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Inhibitory effect of flowering and early fruit growth on leaf photosynthesis in mango

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Summary Carbohydrate and nitrogen contents, chlorophyll fluorescence and gas exchange were measured in leaves from both vegetative and reproductive terminal shoots of 12-year-old flowering mango trees. Reproductive shoot leaves were close to swelling floral buds, inflorescences or panicles bearing set fruits. Leaves close to inflorescences had lower rates of mitochondrial respiration (R_d) and net photosynthesis (A_{net}), and lower stomatal conductance (g_s) and quantum efficiency of photosystem II under actinic light than vegetative shoot leaves. Leaf nitrogen concentration, which decreased from the beginning until the end of flowering, was lower in leaves close to inflorescences than in vegetative shoot leaves. However, these differences and changes were counterbalanced by an increase in leaf mass-to-area ratio so that leaf nitrogen per unit leaf area (N_a) remained nearly constant during the whole flowering period, except in leaves close to panicles bearing set fruits. Net CO_2 assimilation rate simulated by a biochemical model of leaf photosynthesis (Urban et al. 2003) was much higher than A_{net} measured at an ambient CO_2 partial pressure (C_a) of either 36 or 70 Pa. The overestimation of A_{net} was more pronounced in leaves close to inflorescences, to panicles bearing set fruits and to reversing inflorescences (characterized by the appearance of leaves in terminal positions on inflorescences) than in vegetative shoot leaves. It is concluded that low A_{net} in leaves close to inflorescences was probably due neither to changes in N_a nor to a decrease in Rubisco activity induced by low g_s, but rather to a decrease in electron flow in photosystem II. This decrease was not directly associated with higher starch or soluble sugar contents.

Keywords: leaf nitrogen, Mangifera indica, nonstructural carbohydrates, quantum efficiency of radiation use of photosystem II, starch, stomatal conductance.

Introduction

Biochemically based models of leaf photosynthesis, coupled to radiation transfer models, can simulate photosynthesis at the individual plant (Le Roux et al. 2001*b*, Sinoquet et al. 2001) and canopy (Harley et al. 1985, Harley and Tenhunen 1991, Harley and Baldocchi 1995, De Pury and Farquhar 1997) levels. Unfortunately, such models do not serve to model fruit production, mainly because they do not integrate the effects of phenology and cultural practices, except nitrogen fertilization. In fruit production, the effects of flowering and fruiting, which modify source–sink relationships, cannot be overlooked. This is even more critical in tropical fruit production, where the flowering and fruiting phases exceed 6 months at the individual tree scale, depending on climatic conditions. In mango, under the conditions on Réunion Island, flowering usually occurs over 2 months and fruiting over nearly 5 months.

The effect of fruiting on leaf nitrogen content and photosynthesis has been described for several fruit species, including apple (Thiebus-Kaesberg and Lenz 1994), olive (Proietti 2000), peach (Rufat and DeJong 2001) and mango (Urban et al. 2003). Decreases in net photosynthetic assimilation have been reported during the floral period in sweet cherry (Roper et al. 1988) and mango (Shivashankara and Mathai 2000), but no study has investigated changes in leaf nitrogen content. Because proteins of the Calvin cycle and thylakoids represent the majority of leaf nitrogen, photosynthetic capacity (i.e., the maximum rate of carboxylation, the light-saturated rate of electron transport, the rate of phosphate release in triose phosphate utilization and the mitochondrial respiration rate due to phosphorylative oxidations) is strongly related to the amount of leaf nitrogen per unit leaf area (N_a) (Field and Mooney 1986, Evans 1989, Kellomäki and Wang 1997, Walcroft et al. 1997, 2002). In short, observed increases or decreases in net photosynthetic assimilation in the presence of developing flowers may result either from modification of N_a caused by a change in leaf nitrogen concentration or in leaf mass-to-area ratio, or from an increase or decrease in one or more of the limiting biochemical factors of net photosynthesis, mainly ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) activity, ribulose bisphosphate (RuBP) regeneration, and mitochondrial respiration rate. Net CO_2 assimilation rate (A_{net}) may also be reduced by changes in stomatal conductance and associated changes in intercellular CO_2 concentration (C_i). Moreover, low C_i may have an indirect negative effect on A_{net} by lowering the activation state of Rubisco (von Caemmerer and Edmonson 1986, Sage et al. 1990, Meyer and Genty 1999).

The objective of this study was to discriminate among the potential effects of flowering on photosynthesis in mango by examining changes in leaf carbohydrate and nitrogen content, gas exchange and quantum-use efficiency during the flowering season. Measurements were performed on leaves from vegetative terminal shoots (vegetative shoot leaves) and from reproductive terminal shoots close to swelling floral buds, to inflorescences and to panicles bearing set fruits.

Materials and methods

Experimental site and plant material

Measurements were performed on leaves from six 12-year-old *Mangifera indica* L. cv. 'Lirfa,' grafted on 'Maison rouge,' grown in an experimental orchard near Saint-Pierre, Réunion Island (20°52′48″ S, 55°31′48″ E). Trees were spaced 5 m (within rows) by 7 m (between rows) and were about 3 m high, with a northeast–southwest row orientation. Water was supplied every other day on a 100% actual evapotranspiration basis. Stem diameter was monitored with eight linear variable displacement transducers (LVDT, Solartron, Bognor, U.K.). Maximal daytime shrinkage was less than 20 µm for stems with a diameter of 2 to 4 cm, indicating that trees were not water stressed during the trial (data not shown). Trees received 100 kg N ha^{-1} (urea), 20 kg P ha^{-1} (superphosphate) and 100 kg K ha^{-1} (potassium sulphate) on March 1, 2001 (after harvest). Insects and diseases were controlled according to local practice.

The experimental trees were characterized by the simultaneous presence of flower-bearing and nonflower-bearing terminal shoots. Flowering shoots and vegetative shoots were confined to separate scaffold limbs within the same tree. Flowering was not synchronous within flowering scaffold limbs, but all terminal shoots evolved into flowering shoots. Similarly, all terminal shoots remained vegetative on vegetative scaffold limbs. No vegetative flush occurred in any type of scaffold limb during the trial. We labeled one flowering and one vegetative scaffold limb within each tree to follow their behavior. All scaffold limbs were similarly oriented. Four stages of development were considered: vegetative stage, prefloral stage (characterized by the appearance of swelling floral buds), floral stage (characterized by the presence of 4 to 8 cm long inflorescences) and post-floral stage (characterized by the presence of at least three set fruits per panicle with a diameter of at least 2 mm). Measurements were performed from the beginning of August 2001, just before the appearance of swelling floral buds, to the end of September 2001, at fruit set. We checked that swelling buds were indeed floral buds that evolved into inflorescences. Additional measurements were performed at the end of September 2001 on some leaves close to reversing inflorescences (reproductive-to-vegetative shoots, i.e., characterized by the appearance of leaves in terminal positions on inflorescences).

When comparing vegetative shoot leaves (on nonflowering terminals) with leaves close to floral buds or inflorescences, we made sure that all leaves had the same orientation and were at similar heights (about 1.5 m). Fish-eye pictures were taken to ensure that gap fractions were similar (HemiView 3.1 SR1, Delta-T Devices, U.K.).

