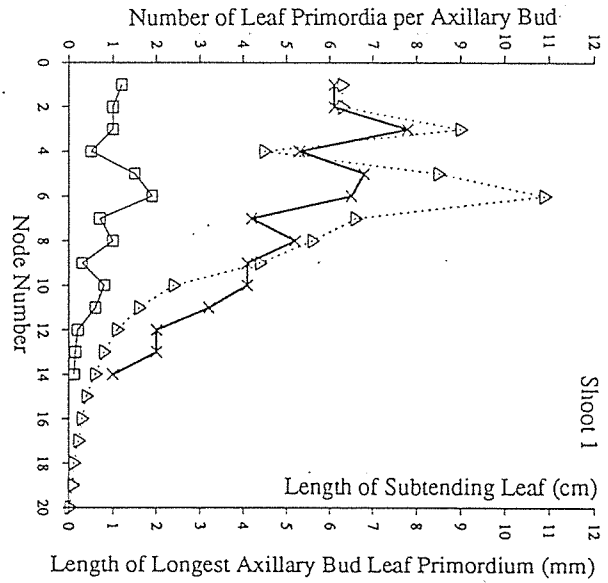
nodes 1 to 32: all buds flowering

33	9.2	3.0	9.4
34	10.6	3.0	9.4
35	10.3	4.0	8.8
36	10.7	4.5	10.8
nodes 37,38,41,43,44,45,46 and 47: buds broken			
39	9.0	3.8	10.9
40	10.6	8.0	10.4
42	10.8	5.0	8.9
48	10.9	15.0	9.0
49	9.5**	4.0	8.5
50	9.0**	3.0	8.3
51	9.3**	4.0	8.0

nodes 52 to 66: all buds flowering

shoot apex located above node 72.

** floral accessory buds growing out



*Passiflora mollissima***Dissection Results**

Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf (cm)
----------	---------------	--------------------	-----------------------

Shoot 1: dissected 15th September

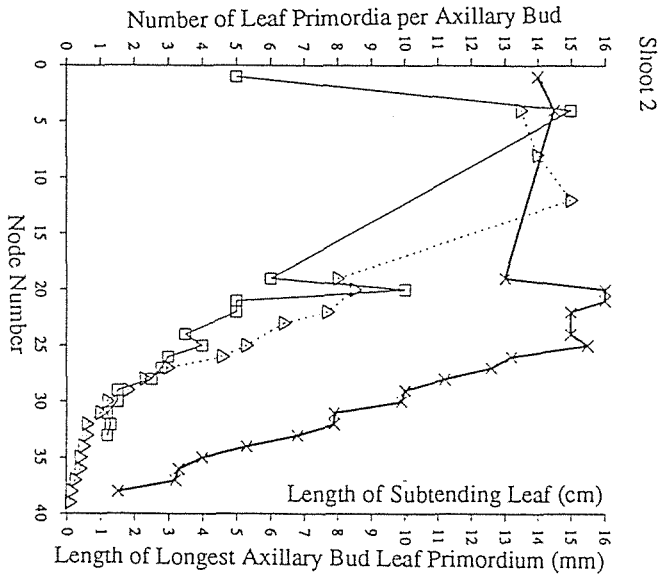
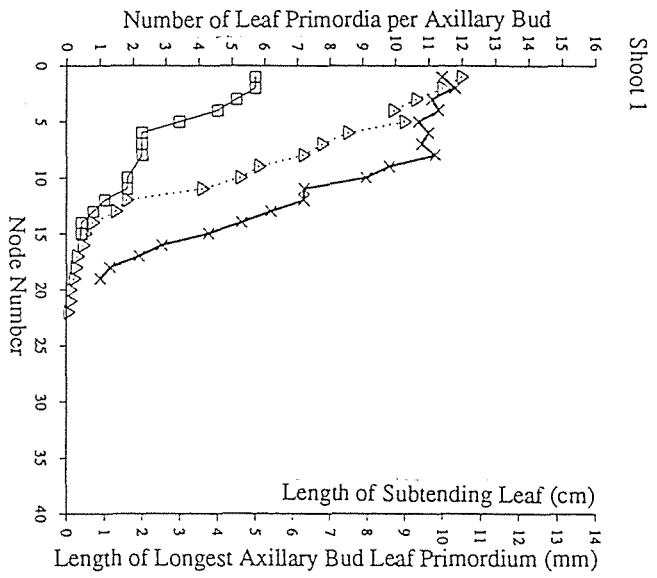
1	11.4	5.0	10.5
2	11.8	5.0	10.0
3	11.1	4.5	9.3
4	11.3	4.0	8.7
5	10.7	3.0	9.0
6	11.0	2.0	7.5
7	10.8	2.0	6.8
8	11.2	2.0	6.3
9	9.8		5.1
10	9.1	1.6	4.6
11	7.2	1.6	3.6
12	7.2	1.0	1.6
13	6.2	0.7	1.3
14	5.3	0.4	0.7
15	4.3	0.4	0.5
16	2.9		0.45
17	2.2		0.3
18	1.3		0.25
19	1.0		0.2

shoot apex located above node 25

Shoot 2: dissected 27th October

1	14.0	5.0	
2	bud absent		
3	bud broken		
4	14.5 - breaking	15.0	13.5
buds between nodes 5 and 18 either broken or absent			
19	13.0	6.0	8.0
20	16.0 - breaking	10.0	
21	16.0	5.0	8.5
22	15.0	5.0	
24	15.0	3.5	6.4
25	15.5	4.0	
26	13.1	3.0	5.3
27	12.6	2.8	4.6
28	11.2	2.5	3.0
29	10.0	1.5	2.3
30	9.9	1.5	1.8
31	7.9	1.2	1.2
32	7.9	1.3	1.0
33	6.8	1.2	0.6
34	5.3		0.6
35	4.0		0.5
36	3.3		0.4
37	3.2		0.4
38	1.5		2.5

shoot apex located above node 48



*Phormium tenax***Dissection Results**

Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf(cm)
----------	---------------	--------------------	----------------------

Plant 1: seedling - dissected 29th May

1			2.0
2			4.8
3	buds not detected		2.2
4			0.25
5			0.01
shoot apex located above node 6			

Plant 2: seedling - dissected 22nd September

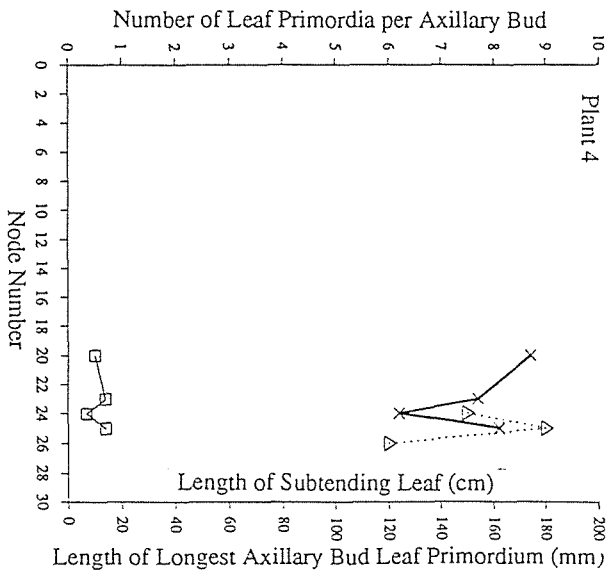
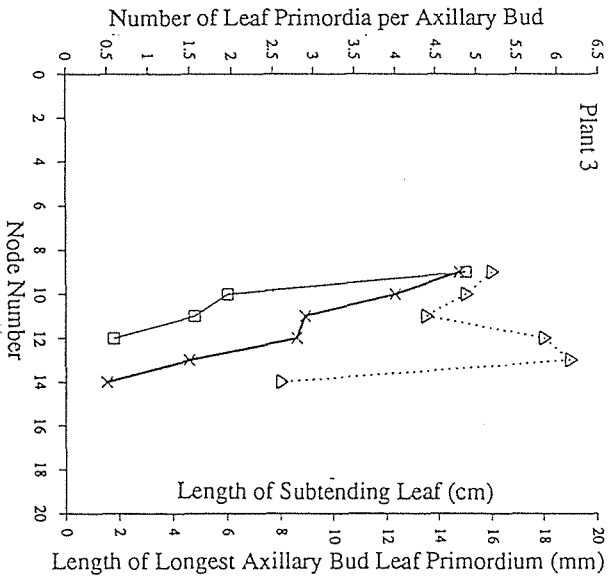
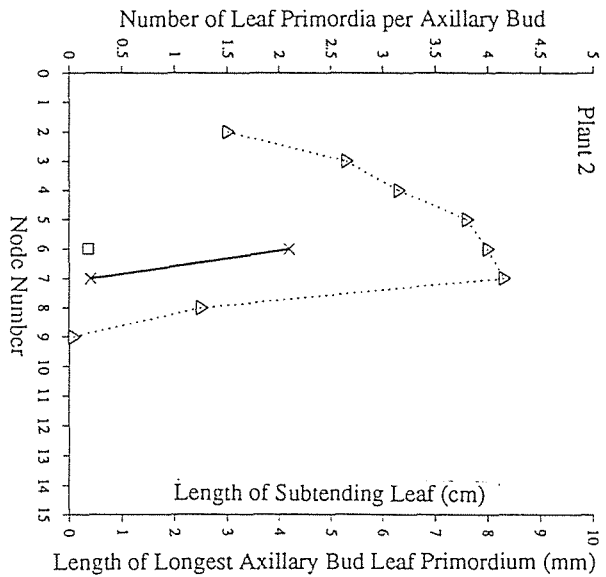
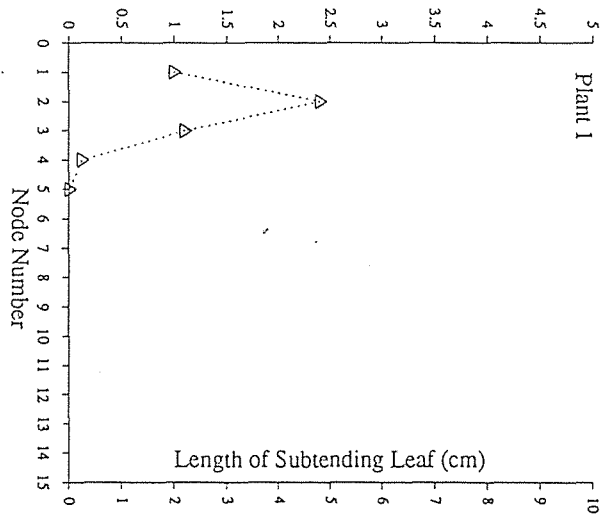
1			
2			3.0
3	buds not detected		5.3
4			6.3
5			7.6
6	2.1	0.36	8.0
7	0.2		8.3
8			2.5
9			0.08
shoot apex located above node 10			

Plant 3: seedling - dissected 1 November

nodes 1 to 8: buds not detected			
9	4.8 - bud broken	15.0	16.0
10	4.0 - bud broken	6.0	15.0
11	2.9	4.8	13.5
12	2.8	1.8	18.0
13	1.5		19.0
14	0.5		8.0
15			0.3
shoot apex located above node 17			

Plant 4: mature plant - dissected 22nd January

nodes 1 to 19: buds not detected			
20	8.7	10.0	
23	7.7	14.0	
24	6.2	7.0	150
25	8.1	14.0	180
26			120
27			80
28			50
29			25
30			1.1
shoot apex located above node 16			



*Pittosporum crassifolium***Dissection Results**

Node No.	Primordia/Bud	Length 1st. Pr.(mm)	Length Sub. Leaf(cm)
----------	---------------	---------------------	----------------------

Shoot 1: Early Bud Break

axillary buds not detected below node 19

7			0.3
9			0.4
11			0.7
13			0.8
15			1.0
18			1.3
20	1	0.1	1.2
21	2	0.1	1.25
22	2	0.1	1.3
23	3	0.25	1.5
24	5	0.3	1.8
25	5	0.35	1.85
26	4	0.3	1.7
27	4	0.3	1.9
28	4	0.28	1.6
29	3	0.25	1.5
30	4	0.25	1.4
31	4	0.28	1.2
32	4	0.2	1.1
33	3	0.2	1.0
34	3	0.18	0.9
35	2	0.1	0.7
36	1	0.15	0.65

buds not detected above node 36; shoot apex located above node 47.

Shoot 2: Late Bud Break

axillary buds not detected below node 10

10	2		1.3
11	2	0.5	1.7
12	4	0.6	2.6
13	5	0.6	4.2
15	6	1.0	5.2
16	7	0.8	5.5
17	8	0.8	5.4
18	8	0.8	5.3
19	8	1.1	5.5
20	10	0.8	5.3
21	9	1.0	5.3
22	9	0.8	5.0
23	9	0.8	5.1
24	9	0.8	4.9
25	10	0.8	4.8
26	10	0.9	4.6
27	9	0.9	4.4
28	9	0.6	4.0
29	8	0.6	3.8
30	7		2.6
31	2		0.2

buds not detected above node 31; shoot apex located above node 47.

