Influence of postharvest temperatures on leaf gas exchange, carbohydrate reserves and allocations, subsequent budbreak, and fruit yield of ‘Braeburn’ apple (Malus domestica) trees

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Abstract Potted ‘Braeburn’ apple (Malus domestica (Borkh.)) trees were grown after harvest in four controlled temperature conditions for 5 weeks to manipulate differences in carbohydrate reserves. Day/night temperatures ranged from 24/19 to 9/4°C. On several occasions, leaf gas exchange and soil respiration were measured and trees were destructively harvested before and after treatment to measure biomass of component parts. Samples were also taken for carbohydrate analysis. After treatment, the trees were returned outdoors and budbreak and fruit growth were measured in the following spring and crop load was measured at the next harvest. Trees at 24/19°C produced new leaves and flowered profusely whereas those at 9/4°C senesced rapidly but these trees grew new roots. Photosynthesis and respiration were highly dependent on temperature, and after 5 weeks of growth there were marked differences in rates between the various treatments.

INTRODUCTION
Production of apples per hectare in New Zealand is significantly higher than in other apple producing countries such as China, the United States, and Germany. For example, New Zealand yields averaged 58 t ha⁻¹ over the 1996–98 seasons whereas for these other countries, yields averaged 9, 26, and 50 t ha⁻¹, respectively (O’Rourke 1999). Although high cropping can partly be attributed to high density planting, it is noteworthy that New Zealand production is based on an average of 850 trees ha⁻¹ whereas tree density in these other countries range from 125 trees ha⁻¹ in China to 1600 trees ha⁻¹ in Germany (O’Rourke 1999). Thus, factors other than planting density apparently contribute to the high New Zealand apple yields.

The length of the growing season in New Zealand after fruit harvest until leaf fall is much longer than for many other apple growing regions in the United States and Europe. This has been implicated as an underlying cause of the high crop yields (Tustin et al. 1997; Wünsche et al. 2000). For apple varieties such as ‘Braeburn’ (Malus domestica (Borkh.)), this
postharvest period can be as long as 2.5 months. In the major apple growing areas in New Zealand, there are relatively mild temperatures (13–20°C for the average daily maximum temperature, Anon. 1980) and sunny conditions (Wünsche et al. 2000) in the period from April until June. Given that apple leaf photosynthesis has optimal rates in the range of 15–35°C (Watson et al. 1978; Lakso 1994; Wünsche unpubl. data), there is a clear expectation that apple leaves should remain photosynthetically active during the postharvest period. Consistent with this, photosynthetic rates of ‘Braeburn’ apple leaves and canopies 20 days after fruit had been harvested have been recently demonstrated by Wünsche et al. (2000) to remain as high as the preharvest maximum rates. Furthermore, in this study, 50 days after harvest, photosynthetic rates remained at nearly 60% of the preharvest rates. Elsewhere, Tustin et al. (1997) have shown for ‘Royal Gala’ that leaf photosynthetic rates of 12–13 μmol m⁻² s⁻¹ occur up to 50 days after harvest. These rates equate to c. 60–70% of maximum apple leaf photosynthetic rates (Flore & Lakso 1989). Elsewhere, for ‘Golden Delicious’ Terhoeven-Urselmans & Blanke (1999) have shown leaf photosynthesis 60 days after harvest remained at c. 4 μmol m⁻² s⁻¹ and concluded that the environmental conditions were the primary limiting factor for photosynthesis. Thus, there is clear evidence that apple trees can continue net acquisition of carbon for several months after fruit harvest, if the environmental conditions are permissive.

Tustin et al. (1997) assessed the hypothesis that the high yields of apple were partly associated with the length of the growing season by carrying out defoliation treatments, both immediately after harvest and 30 days later. These treatments delayed budbreak in spring, reduced initial and final fruit set, and the most severe defoliation treatments reduced fruit size at harvest. By inference, these authors concluded that the treatments caused a loss of carbohydrate reserves, as it is known (Hansen 1977) that these reserves are important for regulating early fruit development. However, no direct measurements of the tree carbohydrate reserves were reported in the study of Tustin et al. (1997). Thus, it remains to be quantified to what extent the period of favourable conditions after harvest, enabling longer photosynthesis and more carbohydrate accumulation and storage, contributes to crop productivity in the subsequent season.