Measurements of leaf photosynthesis and stomatal conductance

Net CO_2 assimilation rate (A_{net}) and leaf diffusive conductance to water vapor (g_s) were measured with an infrared CO_2/H_2O gas analyzer and leaf chamber system with a red/blue light source (LI 6400 and LI 6400-02B, Li-Cor, Lincoln, NE). Measurements were performed in tracking mode to minimize light fluctuations (target value coming from the external sensor, potentially changing every 3 s) on labeled, young, fully expanded leaves, every 2 h from 0800 to 1600 h on August 5 (vegetative shoot leaves, ambient CO_2 partial pressure (C_a) = 36 Pa, n = 12), August 29 (vegetative shoot leaves and leaves close to swelling floral buds and inflorescences, C_a = 36 and 70 Pa, n = 8) and on September 26, 2001 (vegetative shoot leaves and leaves close to inflorescences, panicles bearing set fruits and reversing inflorescences, C_a = 36 and 70 Pa, n = 4). Water vapor pressure deficit at the leaf surface (VPD) was 0.9 to 3.6 Pa. At the end of gas exchange measurements, leaves were harvested, leaf areas measured and leaves frozen in liquid nitrogen.

Additional measurements of A_{net} and g_s were performed on young fully expanded leaves with photosynthetically active flux density (Q) set at 1500 µmol m^{-2} s^{-1} (saturating light), C_a at 36 Pa and leaf temperature (T_l) at 30 °C. Measurements were performed around midday on August 5 (vegetative shoot leaves), August 29 (vegetative shoot leaves and leaves close to swelling floral buds and inflorescences), September 10 (vegetative shoot leaves and leaves close to inflorescences), September 17 (vegetative shoot leaves and leaves close to inflorescences) and September 26, 2001 (vegetative shoot leaves and leaves close to inflorescences, panicles bearing set fruits and reversing inflorescences) (n = 6). Net CO_2 assimilation rate and g_s were calculated according to von Caemmerer and Farquhar (1981).

Biochemical model of leaf photosynthesis

Net CO_2 assimilation rate (µmol CO_2 m^{-2} s^{-1}) in C_3 plants is a function of the carboxylation rate (V_c), the oxygenation rate (V_o) and the rate of CO_2 evolution in light that results from processes other than photorespiration (i.e., mitochondrial respiration, R_d; µmol CO_2 m^{-2} s^{-1}):

$$A_{net} = V_c - 0.5V_o - R_d \quad (1)$$

According to the Harley et al. (1992) version of the model proposed by Farquhar et al. (1980), A_{net} can be expressed as:

$$A_{net} = \left(1 - \frac{0.5O}{\tau C_i}\right)\min(W_c, W_j) - R_d \quad (2)$$

where O is the partial pressure of O_2 in the intercellular air spaces (O = 21 kPa), τ is the specificity factor of Rubisco, C_i is the partial pressure of CO_2 in the intercellular air spaces (Pa),

W_c is the carboxylation rate limited by the amount, activation state or kinetic properties of Rubisco (μmol CO_2 m^{-2} s^{-1}), and W_j is the carboxylation rate limited by the rate of RuBP regeneration (μmol CO_2 m^{-2} s^{-1}). The carboxylation rate W_c is given by:

$$W_c = \frac{V_{cmax} C_i}{C_i + K_c(1 + O/K_o)} \quad (3)$$

where V_{cmax} is the maximum rate of carboxylation (μmol CO_2 m^{-2} s^{-1}), and K_c (Pa CO_2) and K_o (Pa O_2) are the Michaelis constants of Rubisco carboxylation and oxygenation, respectively. The carboxylation rate W_j is controlled by the rate of electron flow J (μmol electrons m^{-2} s^{-1}):

$$W_j = \frac{JC_i}{4(C_i + O/\tau)} \quad (4)$$

$$J = \frac{\alpha Q}{\left(1 + \alpha^2 Q^2 / J_{max}^2\right)^{0.5}} \quad (5)$$

where α is the apparent efficiency of light energy conversion (mol electrons mol^{-1} photons) and J_{max} is the light-saturated rate of electron transport (μmol m^{-2} s^{-1}).

The temperature dependency of V_{cmax} and J_{max} is described by:

$$\frac{e^{c - \Delta H_a / RT_l}}{1 + e^{(\Delta S T_l - \Delta H_d)/RT_l}} \quad (6)$$

where c is a scaling factor, ΔH_a (J mol^{-1}) the activation energy of the given parameter, R is the gas constant (8.3143 J K^{-1} mol^{-1}), T_l (K) is leaf temperature, ΔS (J mol^{-1}) is an entropy term, and ΔH_d (J mol^{-1}) is the deactivation energy of the given parameter. Similarly, the temperature dependency of R_d, τ, K_c and K_o is described by:

$$e^{c - \Delta H_a / RT_l} \quad (7)$$

The scaling factor c for V_{cmax}, J_{max} and R_d was related to N_a^{-1} (Urban et al. 2003) by:

$$c = a_N N_a^{-1} + b_N \quad (8)$$

where a_N and b_N are parameters.

Maximum V_c, J_{max} and R_d were derived from A/C_i curves taken in August. Other parameters were derived from Harley et al. (1992), with the exception of $c(\tau)$, $c(K_c)$, $c(K_o)$, $\Delta H_a(\tau)$, $\Delta H_a(K_c)$ and $\Delta H_a(K_o)$, for which we used the parameters determined from in vivo leaf gas exchange measurements performed on a Rubisco-antisense line of tobacco (*Nicotinia tabacum* L. cv. W38) by Bernacchi et al. (2001)

Leaves were exposed to high irradiance at ambient CO_2 concentration for at least 15 min before starting A/C_i curves. Thirteen measurements were taken (C_a = 200, 180, 160, 140, 120, 100, 80, 60, 40, 30, 20, 10 and 5 Pa CO_2) for each curve. Measurements were performed only on August 7, 8, 9, 10 and 13, 2001 on vegetative shoot leaves (n = 8) because g_s was found to be too low in leaves close to swelling floral buds and inflorescence for reliable measurement of A_{net} as a function of C_i (Terashima et al. 1988). Moreover, g_s could not be maintained above 0.1 mol H_2O m^{-2} s^{-1} even in vegetative shoot leaves after August 15, 2001. Conditions in the leaf chamber were controlled (T_l = 30 °C and VPD (at T_l) = 1.0 + 0.2 kPa). Photosynthetically active flux density was set at 1500 μmol m^{-2} s^{-1}. Best fit V_{cmax}, J_{max} and R_d values were obtained by nonlinear least squares regression (S-Plus 2000, MathSoft International, Bagshot, U.K.). The CO_2 evolution rate after 5 min in the dark was taken as an estimate of R_d. At the end of this procedure, leaf areas were measured and leaves frozen in liquid nitrogen.

Additional measurements of R_d were performed on August 5 (vegetative shoot leaves, n = 8), August 29 (vegetative shoot leaves and leaves close to swelling floral buds and inflorescences, n = 6), September 6 (vegetative shoot leaves and leaves close to swelling floral buds and inflorescences, n = 6), September 11 (vegetative shoot leaves and leaves close to inflorescences, n = 8) and September 26 (vegetative shoot leaves and leaves close to swelling floral buds, inflorescences, panicles bearing set fruits and reversing inflorescences, n = 6).

