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Temperature-dependence of carbon acquisition and demand in relation to shoot and fruit growth of fruiting kiwifruit (*Actinidia deliciosa*) vines grown in controlled environments

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Abstract. Fruiting kiwifruit [*Actinidia deliciosa* (A. Chev.) C.F. Liang *et* A.R. Ferguson] vines were grown in two controlled temperatures of 28/22 and 17/12°C (day/night) for 160 and 215 d, to measure shoot and fruit growth and carbon demand, and to examine competition between fruit and the shoot. Leaf area, internode lengths, fruit diameters, photosynthesis and respiration were measured at regular intervals. The net daily carbon balance per shoot was determined from the net carbon acquisition of shoots, and carbon sequestration as shoot biomass. Vines grown at high temperature had 200% more leaf area, similar stem lengths and 100% more biomass than vines grown at low temperature. Leaf area expansion and stem extension were transiently reduced when fruit growth was maximal. Photosynthetic and respiration rates were affected by temperature, leading to net carbon acquisition of 450 g shoot^{-1} for 28/22°C-grown vines and 253 g shoot^{-1} for 17/12°C-grown vines, 54% being used for leaf, stem and fruit growth. Reallocation of carbon occurred from leaves to fruit, and the consequent reduction in leaf area strongly reduced the overall carbon balance compared with vegetative vines at similar temperatures. The data support the conclusion that at low temperatures especially, there is insufficient carbon to meet the full demands of both fruit and shoot growth.

Introduction

The effects of temperature on the vegetative growth processes of kiwifruit (*Actinidia deliciosa*) have been well described in a number of studies. Specifically, Morgan *et al.* (1985), Laing (1985) and Greer (1996) have shown that shoot elongation, leaf appearance rates, growth rates and photosynthesis are all optimal at 20–25°C and reduced at temperatures above 30°C and below 10°C. These results are consistent with effects of temperature on budbreak in the major growing areas in New Zealand, where temperatures are typically in the range of 12–15°C (Warrington and Stanley 1986).

More recently, Greer (1996), and Greer and Jeffares (1998) have assessed the effects of temperature on the carbon economy of vegetative vines. These results showed vines at high (28/22°C) temperature acquired significantly more carbon through photosynthesis than those at low (17/12°C) temperature, reflected by photosynthetic rates that differed by approximately 25%. Leaf area of high-temperature-grown vines, however, was markedly greater, by about 50%, than that of the low-temperature-grown vines and that was a major cause of the differences in carbon acquisition. In addition, the shoots of vines grown at high temperature produced more overall biomass but, nevertheless, also had a significant surplus of carbon compared with the vines grown at low temperature. In fact, these latter shoots had a negative carbon budget for nearly 50% of the growth period and only just achieved a positive net daily carbon balance.

Fruit are a major sink for carbon resources, as has been demonstrated in crop-load studies. For example, Wünsche *et al.* (2000) showed that leaves of apple trees with little or no crop had marked accumulation of starch and consequently, severely reduced rates of photosynthesis compared with those leaves of trees with high crop loads. Also, in apple trees, leaf photosynthesis increases in direct proportion to crop load (Palmer *et al.* 1997), consistent with the notion of fruit as a strong sink. For kiwifruit vines, it has been shown (Lai *et al.* 1989), that fruit are supplied with carbohydrates mostly from their subtending leaves. Furthermore, once the leaf area per fruit exceeds 225 cm^2

Abbreviations used: CAB, carbon accumulated as biomass; NCA, net carbon acquired; NCB, net carbon balance; PFD, photon flux density.

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per fruit, import of ^{14}C assimilates from outside the fruiting shoot is negligible (Lai *et al.* 1989). With typical crop loads of 540 fruit vine^{-1} (Cooper and Marshall 1992) and canopy leaf areas of 32–39 m^2 vine^{-1} (Green and Clothier 1988; Buwalda *et al.* 1992), kiwifruit vines produce significantly more leaf area than is apparently required to support the crop. This suggests fruit sinks are not as strong in kiwifruit vines as in other crops like apple. It was notable, however, from the Lai *et al.* (1989) study, that both area and photosynthetic rates of individual leaves increased when the leaf area per fruit increased by 4-fold, that is, when vegetative growth became predominant, again in contrast to apple. This again suggests that for kiwifruit vines the vegetative sink was relatively stronger than the fruit.

The kiwifruit vine growth habit is an aggressively-growing liane (Ferguson 1990; Greer and Halligan 2001), and requires extensive management (Cooper and Marshall 1992; Volz *et al.* 1992) to maintain the canopy and full light interception for horticultural production. The practice of summer pruning, thereby reducing vegetative growth to ensure adequate resources are supplied to the fruit (Snelgar *et al.* 1992), is also an indication that vegetative growth is a strong sink for carbon.

Given this apparent demand for carbon to support vegetative growth of kiwifruit vines and the impact of cool temperatures on the carbon economy, it would seem probable that fruiting vines at these temperatures would show marked competition for carbon between the shoot and the fruit. The results of Greer and Jeffares (1998) would, therefore, suggest that vines at cool temperature will produce enough carbon to support either vegetative growth or fruit, but perhaps not both. In contrast, because vines at warm temperatures produce significant surpluses of carbon, these vines should be able to fully support shoot and fruit growth.

The objective of the present study was to assess the hypothesis that kiwifruit vines grown at low temperature have insufficient carbon resources to support both fruit and shoots, and that growth of these organs would be at least impaired compared with non-fruiting vines or those grown at warm temperatures. To assess this hypothesis, fruiting kiwifruit vines were grown at identical temperatures to, and compared with, those in the original study by Greer and Jeffares (1998). Shoot and fruit growth was measured and the carbon economy of these vines determined.

Materials and methods

This study was carried out using facilities at the New Zealand Controlled Environment Laboratory in Palmerston North, New Zealand.

Plant material

Rooted cuttings of *Actinidia deliciosa* cv. Hayward [(A. Chev.) C.F. Liang *et* A.R. Ferguson] were grown in 25-L pots in a 30:30:30 (by volume) gravel:peat:pumice growing medium with incorporated fertilisers. The plants were maintained in an outdoor shelter until early October, when four plants were transferred to each of two controlled environment (CE) rooms. Budbreak occurred within a few days of transfer, and flowering followed by hand-pollination, occurred in mid- to late-November.

