FLOWER-BUD INITIATION IN DECIDUOUS FRUIT TREES WITH PARTICULAR REFERENCE TO APRICOT

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CHAPTER I

INTRODUCTION

'Who, of men, can tell
That flowers would bloom ....' Keats.

In this thesis the author has two aims: (a) to review the literature on flowering in deciduous fruit trees, and (b) to record and discuss, in the light of previous work, experiments designed to elucidate the role of carbohydrates, and the possible role of hormones, in the process of flower-bud initiation in apricot (Prunus armeniaca, L.). The experiments were conducted over the period December, 1968, to February, 1970.

The review is more detailed than may be required for an introduction to the experimental section. This is because most previous work on flower-bud initiation in deciduous fruit trees was carried out some time ago, and there are no recent large reviews on the subject. The review also illustrates how little is known on the process in stone fruits, as most investigations have centred on initiation in apple.

The author in the experimental section has looked at the following factors affecting flower-bud initiation in apricot: shading, defoliation, temperature, light, level of carbohydrate metabolites, level of nitrogen compounds.

In further experiments the herbicide diuron (DCMU) was used to inhibit photosynthesis and so determine the importance of leaf-produced carbohydrates on initiation of flower-buds in the axil of that leaf. The isotope Carbon-14 was also used to substantiate the results of

diuron treatment and to demonstrate translocation patterns within the apricot tree.

The experimental results are not recorded chronologically but appear in the following order:

PART 1: Determination of the importance of shading and defoliation on flower-bud initiation in apricot.

PART 2: The role of temperature and light in flower-bud initiation in apricot.

PART 3: The role of carbohydrates in flower-bud initiation in apricot.

CHAPTER II

REVIEW OF THE LITERATURE

SECTION 1

I. INTRODUCTION

Induction of flower-buds in deciduous fruit trees begins soon after the leaves are formed, and development of these buds continues throughout the growing season and possibly during the winter months (Davis, 1957). In this review and indeed throughout this thesis the processes of induction and development will be termed initiation. Initiation in the following deciduous fruits will be discussed: pome fruits (apple and pear) and stone fruits (cherry, plum, apricot, peach and almond).

During the growing season of these trees, buds are produced at shoot tips (terminal buds), and/or in the axils of leaves (lateral or axillary buds), on shoots and spurs. A bud is considered terminal if more than one leaf scar is found at its base (Gourley and Howlett, 1946).

Leaf or vegetative buds are those from which only a branch or spur may grow, and are often slender and pointed. Flower buds which are frequently borne on very short branches called fruit spurs, tend to be rather plump and rounded, contain the unopened flower(s) and may contain leaves. A bud is termed simple if it contains only leaves or flowers, and mixed if it contains leaves and flowers. Simple buds borne laterally on new shoots and to varying extents on spurs, are found on apricot, plum, peach, cherry and almond. Mixed buds, as on apples and pears, may be lateral on shoots, but more frequently are found terminally on shoots or spurs.

Mixed buds characteristically give rise to a leafy axis with a single flower (quince) or a cluster of flowers (apple and pear) at its apex. From simple buds, one flower (peach, apricot and almond), one to three flowers (plum), or more than three flowers (cherry), arise from a single bud. There are no leaves associated with the flowers of simple buds although the bud scales may expand and persist as in cherry (Chandler, 1957).

II. GROWTH AND FRUITING CHARACTERS OF THE APRICOT

The apricot characteristically produces branch growth as a series of growth "flushes" (Chandler, 1957). In Canterbury strong shoots usually make two flushes of growth, whereas Jackson (1968) reports that several flushes commonly occur on apricot trees grown in Auckland.

After each growth flush the apex stops producing leaves, yellows, and finally abscisses just above a leaf. A temporary resting bud develops at the apex (Jackson, 1968) in the axil of this apical leaf. This distal bud although terminating the shoot is not a true terminal bud but is axillary and continues the growth of the branch (Gourley and Howlett, 1946; Chandler, 1957).

In apricot, flower buds are borne singly, or in groups of two or more, surrounding a leaf bud at each node, on current season's growth. Sometimes flower-buds form quite numerously on shoots in which the internodes are short and the shoot is known as a fruit spur (Gourley and Howlett, 1946), perhaps one to ten inches long (Chandler, 1957).

Bud initials can be detected by eye at about the completion of internode elongation although, at this stage, it is impossible

to determine the difference between flower and vegetative buds (Jackson, 1968). Of the usual three buds in the leaf axils, the central bud is usually vegetative (Knapp and Auchter, 1950; Vjunov, 1957), and develops first while the parent shoots are still actively growing (Vjunov, 1957). The side buds develop later, and differentiate into flower buds if conditions are suitable (Vjunov, 1957). In unfavourable conditions the initials may fail to develop into floral buds and remain dormant.

III. THE PROCESS OF FLORAL INITIATION

The process of floral initiation involves a change in the character of cells proliferating in the meristematic tissue of the shoot. Consequently floral initiation requires specific changes in gene function, either stimulation of certain passive genes or selective inactivation of gene repressors at appropriate times and loci on the desoxyribonucleic acid (DNA) chain (Searle, 1965).

In many plants the reproductive buds are thought to be differentiated from vegetative buds (Gardner, 1966; Romberger, 1967; Turner, 1968). Alternatively vegetative and floral buds may arise separately from undifferentiated tissue. The work of Brooks (1940) in the almond has shown that the carpel (pistil) is not derived from cell layers in the bud that produce the leaf. He found that before any evidence of floral tube formation shows, the apex of the almond flower bud has only two parallel layers of cells while the leaf bud has four.

Fulford (1966) working with apples puts forward the interesting view that the meristem will always form a flower, unless it is prevented from doing so, and that the vegetative phase of development

is the period when successive obstacles to flowering are formed and overcome as the meristem grows.

The flower has been considered to be a modified shoot and the flower parts homologous with leaves (Chandler, 1957). However as Brooks (1940) has warned, perhaps it is not justified to think that the carpel or any other flower part is a modified leaf but only that, like the leaf, it develops from apical meristem.

Once the flower primordia are initiated, differentiation into the various floral parts takes place. Typically, the development of the floral organs is acropetal. Thus their order of development is calyx (sepals), corolla (petals), stamens and pistils (carpels). As the pistils develop, the ovarian cavity is formed. This contains the placentae on which the ovules are borne.

IV. TIME OF FLOWER-BUD INITIATION

Vegetative growth produced during the fruit trees' first years in the orchard is typified by strong shoots, long internodes and often the production of a large number of leaves. Production of this vegetative growth is often extended throughout the growing season in young trees and seems to restrict the number of flower-buds formed. However stone fruits are less affected, and peach may form a considerable number of flower-buds on strong succulent shoots in the second year (Chandler, 1957).

As the trees mature the period of shoot growth is reduced in time with each succeeding year and the trees begin to form flower-buds in greater abundance. This stage is reached within one to four years in stone fruit (earliest in peach, latest in almond) and may

take up to six years in pome fruit. Production of numerous flower-buds for the very first time can be promoted by selection of a dwarfing root-stock which reduces tree vigour (Gardner, 1966), or delayed by pruning practices (Magness, 1917; Magness et al. 1918; Ionova, 1960), by nitrogen manuring and by irrigation practices (May and Antcliff, 1964), all of which may encourage vegetative growth.

Climate may also influence the ability of a fruit tree to come into bearing and its subsequent seasonal fruiting behaviour (May and Antcliff, 1964). Often climate may be responsible for small variations in the time of flower-bud initiation from one season to the next once the tree has settled down. Cloudy dull weather for instance in spring and early summer may delay initiation because of reduced food formation (carbohydrates) in the tree (Chandler, 1957).

Brown (1952) working with apricots found that prolonged periods of dry soil conditions reduced the period of time for flower-bud initiation to occur on these trees.

The annual commencement of flower-bud initiation often depends upon the growth stage of the tree (Davis, 1957), the size of the current season's crop (Barnard, 1938; Davis, 1957), and the stage of growth of the particular shoot on which buds will form (Dorsey and Knowlton, 1925; Micklem, 1938). Goff (1899, 1900, 1901), Swarbrick (1928), and Barnard (1938) working on apple and Barnard and Read (1932-1933) observing pears, plums and apricots, were all of the opinion that flower-buds began initiation about the time when shoot growth ceased. Goff (1901) suggested that the energies of the tree were used for vegetative growth until cessation of shoot growth, after which, they were available for

the formation of fruit-buds.

Chandler (1957) in a further attempt to relate time of flower-bud initiation to some stage of growth, has stated that in pome fruit and stone-fruit trees, flower initiation is near the time when the leaf that subtends these apical and axillary meristems becomes full grown.

V. THE ROLE OF THE SUBTENDED LEAF, AND THE EFFECT OF DEFOLIATION ON FLOWER-BUD FORMATION

Fulford (1966) found that initiation of apple flower-buds was promoted by mature leaves. Heinicke (1966) considers that the ability of lateral buds in apple to develop and in some cases become flower-buds is determined to a great extent by the subtended leaf. Buds in the axils of very small mature apple leaves usually remain small and dormant, or give rise to weak spurs. Conversely large mature leaves usually have in their axils well-developed floral and vegetative buds (Heinicke, 1966).

In several fruit trees, including apples, plums, apricots and the mango (Mangifera indica), removal of leaves, either mechanically or by chemical treatment, results in a failure of flower-bud initiation (Magness, 1917; Roberts, 1923; Swarbrick, 1928; Swarbrick and Naik, 1932; Harley et al. 1942; Reece et al. 1946; Singh, 1948; Fulford, 1960). Conversely, maximum leaf area near the bud favours flower-bud initiation (Swarbrick and Naik, 1932; Haller and Magness, 1933; Fulford, 1962).

Magness (1917) in extensive defoliation studies on apple found that leaf area in one part of the tree will not usually supply

food material to the buds of another part to the extent necessary to cause them to produce fruit-buds. Defoliating one half of a tree had little influence upon the undefoliated portion. The defoliated portion functioned as it would if all the leaves were removed from the whole tree.

These earlier studies on the effects of defoliation on flower-bud initiation in fruit trees were interpreted solely in terms of nutrient supply. However the role of hormones such as auxins and gibberellins in initiation is well established for many plants and it could well be they are of importance in fruit trees. Since leaves are known to be sites of auxin and gibberellin synthesis (Lang, 1965) defoliation effects must also be interpreted in terms of the effect on hormone supply.

SECTION 2

I. FACTORS INFLUENCING FLOWER-BUD FORMATION IN DECIDUOUS FRUIT TREES

These factors can be classified into three broad groups, namely, hormonal, nutritional and cultural.

1. Hormonal factors

a) The photoperiodic response:

The fact that flower-bud initiation in the common deciduous tree fruit species occurs during the summer months has suggested to some workers that these species require long days (LD.) for initiation.

Experimental evidence however, indicates that length of the daylight period does not seem to be an important factor in flower-bud formation in apple (Hoyle, 1955 and Gorter, 1955) or peach (Piringer and Downs, 1958). Wareing (1968) also reports that our common fruit trees, apples, plums, cherries, are relatively insensitive to day length. However long days may be a little more conducive to abundant flower-bud initiation than shorter days, possibly because the longer daylight may cause accumulation of more carbohydrates (Chandler, 1957). A high rate of photosynthesis (Heinicke, 1965) and long days (Gorter, 1965) have both been found to stimulate apple flower-bud initiation presumably to some extent because of carbohydrate build-up. Furthermore Jackson (1968) found that flower-bud initiation in apricots was reduced by low light intensity.

b) Formation of the flowering hormone:

In long-day and short-day plants, the leaves are the organs which receive the photoperiodic stimulus (Knott, 1934; Moshkov, 1937).

In work on fruit trees Harley et al. (1942) concluded from a number of defoliation and leaf/fruit adjustment studies that there was some specific factor responsible for the formation of flower primordia, probably a product of leaf metabolism. They proposed that this factor might resemble a hormone substance and so were one of the first to propose a hormonal control of flower-bud initiation in fruit trees. They reached three important conclusions. Firstly that there is a quantitative relationship between leaf area and blossom bud development; secondly that the movement of the flower-producing substance is away from the bud until the requirements of other tissues have been met; and thirdly that the active amount of leaf area needed to form the flower-producing substance appears to vary with the variety.

It is now generally believed that in fruit trees as in photoperiodic plants a flowering hormone is received by the bud (Chandler, 1957). The existence of this flowering hormone in fruit trees is purely conjecture at the present time, for the identification of such a hormone has not yet been determined in any plant. However the flowering stimulus has been found to be readily transmissible across a graft union in many herbaceous plants (Wareing, 1967), in black currant (El-Antably, 1965) and along connecting stolons in strawberry (Guttridge, 1959), and the occurrence of this transmissible flowering stimuli is not confined to photoperiodic plants (Hillman, 1964). Lang (1952) has reviewed work which shows that day neutral plants can serve as donors of a flowering stimulus to closely related long-day and short-day plants.

Thus the flowering process in day neutral plants such as deciduous fruit trees differs only in that the flowering hormone can be formed under any day length.

c) Effect on flower-bud initiation of other hormones:

Whether a specific flower hormone is active in woody plants such as fruit trees is unknown. However the identified hormones, auxins and gibberellins, have important effects upon flowering in such plants. Gibberellic acid for example, has been shown to completely inhibit flowering in apple (Guttridge, 1962; Marcelle and Sironval, 1963), pear (Griggs and Iwakiri, 1961; Wareing, 1967) and peach (Hull and Lewis, 1959; Stuart and Cathey, 1961) and to partially inhibit flowering in cherry (Hull and Lewis, 1959). Similarly Bradley and Crane (1960) found that development of both floral and vegetative buds was inhibited by applications of gibberellin to branches of Prunus. Higher concentrations were required to inhibit vegetative than reproductive buds. Gibberellic acid also inhibits flower formation in strawberry (Thompson and Guttridge, 1959).

The effect of auxins on floral bud development is poorly documented although promotion of flowering is reported when auxin is applied to pineapple and litchi (Audus, 1965). This appears an indirect effect in that the primary action of auxin in these plants appears to be to reduce vegetative growth and so allow conditions to be more conducive to flowering. In other work Hitchcock and Zimmerman (1943) found that in apple, pear, cherry, peach and plum a summer or early autumn spray of NAA delayed bud burst by up to fourteen days for flower buds, and up to nineteen days for leaf buds in the following spring.

d) Effect of growth inhibitors on flower-bud initiation:

Growth inhibitors have been found to accelerate the time of flower-bud initiation in woody plants (Cathey, 1964) and to increase

the number of flower buds when applied to apples and cherries (Batjer, Williams and Martin, 1964), peaches (Sloane, 1968) and also pears (Modlibowska, 1965). How these effects of inhibitors on flower-bud initiation actually occur can be interpreted in several ways.

Kende, Ninnemann and Lang (1963) suggested that the action of growth retardants on plants was to inhibit the biosynthesis of endogenous gibberellin. Since gibberellin is inhibitory to flowering in many fruit trees the retardants naturally enhance flowering by firstly reducing gibberellin levels, which results in reduced vegetative growth and so more metabolites are available for flower-bud development.

The suggestion of Kende et al. has been demonstrated by Dennis, Upper and West (1965). They found that the principal enzymic site of inhibition of gibberellin biosynthesis by growth retardants Amo-1618* and Phosfon**, was at the site of (-)-Kaurene formation. (-)-Kaurene is a known precursor for gibberellin synthesis (Geissman, Verbiscar, Phinney and Cragg, 1966). The growth retardant CCC*** also inhibits gibberellin biosynthesis, but this inhibition occurs beyond (-)-Kaurene formation (Dennis, Upper and West, 1965). Luckwill (1968) supported this evidence in tests with CCC, which he found inhibited gibberellin synthesis in young expanding apple leaves near the apex.

Alternatively the inhibitors may promote flower-bud initiation by just changing the hormonal balance between natural inhibitors and endogenous gibberellins. Wareing favours this interpretation and found evidence to support his view in work on black currants

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* Amo-1618 is a quaternary ammonium salt of piperidine carboxylate.

** Phosfon is a chlorinated phosphonium salt.

*** [(2-Chloroethyl) trimethylammonium chloride]

(Wareing, 1968). He found that when CCC is applied to this plant, it not only causes a decrease in the level of endogenous gibberellin, but also an increase in endogenous inhibitor, i.e. the effect of CCC is on endogenous hormone levels. This situation may also apply when growth inhibitors are applied to fruit trees.

The simplest explanation of this inhibitor promotion of flower-bud development is that the inhibitor retards vegetative growth; such growth being naturally antagonistic to fruit-bud differentiation. In work on pears Brooks (1964) found that the retardant B 995* stimulated flowering. He attributed this stimulation to the effects B 995 had on the growth of the pear tree. B 995 characteristically reduced terminal growth and stimulated the formation of spur-type growth. In pears most of the flower buds tend to be terminal on spurs or spur branches (Chandler, 1957). Similar results have been obtained by Edgerton and Hoffman (1965) when B 995 was applied to apples.

A further interpretation which may possibly be given is that the inhibitor directly stimulates floral-bud formation. However there is no evidence to support such a simple interpretation. Cathey (1964) is of the opinion that growth retardants promote flowering by modifying activity in the cambium. This results in abnormal types of cells in the xylem and the disappearance of sclerenchymatous cells adjacent to the cortex. The restriction of growth as a result, presumably alters the metabolism and creates conditions conducive to flower initiation.

Another type of inhibitor found to reduce shoot growth and

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* B 995 is N-dimethyl amino succinamic acid

promote flower-bud formation is TIBA*. Greenhalgh (1965) greatly increased initiation in apples after he had applied TIBA to three-year old trees. TIBA reduces the amount of mobile auxin available for transport in the plant (Winter, 1967) and inhibits auxin (Winter, 1967) and other energy dependent transport systems directly (Libbert, 1959).

e) The rest period:

The rest period which is caused by internal factors in the plant can be defined as the period when the plant will not grow, even though environmental conditions are favourable (Samish, 1954). It usually extends from cessation of terminal growth in mid summer or autumn until sufficient chilling has occurred to counteract these restricting factors. Dormancy on the other hand refers to the condition of the bud when internal or external factors prevent growth. This condition generally applies during the period from cessation of terminal growth until bud break in early spring (Dennis and Edgerton, 1961). During the rest, flower initials develop slowly in the bud.

Growth in deciduous fruit trees is inhibited until the tree has been exposed to a certain number of hours at temperatures of $45^{\circ}F$ or lower (Chandler, 1957). More specifically Chandler et al. (1937) noted that if there are not at least two months during which the temperature averages below $48^{\circ}F$, opening of the buds will be considerably delayed, and buds will open unevenly.

Varieties vary in their requirements, but often between 1,000-1,400 hours of low temperatures are needed to enable the leaves and flowers to open satisfactorily from the buds in spring. The

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* 2,3,5-tri-iodobenzoic acid

peach and apricot require at least 1,000 hours at temperatures below 45°F. In peach, if the temperature never falls below 49°F the trees are slow to flower and to come into leaf (Hockings, 1961).

On trees of some species, especially the apricot, the flower buds may nearly all fall off during late winter or early spring if there has been too little weather below 40-45°F after leaf fall. In species with mixed buds like those of the pear, all of the flowers in a bud, or some of them, may die so that it opens only into a leafy spur, or a reduced number of flowers and a leafy spur, if winter chilling has been insufficient (Chandler, 1957).

Overcash and Campbell (1955) found whilst working with peaches, that continuous chilling was more effective in breaking the rest than exposure to intermittent cold.

The responses to chilling is received by the buds of the tree (Kramer and Kozlowski, 1960) and both vegetative and floral buds require chilling to break the rest period (Weinberger, 1950). Frequently there can be a difference in chilling requirements between flower and leaf buds within the one variety, with vegetative buds usually having the higher requirements for chilling (Weinberger, 1950).

The growth inhibitor naringenin which has been found in peach buds is present in low amounts during late summer and autumn, but rises to very high levels in mid winter during rest and dormancy. As the season advances and dormancy is broken the quantity of the inhibitor falls to a minimum by spring (El-Mansy and Walker, 1966). Blommaert (1958) and Hendershott and Bailey (1955) found that the inhibitor content of peach buds dropped as dormancy was broken. As it dropped more rapidly in buds subjected to relatively cold

dormant periods as compared with relatively warm dormant periods, Blommaert felt this suggested that adequate cold stimulated inactivation of the inhibitor.

The studies of Hendershott and Bailey (1955), Blommaert (1958), and El-Mansy and Walker (1966) are quite pertinent in that they relate the inhibitor level to the state of dormancy not rest. Dennis and Edgerton (1961) likewise in their work on peach, found that the inhibitor was related to dormancy, rather than rest. Remembering the definition of dormancy this inhibitor could be the internal factor of dormancy and its formation could be controlled by a daylength cue, the external factor of dormancy. Perception of short days by plants are known to stimulate the synthesis of endogenous growth inhibitors (Kawase, 1961; Cornforth et al. 1965).

In comprehensive studies on flower-bud break in peach, Hendershott and Walker (1959), Erez, Samish and Lavee (1966), and Erez and Lavee (1969) found that auxins, flavonoid compounds, such as naringenin and prunin (naringenin 7-glucoside), and gibberellic acid all took part in the dormancy breaking and bud opening metabolism. This is in agreement with the work of Hendershott and Bailey (1955) who found that an increase in auxin activity accompanied the decline in inhibitor in peach; with the work of Walker and Donoho (1959) who found that gibberellic acid broke the rest period of peach trees, but failed to do so in young apple trees; and with the work of Phillips (1962) who found that naringenin inhibited the dormancy breaking effect of gibberellin in peach buds.

The situation in peach buds may be indicative of the complex interrelationship between growth inhibitors and growth promoters

which probably occurs in all buds of deciduous fruit tree species during this rest period. The inhibitor may be naringenin, abscisic acid or coumarin, the growth promoter an auxin, a gibberellin or even a cytokinin. Whatever endogenous compounds are involved, it is as Dennis and Edgerton (1961) and Wareing (1967) have proposed a delicate balance between inhibitor and promoter which may decide the fate of the bud. For rest to be broken in floral buds, the inhibitor must be broken down by low temperature. For vegetative buds, a chilling requirement and possibly a light requirement are required for rest to be broken (Erez, Samish and Lavee, 1966). Since leafless dormant stems of fruit trees are light perceptive organs (Erez, Samish and Lavee, 1966), phytochrome would appear to be involved in the breaking of the rest period with light transferring the phytochrome pigment to the far-red form and so allowing bud burst (Erez, Samish and Lavee, 1966).