The objectives of the present study were first, to impose different temperatures on potted ‘Braeburn’ apple trees immediately after harvest and then to measure photosynthetic and respiration rates and carbohydrate concentrations. Second, these postharvest effects on subsequent budbreak in spring and crop production in summer were also assessed.

**MATERIALS AND METHODS**

This experiment was carried out using the facilities of the New Zealand Controlled Environment Laboratory in Palmerston North.

**Plant material and growth conditions**

Potted trees of 5-year-old ‘Braeburn’ apple on M9 rootstocks were grown outdoors under uniform conditions throughout the 1996/97 growing season until fruit were harvested in early April. Six trees were then randomly allocated to each of four controlled environments and grown for 5 weeks at day/night temperatures of 24/19, 19/14, 14/9, and 9/4 ± 0.5°C.

The photon flux density (PFD) at mid-tree height was 700 μmol m⁻² s⁻¹ for 10 h. Light was provided by a water-screened array of four high-pressure discharge and four tungsten iodide lamps, as described by Greer et al. (1995). The vapour pressure deficit at each temperature was 0.4/0.2 ± 0.05 kPa (day/night). At the end of this treatment, all leaves were stripped off the plants and the temperature in all treatments reduced to 8/3 ± 0.5°C for an additional 4 weeks. All plants were supplied with a modified Hoaglands nutrient solution (Brooking 1976) throughout the experiment.

At the completion of this stage, four trees from each treatment were returned to outdoors and monitored through the subsequent spring and summer.

**Biomass and phenological measurements**

Before imposing the temperature regimes, two randomly selected trees were destructively harvested and separated into components of leaves, spurs (all ages), 1-year-old wood (current season’s extension shoots), older wood (branches), trunk, main root, coarse roots (>2 mm diam.), and fine roots. From each tissue component, a subsample of c. 1 g was randomly obtained and immediately stored at –80°C for later carbohydrate analysis. The remaining tissues were vacuum-dried at 40°C for up to a week until dry weights were constant. Whole tree leaf area was determined from the measurement (LI-3100 area meter, Licor, Neb., United States) of a
subsample of leaves which were then dried and weighed. Leaf area of each tree was then determined from the total leaf dry weight and the leaf area to dry weight ratio of each subsample.

At the conclusion of the temperature-treatment period, i.e., before the 8/3°C exposure, two trees from each treatment were also destructively harvested and the trees separated into the same components, except that spurs that were flowering were separated from non-flowering spurs as necessary. Carbohydrate subsamples were taken as above and the remaining tissues dried and weighed.

In spring, budbreak was monitored on each of the remaining trees from the four temperature treatments to determine percentage and time of budbreak. At harvest, all fruit were picked and their fresh and dry weights and fruit diameters determined.

**Non-structural carbohydrate determinations**

For each tissue component, a subsample of 0.1 g was ground, lyophilised, and then extracted with 20 ml of 80% ethanol at 60°C. The insoluble residue was analysed for starch and the filtrate dried and sugars and sugar alcohols (sorbitol and inositol) analysed by gas chromatography according to Greer (1998). Carbohydrate concentrations for all tissues were determined from the product of concentration of each constituent and the mean biomass of the particular tree tissue.

**Photosynthesis and respiration**

Ten days after the temperature treatments were imposed, half-way through the temperature treatments, and on the day the treatments ended, leaf respiration was measured in the dark. Four leaves on each tree were measured for each temperature treatment, using a leaf chamber and Ciras (PPSystems, Hitchin, United Kingdom) gas exchange system. One hour after the lights came on leaf photosynthesis was measured using the same gas exchange system and leaf chamber at a saturating PFD of 1200 µmol m⁻² s⁻¹. Leaf temperature was controlled to match the controlled-environment day temperature in each case. Soil respiration was measured with a Ciras (PPSystems, Hitchin, United Kingdom) respiration chamber in two locations around the pot of each of four trees over two succeeding days in all temperature treatments. Measurements were made on three occasions through the experiment.

