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# Girdling decreases photosynthetic electron fluxes and induces sustained photoprotection in mango leaves

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**Summary** Girdling has been suggested as a way to improve earliness and intensity of flowering in mango (*Mangifer indica* L.). However, the accumulation of carbohydrates associated with girdling may result in a decrease in photosynthesis. We assessed the long-term effect of branch girdling during the prefloral period on leaf net photosynthesis ($A_n$) of 3-year old mango trees, cv. Cogshall, growing on La Réunion island. Leaf gas exchange and chlorophyll fluorescence parameters were measured monthly from March to August 2004 on recently matured leaves on girdled and non-girdled branches. Within 28 days after girdling, $A_n$ was reduced by 77% and remained at about 2 μmol $CO_2$ $m^{-2}$ $s^{-1}$ until the beginning of flowering. The decrease in photosynthetic electron transport rate ($J$) and sustained photoprotection (reflected by the decrease in predawn maximal efficiency of photosystem II) effectively protected leaves on girdled branches from photodamage, as shown by the vigorous recovery of $A_n$ and $J$ observed immediately after the appearance of inflorescences. These increases in $A_n$ and $J$ were unaccompanied by a decrease in leaf carbohydrate concentration during the first month following the onset of flowering, indicating that there are carbohydrate-dependent and carbohydrate-independent mechanisms of sink regulation of photosynthesis. It is concluded that girdling does not necessarily lead to irreversible damage, even in the presence of a fourfold increase in leaf starch concentration and in the absence of any sink activity. However, the decrease in leaf nitrogen concentration indicates that there may exist long-term negative effects of branch girdling on photosynthetic capacity. A modified version of the biochemical model of $A_n$ is presented that takes account of the effect of leaf starch concentration on $J$.

*Keywords: carbohydrates, chlorophyll fluorescence, Mangifera indica, nitrogen, photoinhibition, photosynthetic capacity, photosynthesis, starch.*

## Introduction

Girdling (the removal of a ring of phloem) is a common horticultural practice used to manipulate tree growth and development in a variety of fruit species. Its most immediate effect is to stop the basipetal movement of assimilates through the phloem, which results in an accumulation of carbohydrates above the girdle (Roper and Williams 1989, Schaper and Chacko 1993, Di Vaio et al. 2001). Girdling has been suggested as a way to promote floral induction in mango (*Mangifera indica* L.) (Chacko 1991), but it has also been shown to reduce net photosynthesis ($A_n$) in many species including *Malus sylvestris* (L.) Mill. var. *domestica* (Borkh.) (Zhou and Quebedeaux 2003), *Anacardium occidentale* L. (Schaper and Chacko 1993), *Vitis vinifera* L. (Roper and Williams 1989), *Prunus persica* var. nucipersica (Suckow) C.K. Schneid (Di Vaio et al. 2001) and *Mangifera indica* (Lu and Chacko 1998).

Source–sink imbalances can exert feedback downregulation or repression of leaf photosynthesis through carbohydrate accumulation in leaves (Azcon-Bieto 1983, Foyer 1988, Koch 1996, Paul and Foyer 2001, Paul and Pellny 2003). Transient accumulations of carbohydrates in leaves, as observed during the diurnal period, may impair the rate of electron transport (Pammenter et al. 1993). Changes in photosynthetic capacity, not just assimilation rates, are more likely to be observed in association with lasting source–sink imbalances. One hypothetical mechanism is that high concentrations of carbohydrates repress the expression of genes coding for several photosynthetic enzymes (Krapp and Stitt 1995, Koch 1996, Drake et al. 1997). Alternatively, carbohydrates may interact with hormonal signals to control gene expression (Thomas and Rodriguez 1994). There is also some evidence that photosynthetic capacity is related to leaf carbohydrate status through the effect of the latter on phosphate availability (Riesmeier et al. 1993, Sun et al. 1999). In the long term, carbohydrate accumulation may eventually lead to cell death. High sugar concentration has been associated with leaf senescence in several species (Noodén et al. 1997, Wingler et al. 1998, Quirino et al. 2001). Reduced energy utilization by $CO_2$ assimilation, like that resulting from carbohydrate accumulation, in combination with high energy capture is potentially dangerous and can result in over-reduction of the electron transport chain, photoinhibition and oxidative stress caused by photoreduction of oxygen to superoxide in the Mehler-ascorbate peroxidase reaction (Badger 1985). Moreover, reactive singlet oxygen can be formed through reaction of oxygen with triplet chlorophyll released by the breakdown of the chlorophyll–protein complexes in thylakoids (Merzlyak and Hendry 1994).