2. Nutritional factors

a) The level of carbohydrates:

In deciduous fruit trees, namely apple, high levels of carbohydrates have been found to be conducive to flower-bud initiation (Swarbrick, 1927; Haller and Magness, 1933; Davis, 1957; Fulford, 1962). These high levels are associated with maximum leaf area, high rates of photosynthesis and declining vegetative growth of the tree (Chandler, 1957). Such practices as stem girdling, grafting onto weak rootstocks, tying stems into a knot, and restricting root growth by pruning or cultivation in pots, are practical techniques which achieve this high level of carbohydrates within the

tree (Doorenbos, 1968).

Under long-day conditions the level of carbohydrates can be expected to be high. In apples a high rate of photosynthesis (Heinicke, 1965) and long days (Gorter, 1965) stimulated flower-bud initiation. However the rate of photosynthesis can vary greatly from one leaf to another along a shoot of apple (Heinicke and Hoffman, 1933). The size of the leaf will also determine to some extent the level of carbohydrates available to the axillary bud. Large leaves are more conducive to floral initiation compared with small leaves (Heinicke, 1967), and Davis (1957) found that a minimum number of leaves/bud are required to initiate flowers on spurs in apples and cherries.

The stage at which leaves export carbohydrates varies with different species. ^{14}C-translocation pattern studies on peach and apricot revealed that the leaves in this case begin to export before they were fully expanded (Kriedemann, 1968).

b) The level of nitrogen:

If the nitrogen supply to a tree is very low, flower buds will not form (Chandler, 1957).

Under normal conditions of light and water supply, nitrogen will promote flower-bud initiation in deciduous fruit trees (Bradford, 1924; Boynton, 1954; Chandler, 1957; Williams, 1963). However Chandler (1957) thinks that heavy applications of nitrogen may sometimes reduce flower-bud production because of increased use of carbohydrates in growth.

Much of the nitrogen of fruit trees is a major constituent of protoplasm and physiologically active compounds such as enzymes, vitamins and nucleic acids. Thus the tissues in flower and vege-

tative buds in the cambium and in root and stem tips are rich sources of nitrogenous compounds (Kramer and Kozlowski, 1960). High levels of nitrogen also occur in leaves (Oland, 1960).

In autumn, fruit tree roots accumulate high quantities of nitrogen which aids flower-bud initiation, bud development during the winter, and flowering the following spring (Taylor, 1967). Davis (1931) and Oland (1957) also found that the first growth in spring utilizes stored nutrients including nitrogen and that it is not necessary for the fruit tree to draw on the soil supply at this time.

Although the supply of nitrogen is particularly important in the late summer to autumn period, Delap (1967) found that nitrogen applied anytime throughout the season increased the number of flower buds per unit length of shoot.

Harley et al. (1942) found that the early leaf area relative to the size of the developing crop, is of particular importance in determining flower initiation. Thus nitrogen in influencing the development of a large and efficient leaf surface prior to the time of flower formation would influence such initiation.

Heinicke (1934) has proposed that the beneficial effects of nitrogen at some stages of growth may be quite indirect. He found that a late application of nitrogen to apples caused leaves to carry on photosynthesis later in the autumn, building up a higher carbohydrate reserve in the trees.

Finally, Hill-Cottingham and Williams (1967) have suggested that nitrogen stimulates the synthesis of a kinin-like factor in the roots, and that the difference in response to applications at different times depends upon the stage of development of the flower-buds when the factor reaches them.

c) The carbon/nitrogen ratio:

The carbohydrate/nitrogen ratio theory suggested by Kraus and Kraybill in 1918 states that the initiation of flowering is attributed to the attainment of a certain balance between the carbon and nitrogen nutrition of the plant. The theory was based on the result of experiments carried out on the nutrition of tomatoes. An abundance of nitrogenous manures greatly lowered the fruitfulness of these plants and, when coupled with conditions favouring active manufacture of carbon compounds in the leaves, gave rise to lush vegetative growth. When the supply of nitrogen was lowered, while maintaining a high level of carbon nutrition, there resulted plentiful fruiting and reduced vegetative growth, while low levels of both carbon and nitrogen nutrition, as would be expected, greatly reduced both vegetative and reproductive growth.

Although this theory has been widely accepted and has been used to justify many cultural practices, evidence for its application to deciduous fruit trees is lacking. Indeed Potter and Phillips (1927) found that flower-bud initiation in fruit spurs was more closely related to the amount of nitrogen than to any ratio between this element and carbohydrates.

d) General nutrition:

Although the role of other elements in the process of flower-bud initiation has received little study, reduced flower initiation has been observed under zinc (Boynton, 1954) or copper (Wallace, 1961) deficiency in apples and pears.

The level of calcium in the plant is also important as cell division is affected if it is deficient (Meyer, Anderson and Bohning,

1960). Perfil'ev (1962) found a positive correlation existing between the comparative content of calcium in the ash of apple shoots and formation of fruit buds on those shoots.

Eguchi et al. (1958) studied the response of some photoperiodic, vernalizable and day neutral plants to levels of nitrogen and phosphate nutrition. The authors proposed that flowering in many day neutral plants is far more dependent upon nutrition than it is in photoperiodic or vernalizable plants, in which the environmental requirements have been satisfied.

3. Cultural factors

a) The effect of shading on flower-bud initiation:

The problem of shading in fruit trees is a cultural one for within the canopy of any tree there are leaves which receive limited sunlight. In apples, Heinicke (1966) found that two zones, a high light intensity zone of 6,000-11,000 foot candles and a low intensity zone of 400-700 foot candles exists within the canopy of the tree. Judicious pruning can eliminate some of this natural shading but the trend in recent times towards hedge-row plantings of fruit trees has only increased the problem.

Dense shade over the tree reduces photosynthesis and reduces the levels of cellulose and stored carbohydrates. Shade therefore has the effect of increasing the relative percentage nitrogen in the tree, that is relative to the carbohydrate level (Chandler, 1957).

Kraybill (1923) found that shading reduced flower-bud formation in apple and peach. Likewise, Auchter et al. (1926) found that shading of apple during the whole season practically prevented

any blossom-bud formation, even though no crop was borne in that season. During a second season of shading no blossom-buds were formed. They also found that even five weeks of shading in the spring seemed to decrease the number of blossom-buds formed. Later work by Paddock and Charles (1928) suggested that the crucial period for the inhibition of floral-bud initiation by shading was within two weeks after such initiation.

In work on apricot, Jackson (1969) found that shading promoted branch growth by increasing internode length but had little effect on the number of nodes, and as expected initiation of flower-buds was suppressed.

The effects of shading on bud initiation appear to be well documented, but any effects on endogenous hormone levels in fruit trees have not as yet been published. However it is known that light can affect the level of gibberellins and auxins in other plants, so a similar situation could occur in fruit trees. For instance on the evidence obtained by Chailakhyan and Lozhnikova (1964) and through more precise chromatographic experiments by Lang and Reinhard (1961), it appears that light may increase the gibberellin content of plants. Conversely shading could result in a lowering of gibberellin content in fruit trees. Furthermore light can activate the enzymatic destruction of indole-3-acetic acid, the principal auxin in plants (Fang and Butts, 1957). Thus shading would tend to lower the rate of oxidative degradation of IAA and so the auxin content is increased. Since auxin stimulates stem elongation, this may explain the promotion of internode length in most plants as a result of shading and as reported in apricots by Jackson (1969).

b) The presence of fruit and the problem of alternate bearing:

The presence of fruit on the tree, seems to be a dominant factor on the flowering behaviour. The nearer the bud is to the fruit, the stronger the fruits influence so that flower bud initiation and development is inhibited (Davis, 1957). This inhibitory effect of the fruit leads to the problem of alternate bearing in pome and stone fruits.

The fruit effect *per se* is possibly one of competition for carbohydrates and other metabolites (Harvey *et al*. 1942; Fulford, 1962; Kriedemann, 1968), and may depend directly upon the relative quantities of hormones in the respective tissues. Hormones are known to direct the transport of metabolites (Seth and Wareing, 1967; Letham, 1967) and fruits are known to contain quite high levels of hormones (Crane, 1964).

In some varieties, flower and fruit thinning is practised in a good year to ensure sufficient initiation of flowers for the following season. The timing of thinning is very important (Chandler, 1957). Thinning of either blossoms or very young fruit should be carried out prior to the time of flower-bud initiation in that tree if alternate bearing is to be overcome. Having the trees in a healthy state helps to offset this alternate bearing, because the trees are able to carry good crops and initiate flowers at the same time.

c) The effect of branch training on initiation of flower buds:

It has long been claimed by horticulturists, that horizontal training of branches of fruit trees checks vegetative growth and promotes flowering (Shanks, 1922; Halma, 1923; Goldschmidt and Delap, 1950; Tromp, 1967).

The term "gravimorphism" has been suggested by Wareing and Nasr (1958) to cover all morphological tropic responses associated with the promotion of flowering. In work on gravimorphism Wareing and Nasr (1958) found in apples and to a lesser extent in cherries, the orientation of the lateral shoot in relation to gravity, had a marked effect on flower initiation. However in later work these workers were of the opinion that while horizontal training of fruit branches undoubtedly reduced growth (Wareing and Nasr, 1961), there was as yet no evidence that it promoted flowering (Longman, Nasr and Wareing, 1965). Other workers (Magness et al. 1918; Dermine and Monin, 1958; Jonkin, 1962) have also found that the orientation of a branch on an apple tree bears little relation to subsequent flowering and fruiting properties. Where young apple trees are grown under more controlled conditions, however, there is good evidence that gravity affects vegetative growth and stimulates flowering (Mullins, 1965).

Thus it appears questionable even now, whether horizontal training of fruit tree shoots actually promotes flower formation as has long been believed.

CHAPTER III

MATERIALS AND METHODS

1. CULTURE OF PLANTS

In all experiments, young Moorpark apricot trees were grown in two gallon plastic buckets perforated at the base for drainage. The following soil mixture was used: soil 7 parts, compost 3 parts, coarse sand 3 parts. To this mixture basal fertilizer (6 oz./cubic yard) containing 13% N, 18% P, and 48% K was added. In addition, weekly applications of liquid fertilizer (1,000 ml/tree) were given throughout the experiments containing the following elements expressed as ppm: N, 1,000; P, 164; K, 310; S, 187; Mg, 56; Ca, 17; Mn, 4.7; Fe, 2.7; Cu, 1.9; Zn, 1.6; B, 0.3; Mo, 0.05.

Plants were grown in glasshouses where light intensity was approximately 75% of ambient. Heating was used when temperatures fell below 60°F.

2. GROWTH CABINETS

In experiment 6, four controlled-environment cabinets were used. In these cabinets 48 fluorescent tubes (80 watts) and 18 incandescent strip lamps (60 watts) provided a light intensity of approximately 2,200 foot candles at plant height. This intensity was reduced to 450-900 foot candles beneath the canopy of foliage.

3. RADIOACTIVE MATERIAL

20 ml of sodium carbonate - ^{14}C [$Na_2{}^{14}CO_3$] with specific activity 55 mc/mmole, was obtained from the Radiochemical Centre, Amersham, England.

4. ADMINISTRATION OF THE RADIOACTIVE ISOTOPE TO PLANTS

0.5 ml. $Na_2{}^{14}CO_3$ and excess conc. perchloric acid (approximately 4 ml.) were separately injected into a chamber filled with mercury. The formation of $^{14}CO_2$ displaced the mercury and the gas was withdrawn with 1 ml. syringes.

A 5 x 14 cm. polythene bag was placed around a single leaf on one shoot per tree and before sealing with rubber emulsion the bag was flattened to remove all air. Ten ml. of argon:oxygen mixture (70:30) plus 0.5 ml. of $^{14}CO_2$ having an activity of 7.5 uc, was injected into the bag. Treatment was carried out in all cases between 10 a.m. and 11 a.m.

5. DETERMINATION OF RADIOACTIVITY IN PLANT MATERIAL

After exposure for 24 hours, plants were harvested. On the exposed shoot each individual leaf and its axillary buds were separately removed. The vegetative and floral buds derived from the same lateral meristem made up the bud sample for each node. If the lateral meristem was very small and relatively undifferentiated it was included with the young leaf. Care was taken that no portion of stem tissue was included in the bud samples. Eight further leaves and their axillary buds were randomly selected from other parts of the tree to possibly demonstrate that movement of labelled photosynthates occurred in the twenty-four hour period.

Samples were dried at 70°C (158°F) for 24 hours, cooled in a desiccator, weighed immediately after cooling and transferred to 100 ml. B 19/26 quickfit conical flasks. To each flask approximately 30 ml. chromic acid was added to digest plant parts. Chromic acid was prepared by dissolving 63 gram. of sodium dichromate in 35 ml.

distilled water and adding sufficient concentrated H_2SO_4 to make up to one litre volume. On addition of the acid, the top of the flask was immediately fitted with a B 19/26 Thunberg tube containing a 1.5 x 4.5 cm. piece of filter paper (Whatman No. 1) wetted with 1 ml. of 5.0 M NaOH. The Thunberg tube was greased with silicone high vacuum grease before fitting into the flask. The NaOH reacted with the liberated $^{14}CO_2$ from the digested plant samples to form $Na_2{}^{14}CO_3$.

The flasks were left for at least 48 hours with occasional shaking and the Thunberg tube then disconnected. Carbonate around the Thunberg tube was washed down with 0.5 ml. distilled water and the filter paper which had been removed and placed in a 20 ml. low potassium glass counting vial was wetted with this water.

Since such a large number of samples were to be digested, and only a limited number of Thunberg tubes were available, further 150 ml. and 50 ml. flasks were employed in which the filter paper was pinned into rubber bungs for these flasks. Thus the filter paper wetted with NaOH hung directly in the flask just above the digesting plant parts. Care was taken not to run NaOH onto the sides of the flask.

This method was efficient as the $^{14}CO_2$ evolved, quickly came into contact with the NaOH on the filter paper. It was also less time consuming, and eliminated any risk of the filter paper falling into the acid compared with the method using Thunberg tubes.

Filter papers in the counting vials were air dried and to each, 15 ml. of a scintillator solution was added (Funt and Hetherington, 1960). This consisted of a conventional two solute combination of 4 g. 2,5-diphenyloxazole (PPO) and 0.2 g. 1.4 bis-2-

(5 phenlyoxazole) benzene (POPOP) in 1000 ml. of toluene; this had a wavelength spectrum of 3600-4500 Å and a quantum efficiency of between 12-18%.

The glass counting vials were carefully cleaned of finger marks and were now ready for counting.

6. RADIATION DETECTION EQUIPMENT AND METHODS

A liquid scintillation spectrometer was used to detect ^{14}C-activity in the samples. Gill (1964) quotes a 61% counting efficiency for Whatman No. 1 filter paper on which ^{14}C is deposited as a salt and measured in a liquid scintillator.

Vials containing the prepared filter paper were automatically counted in the Packard Tri-Carb Model 3365 liquid scintillation spectrometer. Ten minutes was allowed for counting each sample.

CHAPTER IV

RESULTS

INTRODUCTION

Any of the following bud arrangements may be found at a node of an apricot shoot in the axil of a leaf, and often many different arrangements exist on a single shoot:

1. A single leaf-bud - L
2. Two leaf-buds - L L
3. A leaf-bud with one flower-bud - L F
4. A central leaf-bud partly or completely surrounded by two, three, four or five flower-buds, i.e. -

```
                                        F
F L F,   F L F,   F L F,   F L F,     F   L   F
           F        F F       F       F     F
                                          F
```

5. Two to five flower-buds, i.e. -

```
F F,    F F F,    F F F,    F F F
                    F       F F
```

6. Very occasionally the usual condition of two floral buds with a central vegetative bud is repeated, i.e. -

```
F L F
F L F
```

PART 1: The importance of shading and defoliation on flower-bud initiation.

Experiment 1: Effect of leaf removal and 100% leaf and shoot shading on flower-bud initiation in apricot.

Plate 1 Section of an apricot shoot showing bud arrangements at 4 nodes:

Nodes 1 and 2: 3 floral buds + 1 vegetative bud were present.

Nodes 3 and 4: Only 1 floral and 1 vegetative bud can be seen.

Node 2 demonstrates quite clearly how a central vegetative bud can be surrounded by a number of floral buds.


V
F
X
F
V
3
F
V
2
F
F
V
F
1
F
F

A. EXPERIMENTAL METHODS

(1) Material, treatments and design

Twelve apricot trees, 24-36 months after budding, were pruned hard on December 6, 1968, and placed in a shadehouse. As bud break after pruning was slow, trees were moved into warmer glasshouse conditions on January 10, 1969, and given weekly applications of liquid fertilizer (1,000 ml).

The following treatments were applied on February 1, 1969, to 4 individual shoots on each tree:

1. Control.
2. 100% shade to whole shoot.
3. Alternate leaf removal of the basal 22 leaves on a shoot.
4. Alternate leaf shading (100%) of the basal 22 leaves on a shoot.

The treated shoots on six of the twelve trees had actively growing apices present which continued to produce leaves and nodes for some time after treatment. Presumably conditions within the tree still favoured apical growth. These conditions may have been influenced by the small number of shoots per tree which would have been competing for the root supplied metabolites. Treatments were not extended beyond the basal 22 nodes to include this new growth. Flower-bud counts were restricted to the treated portion of the shoot. In the other six trees, the apex of each treated shoot was removed, leaving exactly 22 leaves for treatment.

100% shading was achieved using black tightly-woven cloth. Leaves were removed to within 10 mm. of the petiole base and these stumps abscissed within two weeks of defoliation.

The experiment was a split plot design with the main plots (presence or absence of the apex) randomised, and the treatments as sub plots. After fifteen weeks the experiment was terminated on May 16, 1969.

B. RESULTS

A survey on lateral bud break on shoots receiving treatments 1, 3 and 4, was made 16 days after treatments were applied. This revealed the following points:

(a) lateral bud break occurred only on shoots where the apex had been removed, and occurred without exception.

(b) looking specifically at the 8 most distal nodes on the shoots receiving treatments 3 and 4, it was found that the presence of the leaf is necessary for lateral bud break, and that 100% leaf shading does not reduce lateral bud break to the extent that leaf defoliation does (Table 1).

Table 1 Effect of alternate leaf removal and leaf shading on lateral bud break in apricot

% Lateral bud break in eight distal nodes where:-	a) Leaves are present	b) Leaves are absent	Significance of diff
Treatment 3: Alternate leaf removal	62.5%	13.04%	**
	a) Leaves unshaded	b) Leaves shaded	
Treatment 4: Alternate leaf shading	48.14%	23.8%	N.S.

Chi-Square test (1df.) ** $P < 0.01$ N.S. Non Significant

Flower-bud counts were made on May 18, 1969, two days after completion of the experiment.

100% shoot shading resulted in gradual abscission of the treated leaves so that by the end of the experiment approximately 75% had abscissed. Some shoot die-back from the tip (approximately 35% of the shoot) also occurred under 100% shoot shading. This reduced the number of nodes at which floral counts could be made. The die-back and leaf abscission could have been attributed to the temperatures inside the bags which were consistently 2 - 7°C (3 - 15°F) higher than ambient.

The results for the experiment are summarised in Table 2.

Table 2 Effect of shoot shading, alternate leaf removal and alternate leaf shading on production of flower-buds and vegetative buds in apricot (n = 6)

Parameter / Treatment	Mean number of flower-buds per shoot	Mean number of flower-buds per node	Mean number of vegetative-buds per node
Apex present			
Control	37.5 a	1.284 ab	0.979 a
100% Shoot Shade	13.8 b	1.452 a	0.930 a
Alternate leaf removal	17.5 b	0.591 bc	0.975 a
Alternate leaf shade (100%)	19.0 b	0.879 abc	0.993 a
Apex removed			
Control	19.0 b	0.978 abc	0.980 a
100% Shoot Shade	8.5 b	0.811 abc	0.965 a
Alternate leaf removal	8.66b	0.464 c	0.993 a
Alternate leaf shade (100%)	11.5 b	0.573 bc	1.000 a
S.E. of Mean			
30 df	± 5.9	± 0.217	± 0.025
C.V. %	85.3	60.5	6.14

Duncan's test figures in the columns differ significantly if not sharing the same letter (P = 0.05)

Control treatments with or without the apex did not differ significantly in the mean number of flower-buds formed per node. However control with the apex produced significantly more flower-buds per shoot because shoots were longer than control without apex. 100% shading with or without the apex did not differ significantly from controls when comparing the same parameter. This could probably be explained in that the leaves were fully mature when shaded so that initiation may have already begun. Shoot die-back also reduced the number of nodes and so the number of buds for counting, which may have exaggerated the flower-buds per node value.

Alternate leaf removal and leaf shading treatments were further analysed as shown in Table 3. The results are quite important for they demonstrate that the leaf is essential for flower-bud initiation irrespective of the presence or absence of the apex. Further divisions of the shoot into proximal and distal regions also showed that the leaf is essential to initiation no matter where it is positioned along the shoot (data not presented).

Leaf shading (100%) on the other hand had no significant effect on the number of flower-buds formed at a node in the distal or proximal regions of a shoot. This treatment thus has no significant effect on the mean number of floral buds formed per node (when the entire shoot is considered) although a reduction in the mean number is quite evident.

Table 3 Effect of alternate leaf removal and leaf shading on flower-bud initiation in apricot (n = 6)

Treatment 3:	Alternate leaf removal		
	Apex remaining		
Treatment / Parameter	Leaf present	Leaf absent	Significance of diff - 10 df
Mean number flower-buds/node	0.916	0.086	**
	Apex removed		
	Leaf present	Leaf absent	
Mean number flower-buds/node	0.928	0.000	**
Treatment 4:	Alternate leaf shading (100%)		
	Apex remaining		
Treatment / Parameter	Leaf unshaded	Leaf shaded	Significance of diff - 10 df
Mean number flower-buds/node	1.072	0.655	N.S.
	Apex removed		
	Leaf unshaded	Leaf shaded	
Mean number flower-buds/node	0.796	0.181	N.S.

Student's t distribution - figures in the rows are compared significant different.