The plants were grown at day/night temperatures of 28/22 ± 0.5°C (referred to as 'high') and 17/12 ± 0.5°C (referred to as 'low') at a photon flux density (PFD) of 800 μmol m^{-2} s^{-1} of photosynthetically active radiation at plant height for 12 h. Irradiance in a diurnal square-wave pattern was provided by a water-screened array of six high-pressure discharge ('Metalarc', 1 kW, GTE; Sylvania, Drummondville, Quebec, Canada) and six tungsten–iodide lamps ('Halogen', 1 kW; Thorn, Enfield, UK). The daylength was extended prior to the main light period by 2 h of supplementary lighting supplied by six tungsten filament lamps (PAR 38, 150 W; GTE; Sylvania, Winchester, KY, USA). The PFD was 8 μmol m^{-2} s^{-1} during this period. The vapour pressure deficit was maintained at 0.6/0.4 ± 0.05 kPa (day/night) in both rooms. The plants were grown for approximately 160 d at high temperature and 214 d at low temperature. This enabled fruit to reach approximately similar stages of development. They were supplied at regular intervals during each day with a half-strength Hoagland's nutrient solution. All vines were grown along a horizontal trellis to ensure the leaves remained normal to the radiation, as described by Greer and Jeffares (1998).

Shoot growth measurements

From the time buds started to expand until late-April, both diameter of leaves and length of the subtending internodes were measured three times per week on two selected shoots on each of four plants in each treatment. The first leaf was defined as the first true leaf excluding bracts. Measurements of diameter commenced when each leaf was > 9 mm across, and of length when each internode was > 3 mm long. Measurements of both leaf diameter and internode length were continued until successive measurements indicated no further changes were occurring. Throughout the experiment, all other shoots were regularly pruned or removed from the vines. The relationship between leaf area (LI3000, Li-Cor, Lincoln, NE, USA) and leaf diameter was determined at the conclusion of the experiment for leaves at each temperature according to Greer (2001). Consequently, area of each leaf was then determined from the diameter measurements. Total shoot leaf area averaged across eight shoots per treatment was calculated over time by accumulating the area of individual leaves on each day of measurement across all nodes. Average shoot extension over time was determined from a comparable accumulation of individual internode lengths on these shoots. Each shoot produced up to 80 leaves at the low temperature and nearly 100 leaves at the high temperature. Dry matter of each leaf was subsequently determined from the relationships between leaf area and dry weight and between stem length and dry weight (Greer 2001).

Maximum length and diameter of each fruit were measured at 3–4-d intervals from 46–60 d after budbreak (about 7–10 d after full bloom) until the completion of the experiment. Dry weight of the developing fruit were back-calculated from these fruit size measurements according to the method of Snelgar *et al.* (1992), which was amended to include the fresh weight to dry weight relationship. This latter relationship was determined for any fruit that had been knocked off during the measurements and those present at the final harvest. At harvest, soluble solid concentration, expressed as °Brix, was also measured on 10 fruit per temperature treatment with a handheld refractometer (N20, Atago, Tokyo, Japan).

Leaf photosynthetic and respiration measurements

At approximately weekly intervals, the photosynthetic rate at the prevailing environmental conditions was measured on each leaf on two

shoots of two plants in each temperature regime from the time leaves were 35 mm in diameter. Respiration was also measured on the same leaves during the initial low light period by covering the leaf with a black cloth. Gas exchange was measured with a leaf chamber and IRGA (LI6400, Li-Cor). Photosynthesis was measured at least 60 min after the main lights came on. All measurements were carried at the respective day temperature and at a PFD of 800 μmol m^{-2} s^{-1}, supplied by a red/blue led lamp (6400-02B, Li-Cor)

Fruit respiration measurements

From the time the fruit were approximately 15 mm in diameter, weekly measurements of respiration were made on each fruit on each vine. A simple cylindrical chamber with a circulating fan was used to enclose the fruit and respiration measured with an IRGA (LCA2; ADC Ltd, Hoddesdon, UK). All measurements were at the day temperature in each room.

Whole-shoot carbon economy

Net daily CO_2 fixation for each leaf was determined by firstly integrating the measured photosynthesis and respiration rates over a 24-h period, assuming the rates were constant in the controlled environments over the day and night (Greer 1999). The net daily CO_2 fixation for the entire shoot (leaves + stem) was then summed for all leaves present, taking into account the changes in shoot leaf area. The rates of photosynthesis and respiration were also assumed to be approximately constant on the days between measurements. Net daily carbon acquisition for the growing shoot was then determined over the entire growth period, taking into account the increase in number of leaves as the stem extended and the molecular fraction of carbon in CO_2 (see Wullschleger *et al.* 1997). Stem respiration for shoots at each temperature, and as shoots extended in length, was estimated following Piller and Meekings (1997). Daily respiratory demand of all fruit on each vine was also assessed, again assuming rates did not differ dramatically between measurement, and again taking into account the growth of each fruit. Net daily carbon acquisition of the entire fruiting shoot was then summed from the leaf, stem and fruit gas exchange.

The net daily shoot carbon balance was then calculated from the difference between net daily carbon acquisition and the daily rate of accumulation of carbon as biomass in leaves, stems and fruit. The biomass carbon content was determined from the estimated daily increments in shoot (leaves, stem and fruit) dry matter, taking into account that approximately 45% of the biomass of kiwifruit shoots and fruit is elemental carbon (Walton and Fowke 1995).

Data analysis

All data were analysed by general linear models (SAS 1996), and least squares means and standard errors were calculated. Curve-fitting to data was carried out with the Bolztmann function, and the calculus/integration function (Origin, Microcal 1997) was used to provide a summation over time of the data for the carbon economy calculations.

Results

Growth and development

Leaf area development

Leaf emergence occurred at a generally constant rate throughout the growing period and all leaves expanded in a curvilinear pattern (not shown). Maximum leaf areas along the shoot varied markedly with nodal position (Fig. 1) on vines at both temperatures, with the largest leaves occurring at node 10, at about 0.027 m^2 in both cases. Further along the shoot, leaf area initially declined markedly until approximately nodes 20–25 and then increased again to reach another peak in size, at approximately node 38 in the low-temperature-grown vines (0.015 m^2) and approximately node 68 in the warm-temperature-grown vines (0.027 m^2). In contrast, although there were some minor perturbations, the cumulative increase in shoot leaf area over time (Fig. 2*A*) was generally constant in both treatments. Rates of increase averaged 0.011 ± 0.003 m^2 d^{-1} for the vines grown at 28/22°C and 0.004 ± 0.001 m^2 d^{-1} for the vines grown at 17/12°C. Consequently, leaf areas of the shoots at the high temperature were twice as large (1.7 ± 0.2 m^2) as those vines at the low temperature (0.75 ± 0.05 m^2), owing to both more and larger leaves at the high nodes.