Formation of reactive oxygen species can lead to membrane damage and eventually cell death.

Although the effect of girdling on photosynthesis in the presence of sink activity has been documented extensively, little is known about the long-term effect of carbohydrate accumulation on photosynthesis in the absence of any sink, as in mango branches girdled with the objective of promoting floral induction. This lack of information may impair our ability to evaluate this technique. It is especially important to establish whether girdling and carbohydrate accumulation can lead to lasting decreases in photosynthetic capacity, or to senescence. With this aim, we tested the hypothesis that girdling in the absence of significant sinks results in long-term decreases in photosynthetic capacity. Specifically, we monitored the nitrogen and nonstructural carbohydrate concentrations of leaves from girdled and non-girdled branches, along with the key parameters of photosynthesis and chlorophyll fluorescence, until flowering. The collected data were used to design a model of the effect of nonstructural carbohydrate accumulation on photosynthesis.

## Materials and methods

### *Plant material and experimental design*

Measurements were performed on leaves from 12 three-year-old trees of *Mangifera indica* cv. Cogshall, grafted on 'Maison rouge', randomly selected within an experimental orchard near Saint-Pierre in La Réunion island (20°52′48″ S, 55°31′48″ E; 290 m a.s.l.). Trees were about 2.5 m high, and were spaced at 4 × 5 m. Trees were grown in 2 × 2 m bottomless "soil pits," 1.5 m deep, lined with plastic film. Water was supplied every day on the basis of 100% replacement of actual evapotranspiration estimated from the equation of Penman-Monteith (Monteith 1965). Fertilizers were supplied and insects and diseases controlled according to the recommendations of the local department of agriculture.

Eighteen branches comprising current-year and previous-year shoots were selected among the experimental trees (six trees with one branch only and six trees with two branches) for being similar in light exposure and initial stem diameter (about 2 cm). All branches had the same south–west to north–east orientation and a similar height above ground (about 1.5 m). Fish-eye pictures were taken and gap fractions calculated following the method of Baret et al. (1993) and Génard and Baret (1994) to ensure that light exposure did not differ among treatments (HemiView 3.1 SR1, Delta-T Devices, U.K.).

Seven branches were girdled (G) on April 1, 2004, and 11 branches were left untreated (NG). Girdling consisted in removing a 10–15 mm wide band of bark in the middle of the main stem of each selected branch. Treatments were randomly distributed among the 12 trees of the trial while avoiding the presence of two G branches on the same tree. The G and NG branches were simultaneously present in five trees and one tree had two NG branches. Leaves were all fully developed at the time of girdling. Vegetative flushing after girdling was exceptional and all new buds were removed. The onset of flowering was assessed by the presence of at least one open flower per panicle. Flowering occurred about 15 days earlier in the G treatment than in the NG treatment, between June 19 and 25, 2004.

One well-lit, mature leaf per branch was selected and tagged on March 29, April 20, May 13, June 9, July 6, July 27 and August 20. The tagged leaves were used for leaf gas exchange, leaf absorptance and chlorophyll fluorescence measurements before nitrogen and carbohydrate analyses.

Effects were evaluated by analysis of variance (ANOVA) followed by Multiple Comparison of Means (S-Plus 4, Mathsoft, Bagshot, U.K.). Results are expressed as means ± standard errors (SE). Differences were assessed as significant at $P < 0.05$.

### *Leaf gas exchange*

Net $CO_2$ assimilation rate ($A_n$) and leaf stomatal conductance to water vapor ($g_s$) were measured before noon on selected clear days to ensure that photosynthetic photon flux ($Q$) was above 1500 μmol $m^{-2}$ $s^{-1}$, i.e., saturating light availability. We used 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) in the tracking mode to minimize light fluctuations (target value coming from the external sensor, potentially changing every 3 s), and a partial pressure of ambient $CO_2$ ($C_a$) = 36 Pa. Leaf temperature ($T_l$) was uncontrolled and ranged from 30 to 34 °C. Water vapor saturation deficit at the leaf surface ($D$) did not exceed 3 kPa. We found that $g_s$ is poorly correlated with $D$ in 'Cogshall' in this range provided that water supply is non-limiting (Urban et al. 2004). Dark respiration ($R_d$) at 30 °C was estimated by measuring the $CO_2$ evolution rate after 5 min in the dark.

