Post-pruning shoot growth increases fruit abscission and reduces stem carbohydrates and yield in macadamia

Lisa M. McFadyen1*, David Robertson1, Margaret Sedgley2, Paul Kristiansen2 and Trevor Olesen1

1 Industry and Investment NSW, Centre for Tropical Horticulture, PO Box 72, Alstonville, NSW 2477, Australia and 2 The University of New England, Faculty of Arts and Sciences, Armidale, NSW 2351, Australia

* For correspondence. E-mail lisa.mcfadyen@industry.nsw.gov.au

INTRODUCTION

The physiology of subtropical evergreen fruit trees is not as well understood as that of deciduous species which have been extensively researched, mainly in northern hemisphere countries. Many subtropical evergreen fruit trees (e.g. avocado, lychee and mango) grow by recurrent flushes (Whiley et al., 1989; Olesen et al., 2002; Olesen, 2005); can flower profusely but set relatively few fruit (Blumenfeld and Gazzit, 1974; McConchie and Batten 1991; Anila and Radha, 2003); and are large trees with a high leaf area to canopy surface area ratio (Possingham, 1986; Menzel et al., 2000). There are no dwarfing rootstocks for most subtropical evergreen fruit trees to pruning, in contrast to the abundance of studies for deciduous species (Mika, 1986).

Macadamia (Macadamia integrifolia, M. integrifolia × tetrathylla) is fairly typical of subtropical evergreen fruit trees. It flushes throughout the year but with peaks in spring and late summer (Stephenson et al., 1986). Flower racemes are initiated in leaf axils and anthesis occurs in early spring (Moncur et al., 1985). Mature trees may produce >10 000 racemes, each consisting of 100–300 flowers but, typically, only around 0.3 % of flowers develop into mature fruit (Urata, 1954; Ito, 1980). Canopy leaf density is high, at >400 leaves per cubic metre in the upper canopy (McFadyen et al., 2010), and trees potentially attain a height of 18 m and a width of 15 m (Cull, 1983) unless managed by pruning.

Macadamia fruit are harvested from the orchard floor between March and August in Australia and trees are usually side-hedged after harvest in early spring during flowering and early fruit development. Hedging is done at this time to avoid interfering with harvest and to maximize the opportunity for trees to compensate for flowers and fruitlets removed, by increasing fruit set on the remaining racemes (Wilkie, 2009). However, hedging at this time reduces yield by between 10 and 20 % (McFadyen and McConchie, 2004; McFadyen et al., 2005). This may be due to an increase in premature fruit abscission caused by reduced assimilate supply resulting from leaf removal and/or competition for assimilates between the young fruit and the post-pruning vegetative flush.
There is evidence that a decrease in assimilate supply, due to either leaf removal or shading, increases early fruit abscission in both deciduous (Quinlan and Preston, 1971; Doud and Feree, 1980; Berüter and Droz, 1991) and evergreen trees (Yuan and Huang, 1988; Mehouachi et al., 1995; Gomez-Cadenas et al., 2000). Competition between shoot and fruit growth, with consequences for fruit abscission, has been demonstrated for deciduous fruit trees. In apple, restriction of vegetative growth by shoot removal reduced fruit abscission and increased yield (Quinlan and Preston, 1971). The role of carbohydrate was demonstrated using 14C to track assimilate movement. Without shoot tip removal, assimilates moved to both shoots and fruit but when the shoot tip was removed assimilate movement was mostly to fruit with only a small amount going to the shoot. In grape, control of vegetative growth, by either shoot tip removal or application of a growth retardant increased initial fruit set but not yield (Cutting and Bower, 1990; Wolstenholme et al., 1990; Whiley et al., 1991); yet in another experiment with avocado, application of a growth retardant increased both fruit number and yield (Adato, 1990). In lychee, shoot growth on pruned branches did not affect fruit abscission in panicles on adjacent branches (Hieke et al., 2002a) but when shoots developed behind panicles, fruit abscission increased (Hieke, 2000). Finazzo et al. (1994) followed the partitioning of 14C assimilate between young shoots and young fruit in avocado and found that partitioning was proportional to the dry weight of the organs. They did not manipulate the trees to test for competition effects.

