Tree Physiology 22, 947–953

Shoot development, chlorophyll, gas exchange and carbohydrates in lychee seedlings (*Litchi chinensis*)

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Received June 26, 2001; accepted January 5, 2002; published online August 1, 2002

Summary Shoot growth, chlorophyll concentrations, gas exchange and starch concentrations were studied in lychee (*Litchi chinensis* Sonn.) seedlings of cultivar "Wai Chee" grown in a heated greenhouse at Nambour in subtropical Australia (27° S). We also examined the effects of shoot defoliation and root pruning on leaf expansion. Shoot growth showed a rhythmic cycle under constant greenhouse conditions, with a mean duration of flushing of 20 days and an interval of 10 days over three cycles. Shoots and leaves expanded in a sigmoidal pattern to about 80 mm and 500 cm^2, respectively, for each flush. Starch concentrations of the lower stem and roots decreased as the young red leaves expanded, and increased as the fully expanded leaves turned dark green. Chlorophyll concentrations and net CO_2 assimilation rate were highest in the fully expanded dark green leaves.

Removing 50% of the area of each fully expanded leaf had little effect on the expansion of younger leaves, but total biomass of defoliated plants was only 60% of that of controls. In contrast, removing half the roots just before bud swelling reduced final leaf area by 80%. We conclude that the young shoot has relatively low rates of photoassimilation until the leaves are fully expanded and dark green, and depends on assimilates from elsewhere in the plant. During leaf expansion, translocation of assimilates to the shoot occurred at the expense of the roots.

Keywords: leaf development, leaf removal, net CO_2 assimilation, root pruning, shoot growth, starch.

Introduction

Shoot growth in lychee (*Litchi chinensis* Sonn.) and related members of Sapindaceae from tropical rainforests, such as longan (*Dimocarpus longan* Lour.) and rambutan (*Nephelium lappaceum* L.) is not continuous (Verheij and Coronel 1991). Generally, there is a rapid period of shoot elongation and leaf expansion followed by a period of leaf maturation, before the next period of shoot growth. In lychee, the duration and interval of growth are strongly related to environmental conditions, with optimum leaf area production occurring at about 29 °C (Batten and Lahav 1994). A similar cycle of shoot growth has been observed in other tropical species such as cacao (*Theobroma cacao* L.) (Greathouse et al. 1971, Sleigh et al. 1984), even when the plants are grown under optimum conditions, and appears to be related to endogenous factors.

In temperate fruit trees, new leaves develop during flowering and fruit development. Many studies have shown that these leaves compete for resources with the developing fruit, although eventually they are net contributors to the carbon economy of the tree (Kriedemann 1968). In contrast, these effects are not well described for tropical trees, although they may also have leaves and fruit developing on the branches at the same time. Wolstenholme (1990) suggested that, in spring, leaves developing next to the newly set fruit compete with the fruit for available resources in some tropical species, such as avocado (*Persea americana* Mill.). Application of the growth retardant paclobutrazol reduced shoot growth and sometimes led to higher yields or larger fruit (Wolstenholme et al. 1990, Whiley et al. 1991). There is some evidence for a similar response in lychee. Batten et al. (1994), for example, showed that drought after flowering reduced terminal shoot growth and doubled the number of fruit per panicle at harvest.

We report on changes in gas exchange, and chlorophyll and starch concentrations during shoot development in lychee seedlings grown in a heated greenhouse. Seedlings were used to test the relationship between development and physiology because growth is confined to a single axis with leaves, stem and roots, without the complications of flowers and fruit. We hypothesized that young leaves would have lower chlorophyll concentrations and photosynthetic rates than mature leaves. We also determined if defoliation and root pruning treatments reduce assimilate production in the seedlings or increase assimilate demand, and reduce shoot extension and leaf expansion.