### *Rate of photosynthetic electron transport, initial quantum yield and leaf absorptance*

Quantum yield of photosystem II ($\Phi_{PSII}$) was measured on the leaves used for the gas exchange measurements with a Li-Cor infrared $CO_2/H_2O$ gas analyzer and LED-based leaf chamber fluorometer system (LI 6400 and LI 6400-40 LCF). We measured $\Phi_{PSII}$ at $Q$ = 2000, 1200, 400 and 10 μmol $m^{-2}$ $s^{-1}$. Measurements were all made at $T_l$ = 30 °C and $C_a$ = 36 Pa. At the end of measurements, leaf absorptance (θ) was measured with a SPAD-502 leaf chlorophyll meter (Soil Plant Analysis Development, Minolta, Osaka, Japan). The relationship between θ and SPAD readings was established with an integrating sphere (data not shown). Three to four readings were taken on each leaf and averaged. Assuming that photosystems I and II absorb equal amounts of light, the total light-driven electron flow ($J$) may be calculated as (Genty et al. 1989):

$$J = 0.5\Phi_{PSII}\theta Q \quad (1)$$

The effect of $Q$ on $J$ may also be described by Smith's equation (Smith 1937), which has often been employed to approximate light responses of photosynthetic electron transport (Tenhunen et al. 1976, Harley et al. 1992, Falge et al. 1996):

$$J = \alpha\theta Q(1 + (\alpha\theta Q/J_{max})^2)^{-0.5} \quad (2)$$

It is theoretically possible to derive $\alpha$ and $J_{max}$, the initial quantum yield and the light-saturated rate of photosynthetic electron transport, respectively, from $\Phi_{PSII}$–$Q$ curves, by combining Equation 1 and Equation 2, provided that $\theta$ is known (Urban et al. 2004). However a high $C_a$ is usually necessary to ensure that photosynthetic electron flux is not limited by utilization of the reducing power. The use of $C_a = 36$ Pa did not prevent us from calculating $\alpha$ but $J_{max}$ values must be considered rough estimates only and are not presented here.

Predawn maximal efficiency of photosystem II ($F_v/F_m$) was measured on tagged leaves to provide an indication of photoinhibition (Butler 1978, Krause 1988).

At the end of all measurements, leaves were harvested and leaf areas measured. Leaves were then frozen in liquid nitrogen for subsequent nitrogen and carbohydrate analyses.

### *Leaf nonstructural carbohydrates and nitrogen concentrations*

Nitrogen and carbohydrate concentrations were assessed on frozen leaf samples taken at the end of the gas exchange and chlorophyll fluorescence measurements. Total nitrogen concentration ($N_m$; g N $g^{-1}$) of each sample was measured on 5 mg of powdered plant material with an elemental analyzer (Carlo Erba Instruments, Milano, Italy), after 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 Co., OH). Starch was determined by enzymatic hydrolysis to glucose (Thievend et al. 1972). Dry mass was assessed after freeze-drying. The masses of starch and soluble sugars were subtracted from the dry mass to obtain the structural dry mass, which was used for calculation of $N_m$ and the leaf mass-to-area ratio ($M_a$; g $m^{-2}$). The amount of leaf nitrogen per unit leaf area ($N_a$; g N $m^{-2}$) was calculated as $N_a = N_m M_a$.

### *Modeling the effect of leaf starch on photosynthesis*

To avoid bias due to the presence of inflorescences, we considered only the data collected from Day 89 to Day 161 (before flowering). Data obtained on leaves from G and NG branches were used to study and model the effect of leaf starch concentration on $\alpha$ and $J$. Linear and nonlinear regressions were performed. For simplicity, we sought to integrate the effect of starch in the biochemical model of leaf photosynthesis of Urban et al. (2003) in the form of a global corrective factor $C_{starch}$ applied to $J$ (Equation 2). The problem with modeling $J$ using such a correction factor is that it does not allow a distinction to be made between the effect of starch accumulation on $\alpha$ on the one hand, and on $J$ independently from its effect on $\alpha$ on the other hand. The correction factor $C_{starch}$ that we derived from our data applies only to leaves in the absence of a sink. Considering that starch accumulation results in a reduction in $J$ independently of its effect on $\alpha$ and that $\alpha$ is negatively affected by starch accumulation only if the latter is associated with the absence of sink activity (see below), we decided to calculate an additional correction factor $C_{starch}'$ that would apply only to leaves affected by starch accumulation in the presence of sink activity, e.g., girdled branches with low fruit load. The procedure involved use of $C_{starch}$ to recalculate new $J_{max}$ values from $\Phi_{PSII}$–$Q$ curves. These new $J_{max}$ values are thus unaffected by starch accumulation. Then a nonlinear regression was performed with the new $J_{max}$ values, the original $J$ and $\alpha$ values, and corresponding $\theta$ and $Q$ data to calculate $C_{starch}'$ from Equation 3:

$$J = C_{starch}'\alpha\theta Q(1 + (\alpha\theta Q/J_{max})^2)^{-0.5} \quad (3)$$