** P < 0.01 N.S. Non Significant

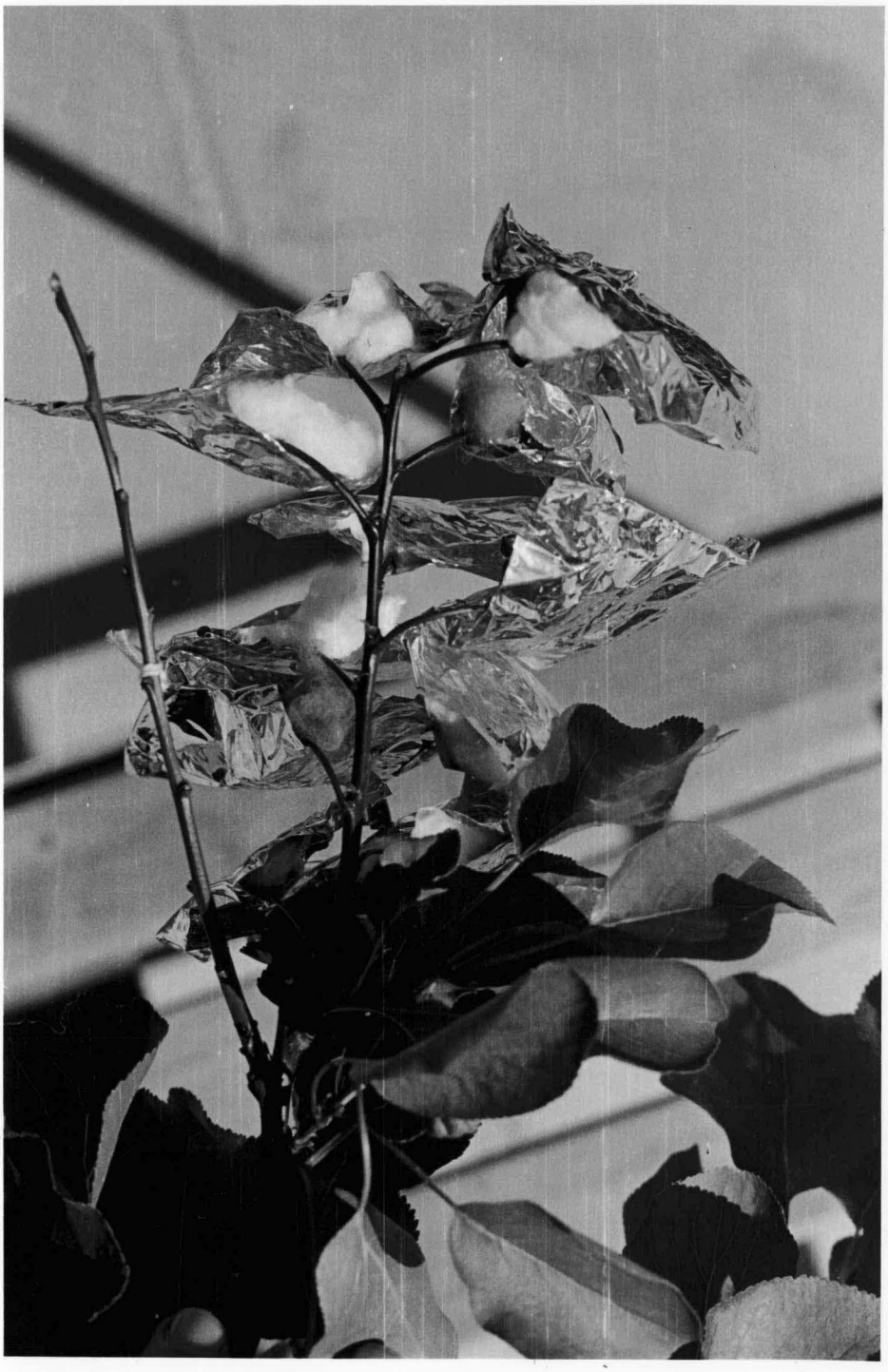


Plate 2 100% individual leaf shading - was obtained using aluminium foil. A small piece of cotton wool was placed around leaf petiole just inside the aluminium cover. This allowed air to circulate into the cover without letting light in.

Experiment 2: Effect of leaf shading, leaf removal and nitrogen level on flower-bud initiation in apricot.

A. EXPERIMENTAL METHODS

(1) Material, treatments and design

Twelve apricot trees, 24-36 months after budding, were used in this experiment. The following treatments were applied to each of five separate shoots on each tree:

1. Control.
2. 50% shading of individual leaves.
3. 100% shading of individual leaves.
4. Alternate leaf removal.
5. Complete leaf removal.

The experiment was a split plot design as nitrogen (1000 ppm) was applied to the roots of six of the twelve trial trees at 4 day intervals throughout the experiment.

Treatments were applied when the shoot apices had stopped producing new leaves, but before the majority of the leaves on the shoot had completed expansion. 100% shading was obtained using aluminium foil and 50% shading using muslin laid in three layers over top and underside of each leaf. The experiment was commenced on March 6, 1969, and terminated on May 22, an interval of eleven weeks.

B. EXPERIMENTAL OBSERVATIONS AND RESULTS

100% shade to leaves caused a large number to abscise very early in the experiment (78% leaf drop had occurred by the thirteenth day from commencement of the experiment). This problem was difficult to overcome and the cause could possibly be attributed to the buildup of

Plate 3 50% individual leaf shading - was achieved by covering top and underside of each leaf with three layers of muslin cloth.

ethylene around the covered leaf. Ethylene has been reported by Abeles and Holm (1967) to promote organ abscission, and leaves are known to produce ethylene (Gawadi and Avery, 1950).

Considerable shoot die-back from the tip occurred in the treatments involving 100% leaf shading (approximately 30%), and total defoliation (approximately 60%).

Flower-bud counts were made 77 days after commencement of the experiment. Flower-bud numbers for the 30 treated shoots receiving nitrogen and the 30 not receiving nitrogen were in total 418 and 311 respectively. An F test on the main plot effect, i.e. the effect of nitrogen, was significant at the 5% level ($F = 7.14^{*}$). However nitrogen failed to improve the mean number of floral-buds formed at each node. The mean figures for the two groups of 30 shoots were 1.023 flower-buds per node for those receiving nitrogen and 1.081 flower-buds per node for those not receiving nitrogen, so it is apparent the nitrogen effect is to increase shoot length and so increase the total number of flower-buds formed per group of 30 shoots, but not to increase the number initiated per node.

The results are summarised in Table 4. 50% shading was not detrimental to flower-bud initiation unless nitrogen was added, when it increased the deleterious effects of shading. Nitrogen failed to improve initiation in the control treatment compared with control receiving no nitrogen. 100% shading greatly reduced floral initiation, this is in contrast with the results in the previous experiment. However, shading was carried out at an early stage of leaf development in this experiment. Total defoliation was as disastrous to flower-bud initiation as was 100% shade.

Table 4 Effect of leaf shading, leaf removal, and nitrogen on flower-bud initiation in apricot (n = 6)

Parameter / Treatment	Mean number of flower-buds per shoot	Mean number of flower-buds per node
No Nitrogen Control	26.333 a	1.612 a
50% Leaf shade	23.833 a	1.723 a
100% Leaf shade	1.366 c	0.556 bc
Alternate leaf removal	12.833 b	1.013 abc
Total Defoliation	5.000 bc	0.500 bc
Nitrogen Control	23.166 a	1.695 a
50% Leaf shade	8.500 bc	0.761 bc
100% Leaf shade	3.833 bc	1.150 abc
Alternate leaf removal	12.000 b	1.143 abc
Total Defoliation	4.333 bc	0.366 c
S.E. of Mean		
40 df	± 3.26	± 0.264
C.V. %	65.72	55.8

The presence of the leaf was again demonstrated to be essential for floral initiation when non-defoliated and defoliated nodes were compared in the alternate leaf removal treatment in Table 5. Nitrogen was able to offset the defoliation effect on floral initiation so it would appear that nitrogen has opposite effects on initiation when either the leaf is removed (positive effect) or when the leaf is shaded (negative effect).

Table 5 Effect of alternate leaf removal and nitrogen on the mean number of flower-buds formed per node in apricot (n = 6)

Treatment for shoot / Analysis of shoot	No Nitrogen	Nitrogen (1000 ppm)	Significance of diff. in rows indicates difference between shoots
Leaves present	1.575	1.393	N.S.
Leaves absent	0.378	1.000	N.S.
Significance of diff. in columns indicates difference along a shoot.	*	N.S.	Student's t distribution used * $P < 0.05$ N.S. Non significant

Experiment 3: Effect of different levels of leaf and shoot defoliation on flower-bud initiation in apricot.

A. EXPERIMENTAL METHODS

(1) Material and Treatments

Ten apricot trees, 24-36 months after budding, had the following treatments applied to each of seven separate shoots on each tree in a randomised block design experiment:

Treatment 1 Control.

Treatment 2 Alternate leaf removal.

Treatment 3 Distal shoot defoliation.

Treatment 4 Proximal shoot defoliation.

Treatment 5 Removal of 25% of each leaf on the treated shoot.

Treatment 6 Removal of 50% of each leaf on the treated shoot.

Treatment 7 Removal of 95% of each leaf on the treated shoot.

Treatments were applied on March 12, 1969. For treatments 3 and 4, the treated shoot was divided into two areas, proximal and distal, each having approximately the same number of nodes.

When treatments were applied shoot apices were still growing, leaves were still expanding, and it was possible the treatments had an effect on internode elongation. For this reason the parameter shoot length was also measured on termination of the experiment.

Removal of portions of individual leaves was made with a cut at right angles to the leaf mid-rib.

B. RESULTS

The experiment was conducted over a period of eleven weeks, and counts and measurements were made on May 29, the day of completion of the experiment.

Results are shown in Table 6. Removal of up to 50% of the leaf had little deleterious effect on floral initiation compared with control. However when up to 95% of each leaf was removed initiation of flower-buds was severely reduced. It would appear from these results that the area of the leaf subtending the flower-buds is critical.

These experimental results also give a clue to the critical time for leaf removal with respect to the formation of flower-buds, as shown in Tables 7a, and 7b.

In Table 7a further analysis of distal and proximal defoliation treatments is carried out which illustrates that removal of a young leaf had a greater inhibitive effect on floral initiation than removal of a mature leaf.

Table 6 Effect of leaf and shoot defoliation on flower-bud production and shoot elongation in apricot (n = 10)

Parameter / Treatment	Mean number of flower-buds per shoot	Mean number of flower-buds per node	Shoot length (cm)
Control	21.2 a A	1.5455 a A	13.26 ab
Alternate leaf removal	14.6 b AB	1.0063 cd BC	14.15 ab
Distal Defoliation	12.9 bc AB	1.2700 b A	11.96 ab
Proximal Defoliation	12.1 bc B	0.8206 de CD	14.96 a
25% Leaf removal	15.6 ab AB	1.2388 bc AB	13.04 ab
50% Leaf removal	17.7 ab A	1.4189 ab A	11.10 b
95% Leaf removal	7.9 c B	0.5869 e D	13.27 ab
S.E. of Mean			
54 df	± 2.121	± 0.085	± 1.046
C.V. %	44.96	23.9	25.3

Duncan's test: Treatments with no common letter are significant different at the 5% level (small letters) or 1% level (capitals).

Table 7a The importance of leaf age at time of leaf removal on the formation of flower-buds in apricot (n = 10)

Parameter / Treatment	Flower-buds per node		Significance of diff - 18 df
	In axils of young leaves	In axils of old leaves	
All young leaves on branch removed.	0.217	1.983	**
All mature leaves on branch removed.	0.722	0.987	N.S.

Student's t distribution - figures in the rows are compared for significant different

** P < 0.01

N.S. Non Significant

Analysis on the results of distal defoliation on flower-bud initiation was looked at more closely in Table 7b in an attempt to discover when defoliation of the young leaf was most critical. To do this, the distal defoliated portion of the treated shoot was further subdivided into basal and topmost halves. The respective mean number of flower-buds per node for these two halves was found not to differ significantly although a trend was quite apparent and it would appear that removal of the topmost leaves, i.e. the youngest leaves had the greatest inhibitive effect on floral initiation.

Table 7 b Importance of leaf age at time of defoliation on flower-bud initiation in apricot (n = 10)

Parameter / Treatment	Mean number of flower-buds per node for the portion of the treated shoot
Proximal (non defoliated) area	1.918 a A
Distal defoliation (Basal half)	0.478 b B
(Topmost half)	0.095 b B
S.E. of Mean	
18 df	± 0.153
C.V. %	59.9

Duncan's test: Treatments with no common letter are significantly different at the 5% level (small letters) or 1% level (capitals).

Alternate leaf removal was also further analysed to provide additional evidence to support the contention that the presence of the subtending leaf is necessary for floral-bud development at that node. Further division of the shoot into proximal and distal halves demonstrated that at any node along a shoot, the presence of the leaf was necessary for flower-bud initiation (Table 8).

Table 8 Effect of alternate leaf removal on flower-bud formation in apricot (n = 10)

Parameter is numbers of flower-buds per	Leaves present	Leaves absent	Significance of diff - 18 df
1) Proximal half of shoot.	62	35	N.S.
2) Distal half of shoot.	37	12	*
3) For entire shoot.	99	47	*

Student's t distribution - figures in the rows are compared for significant difference * $P < 0.05$

N.S. Non Significant

Experiment 4: Effect of proximal and distal shoot defoliation on flower-bud initiation in apricot.

A. EXPERIMENTAL METHODS

(1) Material and treatments

This experiment can really be regarded as a verification of the results and trends which became evident in Experiment 3 when similar treatments were applied to shoots. The aim then as it is in this experiment was to find for flower-bud initiation the most critical time for defoliation.

Eight apricot trees, 34-46 months after budding, were randomly selected from the pool of 32 trees of this age used previously in Experiment 6. Three treatments were applied to the trees:

1. Control.

2. Proximal shoot defoliation.

3. Distal shoot defoliation.

The shoots were still actively growing when treatments were begun on December 19, 1969. The eight basal leaves on each treated shoot were removed in treatment 2 and left on in treatment 3. Distal defoliation was continued throughout the next few weeks and during these latter stages of leaf production, new leaves were removed as soon as they had opened. There was for this treatment then, a gradation in the stage of development the leaf had reached prior to defoliation. The apices on these distally defoliated shoots remained remarkably active in contrast to total defoliation treatments carried out in other experiments in which the apex soon abscissed following leaf removals.

(2) Experimental design

The canopy of each tree was divided into two approximately equal portions. Each treatment was applied to a single shoot and the treatment was repeated twice on all trees, once in each portion, so that half a tree was equivalent to a block. The experiment was a 3 x 16 randomised block design.

B. EXPERIMENTAL RESULTS

The experiment was conducted over a period of eight weeks. Counts and measurements made on February 12, 1970, the day of completion of the experiment, are presented in Tables 9, 10, and 11.

Table 9 Effect of part shoot defoliation on flower-bud production and shoot elongation in apricot (n = 16)

Parameter / Treatment	Mean number of flower-buds per shoot	Mean number of flower-buds per node	Shoot length (cm)
Control	35.88 a	1.3805 a	33.04 a
Proximal shoot defoliation	19.25 b	0.9800 b	21.69 b
Distal shoot defoliation	33.69 a	1.1330 ab	29.43 a
S.E. of Mean			
30 df	± 3.34	± 0.103	± 2.584
C.V. %	45.14	35.34	36.83

Duncan's test:- figures in the columns differ significantly if not sharing the same letter (P = 0.05)

In Table 10, the presence of the leaf was again demonstrated to be necessary at apparently all stages of development, if initiation of floral-buds at that particular node was to occur.

Table 10 The importance of leaf age at time of leaf removal on flower-bud initiation in apricot (n = 16)

Parameter / Treatment	Flower-buds per node		Significance of diff - 30 df
	In axils of young leaves	In axils of old leaves	
All young leaves on branch removed.	0.844	1.916	**
All mature leaves on branch removed.	1.163	0.557	**

Student's t distribution - figures in the rows are compared for significant difference ** P < 0.01

In treatment 3, the distal defoliated area was divided into two equal halves as in Experiment 3. Leaves in the proximal half were predominantly still expanding, and leaves in the distal half were very small when leaves were removed. The results in Table 11 substantiate those of Table 10 in emphasising the importance of the leaf for flower-bud initiation in apricot no matter what its stage of development.

Table 11 Effect of defoliation at various stages of leaf development on flower-bud initiation in apricot

Parameter / Treatment	Mean number of flower-buds per node for the portion of the treated shoot.
Proximal (non defoliated) area	1.916 a A
Distal defoliation (Basal half)	1.331 b B
(Topmost half)	0.366 c C
S.E. of Mean	
30 df	± 0.083
C.V. %	27.75

Duncan's test: treatments with no common letter are significantly different at the 5% level (small letters) or 1% level (capitals).

Thus removal of the very young leaf severely reduces initiation of flower-buds (Table 11), however removal of only mature leaves on a shoot still significantly reduces the amount of flower-buds initiated at such nodes where mature leaves had been present (Table 10).

Experiment 5: Effect of shading and defoliation on flower-bud initiation in apricot.

A. EXPERIMENTAL METHODS

(1) Material, treatments and experimental design

Twelve apricot trees 16-24 months after budding, were used in a randomised block experiment in which four levels of shading and four levels of defoliation were employed to test the "role" of the subtended leaf on axillary flower-bud initiation. In this trial some treatments previously tested in the early experiments were repeated.

Treatments were applied to individual shoots. Each treatment was repeated on every tree, so that a tree is a block and each treated shoot represents a plot. There are 9 x 12 = 108 plots. Treatments were as follows:

Treatment 1 Control.

Treatment 2 Defoliation of whole shoot.

Treatment 3 100% Shading of shoot.

Treatment 4 Alternate leaf shading (100%).

Treatment 5 50% Shading of shoot.

Treatment 6 Alternate leaf shading (50%).

Treatment 7 50% Removal of all leaves.

Treatment 8 50% Removal of alternate leaves.

Treatment 9 Alternate leaf removal.

Shoot apices were still actively producing new nodes and leaves so that the appropriate treatments were applied as these new leaves unfurled. Time of treatment application varied depending on the position of the leaf on the shoot so that treatments which were first applied on December 18, 1969, continued to be applied on new leaves

till January 2, 1970. Total defoliation resulted in little shoot die-back, but 100% shoot shading resulted as usual in premature death of the leaves on such shoots. Alternate leaf shading (100%) caused premature leaf drop of the treated leaves and approximately 70% had abscissed by the completion date for the experiment.

B. RESULTS

Counts and measurements were taken on February 20, 1970. The results appear in Tables 12 and 13.

Table 12 Effect of shading and defoliation on flower-bud initiation in apricot (n = 12)

Parameter / Treatment	Mean number of flower-buds per node	Mean number of flower-buds per shoot
Control	1.291 ab	19.91 ab
Defoliation of whole shoot	0.247 c	-
100% Shading of shoot	0.310 c	-
Alternate leaf shading (100%)	1.483 ab	20.91 ab
50% Shading of shoot	1.534 a	19.91 ab
Alternate leaf shading (50%)	1.553 a	24.41 a
50% Removal of all leaves	1.114 b	15.08 b
50% Removal of alternate leaves	1.536 a	26.41 a
Alternate leaf removal	1.111 b	14.91 b
S.E. of Mean		S.E. of Mean 66 df
88 df	± 0.134	± 2.43
C.V. %	41.4	41.1

Duncan's test: Treatments with no common letter are significantly different at the 5% level (P = 0.05).

The figures for treatments 2 and 3 were not included in the test on the effect the various treatments had on the production of flower-buds as obviously they had severely reduced flower-bud numbers.

This then enabled the remainder of the data to be analysed more accurately.

The shading and defoliation treatments gave some consistent results in the light of previous results. 50% shading again failed to reduce the number of flower-buds formed per node whereas total defoliation and 100% shading were particularly injurious to initiation. The figures for alternate leaf shading (50% and 100%) and alternate leaf removal are more enlightening when further analysed in Table 13. Alternate leaf removal is not as inhibitive to initiation in this experiment as has previously been reported. However the effect of alternate leaf removal is again more pronounced in the distal half of the shoot. This is another demonstration of the importance of leaf age at the time of removal. 100% shading of individual leaves significantly reduced initiation as compared with unshaded leaves whereas 50% shading had no effect.

Table 13 Effect of alternate leaf shading and leaf removal on flower-bud initiation in apricot (n = 12)

Treatment 4:	Alternate leaf shading (100%)		Significance of diff - 22 df
Parameter	Leaves unshaded	Leaves shaded	
Mean number flower-buds per node for those leaves (n = 12)	1.74	1.213	*

(continued overpage)

Table 13 (continued)

Treatment 6:	Alternate leaf shading (50%)		Significance of diff - 22 df
Parameter	Leaves unshaded	Leaves shaded	
Mean number of flower-buds per node for those leaves (n = 12)	1.53	1.56	N.S.
Treatment 9:	**Alternate leaf removal**		**Significance of diff - 22 df**
Parameter	**Leaves present**	**Leaves absent**	
Proximal half of shoot. Mean number of flower-buds per node	1.391	1.149	N.S.
Distal half of shoot. Mean number of flower-buds per node	0.872	0.325	*
Entire Shoot Mean number of flower-buds per node	1.127	0.756	N.S.

Student's t distribution - figures in rows are compared for significant difference

N.S. = Non Significant

* $P < 0.05$

DISCUSSION

PART 1: IMPORTANCE OF SHADING AND DEFOLIATION

In the apricot tree, one leaf is produced at each node of a young shoot, and in the axil of this leaf usually one vegetative bud and a variable number of flower-buds are to be found (see observations in introduction at beginning of chapter). Previous workers (Roberts, 1920, 1923; Haller and Magness, 1933; Heinicke, 1966), investigating the process of flower-bud initiation in deciduous fruits, have considered each leaf and its axillary buds as a separate entity; separate to the extent that the buds will not develop until the subtending leaf has reached a certain size (Chandler, 1957), and the buds are dependent for their carbohydrate supply on these leaves (Magness, Edminster and Gardner, 1917). Germane to the latter suggestion the present experiments on defoliation and shading looked at the effect of leaf metabolites on floral and vegetative bud formation. These metabolites can be grouped as follows: (a) carbohydrates and nitrogenous compounds, either synthesised in the leaf or attracted into it and becoming available to the axillary buds, (b) hormonal metabolites, again either formed in the leaf or attracted to the leaf, in either case becoming available to the axillary buds.