We tested the hypothesis that pruning increases fruit abscission and decreases yield in macadamia through the combined negative effects of leaf area removal and competition from post-pruning shoot growth on carbohydrate availability. This was done by tip-pruning trees at anthesis, allowing some trees to reshoot during the premature fruit abscission period, but removing new shoots as they appeared on others. Shoot growth, changes in fruit number per raceme, branch total non-structural carbohydrates (TNSC) and yield were monitored.

We were also interested in the possibility that regrowth on pruned branches might compete with fruit set on unpruned branches. Mechanically pruning the tops of macadamia trees with a hedging machine (topping) has been used by some growers to control tree size. However, it causes vigorous regrowth and a substantial yield reduction (McFadyen, 2006). If the shoot growth on pruned branches at the top of the canopy competes for resources with fruit set on lower unpruned branches it could help explain the responses observed.

Branches are generally considered to be largely autonomous with regard to carbon supply (Sprugel et al., 1991). However, especially strong sinks such as growing shoots or fruit may draw carbohydrates from sources over long distances. Sprugel and Hinckley (1990) labelled lower branches of Pacific silver fir with 14C. During shoot expansion they found 14C in new leaves all over the tree with concentrations highest on branches near the top of the tree, despite the distance from the labelling site. There is also evidence for carbon transfer between branches to fruit growth sites in macadamia (Trueman and Turnbull, 1994), lychee (Hieke et al., 2002a), peach (Nicolas et al., 2006) and apple (Palmer et al., 1991). Conversely, Marsal et al. (2003) found that peach branches operated largely as independent units with respect to fruit growth. In other studies branch autonomy was reported to vary between seasons [Lacointe et al. (2004) for walnut] and cultivars [Nicolas et al. (2006) for peach].

Sink strength is considered a function of the growth rate, size and number of plant organs (Grossman and DeJong, 1994; Wubs et al., 2009). Tip-pruning maximizes the number of shoots growing concurrently as it synchronizes bud release and flush development amongst branches (Olesen, 2005). As already discussed, shoot growth at the top of a Pacific silver fir was of sufficient sink strength to draw carbohydrates from branches low down on the trunk (Sprugel and Hinckley, 1990). We therefore hypothesized that sink strength of the synchronized flush at the top of a macadamia tree following topping would be sufficient to affect fruit set on lower unpruned branches. This was tested by topping trees and comparing fruit set on upper (pruned) and lower (unpruned) branches, for trees with or without the post-pruning shoots removed. Comparisons were also made with upper and lower branches on untopped control trees.

MATERIALS AND METHODS

Macadamia

Macadamia is native to rainforests on the east coast of Australia, from 23° to 29°S and is grown commercially for its edible kernel. The fruit of the macadamia is a follicle. It has a pericarp (husk) comprising a green fibrous exocarp and a soft thin endocarp that encloses a true seed with a thick hard testa (shell) surrounding a globular embryo (kernel) (Hartung and Storey, 1939). Commercially, the testa and embryo are referred to as a nut. Rapid abscission of flowers and young fruit commences in the first 3 weeks after anthesis, in early spring, and young fruit continue to abscise until 9–10 weeks post anthesis (PA). Thereafter, relatively little abscission occurs (Sakai and Nagao, 1984; Trueman and Turnbull, 1994). Fruit mature at approx. 30 weeks PA (Jones and Shaw, 1943).

Experiment 1: tip-pruning all branches, and suppressing regrowth

The experiment was carried out on 8-year-old, 3-m-high macadamia trees (Macadamia integrifolia × tetraphylla ‘A4’) at the Centre for Tropical Horticulture at Alstonville in northern New South Wales (28.9°S, 153.5°E). Trees were stripped of nuts in March 2005 and internally pruned in June
2005 to minimize any potential for irradiation variation within the canopy to affect measurements and to simplify subsequent tip-pruning and flower and nut counts.