Materials and methods

Plant material

Studies on shoot growth, carbohydrate and chlorophyll concentrations, and gas exchange were conducted on 18-month-

old seedlings of lychee cultivar "Wai Chee" grown in 1.5-l pots containing a 2:1:1 (v/v) mix of sand:peat:soil in a heated greenhouse at Nambour in subtropical Australia (27° S). The defoliation and root pruning experiments were conducted on 30-month-old seedlings grown in 4-l pots. Day/night temperature regime was 30 ± 2/22 ± 2 °C and vapor pressure deficit of the air (VPD) during the day was 0.5 to 1.5 kPa. Every 2 to 4 weeks, seedlings were fertilized with a nutrient solution containing: (mmol l^{-1}) N, 14; P, 2.4; and K, 4.3; and (μmol) S, 20; Mg, 21; Mn, 4.5; Fe, 17.9; Zn, 0.8; Cu, 0.8; and B, 9.1, and given a foliar spray containing 0.2 g l^{-1} each of Mg, Zn and Cu every month. Under these conditions, the plants flushed about every month.

In a preliminary experiment, the relationship between length of the central vein in a leaflet (L_{length}, 10 to 150 mm) and leaf area (L_{area}, cm^2) was established for vigorously growing plants. We used two relationships, one for small leaflets up to 25 mm long (Equation 1), and another for longer leaflets (Equation 2). The areas of the leaflets from each leaf were pooled to calculate total leaf area. The same correlations between leaf area and leaf length were used for control, defoliated and pruned plants:

$$L_{area} = 105.03\{1 - [1 + \exp((L_{length} + 13.85\ln(2^{1/0.07} - 1) - 183.01)/13.84)]^{-0.07}\}, \quad (1)$$

$R^2 = 0.96$, $n = 70$.

$$L_{area} = \frac{-3.67 + 56.71}{1 + \exp[-(L_{length} - 101.26)/33.03]}, \quad (2)$$

$R^2 = 0.96$, $n = 70$.

Shoot growth and carbohydrate concentrations

Growth of eight plants was studied over three flushing cycles commencing in April, May and June. Every 2 to 3 days, shoot extension (S_{length}) and L_{area} were determined, with each flush having four or five new leaves. The growth of the shoots and leaves was described by a modified logistic model (Turner et al. 1996):

$$S_{length} = S_{max}/\{1 + \exp[-k(t - m)]\}, \quad (3)$$

$$L_{area} = L_{max}/\{1 + \exp[-k(t - m)]\}, \quad (4)$$

where S_{max} is maximum shoot length (mm), L_{max} is maximum area of the leaves (cm^2), k is a rate constant (per day), m describes the time to reach maximum growth rate, and t is time in days. This model was fitted to the data by the iterative process of the Marquardt-Levenberg algorithm (SigmaPlot Version 4, Jandel Scientific, San Rafael, CA). Data are presented as means (with standard errors, SE) for each day.

Sets of seedlings were harvested at different stages during the three flush cycles for starch concentration. The flush cycle was described based on modified terminology of Sleigh et al. (1984): F-1 = bud swelling, leaf initiation, unfolding and initial expansion, leaves red; F-2 = leaf expansion, leaves thin, red and green, apical bud dormant; I-1 = leaf expansion completed, leaves light green, apical bud dormant; and I-2 = fully expanded, leaves dark green, apical bud dormant.

The times that the plants were harvested in relation to leaf expansion during the first flush are shown in Figure 1. Plants were harvested early in the morning and divided into leaves of the previous flush, stem of the previous flush, leaves of the older flushes, stem of the older flushes, and roots, and dried at 60 °C, ground and analyzed for starch (Rasmussen and Henry 1990). The seedlings were laid out in a completely randomized design, with the data presented as means (± SE) of six plants per treatment.