The biochemical model of leaf photosynthesis was used to simulate A_{net} (using N_a, Q, T_l, C_a and g_s as entry parameters) in order to compare it with measured A_{net}. Simulated A_{net} was calculated from Equation 2 and the supply function:

$$C_i = C_a - \frac{A_{net}}{g_b} - \frac{A_{net}}{g_s} \quad (9)$$

where g_b is the leaf boundary layer conductance. The system of two equations with two unknowns (A_{net} and C_i) can be manipulated into a quadratic equation with one unknown (A_{net}) with one positive and one negative root.

Measurements of chlorophyll fluorescence

Fluorescence parameters were measured on attached leaves with a portable modulated fluorometer (FMS, Hansatech, Pentney, U.K.). The value of minimal fluorescence, F_o, was measured before dawn or after adaptation to darkness (provided by dark clips) for at least 1 h. Saturating light pulses of 5200 μmol m^{-2} s^{-1} were applied for 0.8 s to obtain maximal fluorescence before dawn (F_m). The parameter F_v/F_m (Butler 1978), calculated as $(F_m - F_o)/F_m$, was used as an indicator of photoinhibition (Krause 1988). Measurements were performed early in the morning and around midday on August 2 (vegetative shoot leaves, n = 12), August 11 (vegetative shoot leaves and leaves close to inflorescences, n = 12), August 29 (vegetative shoot leaves and leaves close to swelling floral buds and inflorescences, n = 8), September 15 (vegetative shoot leaves and leaves close to inflorescences, n = 12) and September 27 (vegetative shoot leaves and leaves close to inflorescences, panicles bearing set fruits and reversing inflorescences, n = 8).

The fraction of photons used in photochemistry by a light-

adapted leaf (Φ_{PSII}) was estimated from $\Delta F/F'_m$ (= $(F'_m - F_s)/F'_m$) (Genty et al. 1989). To obtain maximal fluorescence under actinic light (F'_m), saturating light pulses of 5200 µmol m^{-2} s^{-1} were applied for 0.8 s. F_s is steady state fluorescence. Leaves were adapted to Q = 1500 µmol m^{-2} s^{-1} for 10 min. Measurements were performed from 1100 to 1500 h on August 24 (vegetative shoot leaves and leaves close to swelling floral buds and inflorescences, n = 6), September 10 (vegetative shoot leaves and leaves close to inflorescences, n = 6) and September 26 (vegetative shoot leaves and leaves close to inflorescences, panicles bearing set fruits and reversing inflorescences, n = 6).

Leaf nitrogen and nonstructural carbohydrates

Leaf nitrogen content per unit mass (N_m) was determined with an elemental analyzer (Carlo Erba Instruments, Milan, Italy) following the method of Colombo et al. (1988). Glucose, fructose and sucrose in the leaves were measured with an enzyme-based analyzer (YSI 2007, Yellow Springs Instrument, Yellow Springs, OH). Starch was determined by enzymatic hydrolysis to glucose (Thievend et al. 1972).

Dry mass was assessed by freeze-drying. The masses of starch and soluble sugars were deducted from the dry mass to obtain the structural dry mass from which mass-to-area ratio (M_a) and N_a ($N_a = M_a N_m$) were calculated.

Labeled leaves for gas exchange measurements were sampled. Additional samples were collected as needed to provide six to 12 replicates per treatment and on August 24 and 29, 2001.

Statistical analysis

Treatment effects were evaluated by analysis of variance (ANOVA) followed by multiple comparison of means (S-Plus 4, Mathsoft International). Results are expressed as means ± standard errors (SE). Treatment and time differences were considered significant at $P < 0.05$. Comparisons of slopes of the best fit lines for measured and simulated A_{net} and for g_s as a function of A_{net} were performed by covariance analysis (Scherrer 1984). Differences were considered significant at $P < 0.05$.

Results

Relationship between leaf photosynthetic capacity and leaf nitrogen

The relationships between J_{max} and N_a and between V_{cmax} and N_a of vegetative shoot leaves were described well by the standard model of Urban et al. (2003) (Figures 1A and 1B). Although the plot of the relationship between R_d and N_a was further from the fitting curve of Urban et al. (2003) (Figure 1C), we decided to use their model to simulate A_{net} of both types of leaves. For a given N_a, R_d was significantly lower in leaves close to inflorescences than in vegetative shoot leaves. For leaves close to panicles bearing set fruits, limited data prevented us from deriving a specific relationship, but measured values were described well by the fitted curve corresponding

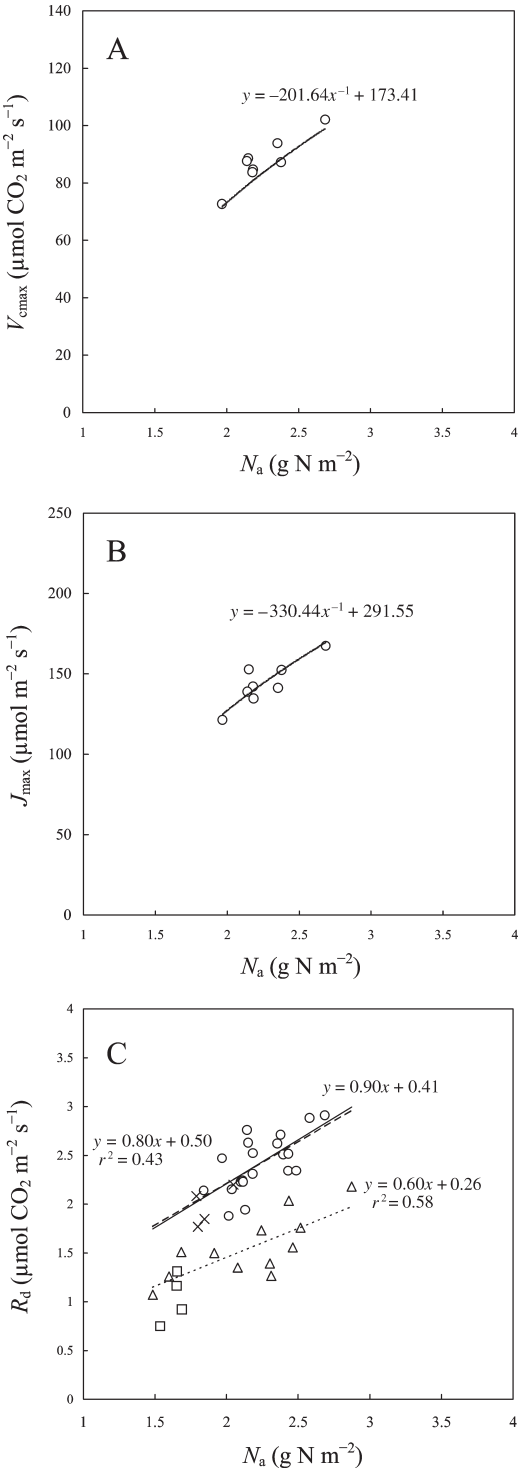

Figure 1. Relationships between the amount of nitrogen per unit leaf area (N_a) and the three key parameters of the photosynthesis model: (A) maximum rate of carboxylation (V_{cmax}); (B) light-saturated rate of electron transport (J_{max}); and (C) mitochondrial respiration (R_d). Measurements were performed on 8 (for V_{cmax} and J_{max}) to 20 (for R_d) vegetative shoot leaves (○), 12 leaves close to inflorescences (△, R_d only), six leaves close to panicles bearing set fruits (□, R_d only) and six leaves close to reversing inflorescences (×, R_d only). The solid lines correspond to the standard model presented by Urban et al. (2003). Best fit lines (C only) correspond to vegetative shoot leaves (– – –) and leaves close to inflorescences (••••).

to leaves close to inflorescences (Figure 1C), which was used to simulate A_{net} of both types of leaves. The relationship between R_d and N_a in leaves close to swelling floral buds did not fit either the standard model or the derived model for leaves close to inflorescences and panicles bearing set fruits (data not shown). Because limited data prevented us from deriving a specific relationship, we decided to use measured values of R_d to simulate A_{net} of this leaf type.