Stem extension

Stem extension rates for the high-temperature-grown vines were initially linear throughout the early part of the growth period (Fig. 2*B*) and averaged 5.8 ± 0.4 cm d^{-1}. However, a marked decline in the extension rate occurred from about 75 d but this was relatively transient, and the rate resumed 110 d after budbreak at 5.0 ± 0.3 cm d^{-1}. Shoot lengths averaged 6.2 ± 0.5 m at the end of the growth stage. For the low-temperature-grown vines, the initial rate of stem extension was 2.6 ± 0.4 cm d^{-1}. There was a minor perturbation in the rate of stem extension occurring from around 76 d, however, after approximately 90 d the extension rate increased to 3.3 ± 0.2 cm d^{-1}, thus, above the initial rate. By the end of the more extended growth period, these vines averaged 6.0 ± 0.2 m, thus, approximately the same length as the high-temperature-grown vines.

Fruit growth

Full bloom occurred on 15 November and 30 November, for the high- and low-temperature-grown plants respectively.

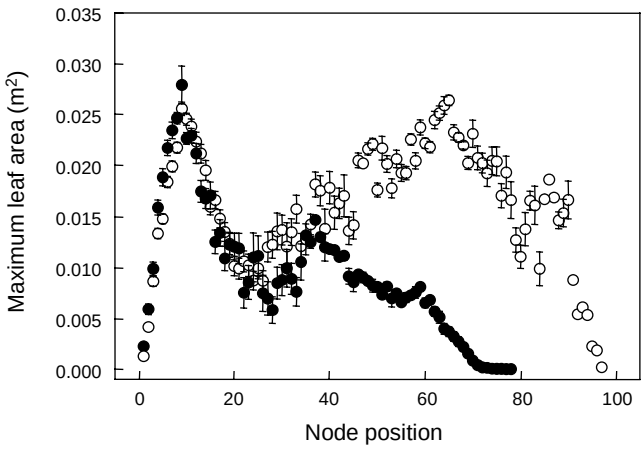

Fig. 1. Mean maximum areas for each leaf at the different node positions along the stem of kiwifruit shoots grown at two controlled temperatures of (○) 28/22°C (day/night) and (●) 17/12°C for 160 and 215 d, respectively (mean ± s.e.). Measurements were determined at the conclusion of the growth period.

Fruit growth patterns differed significantly between vines at the different temperatures (Fig. 3). For those vines grown at high temperature, fruit growth occurred in a continuously curvilinear pattern, while for those vines grown at low temperature, fruit growth followed a double-sigmoid pattern. However, there was no effect of temperature on final mean fruit dry weight since they averaged 18.6 ± 0.8 g and 19.4 ± 0.6 g for the high- and low-temperature treatments, respectively. Crop loads on the vines were 7.7 ± 0.9 and 7.3 ± 1.5 fruit vine^{-1} for the high-and low-temperature-grown vines, respectively and soluble solid content at each harvest averaged 5.2° Brix for both treatments.

Whole-shoot biomass accumulation and partitioning

For the vines grown at high temperature, patterns of total shoot biomass accumulation (Fig. 4) reflected the developmental changes that occurred in shoot leaf area expansion and stem extension. There was a perturbation in shoot leaf dry weight accumulation (Fig. 4*A*) and a more marked perturbation in shoot stem dry weight accumulation (Fig. 4*B*), but leaves and stems averaged 256 ± 14 g and 242 ± 12 g, respectively, by the end of the growth period. Dry weight accumulation of the total fruit per shoot increased in a curvilinear pattern to average 63.3 ± 2.8 g. The perturbation in dry matter accumulation, thus, correlated generally with the period of rapid fruit growth, and rates of both stem and leaf dry matter accumulation increased after fruit growth rates began to decline. These results are indicative of marked competition for resources between the fruit and the shoot.

A similar perturbation occurred in shoot leaf area and stem dry matter accumulation in the low temperature-grown vines (Figs 4*A*, *B*). The relatively small perturbation was surprising given the marked increase in rates of fruit dry matter accumulation between 90 and 120 d (Fig. 4*C*). At the end of the growth stage, leaf and stem dry matter averaged 170 ± 9 g and 127 ± 4 g, respectively while fruit weight averaged 63.7 ± 5.1 g. For the leaves, stem and fruit of the low-temperature-grown vines, dry matter accumulation per shoot was consistently lower than that for the high-temperature-grown vines and total dry matter was 1.8-fold (561 ± 29 g) greater for all components than the low-temperature-grown vines (361 ± 18 g).

For the high-temperature-grown vines, shoot biomass was initially partitioned between leaves and the stem in the proportions of 80% and 20% (Fig. 5*A*). However, the allocation to the stem increased to about 40% within 40 d from budbreak, and remained generally constant, averaging 43.2 ± 0.1% at later stages of the growth period. Allocation to the leaves continued to decline throughout, such that by the end of the growth period, leaves averaged 47.4 ± 0.2% of the total biomass. The allocation of the total shoot biomass to fruit increased relatively rapidly from about 45 d after bloom to about 20% and then reduced slowly to average 11.3 ± 0.1%. Changes in fruit allocation were linearly (P<0.01, r^2=0.98) related to changes in leaf allocation (not

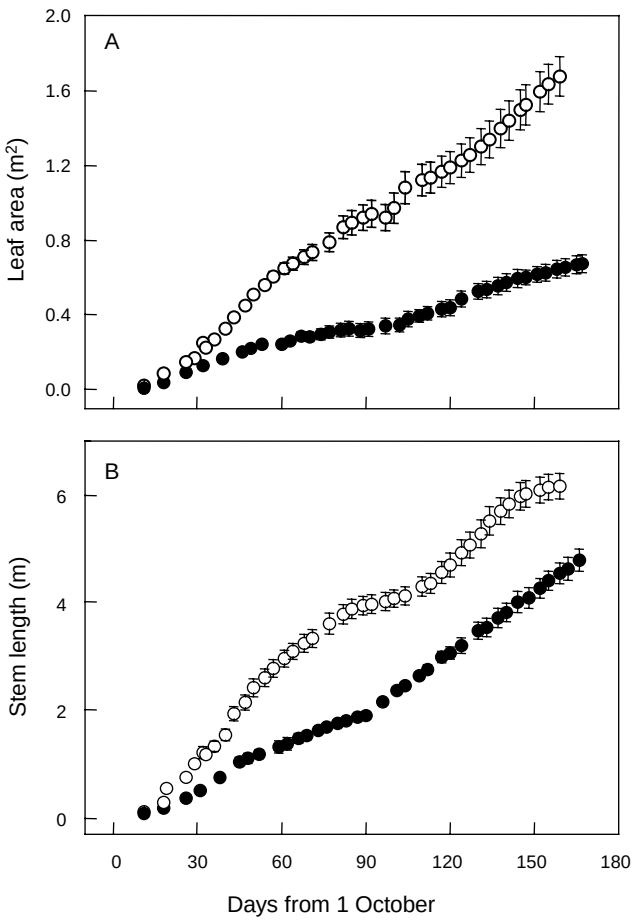

Fig. 2. Leaf area expansion (*A*) and stem extension (*B*) of kiwifruit shoots grown at two controlled temperatures of (○) 28/22°C (day/night) and (●) 17/12°C for 160 and 215 d, respectively (mean ± s.e.).