The model of the effect of starch accumulation on $A_n$ in the presence of sink activity was tested on an independent set of data (November 20, 2002) obtained from gas exchange measurements made on leaves from girdled branches with 10 and 100 leaves per fruit. Leaf starch concentration on a leaf area basis ranged from 1.22 to 25.72 g $m^{-2}$, $N_a$ ranged from 1.46 to 2.68 g N $m^{-2}$, leaf temperature ranged from 26.7 to 35.7 °C and $Q$ ranged from 7 to 2091 μmol $m^{-2}$ $s^{-1}$.

## Results

### *Leaf gas exchanges and nonstructural carbohydrate content*

Girdling reduced $A_n$ and $g_s$ to a similar extent, by 77 and 71% respectively, within 20 days after girdling, and both remained below 2.1 μmol $CO_2$ $m^{-2}$ $s^{-1}$ and 0.06 mol $H_2O$ $m^{-2}$ $s^{-1}$ respectively, until the beginning of flowering (Figures 1A and 1B). The increases in $A_n$ and $g_s$ after the onset of flowering were such that both $A_n$ and $g_s$ had fully recovered at the end of August (Day 233). Girdling had no effect on the intercellular concentration of $CO_2$ in leaves (data not shown). There was no significant difference in $R_d$ between leaves from non-girdled and girdled branches at any time during the trial (data not shown).

Girdling resulted in significant increases in the concentrations of soluble sugars and starch within 20 days (Figures 1C and 1D). The increase was much more pronounced for starch (+174%) than for soluble sugars (+5%). Soluble sugars and starch reached maximum values of 19.2 and 19.5 g $m^{-2}$ respectively, on Day 134 and started to decrease about one month after the onset of flowering. Globally, $A_n$ and $g_s$ were negatively correlated with leaf starch concentrations; however, the increases in $A_n$ and $g_s$ observed immediately after the appearance of inflorescences were not associated with a decrease in leaf carbohydrate concentration during the first month following the onset of flowering.

### *Leaf nitrogen concentration*

Leaf $N_m$ became significantly lower in G leaves than in NG leaves on Day 134: 1.83 versus 1.96% (Figure 2A). Thereafter, the difference in $N_m$ increased and reached a maximum of 14% on Day 188. However, after the onset of flowering, $N_m$ in NG leaves decreased at a higher rate than in G leaves, so that both G and NG leaves had similar $N_m$ (about 1.40%) by the end of August (Day 233). Girdling had no effect on $M_a$ (data not shown), which explains why the differences in $N_a$ between treatments closely matched those in $N_m$ (Figures 2A and 2B).