Leaf nitrogen content in mango leaves as affected by the proximity of swelling floral buds and inflorescences

Leaf nitrogen content per unit mass was low in leaves close to inflorescences, and even lower in leaves close to panicles bearing set fruits (Table 1). However, N_a did not differ among the three leaf types because M_a was slightly, although insignificantly, higher in leaves close to inflorescences and panicles bearing set fruit. There were no differences in N_m, M_a or N_a between vegetative shoot leaves and leaves close to reversing inflorescences (Table 1).

Leaf nitrogen content per unit mass decreased by about 20% from the beginning (August 17) to the end of the flowering period (September 26) in both vegetative shoot leaves and leaves close to inflorescences. On account of slight, although insignificant, increases in M_a, decreases in N_m were not reflected in N_a (Table 1).

On August 17, 2001, N_m was about 4% lower in leaves close to swelling floral buds, whereas M_a and N_a were 13 and 8% higher, respectively.

Effect of flowering and fruit set on the starch and soluble sugars of mango leaves

At the beginning of the flowering season (August 17), concentrations of starch and total nonstructural carbohydrates were higher in leaves close to swelling floral buds than in vegetative shoot leaves (Table 2). Concentrations of starch, soluble sugars and total nonstructural carbohydrates dropped by 74, 16 and 45%, respectively, from August 17 to 24, 2001, in leaves close to inflorescences. Starch increased in vegetative shoot leaves and leaves close to inflorescences by 366 and 836%, respectively, during the flowering period (Table 2). During the same period, soluble sugars remained relatively stable in vegetative shoot leaves (between 8.85 and 10.02 g m^{-2}), whereas they increased by 48% (from 6.42 to 9.53 g m^{-2}) in leaves close to inflorescences. As a result, the initial difference in carbohydrate content between the two leaf types was much reduced by the end of September (Table 2). At the end of September, starch and total nonstructural carbohydrates were lowest in leaves close to panicles bearing set fruits, intermediate in leaves close to reversing inflorescences and highest in leaves close to inflorescences (Table 2).

The ratio of sucrose to total soluble sugars was significantly lower in leaves close to swelling floral buds than in vegetative shoot leaves on August 17, 2001. Between August 17 and 24, 2001, the sucrose-to-total soluble sugars ratio increased by 51% in vegetative shoot leaves and 94% in leaves close to inflorescences (Table 2). It decreased afterwards in both vegetative shoot leaves and leaves close to developing floral buds by

Table 1. Changes in leaf nitrogen concentration, leaf mass-to-area ratio and amount of nitrogen per unit leaf area from the beginning of August until the end of September. Measurements were made on vegetative shoot leaves and on leaves close to swelling floral buds, inflorescences, panicles bearing small set fruits, and reversing inflorescences (n = 6 to 12). Data represent means ± standard errors. For each sample date and parameter, values with different lowercase letters differ significantly ($P < 0.05$). For each type of leaf and parameter, values with different uppercase letters differ significantly ($P < 0.05$).

Measurement date	Vegetative shoot leaves	Leaves close to swelling floral buds	Leaves close to inflorescences	Leaves close to panicles bearing set fruits	Leaves close to reversing inflorescences
Leaf nitrogen concentration (g N g^{-1} structural dry matter)					
August 5	1.85 ± 0.03 B				
August 17	2.05 ± 0.03 b C	1.97 ± 0.02 a			
August 24	1.90 ± 0.04 b B		1.78 ± 0.06 a C		
August 29	1.89 ± 0.07 b B		1.67 ± 0.04 a B		
September 26	1.65 ± 0.04 c A		1.57 ± 0.09 b A	1.38 ± 0.09 a	1.65 ± 0.09 bc
Leaf mass-to-area ratio (g structural dry matter m^{-2})					
August 5	122 ± 4 AB				
August 17	114 ± 3 a A	129 ± 4 b			
August 24	125 ± 4 a B		132 ± 4 a A		
August 29	126 ± 7 a B		134 ± 3 a A		
September 26	133 ± 5 a B		139 ± 8 a A	136 ± 3 a	130 ± 7 a
Amount of nitrogen per unit leaf area (g N m^{-2})					
August 5	2.26 ± 0.08 A				
August 17	2.35 ± 0.09 a A	2.53 ± 0.09 a			
August 24	2.37 ± 0.10 a A		2.35 ± 0.08 a A		
August 29	2.38 ± 0.17 a A		2.24 ± 0.10 a A		
September 26	2.18 ± 0.09 a A		2.20 ± 0.21 a A	1.87 ± 0.13 a	2.15 ± 0.20 a

Table 2. Changes in starch, glucose + fructose + sucrose, total nonstructural carbohydrates and the sucrose-to-total soluble sugars ratio from the beginning of August until the end of September. Measurements were made on vegetative shoot leaves and on leaves close to swelling floral buds, inflorescences, panicles bearing small set fruits, and reversing inflorescences ($n = 6$ to 12). Data represent means ± standard errors. For each sample date and parameter, values with different lowercase letters differ significantly at $P < 0.05$. For each type of leaf and parameter, values with different uppercase letters differ significantly at $P < 0.05$.

Measurement date	Vegetative shoot leaves	Leaves close to swelling floral buds	Leaves close to inflorescences	Leaves close to panicles bearing set fruits	Leaves close to reversing inflorescences
Starch (g m^{-2})					
5 August	2.99 ± 0.27 B				
17 August	3.19 ± 0.21 a B	4.20 ± 0.20 b			
24 August	2.37 ± 0.12 b A		1.10 ± 0.18 a A		
29 August	4.39 ± 0.26 b C		3.97 ± 0.22 a		
26 September	11.1 ± 1.50 c D		10.3 ± 1.47 c C	4.58 ± 0.49 a	6.23 ± 0.88 b
Glucose + fructose + sucrose (g m^{-2})					
5 August	8.47 ± 0.26 A				
17 August	8.60 ± 0.36 a A	9.46 ± 0.32 a			
24 August	8.85 ± 0.27 b A		6.42 ± 0.21 a A		
29 August	8.70 ± 0.34 b A		7.60 ± 0.34 a B		
26 September	10.0 ± 0.43 a B		9.53 ± 0.57 a C	10.1 ± 0.25 a	9.46 ± 0.84 a
Total nonstructural carbohydrates (g m^{-2})					
5 August	11.46 ± 0.48 A				
17 August	11.79 ± 0.56 a A	13.70 ± 0.45 b			
24 August	11.22 ± 0.32 b A		7.52 ± 0.36 a A		
29 August	13.10 ± 0.50 b B		11.6 ± 0.23 a B		
26 September	21.07 ± 1.76 b C		19.8 ± 1.54 b C	14.7 ± 0.7 a	15.7 ± 1.21 a
Sucrose-to-soluble sugars ratio					
5 August	59.8 ± 2.39 C				
17 August	51.7 ± 4.03 b C	36.3 ± 5.9 a			
24 August	78.1 ± 6.68 a D		70.3 ± 7.28 a C		
29 August	31.9 ± 1.77 a B		56.7 ± 6.82 b B		
26 September	25.3 ± 0.81 a A		27.1 ± 1.30 a A	25.1 ± 1.28 a	26.8 ± 2.33 a

68 and 61%, respectively (from August 24 to September 26, 2001). There was no significant difference between vegetative shoot leaves, leaves close to inflorescences, to panicles bearing set fruits and to reversing inflorescences on September 26, 2001.