Twenty-seven trees spread over seven rows were divided into nine ‘blocks’ of three trees; and the three trees in each block were randomly allocated to three treatments. Two trees in each block were tip-pruned in the first week of September 2005, 1 week before full anthesis. Tip-pruning involved removal of at least the most recent flush from all branches. One tree was allowed to regrow (regrowth treatment ‘R’) and the other had new shoots removed on a weekly basis until 22 February 2006 (no regrowth treatment ‘NR’). The third tree was not pruned (control ‘C’).

Racemes per tree were counted around anthesis in the first 2 weeks of September, and the racemes per tree that retained fruit were measured just prior to harvest. Fruit per raceme were counted on 15 tagged racemes distributed evenly around each tree. Counts were made weekly from 2 weeks PA until 14 weeks PA and then fortnightly to 22 weeks PA. Fruit were harvested from the ground on 4 April and 1 May 2006 and the remaining fruit were stripped from the trees on 1 May 2006. Fruit were dehusked and total nut weight per tree recorded. A subsample of 100 nuts was taken from each tree to estimate average nut weight.

Branch samples were collected weekly for carbohydrate analyses from four replicates of each treatment, commencing 3 weeks after pruning (2 weeks PA) and continuing for 9 weeks. One sample per tree was collected at dawn, from the northern quadrant of the tree from a previously tagged branch. For the pruned trees (R, NR) approx. 20 cm of stem was removed from behind the tip-pruning cut. For the C trees, the stems behind the most recently matured flush were sampled and were considered to be of comparable age to the stems sampled from the pruned trees. New shoots around the tip-pruning cut on R stems collected for carbohydrate analysis were excised and dried to constant weight at 60 °C to estimate the timing and rate of post-pruning shoot growth. The remaining leaves on the branch sample were discarded as were leaves on samples from the other treatments. The bark and wood were then dried at 80 °C, ground using a cyclone sample mill (UDY Corporation, Fort Collins, CO, USA) with a 1-mm sieve, and analysed for TNSC as described by Olesen et al. (2006).

Experiment 2: tip-pruning upper branches, and suppressing regrowth

This experiment was carried out on 9-year-old ‘A4’ trees. Average tree height before treatment was 4 m. Fifteen trees were used in the experiment. For ten of these trees, upper branches were pruned at anthesis with a pole hedger to correspond with a 30% reduction in canopy height (tree height – skirt height). On average, 0.9 m of canopy was removed from the top of each tree. The number of racemes removed by pruning was counted for each tree. The remaining five trees were unpruned (control ‘C’). On five of the ten pruned trees, the cut branches were allowed to regrow (regrowth ‘R’). On the other five, shoots were removed on a weekly basis until 18 December 2006 (no regrowth ‘NR’). The experimental design was a randomized complete block with trees assigned to blocks of three trees according to canopy volume, and treatments allocated randomly to trees within each block. After pruning, the unpruned (lower) branches and pruned (upper branches) were identified and tagged accordingly. Corresponding branches on the control trees were identified based on 30% canopy height reduction had these trees been pruned. Racemes on each branch type (lower, unpruned or upper, pruned or control) were counted at anthesis and racemes with fruit were counted at harvest.

On the pruned trees, 20 racemes were tagged at anthesis in the lower canopy (unpruned branches) and another 20 racemes were tagged in the upper canopy (pruned branches). The same number of racemes was tagged on corresponding branches on the control trees. Fruit per raceme were counted fortnightly from 3 to 16 weeks PA and then at 3- to 4-week intervals until 22 weeks PA. Shoot growth following pruning was measured weekly in the R trees by excising new shoots from previously tagged pruned branches and drying them to constant weight at 60 °C. Fruit were stripped from all trees on 26 and 27 March 2007 and dehusked, and the total weight of nuts was recorded separately for upper and lower branches. A subsample of 100 nuts was taken from each tree and canopy position to estimate average nut weight.

**Statistical analyses**

Linear mixed models (ASReml-R software; Butler et al., 2007) were used to analyse treatment, canopy position and time effects on raceme, fruit and nut data; a cubic spline term for time was included as a random effect. F-ratio tests (Wald method) and likelihood ratio tests were conducted to test the statistical significance of the fixed and random effects, respectively. The least significance difference was used to compare means.