In support of the latter contention, leaves, particularly very young leaves of various plants, are known producers of gibberellins (Lockhart, 1957; Okazawa, 1960; Evtushenko, 1961; Jones and Phillips, 1966), auxins (van Overbeek, Vásquez and Gordon, 1947; Leopold, 1955; Stathakopoulos and Erickson, 1967), and inhibitors (Kawase, 1961; Cornforth, Milborrow and Ryback, 1965; Milborrow, 1967; Gabr and Guttridge, 1968; Wareing, 1968). Leaves are also responsible for

the perception of changes in photoperiod (Chailakhyan, 1968), and since they are able to synthesise gibberellins and auxins both of which can attract metabolites (Shindy and Weaver, 1967; Seth and Wareing, 1967), leaves may attract other necessary metabolites for bud development including cytokinins. Cytokinins are produced in the roots of plants (Seth and Wareing, 1965; Weiss and Vaadia, 1965), promote cell division and bud growth (Letham, 1967), and are known to influence the transport of plant metabolites (Letham, 1967), and to stimulate protein metabolism where present in plants (Richmond and Lang, 1957). Thus the effects of shading and defoliation on flower-bud initiation in apricot may be explained by the effects these treatments had on carbohydrate and hormone production. Shading for instance, could be expected to reduce photosynthesis. Similarly removal of all or part of the leaf could likewise reduce photosynthesis. Both treatments might influence the hormonal levels within the leaf and so possibly limit the supply of these factors to the axillary bud.

These experiments have shown that on apricot trees which were growing under the long days of summer, the leaf is necessary for lateral bud break (Table 1). This is contrary to the findings of Champagnat (1955) working with lilac, and Stathakopoulos and Erickson (1967) working with citrus where the mature leaf inhibited lateral bud development. The shoot apex exhibited apical dominance in inhibiting lateral bud break along the shoot. However the apex normally abscisses after a certain period of growth so the importance of the apex on floral-bud initiation along the shoot is probably relatively minor. The author has observed the formation of flower-buds at the base of shoots with or without an apex.

In treatments involving complete shoot defoliation, the apex, if left on, produced very few further nodes and associated leaves and abscissed earlier than a control undefoliated shoot. This abscission could be due to a lack of hormones in the shoot and so a lack of attracting power for metabolites particularly carbohydrates from other parts of the tree. However if leaves were only removed from part of the shoot as with proximal or distal defoliation, the shoot apex remained active for a much longer period of time, compared with defoliated shoots. This was particularly so in Experiment 4 and it would appear that some factor(s) from the leaf help to maintain apical activity on a shoot. Likewise it could be postulated that specific inhibitors may be produced in leaves which exert their effect at the apex so that after a growth "flush", the apex will absciss and the shoot enters a period of summer dormancy. Such specific inhibitors could possibly be produced only in mature leaves and a certain number of mature leaves may be needed before sufficient quantities of this inhibitor can build up and so exert their effect. Inhibitors are known to be produced in leaves (Cornforth, Milborrow and Ryback, 1965), but this inhibitor could perhaps differ from abscisic acid which is known to form in highest quantities in leaves under the influence of short days (Wareing, 1968), because abscission of the apex can occur under any photoperiod.

A. ASSESSMENT OF THE EFFECT OF DEFOLIATION

Defoliation may have two definite effects: it reduces the amount of carbohydrates which can be manufactured, and it reduces the level of hormone metabolites available to the buds. The former effect should not be over-emphasised, since Wareing, Khalifa and

Treharne (1968) found that part defoliation of a shoot caused those leaves remaining to increase their photosynthetic efficiency. They also found that the remaining leaves were greener in colour for a number of different species and explained this on the grounds that partial defoliation reduced the competition between the leaves for cytokinins from the roots and hence increased the amount available to the remaining leaves. This showed up as an increase in total protein content of the leaves.

Defoliation can also have varying effects on the carbohydrate supply available to that shoot, so that removal of all leaves from the distal half of a shoot may not necessarily reduce the supply of carbohydrates to the same extent as removal of all leaves from the proximal half. Heinicke and Hoffman (1933) substantiate this opinion in work on apple where they found that the rate of photosynthesis can vary greatly from one leaf to another along a shoot.

Total defoliation of a shoot severely reduced flower-bud initiation (Tables 4, 12) and the presence of the leaf was absolutely critical for initiation in the axil of that leaf (Tables 3, 5, 8), but not if nitrogen was supplied to the plant (Table 5). Since nitrogen failed to improve initiation at all nodes (i.e. defoliated and undefoliated), it could well be that some factor normally supplied from the leaf was supplied from the roots when additional nitrogen was root applied. This factor which may be a cytokinin, a protein, or some essential amino acid, may have then been translocated to the lateral meristems. At undefoliated nodes it had little effect as sufficient of the factor was being supplied by the leaf. However at defoliated nodes where the factor was limiting, it was able to bring about some improvement in flower-bud initiation.

One of the aims of these defoliation experiments had been to narrow down the period of time at which removal of the leaf was critical. However such a time period cannot be given, and any defoliation in summer or autumn will have some inhibitory effect on initiation in apricot (Tables 6, 7a, 7b, 10, 11) although the effect on the bud in the axil of a leaf diminishes as the leaf gets older. This result is not in absolute agreement with the work of Roberts (1923) working on plum, in which alternate leaf removal at the end of July (equivalent to January in the southern hemisphere) had no inhibitive effect on floral-bud formation.

In experiments 3 and 4, the age at which the leaf was removed was shown to be important (Tables 7a, 7b, 10, 11). Some factor(s) appear to be synthesised in very young through to fully expanded apricot leaves, and are necessary for initiation. The supply of this factor(s) must be maintained right throughout the initiation process, but its importance diminishes the further the initiation process proceeds. Thus the removal of a fully mature old leaf is not nearly as inhibitive to flower-bud initiation as removal of a partly expanded young leaf.

These defoliation studies have also shown (Table 6) that the area of the leaf subtending the buds is critical. This is in agreement with work on plums (Roberts, 1923), and apples (Heinicke, 1966). Removal of 25% or 50% of each leaf on a shoot failed to reduce initiation compared with control. However removal of 95% of each leaf greatly reduced initiation in apricot. Roberts reports similar results for plum during the first few months of the growing season. However he also found that the later in the season part leaf removal was carried out, the less were the differences between 33%, 50% and

66% leaf removal treatments. The parameter measured was average flower-buds per node. In these present experiments, the fact that 50% removal of individual leaves had little effect on initiation (Tables 6, 12) indicates that sufficient leaf area remained to produce sufficient hormone factors and/or carbohydrates and so continue the initiation process. Perhaps part leaves are able to photosynthesise more efficiently in much the same way as Wareing, Khalifa and Treharne (1968) reported for whole leaves (as mentioned earlier in this discussion).

The effect of part leaf removal on the mean number of flower-buds formed per node has further shown that the greater the reduction in leaf area of a shoot the greater was the inhibitive effect on initiation. For instance compared with control 50% removal of every second leaf did not reduce flower-bud initiation to the extent that 50% removal of all leaves did (Table 12). However removal of the same quantity of leaf area from a shoot does not necessarily have the same effect, as shown in Table 6, where complete removal of every second leaf was more inhibitory to flower-bud initiation than 50% removal of all leaves on a shoot. This suggests that not all the factors supplied by the leaf to the buds for development are mobile or how else can the essentiality of the leaf be explained in the alternate leaf removal treatments (Tables 3, 5, 8)? Surely if all factors were completely mobile, then sufficient of this factor(s) would reach the neighbouring nodes. Since this is not the case, it could well be that this factor(s) is produced in quantities sufficient only to affect the axillary buds to that leaf. Alternatively lateral transport may not occur with ease in apricot stem and as neighbouring leaves rarely occur immediately above one another, this would account for the

inability of leaf metabolites produced at one node being able to move to neighbouring defoliated nodes in sufficient quantities to bring about initiation of floral-buds.

B. ASSESSMENT OF THE EFFECT OF SHADING

The influence of shading on hormone and carbohydrate levels is less definite than that of defoliation, since the "factory" has not been reduced in size but may have only had its efficiency lowered. However as light increases the synthesis of hormones in leaves (Leopold, 1955; Chailakhyan, 1968) and is also necessary for photosynthesis, 100% shoot shading was able to reduce flower-bud formation to the same extent as complete shoot defoliation (Tables 4, 12). When comparing 100% shading and total defoliation however, it must be recalled that 100% shoot shading resulted in premature death of the leaves and 100% individual leaf shading resulted in premature leaf abscission, so that these treatments may not differ greatly from total defoliation in their effect. In Experiment 1 100% shoot shading failed to reduce the number of flower-buds formed. This can be explained quite readily because unlike in Experiment 4, shading was applied to relatively mature leaves which had probably formed the hormonal factor(s) necessary for initiation in sufficient quantities to enable continuance of the initiation process.

50% shading to shoots did not affect flower-bud initiation compared with control, whereas 50% removal of all leaves and alternate leaf removal significantly reduced initiation compared with control (Tables 4, 12). Since shading does not have similar effects to leaf removal, it would seem some factor(s) other than photosynthates are derived from the leaf and are required for flower-bud initiation in apricot.

Part shading of whole trees greatly reduces initiation of floral-buds in apricot (Jackson, 1969), but in the present experiments, part shading (50%) of individual leaves (Table 4) or groups of leaves (Table 12) did not affect initiation compared with control except where nitrogen was supplied to the tree via the roots as urea solutions. There are two possible explanations for such a response. Firstly nitrogen may reduce the number of flower-buds initiated under conditions of shading, an assumption not easy to explain. Or alternatively the control treatment with its high level of carbohydrates could possibly make more use of the added nitrogen compared with the shaded shoot which may have a lower level of carbohydrates. However as the control treatment receiving nitrogen did not differ significantly from the control not receiving nitrogen, this reason is likewise rather unsatisfactory.

Since part shading which would be expected to reduce photosynthesis did not affect flower-bud initiation, it seems likely that photosynthates are mobile within the plant and that the bud is not dependent only on the subtending leaf for its photosynthate supply.

PART 2: The role of temperature and light on flower-bud initiation in apricot.

Experiment 6: Effect of daylength, temperature and nutrition on flower-bud formation in apricot.

A. EXPERIMENTAL METHODS

(1) Design of experiment

The experiment was a 2 x 2 x 2 factorial design, to test the following pairs of variables: (a) long days (16 hour photoperiod) v. short days (9 hour photoperiod), (b) high mean temperature (75°F) v. lower mean temperature (60°F), (c) nitrogen (1000 ppm) v. no nitrogen.

(2) Material, Treatments and Methods

Thirty-two trees, 30-42 months after budding were pruned hard and placed in growth cabinets on June 15, 1969. Four controlled environment cabinets were used, eight trees were placed in each cabinet with half of these trees in each case receiving nitrogen applied via the roots. The treatments used were as follows:

Treatment 1	Long days 75°F
Treatment 2	Long days 60°F
Treatment 3	Short days 75°F
Treatment 4	Short days 60°F

The trees prior to pruning had been kept in a glasshouse in which the daylength and night temperatures were similar to ambient.

During the first three weeks, two cabinets were set at a nine hour photoperiod, and the other two at a sixteen hour photoperiod. The temperature was 75°F in all cabinets, and the relative humidity was 80%. This temperature was used throughout all cabinets to induce bud break

from these dormant trees. Since the trees had experienced only a limited period of temperatures below 45°F, the effect of winter chilling in breaking dormancy was far from complete. Consequently as Chandler (1957) has previously reported for apricot, many flower-buds abscissed in response to these warmer temperatures because of inadequate winter chilling. Furthermore not all vegetative buds broke dormancy in reponse to these higher temperatures. The influence of daylength on vegetative bud break in apricot has been presented in the first analysis of data in Table 15.

After three weeks, sufficient bud break had occurred in all cabinets, and treatments 2 and 4 were applied, i.e. two cabinets had their mean temperature lowered to 60°F. In all cabinets approximately 10% of the vegetative buds on the trees had quickly broken dormancy and produced small shoots. Those shoots longer than 2 cm. were removed at this stage prior to beginning the experiment on July 6, 1969.

Nitrogen was applied to the roots of four trees per cabinet for the first time on July 10, and thereafter at 5 day intervals for the remainder of the experiment.

The controlled environment cabinets broke down for a period of twenty-four hours three weeks four days from the date of commencement of the experiment. During this power failure all cabinets were in complete darkness. The effect of this variation from the set treatment conditions, used in the experiment, cannot be assessed.

The experiment was terminated after 12 weeks, that is nine weeks after two of the cabinets had had their mean temperature lowered to 60°F.

B. EXPERIMENTAL RESULTS

The results are summarised in Table 14.

Table 14 Effect of daylength, temperature, and nutrition on production of flower-buds in apricot

Parameter / Treatment	Mean number of flower-buds per node	Mean number of flower-buds per tree
Long days 75°F N_2	1.435 a A	620 a A
Long days 75°F	1.055 b AB	436 b B
Long days 60°F N_2	0.805 b BC	271 c BC
Long days 60°F	0.883 b B	224 c CD
Short days 75°F N_2	0.958 b B	421 b B
Short days 75°F	0.748 b BC	266 c BC
Short days 60°F N_2	0.973 b B	217 c CD
Short days 60°F	0.420 c C	72 d D
S.E. of Mean		
21 df	± 0.102	± 43.14
C.V. %	22.49	27.00

Under conditions of long days, high temperatures (75°F), and high nutrition (1000 ppm Nitrogen) more flower-buds are formed on a tree and the mean number of flower-buds formed per node is highest.

One of the aims of this experiment had been to determine the photoperiod response of apricot. On comparison of the treatments not receiving nitrogen it would appear long days are slightly beneficial to flower-bud initiation:

Long days 75°F	1.055 flower-buds per node
Long days 60°F	0.883 " " " "
Short days 75°F	0.748 " " " "
Short days 60°F	0.420 " " " "

(From Table 14)

However this trend is not evident when comparing the treatments which had received nitrogen:

Long days 75°F N_2	1.435	flower-buds per node
Short days 60°F N_2	0.973	" " " "
Short days 75°F N_2	0.958	" " " "
Long days 60°F N_2	0.805	" " " "

(From Table 14)

In both comparisons temperature does not appear to be greatly important and the slight promotive effect of long days was not as pronounced when nitrogen was added. That is nitrogen tended to make up for the slight inhibitive effect of short days. Nitrogen appears to be used more efficiently under conditions of high mean temperature (75°F) rather than under conditions of low mean temperature (60°F). This was shown in the following figures:

Long Days 75°F N_2	v.	Long Days 60°F N_2
1.435 fl.buds/node		0.805 fl.buds/node
620 fl.buds/tree		271 fl.buds/tree
Short Days 75°F N_2	v.	Short Days 60°F N_2
0.958 fl.buds/node		0.973 fl.buds/node
421 fl.buds/tree		217 fl.buds/tree

In Table 15 the broad effect of each pair of variables on flower-bud formation on all the trees in the four cabinets is tested for significance. These results show that neither nutrition, temperature nor daylength has a significant effect on the number of flower-buds formed per node <u>per se</u>, although it is evident that long days, high temperatures and high nutrition are each singly promotive to flower-bud formation. Thus when all are combined in the treatment Long Days 75°F Nitrogen, the highest number of flower-buds are formed per node as shown in Table 14.

Table 15 Effect of daylength on vegetative bud break, and the effect of daylength, temperature and nutrition on flower-bud formation in apricot

Treatment / Parameter	DAYLENGTH		Significance of diff - 14 df
	Long Days 16 hours 75°F	Short Days 9 hours 75°F	
Mean number of vegetative buds/ tree which had broken dormancy after 2 weeks of respective treatments	56.50	37.12	*
Treatment / Parameter	**DAYLENGTH**		**Significance of diff - 6 df**
	Long Days 16 hours	Short Days 9 hours	
Mean number of flower-buds per tree	387.75	244.0	N.S.
Mean number of flower-buds per node	1.0445	0.7747	N.S.
Treatment / Parameter	**TEMPERATURE**		**Significance of diff - 6 df**
	75°F	60°F	
Mean number of flower-buds per tree	435.75	195.8	*
Mean number of flower-buds per node	1.049	0.770	N.S.
Treatment / Parameter	**NUTRITION**		**Significance of diff - 6 df**
	Nitrogen (1000 ppm)	No Nitrogen	
Mean number of flower-buds per tree	382.25	249.5	N.S.
Mean number of flower-buds per node	1.043	0.777	N.S.

Student's t distribution - figures in the rows are compared for significant difference * $P < 0.05$ N.S. Non Significant

In Table 16 the effect of nitrogen, temperature and daylength on shoot elongation was examined.

Table 16 Effect of nitrogen, temperature and daylength on mean shoot length (cm) in apricot

Nitrogen effect Treatment	Nitrogen (1000 ppm)	No Nitrogen	Significance of diff - 6 df
Long days 75°F	13.372	14.912	N.S.
Long days 60°F	7.288	6.915	N.S.
Short days 75°F	13.080	18.800	*
Short days 60°F	6.072	9.484	N.S.
Temperature effect **Treatment**	**75°F**	**60°F**	**Significance of diff - 6 df**
Long days Nitrogen	13.372	7.288	*
Long days No Nitrogen	14.912	6.915	**
Short days Nitrogen	13.08	6.072	*
Short days No Nitrogen	18.80	9.484	*
Daylength effect **Treatment**	**Long days (16 hr photoperiod)**	**Short days (9 hr photoperiod)**	**Significance of diff 6 df**
75°F Nitrogen	13.372	13.080	N.S.
75°F No Nitrogen	14.912	18.800	*
60°F Nitrogen	7.288	6.072	N.S.
60°F No Nitrogen	14.912	9.484	*

Student's t distribution - figures in the rows are compared for significant difference * $P < 0.05$ ** $P < 0.01$ N.S. Non Significant

It would appear from the results that an increase in temperature had the biggest promotive effect on shoot elongation compared with an increase in daylength and an increase in nutrition. As the number of nodes on these shoots was not significantly increased with an increase in temperature (unpresented data), the temperature effect on shoot elongation was obviously a result of an increase in average internode length.

Increases in nitrogen and in daylength likewise failed to result in a significant increase in the number of nodes (unpresented data).

DISCUSSION

PART 2: The role of temperature and light in the process of flower-bud initiation in apricot.

Plants that have provided the greatest impetus to studies on the mechanism of flowering are those that flower in response to changes in photoperiod. In these, a floral 'stimulus' can be generated reproducibly in the leaves under controlled conditions (Lang, 1952). Such a floral 'stimulus', which can be readily demonstrated, has not as yet been extracted, separated and characterized from any plant (Searle, 1965). However grafting experiments have shown that this floral 'stimulus' or flowering 'hormone', would appear to be the same for all plants irrespective of their photoperiodic reaction (Lang, 1965; Chailakhyan, 1968).

The photoperiod response of apricot is not known, although evidence has been put forward that other deciduous fruit trees such as apple (Gorter, 1955; Hoyle, 1955; Piringer and Downs, 1959), peach (Piringer and Downs, 1959), cherry (Wareing, 1968), and plum (Wareing, 1968), are day neutral plants; that is they can flower under any day length. Thus flower-bud initiation in fruit trees is more likely to be influenced by such factors as temperature, including the need for winter chilling (Chandler, 1957), light intensity (Paddock and Charles, 1928; Jackson, 1968), nutrient supply (Delap, 1967), the presence of a heavy crop on the tree (Davis, 1957), the growth stage of the tree (Davis, 1957; Heinicke, 1967), and many other environmental factors.

In this experiment, temperature, photoperiod and nutrition were all found to individually influence the process of flower-bud initiation on apricot trees.

The effect of temperature on initiation of flower-buds in fruit trees has not been sufficiently recorded. However at higher temperatures it should be possible for enzymatic and non-enzymatic reactions and translocation of metabolites to occur at a faster rate within the plant. This general "quickening up" of the various physiological processes within the plant may account for this increase in initiation at 75°F compared with 60°F. However inhibitory processes would also be speeded up by these higher temperatures. Perhaps the hormonal factor(s) which comprise the floral 'stimulus' may be synthesised in greater amounts at higher temperatures.

The importance of nitrogen on initiation in fruit trees has previously been well documented (Bradford, 1924; Boynton, 1954; Chandler, 1957; Williams, 1963), and in this experiment nitrogen improved initiation under both photoperiods and at either temperature level. The response was however greater at 75°F than at 60°F.

There appears to be a slight improvement in initiation of flower-buds under long day conditions, but the results generally indicate that apricot will form flower-buds under long or short days and so can be regarded as a day neutral plant. It is also significant that the differences in the number of flower-buds formed per node between long day and short day treatments, high and low mean temperatures and under high and low nutrition are virtually all the same. This would also appear to indicate that apricot is a day neutral plant, and as such is influenced in its flowering response by several factors including temperature, photoperiod and nutrition. Long days however may be more conducive to initiation because of the increased photosynthesis, which leads to an accumulation of carbohydrates. High levels of carbohydrates have previously been shown to improve flower-bud initi-

ation in fruit trees (Davis, 1957; Fulford, 1962).

Long days are known to promote gibberellin biosynthesis (Brian, 1958; Chailakhyan and Lozhnikova, 1964), and auxin synthesis (Chailakhyan and Zdanova, 1946) in the leaves of plants irrespective of their photoperiodic reaction. Since gibberellins are known to inhibit flower-bud initiation in fruit trees (Hull and Lewis, 1959; Bradley and Crane, 1960; Stuart and Cathey, 1961; Guttridge, 1962), and auxins "do not play a decisive role in flowering" (Chailakhyan, 1968) these hormones do not appear to be involved in the promotive effect of long days on initiation. Similarly inhibitors such as abscisic acid which usually forms in greater quantities in plants under short days (Wareing, 1968) would seem not to be involved in initiation under long day conditions. However under short day conditions the situation may be different.

Since flower-bud initiation can occur under any photoperiod and since the synthesis of auxins, gibberellins, and many inhibitors in leaves is greatly influenced by photoperiod it could well be that either these growth regulators are not involved in the initiation of flower-buds, or alternatively are only involved at certain concentrations. For instance lower levels of gibberellins in plants growing under short days may have little effect on initiation. However under long days, the level of gibberellins builds up and becomes inhibitory to initiation. Perhaps other as not yet discovered compounds are involved in the floral 'stimulus', the anthesins as proposed by Chailakhyan (1968) florigenic acid as proposed by Lincoln et al. (1961) or even florigen as proposed by early workers investigating the hormone control of flowering.

It would appear however that no one factor is the sole controller of flowering. It would also appear quite obvious that the

known growth substances are not able to satisfy all the requirements for the floral 'stimulus'.

PART 3: The role of carbohydrates in flower-bud initiation in apricot.

Experiment 7: ^{14}C-studies on the movement of photosynthesis in apricot.

A. EXPERIMENTAL METHODS

(1) Material, treatments and method

Details of exposure of apricot trees to $^{14}CO_2$ and subsequent sampling of these trees have been outlined in Chapter III. In each case a single leaf was exposed to $^{14}CO_2$, and leaves of various ages and so development, were selected to indicate variations in photosynthate translocation from such leaves. The treatments were (a) exposure of a very young leaf, (b) exposure of a leaf just finished expansion, (c) exposure of a mature leaf and (d) exposure of a fully expanded partly mature leaf, not as young as (b) or as old as (c) on a shoot where every second leaf had been removed three weeks earlier.