Chlorophyll concentrations and gas exchange

Measurements of chlorophyll concentrations and gas exchange were made on the middle leaf in each flush of seedlings at growth Stages F-1, F-2, I-1 and I-2. For chlorophyll a and b, 0.25 g of fresh leaf was frozen in liquid nitrogen and ground to a fine powder in a mortar with a pestle, with liquid nitrogen. Fifty ml of chilled 100% methanol was added to the powder, and the suspension homogenized for 1 min, and then filtered through Whatman Filter Paper No. 4. There was no pigment left in the residue at this stage. Absorbency of the supernatant was determined with a Helios β spectrophotometer at 653 nm (chlorophyll b) and 666 nm (chlorophyll a). Standard curves were constructed for pure chlorophyll a and b, and Equations 5 and 6 used to calculate the concentrations of chlorophyll in mg g^{-1} fresh weight:

$$\text{Chlorophyll a} = \text{absorbency (at 666 nm)}/2.537 \times 20, \quad (5)$$

$$\text{Chlorophyll b} = \text{absorbency (at 653 nm)}/4.261 \times 20. \quad (6)$$

Net CO_2 assimilation (A) of the seedlings was measured over 4 days. Measurements (three per plant) were made at 1000 h on the middle leaf of each flush with an LI-6200 photosynthesis meter (Li-Cor, Lincoln, NE) equipped with a 1-l chamber. During measurements, temperature in the chamber was 32 ± 2 °C, VPD was 1 ± 0.5 kPa and photosynthetic photon flux density was above 1200 μmol m^{-2} s^{-1}. A record was also kept of the length of the new shoots and leaf new total area per plant. Plants were laid out in a completely randomized design. Data are presented as means (± SE) of three or five plants per harvest.

Defoliation

Defoliation experiments were conducted on 30-month-old seedlings of "Wai Chee" grown in 4-l pots. The plants were laid out in a completely randomized design. Half the area of each fully expanded leaf was removed. This was repeated over three cycles. Unpruned plants served as controls. Every 2 to 3 days, shoot extension and leaf area were determined. At the end of the experiment, the plants were divided into leaves of the previous flush, stem of the previous flush, leaves of the older flushes, stem of the older flushes, and roots, and dried at 60 °C, weighed, ground and analyzed for starch concentration.

