Annals of Botany **80**: 13–21, 1997

Shoot Axillary Bud Morphogenesis in Kiwifruit (*Actinidia deliciosa*)

E. F. WALTON*, P. J. FOWKE†, K. WEIS‡ and P. L. McLEAY§

HortResearch, Ruakura Research Centre, Private Bag 3123, Hamilton, New Zealand

Received: 8 November 1996 Accepted: 11 December 1996

The annual cycle of kiwifruit [*Actinidia deliciosa* (A. Chev.) C. F. Liang et A. R. Ferguson var. *deliciosa* cv. Hayward] shoot axillary bud (first-order axillary bud, FOAB) morphogenesis is described. FOABs developed quickly with the majority of bud scales and leaf primordia present approx. 125 d after budbreak (dab). Mature FOABs had, on average, 23·2 bud scales and leaf primordia. Most second-order axillary structures were also present approx. 125 dab. During the growing season, the second-order structures developed into second-order axillary buds (SOABs) or remained as simple, dome-shaped meristems (SDSMs). At maturity, nearly all FOABs had four SOABs and, on average, 12·4 SDSMs. Most SDSMs were fused to the subtending leaf primordia, but some SDSMs developed so that they were 'free' from the subtending leaf primordia. Third-order axillary meristems (third-order SDSMs) were observed in the axils of most SOABs, and, on average, there were 20·6 per FOAB. Our observations on the development of second-order axillary structures are consistent with evocation in kiwifruit occurring earlier than the generally-accepted time of late summer.

Key words: *Actinidia deliciosa*, bud morphogenesis, development, flowering, evocation.

INTRODUCTION

Kiwifruit [*Actinidia deliciosa* (A. Chev.) C. F. Liang et A. R. Ferguson var. *deliciosa*] is a dioecious, deciduous perennial vine. The aerial structures of the vine can be separated into four components, namely the trunk, leaders, canes and shoots (Fig. 1). In commercial orchards, a mature vine typically has two leaders trained in opposite directions from the trunk along a support structure. A number of canes are then trained perpendicularly from each leader. In spring, a proportion of the axillary buds (first-order axillary buds, FOABs) on each cane break and elongate to produce shoots bearing flowers (Fig. 2). Only the first flush of shoots carries flowers; any later-breaking buds produce only vegetative shoots (Grant and Ryugo, 1982). As shoots develop over the course of the growing season, they lignify and turn brown. After leaf drop in winter, these shoots become the next season's canes. The current commercial winter-pruning system for kiwifruit vines in New Zealand is one of cane replacement in which the previous growing season's canes (principally those with shoots that bore fruit) are removed and the 'new' canes (former shoots) are retained to carry the next growing season's crop. A more detailed account of vine morphology is available in Ferguson (1984).

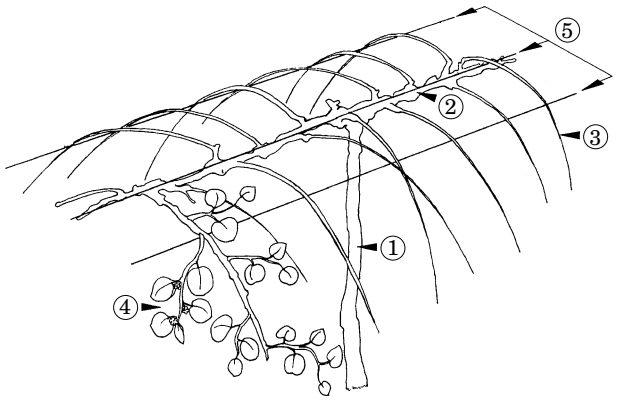


FIG. 1. Schematic of mature kiwifruit vine showing the trunk (1), leaders (2), canes (3) and shoots (4). The wires of the support structure (5) are also shown.

Mature FOAB morphology has been described by Brundell (1975*a*). When observed while dormant in mid-winter, the axils of the bud scales and leaf primordia of FOABs contain second-order structures, namely, second-order axillary buds (SOABs) and simple, dome-shaped meristems (SDSMs; Fig. 3). SOABs (termed 'basal buds') contain up to ten leaf primordia and develop in the most basal nodes of FOABs (Brundell, 1975*a*). SDSMs are found in the nodes distal to SOABs. In spring, just prior to budbreak, the most basal SDSMs start differentiating inflorescences (Brundell, 1975*b*; Polito and Grant, 1984; Watanabe and Takahashi, 1984). Kiwifruit inflorescences are potentially compound dichasia (Ferguson, 1984). Some SDSMs, usually the most basal, fail to differentiate reproductive structures, and abort part way through inflorescence and flower differentiation (Brundell, 1975*b*; Snowball and Considine, 1986; Walton and Fowke, 1993). Lateral flowers on inflorescences can also abort (Brundell,

* For correspondence.

† Current address: AgResearch, Ruakura Agricultural Research Centre, Private Bag 3123, Hamilton, New Zealand.

‡ Current address: Department of Pomology, University of California, Davis, CA 95616, U.S.A.

§ Current address: Waikato Stable Isotope Unit, University of Waikato, Private Bag 3105, Hamilton, New Zealand.