The eight trees used were at least three years old from time of budding, and leaves on shoots with at least twenty leaves were selected for exposure to $^{14}CO_2$.

When buds were removed, extreme care was taken not to include any bark or wood from the adjacent shoot or leaf petiole. The background count 95 counts per minute, represents the extreme, as once a scintillator solution was used three times it was discarded. This figure of 95 cpm was calculated by adding the mean count for a number of vials containing plant parts from unexposed trees, in a scintillator solution which had been used three times, to twice the standard deviation for these counts, i.e. $64.9 + (2 \times 15.4) = 95$ cpm approximately. Naturally for some counts the scintillator solution had only been used once, twice or was previous unused. However records were

not kept of the condition of the scintillator solution for each batch of samples, so it has been necessary to use this high background in all cases.

B. EXPERIMENTAL RESULTS

The counts for the various leaf and bud samples from four of the eight exposed trees (i.e. one replication of each treatment) are detailed in Figures 1 and 2 for treatment a, in Figures 3 and 4 for treatment b, in Figures 5 and 6 for treatment c, and for treatment d in Figures 7 and 8. In each case the exposed shoot is shown in full analysis (Figures 1, 3, 5, 7).

For treatment b, where a leaf just finished expansion was exposed, a Student's t test was carried out on the corrected counts for the leaves and for the buds, as shown in Table 17. This showed that the buds on this shoot were bigger "sinks" than leaves for labelled photosynthates.

Table 17 Differences in the ability of different organs to attract ^{14}C-labelled metabolites

Sum of all counts for buds on Tree 2	Sum of all counts for leaves on Tree 2	Significance of diff - 62 df
1,844,268 cpm/g dry wt.	334,236 cpm/g dry wt.	(4.08) **

Student's t distribution - figures in the row are compared for significant difference ** $P < 0.01$

That is their ability to attract photosynthates was greater than that of leaves when compared on a dry weight basis, this situation was apparent in all treatments.

Figure 1 shows that a very young apical leaf was able to export photosynthates at this stage throughout the shoot on which it was located. However it appears the export may be limited as there was

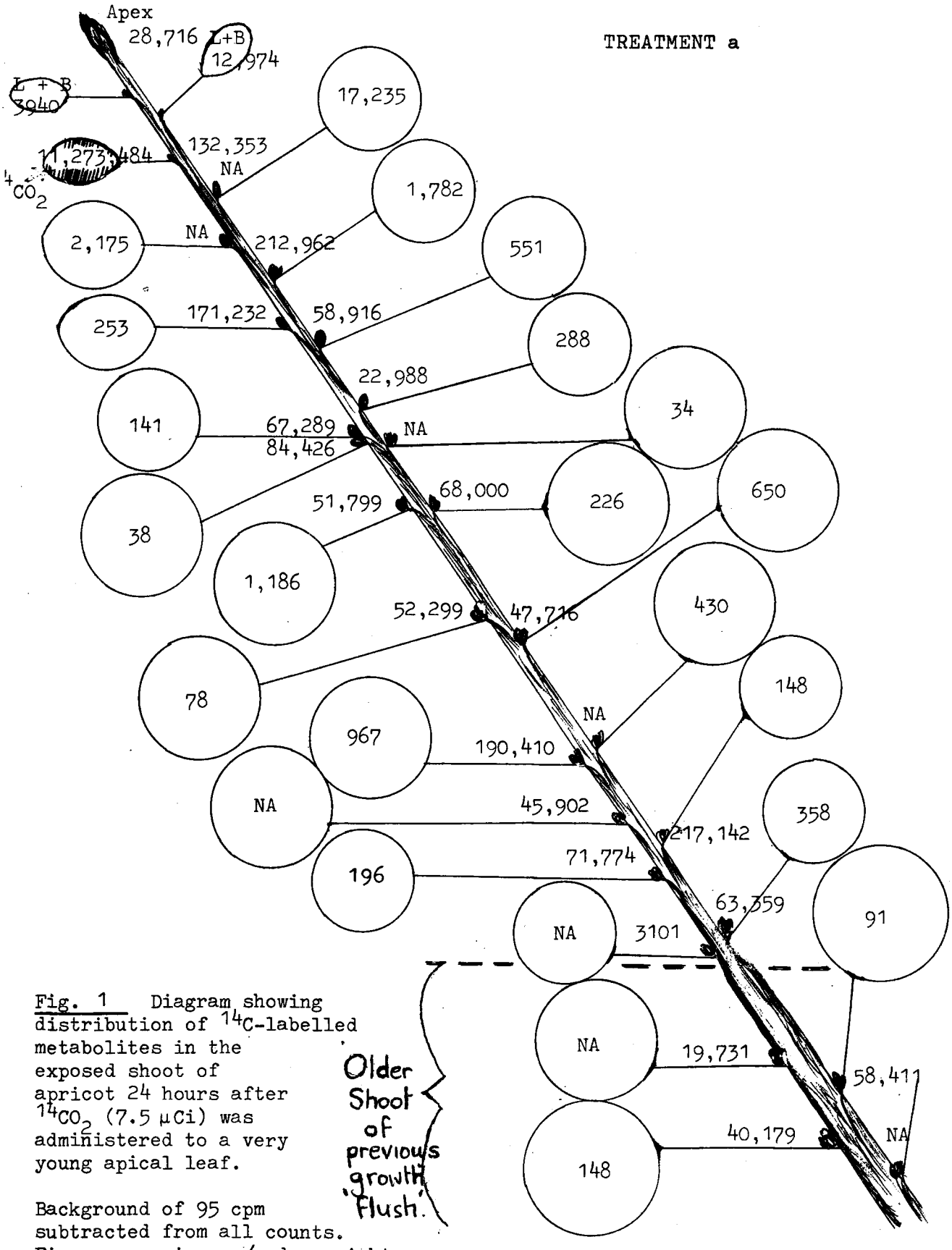


Fig. 1 Diagram showing distribution of ^{14}C-labelled metabolites in the exposed shoot of apricot 24 hours after $^{14}CO_2$ (7.5 µCi) was administered to a very young apical leaf.

Background of 95 cpm subtracted from all counts.
Figures are in cpm/g dry weight.
NA = No Activity
L + B = Leaf + Bud

TREATMENT a

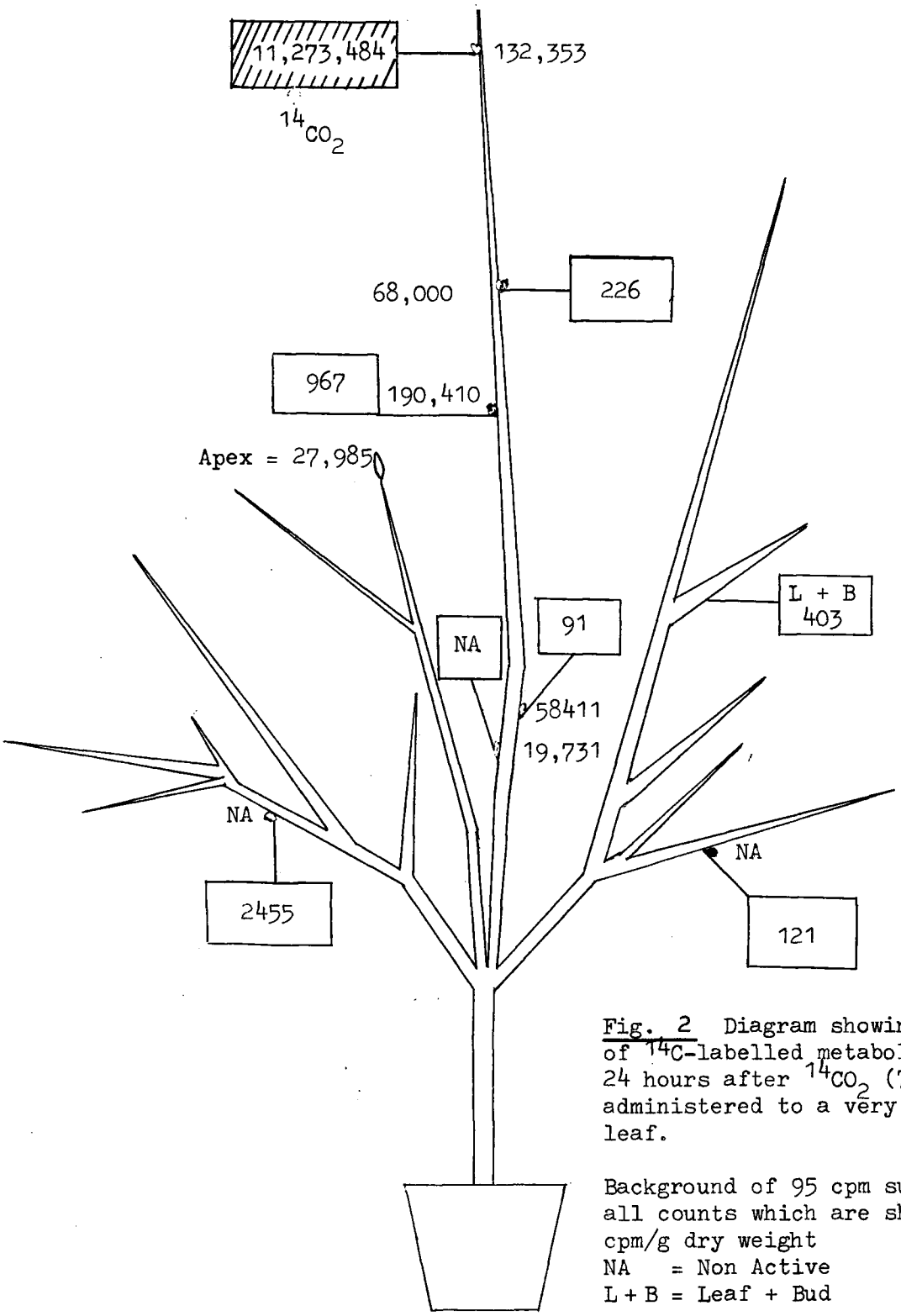


Fig. 2 Diagram showing distribution of ^{14}C-labelled metabolites in apricot 24 hours after $^{14}CO_2$ (7.5 μCi) was administered to a very young apical leaf.

Background of 95 cpm subtracted from all counts which are shown as cpm/g dry weight
NA = Non Active
L + B = Leaf + Bud

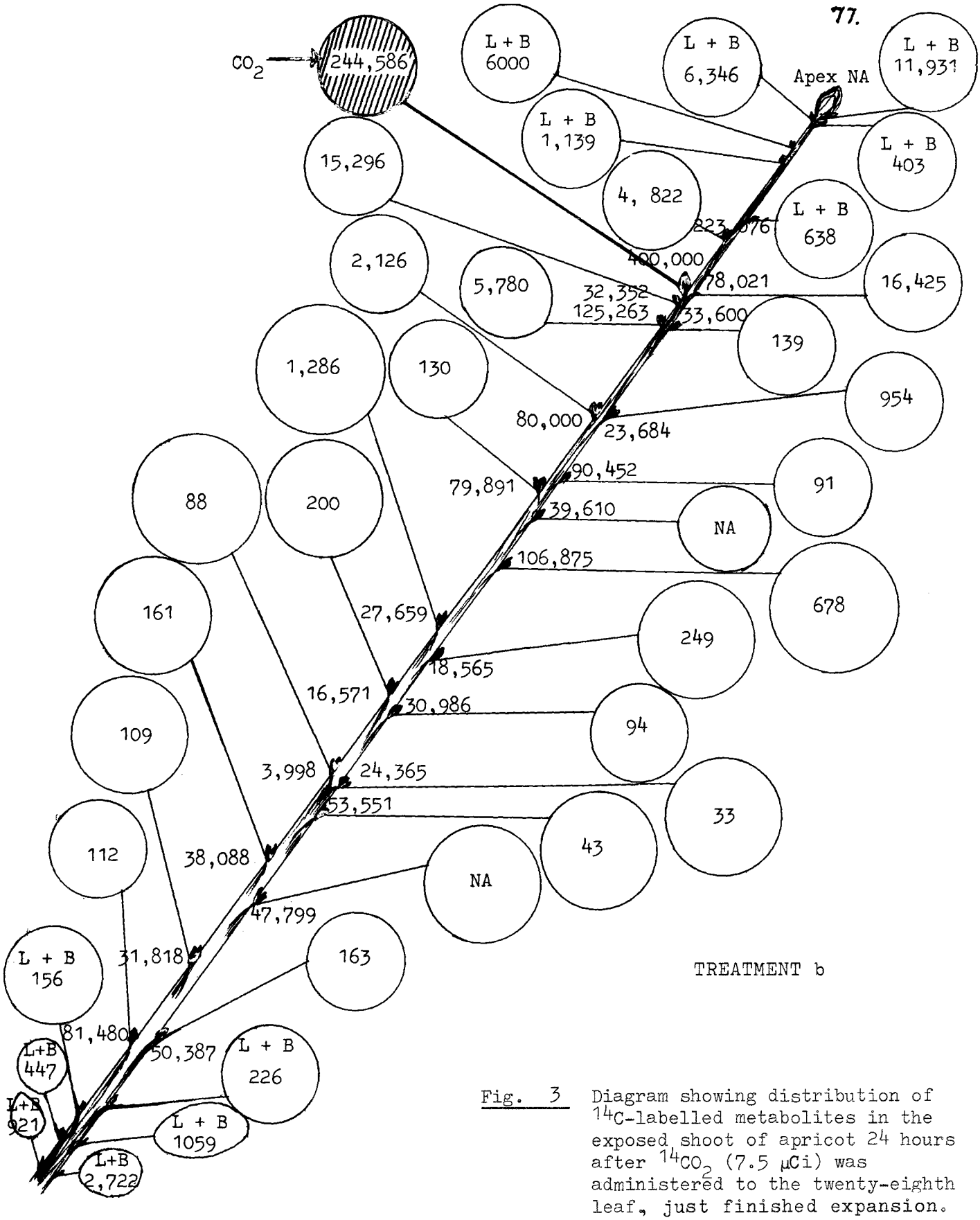
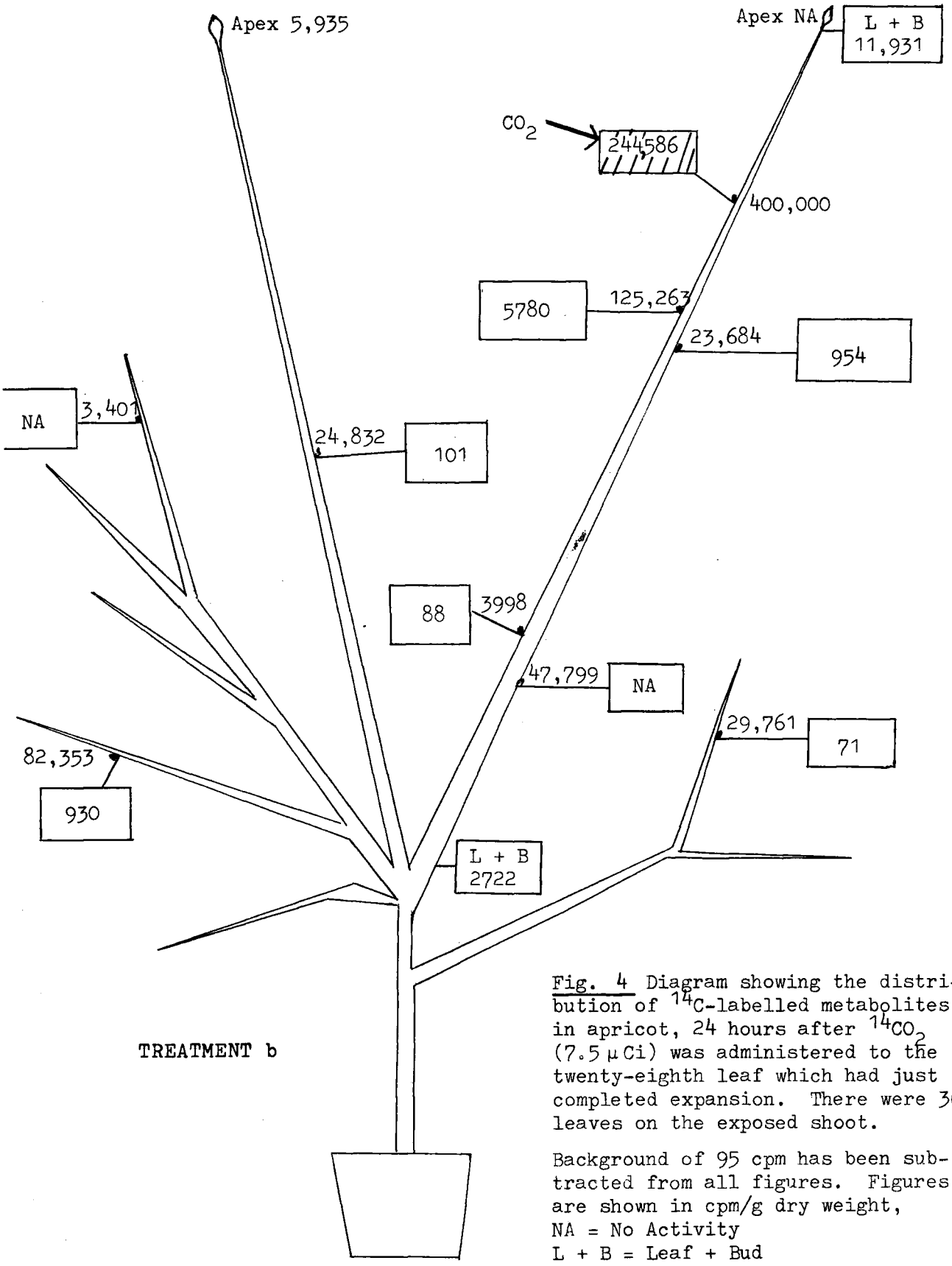


Fig. 3 Diagram showing distribution of ^{14}C-labelled metabolites in the exposed shoot of apricot 24 hours after $^{14}CO_2$ (7.5 μCi) was administered to the twenty-eighth leaf, just finished expansion.

Background of 95 cpm has been subtracted from all figures.
Figures are shown in cpm/g dry weight, NA = No Activity
L + B = Leaf + Bud



TREATMENT b

Fig. 4 Diagram showing the distribution of ^{14}C-labelled metabolites in apricot, 24 hours after $^{14}CO_2$ (7.5 μCi) was administered to the twenty-eighth leaf which had just completed expansion. There were 36 leaves on the exposed shoot.

Background of 95 cpm has been subtracted from all figures. Figures are shown in cpm/g dry weight,
NA = No Activity
L + B = Leaf + Bud