Non-linear regressions (Sigmastat, Jandel Corp., San Rafael, CA, USA) were used to analyse branch TNSC and shoot growth data. For the TNSC data, the Tukey–Kramer method (Sokal and Rohlf, 1995) was used to test if parameters for the upper asymptote and the trough of the curve differed between treatments.

**RESULTS**

**Experiment 1: tip-pruning all branches, and suppressing regrowth**

Fruit number per raceme declined curvilinearly with time (P < 0.0001) from 60–80 fruit per raceme at 2 weeks PA in late September to 1–4 fruit per raceme at 22 weeks PA in mid-February (Fig. 1). There was a significant effect of treatment (P < 0.0001) and a significant interaction between treatment and the spline term for time (P < 0.0001). Fruit abscission was greatest in the R treatment with fruit per raceme first dropping below the other treatments between 4 and 6 weeks PA (P < 0.0001) and remaining lower up to the final sampling date at 22 weeks PA (P < 0.0001). In the NR treatment, fruit per raceme declined relative to the control by 8 weeks PA (P < 0.01) and was still significantly less at the final sampling date (P < 0.05).

Most fruit abscission in the R treatment occurred by 8 weeks PA. In the C and NR treatments, fruit abscission rate slowed
slightly at around 5 weeks PA and then increased briefly, until around 9 weeks PA after which there was very little further abscission.

The percentage of racemes that carried fruit at the end of the season was also lowest for the R treatment (Table 1; \( P < 0.05 \)). C and NR treatments were not significantly different (\( P > 0.05 \)). Treatment effects on fruit retention were strongly reflected in final yield, with the R trees yielding only 12% and 16% of the C and NR trees, respectively (Table 1; \( P < 0.05 \)) and NR trees producing 63% of the yield of the C trees (\( P < 0.05 \)). Nut weight was highest in the R treatment (Table 1; \( P < 0.05 \)) presumably because fruit number per tree was substantially lower than the other treatments (Table 1; \( P < 0.05 \)).

![Graph showing fruit number per raceme over time for each treatment](image)

**Table 1.** Raceme number at anthesis, percentage of racemes with fruit at maturity, fruit number per tree, individual nut weight and nut weight per tree for macadamia trees on which all branches were tip-pruned at anthesis and subsequently developed new shoots (regrowth) or had new shoots removed weekly (no regrowth) (control trees were unpruned)

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Raceme number at anthesis</th>
<th>Percentage of racemes with fruit at maturity</th>
<th>Fruit number per tree</th>
<th>Individual nut weight (g)</th>
<th>Nut weight per tree (kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>613 ± 87&lt;sup&gt;a&lt;/sup&gt;</td>
<td>58 ± 4&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1009 ± 128&lt;sup&gt;a&lt;/sup&gt;</td>
<td>8.1 ± 0.2&lt;sup&gt;a&lt;/sup&gt;</td>
<td>8.1 ± 1.0&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>No regrowth</td>
<td>601 ± 112&lt;sup&gt;a&lt;/sup&gt;</td>
<td>68 ± 8&lt;sup&gt;b&lt;/sup&gt;</td>
<td>649 ± 84&lt;sup&gt;b&lt;/sup&gt;</td>
<td>8.0 ± 0.2&lt;sup&gt;a&lt;/sup&gt;</td>
<td>5.1 ± 0.6&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Regrowth</td>
<td>731 ± 182&lt;sup&gt;a&lt;/sup&gt;</td>
<td>10 ± 2&lt;sup&gt;b&lt;/sup&gt;</td>
<td>92 ± 34&lt;sup&gt;c&lt;/sup&gt;</td>
<td>10.5 ± 0.3&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.9 ± 0.3&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

Values are means ± s.e. (\( n = 9 \))

Treatment means followed by a different letter are significantly different (\( P < 0.05 \)).