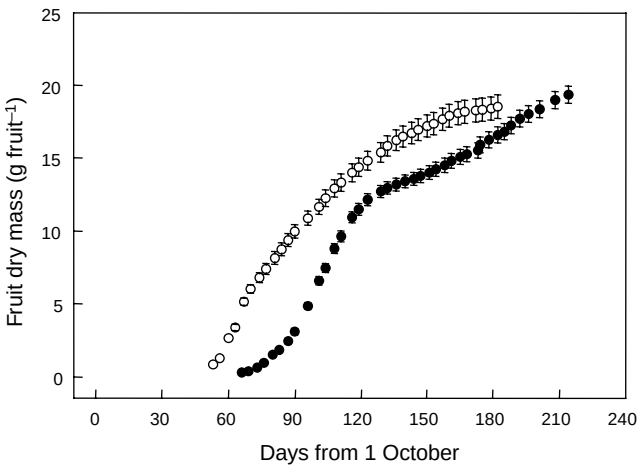

Fig. 3. Average fruit growth (mean ± s.e.) of kiwifruit vines grown at two controlled temperatures of (○) 28/22°C (day/night) and (●) 17/12°C for 160 and 215 d, respectively (mean ± s.e.).

shown); hence, fruit growth was directly at the expense of allocation of biomass to leaves.

The vines grown at the low temperature (Fig. 5*B*) had similar shifts in biomass allocation, although stems remained generally constant throughout at 35.6 ± 0.1% and leaf biomass allocation declined in direct proportion ($P<0.01$, $r^2=0.97$) to the increase in fruit allocation per shoot. By the end of the growth period, the leaf biomass averaged 47.1 ± 0.1% and fruit biomass averaged 17.7 ± 0.1% of the total. Thus, even though allocation to leaves was similar, there were differences in allocation between the vines grown at the two temperatures. Relatively more biomass was allocated to fruit at low temperature and more to stems at high temperature.

Gas exchange

Early in the season, the earliest emerging leaves had the highest rates of photosynthesis at about 14 μmol m^{-2} s^{-1} for the high-temperature-grown vines (Fig. 6*A*), but the rates declined for the most recently emerged leaves to about 4 μmol m^{-2} s^{-1}. By contrast, respiration increased for leaves along the shoot to about 4 μmol m^{-2} s^{-1}, thus, indicating that the young, expanding leaves had virtually no net carbon gain. This pattern for both photosynthesis and respiration for leaves along the shoot continued throughout the season, although rates of photosynthesis for the older leaves had declined to about 8 μmol m^{-2} s^{-1} by the time the growth period had finished.

Similar results occurred with the low-temperature-grown vines (Fig. 6*B*), except that respiration did not increase along the shoot to the same extent as in the high-temperature-grown vines. This was probably because of the low night temperature (12°C), which would have reduced the rate of respiration. It was also notable that in mid-season the mid-aged leaves (nodes 10–15) actually had the highest rates of photosynthesis (up to 16 μmol m^{-2} s^{-1}). Late in the growing season, rates of photosynthesis along the shoot were similar and were typically around 8–9 μmol m^{-2} s^{-1}.

Over the entire growth period, photosynthetic rates averaged 7.6 ± 0.2 and 9.2 ± 0.2 μmol m^{-2} s^{-1}, while respiration rates averaged 1.6 ± 0.1 and 1.2 ± 0.1 μmol m^{-2} s^{-1} for the high- and low-temperature-grown vines, respectively.

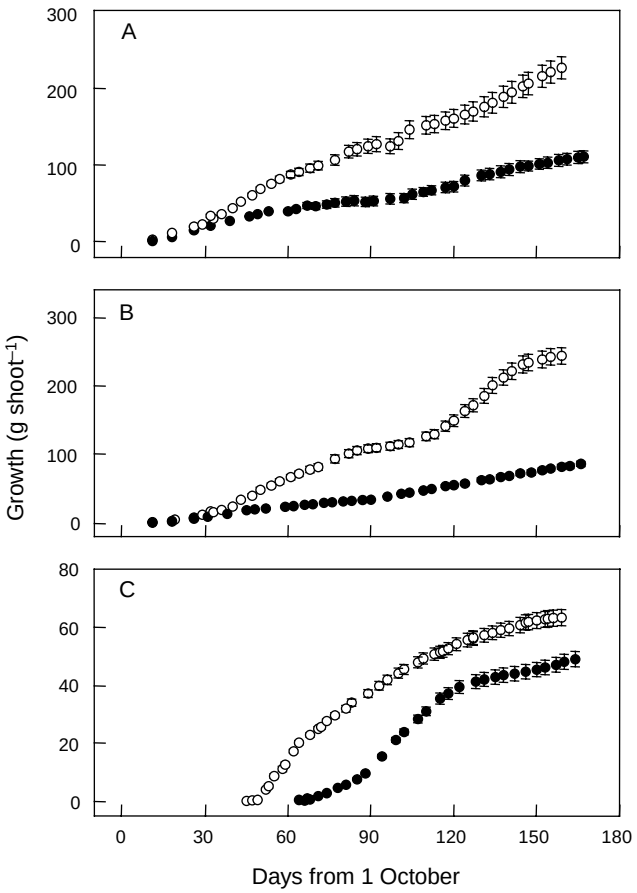

Fig. 4. Average cumulative growth of leaves (*A*), stems (*B*), and fruit load (*C*) of shoots of kiwifruit vines grown at two controlled temperatures of (○) 28/22°C (day/night) and (●)17/12°C for 160 and 215 d, respectively (mean ± s.e.).