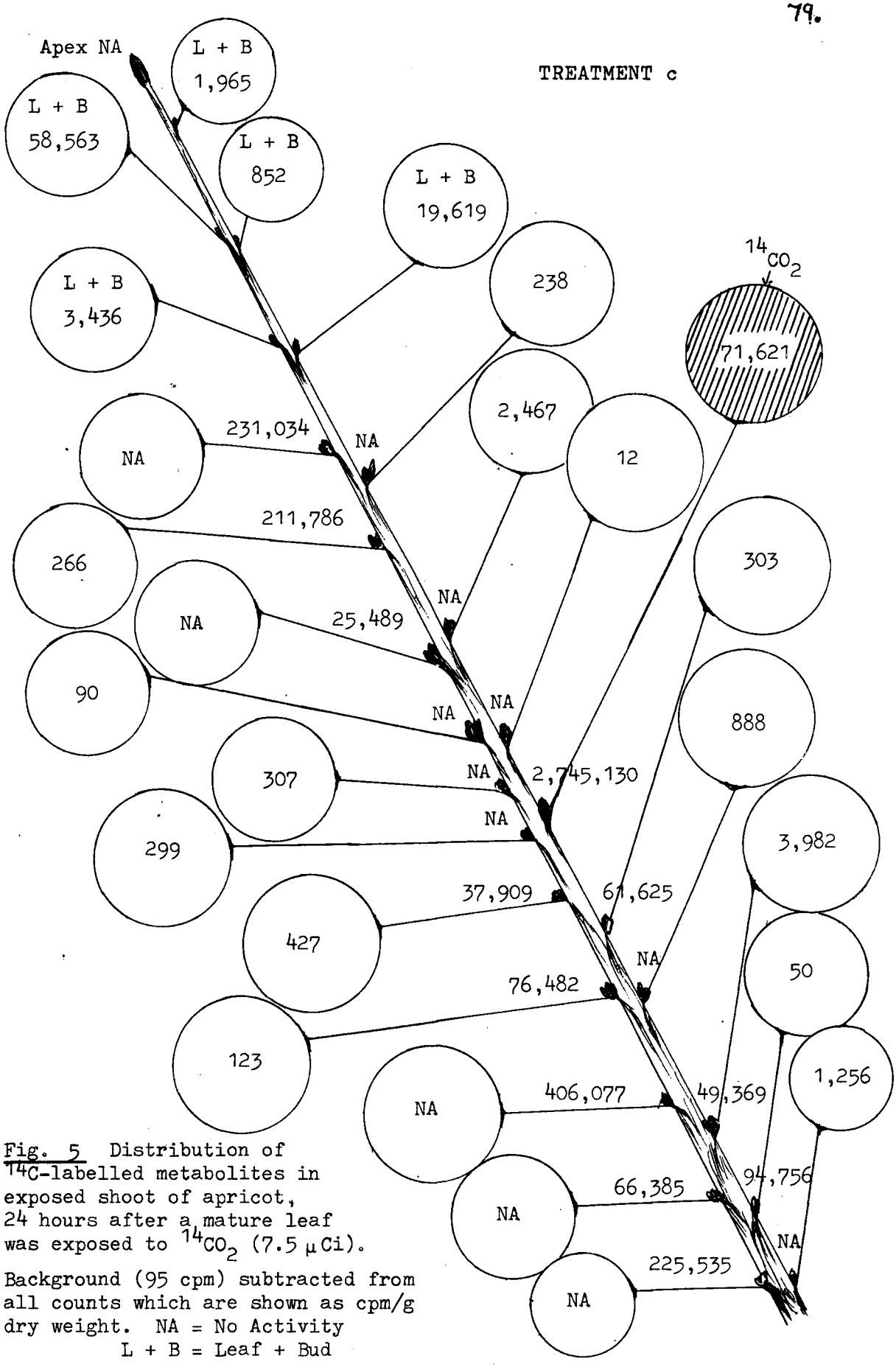
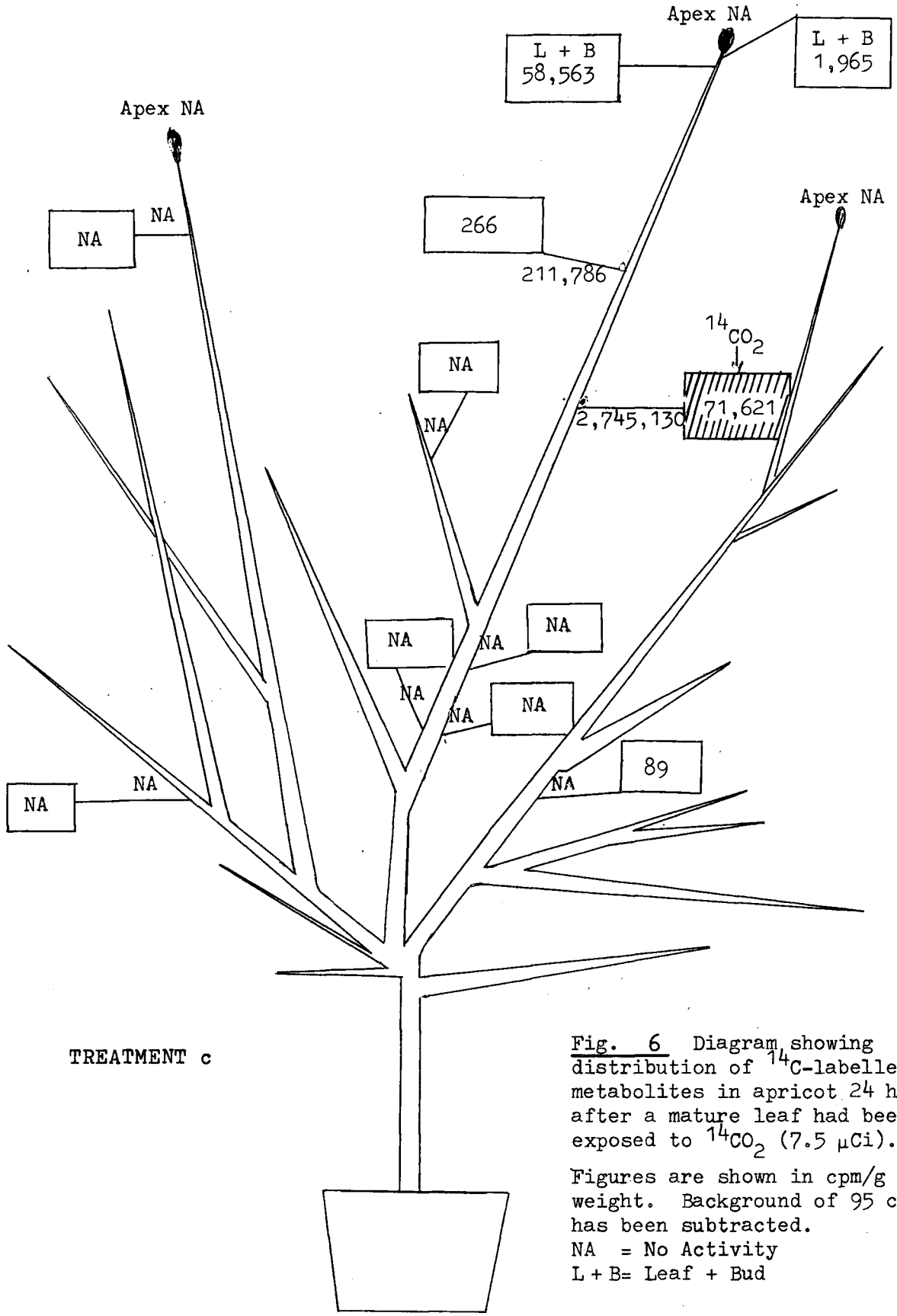


Fig. 5 Distribution of ^{14}C-labelled metabolites in exposed shoot of apricot, 24 hours after a mature leaf was exposed to $^{14}CO_2$ (7.5 μCi).

Background (95 cpm) subtracted from all counts which are shown as cpm/g dry weight. NA = No Activity
L + B = Leaf + Bud



TREATMENT c

Fig. 6 Diagram showing distribution of ^{14}C-labelled metabolites in apricot 24 hours after a mature leaf had been exposed to $^{14}CO_2$ (7.5 μCi).

Figures are shown in cpm/g dry weight. Background of 95 cpm has been subtracted.
NA = No Activity
L + B= Leaf + Bud

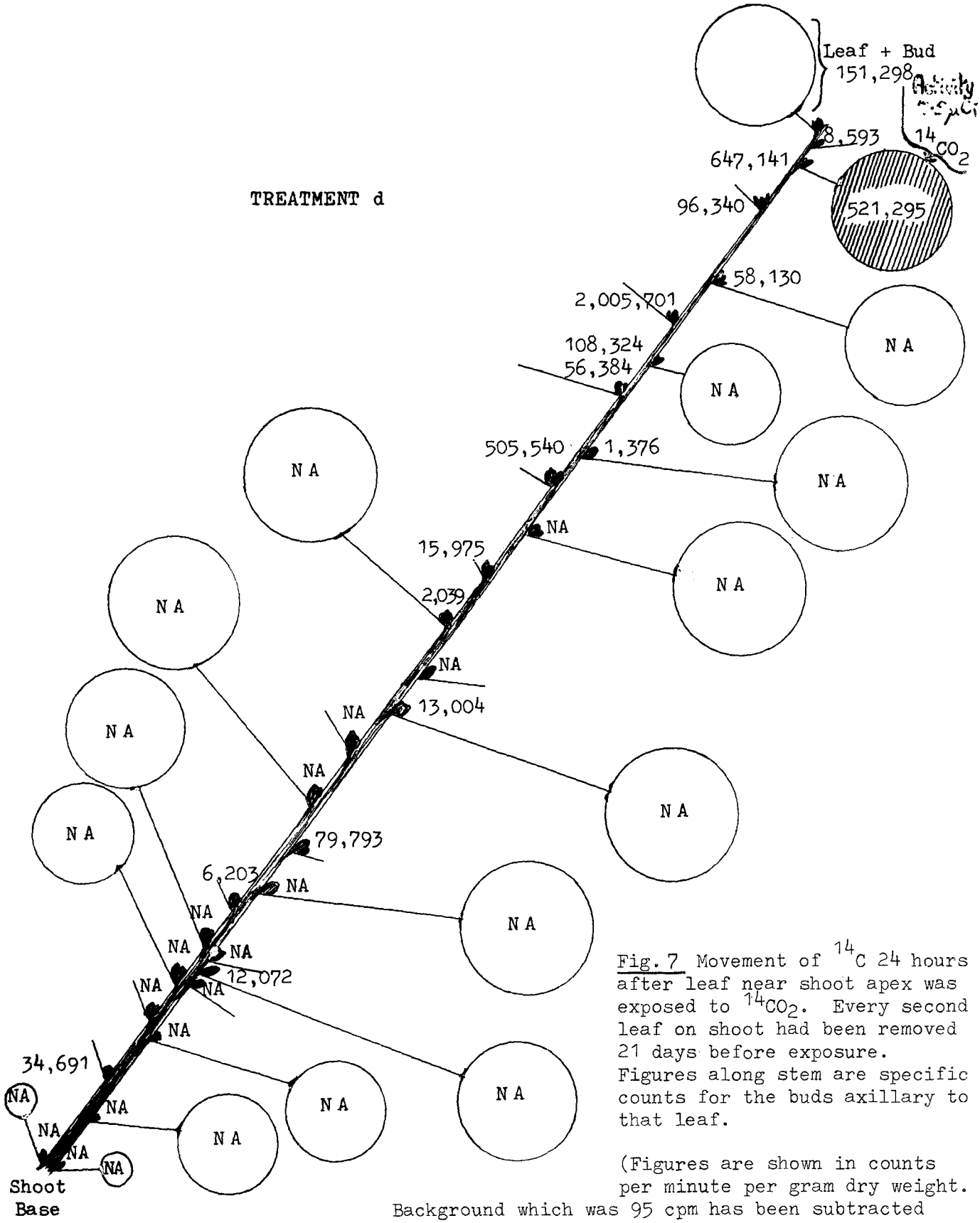


Fig. 7 Movement of ^{14}C 24 hours after leaf near shoot apex was exposed to $^{14}CO_2$. Every second leaf on shoot had been removed 21 days before exposure. Figures along stem are specific counts for the buds axillary to that leaf.

(Figures are shown in counts per minute per gram dry weight. Background which was 95 cpm has been subtracted from all counts prior to conversion on a dry weight basis.
NA = non active after removal of background.)

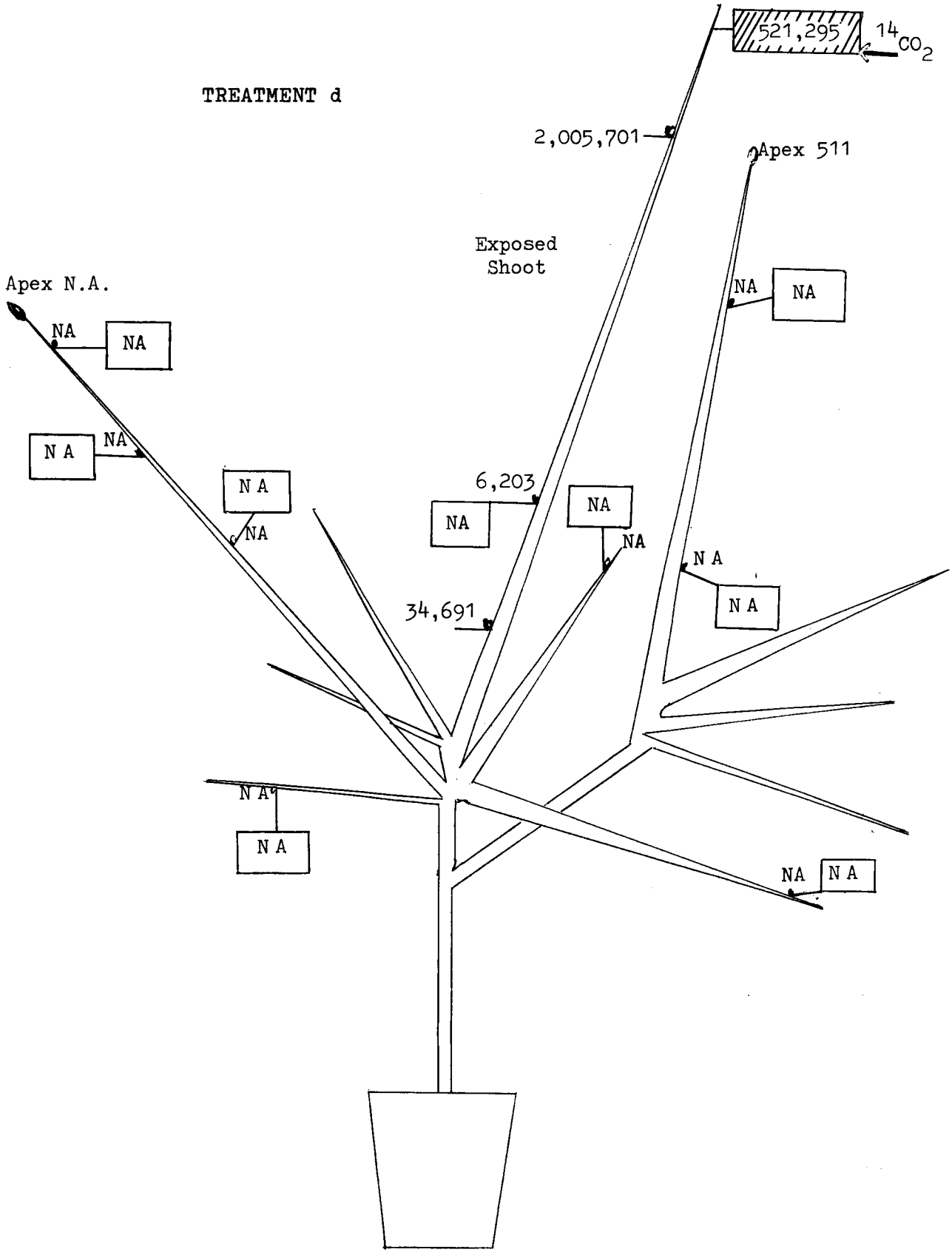


Fig. 8 Randomly selected leaf and bud samples indicating movement of ^{14}C in tree 24 hours after leaf exposure to $^{14}CO_2$ (7.5 μCi)

little activity in the leaves on the previous growth 'flush'. Likewise there was some translocation of the labelled photosynthates to other parts of the tree, but again the movement was not universal (Figure 2).

When a leaf just finished expansion was exposed to $^{14}CO_2$, it appears that the labelled photosynthates formed in that leaf were exported to all parts of the shoot on which it was located (Figure 3), and to almost all parts of the tree (Figure 4). In contrast, when a fully mature leaf was exposed, there was virtually no labelled ^{14}C-compounds found in the leaf or the bud samples from various parts of the tree (Figure 6). Similarly export throughout the shoot was also reduced, consequently a very high activity was found in the axillary buds of the exposed leaf (2,745,130 cpm/gram dry weight). It would appear from this figure, that at this stage in the ontogeny of the leaf photosynthates formed in that leaf are principally exported to the flower and vegetative buds initiated in the axil of that leaf.

In treatment d, every second leaf had been removed three weeks prior to the exposure of a fully expanded partly mature leaf to $^{14}CO_2$. (Defining maturity, the author considers that once a leaf has fully expanded, has taken on a darker green colouration, and the leaf itself thickens so that if feels harder when rubbed between the fingers, it can be considered mature). The fact that labelled photosynthates are to be found in 64% of the bud samples taken from defoliated nodes on a shoot where all but one leaf was non active, and on which 53% of the bud samples taken from non defoliated nodes were non active, indicates that buds without their subtending leaf are still vascularly connected to the central stele of the shoot (Figure 7).

The counts for the leaves and buds on this shoot on which the partly mature fully expanded leaf was exposed are relatively low when compared with treatments a, and b, and it could well have been that in this particular tree the roots had had a high requirement for photosynthates at the time when the exposed leaf was exporting so that much labelled photosynthate moved to the roots which unfortunately were not sampled. This may account for the lack of activity in the random leaf and bud samples taken from various parts of the tree, as well as the lack of high activity throughout the shoot on which the exposed leaf was attached.

Finally one point which was of some surprise was the overall lack of high activity in the apices sampled from the four trees. Admittedly the apex had yellowed on the treated shoot in treatment b, and on a sample shoot in treatment d. Yellowing is the stage prior to abscission so perhaps these apices were no longer vascularly connected. However the results do reveal that only four of the nine apices had activity above background and only in treatment a, was the apex able to attract any sizeable amounts of labelled photosynthates. Their ability to attract metabolites in this case, did not compare very favourably with axillary buds on a dry weight basis.

Experiment 8: Effect of DCMU and sugar on flower-bud initiation in apricot.

A. EXPERIMENTAL METHODS

The herbicide diuron, also known as DCMU (3- (3,4-dichlorophenyl) -1,1-dimethylurea) is a photosynthesis inhibitor, (Bishop, 1958), inhibiting the photochemical phase involving the photolysis of water (Minshall, 1960) and also inhibiting the cytochrome reduction associated with photosynthesis (Duysens, Amesz, and Kamp, 1961). Such inhibitors have previously been reported for other phenylureas (Moreland et al., 1958).

Diuron has further been found to inhibit (oxidative) photosynthetic phosphorylation (Bishop, 1958; Hilton, Jensen and Hull, 1963).

The inhibitory action of diuron on photosynthesis apparently persists for some time. In barley treated with diuron, photosynthesis was still less than 5% of control two weeks after application (Prasad pers. comm.).

Hilton (1959) in a search for metabolites that are able to reverse this inhibitory action of the phenylureas, found carbohydrates effective. Later work by Genter and Hilton (1960) illustrated at least a partial protection from injury caused by fenuron, diuron, monuron, neburon, and DMU (1,1-Dimethyl urea), if sucrose solutions were also applied.

(1) Material and treatments

Ten apricot trees, 16-24 months after budding, had the following treatments applied on January 4, January 25, and February 7, 1970:

Treatment 1 Control.

Treatment 2 Agral (Wetting Agent).

Treatment 3 3×10^{-5} M DCMU + Agral.

Treatment 4 6×10^{-5} M DCMU - Agral.

Treatment 5 9×10^{-5} M DCMU + Agral.

Treatment 6 3×10^{-5} M DCMU + 10% Sucrose + Agral.

Treatment 7 6×10^{-5} M DCMU + 10% Sucrose + Agral.

Treatment 8 9×10^{-5} M DCMU + 10% Sucrose + Agral.

Treatment 9 10% Sucrose + Agral.

DCMU and sucrose were both applied as solutions painted onto individual leaves but not to buds. Both the top and underside of each leaf was painted.

The experiment which was analysed as a mixed level split plot design, was terminated on February 19, 1970, and flower-bud counts were made on that day.

B. EXPERIMENTAL OBSERVATIONS AND RESULTS

The application of sucrose appeared to overcome some effects of DCMU. Comparison of treatments with or without sucrose at all levels of DCMU demonstrated that DCMU when applied without sugar resulted in chlorophyll breakdown, so that the leaves were yellowed between the veins. This breakdown presumably occurred because photosynthesis no longer took place. Treatments in which DCMU and sugar were applied together obviously had differing effects on the leaf as the leaf blade remained dark green at all stages.

In Table 18, DCMU at all concentrations failed to reduce the mean number of flower-buds formed per node as compared with controls without sugar, or the control treatment with sugar. This indicates that either the DCMU did not work and so in fact photosynthesis was unaffected or alternatively that photosynthesis was stopped, but hormone production in the leaf remained unaffected. Since carbohydrates could supposedly be moved from other parts of the tree, then initi-

ation processes were able to continue, as both hormones and carbohydrates were still available to the buds. In view of the chlorotic effects which were observed in the leaf which one could expect could quite likely accompany a breakdown of photosynthesis, and in view of the reversible effect of sugar on such chlorosis the latter suggestion would appear to be more correct.

Table 18 Effect of DCMU and sugar on flower-bud initiation in apricot

Parameter / Treatment	Mean number of flower-buds per shoot	Mean number of flower-buds per node
No Sucrose		
Control (No Wetting Agent)	31.9 ab	1.570 a
Control (+ Wetting Agent)	52.7 a	1.719 a
3 x 10^{-5} M DCMU	37.8 ab	1.628 a
6 x 10^{-5} M DCMU	41.9 ab	1.649 a
9 x 10^{-5} M DCMU	48.0 ab	1.646 a
10% Sucrose		
Control (+ Wetting Agent)	39.2 ab	1.671 a
3 x 10^{-5} M DCMU	36.1 ab	1.646 a
6 x 10^{-5} M DCMU	49.2 ab	1.565 a
9 x 10^{-5} M DCMU	29.1 b	1.475 a
S.E. of Mean		
72 df	± 6.8	± 0.097
C.V. %	52.9	18.89

Duncan's test: figures in the columns differ significantly if not sharing the same letter (P = 0.05).

Experiment 9: Effect of sugar and nitrogen on flower-bud initiation in apricot.

A. EXPERIMENTAL METHODS

(1) Material and treatments

Apricot trees, 16-24 months after budding, had the following treatments applied to two branches of each of ten trees:

1. Control (No Tween 20).
2. Control (Tween 20).
3. 1% Urea + Tween 20.
4. 10% Sucrose + Tween 20.
5. 1% Urea + 10% Sucrose + Tween 20.

The experiment was a randomised block design and treatments were applied at weekly intervals commencing on December 27, 1969. All treatments were painted on the top and underside of individual leaves taking particular care not to apply any to the axillary buds. When treatments were applied, the shoots were still elongating and the apices were producing nodes and leaves quite quickly. Thus the treatments were being applied at a stage early enough to have an effect on the process of initiation.

B. EXPERIMENTAL RESULTS

The experiment was terminated on February 21, 1970. The treatments had been applied eight times in all and the results are shown in Table 19. There was no response to urea or sucrose solutions or to a combination of these nutrients. Possibly the apricot is not able to absorb sucrose solutions applied to leaves, or has not the enzyme urease in the leaf to enable breakdown of the absorbed urea.

Table 19 Effect of sucrose and urea on flower-bud initiation in apricot

Parameter / Treatment	Mean number of flower-buds per node per shoot
Control	1.708 a
Control + Tween 20	1.755 a
1% Urea + Tween 20	1.872 a
10% Sucrose + Tween 20	1.688 a
1% Urea + 10% Sucrose + Tween 20	1.884 a
S.E. of Mean 76 df	± 0.07
C.V. %	17.57

Duncan's test: figures in the column differ significantly if not sharing the same letter (P = 0.05)

DISCUSSION

PART 3 IMPORTANCE OF CARBOHYDRATES

Early workers on flower-bud initiation in fruit trees related the effect of defoliation, shading, nitrogen manuring, and certain cultural practices to the carbohydrate level within the tree. They also attached great importance to the ratio of the level of carbohydrates with the level of nitrogen compounds in the plant (Magness, Edminster and Gardner, 1917; Roberts, 1920, 1923; Harvey and Murneek, 1921; Swarbrick, 1928; Haller and Magness, 1933).

In these experiments, ^{14}C-radioisotope studies have demonstrated that carbohydrates manufactured in a leaf are exported throughout that shoot (Figures 1, 3, 5, 7) and that buds are big "sinks" for photosynthates, much bigger "sinks" in fact than leaves (Table 17).

Buds are also able to attract photosynthates irrespective of the presence or absence of the subtending leaf. This was demonstrated in treatment d of Experiment 7, where every second leaf on the treated shoot had been removed three weeks prior to the exposure of a partly mature leaf to $^{14}CO_2$ for 24 hours. High activity was found in most buds on the treated shoot, which showed that buds at defoliated nodes were still vascularly connected to the central stele of the stem.

Labelled photosynthates were also found to be transported from the exposed leaf throughout the tree (Figures 2, 4). This movement did not occur in all exposed trees and obviously depends on the current needs of the shoot at any particular point in time. Thus a shoot with many developing buds in the axils of its leaves is unlikely to be a big exporter of photosynthates.