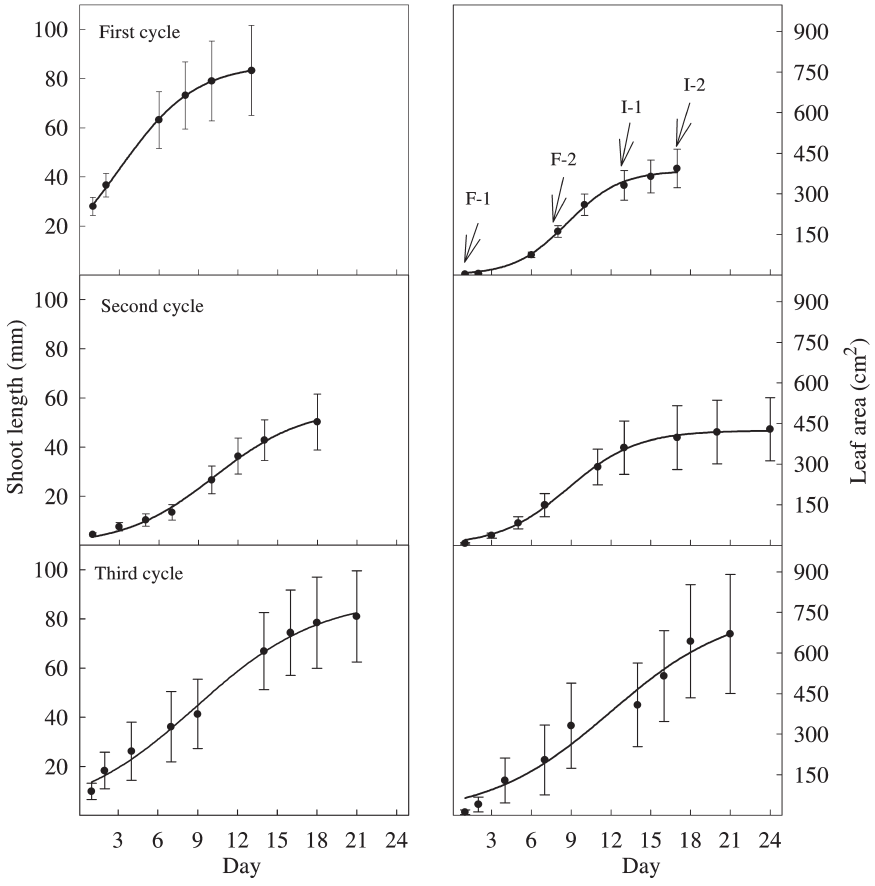

Figure 1. Growth of the shoots and leaves over three flushing cycles. Data are the means (± SE) of eight plants. Regressions ($R^2 > 0.97$; $P < 0.001$) for shoot extension are $S_{length1} = 85/\{1 + \exp[-0.34(day - 3)]\}$, $S_{length2} = 56/\{1 + \exp[-0.29(day - 10.2)]\}$ and $S_{length3} = 88/\{1 + \exp[-0.22(day - 8.9)]\}$; and for leaf area are $L_{area1} = 386/\{1 + \exp[-0.50(day - 8.7)]\}$, $L_{area2} = 423/\{1 + \exp[-0.39(day - 8.8)]\}$ and $L_{area3} = 764/\{1 + \exp[-0.22 (day - 12.0)]\}$ for the first, second and third cycles, respectively.

Values presented are means (± SE) of eight plants per treatment.

Root pruning

Experiments were conducted on 30-month-old seedlings of "Wai Chee" grown in 4-l pots. The plants were laid out in a completely randomized design. Pruning was carried out to remove 50% of the potting medium and associated roots at Stage I-2 of shoot development. The control pots were disturbed, but not pruned. It was not possible to determine the actual root volume, length or area remaining in the pots after pruning. Presumably, the proportion of root volume removed was less than 50%, because more roots are found in the center of the pots than on the edges. Stem extension and leaf area were determined every 2 to 3 days over a single flush cycle. Values presented are means (± SE) of eight plants per treatment.

Results

Shoot growth and carbohydrate concentrations

Seedlings raised in the heated greenhouse exhibited cyclical growth from April to August. Each flush produced four or five leaves. Initially, there was a short period of stem elongation with some leaf unfolding, but without significant expansion, then a period of stem elongation and leaf expansion, and finally just leaf expansion. The duration of flushing was 15 ± 1 days, 24 ± 3 days and 18 ± 2 days, in the first, second and third cycles, whereas the intervals between flushes were 8 ± 1 days and 12 ± 1 days, respectively.

The empirical growth model fitted the data well. A small value of the coefficient m (days) indicates earlier completion of shoot or leaf growth. A high value of the coefficient k (per day) indicates that the shoot or leaf reached S_{max} or L_{max} more rapidly. The first and second leaves were larger and grew more quickly than the last leaf (Figure 2) and had higher values of L_{max} (116 ± 1, 128 ± 1 and 65 ± 1 cm^2) and k (0.69 ± 0.03, 0.61 ± 0.02 and 0.49 ± 0.03 days), but lower values of m (7.1 ± 0.1, 8.3 ± 0.1 and 9.2 ± 0.2 days).

Stems grew more slowly in the second and third cycles than in the first cycle (Figure 1), possibly because of lower temperatures in the greenhouse. The decrease in stem growth rate was reflected in lower values of k and higher values of m. Similarly, leaf area expansion was slower in the second and third cycles than in the first cycle.

Mean starch concentrations were slightly lower in May (3.2 ± 0.3%) and June (3.3 ± 0.3%) than in April (4.4 ± 0.3%). Among the different plant parts, starch concentrations were higher in the stem of the old flushes (5.5 ± 0.4%) and roots (6.9 ± 0.4%) than in the leaves of the previous flush (1.4 ± 0.2%), leaves of the old flushes (1.3 ± 0.1%) and stem of the previous flush (3.1 ± 0.2%). Starch concentrations in the stem of old

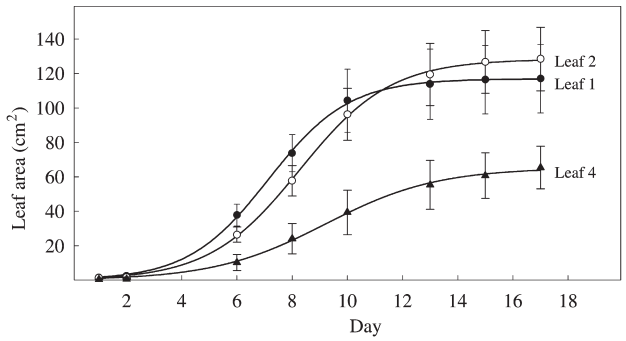

Figure 2. Growth of the first, second and last leaf over the first flushing cycle. Data are the means (± SE) of eight plants. The curves are fits of Equation 4.

flushes and roots decreased from Stages F-1 to F-2 and I-1 and then increased at Stage I-2 (Table 1).