Gas exchange in mango leaves during flower bud development and flowering

Net photosynthetic assimilation rate and g_s of vegetative shoot leaves changed little over time (Table 3). Leaves close to swelling floral buds, inflorescences and panicles bearing set fruits had substantially lower values of both A_{net} and g_s than vegetative shoot leaves. Net CO_2 assimilation rate was higher in leaves close to reversing inflorescences than in leaves close to inflorescences or panicles bearing set fruits, whereas there were no differences in g_s.

Intercellular CO_2 concentration did not differ significantly between leaves close to inflorescences and vegetative shoot leaves, except on September 17 and 26, 2001 (Table 3). Intercellular CO_2 concentration changed little over time in either vegetative shoot leaves or leaves close to inflorescences. Intercellular CO_2 concentration was lowest in leaves close to reversing inflorescences.

A strong linear relationship was observed between g_s and A_{net} on August 5, 2001 (Figures 2A and 2B). This relationship completely disappeared in leaves close to swelling floral buds on August 29 but was restored during the flowering period. The slopes of the best fit lines were found to be slightly, although significantly, different between vegetative shoot leaves, leaves close to inflorescences, leaves close to panicles bearing set fruits, and leaves close to reversing inflorescences (Figure 2C).

Mitochondrial respiration rate increased in vegetative shoot leaves from 1.82 to 2.75 μmol CO_2 m^{-2} s^{-1} from early August to September 11, 2001, before declining slightly to 2.17 μmol CO_2 m^{-2} s^{-1} on September 26, 2001 (Table 4). On August 29 and September 6, 2001, R_d was 39 to 51% higher in leaves close to swelling floral buds and 13 to 35% lower in leaves close to inflorescences than in vegetative shoot leaves. On September 26, R_d was lowest, around 1 μmol CO_2 m^{-2} s^{-1}, in leaves close to panicles bearing set fruits, while similar in magnitude in all other types of leaves. The R_d/A_{net} ratio was

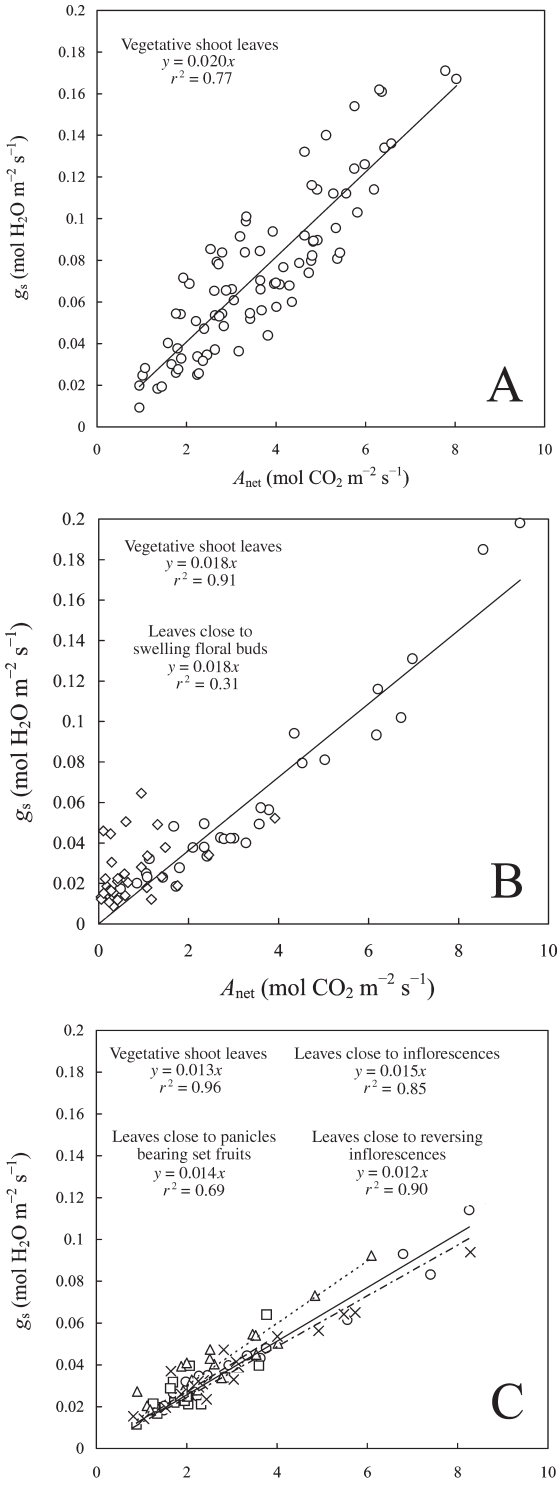

Figure 2. Relationship between stomatal conductance (g_s) and leaf net photosynthesis (A_{net}) on (A) August 5, (B) August 29 and (C) September 26, 2001. Measurements were made on vegetative shoot leaves (○) and on leaves close to swelling floral buds (◇), inflorescences (△), panicles bearing small set fruits (□) and reversing inflorescences (×) (n = 4 to 12). Best fit lines are for (a–c) vegetative shoot leaves (——) and (c) leaves close to inflorescences (····), panicles bearing small set fruits (– – –), and reversing inflorescences (–·–). The best fit line for leaves close to swelling floral buds (c, only) merges with that for vegetative leaves and is not represented.

high in all types of leaves, approaching 100% in leaves close to swelling floral buds (Tables 3 and 4).

Simulated A_{net} of vegetative shoot leaves and leaves close to inflorescences

The biochemical model overestimated A_{net} of vegetative shoot leaves by 29% on August 17, 2001, at the time of floral bud swelling (Figure 3A). The overestimation of A_{net} during the floral phase was 47 to 52% in vegetative shoot leaves and 76 to 95% in leaves close to inflorescences. The model failed to simulate A_{net} of leaves close to swelling floral buds (data not shown). The overestimation of A_{net} was 76% in leaves close to panicles bearing set fruits and 61% in leaves close to reversing inflorescences. The observed differences in slope between leaves of different origin were confirmed at C_a = 70 Pa (Figures 3B–D). Overestimation of A_{net} was less pronounced at C_a = 70 Pa than at C_a = 36 Pa, whatever the origin of the leaves.

Chlorophyll fluorescence parameters in mango leaves during flower bud development and flowering

The maximum quantum efficiency of photosystem II, measured before dawn and around midday, remained high throughout the trial, and there were no significant differences in predawn and midday F_v/F_m in any type of leaf, except those close to inflorescences (data not shown).