0305-7364/97/070013+09 $25.00/0 bo960381

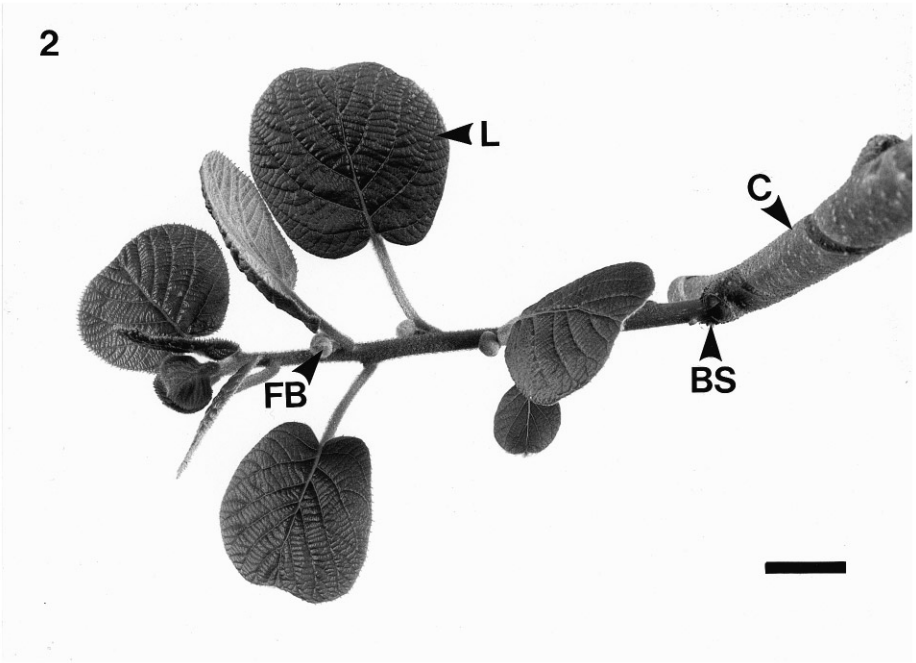


FIG. 2. Flowering shoot of kiwifruit produced from a mature first-order axillary bud (FOAB) in spring. The shoot arises from a cane (C). Second-order axillary buds (SOABs) (not visible) are subtended by bud scales (BS) and flower buds (FB) by leaves (L). Nodes distal to the last flower bud (labelled) are where the next seasons FOABs will develop. Bar = 15 mm.

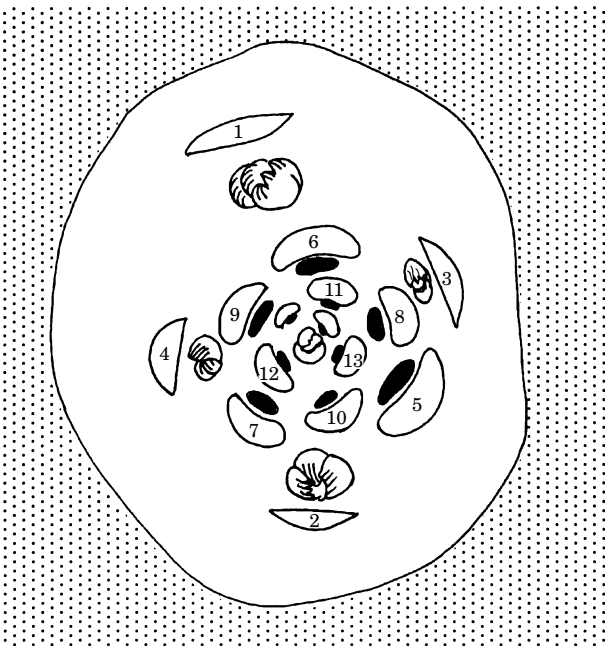


FIG. 3. Schematic of a mature FOAB in winter showing relative positions of second-order axillary structures. The bud scales (nodes 1–4) subtend the SOABs. The leaf primordia (numbered only up to node 13) subtend SDSMs (in black). ⊡, represents the tissue surrounding the bud.

1975*b*; Polito and Grant, 1984), and so, in the pistillate kiwifruit cultivar 'Hayward', inflorescences bearing one, two or three flowers can be found. SDSMs distal to those that differentiate into inflorescences, develop into 'new' FOABs during the forthcoming growing season (Table 1, Year I) and may produce floral shoots during the subsequent spring (Table 1, Year II).

TABLE 1. *Seasonal cycle of vine growth and first-order axillary bud (FOAB) development*

Year	Season	Developmental stage
I	Spring	Budbreak and shoot extension
		Commencement of FOAB development
	Summer	Presumed start of FOAB evocation
	Autumn	Leaf abscission
	Winter	Vine dormant
II	Spring	Budbreak and extension of FOABs into shoots
		Differentiation of basal SDSMs into inflorescences and flowers
		Flowering and fruit set
	Summer	Fruit development
	Autumn	Fruit harvest
		Leaf abscission
	Winter	Vine dormant

Evocation is the inductive process whereby a meristem becomes committed to reproductive development through a change in developmental state (McDaniel, 1994). The expression of that state leads to the initiation of the floral apex and ultimately to the formation of flower(s) (McDaniel, 1994). Evocation of the developing FOABs of kiwifruit has been investigated by several research groups using sequential shoot-defoliations (Davison, 1974; Snelgar and Manson, 1992; Snowball, 1996). However, shoot-defoliation experiments not only remove the putative source of the inductive signal, but also the source of photosynthate, and so, as

stated by Snelgar and Manson (1992) 'any deductions based on data obtained using the defoliation technique must be considered tentative'. None the less, using this methodology, evocation is generally accepted to occur during late-summer to autumn of the season prior to inflorescence differentiation (Table 1, Year I), based on Davison (1974), although Snelgar and Manson (1992) suggested that evocation may start earlier in the older, more developed FOABs. Most recently, Snowball (1996) giving more weight to the effect of the loss of photosynthate, postulated that evocation may not occur until immediately prior to flower differentiation in spring (Table 1, Year II).

This paper provides a comprehensive anatomical description of first-order axillary bud (FOAB) morphogenesis in kiwifruit. As our overall interest is the regulation of flowering in kiwifruit, emphasis was given to the timing of the appearance and development of the second-order axillary structures that can potentially differentiate into inflorescences and flowers. We wished to know, firstly, when these structures appeared, as this may give an indication as to when evocation actually occurs in kiwifruit and secondly, to provide information useful in improving current orchard management practices for this crop. While the results presented here do not define the time of evocation in kiwifruit *per se*, they support the earliest time of evocation proposed by Snelgar and Manson (1992), and provide the necessary foundation for future molecular studies.

MATERIALS AND METHODS

Developing FOABs were collected from shoots on mature kiwifruit vines (from the pistillate cultivar 'Hayward') growing in a commercial orchard near Te Puna in the Bay of Plenty, New Zealand (37° 42′ S, 176° 05′ E). Mean monthly climatological data for a nearby site (Tauranga) are available from the New Zealand Meteorological Service's published summaries (Ministry of Transport, New Zealand Meterological Service, 1983). Vines were managed according to normal orchard practice (Sale, 1990). Buds were collected after approx. 14 d intervals from early spring (28 Sept. 1990) until late winter (9 Aug. 1991). On each sampling date, the FOAB at the fifteenth node was collected from ten emergent shoots. That node was selected as it was two or three nodes distal to the last flower or fruit and, therefore, those FOABs were among the most developmentally advanced on the vine. To ensure correct node identification, shoots were tagged and the number of nodes to the first flower recorded prior to abscission of the bud scales and any vestigial leaves. To ensure that sufficient FOABs would break over a relatively short period and thereby reduce sample-to-sample variation, the vines were sprayed with a 30 g l^{-1} hydrogen cyanamide solution (in the form of 'Hi-cane', SKW Trostberg AG, Germany) with an airblast sprayer on 10 Aug. 1990. This treatment follows standard orchard practice (Henzell and Briscoe, 1986, 1988), and has negligible adverse long-term or carry-over effects on the vine during the current or subsequent seasons (Henzell, Briscoe and Gravett, 1991). Budbreak (the time when 10% of FOABs had developed shoots 10 mm long) was 9 Sept. 1990.