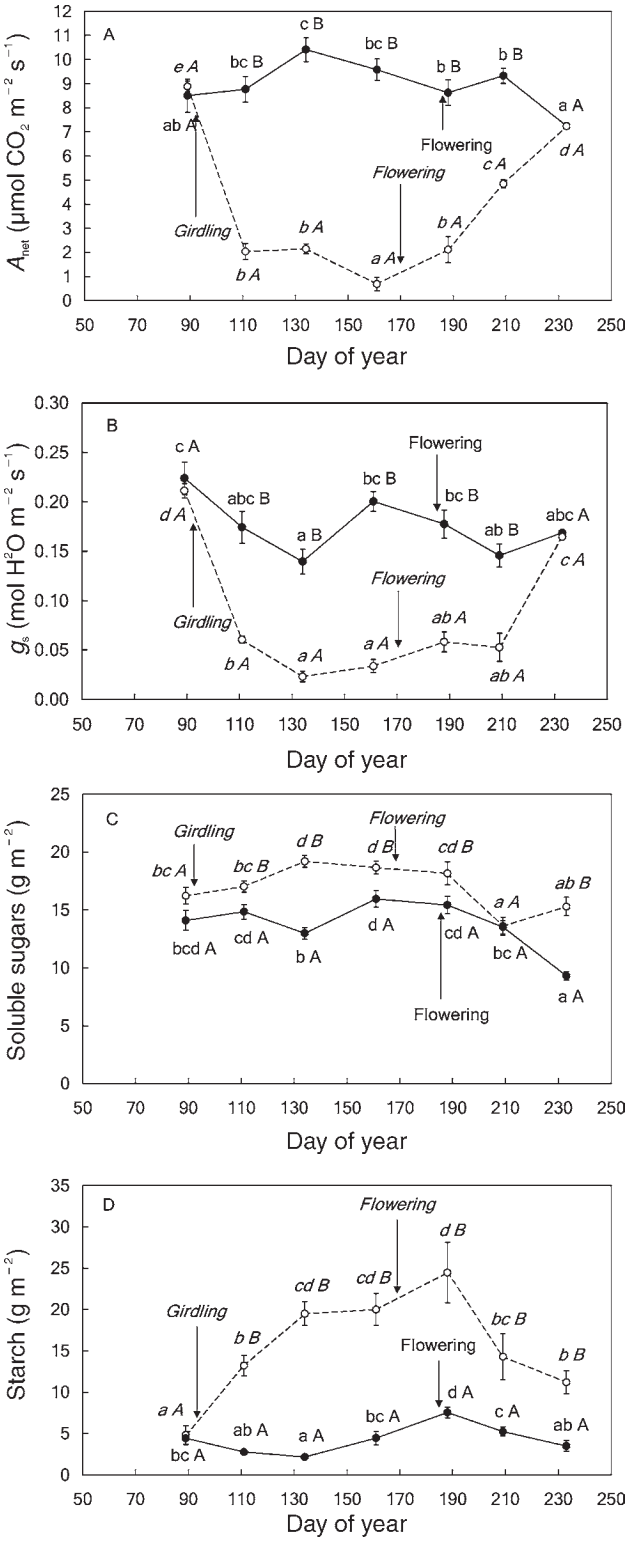


Figure 1. Effects of girdling and flowering on net photosynthetic assimilation rate, $A_n$ (A), leaf diffusive conductance, $g_s$ (B), and the concentrations of soluble sugars (C) and starch (D) expressed on a leaf area basis. Measurements were made on leaves from girdled branches (○) ($n = 11$) and non-girdled branches (●) ($n = 7$). Vertical bars represent SE. For each date, values with different uppercase letters differ significantly at $P < 0.05$. For each treatment, values with different lowercase letters differ significantly at $P < 0.05$.

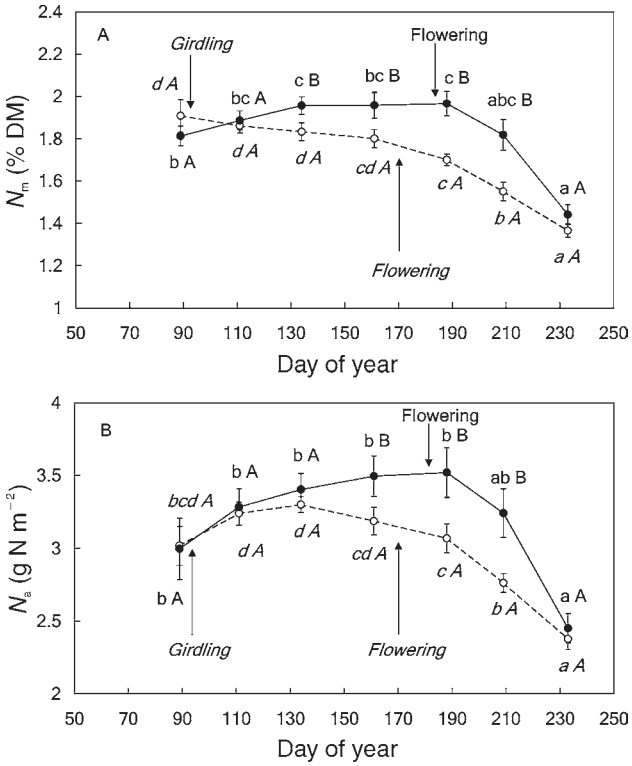


Figure 2. Effects of girdling and flowering on leaf nitrogen concentration expressed on a dry matter basis, $N_m$ (A), and the amount of nitrogen per unit leaf area, $N_a$ (B). Measurements were made on leaves from girdled branches (○) ($n = 11$) and non-girdled branches (●) ($n = 7$). Vertical bars represent SE. For each date, values with different uppercase letters differ significantly at $P < 0.05$. For each treatment, values with different lowercase letters differ significantly at $P < 0.05$.