Carbon acquisition was calculated from the daily integration of photosynthesis and respiration and total leaf area of the trees at each measurement date and then summed over the period of study according to the method of Greer & Jeffares (1998).

**Data analysis**

All data were analysed using general linear models (SAS 1996) and least squares means and standard errors calculated.

**RESULTS**

**Changes in dry matter**

For the 24/19°C especially and to a lesser extent for the 19/14°C treatments, there was new leaf growth on many spurs during the 5-week exposure, whereas for the 9/4°C treatment there was considerable senescence and abscission. This is reflected in the differences in leaf dry matter (DM) between these various treatments (Table 1), however, because of high inter-tree variability, the differences were not significant. Nevertheless, after 5 weeks of temperature treatment, leaf DM was positively and linearly ($P < 0.01, r^2 = 0.98$) correlated with temperature (not shown).

In addition to the new leaf growth, at the two higher temperatures, the trees also produced new flowers during the treatment to these temperatures, with a mean of 145 –1 tree at 24/19°C and 47 –1 tree at 19/14°C. However, the flower DM contribution was $3.4 ± 0.3\%$ of total DM at 24/19°C and 0.6 ± 0.2% at 19/14°C.

Dry matter of the current season shoots, branches, and trunk across all the treatments was too variable to assess any changes (Table 1), again indicating inter-tree variability in DM before the start of the treatments.

Dry matter of fine and coarse roots and the main root was significantly different from the start of the treatment, at least for some temperature regimes, notably those trees at the low temperatures. This is also reflected in marked differences in the root/shoot (below to total above ground) ratio between the treatments (not shown), which increased across the whole temperature range (9°–24°C) in a curvilinear ($P < 0.01, r^2 = 0.98$) fashion from 0.36 to 0.47. Furthermore, total root biomass initially contributed c. 18% to the total biomass of the controls but, after the 5 weeks of treatment, this increased to 24% for the trees grown at 24/19°C and 30% for the trees grown at 9/4°C.
Changes in carbohydrates over the growth period

Carbohydrate concentration

At the start of the experiment, leaves had a high concentration of sorbitol and similar but low concentrations of soluble sugars and starch (Fig. 1). For the other tree components, starch was the predominate carbohydrate but the highest concentrations were in roots and especially the coarse and fine roots where the concentration exceeded 250 mg g\(^{-1}\). This pattern of differences in carbohydrate concentration between the different tree components was generally retained after the 5 weeks of growth at the different temperatures, nevertheless, there were some specific changes at the different temperatures. Leaf starch concentration remained similar across all temperatures, sorbitol declined whereas soluble sugar concentrations were generally similar. For spurs, concentrations of starch and soluble sugars were also unaffected by temperature whereas sorbitol concentration declined slightly with increasing temperature.

For the flowers at the highest temperature treatment, there were very low starch concentrations and relatively high soluble sugar concentrations, with the sorbitol concentration intermediate. However, at 19/14°C, the concentrations of all components were similar, but, with the exception of starch, significantly lower than the flowers at 24/19°C.

In general, for all the woody fractions, there were similar concentrations of starch (average of 94 mg g\(^{-1}\)) across the four temperature treatments and in comparison with the initial concentration (125 mg g\(^{-1}\)). On the other hand, sorbitol concentration tended to be highest in the trees at 14/9°C (c. 45 mg g\(^{-1}\)), at least for the first year and older branches, but significantly lower than the initial concentration. By contrast, the soluble sugar concentrations in all woody fractions were highest in the trees at 9/4°C (c. 35 mg g\(^{-1}\)) and were markedly above the initial concentrations. For trees at the higher temperatures, soluble sugar concentrations in the woody fractions were low and no different from the initial concentrations.

For the main root fraction, temperature had little effect on starch concentration and there was little change from the initial concentration, but this tree component had the lowest overall concentration of the root fractions (c. 100 mg g\(^{-1}\)). The starch concentration of coarse roots was highest at c. 300 mg g\(^{-1}\). At all temperatures, however, starch declined relative to the other carbohydrates.