**FIG. 1.** Fruit number per raceme over time, in macadamia trees on which all branches were tip-pruned at anthesis and subsequently developed new shoots (B: regrowth) or had new shoots removed weekly (C: no regrowth). Control trees (A) were unpruned. Points are the observed means of 15 racemes per tree. Lines are predicted values, using a linear mixed model. Comparison of fitted curves for control, regrowth and no regrowth, as indicated, treatments is shown in (D). There was a significant effect of treatment (\( P < 0.0001 \)) and a significant interaction with a spline term for time (\( P < 0.0001 \)).
Dawn TNSC fell and rose in all treatments during the sampling period, but the timing of fluctuations varied (Fig. 2). The decline in TNSC in the R trees occurred earlier than in the NR trees (Tukey–Kramer $P < 0.05$ for parameter $c$, the time when the minimum concentration of TNSC occurred, in the non-linear function) and took place between 5 and 6 weeks PA. This decline occurred around the time of early shoot growth (Fig. 3) and the increase in fruit abscission relative to the other treatments (Fig. 1). In contrast, TNSC in the NR treatment, which had virtually no shoot growth, remained steady over this period not declining until 6–8 weeks PA, when TNSC in the R treatment were recovering (Fig. 2). The recovery of TNSC in the R treatment coincided with the maximum rate of shoot dry weight increase (Figs 2 and 3).

The timing of the minimum TNSC in the C treatment occurred between, and was not significantly different from, the timings of the minima for the R and NR treatments (Tukey–Kramer $P > 0.05$ for parameter $c$). There was no significant difference in parameter $a$, the maximum concentration of TNSC, between treatments (Tukey–Kramer $P > 0.05$). Estimates of parameters $a$ and $c$ and their standard errors from the fitted non-linear functions are presented in Table 2.

**Experiment 2: tip-pruning upper branches, and suppressing regrowth**

Fruit number per raceme declined curvilinearly with time ($P < 0.0001$) from 50–70 fruit per raceme at 3 weeks PA to 1–3 fruit per raceme at 23 weeks PA (Fig. 4). There was a significant effect of treatment ($P < 0.0001$) and a significant interaction between treatment, canopy position and the spline term for time ($P < 0.0001$).

In the upper canopy, fruit abscission was greatest in the R treatment with fruit per raceme dropping below the other treatments between 5 and 6 weeks PA ($P < 0.05$) and remaining

![Fig. 2. Dawn levels of stem total non-structural carbohydrates (TNSC) over time, in macadamia trees on which all branches were tip-pruned at anthesis and subsequently developed new shoots (B: regrowth) or had new shoots removed weekly (C: no regrowth). Control trees (A) were unpruned. Points are observed values for one sample per tree. Lines are predicted values from the fitted non-linear function, $y = a - db^e^{x-c}/[1 + e^{x-c}]$, where $y$ and $y$ are variables ($y =$ TNSC, $x =$ weeks post anthesis) and $a$, $b$, $c$ and $d$ are parameters. The upper asymptote and the trough of the curve occur at $y = a$ and $x = c$, respectively. Comparison of fitted curves for control, regrowth and no regrowth, as indicated, is shown in (D). Parameter $c$, the time when the minimum concentration of TNSC occurred, for the regrowth treatment was significantly less than for the other treatments (Tukey–Kramer $P < 0.05$). There was no significant difference in parameter $a$, the maximum concentration of TNSC, between treatments.](image-url)
lower until the final sampling date (Fig. 4). The divergence in the pattern of fruit abscission between 5 and 6 weeks PA coincided with early shoot development (Fig. 5). There were no significant differences in fruit per raceme between C and NR treatments in the upper canopy ($P > 0.05$).

In the lower canopy, fruit number per raceme was slightly higher in the NR treatment relative to the R treatment only from 9 to 14 weeks PA ($P < 0.05$) with no significant difference at the final sampling date ($P > 0.05$) (Fig. 4). When raceme number per tree at anthesis was incorporated as a covariate in ANOVAs for individual sampling dates the only significant difference occurred at 11 weeks PA ($P < 0.05$). Treatment C was not significantly different from the other treatments ($P > 0.05$).