However differences in $N_a$ between treatments were significant only between Days 161 and 209. Differences were about 13% on Day 161 and 15% on Day 209.

### *Correction of rate of photosynthetic electron flow in the model of leaf photosynthesis*

Girdling had no significant effect on θ (data not shown). Photosynthetic electron transport rate measured at either $Q = 400$ or 2000 μmol $m^{-2}$ $s^{-1}$ followed a similar pattern to $A_n$ (Figures 3A and 3B). Because $J$ appeared to be negatively correlated with starch, we tried to express $J$ as a function of area-based leaf starch concentration and $Q$. The best fit was provided by the relationship (Figures 4A an 4B):

$$J = (a(Q + b))e^{-c[\text{starch}]a} \quad (4)$$

where $a$, $b$ and $c$ represent coefficients, and were evaluated at 0.0434, 72.8 and 0.0412, respectively. The correction factor $C_{starch}'$ for leaves accumulating carbohydrates in the presence of sink activity was equal to $e^{-0.0398*[starch]a}$.

The modified model of leaf photosynthesis of Urban et al. (2003) that incorporated the correction factor for $J$ (Equation 2) performed better than the uncorrected model. The slope of the relationship between simulated and measured values of

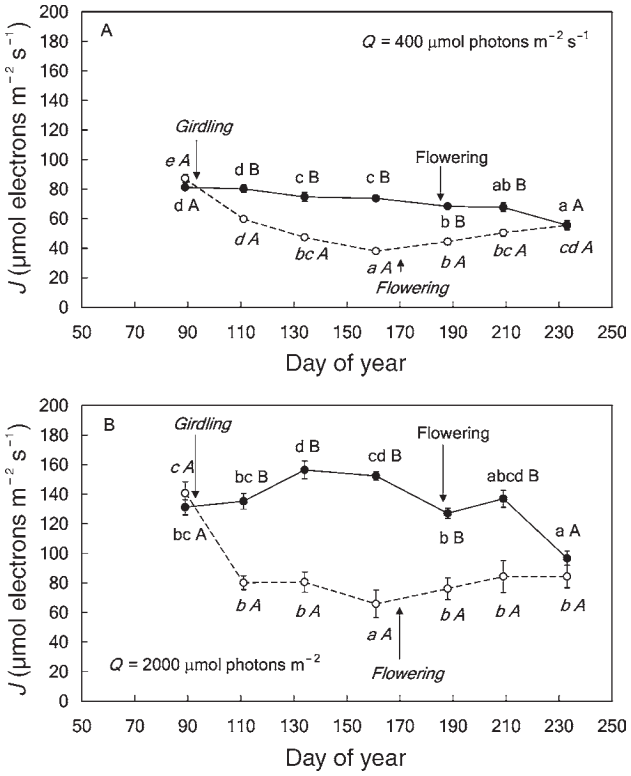


Figure 3. Effects of girdling and flowering on total photosynthetic electron flux, $J$, measured at $Q = 400$ (A) and 2000 (B) μmol photons $m^{-2}$ $s^{-1}$. Measurements were made on leaves from girdled branches (○) ($n = 11$) and non-girdled branches (●) ($n = 7$). Vertical bars represent SE. For each date, values with different uppercase letters differ significantly at $P < 0.05$. For each treatment, values with different lowercase letters differ significantly at $P < 0.05$.