Quantum efficiency of photosystem II under actinic light was lower in leaves close to swelling buds than in vegetative shoot leaves, and even less in leaves close to inflorescences, on August 24, 2001 (Table 5). The difference in Φ_{PSII} between vegetative shoot leaves and leaves close to inflorescences was confirmed on September 10 and 26. Whereas Φ_{PSII} remained around 0.20 in leaves close to inflorescences, Φ_{PSII} of vegetative shoot leaves decreased from 0.37 to 0.26 between September 10 and 26, 2001. Quantum efficiency of photosystem II under actinic light of leaves close to reversing inflorescences did not differ significantly from that of leaves close to inflorescences or to panicles bearing set fruits.

Discussion

Changes in leaf nitrogen

Leaf nitrogen concentration per unit mass was lower in leaves close to developing inflorescences than in vegetative shoot leaves (Table 1). Such differences in nitrogen concentration have been attributed to the proximity of strong sinks, such as fruits (Taylor and May 1967, Taylor and Van den Ende 1969, Lenz 2000). Miyazaki et al. (2002) observed that leaves of reproductive shoots of *Styrax obassia* Sieb. & Zucc. had lower N_m than leaves of nonreproductive shoots. Leaf nitrogen concentration per unit mass was lower in leaves close to panicles bearing set fruits than in leaves close to inflorescences, but higher in leaves close to reversing inflorescences, suggesting that demand for nitrogen increases with fruit set, but decreases with reversion. The decrease in N_m during the floral period was more pronounced in vegetative shoot leaves than in leaves close to inflorescences (Table 1), indicating that nitrogen was

Table 3. Changes in leaf net photosynthesis, stomatal conductance and intercellular CO_2 concentration from the beginning of August until the end of September (photosynthetically active flux density = 1500 µmol m^{-2} s^{-1}, leaf temperature = 30 °C). Measurements were made on vegetative shoot leaves and on leaves close to swelling floral buds, inflorescences, panicles bearing small set fruits, and reversing inflorescences ($n = 6$). Data represent means ± standard errors. For each sample date and parameter, values with different lowercase letters differ significantly ($P < 0.05$). For each type of leaf and parameter, values with different uppercase letters differ significantly ($P < 0.05$).

Measurement date	Vegetative shoot leaves	Leaves close to swelling floral buds	Leaves close to inflorescences	Leaves close to panicles bearing set fruits	Leaves close to reversing inflorescences
Leaf net photosynthesis (µmol CO_2 m^{-2} s^{-1})					
August 5	6.60 ± 1.88 AB				
August 29	6.35 ± 0.38 c B	3.69 ± 0.76 a	5.16 ± 0.18 b C		
September 10	6.74 ± 1.07 b AB		3.48 ± 0.33 a AB		
September 17	5.42 ± 0.21 a A		4.72 ± 0.63 a BC		
September 26	6.27 ± 0.69 c AB		3.24 ± 0.34 a A	4.40 ± 0.49 b	5.48 ± 0.77 bc
Stomatal conductance (mol H_2O m^{-2} s^{-1})					
August 5	0.13 ± 0.02 A				
August 29	0.12 ± 0.01 c A	0.07 ± 0.01 a	0.09 ± 0.01 b A		
September 10	0.10 ± 0.02 b A		0.06 ± 0.01 a A		
September 17	0.11 ± 0.01 a A		0.09 ± 0.02 a A		
September 26	0.11 ± 0.02 b A		0.07 ± 0.01 a A	0.08 ± 0.01 a	0.06 ± 0.01 a
Intercellular CO_2 concentration (Pa)					
August 5	23.8 ± 0.8 A				
August 29	25.3 ± 0.6 a A	27.1 ± 1.7 a	24.4 ± 0.9 a A		
September 10	26.5 ± 1.4 a AB		27.3 ± 1.0 a B		
September 17	26.6 ± 0.4 b B		25.4 ± 0.3 a AB		
September 26	23.9 ± 0.4 b A		25.9 ± 0.5 c AB	25.6 ± 0.9 c	18.1 ± 1.0 a

Table 4. Changes in mitochondrial respiration from the beginning of August until the end of September. Measurements were performed at leaf temperature = 30 °C on vegetative shoot leaves and on leaves close to swelling floral buds, inflorescences, panicles bearing small set fruits, and reversing inflorescences ($n = 6$ to 8). Data represent means ± standard errors. For each sample date, values with different lowercase letters differ significantly ($P < 0.05$). For each type of leaf, values with different uppercase letters differ significantly ($P < 0.05$).

Measurement date	Vegetative shoot leaves	Leaves close to swelling floral buds	Leaves close to inflorescences	Leaves close to panicles bearing set fruits	Leaves close to reversing inflorescences
August 5	1.82 ± 0.24 A				
August 29	2.44 ± 0.17 b BC	3.69 ± 0.37 c	1.59 ± 0.11 a A		
September 6	2.65 ± 0.15 b BC	3.68 ± 0.22 c	2.25 ± 0.12 a C		
September 11	2.75 ± 0.09 b C		1.97 ± 0.12 a BC		
September 26	2.17± 0.18 b AB		1.89 ± 0.18 b AB	1.03 ± 0.14 a	2.19 ± 0.36 b

mobilized from leaves distant from the developing inflorescences, possibly to meet the increased demand for nitrogen during panicle development, when nitrogen reserves of nearby leaves, and maybe other organs, become exceedingly depleted.

It was surprising that increases in M_a made up for the observed changes in N_m, so that N_a remained almost constant regardless of the stage of floral development and the position of leaves with respect to inflorescences (Table 1). The maintenance of a nearly constant high value of N_a over time was reflected by the preservation of high F_v/F_m throughout the floral period. In other species, like *S. obassia*, M_a is lower in leaves of reproductive shoots than in leaves of nonreproductive shoots (Miyazaki et al. 2002). The literature reports that decreases in M_a, rather than N_m, occur in most shrub and tree species (Niinemets et al. 1998, Rosati et al. 2000, Le Roux et al. 2001*a*), including mango (Urban et al. 2003), as the result of the progressive shading that results from canopy development and, in some cases, the associated increase in leaf age. Our results show that a rapid increase in M_a is also possible. We have no explanation for such behavior.

It has been hypothesized that leaf nonstructural carbohydrate content is the driving force behind photosynthetic acclimation (Dewar et al. 1998, Kull and Kruijt 1999). In mango, leaf carbohydrate content was found to be neither the signal promoting N_a, and thus photosynthetic capacity, in leaves close to developing fruits, nor the signal for photosynthetic ca-