The entire shoot was removed during FOAB collection and the distance from the base of the shoot to the fifteenth node, and the width of the subtending leaf at node 15 were measured. These measurements were made so that in the future the extent of FOAB development could be estimated from leaf and/or shoot phenology. FOABs were excised with surrounding supporting tissue and immediately fixed in FAA with vacuum aspiration. Ethanol-dehydrated tissue was embedded in Paraplast paraffin (melting point 56 °C), (Oxford, St Louis, Missouri, USA). Between five and ten FOABs from each sampling date (depending on bud age) were serially sectioned at 10 μm. All FOABs were sectioned transversely to facilitate the accurate counting of the structures of the bud. By the end of the sampling period each FOAB yielded up to 100 sections, even when the upper portion of the bud had been excised (see below). Sections were stained with tannic acid/ferric chloride, with a counterstain of safranin and fast green (Schneider, 1973). Trichome lignification was determined by staining with phloroglucinol (Johansen, 1940).

Developing FOABs collected from December onwards caused significant problems in sectioning because of the large numbers of lignifying trichomes. Although this problem was largely overcome by excising the upper portion of the bud and plucking most trichomes from the bud scales and outer leaf primordia with fine forceps, a number of FOABs were still destroyed during the sectioning process. Final numbers of FOABs sectioned at each sampling date ranged from four to nine.

Sections were examined to determine the numbers of bud scales and leaf primordia in the developing FOABs, and the types and locations of any evident second-order axillary structures. To facilitate the correct assignation of node numbers within each FOAB, up to ten sections were selected for scanning with a video camera attached to the microscope. The resultant images were printed and from these the phyllotaxis of each bud was determined. Basal transverse-sectional areas of SDSMs were determined from the scanned images to determine the date of growth cessation and their ultimate size. The images were analysed using IPLab Spectrum 3.1 (Signal Analytics, Vienna, Virginia, U.S.A.).

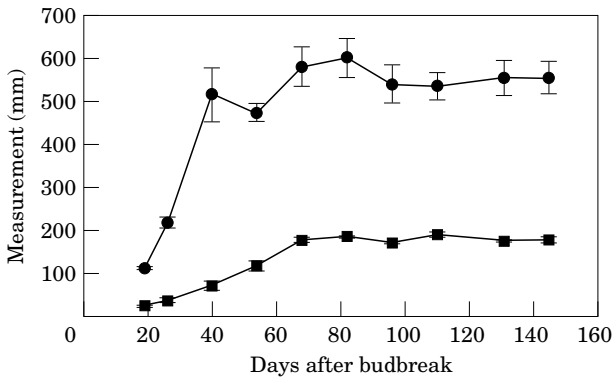
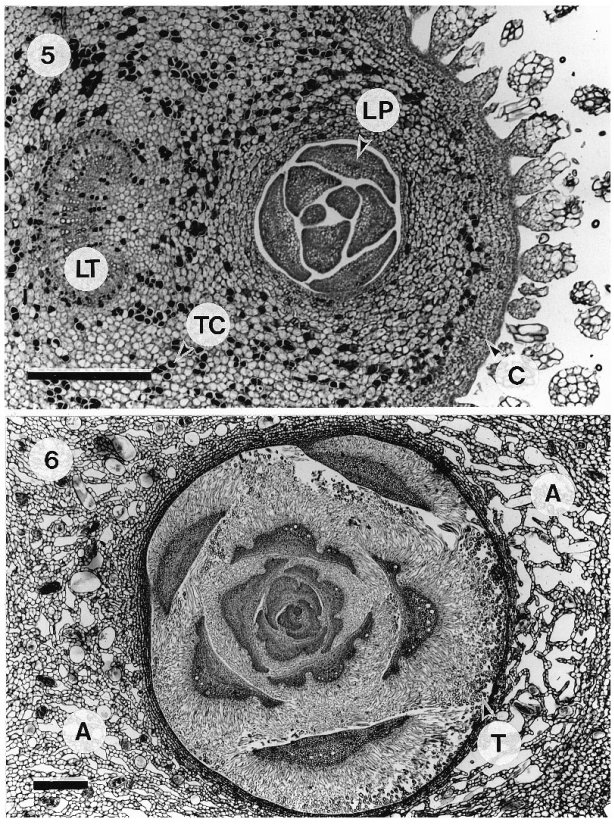


FIG. 4. Mean shoot lengths (to node 15, ●) and mean widths of leaves subtending node 15 (■) during the growing season. Vertical bars are ± s.e.



FIGS. 5–6. Transverse sections (midway through serial series) of developing FOABs. LP, Leaf primordium. FIG. 5. FOAB 40 dab, embedded in tissue derived from the stem cortex and/or leaf base; this section shows a total of eight budscales and leaf primordia. Note random arrangement of tanniniferous cells (TC). LT, Leaf trace to the subtending leaf. FIG. 6. FOAB 72 dab; this section shows a total of 14 budscales and leaf primordia. Note the greater development of arenchyma (A) on adaxial size of bud (right hand side of photograph) and the lignified trichomes (T) around the periphery of the FOAB. Bars = 0·5 mm.

RESULTS

Stem and subtending leaf growth

Shoots (between the base and the fifteenth node) increased in length until approx. 40 dab (Fig. 4). At that time, node 15 was approx. 500 mm from the base of the cane. The leaf subtending node 15 continued to expand until approx. 70 dab, by which time it was approx. 175 mm in width (Fig. 4).

Tissue surrounding first-order buds

At the beginning of the season, the FOABs were completely embedded in tissue derived from the stem cortex and/or leaf petiole (Fig. 5). As development proceeded, the buds protruded through that surrounding tissue, so that by the end of the growing season a small ostiole (approx. 2–3 mm in diameter) containing brown trichomes was visible. Collenchyma development under the epidermis of the surrounding tissue was first seen 26 dab and it reached maximum development as a layer approx. 4 or 5 cells thick (Fig. 5).