Chlorophyll concentrations and gas exchange

Total chlorophyll concentrations in the leaves were higher at Stage I-2 than at Stages F-1, F-2 and I-1 (Table 2), mainly because of higher chlorophyll a concentrations, although there was also some effect on chlorophyll b concentrations. The changes in chlorophyll concentrations reflected changes in the color of leaves, which were red at F-1, red-green at F-2, light green at I-1 and dark green at I-2.

Net CO_2 assimilation per unit leaf area increased by a factor of 20 as the flush developed, with the greatest difference between Stages I-1 and I-2 (Table 2). These changes reflected differences in leaf color and chlorophyll concentrations rather than leaf size. Leaves at I-1 were 75% expanded, but only had half the CO_2 assimilation per unit leaf area of leaves at I-2.

Table 1. Starch concentrations (% of dry weight) in different parts of lychee seedlings at four stages of flush development. Data are means (± SE) of 18 plants per treatment pooled from three harvests.

Plant part	F-1	F-2	I-1	I-2
Leaves (previous flush)	1.9 ± 0.5	1.0 ± 0.2	1.1 ± 0.2	1.8 ± 0.2
Leaves (old flushes)	1.4 ± 0.2	0.9 ± 0.1	1.2 ± 0.2	1.5 ± 0.2
Stem (previous flush)	3.7 ± 0.2	2.9 ± 0.3	2.4 ± 0.3	3.4 ± 0.4
Stem (old flushes)	8.2 ± 0.4	4.8 ± 0.8	3.6 ± 0.7	5.6 ± 0.8
Roots	9.6 ± 0.5	6.5 ± 0.8	5.2 ± 0.8	6.1 ± 0.8

Defoliation

Removing 50% of the area of fully expanded leaves did not consistently change the pattern of shoot extension or leaf expansion over three cycles (Figure 3). Shoots of control and defoliated plants had a sigmoid growth pattern and took 22 to 35 days to reach a length of 110 to 170 mm. Similarly, they took 29 to 36 days to reach a leaf area of 800 to 1600 cm^2. In the first two cycles, stem extension was slightly slower in the controls than in the defoliated plants. The empirical model fitted the data well, with similar S_{max} values, but lower k and higher m values in the controls than in the defoliated seedlings in the first two cycles.

The controls had lower leaf area per plant than the pruned seedlings in the second and third cycles, and slower leaf growth in the second cycle (Figure 3). Thus, L_{max} was lower in September and November, and k lower and m higher in September. Thus, defoliation did not slow shoot development or lengthen the time to reach maximum values. In contrast, there were differences in the values of S_{max}, L_{max}, m and k during the different flushes in August, September and November (Figure 3), reflecting differences in greenhouse temperature.

Defoliated plants had lower leaf dry biomass than control plants after the three cycles (Table 3). However, the biomass of old stems and especially roots was also much lower. Starch concentrations in the defoliated plants were lower in the stems of the previous and the old flushes and in the roots compared with controls (Table 3). Defoliation had no effect on foliar starch concentrations of the remaining leaves. Highest starch concentrations were found in the old stem and roots of controls.

Root pruning

The root-pruned plants had only 20% of the final stem extension and leaf area of the controls (Figure 4). Equations 3 and 4 fitted the data for the controls (S_{max} = 125 ± 1 mm, m = 13.2 ± 0.2 days and k = 0.22 ± 0.01 days) (L_{max} = 495 ± 14 cm^2, m = 24.0 ± 0.4 days and k = 0.26 ± 0.02 days), but not the data for the root-pruned plants.