There were significant interactions between treatment and canopy position for raceme number at anthesis ($P < 0.05$), percentage of racemes with fruit at maturity ($P < 0.05$), fruit number per tree ($P < 0.01$), nut weight ($P < 0.01$) and yield ($P < 0.01$). In the upper canopy, the R treatment had the lowest percentage of racemes that carried fruit to maturity, the lowest fruit number per tree and yield, and the highest nut weight (Table 3; $P < 0.05$). There were no differences between the C and NR treatments in the upper canopy (Table 3; $P > 0.05$). In the lower canopy, there were no differences between treatments in the percentage of racemes with fruit at maturity or yield (Table 3; $P > 0.05$). However the NR treatment had fewer fruit than the C treatment ($P < 0.05$), and the R treatment had larger nuts than the C treatment ($P < 0.05$). Treatment C in the lower canopy had a higher number of racemes at anthesis than all the other treatment x canopy position combinations ($P < 0.05$).

**Table 2.** Parameter estimates of interest ($\pm$ s.e.) for non-linear functions fitted to dawn levels of stem TNSC over time in macadamia trees

<table>
<thead>
<tr>
<th>Treatment</th>
<th>$a$</th>
<th>$b$</th>
<th>$c$</th>
<th>$d$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>4.1 ± 0.5</td>
<td>0.8 ± 0.3</td>
<td>7.3 ± 0.4</td>
<td>9.6 ± 6.1</td>
</tr>
<tr>
<td>No regrowth</td>
<td>3.1 ± 0.2</td>
<td>2.3 ± 0.7</td>
<td>7.9 ± 0.2</td>
<td>2.7 ± 0.9</td>
</tr>
<tr>
<td>Regrowth</td>
<td>3.3 ± 0.2</td>
<td>2.9 ± 3.9</td>
<td>6.5 ± 0.2</td>
<td>2.0 ± 0.8</td>
</tr>
</tbody>
</table>

Trees were either unpruned (control) or had all branches tip-pruned at anthesis and subsequently developed new shoots (regrowth) or had new shoots removed weekly (no regrowth). The maximum TNSC concentration (upper asymptote) and time of minimum TNSC concentration (location of trough) for each curve occur at $y = a$ and $x = c$, respectively (details in Fig. 2).
TABLE 3. Raceme number at anthesis, percentage of racemes with fruit at maturity, fruit number per tree, individual nut weight and nut weight per tree for macadamia trees on which upper branches were tip-pruned at anthesis and subsequently developed new shoots (regrowth) or had new shoots removed weekly (no regrowth) (control trees were unpruned)

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Raceme number at anthesis</th>
<th>Percentage of racemes with fruit at maturity</th>
<th>Fruit number per tree</th>
<th>Individual nut weight (g)</th>
<th>Nut weight per tree (kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper branches</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>887 ± 309^a</td>
<td>50 ± 8^a</td>
<td>857 ± 99^a</td>
<td>7.3 ± 0.2^a</td>
<td>6.3 ± 0.7^a</td>
</tr>
<tr>
<td>No regrowth</td>
<td>878 ± 241^a</td>
<td>52 ± 9^a</td>
<td>877 ± 136^a</td>
<td>7.6 ± 0.2^a</td>
<td>6.7 ± 1.0^a</td>
</tr>
<tr>
<td>Regrowth</td>
<td>1086 ± 333^a</td>
<td>27 ± 3^a</td>
<td>416 ± 110^a</td>
<td>8.6 ± 0.2^a</td>
<td>3.5 ± 0.9^a</td>
</tr>
<tr>
<td>Lower branches</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>2291 ± 634^b</td>
<td>40 ± 6^ab</td>
<td>1177 ± 49^c</td>
<td>7.4 ± 0.3^c</td>
<td>8.7 ± 0.4^c</td>
</tr>
<tr>
<td>No regrowth</td>
<td>947 ± 289^b</td>
<td>45 ± 6^c</td>
<td>884 ± 98^a</td>
<td>7.6 ± 0.2^ac</td>
<td>6.7 ± 0.7^ac</td>
</tr>
<tr>
<td>Regrowth</td>
<td>1400 ± 392^c</td>
<td>42 ± 10^a</td>
<td>946 ± 111^ce</td>
<td>8.2 ± 0.1^c</td>
<td>7.7 ± 0.8^ce</td>
</tr>
</tbody>
</table>

Values are means ± s.e. (n = 4 and 5 for control and pruned trees, respectively). Treatment means followed by a different letter are significantly different (P < 0.05).