Concurrent with collenchyma development, the tissue adjacent to the FOABs started to differentiate into aerenchyma. Development of aerenchyma commenced at the base of the FOABs and tended to be on the adaxial side of the FOABs, that is, the side away from the petioles of the axillant leaves (Fig. 6). Mature aerenchyma was composed of uniseriate files of cells traversing large voids in the tissue (Fig. 7). The thickening of the walls of the cells comprising the files was perpendicular to the axis of the file. Eighty-two d after budbreak, aerenchyma showed evidence of collapse in the tissue surrounding distal ends of the buds, that is, the voids were no longer extant, but the cells themselves appeared to be intact (Fig. 8).

A periderm, under the epidermis of the tissue surrounding the FOAB, was visible in one sample taken 68 dab, but was present in all samples 82 dab (Fig. 9).

Idioblasts

Two types of idioblasts were seen: the first type formed early (26 dab) as cells containing bundles of raphides surrounded by mucilage (Fig. 10). Initially these cells were found only in the distal portions of the bud scales and leaf primordia of the FOABs, but with time their distribution became ubiquitous in the bud and surrounding tissue. With FOAB development, the raphide-containing cells became larger, increasing in diameter to approx. 8 to 10 times that of adjacent cells.

The second type of idioblasts, tanniniferous cells, were first seen 54 dab. They were found randomly scattered throughout the tissue surrounding the FOABs (Fig. 5) but tended to be less common in the aerenchyma.

Bud scales and leaf primordia

At the first sampling date (19 dab), there were, on average, six bud scales and/or leaf primordia present within each FOAB (Fig. 11). Bud scales arose from the most basal nodes (the first developed) and when mature, were densely covered with brown trichomes on their abaxial surface. Leaf primordia were at nodes distal to the bud scales, the larger and more developed of which were also covered with trichomes on their abaxial surfaces. By 96 dab, nearly all of the bud scales and leaf primordia were present (Fig. 11). In mature FOABs, the mean total number of bud scales and leaf primordia was 21·2 (s.e. = 0·96), but ranged between 21 and 26.

Trichomes were uniseriate and visible on the outermost bud scales at the first sampling date. Their lignification started with the apical cell and proceeded cell by cell to their base. Trichome lignification commenced 54 dab with the trichomes located on the tips of the bud scales. By 82 dab these trichomes were completely lignified. Consequently, at that time, transverse sections of a developing FOAB, midway through the serial series, had rings of lignified trichomes around their periphery (Fig. 6). Most of the remaining trichomes had lignified by approx. 96 dab.

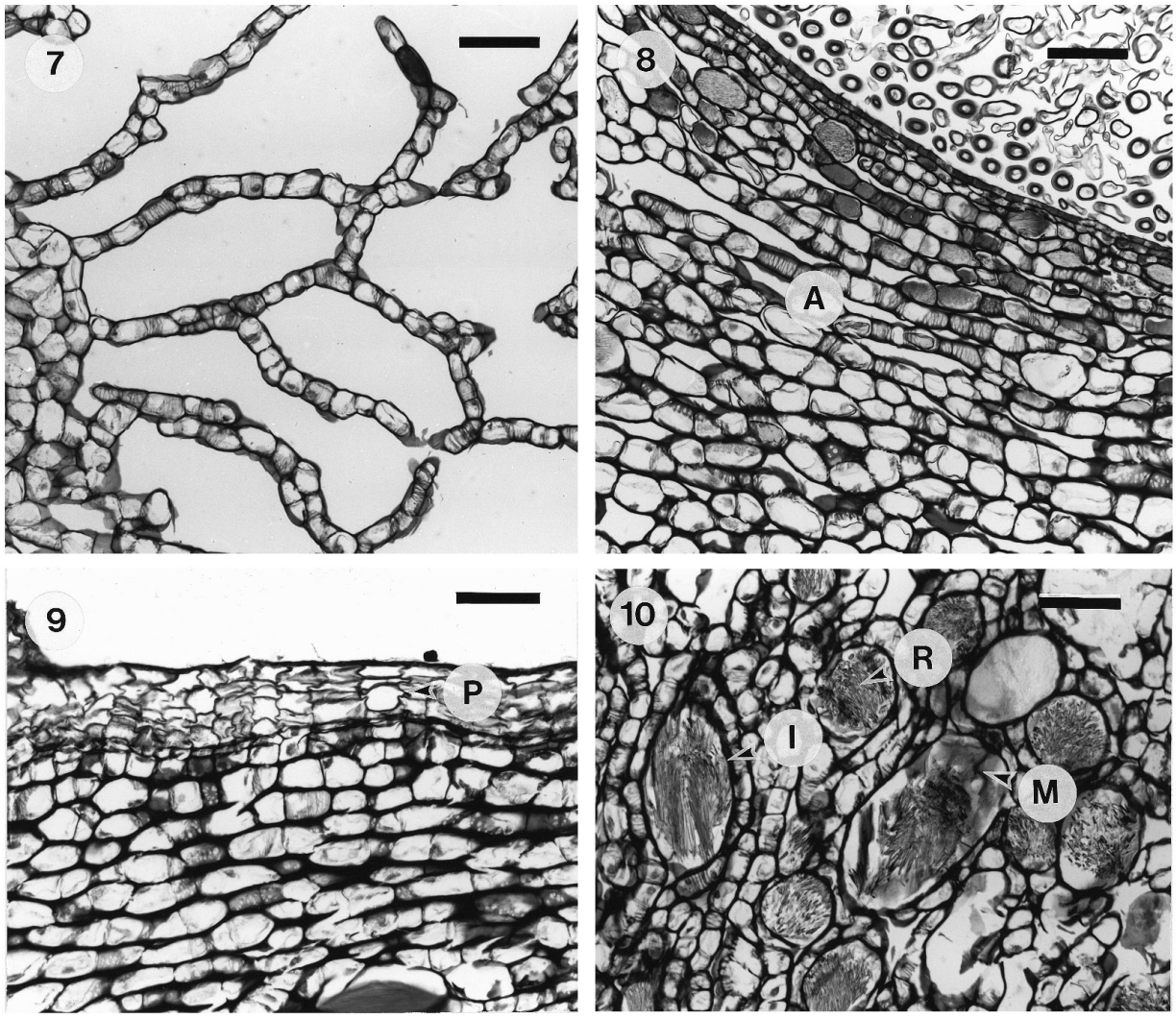


FIG. 7. Mature aerenchyma in tissue surrounding FOABs (40 dab). Note that the thickening of the walls of individual cells is perpendicular to the axis of the file of cells. FIG. 8. Collapsed aerenchyma (A) in tissue surrounding FOABs (82 dab). Note that the individual cells are still intact. FIG. 9. Periderm with four or five cell layer phellem (P) (152 dab). FIG. 10. Idioblastic cells (I) containing raphides (R) and mucilage (M) viewed under polarising light (152 dab). Bars = 0·1 mm.