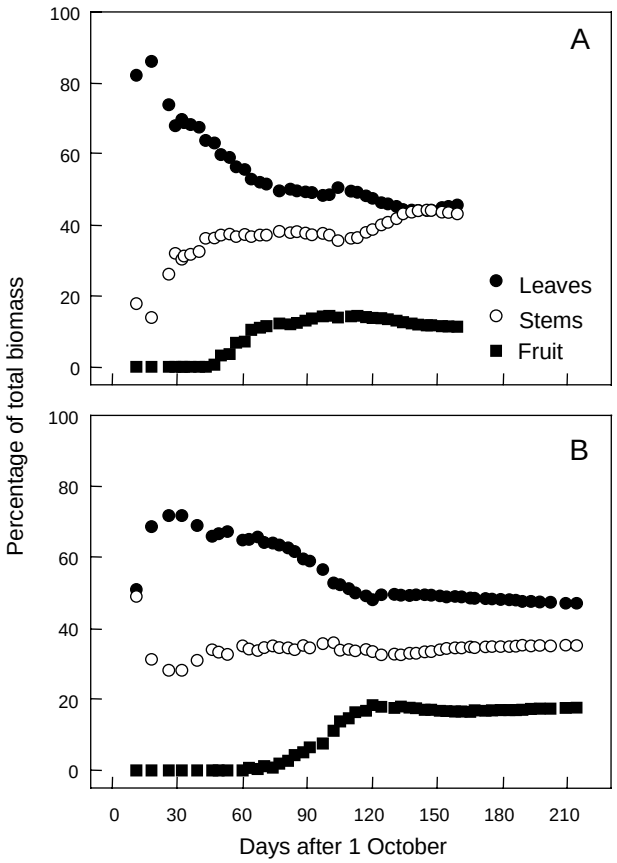

Fig. 5. Changes in the partitioning of the total biomass between leaves (●), stem (○) and fruit (■) of shoots of kiwifruit vines grown at two controlled temperatures of 28/22°C (*A*) and 17/12°C (*B*) for 160 and 215 d, respectively.

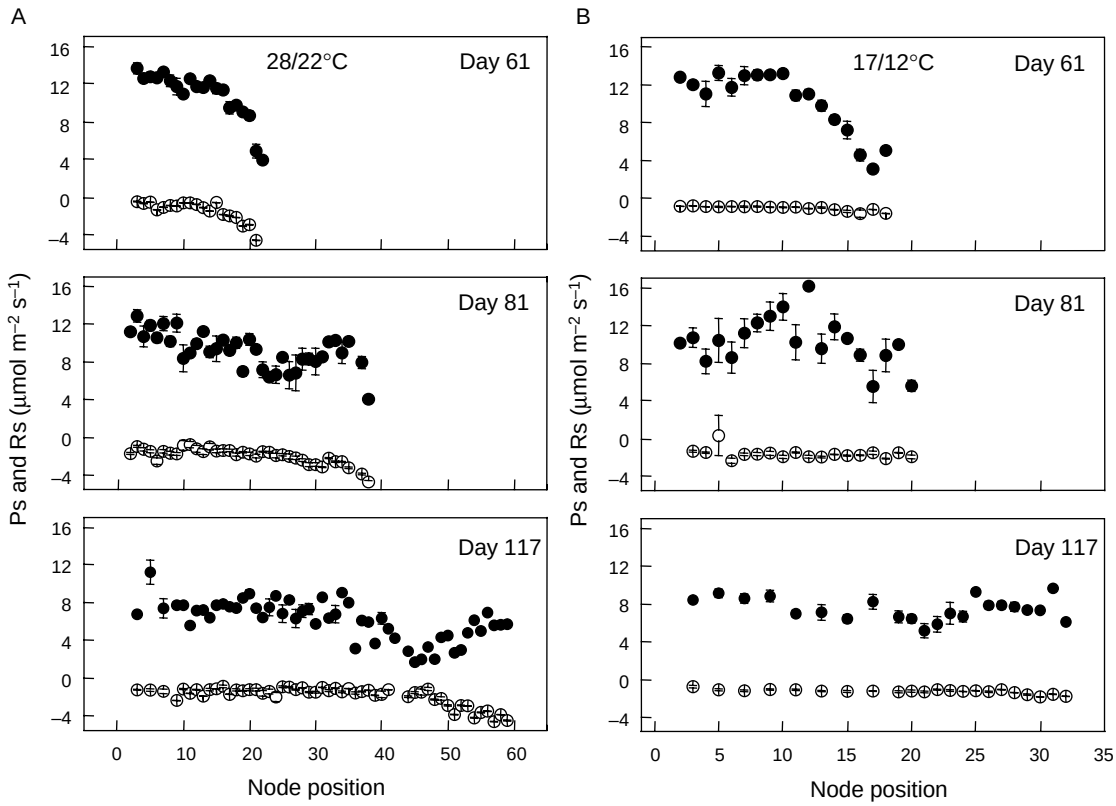

Fig. 6. Changes in photosynthesis (Ps, ●) and respiration (Rs, ○) (mean ± s.e.) along kiwifruit shoots at three times during the study for vines grown at two controlled temperatures of 28/22°C (*A*) and 17/12°C (*B*) for 160 and 215 d, respectively.

Fruit respiration

Respiration rates were relatively high shortly after anthesis (Fig. 7) and in the range of 1.5–2.5 g C g^{-1} dry wt d^{-1}. However, within a few weeks after anthesis, the rates of respiration of the fruit had declined markedly and remained constant and very low at 10.6–15.5 mg C g^{-1} dry wt d^{-1}. For the plants grown at the high temperature, fruit respiration over the period of fruit development averaged 17.8 ± 1.9 mg C g^{-1} dry wt d^{-1}, while those grown at low temperature averaged 22.7 ± 1.3 mg C g^{-1} dry wt d^{-1}.

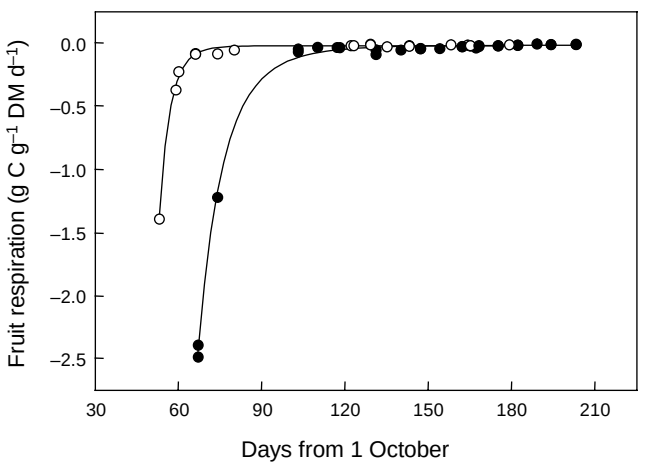

Fig. 7. Changes in fruit respiration (mean ± s.e.) for kiwifruit vines grown at two controlled temperatures of 28/22°C (○) and 17/12°C (●) for 160 and 215 d, respectively.

Net carbon balance

Net daily carbon acquisition

For the high-temperature-grown vines, net daily rate of carbon acquisition per shoot increased in a generally linear pattern from approximately 20 d after budbreak until harvest (Fig. 8*A*). However, there was a major perturbation from about day 75, when the rate apparently declined for approximately 20 d, but thereafter the rate increased again. By the end of the growth stage, these vines were acquiring carbon at a rate of nearly 7 g C shoot^{-1} d^{-1}, and over the entire period achieved a net total of 450 g C shoot^{-1}.