Node No.	Primordia/Bud	Length 1st. Pr.(mm)	Length Sub. Leaf(cm)
----------	---------------	---------------------	----------------------

Shoot 3: Fully Developed Shoot in Early Winter

axillary buds not detected below node 8

8	2	0.4	3.0
9	7	0.6	3.5
10	7	0.7	3.7
11	9	1.0	4.0
12	11	1.1	4.0
13	11	1.2	4.2
14			4.4
15	13	1.3	4.5
16	14	1.3	4.5
17	12	1.2	4.0
18	11	1.1	4.2
19	13	1.3	4.0
20	13	1.2	4.0
21	13	1.3	4.0
22	15	1.4	4.0
23	15	1.5	3.8
24	20	1.8	4.5
25	19	2.1	4.2
26	18	2.0	4.0

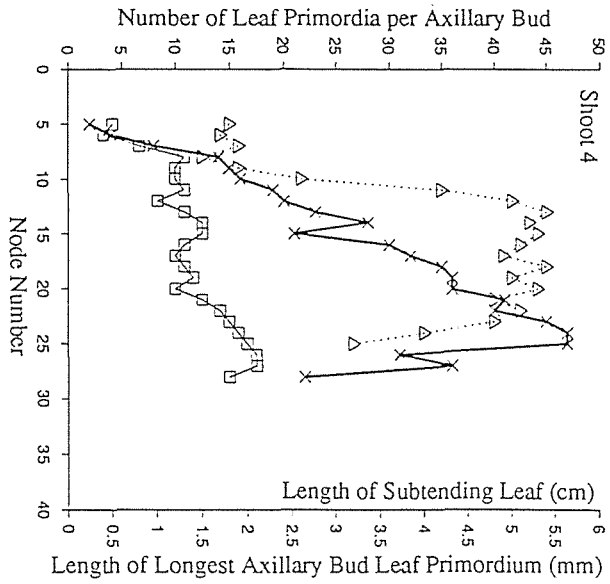
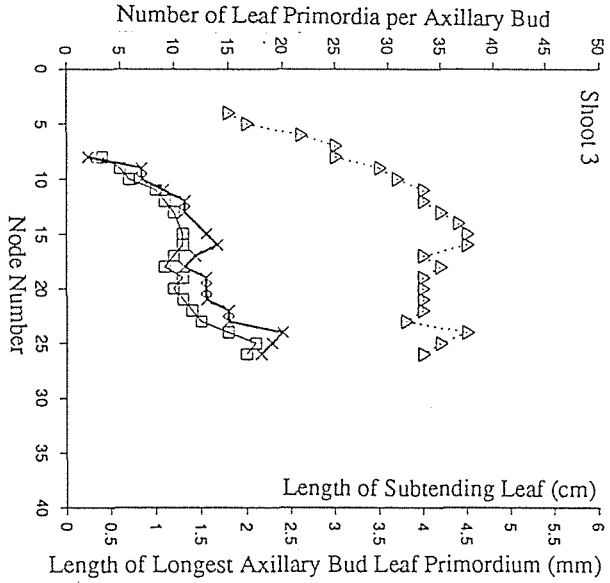
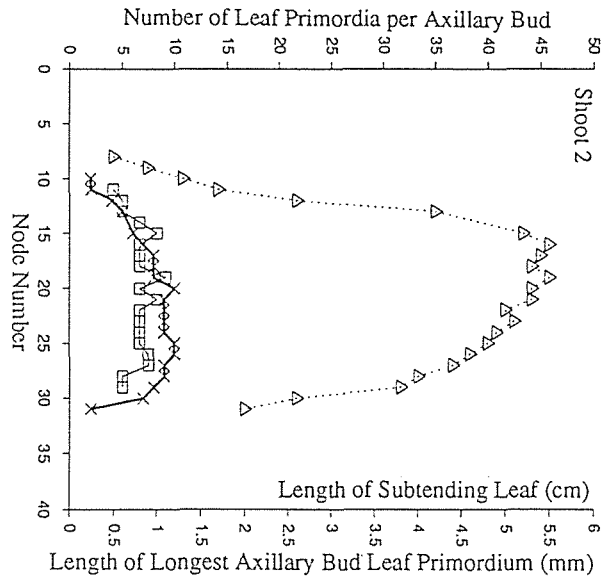
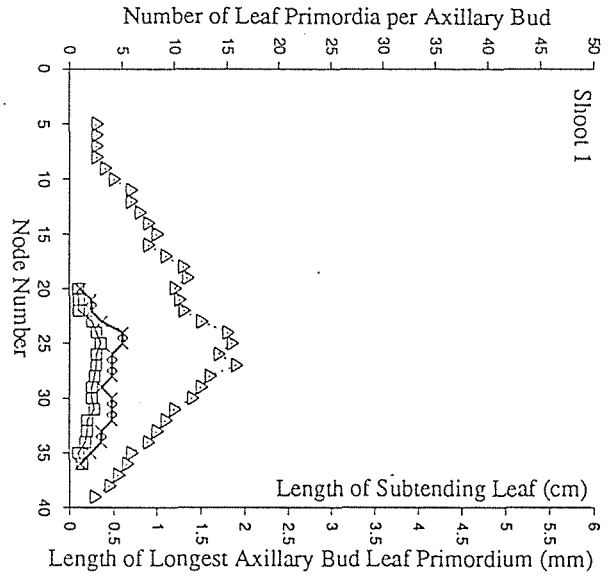
buds not detected above node 26; shoot apex located above node 57.

Shoot 4: Fully Developed Shoot in Mid Winter

axillary buds not detected below node 4

5	2	0.5	1.8
6	4	0.4	1.7
7	8	0.8	1.9
8	14	1.3	1.5
9	15	1.2	1.9
10	16	1.2	2.6
11	19	1.3	4.2
12	20	1.0	5.0
13	23	1.3	5.4
14	28	1.5	5.2
15	21	1.5	5.3
16	30	1.3	5.1
17	32	1.2	4.9
18	35	1.3	5.4
19	36	1.4	5.0
20	36	1.2	5.0
21	41	1.5	4.8
22	40	1.7	5.1
23	45	1.8	4.8
24	47	1.9	4.0
25	47	2.0	3.2
26	31	2.1	
27	36	2.1	
28	22	1.8	

buds not detected above node 28; shoot apex located above node 79



*Salix fragilis***Dissection Results**

Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf (cm)
----------	---------------	--------------------	-----------------------

Shoot 1: one week after bud break; dissected 2nd October

1	6.2	0.6	2.0
2	5.2	0.8	3.0
3			3.8
4	1.1		4.0
5	2.3	0.1	4.6
6	1.5		4.5
7	1.5		4.0
7	1.5		4.0
8	1.9		3.8
9	1.3		3.0
10	1.3		2.3
11	1.0		1.8
12	0.3		1.6
13			1.3
14			0.9
15			0.6
16			0.4
17			0.15

shoot apex located above node 19

Shoot 2: dissected 17th October

1			1.4
2			1.5
3			2.5
4			3.0
5	6.0	0.5	4.1
6	7.1	1.0	4.9
7	8.2	1.5	6.0
8	8.4	2.0	8.0
9	8.2	1.8	8.9
10	8.2	1.7	9.6
11	7.6	1.5	8.3
12	7.2	1.7	6.5
13	5.5	1.2	4.6
14	4.2	0.5	3.0
15	2.8		2.6
16	1.3		1.8
17	0.5		1.3
18			0.8
19			0.43
20			0.28
21			0.15
22			0.1

shoot apex located above node 25

Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf (cm)
----------	---------------	--------------------	-----------------------

Shoot 3: dissected 23rd November

4	10.0		
5	9.0	1.0	
6	9.0	1.2	4.4
7			1.0
8	10.5	2.0	7.0
9	12.3	2.4	9.0
10	12.3	2.4	10.0
11	13.6	2.7	8.5
12	12.1	2.9	8.0
13	13.4	3.0	9.0
14	14.7	3.2	11.1
15	13.9	3.7	11.0
16	13.8	3.8	11.7
14	14.7	3.2	11.1
15	13.9	3.7	11.0
16	13.8	3.8	11.7
17	13.2	4.1	11.0
18	12.9	3.5	10.0
19	12.3	3.5	10.5
20	8.4	1.4	8.5
21	6.2	1.3	9.5
22	5.7	1.3	9.0
23	5.3	1.3	9.0
24	5.0	1.2	7.0
25	4.0		4.3
26	2.0		2.5
27	1.0		0.6
28			0.2
29			0.2

shoot apex located above node 33

Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf (cm)
----------	---------------	--------------------	-----------------------

Shoot 4: dissected 24th January

6	9.0	1.0	
7	11.8	2.8	
8	12.2	3.8	
9	14.0	4.7	
10	14.9	5.2	11.3
11	14.9	5.5	12.5
12	15.9	6.1	12.5
13	15.9	6.2	12.0
14	16.3	7.8	16.0
15	16.7	7.0	16.5
16	16.8	6.9	16.0
17	17.2	7.0	17.0
18	17.4	7.8	14.0
19	17.3	7.4	16.0
20	17.0	7.0	16.5
21	17.4	7.7	14.0
22	16.9	7.2	14.0
23	16.4	7.6	15.0
24	15.9	6.4	9.3
25	15.8	7.0	13.9
26	15.2	7.0	11.2
27	13.4	5.9	
28	13.2	6.0	14.0
29	13.4	6.0	11.3
30	12.6	6.0	14.5
31	13.7	7.0	16.0
32	11.8	5.8	9.5
33	11.3	5.4	11.5
34	10.2	4.5	9.0
35	9.4	3.9	3.0
36	9.0	3.5	5.2
37	6.7	1.9	4.5
38	4.9	1.0	3.3
39	2.5	0.3	1.8
40	0.5		0.6

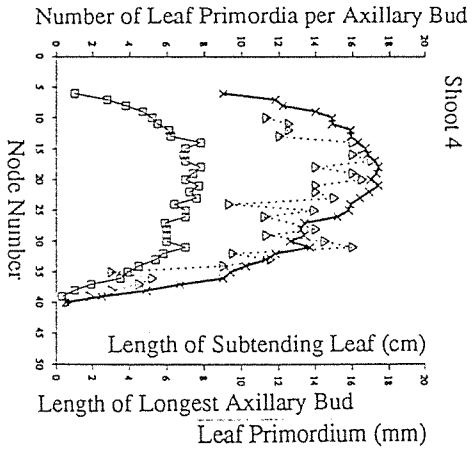
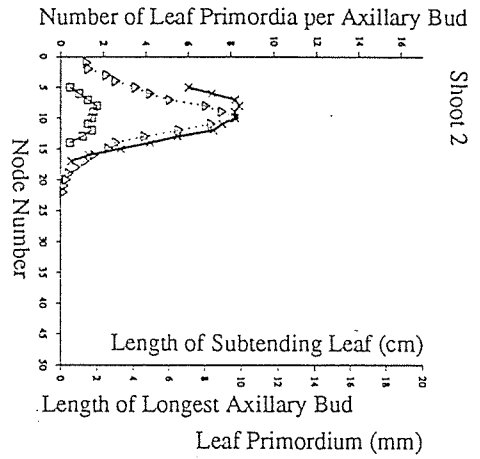
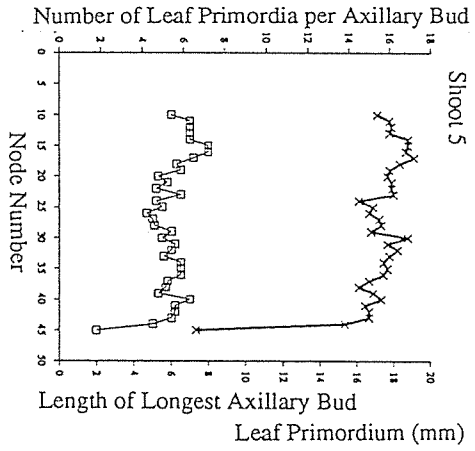
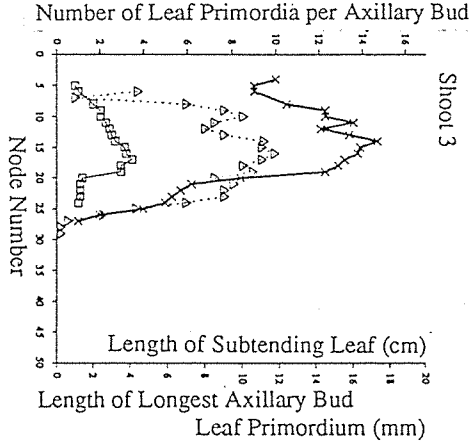
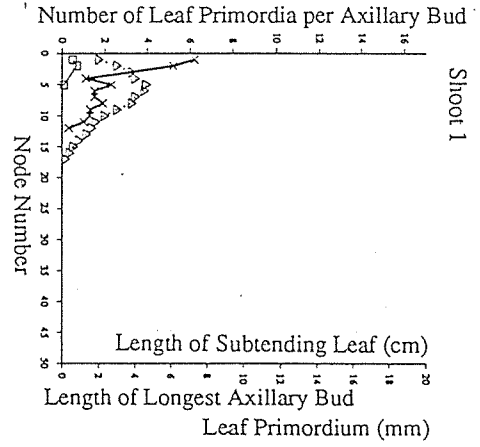
shoot apex located above node 45

Node No. Primordia/Bud Length 1st Pr.(mm)

Shoot 5: dissected 25th March

10	15.4	6.0
11	16.0	7.0
12	16.1	7.0
13	16.0	7.0
14	16.9	7.0
15	16.9	8.0
16	16.8	8.0
17	17.2	7.2
18	16.5	6.3
19	16.0	6.5
20	15.9	5.3
21	16.1	5.8
22	16.1	5.2
23	16.2	6.5
24	14.4	5.2
25	15.2	5.5
26	15.0	4.7
27	15.5	5.0
28	15.6	5.1
29	15.1	6.0
30	16.9	5.5
31	15.9	6.2
32	16.4	6.0
33	16.0	5.6
34	15.7	6.5
35	15.9	6.5
36	15.7	6.5
37	15.0	5.8
38	14.5	5.7
39	15.2	5.3
40	15.6	7.0
41	14.8	6.2
42	15.0	6.2
43	15.0	6.0
44	13.8	5.0
45	6.6	2.0

shoot apex senescent



*Sambucus nigra***Dissection Results**

Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf (cm)
----------	---------------	--------------------	-----------------------

Shoot 1: dissected 18th September

3			2.8
4	2.2	0.7	5.5
6	2.0	0.6	3.4
7	1.2		1.9
8			0.6

shoot apex located above node 10

Shoot 2: dissected 16th October

1			2.5
2			7.5
3	4.3	1.8	12.0
4	4.3	1.8	16.0
5	4.1	2.0	20.7
6	3.9	2.0	18.0
7	3.8	2.0	11.0
8	2.8	1.4	5.3
9	2.5	0.36	1.9
10	1.0		0.9

shoot apex located above node 14

Shoot 3: dissected 1st December

2	8.0		21.5
3	7.9		22.2
4	8.6	4.2	20.0
5	7.4		18.5
6	7.4		21.5
7	7.0	3.0	25.0
8	5.9	3.5	25.0
9	6.1	3.0	21.2
10	5.9	3.0	24.0
11	5.4	3.0	22.2
12	4.7	3.0	16.5
13	3.5	1.7	9.0
14	2.8	1.0	3.8
15	1.9	0.24	1.1
16			0.4