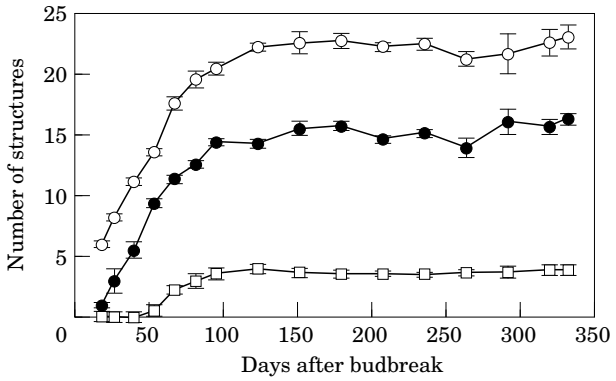


FIG. 11. Mean numbers of bud scales and leaf primordia (○), second-order axillary structures (●) and SOABs (□) developing in FOABs at node 15. The number of SDSMs is the difference between the number of second-order axillary structures and the number of SOABs. Vertical bars are ± s.e.

Second-order axillary structures

Second-order axillary structures were borne singly at nodes of FOABs and subtended by either budscales or leaf primordia as per Fig. 3. The first second-order axillary structure was seen in the most basal node 19 dab (Fig. 11). Numbers of second-order axillary structures increased steadily until approx. 124 dab (early January; mid-summer), by which time there were approx. 14 axillary structures per FOAB. The appearance of the second-order axillary structures lagged behind the appearance of budscales and leaf primordia by approx. 27 d. At the end of the sampling period there were, on average, 16·4 (s.e. = 0·51; range 15–18) second-order axillary structures per FOAB.

All second-order axillary structures first appeared as meristems, but as the season progressed they either developed into SOABs (Fig. 12) or remained as meristems (SDSMs). SOABs differentiated in the most basal nodes of

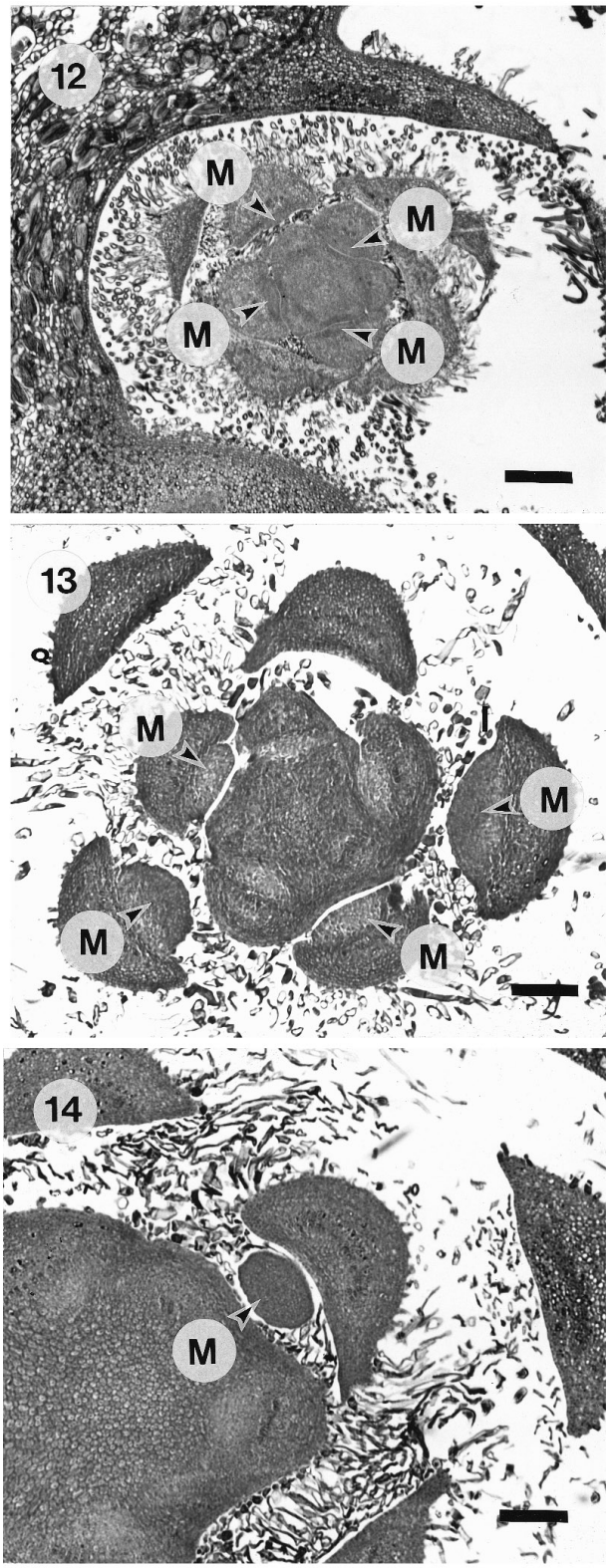


FIG. 12. Transverse section of a SOAB (in node 1 of the FOAB) showing third-order axillary meristems in the axils of second-order leaf primordia (180 dab). In this particular section, third-order axillary meristems (M) can be seen in nodes 5, 7, 8 and 9. (Note that many trichomes had been plucked from this bud prior to sectioning.) FIG. 13. Transverse section through FOAB showing 'fused' SDSMs on primary bud axis (264 dab). In this particular section, SDSMs (M) can be seen in nodes 8, 9, 11 and 12; but meristem initials can be seen in nodes 13, 14 and 15. (Note that many trichomes had been plucked from this bud prior to sectioning.) FIG. 14. Transverse section showing 'free' SDSM (M) in node 9 of a FOAB (292 dab). (Note that many trichomes had been plucked from this bud prior to sectioning.) Bars = 0·2 mm.