DISCUSSION

Experiment 1: tip-pruning all branches, and suppressing regrowth

Tip-pruning of macadamia trees around the time of anthesis produced a vegetative flush that coincided with the premature fruit abscission period and increased fruit abscission, reducing final set and yield. The removal of leaf area alone, through pruning (NR), also reduced fruit set and yield, but the effects were not as great as those associated with shoot regrowth. In lychee, removal of mature leaves by pruning also reduced yield. Trees pruned at a time that allowed one vegetative flush to develop before flowering produced a higher yield than trees pruned at a later time that did not allow regeneration of the canopy before flowering (Menzel et al., 2000).

The pattern of carbohydrate depletion in the branches of the R treatment was consistent with the hypothesis that shoot growth competes with developing fruitlets for assimilates. Rapid depletion of branch TNSC in the R treatment occurred between 5 and 6 weeks PA, which was around the time of early shoot growth from pruned branches and a decrease in fruit number relative to C and NR treatments.

It is likely that the decline in carbohydrates in the R treatment was largely due to shoot growth. Judging from depletion patterns in the NR treatment trees, on which there was virtually no shoot growth, accelerated demand on branch TNSC from fruit growth did not commence until after 6 weeks PA. By this time, branch TNSC in the R treatment had already started to recover. The early recovery in TNSC may have reflected a combination of reduced fruit demand caused by accentuated fruit abscission, and maturation of the new shoots to the status of net carbon producers. The former effect is similar to that observed for oil palm where stem TNSC increased following fruit removal by pruning (Legros et al., 2009).

Similar fluctuations in stem carbohydrate during shoot development have previously been observed for macadamia and lychee. In lychee, starch concentrations in stems decreased from early leaf expansion up to and during the period of maximum leaf area increase, and recovered during leaf maturation (Hieke et al., 2002b). In macadamia, stem TNSC declined during the early stages of shoot development but recovered before the maximum rate of shoot dry weight accumulation occurred (Olesen et al., 2006). The authors suggested this pattern indicated that early shoot growth represented a strong sink for carbohydrates but that as the leaves became net carbon contributors they allowed for a simultaneous increase in shoot growth rate and recharge of carbohydrate reserves. In the present study, a similar pattern of decline and recharge of carbohydrates in relation to shoot growth rate generally supports this view, although it was found that the minimum carbohydrate concentration occurred at approximately the same time as the maximum rate of new shoot dry weight accumulation. Stephenson et al. (1989), on the other hand, did not find any evidence that a developing flush depleted carbohydrate reserves in macadamia. They found that trees which had had their reproductive growth restricted by a combination of ethephon sprays, to abort developing racemes, and regular raceme removal, did not show a reduction in trunk carbohydrate concentrations during the period of flush development. This may have been because their sampling interval was monthly whereas in the present study and that of Olesen et al. (2006) stem carbohydrate levels declined and recovered within this interval and so may not have been detected in a monthly sampling schedule.

The maximum draw-down of TNSC in the NR trees occurred 8 weeks PA and corresponded with accelerated fruit drop. The R trees showed no evidence of fruit drop after 8 weeks PA, presumably because the massive fruit drop 2 weeks earlier during the regrowth phase had reduced fruit–fruit competition and made the trees insensitive to an increase in fruit growth rate. There is support for this in that the TNSC levels in the R trees had been restored by 8 weeks PA.