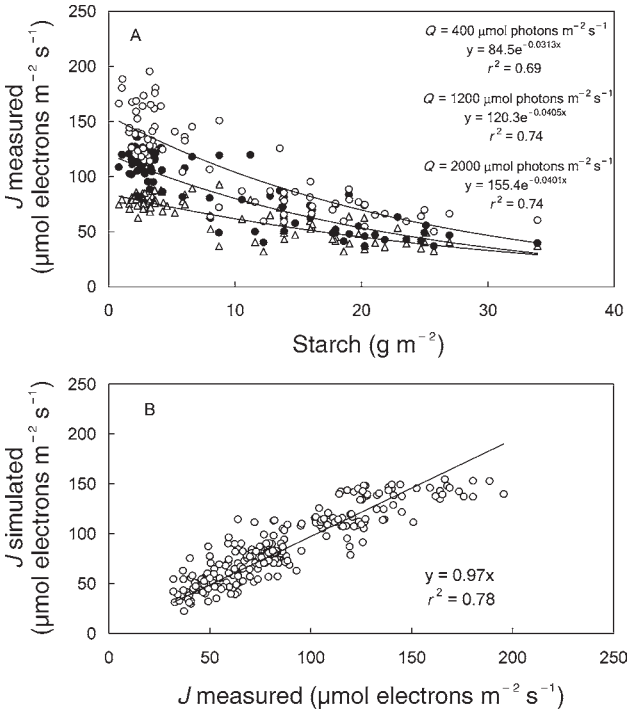


Figure 4. Relationship between total photosynthetic electron flux, $J$, measured at $Q = 400$ (△), 1200 (●), and 2000 (○) μmol photons $m^{-2}$ $s^{-1}$, and the amount of starch per unit leaf area (A). Best fit lines at each $Q$ value were assessed from all measurements performed on both girdled and non-girdled leaves from Day 89 until Day 161 (before flowering). Comparison between measured $J$ and $J$ simulated with Equation 4 (B). Data were obtained from measurements made on leaves from both girdled and non-girdled branches from Day 89 until Day 161 (before flowering).

$A_n$ was 1.03 for the modified model and 1.27 for the uncorrected model, resulting in an increase in $r^2$ from 0.32 to 0.76 (Figure 5).

### *Quantum efficiency of photosystem II*

Girdling had no significant effect on $F_0$ (data not shown). By contrast, the negative effects of girdling on $F_m$, $F_v/F_m$ and α were apparent within 20 days (Figures 6A, 6B and 6C). On Day 119, $F_m$, $F_v/F_m$ and α were 21, 9 and 5% lower, respectively, in G leaves than in NG leaves. Globally, $F_m$, $F_v/F_m$ and α in G leaves followed the same temporal pattern as $A_n$, $g_s$ and $J$ (Figures 1A, 1B, 3A and 3B). Both $F_v/F_m$ and α were negatively correlated with leaf starch concentration (Figures 7A and 7B).

## Discussion

### *Effects of girdling on photosynthesis and leaf nitrogen concentration*

Lower $g_s$ in G leaves was not associated with lower $C_i$, demonstrating that the depressing effect of girdling on $A_n$ is not attrib-

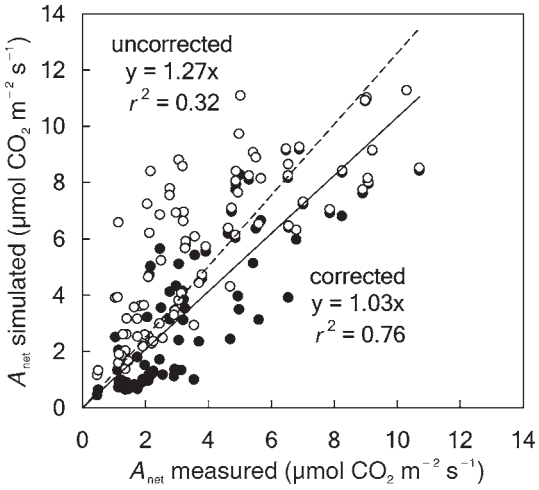


Figure 5. Comparison between measured $A_n$ and $A_n$ simulated with the original biochemical model of Urban et al. (2003) (○), and $A_n$ simulated with the same model corrected for starch accumulation (●). Data were obtained from measurements made on leaves from non-girdled and girdled branches with 10 and 100 leaves per fruit on November 20, 2002.