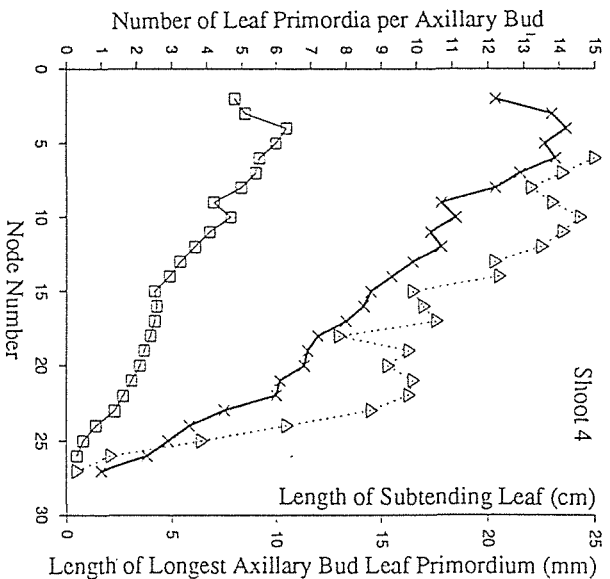
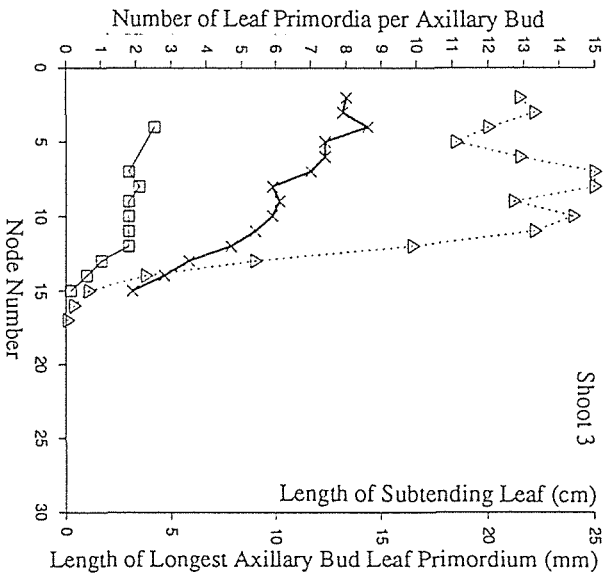
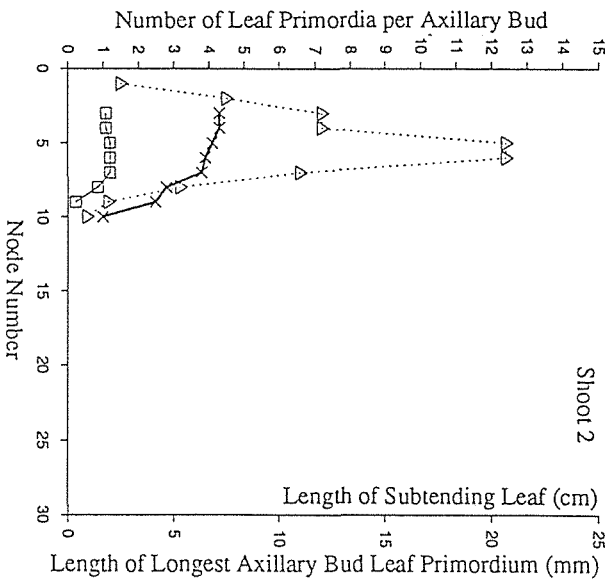
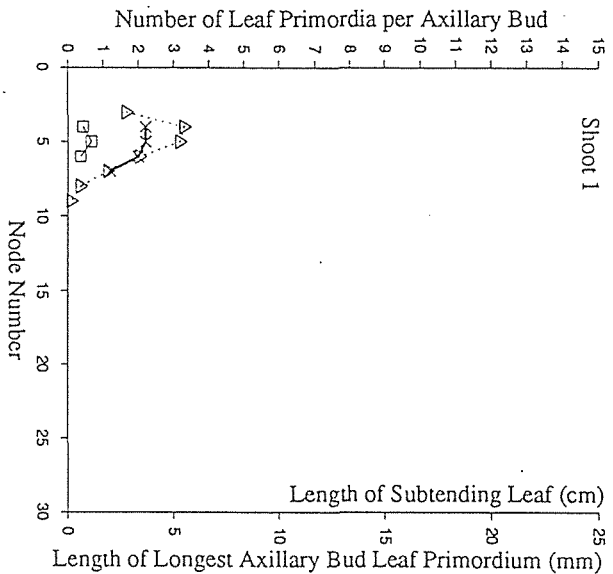
shoot apex located above node 19

Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf (cm)
----------	---------------	--------------------	-----------------------

Shoot 4: dissected 21st February

2	12.2	8.0	
3	13.8	8.5	
4	14.2	10.5	
5	13.6	10.0	
6	13.9	9.2	27.0
7	12.9	9.0	23.5
8	12.2	8.3	22.0
9	10.7	7.0	23.0
10	11.1	7.8	24.3
11	10.4	6.8	23.5
12	10.7	6.1	22.5
13	9.9	5.4	20.3
14	9.3	4.9	20.5
15	8.7	4.2	16.5
16	8.5	4.3	17.0
17	8.0	4.2	17.6
18	7.2	4.0	13.0
19	6.9	3.7	16.3
20	6.8	3.5	15.3
21	6.1	3.1	16.5
22	6.0	2.7	16.3
23	4.5	2.3	14.5
24	3.5	1.4	10.5
25	2.9	0.8	6.4
26	2.3	0.5	2.1
27	1.0		0.5

shoot apex located above node 30



*Solanum aviculare***Dissection Results**

Node no.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf(cm)
----------	---------------	--------------------	----------------------

Plant 1

1	3.5	0.2	
2	4.1	0.37	
3	4.1	0.35	
4	4.2	0.4	
5	3.7	0.35	
6	3.3	0.4	
7	3.2	0.4	
8	2.5	0.35	6.5
9	3.1	0.45	4.8
10	2.5	0.3	5.0
11	2.3	0.2	1.5
12	1.5		1.5

shoot apex located above node 18

Plant 2

2	6.3	1.8	
3	7.3	3.0	
4	7.8	3.0	
5	6.8	2.4	
6	6.8	1.7	
7	5.4	1.0	
8	6.1	1.0	
9	5.1	1.0	7.5
10	5.9	2.5	
11	5.6	2.0	11.0
12	5.0	1.0	7.0
13	4.2	1.3	9.5
14	5.6	1.2	12.5
15	5.9	1.2	12.5
16	4.2	1.0	10.2
17	3.1	0.35	5.3
18	2.5	0.1	3.1
19	2.0		1.8
20	bud not detected		0.85
21	1.8		0.6

shoot apex located above node 21 - flowering

Node no.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf(cm)
----------	---------------	--------------------	----------------------

Plant 3

buds below node 5 not examined

5	8.5		
7	7.9		
10	5.1	0.8	11.3
11	5.0	0.9	11.5
12	4.6	0.5	12.0
13	4.5	1.0	15.0
14	5.4	1.0	13.5
15	4.2	0.6	10.5
16	3.4	0.5	6.0
17	3.2	0.5	4.5
18	3.3	0.6	2.3
19	6.0	1.6	1.5
20	7.1	2.2	1.1

shoot apex located above node 20 - flowering

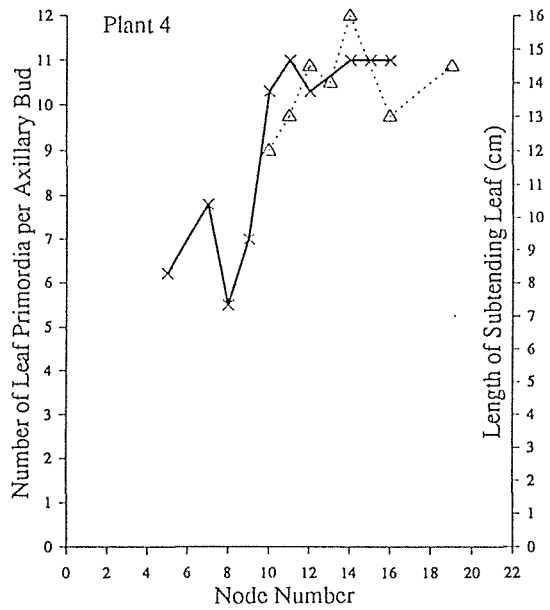
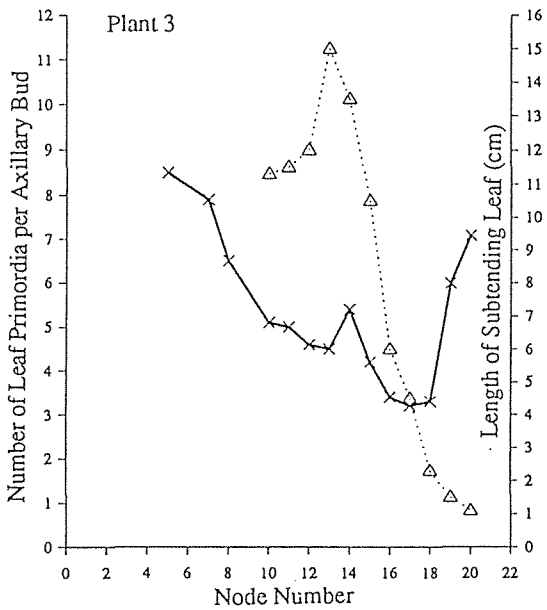
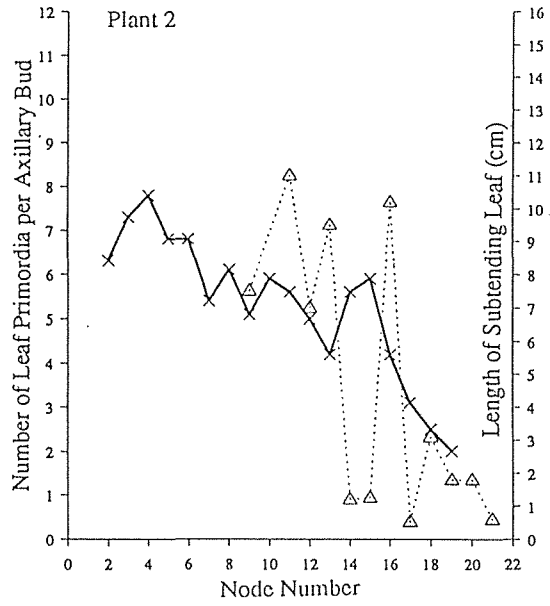
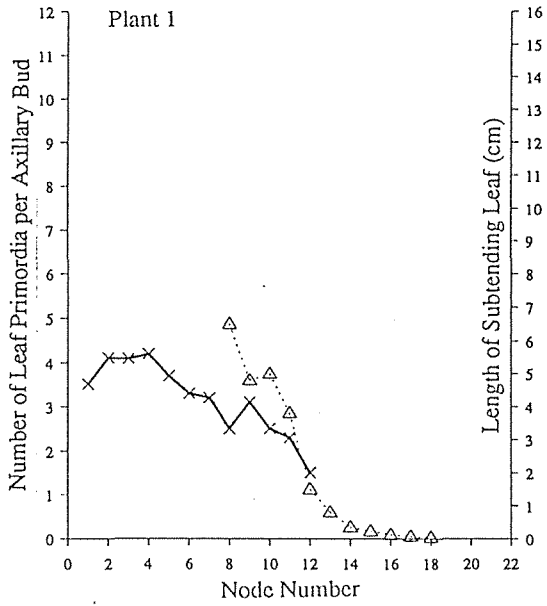
Plant 4

buds below node 5 not examined

5	6.2		
7	7.8		
8	5.5		
9	7.0	2.1	
10	10.3	4.5	12.0
11	11.0	5.0	13.0
12	10.3	5.0	14.5
13			14.0
14	11.1	4.0	16.0
15	11.0	1.0	
16	11.0	13.0	13.0

buds at nodes 17,18 and 19: broken to form large shoots;
shoot apex located above node 19 - flowering

Solanum aviculare



*Solanum tuberosum***Dissection Results**

Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf (cm)
----------	---------------	--------------------	-----------------------

Shoot 1: approximately 2.5 cm in height

1	11.2		0.15
2	8.1	1.3	0.15
3	8.3	1.2	0.2
4	7.4	1.5	0.45
6	7.4	1.9	
7	7.8	2.0	0.5
8	7.8	1.5	1.2
9	7.8	2.1	2.1
10	6.9	1.4	2.0
11	5.3	1.0	1.0
12	4.5		0.9
13	3.2		0.7
14	2.6		0.7
15	0.5		0.3

shoot apex located above node 21 - flowering

Shoot 2: approximately 5 cm in height

1	9.3	1.9	
2	10.1	2.7	2.7
3	9.1	2.5	2.5
4	9.1	2.9	3.8
5	8.1	2.8	3.1
6	7.5	1.8	2.7
7	6.0	1.5	1.9
8	2.8	1.0	1.0
9	4.5	0.7	1.1
10	2.6		0.7
11	1.3		0.5
12	1.0		0.3
13	0.9		0.2
14	0.7		0.15
15	3.5		
16	3.7		

shoot apex located above node 16 - flowering

Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf (cm)
----------	---------------	--------------------	-----------------------