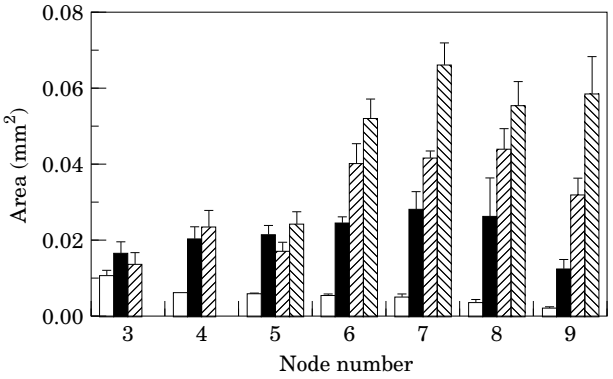


FIG. 15. Mean transverse-sectional areas of second-order axillary meristems at nodes 3–9 from FOABs (at node 15) at 54 (□), 68 (■), 264 (▨) and 334 (▧) dab. Vertical bars are the s.e.

developing FOABs. In mature FOABs there were four SOABs, except in two cases where there were five. The first SOABs were seen 54 dab at node 1 (as determined by the initiation of the first leaf primordia on meristems), 68 dab at nodes 2 and 3, and 82 dab at node 4. By 96 dab, the increase in the number of leaf primordia in SOABs at node 1 was negligible. By the end of the sampling period the mean number of leaf primordia in a SOAB at node 1 was 13·5 (s.e. = 1·0; range 11–16). Similar trends were observed for SOABs in more distal nodes, though they were less distinct for buds at nodes 3 and 4. The mean numbers of leaf primordia (with s.e. and ranges in parentheses) for mature SOABs at nodes 2, 3 and 4 were 11·8 (1·2; 9–16), 6·5 (1·1; 3–8) and 5·6 (0·74; 4–8), respectively. Third-order axillary meristems were frequently observed within the axils of the SOABs (Fig. 12) and were first observed 82 dab. By the end of the sampling period, SOABs at node 1 had, on average, 9·2 (s.e. = 0·85; range 7–11) third-order axillary meristems. Numbers of third-order axillary meristems for nodes 2, 3 and 4 (with s.e. and ranges in parentheses) were 8·2 (0·58; 7–10), 2·2 (1·0; 0–4) and 1·0 (0·63; 0–3), respectively. Consequently, on average, each FOAB contained 20·3 third-order axillary meristems.

A single third-order axillary bud was seen in the first node of the most basal SOAB from a sample collected 152 dab. That bud had eight leaf primordia and at least one fourth-order axillary meristem.

By the end of the sampling period, SDSMs were found only at node 5 and those distal. The first SDSMs at node 5 were seen 40 dab. By the end of the season, there remained 12·4 (s.e. = 0·51; range 11–14) SDSMs per FOAB (Fig. 11). All SDSMs were more or less elliptical in shape when viewed in transverse section (Fig. 13), but those in the basal nodes were the most elongated. Most SDSMs were 'fused' to the subtending leaf primordia in all sections examined (Fig. 13), but some SDSMs developed so that they were

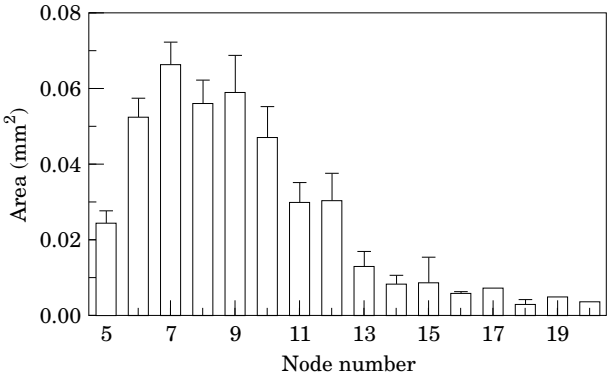


FIG. 16. Mean transverse-sectional areas of SDSMs from FOABs (at node 15) at 334 dab. Vertical bars are the s.e.

'free' from their subtending leaf primordia in the more distal sections (Fig. 14).

At 54 dab, the largest SDSM was the most basal (node 3; Fig. 15), since by that time the meristems that had been at nodes 1 and 2 had differentiated into SOABs. By 68 dab, the largest SDSMs were located at nodes 4–8, and by 264 dab the largest SDSMs were located at nodes 6 and distal. The SDSM at node 3 had stopped growing by approx. 54 dab and the SDSMs at nodes 4 and 5 had stopped growing by 68 dab. The SDSMs at nodes 6 and distal, continued to grow during dormancy, while the vine was leafless. At the end of the sampling period, SDSMs at node 5 were less than half the size of those at the nodes immediately distal, and the SDSMs at nodes 13 and distal were similar in size to each other (Fig. 16).

DISCUSSION

Although FOABs at node 15 of the shoots are on the vine for approx. 12 months, most of their development occurs over a much shorter period of time. The majority of budscales and leaf primordia were present by approx. 125 dab. The second-order axillary structures also appeared over a relatively short period of time, and although their appearance followed behind the budscales and leaf primordia by about 27 d, the majority of second-order axillary structures were also present by 125 dab. This time in bud development was approx. 55 d after the end of subtending leaf expansion, and approx. 85 d after the end of the shoot extension (to node 15).

The mean numbers of structures reported here for mature FOABs is slightly larger, and the timing of their appearance is much earlier (approx. 5 weeks), than that reported by Snowball (1995). Some of this difference is due to the ability to detect the initial stages of meristem differentiation given the higher resolution afforded by anatomical microscopy as opposed to dissections. However, most of the difference in timing is likely to be due to hydrogen cyanamide being used in this study to maximize, and synchronize, budbreak. This treatment also advances the date of budbreak (Henzell and Briscoe, 1986), and so the earlier resumption in growth leads to earlier FOAB development relative to untreated vines. It is worthwhile to note that the similar numbers of structures in mature FOABs in this study and that of Snowball (1995) indicates that hydrogen cyanamide treatment has negligible effect on the ultimate development of FOABs.