### Table 1

<table>
<thead>
<tr>
<th>Treatment (°C)</th>
<th>Main root (g)</th>
<th>Fine roots (g)</th>
<th>Coarse roots (g)</th>
<th>Trunk (g)</th>
<th>Older wood (g)</th>
<th>Flowers (g)</th>
<th>Spurs (g)</th>
<th>Leaves (g)</th>
<th>Total (g)</th>
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<tbody>
<tr>
<td>Initial</td>
<td>197.5 ± 7</td>
<td>34.8 ± 4.4</td>
<td>45.2 ± 5.2</td>
<td>63.4 ± 2.0</td>
<td>45.4 ± 4.3</td>
<td>39.5 ± 2.2</td>
<td>48.6 ± 2.7</td>
<td>97.5 ± 7</td>
<td>501.2 ± 15</td>
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<tr>
<td>9/4</td>
<td>162.2 ± 10</td>
<td>55.2 ± 1.7</td>
<td>55.2 ± 1.7</td>
<td>69.4 ± 1.6</td>
<td>50.1 ± 4.3</td>
<td>47.1 ± 2.7</td>
<td>50.4 ± 2.7</td>
<td>97.1 ± 7</td>
<td>428.2 ± 12</td>
</tr>
<tr>
<td>14/9</td>
<td>187.4 ± 24</td>
<td>68.9 ± 1.4</td>
<td>35.9 ± 5.9</td>
<td>67.4 ± 1.6</td>
<td>50.4 ± 4.3</td>
<td>43.2 ± 2.5</td>
<td>50.4 ± 2.7</td>
<td>100.1 ± 7</td>
<td>480.9 ± 19</td>
</tr>
<tr>
<td>19/14</td>
<td>207.0 ± 37</td>
<td>20.9 ± 8.6</td>
<td>66.4 ± 1.6</td>
<td>70.9 ± 1.2</td>
<td>50.4 ± 4.3</td>
<td>41.3 ± 2.5</td>
<td>50.4 ± 2.7</td>
<td>107.9 ± 7</td>
<td>538.9 ± 25</td>
</tr>
<tr>
<td>24/19</td>
<td>218.0 ± 20</td>
<td>27.2 ± 9.8</td>
<td>72.8 ± 2.0</td>
<td>72.8 ± 2.0</td>
<td>35.4 ± 4.8</td>
<td>48.6 ± 2.7</td>
<td>50.4 ± 2.7</td>
<td>112.8 ± 7</td>
<td>578.8 ± 27</td>
</tr>
</tbody>
</table>

**Changes in dry matter (mean ± SE, N = 2) for each component of the 'Braeburn' apple (Malus domestica) trees grown for 5 weeks at four different temperature regimes.**
Fig. 1  Concentrations (mean ± SE) of starch, sorbitol, and soluble sugars for leaves, flowers, spurs, current season's branches (1-year wood), older branches (older wood), trunk, fine roots, coarse roots, and the main root (i.e., the rootstock) as a function of the treatment temperatures. Concentrations of each component at the start of the treatments are indicated as “initial.” Note all leaves for the 9/4°C treatment were dead so no carbohydrates were measured and spurs were not separated from the current season branches at the initial harvest. (DW, dry weight.)
Fig. 2  Amounts (mean ± SE) of starch, sorbitol, and soluble sugars for leaves, flowers, spurs, current season’s branches (1-year wood), older branches (older wood), trunk, fine roots, coarse roots, and the main root (i.e., the rootstock) as a function of the treatment temperatures. Concentrations of each component at the start of the treatments are indicated as “initial”. (DW, dry weight.)
to the initial concentration although there was a weak trend for it to decline with increasing temperature. A stronger but similar pattern occurred with the fine roots in that at the two lower temperatures starch concentration remained unchanged over the 5 weeks but from 14/9°C to 24/19°C starch concentration declined progressively.

Sorbitol concentration in all the root fractions was lower (60%) than at the start, but temperature had little effect. Temperature also had no effect on soluble sugars in the roots and the different components differed only slightly in concentration.