A similar, though more marked, decline in the rate of carbon acquisition also occurred with the low-temperature-grown vines (Fig. 8*D*) at about day 120. In this instance, however, the rate of carbon acquisition actually declined by about 25% before increasing to a maximum rate of 2 g C shoot^{-1} d^{-1}. Total carbon acquisition for these vines was 253 g C shoot^{-1}.

Daily carbon accumulation as biomass

Daily rates of sequestration of carbon into biomass were highly variable in both treatments (Figs 8*B*, *E*). For the high-temperature-grown vines, after an initial increase to about 2.5 g C shoot^{-1} d^{-1} there was a discernible reduction in the rate down to less than 1 g C shoot^{-1} d^{-1} at about day 90. Thereafter, the rate increased again to a maximum of about 3 g C shoot^{-1} d^{-1} before it declined again. Over the entire growth period, these shoots accumulated a total of 244 g C shoot^{-1}.

For the low-temperature-grown vines, sequestration of carbon into biomass was relatively low at about 0.5 g C shoot^{-1} d^{-1} for approximately the first 80 d. It then increased to a peak of 1.5 g C shoot^{-1} d^{-1} at around day 105, and then progressively declined back to about 0.5 g C shoot^{-1} d^{-1} by the end of the growth period. The total carbon sequestered into shoot biomass for these low-temperature-grown vines was 137 g C shoot^{-1}.

Net daily carbon balance

The net daily carbon balance of the high-temperature-grown vines became increasingly negative from budbreak for about 45 d, when net daily carbon balance was most negative at –1.8 g C shoot^{-1} d^{-1} (Fig. 8*C*). Thereafter, the net carbon balance began to increase but only became positive 60 d after budbreak, with the rate increasing strongly to reach a maximum of about 6 g C shoot^{-1} d^{-1} by the end of the growth stage. Over the entire growth stage, these vines had a net carbon gain of 206 g shoot^{-1}. This surplus was exported out of the shoots, presumably to the trunk and roots of the vines.

In contrast, the low-temperature-grown vines initially had a slightly negative net daily carbon balance (Fig. 8*F*), which became positive about 45 d after budbreak. The carbon balance remained relatively low and only just started to increase after about 150 d after budbreak, to nearly 2 g C shoot^{-1} d^{-1}. Over the entire growth stage, these vines had a net carbon gain of 116 g C shoot^{-1}, again exported out of the shoots to other sinks.

Comparison of the shoot carbon economies of fruiting and vegetative vines

Shown in Table 1 are the data for the present study and that of Greer and Jeffares (1998) for the total carbon fixed, sequestered as biomass and the estimated surpluses for shoots of kiwifruit vines grown at the two temperatures. Note that as Greer and Jeffares (1998) used a different growth period, the data for the present experiment in Table 1 has been recalculated to match the shorter durations used in the original study, and enable direct comparison.

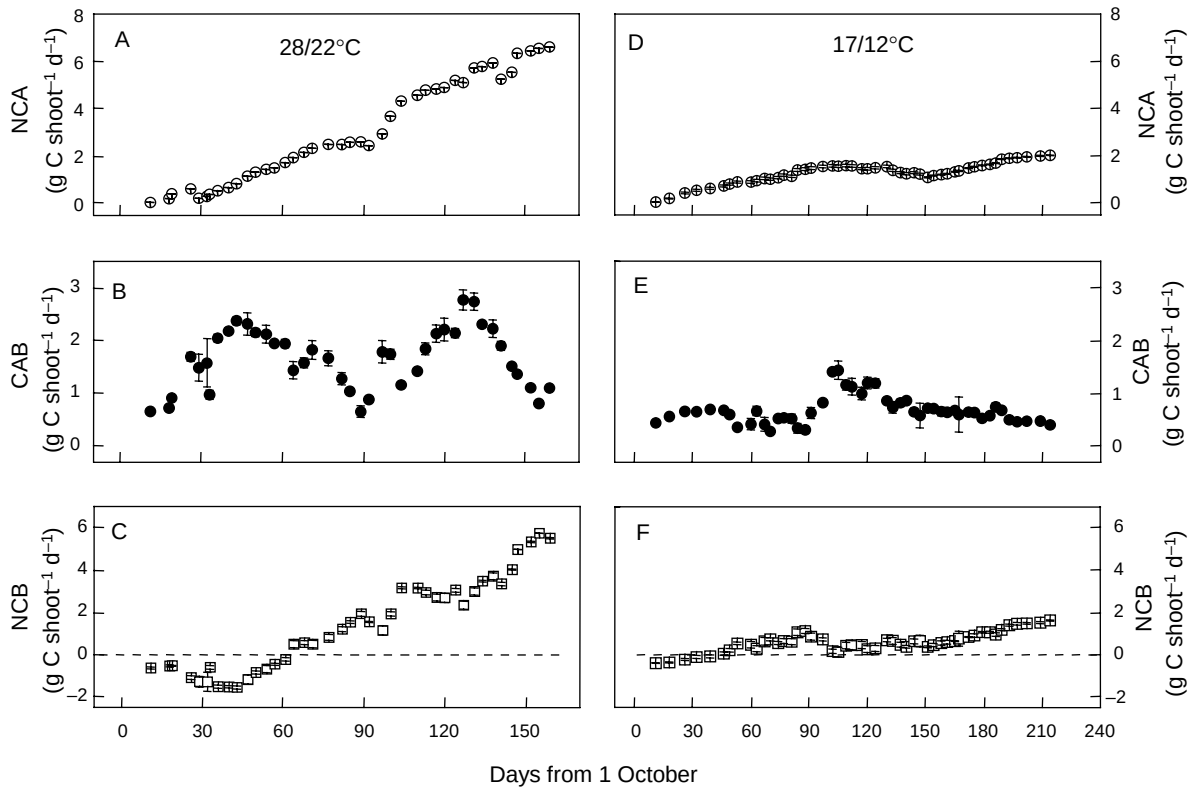

Fig. 8. Changes in the estimated (mean ± s.e.) net daily carbon acquisition (*A*, *D*), net daily carbon accumulation as biomass (*B*, *E*) and the net daily carbon balance (*C*, *F*) of shoots of kiwifruit vines grown at two controlled temperatures of 28/22°C (*A–C*) and 17/12°C (*D–F*) for 160 and 215 d, respectively. The dotted line in *C* and *F* represents when the net daily carbon balance is zero.

For the vegetative vines grown at high temperature, the net carbon fixed was 387 g C shoot^{-1}, while fruiting vines fixed 281 g C shoot^{-1}. At the low growth temperature, fruiting and vegetative vines both fixed about 125 g C shoot^{-1}.