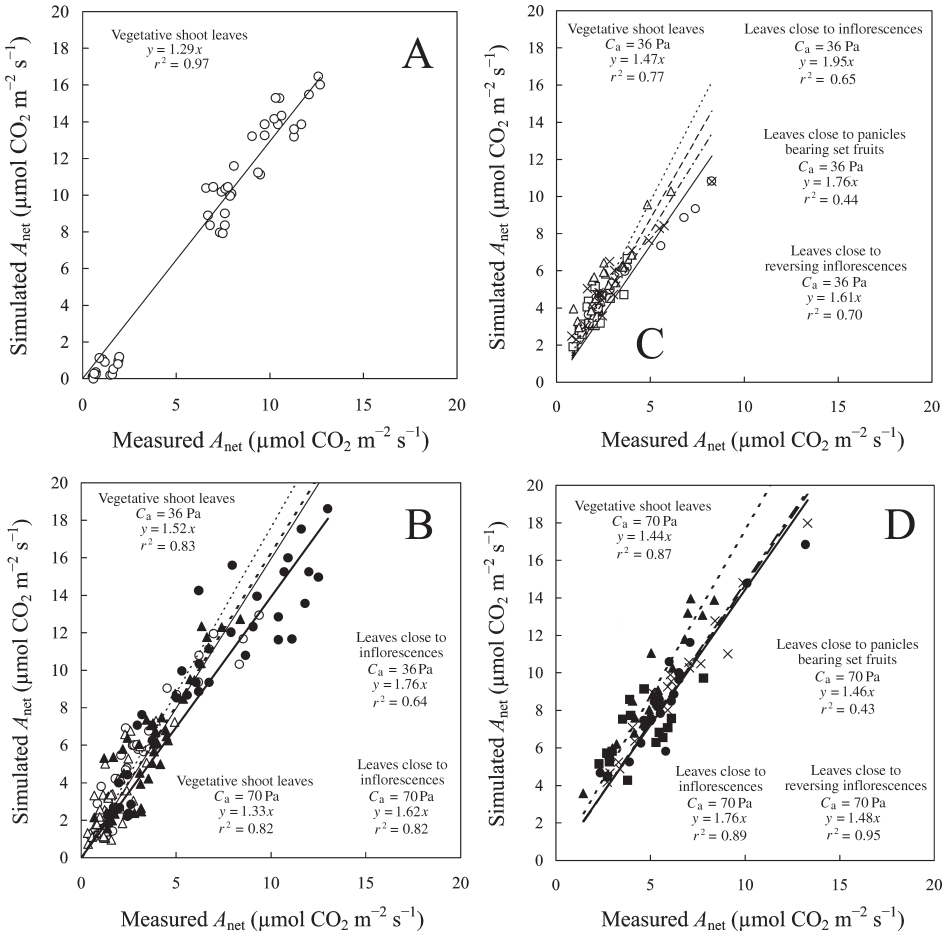

Figure 3. Comparison of simulated and measured leaf net photosynthesis (A_{net}) on (A) August 5 (ambient CO_2 partial pressure (C_a) = 36 Pa), (B) August 29 (C_a = 36 and 70 Pa), (C) September 26 (C_a = 36 Pa) and (D) September 26, 2001 (C_a = 70 Pa). Simulations used the biochemical model. Measurements were performed on vegetative shoot leaves (○) and on leaves close to swelling floral buds (◇), inflorescences (△), panicles bearing small set fruits (□), and reversing inflorescences (×) (n = 4 to 12). Best fit lines correspond to vegetative shoot leaves (——) and leaves close to inflorescences (····), panicles bearing small set fruits (– – –), and reversing inflorescences (– · –). Open symbols and standard lines correspond to C_a = 36 Pa. Closed symbols and thick lines correspond to C_a = 70 Pa. Data corresponding to swelling floral buds and inflorescences were pooled, as they were not different.

pacity acclimation to light (Urban et al. 2003). Although carbohydrate and nitrogen concentrations seemed to vary in opposite directions from the beginning until the end of the flowering period, we found no clear evidence for the involvement of leaf carbohydrates in the observed variations in leaf nitrogen concentration (Tables 1 and 2). Carbohydrate content may not always reflect plant nitrogen status, especially when nitrogen status is high (Ono et al. 2001). The decreases in N_m and N_a in leaves close to panicles bearing set fruits were associated with a decrease in leaf carbohydrate concentration, probably as a consequence of an increased demand for both nitrogen and energy of the developing fruits.

Increases in N_a in mango leaves close to developing fruits and decreases in N_a as a consequence of canopy development were attributed mainly to increases and decreases, respectively, in M_a (Urban et al. 2003). Changes in leaf nitrogen content and photosynthetic capacity may also result from depletion of leaf nitrogen by sinks such as developing flowers or fruits, demonstrating that there is more than one trigger for changes in leaf nitrogen content and photosynthetic capacity

Table 5. Changes in the quantum efficiency of photosystem II under actinic light from the beginning of August until the end of September. Measurements were made (at leaf temperature = 30 °C and photosynthetically active flux density = 1500 μmol m^{-2} s^{-1}) on vegetative shoot leaves and on leaves close to swelling floral buds, inflorescences, panicles bearing small set fruits, and reversing inflorescences (n = 6). Data represent means ± standard errors. For each sample date, values with different lowercase letters differ significantly (P < 0.05). For each leaf type, values with different uppercase letters differ significantly (P < 0.05).

Measurement date	Vegetative shoot leaves	Leaves close to swelling floral buds	Leaves close to inflorescences	Leaves close to panicles bearing set fruits	Leaves close to reversing inflorescences
August 24	0.34 ± 0.02 c B	0.29 ± 0.03 b	0.20 ± 0.01 a B		
September 10	0.37 ± 0.04 b B		0.21 ± 0.01 a B		
September 26	0.26 ± 0.02 b A		0.17 ± 0.01 a A	0.19 ± 0.04 a	0.21 ± 0.05 ab

during tree development.

Changes in leaf carbohydrate content

Although leaf starch concentration was lowest in leaves close to inflorescences (Table 2), leaf starch was globally higher during the floral period, from floral bud swelling to fruit set, than at any other period of the year (data not shown), regardless of leaf position with respect to inflorescences, confirming previous observations on mango (Paulas and Shanmugavelu 1989). Starch concentrations are higher in all parts of flowering lychee trees than in nonflowering but vegetatively flushing trees (Menzel et al. 1995). Similarly, starch is present in excess in avocado leaves during flower development (Thorp et al. 1993). Although we lack data from trees that remained entirely vegetative, a higher leaf starch content may be a distinctive feature of tropical fruit trees with flowering potential. Observations by Day et al. (1995) on *Boronia megastigma* Nees, Rideout et al. (1992) on tobacco, and Yu et al. (2000) on mutants of *Arabidopsis thaliana* L. with reduced capacity for starch synthesis suggest that starch accumulation may play an important role in floral initiation of shrubs and herbaceous plants as well.

Reserves of starch, soluble carbohydrates and total nonstructural carbohydrates were all strongly depleted in leaves close to developing inflorescences at the beginning of the floral period (August 24, 2001), whereas the sucrose-to-total soluble sugars ratio increased in both vegetative shoot leaves and leaves close to inflorescences from August 17 to 24, 2001 (Table 2). Corbesier et al. (1998) observed in *A. thaliana* that floral induction was associated with a large, transient and early increase in carbohydrate export from leaves. Their observations support the ideas that phloem carbohydrates have a critical function in floral transition and that floral induction increases the capacity of the leaf phloem-loading system. Similarly, the sucrose in leaf exudates of *Lolium temulentum* L. increased when flowering was induced (Périlleux and Bernier 1997), whereas a decrease in sucrose-phosphate synthase activity reduced reproductive sink development in rice (Ono et al. 1999). Surprisingly, no decrease in either starch or soluble sugars was observed in mango leaves close to swelling floral buds (Table 2). In mango, however, floral induction occurs after the bud has started to grow (Batten and McConchie 1995), so swelling buds are not yet floral buds. Thus, a correlation between floral induction and leaf carbohydrate content in mango is more likely to be apparent when floral organs emerge than at the swelling bud stage. On August 24, 2001, at the beginning of the floral period, there was a decrease in starch and soluble sugars, supporting observations that starch and then soluble sugars decreased in association with floral initiation and floral bud development in *Boronia megastigma* after an initial period of carbohydrate accumulation (Day et al. 1995).