Overall, total carbohydrate concentrations averaged 242 ± 26 mg g⁻¹ at the start of the treatments and thereafter averaged 209 ± 25, 203 ± 21, 189 ± 20, and 169 ± 15 mg g⁻¹ for the 9/4, 14/9, 19/14, and 24/19°C treatments, respectively. Thus, at both higher temperatures, the mean total concentration declined by 18–30% whereas for the two lower temperatures, mean total concentration declined slightly over the treatment period.

**Carbohydrate content**

Starch content in leaves, spurs, and flowers was very low across all temperatures and little changed from the initial concentration (Fig. 2). Leaf sorbitol content was higher than the spur and flower contents but again temperature had little effect. A similar result occurred for soluble sugar content for leaves and spurs whereas for flowers, between 19/14 and 24/19°C, the soluble sugar content increased markedly.

Before treatment, the woody fraction, but especially the trunk and older branches, had the most carbohydrate, where starch content averaged 60–90 g. In these two fractions, sorbitol and soluble contents were also markedly higher than any other component of the tree. The roots also had a moderate starch content, averaging c. 40–50 g.

In most cases, after 5 weeks of treatment the carbohydrate content in the different tree fractions had declined significantly but effects of temperature were, nevertheless, still discernible. For the woody fractions, the decline in starch content was generally greatest on trees at 9/4°C and, on average, least on trees at 19/14°C. Differences in starch content between the various woody components, however, remained strong.

Sorbitol content of each woody component also declined after the 5 weeks of growth, with the decline generally least on trees at 14/9°C and most on trees at both 9/4 and 24/19°C. By contrast, soluble sugar content of each woody fraction was strongly affected by temperature. Those trees at 9/4°C retained or even slightly increased their sugar content compared to the initial levels. However, as the temperature increased, there was a generally linear decline in the soluble sugar content, most notably in the trunk and older branches.

Starch content of fine roots also increased over the 5 weeks in trees at 9/4°C but across the other temperatures declined in a linear pattern such that on trees at 24/19°C, there was a marked decline in starch content. By contrast, the starch content of the main root increased over the 5 weeks, most notably on trees at 19/14°C. For coarse roots, starch content declined most at 9/4°C and least at 14/9°C.

Sorbitol content of all root fractions was relatively small and differed little between the various temperatures and from the initial content. Soluble sugar content of the main root increased from the start but temperature had little effect on this or the other root fractions. However, the main root had a
significantly higher soluble sugar content than the fine roots which, in turn, had a significantly higher content that the coarse roots.

The total amounts of carbohydrate for the whole trees averaged 464 ± 42 g at the start of the treatment and averaged 360 ± 26, 424 ± 28, 439 ± 65, and 331 ± 10 g after treatment for the 9/4, 14/9, 19/14, and 24/19°C treatments, respectively. Thus, in all cases, the total amount of carbohydrate apparently decreased during treatment, by 20–30% at the two extreme temperatures and 5–10% at the two moderate temperatures, but these largely reflected the differences in tree biomass (Table 1).

**Photosynthesis and respiration**

After 10 days at each temperature, photosynthetic rates (Fig. 3A) ranged from c. 5 to 9 µmol m⁻² s⁻¹, generally increasing as the temperature increased. However, thereafter, there were marked differences in photosynthesis between the trees at the different temperatures. The trees at the highest temperature consistently increased to 12 µmol m⁻² s⁻¹. Photosynthesis at the two intermediate temperatures increased only slightly to c. 9 µmol m⁻² s⁻¹. In keeping with leaf senescence of the trees at 9/4°C, photosynthesis declined consistently to negligible rates by Day 37. At this time, differences in photosynthetic rates between the four treatments were highly significant.

Differences in leaf respiration (Fig. 3B) between the trees at the different temperatures were small after 10 days at each temperature, ranging between 1.5 and 2.0 µmol m⁻² s⁻¹. As the leaves senesced at 9/4°C, rates of respiration also declined whereas the rates for the trees at the other treatments were generally constant or increased slightly over time. However, trees at 19/14°C had, on average, higher respiration rates than those at 24/19 and 14/9°C.