Discussion

Lychee seedlings grown in a heated greenhouse exhibited cycles of shoot extension and leaf growth. There were large differences in the concentrations of chlorophyll and starch, and

Table 2. Chlorophyll concentrations and net CO_2 assimilation (A) at four stages of flush development. Total leaf area per flush is also presented. Values for chlorophyll concentrations are the means (± SE) of five plants per treatment. Values for A and leaf area are the means (± SE) of 12 plants per treatment pooled over 4 days.

Stage	Chlorophyll a (mg g^{-1} fresh weight)	Chlorophyll b (mg g^{-1} fresh weight)	Total chlorophyll (mg g^{-1} fresh weight)	A (μmol CO_2 m^{-2} s^{-1})	Total leaf area per flush (cm^2)
F-1	0.96 ± 0.06	0.34 ± 0.02	1.30 ± 0.09	0.3 ± 0.3	315 ± 80
F-2	0.87 ± 0.09	0.23 ± 0.03	1.11 ± 0.13	1.6 ± 0.3	1063 ± 52
I-1	2.24 ± 0.28	0.75 ± 0.10	2.98 ± 0.38	2.7 ± 0.2	1263 ± 227
I-2	8.18 ± 0.58	2.87 ± 0.20	11.04 ± 0.78	5.8 ± 0.3	1568 ± 286

Table 3. Effects of 50% defoliation on plant dry biomass and starch concentrations in different parts of lychee seedlings after three flushing cycles. Values are the means (± SE) of four or eight plants per treatment.

Plant part	Dry biomass (g plant^{-1})		Starch concentration (% of dry weight)	
	Control	Defoliated	Control	Defoliated
Leaves (previous flush)	8.6 ± 0.7	4.3 ± 0.3	1.5 ± 0.2	1.5 ± 0.3
Stem (previous flush)	1.8 ± 0.2	1.6 ± 0.2	1.9 ± 0.1	1.2 ± 0.1
Leaves (older flushes)	27.0 ± 2.8	14.0 ± 1.0	0.7 ± 0.1	0.8 ± 0.1
Stem (older flushes)	27.5 ± 4.1	20.3 ± 2.1	3.8 ± 1.0	1.4 ± 0.1
Root	20.4 ± 2.9	11.4 ± 1.0	5.8 ± 2.4	2.2 ± 0.3
Total plant	85.3 ± 9.1	51.6 ± 4.4	–	–

gas exchange during the flushes. Defoliation and root pruning altered the patterns of shoot and root growth. Therefore, we conclude that developing leaves are strongly dependent on assimilates from the rest of the plant.

Pattern of shoot growth

The developing shoots and leaves of our lychee seedlings followed the modified logistic growth model of Turner et al. (1996). Seedling growth was slower during the coolest months, which agrees with previous reports on leaf expansion (Batten and Lahav 1994). In our model, a small value of m (days) indicates earlier completion of shoot or leaf growth, whereas a high value of k (per day) indicates that S_{max} or L_{max} was reached more rapidly. A species with a small value of m would have a relatively short period of leaf or shoot extension. Similarly, a species with a high value of k would have the bulk of shoot elongation or leaf expansion completed very early during the growth period.

There were generally about 20 to 25 days of stem extension and leaf expansion and then an interval of about 8 to 12 days before the next flush. The last leaf produced was smaller than the earlier leaves, suggesting competition within a flush. There is also evidence of competition in cacao, because removing the first few leaves of a flush increased the size of the other leaves (Machado and Hardwick 1987).

Assimilate production and distribution

Seedling photosynthesis varied with leaf development. The young red leaves had low CO_2 assimilation rates that were reflected in their chlorophyll concentration. There was an 8.5-fold increase in total chlorophyll concentration during development from young red leaves to mature dark green leaves. Leaves at Stage I-1 had completed 75% of their expansion, but were light green compared with fully expanded dark green leaves. However, A of Stage I-1 leaves was only half that of fully expanded leaves. Net CO_2 assimilation generally increases during leaf ontogeny, often reaching a maximum at about full leaf expansion and then decreases during senescence in deciduous trees such as apple (*Malus* Mill.; Kennedy and Johnson 1981). In tropical trees such as avocado, however, the peak in CO_2 assimilation often occurs after full leaf expansion (Schaffer et al. 1991).