Variations in photosynthate export from the exposed leaf were also observed and it appears apricot leaves become contributing organs well before they achieve full size. Kriedemann (1968) has also reported this fact. In this respect then apricot resembles peach (Kriedemann, 1968), grape (Hale and Weaver, 1962), and a vast majority of agronomic plants (Wardlaw, 1968), but differs from citrus (Kriedemann, 1969b). In orange (Kriedemann, 1969a) and lemon (Kriedemann, 1969b), little export of labelled photosynthate occurred until the leaf was fully mature.

However the work of Kriedemann (1968) on apricot differs from the present study because Kriedemann removed shoots from trees, kept them in water, and exposed a terminal leaf to $^{14}CO_2$ after separation from the tree. Thus photosynthates formed in the exposed leaf were not able to be exported out of the shoot as could normally happen, and which was shown to happen in Figures 2 and 4 in this study. This then could account for Kriedemann's observation that "mature apricot leaves showed extensive import from a terminal source leaf".

The author suggests from the isotope work reported here than an apricot leaf exports photosynthates to the axillary buds, the shoot, and to the tree to some extent, from the stage when it is partly expanded, about one-third, to the stage when it is fully expanded. Once the leaf begins to mature (see Results for definition of maturity) export to the tree is greatly reduced, to the shoot is partly reduced, and a great deal of the photosynthates formed in the leaf are utilized in the process of initiation of floral buds and a vegetative bud in the axil of that leaf.

The results obtained from these ^{14}C-radioisotope studies have

also shown that a reduced supply of carbohydrates from the subtending leaf to the axillary buds would hardly limit floral initiation at that node, as carbohydrates are very mobile and are readily available from other leaves somewhere in the tree canopy. The experiments using DCMU substantiate this contention. DCMU is a known photosynthesis inhibitor (Bishop, 1958) and yet when applied to all leaves on a shoot it failed to reduce flower-bud initiation on that shoot compared with control. This would indicate that carbohydrates were transported into these DCMU treated shoots and since the leaves were still able to manufacture hormones, all factors necessary for flower-bud formation were present. The sugar applied in some treatments appeared to alleviate the inhibitive effect of DCMU on chlorophyll breakdown. However there was no response in initiation to this addition of sucrose to the leaf (Table 18). This result was repeated in Experiment 9 (Table 19), where foliar applications of 1% Urea, 10% Sucrose and 1% Urea + 10% Sucrose were unable to increase flower-bud initiation as compared with control. The lack of response to urea is not surprising as leaves of stone fruits contain little urease, an enzyme initially responsible for the breaking down of urea (Baxter, 1958), and are not nearly as responsive as apple to foliar urea sprays (Norton and Childers, 1954).

CHAPTER V

GENERAL DISCUSSION

In the three discussions at the conclusion of each experimental section, a number of important facts have arisen which when linked with various observations noted during the conduct of these experiments, may allow the following pattern of shoot growth and subsequent axillary flower-bud formation in apricot to be presented.

1. Initiation of vegetative and floral buds in the leaf axils on shoots of apricot.

The meristematic activity and tissue differentiation at the apex of a shoot leads to the formation of nodes and associated leaves arranged in an alternate pattern along the shoot. At each node meristematic tissue is present in the axil of each leaf. This meristematic area is indicated by a small "hump" which in the early stages of development is covered by ligule-like structures. These structures may persist in the axil of the leaf for some time after they have opened to expose the "hump", but eventually they will abscise. Their function in the early stages of lateral meristem development would appear to be to protect this delicate tissue from drying out.

The exact pattern of development which occurs within this lateral meristem leading to the formation of separate floral and vegetative buds has not been investigated in this study. However it would appear that the development of floral buds is particularly sensitive to 'stimuli' arising from other parts of the tree, so that conditions suitable for flower-bud initiation within the lateral meristem can be readily modified. The effect of various stimuli will also vary depending on the stage of development of the flower-bud. Thus a stimulus may need to:-

(1) be continuously available to the lateral meristem during the development of floral buds, or

(2) be available at only one particular stage during the development of flower-buds, or

(3) be available at the correct level or concentration at a particular stage, for instance in the early induction of flower-buds, or

(4) be available in the correct sequence where more than one stimulus is required for flower-bud formation. For instance flower-bud development may require Stimulus A from the leaves right throughout development, and Stimuli B, C and D in that order arriving from different sources to the lateral meristem.

When all the requirements for flower-bud initiation are satisfied, multiple flower-bud development occurs in the leaf axils, and often when this occurs, it is noticed that lateral vegetative buds may be absent.

In the experiments reported here, removal of the subtending leaf at any stage during the development of the flower-buds has an inhibitory effect on such development. The earlier the removal of the leaf the greater is the effect on floral initiation and it would appear that a stimulus from the leaf is continuously required for the initiation of flower-buds (i.e. induction and development as defined on page 3).

The removal of leaves does not appear to affect greatly the development of vegetative buds and in fact these buds appear to be far less dependent on reception of stimuli derived from the subtending leaf. Completely defoliated shoots still had a vegetative bud initiated at each node, although such buds were smaller in size compared with vegetative buds on non-defoliated shoots. In addition, the development of

vegetative buds appears to be relatively unaffected by shading, changes in daylength, changes in temperature, even changes in nutrition (Data not presented). However early shoot pruning did have an effect on initiation of vegetative buds. In apricot when elongating shoots were pruned to approximately half of their original length, there developed from the undifferentiated meristematic tissue in the axils of the topmost leaves a number of vegetative buds, usually three. Floral buds failed to develop from these lateral meristems. This occurrence of multiple vegetative bud formation is very rare in apricot, and it appears that of all the treatments applied to apricot shoots, this is the only treatment which promoted such a response.

Brooks (1940) and Phillipson (1949) report the same phenomenon in plants other than apricot, provided the pruning is carried out at an early stage in the development of the lateral meristem. They provide no explanation for such an occurrence. However it could well be that if an accumulation of metabolites occurred at the distal end of the pruned shoot, remembering that sap tends to flow to the highest point on a shoot, this accumulation may promote initiation of vegetative buds rather than floral buds.

It would seem from the presented observations that for the development of vegetative and floral buds, different stimuli appear to be required.

2. Role of the shoot apex on flower-bud initiation.

The role of the shoot apex on flower-bud initiation in apricot does not appear to be very important. Thus in Experiment 1, flower-bud formation occurred on shoots irrespective of the presence or absence of the apex. In this Experiment, the presence of the apex

on the treated shoots of half the trees was maintained by limiting the total number of shoots on the tree. Normally, flower-bud initiation in apricot as in other fruit trees, occurs principally after cessation of shoot growth (Barnard and Read, 1932, 1933). But these experiments show that this cessation is not mandatory for flower-bud initiation. At cessation of shoot growth the apex has quickly yellowed and abscissed so hence is not present on a shoot when the majority of the flower-buds initiate.

3. The role of the subtending leaf on flower-bud initiation.

In the defoliation treatments carried out in the first five experiments reported in this thesis, the following was observed:

(a) removal of a very young leaf severely reduces flower-bud initiation at that node (Tables 7a, 10, 11)

(b) removal of a fully expanded leaf reduces flower-bud initiation at that node (Table 10) but not always to the extent of (a) (Table 7a).

(c) removal of 25% of a leaf slightly reduces initiation of flower-buds at that node (Table 6).

(d) removal of 50% of a leaf slightly reduces flower-bud initiation at that node (Tables 6, 12).

(e) removal of 95% of a leaf greatly reduces flower-bud initiation at that node (Table 6).

(f) alternate leaf removal along a shoot showed that initiation at non-defoliated nodes was not significantly less than flower-bud initiation on the control shoots. However initiation at defoliated nodes was significantly reduced compared with control or with non-defoliated nodes (Tables 3, 5, 8).

From these results it would seem that some factor arising from the leaf is essential for flower-bud initiation to take place in the axil of that leaf. This factor would also seem to be either produced in small quantities or to be immobile (as indicated in (f)), because alternate leaf removal has shown that the leaf factor is not able to move to neighbouring defoliated nodes and so partly or wholly compensate for the loss of the subtending leaf.

The formation of this leaf factor was only slightly inhibited by 50% shading of the leaf (Tables 4, 12), but was inhibited by 100% shading (Tables 2, 4, 12), and by removal of greater than 50% of the leaf as reported in this study and in the work of Roberts (1923).

The formation of this leaf factor would seem to occur under long days (16 hours light) or short days (9 hours light), and at low (60°F) or high (75°F) temperatures, as revealed by the results of the controlled environment experiment (Experiment 6). However long days and high temperatures were slightly more promotive of flower-bud initiation though not significantly so.

Thus the characteristics of this leaf factor would seem to be as follows:

(1) synthesis may be promoted by light,

(2) synthesis is not greatly affected by light intensity otherwise 50% shading would have had an inhibitive effect,

(3) synthesis would not seem to be greatly influenced by daylength,

(4) higher temperatures may be slightly promotive to the synthesis of this leaf factor,

(5) sufficient quantities can be formed in only 50% of the leaf to promote flower-bud initiation,

(6) it may be formed in small quantities, or

(7) movement in the plant may be restricted to movement from the leaf to the axillary buds but not along the stem.

The nature of this leaf factor could take many possible forms but three obvious and most likely suggestions are that this factor belongs to one of the following classes:

(i) Products of photosynthesis (possibly carbohydrates).

(ii) Nitrogenous compounds, such as an essential amino acid or a protein.

(iii) Hormones, this includes both growth promoters and growth inhibitors.

4. Carbohydrates as the essential leaf factor.

The requirement for a continuous supply of carbohydrates for flower-bud initiation is understandable as active cell division and expansion requiring such metabolites is taking place in the lateral meristem. However are these carbohydrates the factors necessary for initiation?

^{14}C-studies have illustrated the mobility of photosynthates produced in one leaf along an apricot shoot. This movement into the shoot, and into the other leaves and buds on that shoot appears to take place to some extent right throughout the ontogeny of a leaf. Likewise a single leaf can supply photosynthates to other parts of the tree especially when the leaf is young (Figures 2, 4). Thus carbohydrates appear to be very mobile. Further evidence to support

such a contention was obtained in Experiment 8, where all the leaves on a shoot were treated with DCMU, a photosynthesis inhibitor. Assuming DCMU did inhibit photosynthesis in apricot as it does in other plants, these shoots then had leaves incapable of synthesising carbohydrates in very high quantities. However initiation of flower-buds on these shoots was not affected by this lack of carobhydrates from the leaves (Table 18), and so one can only conclude that carbohydrates were able to be moved from other parts of the tree. If carbohydrates from all parts of a tree are able to be "pooled" and subsequently redistributed, then it appears likely that carbohydrates only become limiting when large areas of the tree are shaded as has been shown by Harley et al. (1942) and Jackson (1968).

Fifty per cent leaf and shoot shading had little inhibitory effect on flower-bud initiation. As such shading could be expected to reduce photosynthesis to some extent in those parts, it can only be assumed that initiation of flower-buds remained unaffected by such treatments because carbohydrates were able to move quite readily to such leaves and shoots from other parts of the tree. 50% leaf removal could likewise be expected to have inhibitory effects on initiation. However this too was without significant effect on flower-bud initiation presumably because carbohydrates were not a limiting factor.

The ^{14}C-studies also indicated that a leaf admittedly in an enriched carbon dioxide atmosphere, was capable of producing quite large quantities of photosynthates, even in a period of 24 hours.

The author feels that in the light of the presented evidence showing that carbohydrates are mobile in apricot, and are formed in high quantities in leaves it is very doubtful if carbohydrate is the essential leaf factor.

5. Nitrogen compounds as the essential leaf factor.

Nitrogen when applied to the roots of apricot trees is able to improve initiation under some conditions as in the growth cabinet experiment (Table 15) but failed to improve initiation to the same extent when applied to trees in Experiment 2 (Table 4).

Nitrogen when applied as a foliar spray of urea failed to improve initiation in the axils of the treated leaves (Table 19), and in other work done during this investigation (unpresented).

Numerous reviews on nitrogen metabolism show that nitrogenous compounds are present in quite high amounts, particularly in leaves where secondary amino acid synthesis can take place. Nitrogen compounds are also quite mobile in plants at least in some forms. Thus if nitrogen compounds were the essential leaf factor one could expect that due to their mobility and their occurrence in plants in quite high amounts, these compounds would be available to the lateral meristem at all nodes irrespective of the presence or absence of a leaf. However alternate leaf removal treatments as already emphasised, have shown that the leaf factor is either immobile, or produced in small quantities, as initiation of flower-buds was greatly reduced at defoliated nodes. On these grounds it would appear very unlikely that nitrogen compounds were in fact the essential leaf factor, although admittedly, the case against nitrogen compounds has not received as much study in this investigation as the case against carbohydrates.

6. Hormones as the essential leaf factor.

Since this leaf factor appears to be either immobile, and/or occurs in relatively low amounts in the leaves, and since carbohydrates and nitrogen compounds do not comply with these requirements, hormones

in the leaf appeal as the obvious remaining alternative for this factor.

The role of hormones in flower-bud initiation in apricot has received little study, although Bradley and Crane (1960) found that gibberellic acid (GA_3) will reduce flower-bud initiation in apricot and Jackson (pers. comm.) found that the growth retardants CCC and B 995 were unable to improve initiation in apricot to the extent that these retardants could in other fruit trees (Cathey, 1964; Modlibowska, 1965; Sloane, 1968).

In this investigation no work has been carried out to measure the levels of hormones in apricot leaves at various stages of leaf development. Such a study would be of great interest in the light of present knowledge that hormones are produced in leaves, often in quite small amounts, and that such synthesis is promoted by light of variable intensity and period depending on the photoperiodic response of the plant. Hormones can also be relatively immobile in plants compared with carbohydrates, particularly growth promoters such as cytokinins. In the flowering response of photoperiod sensitive plants hormones are known to be involved and in the most recent comprehensive review on flowering by Chailakhyan (1968), many hormones have been proposed as having possible roles in the flowering process of plants.

In apricot therefore, it could well be that the factor which forms in the leaf, and is so essential for initiation of flower-buds in the axil of that leaf may be of a hormonal nature.

CHAPTER VI

SUMMARY

1. In the apricot one leaf is produced at each node of a young shoot, and in the axil of this leaf one vegetative bud and a variable number of flower-buds are formed.

2. The subtending leaf produces some factor which is essential for flower-bud initiation to occur in the axil of that leaf.

3. The factor from the leaf is either produced in small quantities or is relatively immobile as shown by alternate leaf removal treatments.

4. The level of the factor from the leaf does not appear to be greatly affected by 50% leaf shading.

5. The level of the factor may be affected by 100% leaf shading depending on the age of the leaf at the time of shading.

6. The level of the factor from 50% of the leaf is still sufficient to bring about quite good flower-bud initiation at that node.

7. The level of the factor from only 5% of the leaf is insufficient to promote high flower-bud initiation at that node.

8. The synthesis of this leaf factor may be influenced by daylength, temperature and nutrition, but from the controlled environment experiment synthesis is not absolutely dependent on any one of these cues. Because of this lack of dependence on daylength apricot would appear to be a day neutral plant and so does not differ from many other deciduous fruit trees.

9. The nature of this leaf factor remains unknown although it would not appear to be a carbohydrate, or a nitrogenous compound, but may most probably be a hormonal compound.

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APPENDIX A

Table Experiment 1 - Basic data - Number of flower-buds per shoot

Replication No. \ Treatment		1	2	3	4
No Apex	1	4	0	5	15
	2	22	0	7	2
	3	34	0	18	26
	4	18	24	8	16
	5	32	27	8	6
	6	4	0	6	4
Total		114	51	52	69
Apex	1	33	10	16	12
	2	16	17	10	6
	3	47	28	19	29
	4	0	14	11	8
	5	89	0	15	29
	6	40	14	34	30
Total		225	83	105	114

Table Experiment 1 - Basic data - Number of vegetative buds per node

Replication No. \ Treatment		1	2	3	4
No Apex	1	1.00	1.00	1.00	1.00
	2	1.00	1.00	1.00	1.00
	3	1.00	1.00	1.00	1.00
	4	1.00	0.86	1.00	1.00
	5	0.88	0.93	0.96	1.00
	6	1.00	1.00	1.00	1.00
Total		5.88	5.79	5.96	6.00
Apex	1	0.93	0.71	1.00	1.00
	2	1.00	1.00	1.00	1.00
	3	0.95	0.87	1.00	1.00
	4	1.00	1.00	1.00	1.00
	5	1.00	1.00	0.85	0.95
	6	1.00	1.00	1.00	1.00
Total		5.88	5.58	5.85	5.95

Table Experiment 1 - Basic data - Number of flower-buds per node

Replication No. \ Treatment		1	2	3	4
No Apex	1	0.077	0.000	0.263	0.500
	2	0.917	0.000	0.350	0.038
	3	1.700	1.288	0.750	1.182
	4	1.125	1.710	0.670	1.000
	5	1.882	1.800	0.348	0.500
	6	0.167	0.065	0.400	0.222
Total		5.868	4.863	2.781	3.442
Apex	1	1.151	1.429	0.390	0.545
	2	0.516	1.000	0.526	0.273
	3	1.661	1.867	0.924	1.320
	4	0.776	0.778	0.282	0.450
	5	2.023	1.890	0.730	1.320
	6	1.574	1.750	0.692	1.364
Total		7.701	8.714	3.544	5.272

Table Experiment 2 - Basic data - Number of flower-buds per shoot

Replication No. \ Treatment		1	2	3	4	5
No Nitrogen	1	16	4	0	6	5
	2	39	7	0	24	40
	3	20	0	0	14	13
	4	29	0	0	14	34
	5	20	0	10	6	23
	6	34	19	0	13	28
Total		158	30	10	77	143
Nitrogen (1000 ppm)	1	39	7	11	12	11
	2	19	12	0	13	8
	3	9	0	0	7	9
	4	21	2	1	14	9
	5	19	1	11	18	2
	6	32	4	0	8	12
Total		139	26	23	72	51

Table Experiment 2 - Basic data - Number of flower-buds per node

Treatment / Replication No.		1	2	3	4	5
No Nitrogen	1	0.762	0.222	0.000	0.545	0.714
	2	2.053	0.778	0.000	1.412	2.105
	3	1.667	0.000	0.000	1.273	1.300
	4	2.071	0.000	0.000	1.167	1.889
	5	1.429	0.000	0.833	0.545	1.643
	6	1.889	2.375	0.000	0.929	1.867
Total		9.871	3.375	0.833	5.871	9.518
Nitrogen (1000 ppm)	1	2.167	0.636	1.375	1.200	1.000
	2	1.727	0.923	0.000	1.300	0.889
	3	0.900	0.000	0.000	0.636	0.818
	4	1.615	0.133	0.250	1.077	0.750
	5	1.462	0.100	1.375	1.800	0.167
	6	1.882	0.444	0.000	0.889	1.000
Total		9.753	2.236	3.000	6.902	4.624

Table Experiment 3 - Basic data - Number of flower-buds per node

Treatment / Replication No.	1	2	3	4	5	6	7
1	2.2727	1.0000	1.3636	1.5555	1.7692	1.2500	1.8000
2	1.6250	1.1875	1.6000	1.1666	1.2666	0.2000	1.7000
3	2.2352	0.9230	2.5714	0.8571	1.4000	0.0833	2.0833
4	1.6153	1.4545	0.7500	0.6428	1.3076	0.5000	1.1666
5	2.0769	1.6470	1.6666	1.3333	1.7000	0.9090	2.0000
6	0.9444	0.6000	1.2105	0.0000	1.0000	0.4000	1.3333
7	1.9230	1.4210	1.1000	0.8181	1.6666	0.3846	1.3076
8	1.1428	0.6153	1.3333	0.7857	1.1250	1.0000	1.0909
9	0.5000	1.2142	0.2727	1.0476	0.7690	0.8421	0.8333
10	1.1000	0.0000	0.8333	0.0000	0.3846	0.3000	0.8750
Total	15.4353	10.0626	12.7014	8.2064	12.3880	5.8690	14.1894

Table Experiment 3 - Basic data - Number of flower-buds per shoot

Treatment / Replication No.	1	2	3	4	5	6	7
1	24	10	15	28	23	20	27
2	26	19	16	14	19	3	17
3	38	12	18	12	21	1	25
4	21	16	6	9	17	6	14
5	27	28	15	16	17	10	24
6	17	9	23	0	15	6	24
7	25	27	11	9	20	5	17
8	16	8	12	11	9	9	12
9	7	17	3	22	10	16	10
10	11	0	10	0	5	3	7
Total	212	146	129	121	156	79	177

Table Experiment 3 - Basic data - Shoot length (cm)

Treatment / Replication No.	1	2	3	4	5	6	7
1	10.7	9.8	13.4	24.8	13.4	19.7	16.7
2	18.4	16.2	12.6	12.5	16.0	14.5	9.5
3	16.9	14.5	14.1	14.8	17.7	13.6	11.6
4	10.9	13.6	9.1	9.9	14.1	9.4	9.2
5	12.9	17.2	12.7	13.9	12.4	11.6	11.4
6	17.5	17.4	18.9	12.7	13.9	12.7	17.1
7	11.8	19.5	9.3	8.5	11.0	12.7	11.1
8	13.0	12.6	11.6	16.4	6.7	8.9	9.7
9	11.1	12.6	6.1	20.7	12.1	18.9	9.2
10	9.4	8.1	11.8	12.7	13.1	10.7	5.5
Total	132.6	141.5	119.6	146.9	130.4	132.7	111.0

Table Experiment 4 - Basic data - Number of flower-buds per node

Treatment / Replication No.	1	2	3	4	5	6	7	8	9
1	1.417	0.425	0.800	1.765	1.600	1.706	1.615	1.438	1.615
2	0.286	0.000	0.300	0.143	0.722	1.500	0.118	0.625	0.240
3	2.267	1.636	0.000	1.556	2.056	2.154	2.364	2.955	2.364
4	1.538	0.444	0.078	1.778	2.529	2.417	1.500	1.538	1.111
5	2.000	0.000	0.429	1.824	2.000	2.286	1.600	1.917	1.222
6	0.357	0.000	0.588	1.471	0.273	0.472	0.167	1.000	1.571
7	1.300	0.000	0.833	1.056	1.500	1.154	0.419	1.784	0.929
8	1.642	0.000	0.000	1.667	1.667	1.724	1.133	1.950	1.778
9	0.000	0.000	0.000	1.077	1.556	0.029	0.000	0.267	0.000
10	0.902	0.000	0.091	1.730	1.500	1.824	1.636	1.572	0.818
11	2.200	0.214	0.000	1.727	2.059	2.364	1.640	1.909	1.179
12	1.588	0.250	0.000	2.000	0.941	1.000	0.688	1.474	0.500
Total	15.497	2.969	3.119	17.794	18.403	18.630	12.880	18.429	13.327

Table Experiment 4 - Basic data - Number of flower-buds per shoot

Treatment / Replication No.	1	2	3	4	5	6	7	8	9
1	27	4	1	28	16	17	11	28	11
2	33	3	5	19	35	52	41	42	33
3	0	0	0	14	28	1	0	4	0
4	37	0	0	26	30	31	18	33	9
5	23	0	0	15	15	24	16	39	16
6	13	4	5	19	12	15	5	25	14
7	5	0	0	25	3	17	2	10	11
8	26	4	3	31	26	32	24	23	11
9	20	0	1	16	43	29	15	20	20
10	34	36	10	14	37	28	26	65	27
11	4	3	3	2	13	18	2	5	6
12	17	17	7	30	16	29	21	23	21
Total	239	71	35	239	274	293	181	317	179

Note: In the analysis of the data in Table Treatments 2 and 3 were note included because flower-bud formation had quite obviously been reduced.