Soil respiration (Fig. 4) differed significantly between all temperature treatments when first measured, increasing more than 4-fold from the lowest rate at 9/4°C to the highest rate at 24/19°C. Over the course of the treatments, rates of soil respiration declined, most notably at the two higher temperatures, such that by the end of the treatments, the rates differed c. 3-fold. Thus, there was still a strong effect of temperature on rates of soil respiration.

The net carbon fixation (photosynthesis plus respiration) over the 37 days of treatment was 188.8 g tree⁻¹ for the 24/19°C treatment and 121.9, 138.1, and 23.9 g tree⁻¹, for the 19/14, 14/9, and 9/4°C treatments, respectively.

**Budbreak and fruit growth**

The percentage budbreak for the apple trees during spring (Fig. 5A) was significantly and curvilinearly dependent on the growth temperatures. Budbreak for the trees at the two lower temperatures averaged nearly 100% whereas for trees grown in the 19/14 and 24/19°C treatments, budbreak was lower at c. 80 and 50%, respectively, probably because of the flowering that occurred during exposure to the temperature regimes. For the trees grown in the 9/4°C treatment, time to 50% budbreak was the earliest at 27 October and delayed by 3, 4, and 15 days for the trees in the 14/9, 19/14, and 24/19°C treatments, respectively. For comparison, budbreak
in trees grown continuously outdoors was 5 days after the trees at 9/4°C.

Although there were initially larger fruit diameters for the trees in the 24/19°C treatment, fruit growth over the growing season generally did not differ significantly between the treatments (Fig. 5B). However, at harvest, fruit from the 9/4°C treated trees were significantly larger than for all other treatments. The mean fresh weight at harvest was 187 ± 12, 169 ± 10, 176 ± 11, and 243 ± 12 g apple⁻¹ for the trees treated at 24/19, 19/14, 14/9, and 9/4°C, respectively. Thus, fruit fresh weight confirmed that the 9/4°C treated trees had the largest fruit.

**Crop load**

Crop load (Fig. 6) was significantly affected by temperature, with a maximum crop load of 70 ± 3 fruit tree⁻¹ on those treated at 19/14°C and lower crop loads for those trees treated at both the highest and lowest temperatures.

Dry matter yield of fruit averaged 1.2 ± 0.14 kg tree⁻¹ for the trees in the 24/19°C treatment and 2.0 ± 0.14, 1.7 ± 0.12, and 1.1 ± 0.08 kg tree⁻¹ for those trees in the 19/14, 14/9, and 9/4°C treatments, respectively. Thus overall fruit yield was highest at the moderate temperature.

**DISCUSSION**

The growth of ‘Braeburn’ apple trees in the postharvest period was strongly influenced by temperature. At the higher temperatures, a new flush of growth occurred, including both leaves and flowers, whereas at the lowest temperature leaf senescence occurred, such that few green leaves remained on the trees after the 5 weeks of treatment. As a consequence of these two different outcomes, over the temperature range studied and after treatment, the amount of leaf DM was strongly and linearly temperature-dependent. New root growth also occurred, though most notably for the trees at the lowest temperature and least at the highest temperature.

However, soil respiration increased markedly with the increase in temperature, inferring loss of carbon from root respiration at the higher temperatures compared with that at the lower temperatures.

Consistent with earlier data (Watson et al. 1978), leaf photosynthesis of these apple trees was also highly temperature-dependent, generally increasing with increasing temperature. However, this dependency became more marked with time at each temperature, since photosynthesis increased...
markedly on the trees in the 24/19°C treatment and declined precipitously as the leaves senesced in the 9/4°C treatment. Rates of leaf respiration also differed between the four temperatures but, with the exception of the senescing leaves, did not change much over time. Thus, for the trees at the three higher temperatures, there was a high level of carbon fixation. It progressively increased over time at the highest temperature but remained steady at the two intermediate temperatures. The imposition of these different temperatures was, therefore, highly successful in manipulating the amount of carbon fixed by the trees.