In lychee, most of the changes in carbohydrate concentration are attributable to changes in starch concentration, with soluble sugars representing only a small fraction of the carbohydrate pool. If growth exceeded CO_2 assimilation, we would

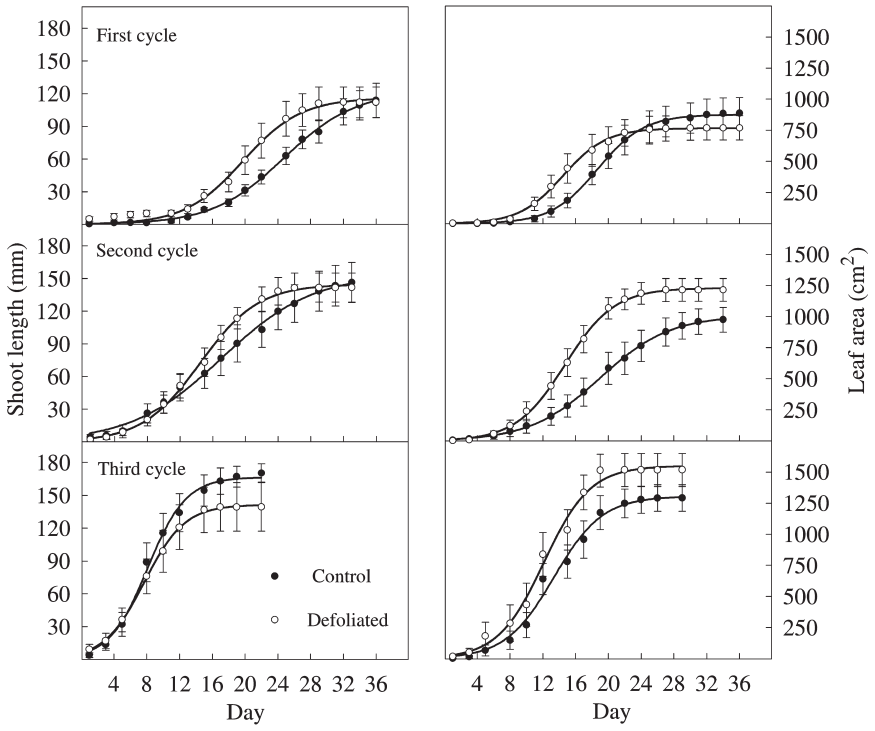

Figure 3. Effects of defoliation on the growth of the shoots and leaves over three flushing cycles (subscripts 1–3). Half the area of each fully expanded leaf was removed. Data are the means (± SE) of eight plants per treatment. Regressions ($R^2 > 0.99$; $P < 0.001$) for shoots for controls (subscript C) are $S_{length1C} = 122/\{1 + \exp[-0.23(day - 24.8)]\}$, $S_{length2C} = 154/\{1 + \exp[-0.18\ (day - 17.1)]\}$ and $S_{length3C} = 167/\{1 + \exp[-0.42(day - 8.1)]\}$; and for defoliated plants (subscript D) are $S_{length1D} = 116/\{1 + \exp[-0.28\ (day - 19.7)]\}$, $S_{length2D} = 145/\{1 + \exp[-0.28\ (day - 14.5)]\}$, and $S_{length3D} = 141/\{1 + \exp[-0.41\ (day - 7.7)]\}$. Regressions ($R^2 > 0.99$; $P < 0.001$) for leaf area for controls (subscript C) are $L_{area1C} = 876/\{1 + \exp[-0.35\ (day - 18.7)]\}$, $L_{length2C} = 1008/\{1 + \exp[-0.23\ (day - 18.9)]\}$, and $L_{length3C} = 1305/\{1 + \exp[-0.34(day - 13.3)]\}$; and for defoliated plants (subscript D) are $L_{length1D} = 767/\{1 + \exp[-0.38(day - 14.4)]\}$, $L_{length2D} = 1229/\{1 + \exp[-0.33(day - 14.7)]\}$, and $L_{length3D} = 1549/\{1 + \exp[-0.35(day - 12.1)]\}$ for the first, second and third cycles, respectively.