Shoot 3: approximately 35 cm in height

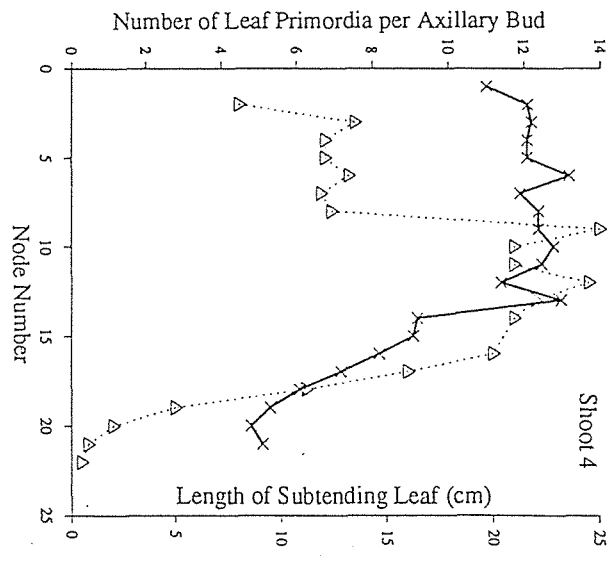
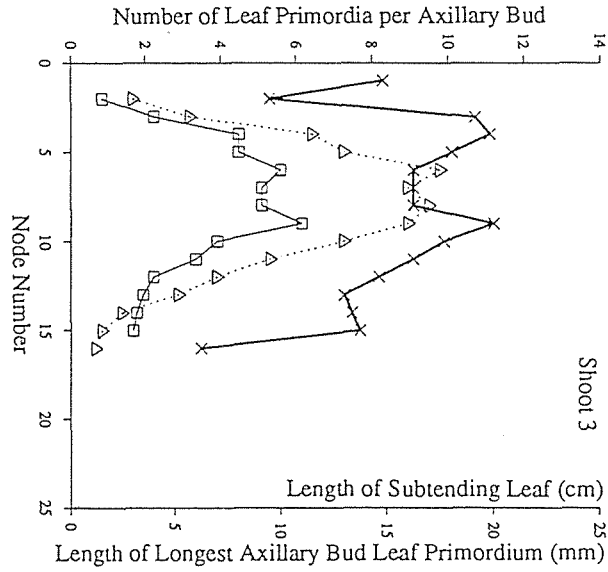
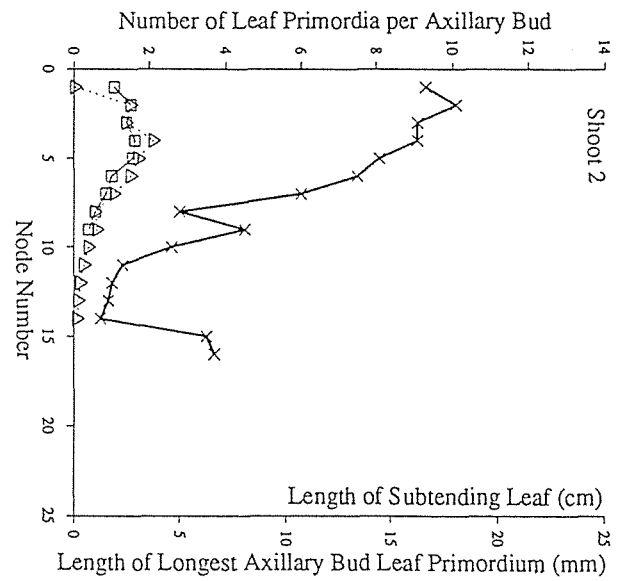
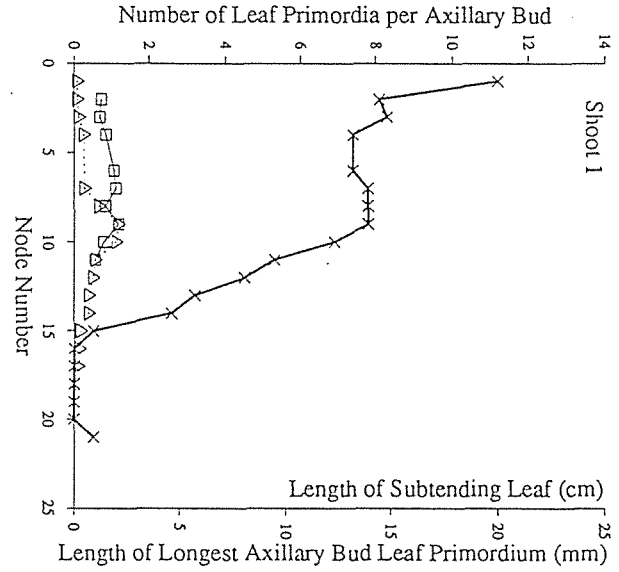
1	8.3		
	4.0		
2	5.3	1.5	3.0
	2.0		
3	10.7	4.0	5.7
4	11.1	8.0	11.5
5	10.1	8.0	13.0
6	9.1	10.0	17.5
7	9.1	9.1	16.0
8	9.1	8.0	17.0
9	11.2	11.0	16.0
10	9.9	7.0	13.0
11	9.1	6.0	9.5
12	8.2	4.0	7.0
13	7.3	3.5	5.2
14	7.5	3.2	2.5
15	7 - flowering	3.0	1.5
	2 - flowering		
16	3 - flowering		1.2

shoot apex located above node 16 - consisting of 12 flower primordia at various stages of development.

Shoot 4: approximately 70 cm in height

1	11		
	9		
2	12.1		8.0
3	12.2		13.5
4	12.1		17.0
5	12.1		16.5
6	13.2		22.0
7	11.9		22.0
8	12.4		23.0
9	12.4		25.0
10	12.8		21.0
11	12.5		21.0
12	11.4		24.5
13	13.0		22.0
14	9.2		21.0
15	9.1		
	flowering accessory bud		
16	8.2		20.0
17	7.2		16.0
18	6.1		11.2
19	5.3		5.0
20	4.8		2.0
21	5.1		0.8

shoot apex located above node 21 - flowering



*Stachys sylvatica***Dissection Results**

Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf(cm)
----------	---------------	--------------------	----------------------

Plant 1: seedling

1	1.7	0.08	1.4
2	1.8	0.08	2.4
3			0.25
4			0.03

stem apex located above node 5

Plant 2: seedling

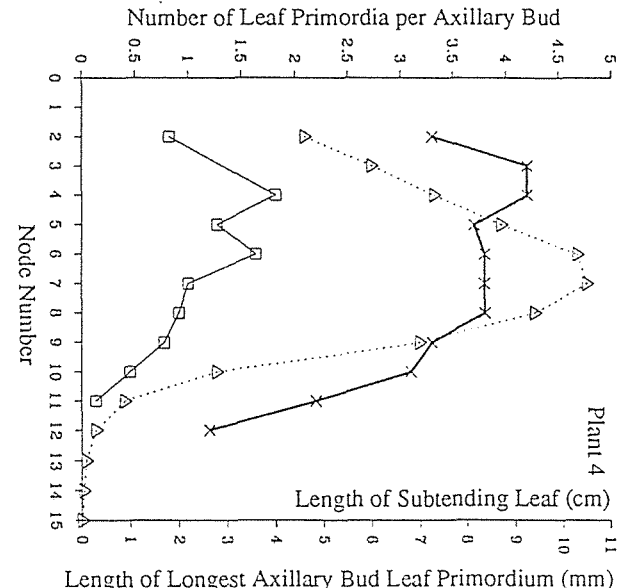
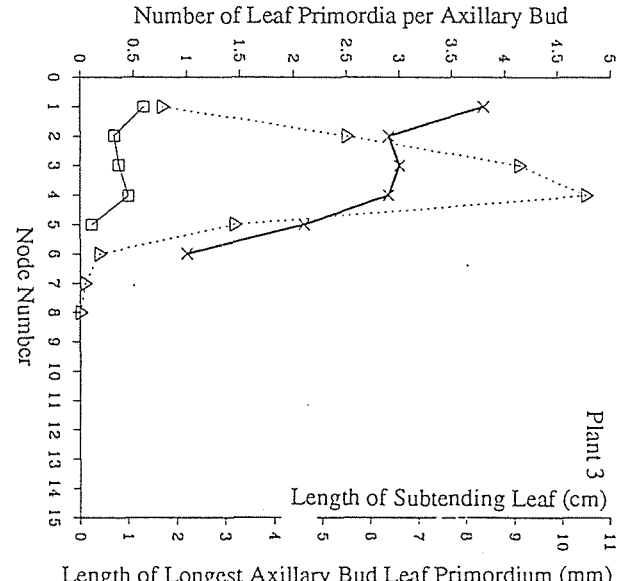
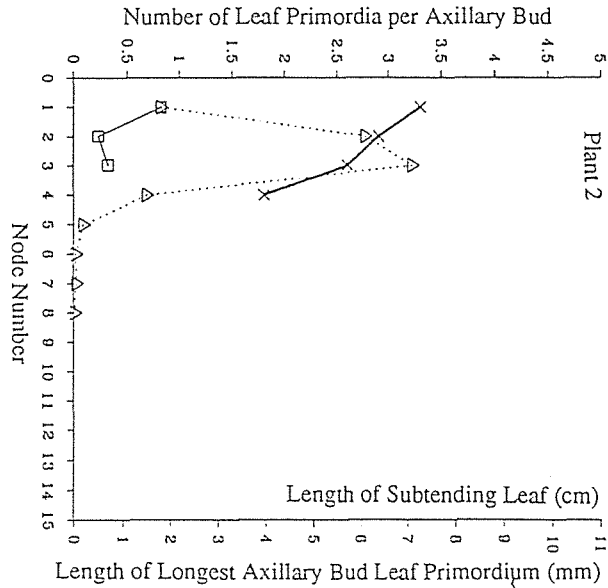
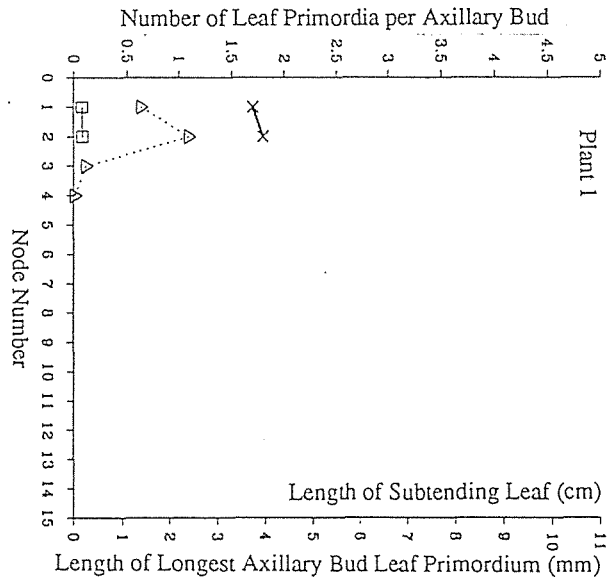
1	3.3	1.8	1.8
2	2.9	0.5	6.1
3	2.6	0.7	7.1
4	1.8	1.5	
5			0.2
6			0.05

stem apex located above node 7

Plant 3: seedling

1	3.8	1.3	1.7
2	2.9	0.7	5.5
3	3.0	0.8	9.1
4	2.9	1.0	10.5
5	2.1	0.25	3.2
6	1.0		0.4
7			0.11
8			0.02

stem apex located above node 8



*Tradescantia fluminensis***Dissection Results**

Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf(cm)
----------	---------------	--------------------	----------------------

Shoot 1

1	3.0	0.9	1.3
2	3.2	0.6	4.5
3	2.9	0.5	4.7
4	2.8	0.3	4.5
5	1.9	0.15	3.8
6	0.5		2.2

shoot apex located above node 9

Shoot 2

1	4.4		
2	4.4		
3	4.3		4.0
4	4.2		4.0
5	4.1		4.2
6	4.1	1.0	4.5
7	4.6	1.0	4.4
8	4.3	0.7	4.0
9	3.6		4.1
10	2.8		3.8
11	1.2		3.0

shoot apex located above node 16

Shoot 3

1		2.2	
2	bud broken	6.0	
3	5.1 - broken	2.0	4.8
4	5.2 - broken	2.2	4.8
buds at nodes 5,6, and 7: broken			
8	6.0 - breaking	4.2	5.2
9	4.6	1.1	5.4
10	4.9	1.2	5.6
11	5.3	1.7	5.6
12	4.5	1.0	5.3
13	4.4	1.0	5.0
14	4.2	0.8	4.8
15	4.1	0.7	4.7
16	4.0	0.6	4.4
17	3.2	0.5	3.9
18	1.7	0.1	2.9
19	1.0		1.4

shoot apex located above node 23

Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf(cm)
----------	---------------	--------------------	----------------------