SOAB morphology is far more complex than has been previously reported by Brundell (1975*a*) and Snowball (1995). Though SOABs were variable in the extent of their development, those found in nodes 1 and 2 of the FOAB were always larger (approx. twice as many leaf primordia) than those found in nodes 3 and 4. The largest SOAB had 16 leaf primordia. Most SOABs contained third-order axillary meristems (SDSMs), and in one case, a SOAB was seen with a third-order axillary bud, containing at least one fourth-order axillary meristem. On average, mature SOABs contained 20·6 third-order axillary meristems. Though SOABs do not normally develop, when they do they can produce floral shoots (Walton, 1996). The resultant inflorescences and flowers must develop from the third-order axillary meristems. Consequently, some of these third-order axillary meristems, in addition to the more basal second-order axillary meristems (SDSMs), gain the competency to differentiate inflorescences and flowers.

The size distribution of SDSM transverse-sectional areas reported here for the last sampling date is similar to that reported by Watson and Gould (1994) for *Actinidia chinensis* Planch. var. *chinensis*, once the node numbering system is adjusted to take account of the four SOABs found in the four basal nodes of each FOAB. However, the maximum, average transverse-sectional area reported here for SDSMs from *A. deliciosa* is approx. a quarter of that reported by Watson and Gould (1994) for *A. chinensis*. The smaller SDSMs in *A. deliciosa* are likely to be due to the FOABs being collected earlier in the growing season, when they are less developed, rather than a true taxonomic difference.

The trichomes on the abaxial surfaces of the budscales and leaf primordia were uniseriate. Mature leaves on the other hand have stellate trichomes on their abaxial surfaces (Ferguson, 1984), while fruit are covered with short uniseriate (Schmid, 1978) and multicellular trichomes (Hopping, 1976; Schmid, 1978). Like bud trichomes, fruit trichomes are also lignified (Schmid, 1978). The idioblastic cells containing raphides and surrounded by mucilage reported here are not dissimilar to those reported in other parts of the kiwifruit vine, namely, roots (Lemon and Considine, 1993; Wang, Gould and Patterson, 1994), stems (Ferguson, 1984) and fruit (Perera *et al.*, 1990).

By the end of the sampling period, there were approx. 16 axillary structures in each FOAB, of which the most basal four were SOABs, the others remained as SDSMs. The most basal SDSM (node 5) usually aborts during the inflorescence and flower differentiation (Brundell, 1975*b*; Snowball and Considine, 1986; Walton and Fowke, 1993), suggesting a link between its smaller size and location, and its ultimate developmental fate. On shoots, the nodes that are most likely to bear flowers are nodes 6–12 (Walton and Fowke, 1993) and these are the nodes where the largest SDSMs are located. This suggests that there may also be a link between 'large' SDSM size and the ability to differentiate inflorescences and flowers. The new season's developing FOABs develop from the more distally located SDSMs and these

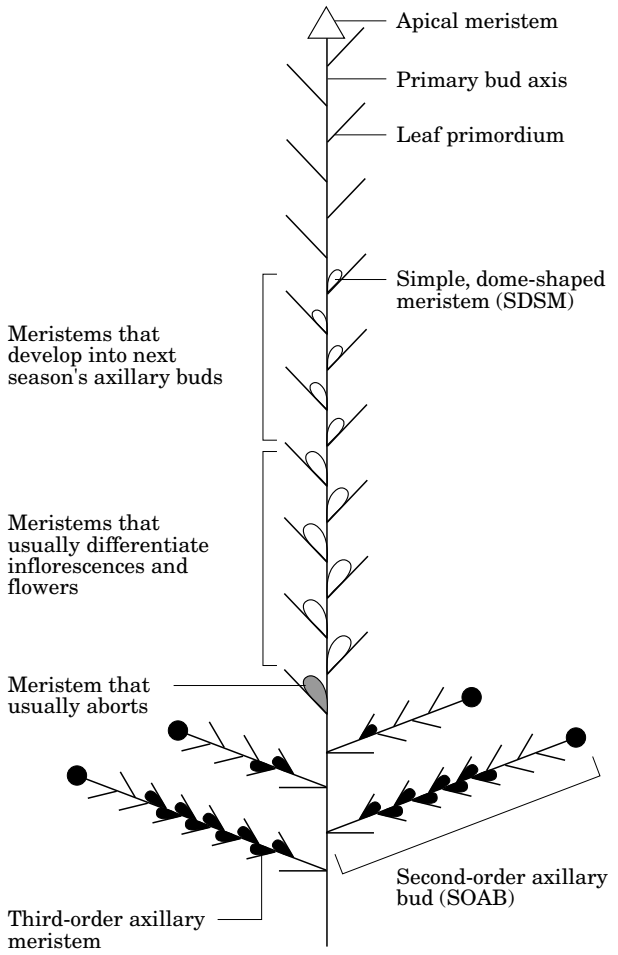


FIG. 17. Schematic of a mature FOAB at node 15. The numbers of structures depicted are mean numbers per bud. The ultimate developmental fates of the SDSMs are based on Walton and Fowke (1993).

meristems tended to be smaller. Consequently, the developmental fates of the axillary structures on the primary bud axis are linked to their nodal position. All second-order axillary structures were initially meristems (SDSMs), but only the most basal four developed into SOABs. It is likely that an event or trigger occurs during the development of the FOAB which prevents the meristems in nodes 5 and distal developing into SOABs. As the meristems in nodes 5 and basal had stopped increasing in size by 68 dab, but the meristems in nodes 6 and distal continued to grow, this suggests that the switch in developmental fates occurs about this time or earlier. That switch may be evocation. This relatively early timing of evocation in kiwifruit is in close agreement with the 'early' start of evocation (approx. 73 dab) proposed by Snelgar and Manson (1992). The early timing of floral evocation is also supported by the observation that primary *Actinidia eriantha* shoots 'tipped' in late spring and early summer can produce secondary shoots bearing flowers (Walton, 1995). Also, grape, which is similar to kiwifruit in that its flowers do not differentiate until the spring of anthesis (Pratt, 1971; Srinivasan and Mullins, 1981), undergoes evocation early in development, approx. 14–18 d before anlagen (equivalent to SDSMs in kiwifruit) initiation (Lavee, Regev and Samish, 1967), approx. 40–45 d after bud formation.

Our observations are consistent with evocation in kiwifruit occurring earlier than the generally accepted time of late-summer, and support the early start to evocation proposed by Snelgar and Manson (1992). We are currently analysing the expression of kiwifruit floral homeotic genes to obtain a molecular marker for evocation in this crop.