Of the carbon sequestered as shoot biomass, fruiting vines grown at high temperature accumulated about the same amount of carbon as vegetative vines (approximately 190 g shoot^{-1}), but as a proportion of that fixed, fruiting vines sequestered 71% compared with 47% for vegetative vines. In contrast, low-temperature-grown vegetative vines sequestered nearly twice as much carbon as fruiting vines, but of that fixed, vegetative vines accumulated 92% as shoot biomass, whereas fruiting vines accumulated 70% as shoot biomass.

Shoots of both fruiting and vegetative vines at high growth temperature had a net carbon surplus, but at about 200 g C shoot^{-1}, the surplus for the vegetative vines was nearly 2.5-fold greater than for the fruiting vines. In contrast, shoots of vines grown at low temperature produced a slightly greater carbon surplus than shoots of vegetative vines, but in general, the surpluses for both were small.

Discussion

The overall growth and development of fruiting kiwifruit vines was markedly affected by temperature. The high-temperature-grown vines had more than twice the leaf area, similar shoot lengths and approximately twice as much leaf and stem biomass as those vines grown at low temperature. These results are, thus, comparable with those determined for vegetative vines in the original studies by Greer and Jeffares (1998) and Morgan *et al.* (1988), in that temperature had major effects on both growth and development. However, of concern here was the impact the presence of fruit had on the growth and developmental properties of the vines and the effects of temperature. Comparison of these data with those from Greer and Jeffares (1998) reveals that, at both temperatures, vegetative vines had about 50% more leaf area than fruiting vines at a comparable developmental stage. This is reflected in marked differences in size of the largest leaf (0.045 *cf.* 0.027 m^2). Furthermore, the pattern of leaf area distribution along the shoot was markedly different from that of vegetative vines (*cf.* Greer 1996; Greer 2001). In the latter cases, leaf area declined in a consistent pattern along the shoot whereas with fruit present, a bimodal distribution of leaf area occurred. Expansion of leaves emerging from the early to middle phase of the growth period was, therefore, apparently affected by the presence of flowers and fruit, while later emerging leaves were apparently unaffected.

Differences in stem lengths between vegetative and fruiting vines were also affected by temperature and, on average, were 20 and 40% longer in the vegetative vines at high and low temperature, respectively. Consistent with this, grapevines with and without fruit had similar (34%) differences in leaf area, but even greater (2.5-fold) differences in stem length (Petrie *et al.* 2000*a*; see also Edson *et al.* 1995*a*) than observed here. Apple trees with and without crop had 67% more leaf area on the non-cropping trees (Wünsche *et al.* 2000; see also Fujii and Kennedy 1985). These data consistently show that leaves are an alternative sink for carbon when fruit are absent.

In contrast, fruiting kiwifruit vines at high temperature had about 40% more leaf biomass than vegetative vines, primarily owing to leaves being thicker (147 *cf.* 77 g m^{-2}), and this difference was retained throughout the growth period. Fruiting vines grown at low temperature also had about 30% more leaf biomass than vegetative vines, again from thicker leaves (223 *cf.* 198 g m^{-2}). The increase in leaf biomass on fruiting kiwifruit vines was, thus, temperature-dependent. For comparison, grapevines without fruit and grown at 24/15°C had 38% more leaf biomass than fruiting vines (Petrie *et al.* 2000*a*) while non-fruiting Seyval grapevines had nearly 60% more leaf biomass than fruiting vines (Edson *et al.* 1995*a*). In contrast, at a comparable development stage, stem biomass was greater in vegetative kiwifruit vines at both temperatures, by about 20% for vines grown at high temperature and nearly double for vines grown at low temperature. Non-fruiting grapevines also had the greater (2.8-fold, Edson *et al.* 1995*a*; 3.3-fold, Petrie *et al.* 2000*a*)

Table 1. Comparison of the shoot carbon economy of kiwifruit vines grown at two temperatures either with (+) or without (-) fruit

Data from Greer and Jeffares (1998). Note that a new method of integration of the original data (see methods) gave quantitatively different values to those published. However, these new data do not materially affect the conclusions in Greer and Jeffares (1998). The total net carbon acquired (NCA), the total carbon accumulated as biomass (CAB) and the net carbon balance (NCB) is included. For comparison, the shoot leaf areas are also included. Data for the fruiting vines were calculated over 130 d to match that for vegetative vines

Temperature (°C)	Fruit	Shoot leaf area (m^2)	NCA (g C shoot^{-1})	CAB (g C shoot^{-1})	NCB (g C shoot^{-1})
28/22	–	1.89	387	181	206
	+	1.22	281	199	82
17/12	–	0.89	126	116	10
	+	0.59	123	85	38

stem biomass These results conform with the stems being a strong carbon sink in the absence of fruit. Although there was 18% more total shoot biomass on the fruiting vines at high temperature, fruit accounted for approximately 12% of this increase. For vines grown at low temperature, however, fruiting vines had only about 75% of the total shoot biomass of the vegetative vines. Thus, these data support our hypothesis that at low temperatures, fruit have a more negative effect on the growth of stems and leaves than at high temperatures.

When the dynamics of leaf and stem growth were considered, it was clear that fruit had a marked, though somewhat transient, impact on shoot growth patterns. A comparison of stem extension rates of vegetative (Fig. 2; Greer and Jeffares 1998) and fruiting vines (Fig. 2*B*) reveals a distinct depression in the rates on the fruiting vines from about 80 d after budbreak. This depression was also apparent in rates of leaf area expansion, especially for those leaves emerging at the time of fruit growth. Consequently, fruiting vines had markedly smaller leaf areas over all leaves than vegetative vines. No such depression in leaf expansion or stem extension rates occurred on vegetative kiwifruit vines or in grapevines (Edson *et al.* 1995*a*; Petrie *et al.* 2000*a*).

Although the timing of the growth depression did not precisely coincide with the time of maximum fruit growth rates, the rates were still relatively high when the growth depression occurred. However, stem extension resumed at near the original rate at a time about when fruit growth rates had begun to decline, and achieved about the same overall length as the vegetative vines. No such effect was observed in grapevines, even though the crop load was about 60% of the total biomass (Petrie *et al.* 2000*a*) compared with 11–18% for the kiwifruit vines. Fruit on low-temperature-grown vines, in contrast, had a distinctive and marked change in growth rates, following a double-sigmoid growth pattern, which is typical of kiwifruit (*cf.* Hall *et al.* 1996; Richardson *et al.* 1997). This had a smaller effect on the dynamics of shoot growth compared with the growth pattern at high temperature. Nevertheless, the effect was still coincident with the time of maximum fruit growth. Therefore, the presence of fruit unequivocally affects developmental growth patterns and biomass accumulation of kiwifruit vines and other perennial crops.