Shoot 4

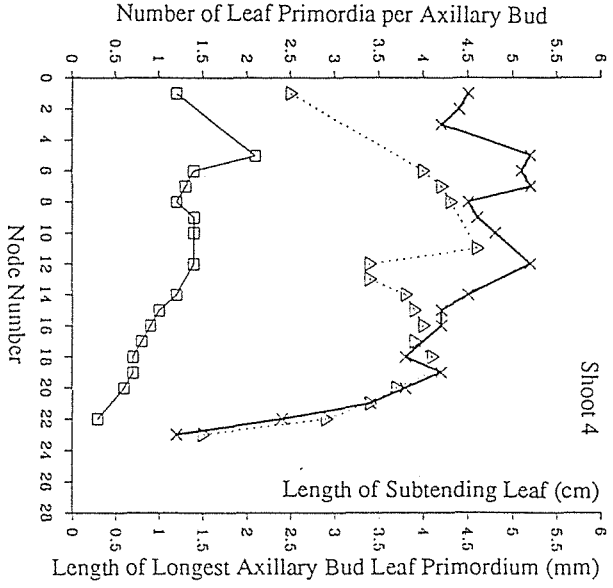
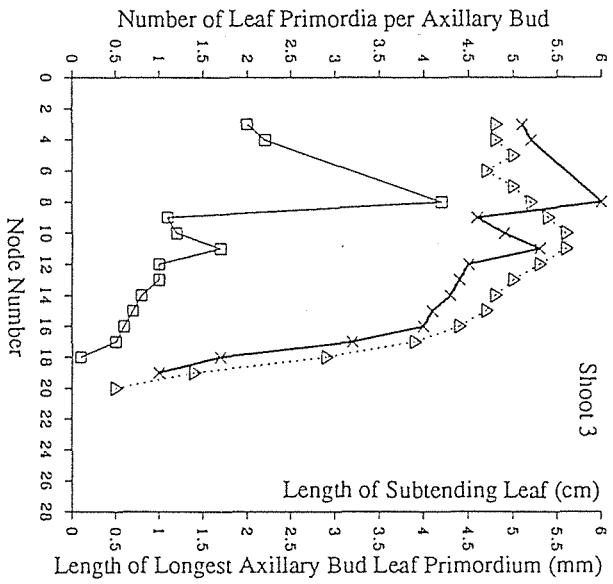
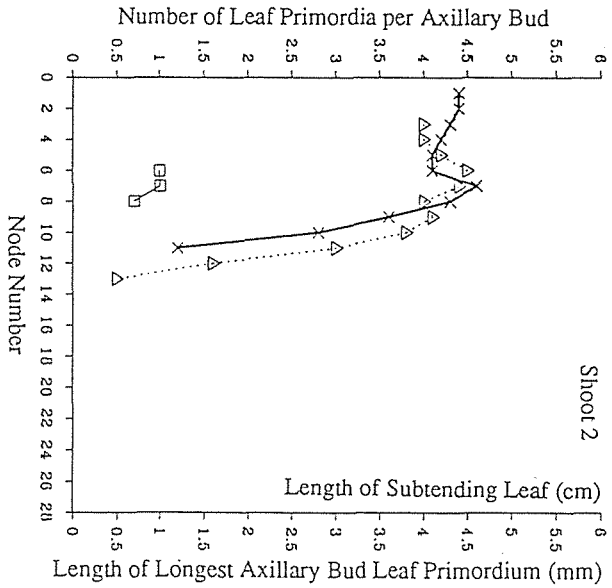
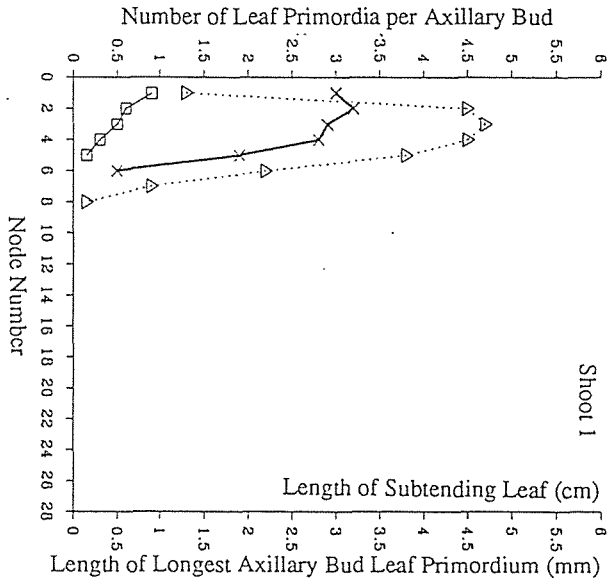
1	4.5	1.2	2.5
2	4.5		
3	4.2		
4	bud absent		
5	5.2	2.1	
6	5.1	1.4	4.0
7	5.2	1.3	4.2
8	4.5	1.2	4.3
9	4.6	1.4	
10	4.8	1.4	
11	5.0	1.4	4.6
12	5.2	1.4	3.4
13	bud broken		3.4
14	4.5	1.2	3.8
15	4.3	1.0	3.9
16	4.2	0.9	3.9
17	4.0	0.8	3.9
18	3.8	0.7	4.0
19	4.2	0.7	4.1
20	3.8	0.6	3.7
21	3.4		3.4
22	2.4	0.3	2.9
23	1.2		1.5

shoot apex located above node 28

Plant 4: shoot on an adult plant

2	3.3	1.8	4.6
3	4.2		6.0
4	4.2	4.0	7.3
5	3.7	2.8	8.7
6	3.8	3.6	10.3
7	3.8	2.2	10.5
8	3.8	2.0	9.4
9	3.3	1.7	7.0
10	3.1	1.0	2.8
11	2.2	0.3	0.9
12	1.2		0.3
13			0.1

stem apex located above node 16



*Trifolium repens***Dissection Results**

Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf(cm)
----------	---------------	--------------------	----------------------

Plant 1: dissected 1st June

1	(cotyledonary node) bud not detected		0.6
2	0.5		2.6
3			0.8
4			0.08
shoot apex located above node 5			

Plant 2: dissected 2nd July

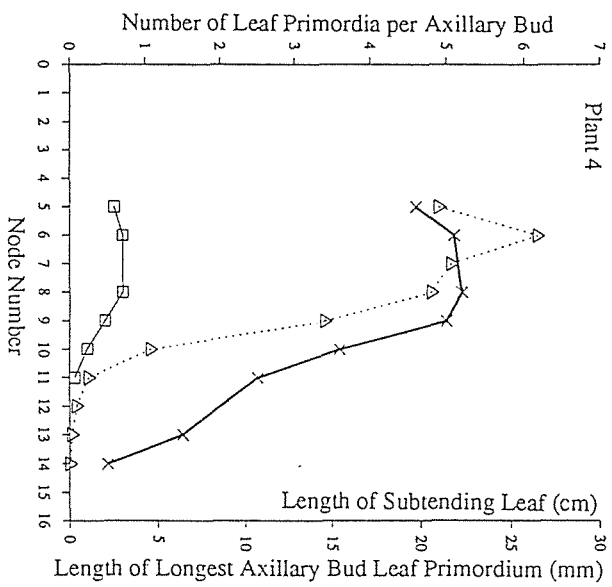
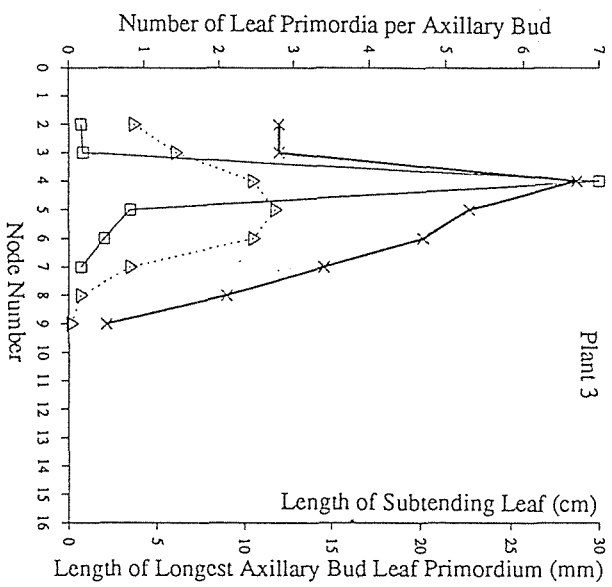
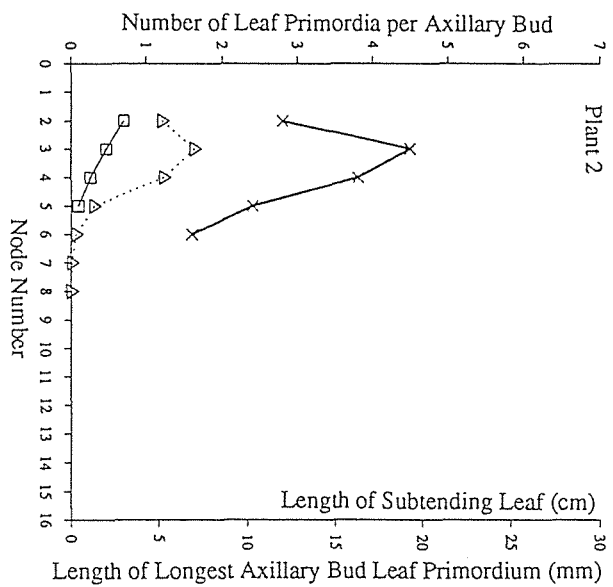
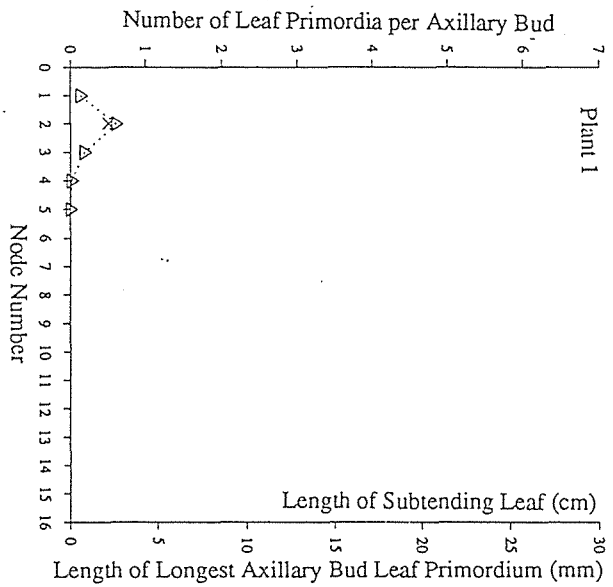
1	bud not detected		
2	2.8	3.0	5.2
3	4.5	2.0	7.0
4	3.8	1.1	5.3
5	2.4	0.4	1.3
6	1.6		0.3
shoot apex located above node 9			

Plant 3: dissected 10th July

1	1.7		
2	2.8	0.7	3.7
3	2.8	0.8	6.1
4	6.7 - broken	30.0	10.5
5	5.3	3.5	11.8
6	4.7	2.0	10.5
7	3.4	0.7	3.5
8	2.1		0.7
9	0.5		0.17
shoot apex located above node 11			

Plant 4: dissected 14th August

1	bud not detected		
buds at nodes 2,3 and 4: broken.			
5	4.6	2.5	21.0
6	5.1	3.0	26.5
7	broken		21.7
8	5.2	3.0	20.6
9	5.0	2.0	14.6
10	3.6	1.0	4.6
11	2.5	0.3	1.1
12	bud not dissected		0.4
13	1.5		0.15
14	0.5		0.05
shoot apex located above node 16			



*Tropaeolum majus***Dissection Results**

Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf (cm)
----------	---------------	--------------------	-----------------------

Shoot 1: dissected 18th September

1	7	3	45.0
2	7.8	3	56.0
3	6.6	1.5	43.5
4	6.5	1.5	
5	6.2	1.3	25.0
6	flowering		5.5
7	5.1	0.5	1.9
8	3.0		0.9
9	flowering		0.3
10	2.0		0.2
11	1.0		0.13

shoot apex located above node 18

Shoot 2: dissected mid November

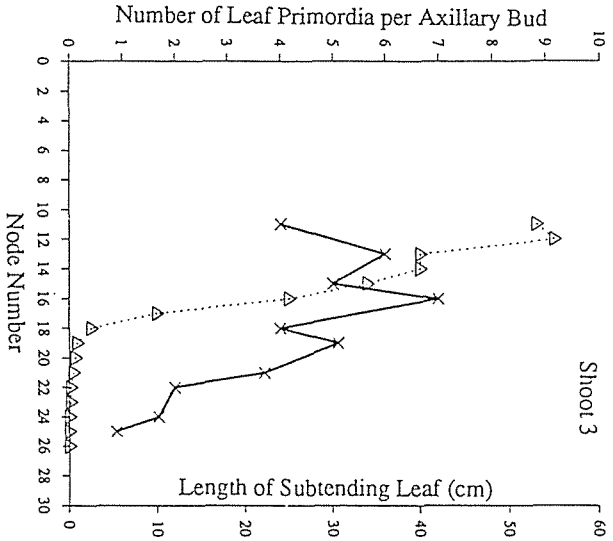
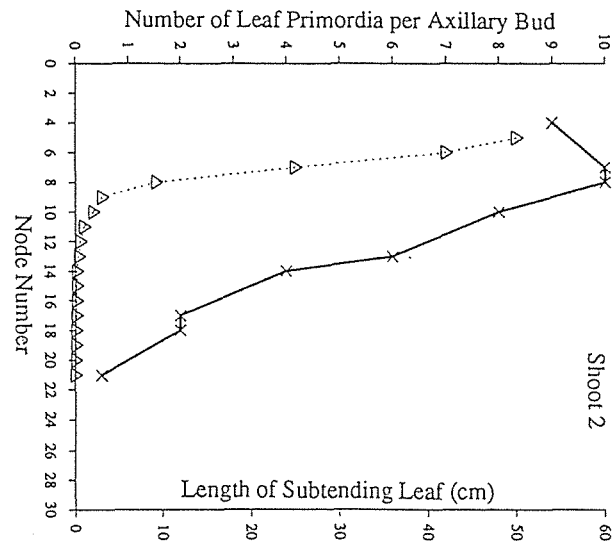
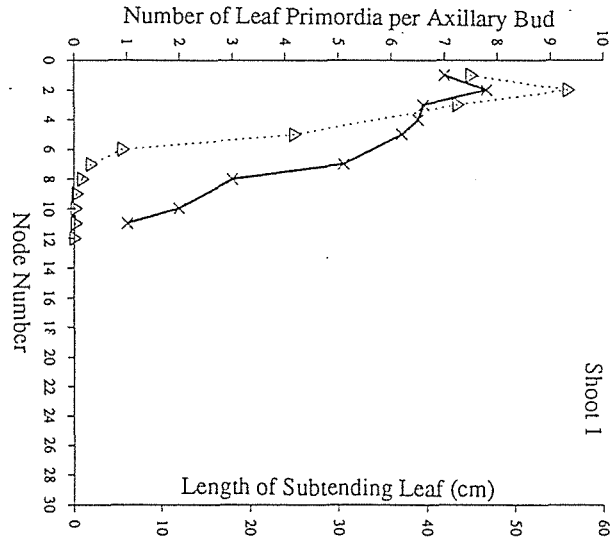
4	9.0		
5	flowering		50.0
6	flowering		42.0
7	10.0	2.5	25.0
8	10.0	2.0	9.2
9	flowering		3.0
10	8.0	1.5	2.0
11	flowering		1.0
12	flowering		6.0
13	6.0	0.8	0.4
14	4.0	0.4	0.2
15	flowering		0.2
16	flowering		1.5
17	2.0		0.13
18	2.0		0.1
19	flowering		0.07
20	flowering		0.06
21	0.5		0.04

shoot apex located above node 27

Shoot 3: dissected 7th February

11	4 - flowering	3.0	53.0
12	flowering		55.0
13	6 - flowering	4.0	40.0
14	flowering		40.0
15	5 - flowering	4.0	34.0
16	7.0		25.0
17	flowering		10.0
18	4 - flowering	1.0	2.5
19	5.1	1.0	0.9
20	flowering		0.7
21	3.7	3.2	0.5
22	2.0		0.2
23	flowering		0.19
24	1.7		0.1
25	0.9		0.7

shoot apex located above node 29



Ulmus procera cv. Van Houlte**Dissection Results**

Node No. Primordia/Bud Length Sub. Leaf (cm)