Some of this fixed carbon was used for structural growth, such as the flush of new leaf and flowers, at the high temperatures. However, it was unclear how new root growth occurred at the lowest temperature, given that little carbon was fixed in these trees. Fine roots increased in both starch and soluble sugar content at the lowest temperature, possibly at the expense of the coarse roots and also the trunk and branches, perhaps suggesting mobilisation of reserves had occurred to support this root growth. The decline in fine root starch content and concentration with increased temperature, the decline in root growth and the increase in soil respiration at least conforms with differences in mobilisation occurring at the different temperatures. The shift in allocation of biomass to roots, especially at the lowest temperature, is also strongly supportive of root growth occurring from mobilised reserves.

The trees stored the majority of the non-structural carbohydrates as starch, both in the roots and shoots, as indicated by both the high concentrations and amounts of starch. Total carbohydrate concentrations were highest in the fine and coarse roots but these both declined with increased temperature to below the concentrations at the start of the treatments. This probably conforms with the increase in respiratory carbon loss from these roots with increased temperature. However, the trunk and older wood had the greater amounts of carbohydrate and although there were some effects of temperature, all woody fractions apparently declined in starch and even sorbitol content, over the duration of the treatments. Thus differences in total concentration and amounts of carbohydrate did not conform with differences in photosynthesis or in the net carbon balance. Although the trees at the highest temperature fixed significantly more carbon than all other treatments, their total carbohydrate concentration did not change significantly. Some fraction of the current photosynthate was apparently used in new growth and the marked decrease in soluble sugar content of the woody fractions with increased temperature is at least consistent with this. This may account for some of the apparent anomaly between the carbon fixed and the pools of carbohydrate. However, high tree-to-tree variability may have also obscured the real trends.

Did the differences in concentrations of carbohydrate between the trees of the various treatments have any influence on their subsequent budbreak in spring? Certainly the lower concentration of total carbohydrate in the trees treated at high temperatures conformed with their significantly delayed time of budbreak and possibly also their lower percentage budbreak. However, the high incidence of flowering of the trees treated at 24/19°C (c. 150 flowers tree⁻¹) during the treatment may have also reduced the availability of buds and hence affected their percentage and delayed budbreak. On the other hand, the earliest budbreak occurred in the trees treated at 9/4°C, consistent with the chilling requirements for budbreak being best met by these temperatures (Shaltout & Unrath 1983). The other intermediate temperature treatments had relatively high percentage budbreak and time of budbreak was delayed only by a few days compared to the 9/4°C treatment. Notably, the time of budbreak of these trees treated at intermediate temperatures conformed with natural budbreak occurring, suggesting chilling requirements had been also met for these treatments. It seems unlikely, therefore, that in this study the differences in carbohydrate concentrations could be related to differences in budbreak.

Fruit growth over summer was generally unaffected by the temperature treatments. However, Warrington et al. (1999) have shown early season temperatures to have the greatest effect on fruit size. It would seem most likely, therefore, that spring rather than postharvest temperatures had the dominant affect on fruit growth. It is likely that crop loads also had an influence on fruit size and this may have accounted for some of the observed seasonal differences in fruit size between the treatments. It was notable, however, that the trees treated at 19/14°C trees carried the largest crop load and the highest yield (DM) compared with all other treatments while those trees at 14/9°C also had a high yield. The total yields for those trees at 24/19 and 9/4°C were similar. Thus, in both cases where there were high amounts of carbohydrate then there was also a concomitantly higher yield.
Equally, when amounts of carbohydrate were low, as occurred in the trees treated at both 24/19 and 9/4°C, there was a concomitant reduction in yield. These data provide support for the hypothesis that total fruit yield at harvest was at least partially dependent on the carbohydrate reserves established before leaf fall in the previous crop year.

In conclusion, Tustin et al. (1997) and Wünsche & Palmer (1997) both postulated that high yield of New Zealand apple orchards was related to the length of the previous postharvest season. Although the present study confirmed that carbohydrate reserves could be manipulated by temperature-induced changes in carbon fixation in the postharvest period, the data were not able to verify a relationship between carbohydrates in autumn and tree performance in the subsequent growing season. High inter-tree variability as well as unintended changes in biomass and development may have obscured such a relationship. Thus it still remains to demonstrate that high apple yields in New Zealand orchards are related to the long postharvest growing season.

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