SUMMARY

A schematic of a typical FOAB at node 15 is presented in Fig. 17. At maturity, each FOAB had approx. 23 bud scales and leaf primordia and approx. 16 second-order axillary structures, of which four were SOABs and 12 were SDSMs. Most SOABs contain third-order axillary meristems in their more basal nodes. Based on the assessments of floral shoots by Walton and Fowke (1993), the basal six or seven SDSMs (the larger meristems) differentiate into inflorescences and flowers, although the most basal one or two SDSMs abort part way through the process. The remainder of the SDSMs (the smaller meristems) develop into the next seasons' FOABs, thus reiterating the developmental cycle.

ACKNOWLEDGEMENTS

We thank Murray Hopping for his thought-provoking comments at the beginning of this study, Neil and Max Thompson for the use of their orchard for sample collection, Paul Sutherland for assistance with the photography and John Green for the use of his image analysis suite. This work was supported by grants from the New Zealand Foundation for Research Science and Technology and the New Zealand Kiwifruit Marketing Board.

LITERATURE CITED

Brundell DJ. 1975*a*. Flower development of the Chinese gooseberry (*Actinidia chinensis* Planch.). I. Development of the flower shoot. *New Zealand Journal of Botany* **13**: 473–483.

Brundell DJ. 1975*b*. Flower development of the Chinese gooseberry (*Actinidia chinensis* Planch.). II. Development of the flowering bud. *New Zealand Journal of Botany* **13**: 485–496.

Davison RM. 1974. Flowering of kiwifruit. In: *Proceedings of Kiwifruit Seminar, Tauranga, 19 Sept. 1974*. Tauranga, New Zealand: Ministry of Agriculture and Fisheries, 13–16.

Ferguson AR. 1984. Kiwifruit: A botanical review. *Horticultural Reviews* **6**: 1–64.

Grant JA, Ryugo K. 1982. Influence of developing shoots on flowering potential of dormant buds of *Actinidia chinensis*. *HortScience* **17**: 977–978.

Henzell RF, Briscoe MR. 1986. Hydrogen cyanamide: A tool for consistently high kiwifruit production. *New Zealand Kiwifruit Special Publication* **1**: 8–11.

Henzell R, Briscoe M. 1988. Hydrogen cyanamide–a wonder chemical? *New Zealand Kiwifruit* **46**: 17.

Henzell RF, Briscoe MR, Gravett I. 1991. Improving kiwifruit vine productivity with plant growth regulators. *Acta Horticulturae* **297**: 345–350.

Hopping ME. 1976. Structure and development of fruit and seeds in Chinese gooseberry (*Actinidia chinensis* Planch.). *New Zealand Journal of Botany* **14**: 63–68.

Johansen DA. 1940. *Plant microtechnique*. New York: McGraw-Hill.

Lavee S, Regev U, Samish RM. 1967. The determination of induction and differentiation in grape vines. *Vitis* **6**: 1–13.

Lemon CW, Considine, JA. 1993. Anatomy and histochemistry of the root system of the kiwifruit vine, *Actinidia deliciosa* var. *deliciosa*. *Annals of Botany* **71**: 117–129.

McDaniel CN. 1994. Photoperiodic induction, evocation and floral initiation. In: Greyson RI, ed, *The development of flowers*. Oxford: Oxford University Press, 25–43, 267–307.

Ministry of Transport, New Zealand Meteorological Service. 1983. *Summaries of climatological observations to 1980*. *New Zealand Meteorological Service Miscellaneous Publication 177*. Wellington, New Zealand: New Zealand Meteorological Service, 20.

Perera CO, Hallet IC, Nguyen TT, Charles JC. 1990. Calcium oxalate crystals: The irritant factor in kiwifruit. *Journal of Food Science* **55**: 1066–1069, 1080.

Polito VS, Grant JA. 1984. Initiation and development of pistillate flowers in *Actinidia chinensis*. *Scientia Horticulturae* **22**: 365–371.

Pratt C. 1971. Reproductive anatomy of cultivated grapes—A review. *American Journal of Enology and Viticulture* **22**: 92–109.

Sale PR. 1990. *Kiwifruit growing*. Wellington, New Zealand: GP Books.

Schmid R. 1978. Reproductive anatomy of *Actinidia chinensis* (Actinidiaceae). *Botanische Jahrbuecher für Systematik Pflanzengeschichte und Planzengeographie* **100**: 149–195.

Schneider H. 1973. Methods for botanical sciences. In: Clark G, ed. *Staining procedures used by the Biological Stain Commission*. Baltimore: Williams and Wilkins, 198–199.

Snelgar WP, Manson PJ. 1992. Determination of the time of flower evocation in kiwifruit vines. *New Zealand Journal of Crop and Horticultural Science* **20**: 439–447.

Snowball AM. 1995. The seasonal cycle of leaf, shoot and bud development in kiwifruit. *Journal of Horticultural Science* **70**: 787–797.

Snowball AM. 1996. The timing of flower evocation in kiwifruit. *Journal of Horticultural Science* **71**: 335–347.

Snowball AM, Considine J. 1986. Flowering in kiwifruit (*Actinidia deliciosa* Liang et Ferguson): positional effects and development. *Acta Horticulturae* **175**: 85–89.

Srinivasan C, Mullins MG. 1981. Physiology of flowering in the grapevine—A review. *American Journal of Enology and Viticulture* **32**: 47–63.

Walton EF. 1995. Occurrence of secondary floral shoots in summer on *Actinidia eriantha* Benth. *New Zealand Journal of Crop and Horticultural Science* **23**: 341–343.

Walton EF. 1996. Occurrence of multiple shoots bearing flowers arising from a single axillary bud in kiwifruit (*Actinidia deliciosa*). *New Zealand Journal of Crop and Horticultural Science* **24**: 95–97.

Walton EF, Fowke PJ. 1993. Effect of hydrogen cyanamide on kiwifruit shoot flower number and position. *Journal of Horticultural Science* **68**: 529–534.

Wang Z-Y, Gould GS, Patterson KJ. 1994. Structure and development of mucilage-crystal idioblasts in the roots of five *Actinidia* species. *International Journal of Plant Sciences* **155**: 342–349.

Watanabe K, Takahashi B. 1984. Flower bud differentiation and development of kiwi (*Actinidia chinensis* Planch.). *Journal of the Japanese Society of Horticultural Science* **53**: 259–264.

Watson M, Gould KS. 1994. Development of flat and fan-shaped fruit in *Actinidia chinensis* var. *chinensis* and *Actinidia deliciosa*. *Annals of Botany* **74**: 59–68.