Shoot 1: dissected 18th October

1	3.0	
2	6.1	
3	7.1	3.9
4	7.8	7.1
5	8.2	7.0
6	8.0	7.8
7	8.1	5.7
8	7.4	4.8
9	5.1	0.8
10	3.5	0.45
11	0.5	0.2

shoot apex located above node 14

Shoot 2: dissected 4th December

1	13.0	6.5
2	13.5	10.0
3	14.1	10.5
4	14.9	13.5
5	15.3	13.5
6	15.0	14.0
7	14.5	12.0
8	15.1	10.0
9	13.1	8.5
10	13.5	9.5
11	13.5	12.5
12	13.7	12.0
13	13.1	13.5
14	11.0	10.2
15	10.2	5.2
15	10.2	5.2
16	8.8	2.4
17	6.2	0.7
18	4.3	0.3
19	2.4	0.25
20	1.5	0.14

shoot apex located above node 25

Node No. Primordia/Bud Length Sub. Leaf (cm)

Shoot 3: dissected 1st February

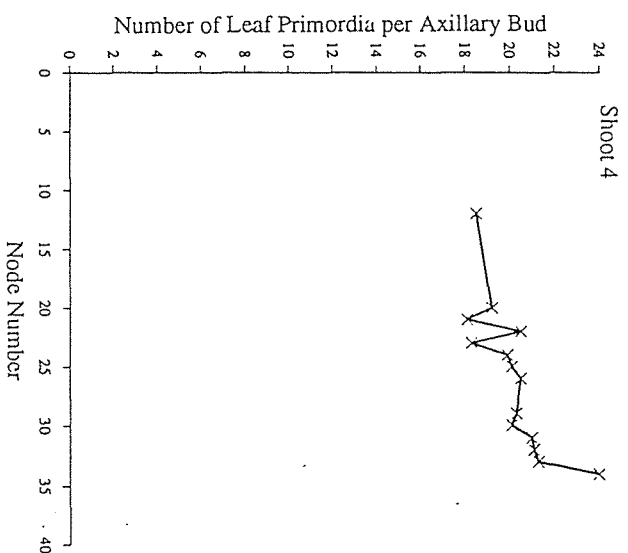
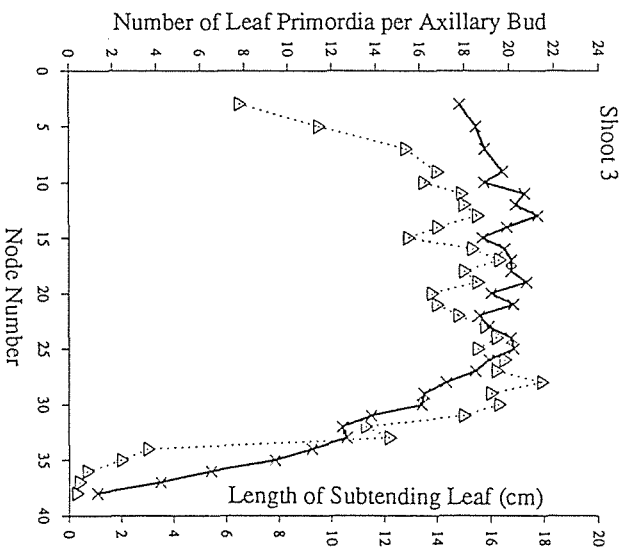
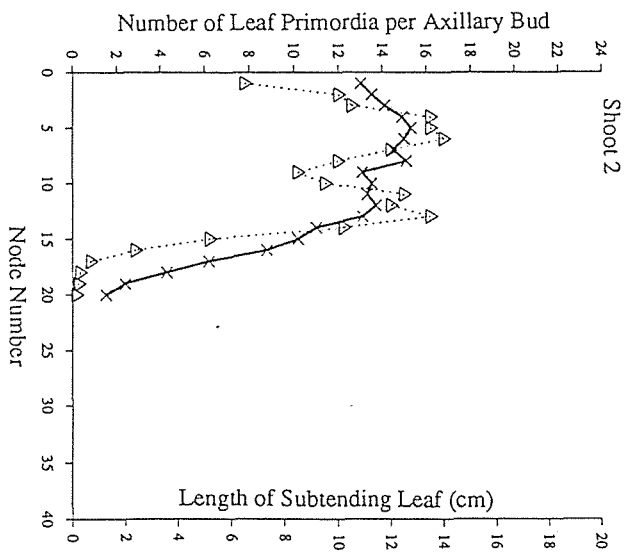
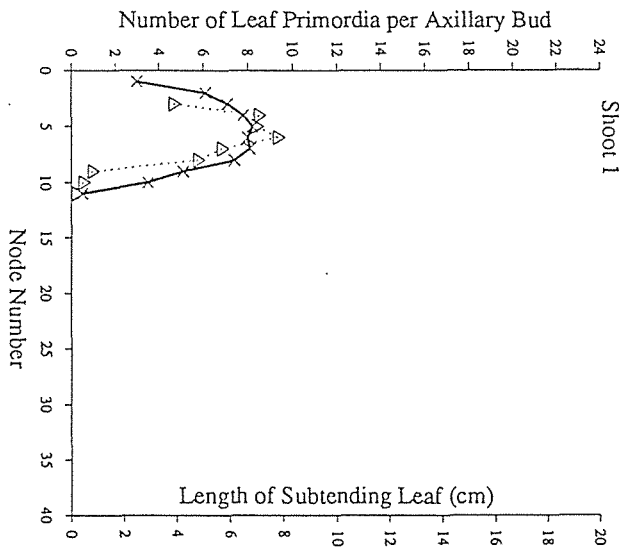
3	17.8	6.5
5	18.5	9.5
7	18.9	12.8
9	19.7	14.0
10	18.9	13.5
11	20.7	14.9
12	20.3	15.0
13	21.3	15.5
14	19.9	14.0
15	18.8	12.9
16	19.8	15.3
17	20.1	16.3
18	20.1	15.0
19	20.8	15.5
20	19.2	13.8
21	20.2	13.8
22	18.7	14.8
23	19.1	15.8
24	20.1	16.2
25	20.2	15.5
26	19.1	16.5
27	18.5	16.2
28	17.2	17.9
29	16.2	16.0
30	16.1	16.3
31	13.8	15.0
32	12.5	11.3
33	12.7	12.2
34	11.1	3.0
35	9.4	2.0
36	4.2	0.4
37	1.3	0.3

shoot apex located above node 45

Shoot 4: dissected 13th July

12	18.5
nodes 13 to 16:	buds senescent
nodes 17 to 19:	buds broken
20	19.2
21	18.1
22	20.5
23	18.3
24	19.9
25	20.1
26	20.5
29	20.3
30	20.1
31	20.1
32	21.2
33	21.3
34	24.0

shoot apex senescent; bud at node 34 will be the new shoot apex next season



Viburnum japonicum

Dissection Results

Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf (cm)
----------	---------------	--------------------	-----------------------

Shoot 1: dissected 12th September

1			2.2
2	1.3		7.5
3			2.6
4			0.15
shoot apex located above node 5			

Shoot 2: dissected 26th October

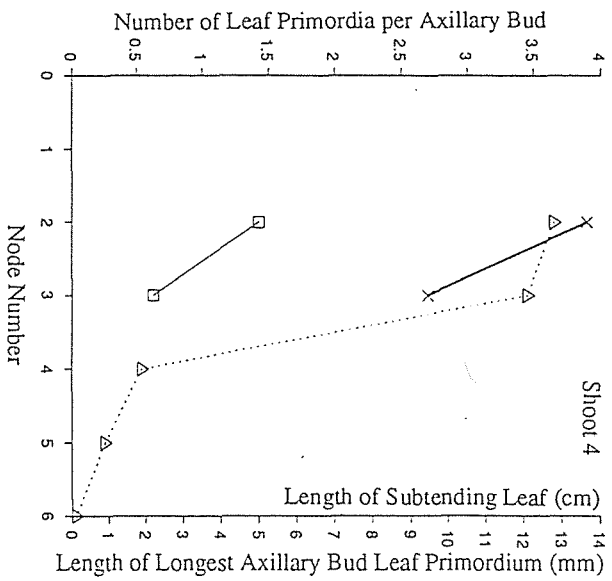
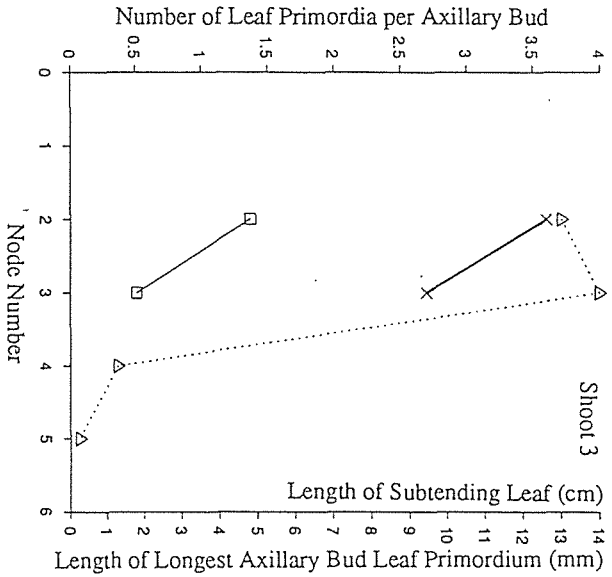
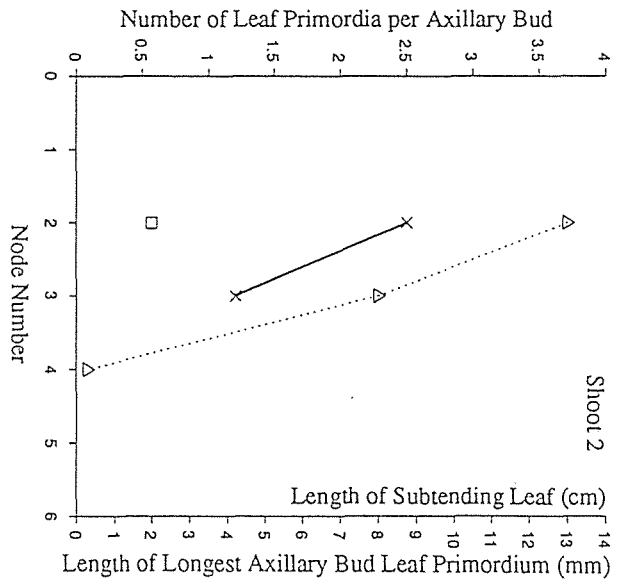
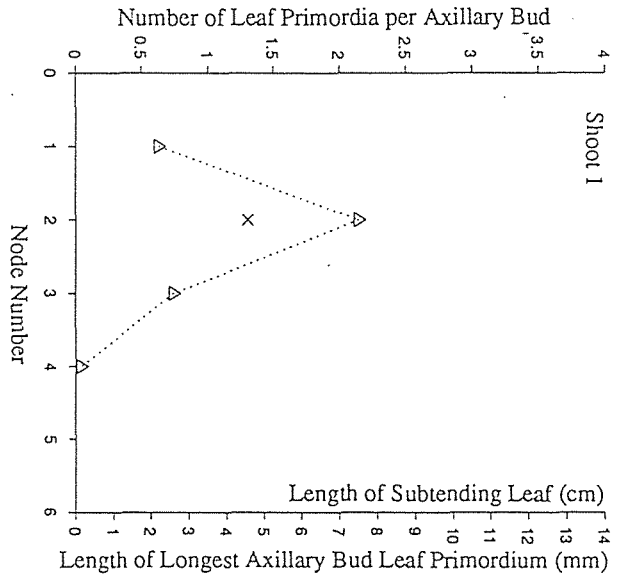
2	2.5	2.0	13.0
3	1.2		8.0
4			0.3
shoot apex located above node 5			

Shoot 3: dissected 27th November

2	3.6	4.8	13.0
3	2.7	1.8	14.0
4			1.3
5			0.26
shoot apex located above node 6			

Shoot 4: dissected 5th February

2	3.9	5.0	12.8
3	2.7	2.2	12.1
4			1.9
5			0.9
6			0.12
shoot apex located above node 6 - flowering			



Vicia faba

Dissection Results

Node No.