Notwithstanding the presence of developing inflorescences, the soluble carbohydrate concentration increased in leaves close to inflorescences from August 24, 2001, until the end of the flowering period. The sucrose-to-total soluble sugars ratio decreased too, confirming that phloem loading had decreased. It appears that, after an initial phase of phloem-loading stimulation associated with floral initiation, the development of floral buds had the opposite effect. It is difficult to reconcile this effect with the need to support flowering. We have no data on starch and soluble sugar contents of reproductive shoot stems, but it seems probable that the soluble sugars needed to support flowering were produced through starch conversion in stems, as in avocado (Liu et al. 1999) or other plant organs.

After an initial decrease, starch increased steadily in leaves close to inflorescences until the end of the flowering period (Table 2). The observed increase in starch may be the result of a regulatory process linked to floral initiation (Eimert et al. 1995). This hypothesis is consistent with the substantial decrease in starch observed in leaves close to panicles bearing small set fruits, i.e., when floral initiation was over and fruit-bearing panicles acted only as sinks. Alternatively, leaf starch accumulation may be attributed to a regulatory mechanism preventing down-regulation of photosynthesis due to the accumulation of soluble carbohydrates (Foyer 1988). Because transient accumulations of soluble carbohydrates in leaves, as observed during the diurnal period, may impair the rate of electron transport (Pammenter et al. 1993), the synthesis of leaf starch may alleviate reductions in photosynthesis caused by feedback regulation (Sun et al. 1999). Although, in the present study, starch accumulation apparently did not prevent soluble carbohydrate concentration from increasing during flowering in leaves close to inflorescences (Table 2), it cannot be ruled out that, in the absence of starch accumulation, soluble sugars would have increased even more.

Temporal changes in starch concentration of vegetative shoot leaves paralleled those of leaves close to inflorescences, suggesting that the depleting and stimulating effects of floral induction and floral initiation on leaf starch may reach leaves far from, as well as close to, inflorescences.

Interpreting the effect of flowering on photosynthesis

Our results (Table 3) confirm the negative effect of flowering on A_{net} observed in mango by Shivashankara and Mathai (2000). Decreases in A_{net} in leaves close to developing flowers may theoretically result from (i) a decrease in N_a caused by a decrease in N_m or M_a; (ii) a decrease in Rubisco activity or RuBP regeneration, or an increase in R_d; or (iii) a decrease in g_s and the associated decrease in C_i. The last has a direct negative effect on A_{net}, but may also have an indirect effect, because it has been observed that a decrease in C_i may result in a decrease in the activation state of Rubisco (von Caemmerer and Edmonson 1986, Sage et al. 1990, Meyer and Genty 1999). Intercellular CO_2 concentration was no lower in leaves close to inflorescences than in vegetative shoot leaves, except on September 17, 2001 (Table 3). On September 26, 2001, C_i was even higher in leaves close to inflorescences. Low C_i can thus probably be eliminated as the determinant of the lower rates of A_{net} observed in leaves close to inflorescences.

The amount of leaf nitrogen per unit leaf area did not differ between leaves close to inflorescences and vegetative shoot leaves (Table 1). Differences in A_{net} between leaves close to in-

florescences and vegetative shoot leaves thus cannot be explained by differences in N_a.

The biochemical model of leaf photosynthesis substantially overestimated A_{net} in all types of leaves (Figures 3A and 3B), indicating either that the model of Urban et al. (2003) did not apply during the flowering period or that A_{net} was globally limited during the flowering period by one or more factors other than N_a and g_s. Overestimation of A_{net} by the biochemical model may indicate that part of the nitrogen present in the leaves during the flowering period was not invested in the photosynthetic machinery. Such an assumption questions the relationship between photosynthetic capacity and N_a (Field and Mooney 1986, Evans 1989, Kellomäki and Wang 1997, Walcroft et al. 1997, 2002). Although unlikely, this hypothesis cannot be ruled out because we have no direct data about the major components of photosynthetic capacity for the bulk of the flowering period. If we assume that A_{net} was reduced by limiting factors, the greater overestimation of A_{net} by the biochemical model in leaves close to inflorescences compared with vegetative shoot leaves (Figures 3B–D) may be attributed to either a decrease in Rubisco activity, an increase in R_d or a decrease in RuBP regeneration.

Low g_s in leaves close to inflorescences compared with vegetative shoot leaves generally did not result in lower C_i (Table 3). Moreover, increasing C_a from 36 to 70 Pa did not reduce the overestimation of A_{net} by the model in leaves of any type (Figure 3), suggesting that the activation state of Rubisco was not negatively affected by the depressing effect of flowering on g_s.

Differences in R_d did not account for the observed decrease in A_{net} in leaves close to inflorescences when compared with vegetative shoot leaves, because R_d was substantially lower in leaves close to inflorescences (a decrease in R_d would have increased A_{net}). We have no explanation for the observed increase and decrease, respectively, in R_d in leaves close to swelling floral buds and to panicles bearing set fruits. Such variations in R_d leave in question the robustness of existing models and call for further improvements in R_d modeling.

It may be hypothesized that the observed differences in overestimation of A_{net} between leaves close to inflorescences and vegetative shoot leaves were mainly due to differences in RuBP regeneration. This is consistent with the observation that Φ_{PSII}, and thus most probably the rate of electron transport in photosystem II, was substantially higher in vegetative shoot leaves than in leaves close to inflorescences (Table 5). Photosynthetic electron fluxes are believed to be linked to leaf carbohydrate content, but this was obviously not the case in our study; Φ_{PSII} was highest in vegetative shoot leaves whereas starch, soluble carbohydrate and total nonstructural carbohydrate concentrations were lowest in leaves close to inflorescences (Tables 2 and 5). This suggests that one or more factors other than carbohydrate accumulation accounted for the observed decrease in Φ_{PSII} in leaves close to inflorescences. It also raises the question of the mechanism by which inflorescences inhibited the rate of photosynthetic electron flow in photosystem II.

We have insufficient evidence to determine whether g_s had a direct inhibiting effect on A_{net} or whether the decreases in both g_s and A_{net} were merely concomitant. Cowan and Farquhar (1977) hypothesized that stomata were regulated to maximize A_{net} while minimizing water losses through transpiration. This hypothesis underlies the models of Ball et al. (1987) and Leuning (1995), where g_s is linearly correlated with A_{net}. Except on August 29, 2001, g_s was found to be well correlated with A_{net} in all types of leaves (Figure 2), but the slope of the linear relationship between g_s and A_{net} differed significantly among treatments (Figure 2), suggesting that the coregulation of A_{net} and transpiration was affected, if only moderately, by the proximity of either developing or reversing inflorescences, or panicles bearing set fruits.

Conclusion

In mango, flowering inhibits A_{net} of leaves both close to and far from inflorescences; although the effect is most pronounced in leaves closest to inflorescences. Differences in N_a do not seem to explain the low A_{net} of leaves close to inflorescences relative to vegetative shoot leaves. Our inability to obtain reliable A/C_i curves for leaves close to inflorescences prevented us from establishing definitely whether low A_{net} in these leaves was related to Rubisco activity and RuBP regeneration. However, indirect evidence suggests that low RuBP regeneration is responsible. Lower Φ_{PSII} in leaves close to inflorescences was not linked to either starch or soluble sugars or total nonstructural carbohydrate concentration.

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