The presence of fruit on perennial vines and trees is well known to have a major effect on the photosynthetic rates of these plants. Notably photosynthesis becomes down-regulated in the absence of the fruit sink (Flore and Lakso 1989; Edson *et al.* 1993; Gucci *et al.* 1995; Petrie *et al.* 2000*b*; Wünsche *et al.* 2000). Consistent with this, photosynthetic rates of kiwifruit leaves on vines with fruit were, on average, 17–21% higher at both growth temperatures than in the vegetative vines. Downton *et al.* (1987) and Edson *et al.* (1995*b*) both observed similar differences to those reported here for grapevine leaf photosynthesis although elsewhere, photosynthesis was unaffected by the presence of fruit (Chaumont *et al.* 1994). Fruit-bearing and non-fruiting pecan trees also had similar differences in photosynthesis (Wood 1988) to that reported in the present study. In contrast, photosynthesis of sweet cherry was unaffected by the presence or absence of fruit (Roper *et al.* 1988). Thus, there is a general, though not universal, response of leaf photosynthesis to the presence of fruit.

Kiwifruit leaf respiration also differed between fruiting and vegetative vines (*cf.* Greer and Jeffares 1998), with the rates about twice as high on the fruiting vines at both temperatures. This probably reflects the proportionally higher biomass per leaf of the fruiting leaves and hence, the higher maintenance respiration costs (McKree 1986) compared with the vegetative leaves. In contrast, leaf respiration did not differ between fruiting and non-fruiting apple trees (Fujii and Kennedy 1985), although Wibbe and Blanke (1995) did measure higher leaf respiration in fruiting compared with non-fruiting apple trees. These authors attributed this result to stomatal closure in non-fruiting plants but changes in biomass allocation per leaf (not assessed) may have explained their results.

Fruiting vines at high growth temperatures fixed much less carbon than vegetative vines over a comparable time (Table 1). This occurred despite the higher photosynthetic rates (on average, 9.2 ± 0.2 *cf.* 7.6 ± 0.07) of the fruiting vines. However, as shown earlier, the fruit had negative impacts on leaf area expansion patterns compared with those of vegetative vines, such that the fruiting shoots both lagged sharply behind in development of leaf area (e.g. 0.9 *cf.* 1.3 m^2 on day 90) and had smaller leaves. These latter effects contributed to markedly lower daily rates of net carbon acquisition for over 100 d, such that these fruiting vines fixed only about 75% of the carbon fixed by vegetative vines. This contrasts with grapevines, where vines without fruit fixed 22% less carbon than fruiting vines (Downton *et al.* 1987). Similarly, apple trees without fruit fixed 35% less carbon than trees with fruit (Wibbe and Blanke 1997). Kiwifruit vines, thus, differed from these and other species (see also Flore and Lakso 1989). It remains uncertain why leaf area expansion of kiwifruit vines was so strongly influenced by fruit, especially since leaves of fruiting vines accumulated more biomass per area than vegetative vine leaves.

Because of the increased demand for carbon from the leaves and fruit and also the relatively high stem demand, the high-temperature-grown vines sequestered slightly more (10%, Table 1) carbon into biomass than vegetative vines, at a comparable growth stage. In comparison, grapevines with fruit sequestered approximately 37% more carbon into leaf and stem biomass than vegetative vines (Petrie *et al.* 2000*a*). Similar differences were observed in cucumber (Janoudi and Withers 1993), strawberry (Hancock and Cameron 1986) and

apple (Maggs 1963; Avery 1969). Thus, kiwifruit vines at high temperatures were comparable with other species in having a higher demand for carbon with fruit as an extra sink.

Allocation of the total shoot biomass to stems of fruiting vines altered little over the growth period in both treatments. Thus, allocation of carbon to fruit during the active growth phase was almost entirely at the expense of leaves. This appears surprising given the marked effects of fruiting on the dynamics of shoot extension. Furthermore, relative to vegetative vines, biomass accumulation per m^2 by leaves of fruiting vines actually increased. It may be, therefore, that some aspect other than the carbon economy accounts for the effect of fruit on stem growth and development. However, the analysis here only assessed net changes in carbon sequestration into biomass of the shoot. It may be that shifts in carbohydrate between short- and long-term reserve pools (Henton *et al.* 2002), especially in the roots, might accommodate the apparent contradictions in stem and leaf biomass demands on fruiting kiwifruit vines. Further work is needed to resolve this.

The net carbon balance of the shoots of fruiting vines was only slightly positive (82 g $shoot^{-1}$) compared with that occurring with shoots of vegetative vines at comparable growth stages. Field-grown grapevines (Downton and Grant 1992), when compared over comparable dry weights, had a similar net surplus of carbon. This net surplus strongly conforms with the conclusion of Lai *et al.* (1989) that, with the leaf area per fruit carried by these kiwifruit vines, export rather than import of carbon occurred in the shoots of the fruiting vines. Furthermore, consistent with our hypothesis, the shoots of kiwifruit vines at high temperature produced more than enough carbon to support fruit and vegetative growth.

Photosynthetic rates of leaves on fruiting vines grown at low temperature also increased (7.6 ± 0.2 *cf.* 6.5 ± 0.1), consistent with rates determined by Laing (1985). As with high temperature, fruit had a negative effect on the development of leaf area on vines grown at low temperature, by 30%, yet shoots of fruiting vines acquired as much carbon as vegetative vines in a comparable time (Table 1). Thus, increased photosynthesis appeared to match the decreased leaf area. Higher rates of photosynthesis in mid-season (Fig. 5) also probably contributed to the high rates of carbon fixation. However, compared with the vegetative vines, fruiting vines sequestered about 26% less carbon into overall shoot biomass. Thus, allocation of carbon for fruit growth at low temperatures was also at the expense of leaves. This suggests that redistribution of carbon from leaves to fruit is a more general process for kiwifruit vines. However, as at high temperatures, internal cycling between carbohydrate pools may have occurred and stems may have also contributed carbon to the fruit.

In summary, the hypothesis that at low temperatures, kiwifruit vines acquire just enough carbon to meet leaf and stem growth demands and, therefore, are not able to sustain both fruit and vegetative growth was at least partially confirmed by this study. Perhaps surprisingly, fruit also had a more negative effect on stem growth and leaf area expansion at high temperatures than might have been expected, based on the carbon economy. Because of these negative impacts, a longer growth period was required, at both temperatures, to meet the carbon demands for fruit growth and to achieve similar stem and leaf growth to that of vegetative vines. Fruit were, as in many other species, a strong sink for carbon of kiwifruit vines, yet the demand was relatively transient. Consequently, resumption of vegetative growth occurred, particularly at high temperatures. This behaviour conforms with a characteristic growth habit of this species, that is, strong vegetative regrowth occurring in summer.

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