Primordia/Bud

Plant 1: approximately 1 cm in height1: cotyledonary node -
buds dissected from one
side in all plants

3.2	0.5	0.3	
2	4.2	2.1	0.5
3	1.3	0.5	
4	1.9	0.5	

buds not detected at nodes 5, 6 and 7; shoot apex located above node 9 - apparently flowering

Plant 2: approximately 2 cm in height

1	6.2	5.8	2.2	2.1
2	6.3	4.1	2.6	
3	4.8	3.7	0.5	
4	4.3	2.1		
6	1.2			

buds not detected at nodes 7 and 8; shoot apex located above node 13

Plant 3: approximately 30 cm in height

1	6.2	1.3	2.0	
2	6 - flowering		5 - flowering	5.2
3	4 - flowering		4.2	1.1
4	4 - flowering		4.2	1.3
5	5.3	2.2		
6	3 - flowering			
7	4.5			
8	3 - flowering			
9	2 - flowering			

buds at nodes 10, 11 and 12 flowering; shoot apex located above node 14 flowering -

Plant 4: approximately 40 cm in height

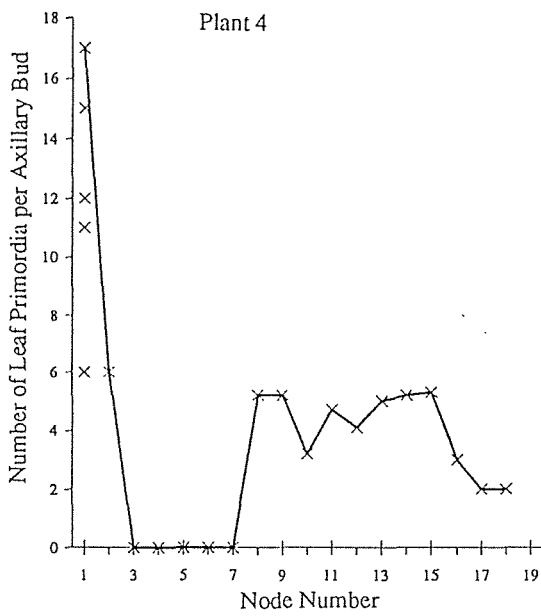
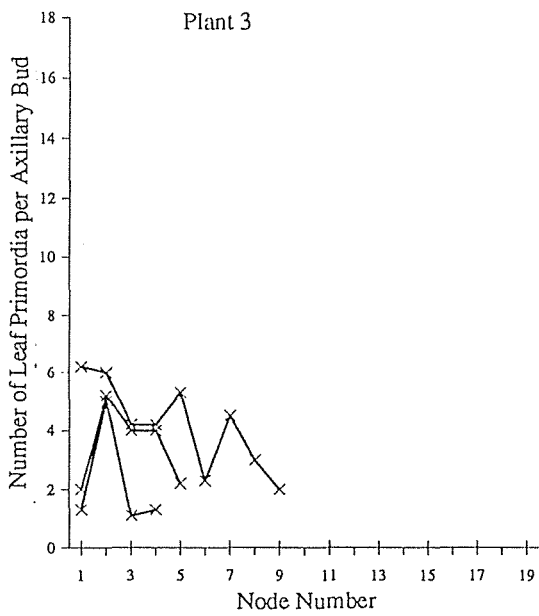
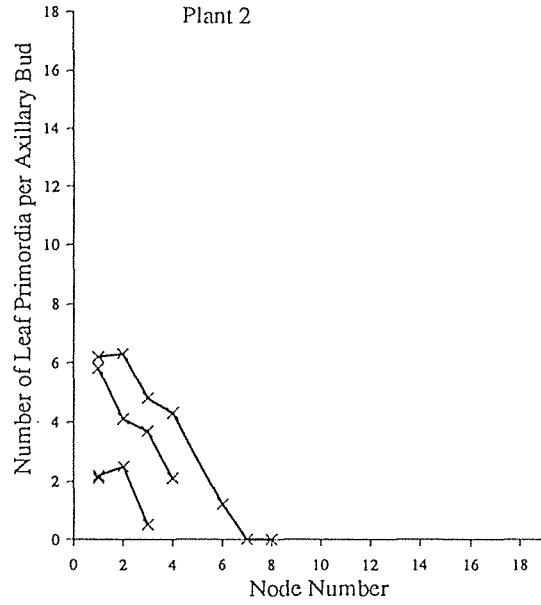
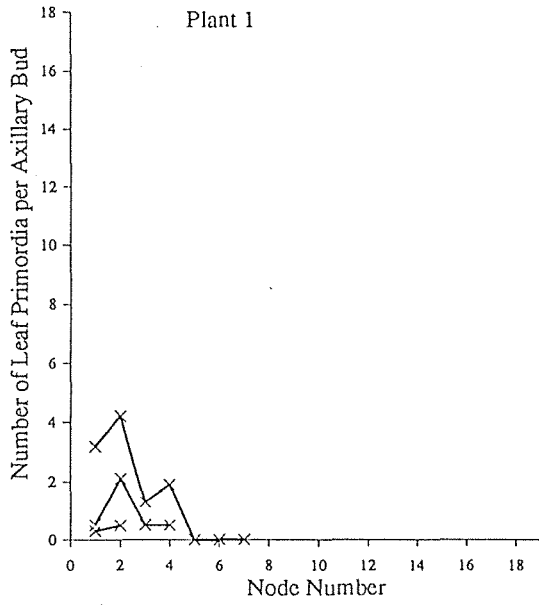
1	17, 15, 12, 11 - all flowering	6.0
2	6 - flowering	

buds not detected at nodes 3 to 7

8	5.2
9	5.2
10	3.2
11	4.7
12	4.1
13	5.0
14	5.2
15	5.3
16	3.0
17	2 - flowering
18	2.0

shoot apex located above node 18 - flowering

Vicia faba



*Vitis arnurensis***Dissection Results**

Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Subt. Leaf (cm)
----------	---------------	--------------------	------------------------

Shoot 1: dissected 2nd October

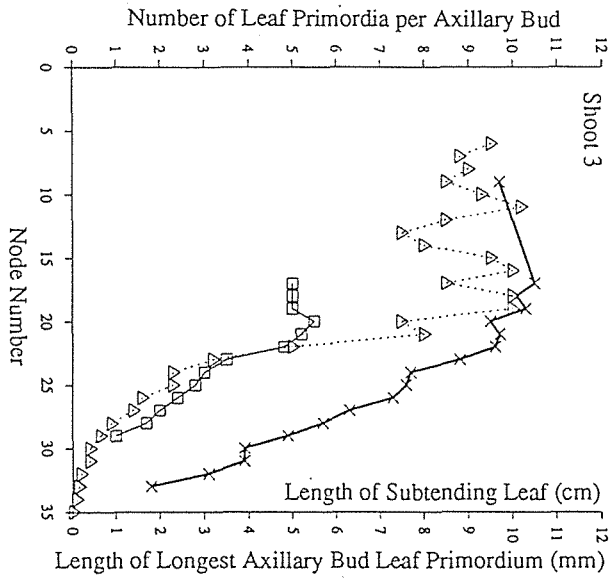
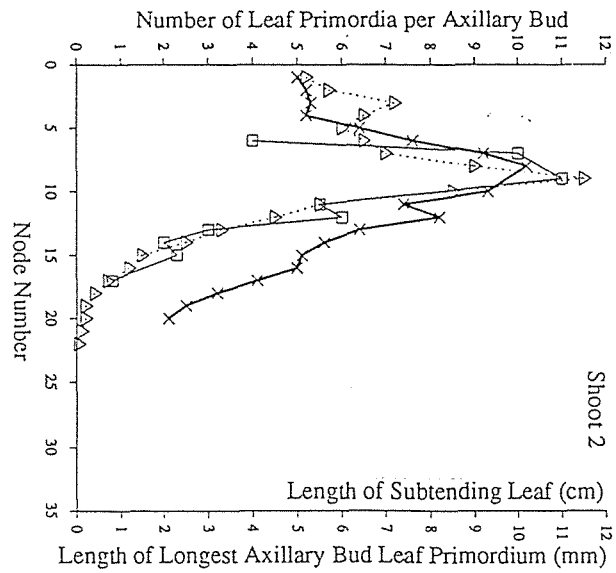
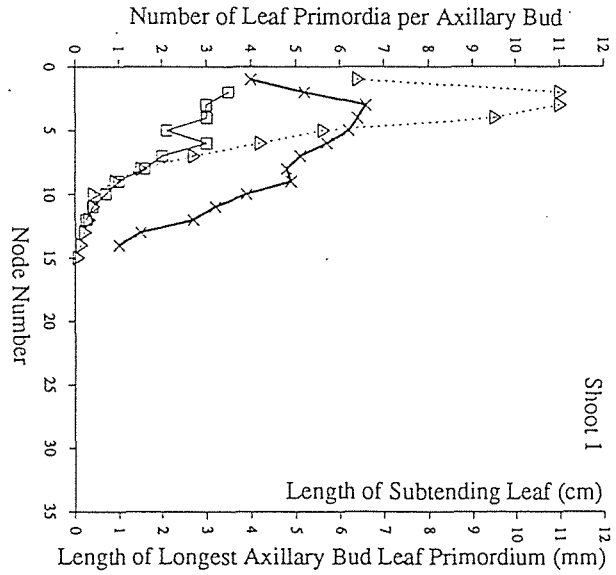
1	4.0		6.4
2	5.2	3.5	11.0
3	6.6	3.0	11.0
4	6.4	3.0	9.5
5	6.2	2.1	5.6
6	5.7	3.0	4.2
7	5.1	2.0	2.7
8	4.8	1.6	1.5
9	4.9	1.0	0.9
10	3.9	0.7	0.4
11	3.2	0.4	0.4
12	2.7	0.25	0.3
13	1.5		0.2
14	1.0		0.12

shoot apex located above node 17

Shoot 2: dissected 7th December

1	5.0		5.2
2	5.2		5.7
3	5.3		7.2
4	5.2		6.5
5	6.4		6.0
6	7.6	4.0	6.5
7	9.2	10.0	7.0
nodes 8,9 and 10: buds broken			
11	7.4	5.5	5.5
12	8.2	6.0	4.5
13	6.4	3.0	3.3
14	5.6	2.0	2.5
15	5.1	2.3	1.5
16	5.0		1.2
17	4.1	0.8	0.7
18	3.2		0.4
19	2.5		0.2
20	2.1		0.2

shoot apex located above node 25



Zea mays

Dissection Results

Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf(cm)
----------	---------------	--------------------	----------------------

Plant 1

1	bud not detected		4.0
2	2.2	0.36	15.0
3	3.1	0.38	21.0
4	1.8	0.25	17.0
5	0.2		7.5

stem apex located above node 10

Plant 2

1	bud not detected		1.1
2	6.1	0.7	9.4
3	6.1	1.0	19.6
4	6.3	0.9	31.7
5	4.1	0.4	26.0
6	1.2		12.2
7			1.5
8			0.5

stem apex located above node 13

Plant 3

3	3.2	1.0	18.0
4	8.2	1.4	32.5
5	8.3	2.0	53.0
6	8.4	2.1	69.5
7	6.2	1.6	62.0
8	5.3	1.0	46.0
9	5.0		23.0
10	4.0	0.4	6.5
11	3.0	0.1	1.6
12			0.5

stem apex located above node 16 - flowering.

Plant 4

2	4.3	1.7	0.7
3	6.0	1.8	32.0
4	8.2	3.0	50.0
5	8.1	3.5	74.0
6	10.0	5.2	77.5
7	10.0- flowering	5.0	82.0
8	9.0- flowering	6.5	69.0
9	8.0- flowering	6.0	50.0
10	0.5	0.1	32.0
11			23.0
12			16.0
13			10.5
14			4.3

stem apex located above node 14 - flowering

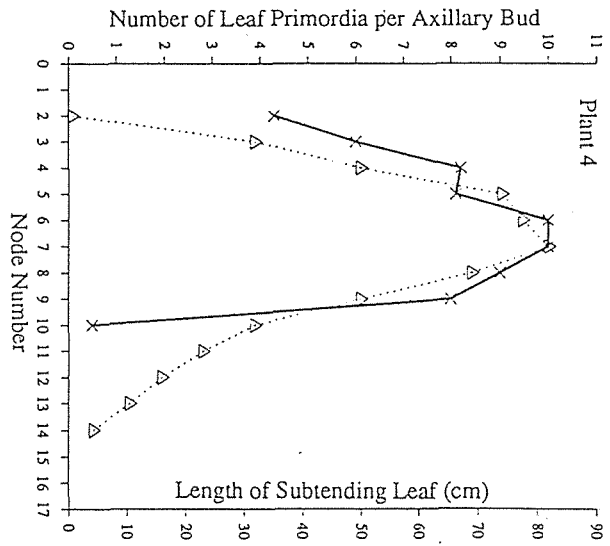
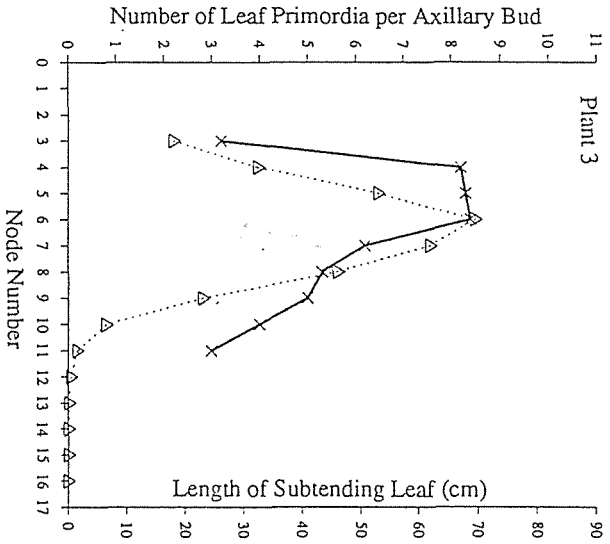
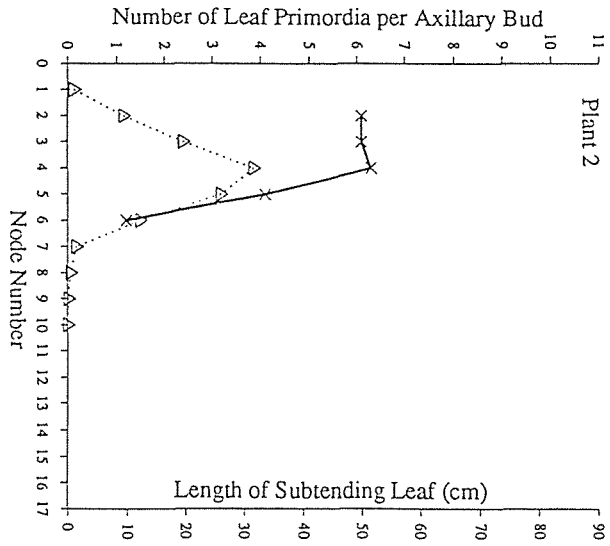
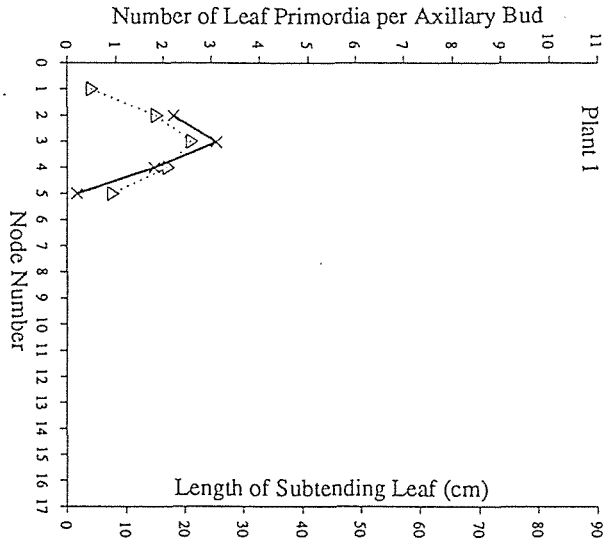
Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Subt. Leaf (cm)
----------	---------------	--------------------	------------------------