Table Experiment 5 - Basic data - Number of flower-buds per node

Replication No. \ Treatment	1	2	3
1	1.400	1.853	0.467
2	1.250	1.848	1.056
3	0.920	1.125	1.188
4	1.643	1.130	0.909
5	1.393	1.207	1.348
6	1.688	1.211	1.806
7	1.633	0.633	0.611
8	1.217	0.706	0.800
9	1.153	0.925	1.700
10	1.356	1.039	1.200
11	1.417	1.161	0.784
12	1.000	1.061	0.720
13	1.533	0.647	1.000
14	1.000	1.409	0.444
15	1.857	1.280	0.647
16	1.629	0.897	1.000
Total	22.089	18.132	15.680

Table Experiment 5 - Basic data - Number of flower-buds per shoot

Replication No. \ Treatment	1	2	3
1	44	11	23
2	52	31	8
3	9	32	11
4	46	26	29
5	17	40	17
6	34	27	12
7	53	36	15
8	30	35	18
9	28	35	31
10	49	46	56
11	54	19	11
12	39	24	12
13	46	63	7
14	23	61	19
15	35	27	19
16	15	26	20
Total	574	539	308

Table Experiment 5 - Basic data - Shoot length (cm)

Treatment / Replication No.	1	2	3
1	31.4	38.3	14.3
2	10.8	33.9	17.6
3	30.2	24.9	17.1
4	34.4	25.3	24.5
5	34.4	30.1	25.2
6	47.4	39.6	44.4
7	43.0	30.4	17.4
8	33.2	33.4	15.7
9	36.5	34.4	11.2
10	62.5	27.9	7.6
11	30.1	33.7	19.9
12	20.2	34.6	35.3
13	36.0	13.0	24.8
14	4.6	22.4	16.1
15	37.8	25.3	17.8
16	36.1	23.7	38.2
Total	528.6	470.9	347.1

Table Experiment 5 - Basic data- defoliation at various stages of leaf development. Parameter measured is flower-buds per node.

Replication No.	PROXIMAL AREA OF SHOOT LENGTH Flower-buds per node where leaves ar present	DISTAL AREA OF Flower-buds per node, leaves removed when partly expanded.	SHOOT LENGTH Flower-buds per node, leaves removed when very small.
1	3.000	2.307	0.857
2	3.000	2.167	0.846
3	1.750	1.375	0.250
4	1.750	1.143	0.500
5	1.750	1.300	0.727
6	1.875	1.667	0.400
7	1.625	0.545	0.000
8	1.500	0.923	0.000
9	2.500	1.333	0.000
10	2.000	1.000	0.222
11	2.375	1.417	0.000
12	1.857	1.615	0.077
13	1.333	0.500	0.000
14	1.714	1.171	0.875
15	1.500	1.375	1.000
16	1.125	1.454	0.100
Total	30.654	21.292	5.854

APPENDIX B

Table Experiment 6 - Basic data - Total numbers of flower-buds per tree

Treatment / Replication No.		16 hours light Long Days 75°F	16 hours light Long Days 60°F	9 hours light Short Days 75°F	9 hours light Short Days 60°F
No Nitrogen	1	408	219	381	36
	2	381	132	305	78
	3	494	272	155	29
	4	462	274	223	146
	Total	1745	897	1064	289
Nitrogen (1000 ppm)	1	631	264	223	168
	2	706	283	461	318
	3	429	254	495	165
	4	719	283	505	217
	Total	2485	1084	1684	868

Table Experiment 6 - Basic data - Mean numbers of flower-buds per node

Treatment / Replication No.		16 hours light Long Days 75°F	16 hours light Long Days 60°F	9 hours light Short Days 75°F	9 hours light Short Days 60°F
No Nitrogen	1	1.05	0.78	0.79	0.35
	2	1.26	1.04	0.38	0.64
	3	1.11	1.20	1.25	0.18
	4	0.80	0.51	0.57	0.51
	Total	4.22	3.53	2.99	1.68
Nitrogen	1	1.63	0.88	0.93	1.08
	2	1.50	0.70	1.14	1.09
	3	1.30	0.77	0.99	0.79
	4	1.31	0.87	0.77	0.93
	Total	5.74	3.22	3.83	3.89

APPENDIX C

Table Experiment 7. Basic data for treatment a; a small young leaf was exposed to $^{14}CO_2$ for 24 hours, background of 95 counts per minute has been subtracted from raw counts

Leaf Number	Raw cpm	Corrected cpm	Dry Wt.	cpm/g Dry wt.	Comments
1	86	N.A.	0.0522 gms	———	Numbering from
2	141	46	0.1284 "	358.2	base of shoot.
3	129	34	0.1739 "	195.5	
4	125	30	0.2029 "	147.6	
5	45	N.A.	0.2011 "	———	
6	207	112	0.2604 "	430.1	
7	333	238	0.2462 "	966.6	
8	258	163	0.2509 "	649.6	
9	113	18	0.2317 "	77.7	
10	153	58	0.2568 "	225.9	
11	375	280	0.2361 "	1,185.9	
12	103	8	0.2363 "	33.9	
13	102	7	0.1839 "	38.1	
14	125	30	0.2129 "	140.9	
15	147	52	0.1805 "	288.1	
16	175	80	0.1452 "	550.9	
17	140	45	0.1782 "	252.5	
18	345	250	0.1403 "	1,781.8	
19	373	278	0.1278 "	2,175.2	
20	1,460	1,365	0.0792 "	17,234.8	
21	422.535	422,440	0.037472 "	11,273,484.0	Exposed Leaf.
22	649	554	0.0427 "	12,974.2	
23	214	119	0.0302 "	3,940.4	
24	180	85	0.00296 "	28,716.2	Apex of shoot.
25	90	N.A.	0.0736 "	———	}
26	107	12	0.0811 "	147.9	}
27	113	18	0.1988 "	90.5	}
28	75	N.A.	0.1647 "	———	}Background
29	311	216	0.0880 "	2,454.5	} NA = No activity
30	124	29	0.2395 "	121.1	} after subtrac-
31	148	53	0.0019 "	27,894.7	} tion of back-
32	166	71	0.1760 "	403.4	} ground.

Table Experiment 7. Basic data for treatment a.

Bud Number	Raw cpm	Corrected cpm	Dry Wt.	cpm/g Dry Wt.	Comments
2	178	83	0.00131	63,358.7	
3	184	89	0.00124	71,774.1	
4	323	228	0.00105	217,142.0	
5	151	56	0.00122	45,901.6	
6	91	N.A.	0.00207	——	
7	373	278	0.00146	190,410.0	
8	189	94	0.00297	47,715.7	
9	186	91	0.00174	52,298.8	
10	197	102	0.00150	68,000.0	
11	167	72	0.00139	51,798.5	
12	66	N.A.	0.00175	——	
13	198	103	0.00122	84,426.0	NA = No activity
14	167	72	0.00107	67,289.7	after subtraction
15	115	20	0.00087	22,988.0	of background
16	171	76	0.00129	58,914.7	
17	220	125	0.00073	171,232.0	
18	210	115	0.00054	212,962.0	
19	41	N.A.	0.0010	——	
20	62	N.A.	0.0004	——	
21	140	45	0.0034	132,352.9	Bud in axil of exposed leaf
26	140	45	0.00112	40,178.6	}
27	192	97	0.00166	58,433.7	}
28	139	44	0.00223	19,730.9	} Background
29	53	N.A.	0.0004	——	}
30	44	N.A.	0.0008	——	}
31	82	N.A.	0.0010	——	}

Table Experiment 7. Basic data for treatment b; a newly expanded leaf was exposed, background of 95 cpm has been subtracted from raw counts

Leaf Number		Raw cpm	Corrected cpm	Dry Wt.	cpm/g Dry Wt.	Comments
	1	144	49	0.0180 gms	2,722.2	Numbering from
	2	142	47	0.0510 "	921.5	base of shoot.
	3	145	50	0.0472 "	1,059.3	
	4	137	42	0.0939 "	447.2	
	5	124	29	0.1861 "	155.8	
	6	133	38	0.1681 "	226.0	
	7	127	32	0.2859 "	111.9	
	8	135	40	0.2456 "	162.8	
	9	130	35	0.3222 "	108.6	
	10	77	N.A.	0.3772 "	———	
	11	149	54	0.3350 "	161.2	
	12	110	15	0.3456 "	43.4	
	13	107	12	0.3572 "	33.6	
	14	123	28	0.3171 "	88.3	
	15	127	32	0.3418 "	93.6	
	16	158	63	0.3150 "	200.0	
	17	163	68	0.2731 "	249.0	
	18	489	394	0.3064 "	1,285.9	
	19	282	187	0.2759 "	677.7	
	20	85	N.A.	0.2667 "	———	
	21	127	32	0.2455 "	130.3	
	22	117	22	0.2425 "	90.7	
	23	336	241	0.2526 "	954.0	
	24	600	505	0.2375 "	2,126.3	
	25	125	30	0.2149 "	139.6	
	26	1,339	1,244	0.2152 "	5,780.0	
	27	2,703	2,608	0.1705 "	15,296.2	
Exposed	28	29,103	29,008	0.1186 "	244,586.8	Exposed leaf.
	29	2,301	2,206	0.1343 "	16,425.2	
	30	530	435	0.0902 "	4,822.0	NA = No activity
	31	148	53	0.0831 "	637.7	after subtraction
	32	158	63	0.0553 "	1,139.2	of background
	33	329	234	0.0390 "	6,000.0	cpm = counts per
	34	147	52	0.0312 "	1,666.6	minute
	35	82	N.A.	0.0150 "	———	
	36	100	5	0.0124 "	403.2	
	37	128	33	0.0052 "	6,346.1	
	38	137	42	0.00352 "	11,931.0	
Apex	39	85	N.A.	0.0050 "	———	Apex
B6	40	128	33	0.00556 "	5,935.0	}
B6	41	128	33	0.3276 "	100.7	} Background
B6	42	242	147	0.1580 "	930.3	}

Table Experiment 7. Basic data for treatment b (cont.)

		Raw cpm	Corrected cpm	Dry Wt.	cpm/g Dry Wt.	Comments
Bud	6	91	N.A.	0.00108 gms	———	Numbering from
	7	161	66	0.00081 "	81,480.0	base of shoot
	8	160	65	0.00129 "	50,387.0	
	9	137	42	0.00132 "	31,818.1	
	10	171	76	0.00159 "	47,798.7	
	11	159	64	0.00168 "	38,095.2	
	12	198	103	0.00196 "	52,551.0	
	13	143	48	0.00197 "	24,365.4	
	14	102	7	0.00176 "	3,977.3	NA means no activ-
	15	161	66	0.00213 "	30,985.9	ity after back-
	16	124	29	0.00175 "	16,571.4	ground has been
	17	139	44	0.00237 "	18,565.4	subtracted.
	18	147	52	0.00188 "	27,659.5	
	19	266	171	0.00160 "	106,875,0	
	20	156	61	0.00154 "	39,610.3	
	21	242	147	0.00184 "	79,891.0	
	22	113	18	0.00199 "	90,452.0	
	23	140	45	0.00190 "	23,684.2	
	24	175	80	0.00100 "	80,000.0	
	25	136	41	0.00122 "	33,606.5	
	26	214	119	0.00095 "	125,263.1	
	27	128	33	0.00102 "	32,352.9	
Exposed	28	423	328	0.00082 "	400,000.0	Buds in axil of
	29	166	71	0.00091 "	78,021.9	the exposed leaf
	30	240	145	0.00065 "	223,076.9	
	41	132	37	0.00149 "	24,832.2	
	42	137	42	0.00051 "	82,352.9	

Table Experiment 7. Basic data for treatment c; a fully matured old leaf was exposed to $^{14}CO_2$ for 24 hours, background of 95 cpm has been subtracted from raw counts

Leaf Number	Raw cpm	Corrected cpm	Dry Wt.	cpm/g Dry Wt.	Comments
1	147	52	0.0414 gms	1,256.0	Numbering from
2	52	N.A.	0.1135 "	———	base of shoot
3	101	6	0.1193 "	50.3	
4	65	N.A.	0.1964 "	———	
5	916	821	0.2062 "	3,981.6	
6	71	N.A.	0.2301 "	———	
7	350	255	0.2873 "	887.5	
8	126	31	0.2520 "	123.0	
9	188	93	0.3067 "	303.2	
10	212	117	0.2743 "	426.5	
11	216	121	0.4052 "	298.6	
12	14,634	14,539	0.2030 "	71,620.6	Exposed leaf

Table Experiment 7. Basic data for treatment c (cont.)

Leaf Number	Raw cpm	Corrected cpm	Dry Wt.	cpm/g Dry Wt.	Comments
13	154	59	0.1920 gms	307.3	Numbering from base of shoot.
14	100	5	0.4195 "	11.92	
15	117	22	0.2454 "	89.65	
16	94	N.A	0.3025 "	-	
17	662	567	0.2298 "	2,467.4	
18	166	72	0.2709 "	265.8	
19	145	50	0.2104 "	237.6	
20	60	N.A	0.1982 "	-	N.A = No Activity after subtraction of background
21	1,796	1,701	0.0867 "	19,619.3	
22	330	235	0.0684 "	3,435.7	
23	148	53	0.0622 "	852.1	
24	3,070	2,975	0.0508 "	58,562.9	
25	162	67	0.0341 "	1,964.8	
Apex 26	82	N.A	0.00221 "	-	Apex
B6 27	118	23	0.2583 "	89.0	
B6 28	41	N.A	-		
B6 29	37	N.A	-	-	
B6 30		N.A	-	-	Background
B6 31		N.A	-	-	
B6 32		N.A	-	-	
B6 33		N.A	-	-	
B6 34		N.A	-	-	
Bud 1	81	N.A	0.000933 gms	-	
2	390	295	0.001308 "	225,535.1	
3	254	159	0.001678 "	94,755.6	
4	205	110	0.001657 "	66,385.0	
5	192	97	0.001965 "	49,363.8	
6	536	441	0.001086 "	406,077.3	
7	84	N.A	0.001778 "	-	
8	215	120	0.001569 "	76,481.8	
9	205	110	0.001785 "	61,624.6	
10	169	74	0.001952 "	37,909.8	
11	92	N.A	0.001411 "	-	
12	2,777	2,682	0.000977 "	2,745,130.0	Bud in axil of exposed leaf.
13		N.A	0.001903 "	-	
14		N.A	0.003133 "	-	
15		N.A	0.001251 "	-	
16	125	30	0.001177 "	25,488.5	
17		N.A	0.000903 "	-	
18	210	115	0.000543 "	211,786.0	
19	87	N.A	0.000468 "	-	
20	162	67	0.000290 "	231,034.4	
27		N.A		-	
28		N.A		-	
29		N.A		-	
31		N.A		-	Background
32		N.A		-	cpm = counts/ minute
33		N.A		-	
34		N.A		-	N.A = No activity after subtraction of background

Table Experiment 7. Basic data for Treatment d; Fully expanded new leaf exposed, every second leaf had been removed 3 weeks prior to exposure

Leaf Number	Raw Counts	Background of 95 cpm sub-tracted - Corrected counts	Dry Wt of Leaf (gm)	cpm/g Dry Wt	
1	58	N.A	0.0346		Numbering from base of shoot
2	72	N.A	0.1358		
3	35	N.A	0.0692		
5	41	N.A	0.2818		
7	44	N.A	0.2729		
9	61	N.A	0.3052		
11	29	N.A	0.3139		
13	49	N.A	0.2938		
15	87	N.A	0.4340		
17	42	N.A	0.4040		
19	59	N.A	0.3766		
21	62	N.A	0.3426		
23	94	N.A	0.2208		
25	90	N.A	0.2981		
27	87	N.A	0.1250		
29	116,865	116,770	0.2243	521,295	Leaf exposed to $^{14}CO_2$ for 24 hrs
31	538	443	0.2928	151,298	
32	97	2	0.0448	511	
33	69	N.A	0.3674		
34	79	N.A	0.3839		
35	89	N.A	0.3369		
36	94	N.A	0.1866		Background
37	91	N.A	0.1307		
38	92	N.A	0.5509		NA = No Activity after subtraction of background.
39	80	N.A	0.9135		
40	73	N.A	0.2741		
41	84	N.A	0.0292		cpm = counts per minute

Table Experiment 7. Basic data for Treatment d.

Bud Number	Raw Counts	Background of 95 cpm sub-tracted - Corrected counts	Dry Wt of Bud (gm)	cpm/g Dry Wt	
1	64	N.A	0.000606		Numbering from base of shoot.
2	73	N.A	0.001694		
3	61	N.A	0.000699		
4	198	103	0.002969	34,691	
5	74	N.A	0.002729		
6	69	N.A	0.002834		
7	94	N.A	0.004559		
8	29	N.A	0.003669		
9	144	49	0.004059	12,072	
10	49	N.A	0.005199		
11	72	N.A	0.003694		

Table Experiment 7. Basic data for Treatment d (cont.)

Bud Number	Raw Counts	Background of 95 cpm subtracted - Corrected counts	Dry Wt of Bud (gm)	cpm/g Dry Wt	
12	127	32	0.005159	6,203	Numbering from base of shoot
13	24	N.A	0.005929		
14	450	355	0.004449	79,793	
15	47	N.A	0.005815		
16	90	N.A	0.005049		
17	176	81	0.006229	13,004	
18	57	N.A	0.004899		
19	106	11	0.005394	2,039	
20	162	67	0.004194	15,975	
21	74	N.A	0.005487		
22	1,783	1,688	0.003339	505,540	
23	100	5	0.003634	1,376	
24	269	174	0.003086	56,384	
25	488	393	0.003628	108,324	
26	3,613	3,518	0.001754	2,005,701	Buds in axil of the exposed leaf
27	233	138	0.002374	58,130	
28	224	129	0.001339	96,340	
29	2,393	2,298	0.003551	647,141	
30	127	32	0.003724	8,593	
31	65	N.A	0.003914		NA = No activity after subtraction of background
32	64	N.A	0.005436		
33	78	N.A	0.003434		
34	71	N.A	0.003694		
35	60	N.A	0.003741		
36	43	N.A	0.002119		
37	91	N.A	0.006907		
38	77	N.A	0.004504		
39	61	N.A	0.005314		
40	55	N.A	0.034383		

Table Experiment 8. Basic data - Number of flower-buds per node

Treatment / Replication No.		1	2	3	4	5
No Sugar	1	1.727	1.815	1.364	1.870	1.690
	2	1.741	1.951	1.871	1.988	1.577
	3	1.188	1.327	1.097	1.563	1.758
	4	1.913	2.214	1.893	1.233	2.886
	5	1.688	1.167	1.478	1.615	1.382
	6	1.182	1.357	1.571	1.600	0.889
	7	2.481	2.619	2.200	1.727	1.258
	8	1.821	1.176	1.259	1.125	2.207
	9	0.729	1.522	1.650	1.844	0.852
	10	1.231	2.042	1.895	1.923	1.533
	Total	15.701	17.190	16.278	16.488	16.456
	Mean	1.570	1.719	1.628	1.649	1.646
Sugar	1		1.923	2.357	2.414	2.097
	2		1.690	1.417	1.821	1.167
	3		2.300	1.806	1.320	1.188
	4		1.750	1.250	2.000	1.800
	5		1.481	1.316	1.526	1.500
	6		1.333	1.769	1.167	1.500
	7		1.091	1.375	1.050	1.333
	8		2.345	2.200	2.125	1.778
	9		1.118	1.111	1.000	1.000
	10		1.674	1.857	1.222	1.389
	Total		16.705	16.458	15.645	14.752
	Mean		1.670	1.649	1.565	1.475

Table Experiment 8. Basic data - Number of flower-buds per shoot

Replication No. \ Treatment	1	2	3	4	5
1	19	49	30	43	39
2	47	80	58	61	41
3	19	69	34	19	58
4	44	62	53	35	101
5	16	98	36	75	47
6	27	21	34	42	21
7	13	38	44	48	39
8	67	55	22	19	64
9	51	20	34	18	24
10	16	35	33	59	46
Total	319	527	378	419	480
1		25	66	140	65
2		49	34	51	21
3		46	65	33	19
4		21	14	54	45
5		40	25	29	27
6		40	23	14	30
7		12	11	42	16
8		68	55	68	32
9		19	10	39	11
10		72	52	22	25
Total		392	361	492	291

Table Experiment 9. Basic data - Number of flower-buds per node

Treatment / Replication No.	1	2	3	4	5
1	1.833	1.786	2.210	2.450	2.300
2	2.000	2.111	2.210	2.150	2.095
3	1.833	1.565	1.526	0.941	1.500
4	1.538	1.318	1.563	1.400	1.714
5	2.000	1.778	1.500	1.833	1.612
6	2.070	1.643	2.375	1.385	2.267
7	2.000	1.475	2.545	2.045	1.833
8	2.000	2.000	2.294	1.611	2.000
9	1.140	1.333	1.462	1.385	2.278
10	1.688	1.900	1.769	2.083	2.083
11	1.464	1.320	1.133	1.833	1.545
12	1.000	2.438	1.565	1.690	1.463
13	1.857	2.053	2.375	2.333	2.273
14	2.067	2.278	2.286	2.314	2.333
15	1.667	1.591	1.000	0.231	1.760
16	1.643	1.421	1.960	1.556	1.613
17	1.538	1.882	1.810	1.526	1.357
18	1.083	1.211	1.240	1.045	1.059
19	2.364	2.238	2.375	2.000	2.000
20	1.375	1.765	2.235	1.938	2.600
Total	34.164	35.109	37.433	33.749	37.685
Mean	1.708	1.755	1.851	1.687	1.884