The depletion of stem TNSC in the C treatment reflected the combined demands of flush development and fruit growth. The timing of recovery, at around 7 weeks PA was earlier than observed for macadamia by Stephenson et al. (1989) who reported that trunk carbohydrate concentrations declined until around 12 weeks PA in mid-December. The recovery in the present study may have related to a temporary reduction in demand from fruit growth due to the increase in fruit abscission that occurred at approximately the same time. A similar but sharper recovery in TNSC occurred in the NR treatment that corresponded with a sharper increase in fruit abscission.
In discussions on competition between vegetative and reproductive growth, observations that fruit are dominant sinks and that new shoots, although initially a drain on resources, quickly become net contributors, are sometimes used to relegate the potential for vegetative growth to affect yield (Huett, 1996; Hieke et al., 2002a). However, while it is generally considered that reproductive sinks have a higher priority for nutrients and water than other plant parts (Wardlaw, 1990; Trifilo et al., 2010) it is not always the case, especially when reproductive structures are small and/or not growing rapidly (Wright, 1989; Marcelis, 1993; Grossman and De Jong, 1994). The present study demonstrates that macadamia fruit are not strong sinks until at least 8 weeks PA, and are vulnerable during early development to competition for carbohydrates from early shoot growth. The results have practical implications for macadamia management. It is likely that hedging at a time that avoids stimulating shoot growth during the premature fruit abscission period will minimize the negative effect of hedging on yield.

**Experiment 2: tip-pruning upper branches, and suppressing regrowth**

This experiment provided evidence for branch autonomy in macadamia with respect to shoot growth. In the R treatment, where new shoots were allowed to develop behind the pruning cuts, there was a substantial increase in fruit abscission in the upper part of the canopy but little effect on fruit abscission in the lower canopy, when compared with the NR treatment, where new shoots were removed weekly.

There was, however, evidence for resource movement between different parts of the canopy in response to fruit growth. In the whole tree pruning experiment, the NR treatment had fewer fruit than the C treatment, presumably due to lower overall canopy photosynthesis, as discussed previously. In the partial tree pruning experiment, the pruned parts of the NR treatment (upper branches) and the corresponding parts of the C treatment held similar numbers of fruit. This may have been caused by movement of sugars from the lower part of the canopy of the NR treatment to the upper part to compensate for the loss of leaves in the upper part, or, alternatively, movement of sugars from the C treatment upper canopy to the lower canopy to compensate for the higher number of racemes and greater sink strength. This is consistent with Trueman and Turnbull (1994) who showed that defoliation of branches did not affect fruit set on those branches, suggesting that the branches were supported by carbohydrates from elsewhere in the tree.

Thus macadamia branches appear to be autonomous with respect to shoot growth but less so with respect to fruit growth. Hieke et al. (2002a) came to a similar conclusion with respect to lychee and suggested that the differential branch autonomy observed for shoot and fruit growth reflected differences in sink strength.

Earlier work by McFadyen (2006) found that topping trees in November caused a 16% reduction in yield in the year of application, a comparable reduction to that reported here for the R treatment, even though her trees were topped 2 months later than trees in the present study. She also found a much greater reduction in yield in the second year following topping that corresponded with pronounced vertical shoots at the tops of the trees. From the work above, this greater reduction in yield was unlikely to be related to competition between vegetative growth at the top of the canopy and fruit set in the lower canopy. A more likely explanation is that there was less flowering and/or more abscission of fruit in the upper part of the canopy.

**Conclusions**

This is the first demonstration of competition between fruit abscission and leafy shoot development in an evergreen recurrent flushing tree in response to pruning. The variations in the levels of reserve carbohydrates support the hypothesis that the young shoots and fruit competed for assimilates. The effect appears to have been quite local, with leafy shoot development in one part of the canopy having little effect on fruit abscission in another part of the canopy.

The results have major implications for the timing and approach to canopy management practices in macadamia and, more generally, for our understanding of the control of the timing, extent and spatial separation of vegetative and reproductive shoot development within evergreen tree canopies.

**ACKNOWLEDGEMENTS**

We thank Russell Priddle, Alistair Janetzki and Magda Verbeek for technical assistance, Richard Meyer for carbohydrate analyses, and Stephen Morris for assistance with and advice on statistical analyses and ‘R’ programming. We also thank Stephen Morris and Donald Irving for comments on drafts of the manuscript. This work was supported by funding from the Australian Macadamia Society and Horticulture Australia Ltd (project number MC04024).

**LITERATURE CITED**


Jones WW, Shaw L. 1943. *Final report MC01037*


McFadyen LM. 2006. *Maintaining existing canopy management sites, final report MC01077*