Shoot 3: dissected 25th January

nodes 1 to 8 and 10 to 16: buds broken and/or senescent

9	9.7		8.5
17	10.5	5.0	8.5
18	10.1	5.0	10.0
19	10.3 - breaking	5.0	10.0
20	9.5	5.5	7.5
21	9.7	5.2	8.0
22	9.6	4.8	5.0
23	8.8	3.5	3.2
24	7.7	3.0	2.3
25	7.7	2.8	2.3
26	7.3	2.4	1.6
27	6.3	2.0	1.4
28	5.7	1.7	0.9
29	4.9	1.0	0.65
30	3.9		0.4
31	3.9		0.4
32	3.1		0.2
33	1.8		0.15

shoot apex located above node 38



SECTION 2

Data for the four graphs in chapter 2

Data for the graph (FIG. 2.3a) relating internode length to leaf length in *Muehlenbeckia australis*.

Node	Internode Length Below Leaf (mm)	Leaf Length (mm)
2	42	60
3	45	70
4	57	72
5	60	73
6	68	65
7	65	57
8	55	52
9	60	
10	65	53
11	65	51
12	63	32
13	56	27
14	37	21
15	22	16
16	9	16
17	5	11
18	2	9
19	1	7

Data for the graph (FIG. 2.3b) relating internode length to leaf length in *Melicytus ramiflorus*.

Node	Internode Length Below Leaf (mm)	Leaf Length (mm)
2	11	115
3	8	124
4	13	110
5	13	110
6	16	135
7	11	130
8	13	126
9	15	145
10	10	128
11	13	105
12	11	96
13	7	72
14	4	63
15	1	46
16	0.5	30

Data for the graph (FIG. 2.3c) relating internode length to leaf length in *Hebe speciosa*.

Node	Internode Length Below Leaf (mm)	Leaf Length (mm)
10	10	45
11	10	48
12	11	50
13	11	55
14	11	55
15	11	55
16	9	52
17	7	44
18	5	33
19	4	23
20	3	12
21	2	7
22	1	5
23		3
24		1.2

Data for the graph (FIG. 2.3d) relating internode length to leaf length in *Passiflora mollissima*.

Node	Internode Length Below Leaf (mm)	Leaf Length (mm)
1	70	105
2	70	100
3	55	93
4	60	87
5	55	90
6	40	75
7	35	68
8	30	63
9	35	51
10	23	46
11	10	36
12	6	16
13	4	13
14	2	7
15	1	5

Data from the four experiments used as examples to show the method of calculation of axillary bud growth depression in chapter 6.

Dissection Results

Node No.	Primordia/Bud	Length 1st Pr.(mm)	Length Sub. Leaf (cm)
Shoot 1 (FIG. 6.1)			
15			8.5
16	14.5	3.8	9.0
17	14.1	3.8	9.0
18	16.7	4.0	
19	14.0	4.0	11.0
20	13.5	4.0	10.0
Shoot 2 (FIG. 6.2)			
12	11.3	3.0	14.0
13			
14			
15	11.1	2.6	13.5
16			
17			
18			
19	9.6	2.0	12.5
20	9.0	2.2	13.4
21	8.6	2.2	12.5
22	7.3	1.4	
23	5.6	0.7	
24	5.4	1.1	0.6
25	5.2	1.0	5.2
26	3.8	0.25	3.8
27	2.1	0.1	2.6
28	1.9		1.8
Shoot 3 (FIG. 6.3)			
10	12.9	3.0	12.5
11	13.0	3.1	11.8
12	12.6	4.7	10.5
13	11.3	2.2	
14	12.8	4.5	8.5
15	11.8	4.5	6.0
16	8.5	1.7	
17	10.5	3.2	9.0
18	9.7	3.0	13.5
Shoot 4 (FIG. 6.4)			
1	11.5	4.3	16.5
2	10.8	3.2	16.3
3	10.0	3.2	16.0
4	9.9	3.0	16.0
5	8.7	2.9	5.3
6	8.9	2.8	16.0
7	8.2	2.1	12.0
8	7.3	2.1	10.2
9	6.9	2.0	8.5

Bibliography

- ALI, A., FLETCHER, R.A. Hormonal Interaction in Controlling Apical Dominance in Soybeans. Canadian Journal of Botany. **49**: 1727, 1971.
- BARKER, W.G., STEWARD, F.C. Growth and Development of the Banana Plant. Annals of Botany. **26**: 389, 1962.
- BOOKER, C.E., DWIVEDI, R.S. Ultrastructure of Meristematic Cells of Dormant and Released Buds in *Tradescantia paludosa*. Experimental Cell Research. **82**: 255-61, 1972.
- CHAMPAGNAT, M. Les correlatons sur le rameau d'un a des vegetaux ligneux. Phyton. **4**: 1-102, 1954.
- CUTTER, E.G. Recent Experimental Studies of the Shoot Apex and Shoot Morphogenesis. Botanical Review. **31**: 7-113, 1965.
- CUTTER, E.G. Patterns of Organogenesis in the Shoot p.221. In Trends in Plant Morphogenesis. Edited by E.G.Cutter. London: Longmans, 1966
- CUTTER, E.G. Regulation of Branching in Decussate Species with Unequal Lateral Buds. Annals of Botany. **36**: 207-20, 1971.
- CUTTER, E.G. Plant Anatomy: Experiment and Interpretation. Part 2. Organs. London: Arnold, 1971. p.62.
- CUTTER, E.G. A morphogeneticists view of correlative inhibition in the shoot p.51-73. In The Dynamics of Meristem Cell Populations. Edited by M.M. Miller and C.C. Kuehnert. New York: Plenum, 1972.
- DORFLING, K. Uber Das Wuchsstoff-Hemmstoffsystem von Acer pseudoplatanus L. II Die Bedeutung von "Inhibitor B" fur die Korrelative Knospenhemmung und fur die Regulation der Kambiumtatigkeit. Planta **60**: 413-33, 1964.

- ESAU, K. Apical Meristems - The Origin of Branches. p.109-112. In Plant Anatomy. New York: Wiley, 1965.
- FLETCHER, G.M., DALE, J.E. Growth of Tiller buds in Barley: Effects of Shade Treatment and Mineral Nutrition. Annals of Botany. **38**: 63-76, 1973.
- FOSTER, A.S., GIFFORD, E.M. Comparative Morphology of Vascular Plants. San Francisco: W.H. Freeman, 1966 p.34.
- GOEBEL, K. Botanische Zeitung. **38**: 800, 1880.
- GOODWIN, P.B., CANSFIELD, P.E. The Control of Branch Growth on Potato Tubers. III The Basis of Correlative Inhibition. Journal of Experimental Botany. **18**: 297-307, 1967.
- GOULD, K.S., CUTTER, E.G., YOUNG, J.P.W., CHARLTON, W.A. Positional differences in size, morphology, and *in vitro* performance of pea axillary buds. Canadian Journal of Botany. **65**: 406-11, 1987.
- HALLE, F. and others. Tropical Trees and Forests. Berlin: Springer Verlag, 1978 p.43-46
- HOAD, G.V. Effect of Moisture Stress on Abscissic Acid Levels in *Ricinis communis* L. with Particular Reference to Phloem Exudate. Planta. **113**: 367-72, 1973.
- KUSE, G. Correlative growth of lateral buds in *Ipomoea batatus* shoots. Mem. Coll. Sci. Kyoto. B. **28**: 431-453, 1961.
- McDANIEL, C.N. Determination for Growth Pattern in Axillary Buds of *Nicotiana tabacum* L. Developmental Biology. **66**: 250-55, 1978.
- McDANIEL, C.N., SANGREY, K.A., SINGER, S.R. Node counting in axillary buds of *Nicotiana tabacum* cv. Wisconsin 38. American Journal of Botany. **76**(3): 403-8, 1989.

- McINTYRE, G. Environmental control of apical dominance in *Phaseolus vulgaris*. Canadian Journal of Botany. **46**: 147-55, 1968.
- MORELAND, C.F. Factors affecting development of cotyledonary buds of the common bean, *Phaseolus vulgaris*. Memoirs. Cornell University Agricultural Experiment Station. **167**, 1973.
- NAYLOR, J.M. Control of Nuclear Processes by Auxin in Axillary Buds of *Tradescantia paludosa*. Canadian Journal of Botany. **36**: 221-232, 1958.
- NELSON, T., LANGDALE, J.A. Patterns of Leaf Development in C4 Plants. The Plant Cell. **1**: 3-13, 1989.
- NEVILLE, P. Influence de la feuille, a ses premiers stades, sur la morphogenese vegetative chez *Gleditschia triacanthos* L.. Bulletin. Societe Botanique de France. **108**: 120-127, 1961.
- PHILLIPS, I.D.J. Apical dominance. Annual Review of Plant Physiology. **26**: 341-67, 1975.
- RICHARDS, J.H. Developmental potential of axillary buds of water hyacinth, *Eichhornia crassipes* Solms.. American Journal of Botany. **69**(4): 615-22, 1982.
- SACHS, T., THIMANN, K.V. The Role of Auxins and Cytokinins in the Release of Axillary Buds from Dominance. American Journal of Botany. **54**: 136, 1967.
- SAWNHEY, V.K., NAYLOR, J.M. *In vitro* studies of the dormancy of excised axillary buds of *Tradescantia paludosa*. Journal of Plant Growth Regulation. **1**: 49-59, 1982.
- SHARMAN, B.C. Leaf and Bud Initiation in the Gramineae. Botanical Gazette. **106**: 269, 1945.
- SHELDRAKE, A.R. The Production of Hormones in Higher Plants. Biological Review. **48**: 509-59, 1973.

- SNOW, M., SNOW, R. The determination of axillary buds. New Phytologist. **41**: 13-22, 1942.
- SNOW, M., SNOW, R. The dorsiventrality of leaf primordia. New Phytologist. **58**: 188-207, 1959.
- STEEVES, P.A., SUSSEX, I.M. Patterns in Plant Development. Englewood Cliffs, New Jersey: Prentice Hall Inc. 1972
- SUSSEX, I.M. Developmental programming of the shoot meristem. Cell. **56**: 225-9, 1989.
- TAMAS, I.A., SCHLOSSBERG, J.L. Hormonal control of axillary bud growth in cultured stem segments of *Phaseolus vulgaris* L.. Horticultural Science. **17**: 484, 1982.
- THIMANN, K.V., SACHS, T., MATHUR, S.N. The mechanism of apical dominance in *Coleus*. Physiologia Plantarum. **24**: 68-72, 1971.
- THIMANN, K.V., SKOOG, F. Studies on the Growth Hormone of Plants. III. The Inhibiting Action of the Growth Substance on Bud Development. Proceedings of the National Academy of Science, U.S.A. **19**: 714-16, 1933.
- THIMANN, K.V., SKOOG, F. On the Inhibition of Bud Development and other Functions of Growth Substances in *Vicia faba*. Proceedings of the Royal Society B. **114**: 317-39, 1934.
- TUCKER, D.J. Apical dominance in the "Rogue" tomato. Annals of Botany. **41**: 181-90, 1976.
- TUCKER, D.J., MANSFIELD, T.A. A discussion in relation to current hypotheses of correlative inhibition. Journal of Experimental Botany. **24**: 731-40, 1973.
- WARDLAW, C.W. Preliminary observations on the Development of Buds on the Rhizome of *Matteuccia struthiopteris* Tod.. Annals of Botany. **7**: 171-84, 1943.

- WARDLAW, C.W. Experimental observations on the Development of Buds in *Onoclea sensibilis* and in Species of *Dryopteris*. Annals of Botany. **7**: 357-72, 1943.
- WARDLAW, I.F., MORTIMER, D.C. Carbohydrate movement in pea plants in relation to axillary bud growth. Canadian Journal of Botany. **48**: 229, 1970.
- WAREING, P.F., SAUNDERS, P.F. Hormones and Dormancy. Annual Review of Plant Physiology. **22**: 261-88, 1971
- WENT, F. Experiments on bud growth. American Journal of Botany. **26**: 109-17, 1939.
- WETMORE, R.H., GARRISON, R. The Morphological Ontogeny of the Leafy Shoot. p.187-99. In Trends in Plant Morphogenesis, edited by E.G. Cutter. London: Longmans, 1966.
- YUN, K.B., NAYLOR, J.M. Regulation of cell reproduction in bud meristems of *Tradescantia paludosa*. Canadian Journal of Botany. **51**: 1137-1145, 1973.
- ZAMSKI, E., SCHLOMIT OSHRI, ZIESLIN, N. Comparative morphology and anatomy of axillary buds along a rose shoot. Botanical Gazette. **146**(2): 208-212, 1985.