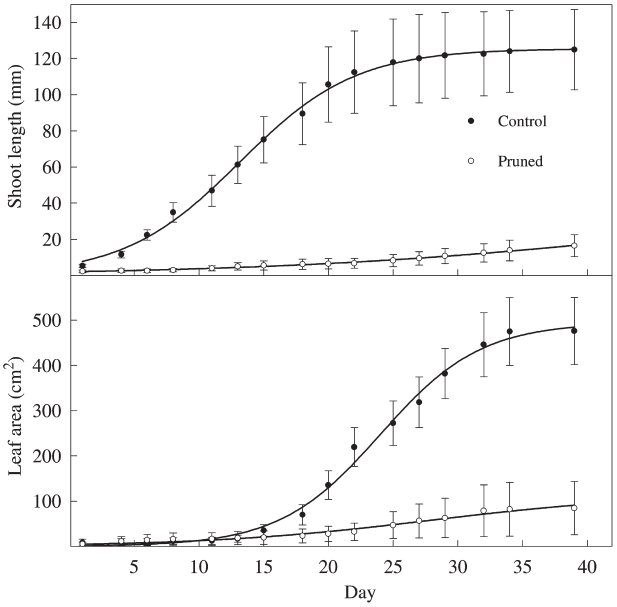

Figure 4. Effect of root pruning on the growth of the shoots and leaves over a single cycle. Half the volume of the root medium was removed at Stage F-1 of flush development. Data are the means (± SE) of eight plants per treatment.

expect starch reserves to decline. On the other hand, if growth was less than assimilation, starch concentrations should increase. Starch concentrations in leaves and the young stem were below 4% and did not vary with plant development, whereas starch concentrations were much higher in the old stem and roots, and declined during the period of maximum leaf growth (F-1 to I-1), and then rose during leaf maturation (I-2). These results suggest that the demand for assimilates exceeded supply during early leaf development.

Responses to defoliation and root pruning

Defoliation and root pruning were used to assess the impact of changing assimilate production and demand on flush development. These treatments were expected to affect shoot and leaf growth. Removing part of the leaves when they were fully expanded had a small effect on the growth of new flushes. Defoliation had no effect on stem extension and leaf expansion. The data on plant dry biomass showed that flushes used assimilates that normally supported the lower stem and roots. Starch concentrations in the lower stems and roots were also lower in defoliated plants than in controls.

In contrast, root pruning reduced leaf expansion by 80%. Similar findings have been reported by Sleigh et al. (1984) who removed 25 and 50% of the root systems of cacao seedlings growing in a heated greenhouse, when the leaves were mature. The control plants took 5 days to start flushing and flushed for 25 days. These values were extended to 6 to 18 days, and 28 to 31 days in pruned plants.

Changes in starch concentrations with leaf development, and the responses to defoliation and root pruning suggest that lychee leaf flushes are strong sinks for assimilates from the rest of the plant. These assimilates can come from current assimilation or stored reserves. Because starch concentrations declined in intact plants, it appears that demand by the developing flushes, roots and other plant parts at this time exceeds the capacity of the mature leaves to export assimilates. The developing leaves of cacao (Hardwick et al. 1982) are strong sinks for ^{14}C assimilates fed to mature leaves, whereas roots were favored when shoot development ceased. Hardwick et al. (1982) fed $^{14}CO_2$ to the third youngest mature leaf, and found that during flushing, label was mainly found in the developing leaves, whereas the stem and roots were the main sink when the leaves were mature. Similar results have been reported for avocado (Whiley and Schaffer 1993), citrus (*Citrus sinensis* Pers.; Kriedeman 1969) and pecan (*Carya illinoensis* Koch; Davis and Sparks 1974). Root pruning might also be expected to influence water and nutrient uptake of the plants, although none of our root-pruned lychee seedlings wilted or showed symptoms of nutrient deficiency.

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