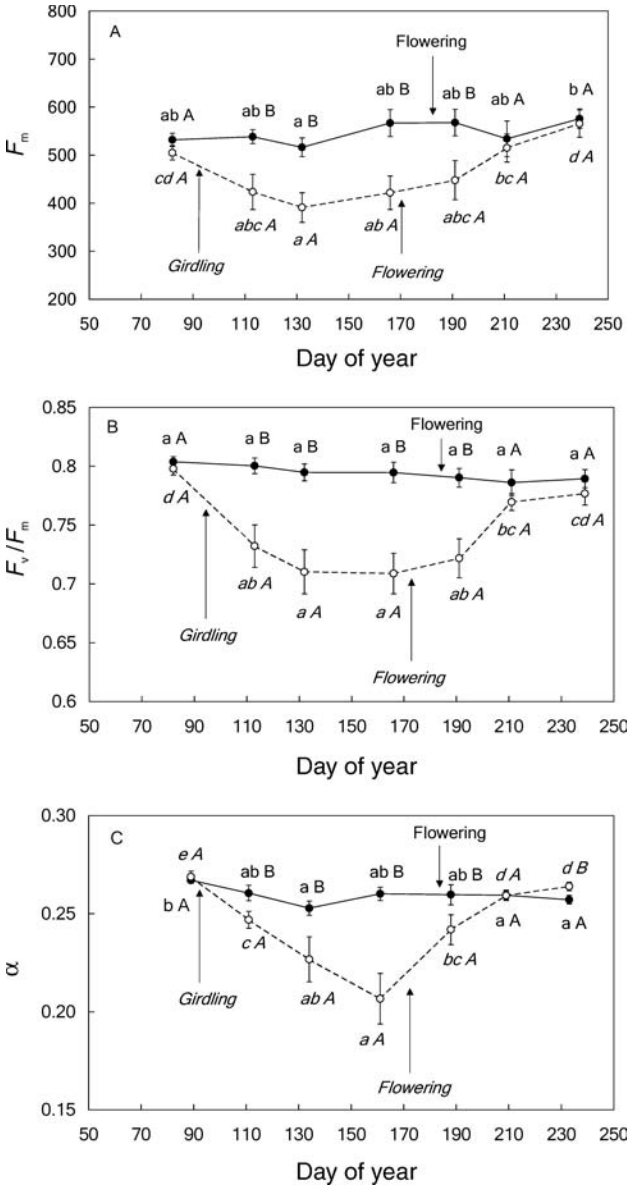


Figure 6. Effects of girdling and flowering on maximum fluorescence, $F_m$ (A), maximum quantum efficiency of photosystem II, $F_v/F_m$ (B), and initial quantum efficiency of photosystem II, α (C). Measurements were made on leaves from girdled branches (○) ($n = 11$) and non-girdled branches (●) ($n = 7$). Vertical bars represent SE. For each date, values with different uppercase letters differ significantly at $P < 0.05$. For each treatment, values with different lowercase letters differ significantly at $P < 0.05$.

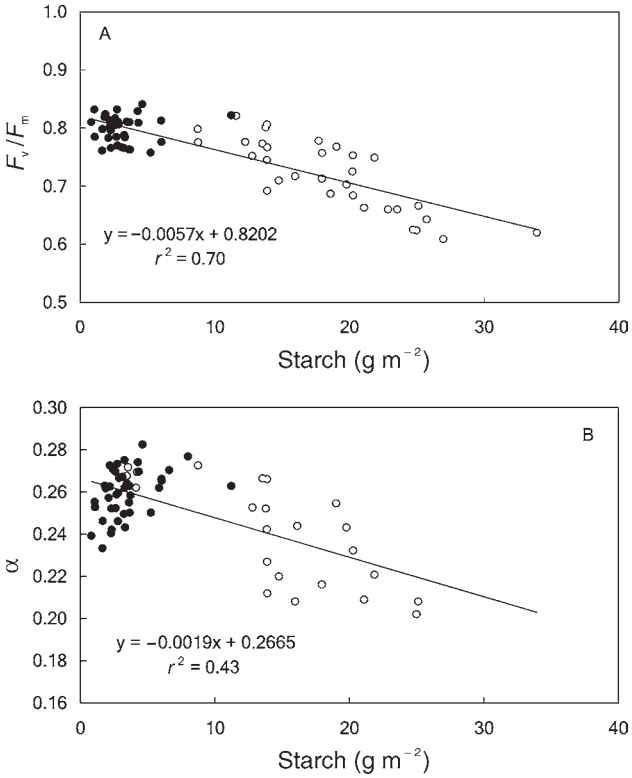


Figure 7. Relationship between the maximum quantum efficiency of photosystem II photochemistry, $F_v/F_m$, (A) and the initial quantum efficiency of photosystem II photochemistry, α (B), and the amount of starch per unit leaf area. Best fit lines were assessed from all measurements made on both girdled and non-girdled leaves from Day 89 until Day 161 (before flowering). Symbols: ● = non-girdled leaves and ○ = girdled leaves.

utable to a $g_s$-associated decrease in $C_i$. As observed previously on girdled mango branches carrying different fruit loads (Urban et al. 2004), girdling did not result in an increase in $R_d$. By contrast, $J$ was greatly decreased by girdling. The inhibiting effects of girdling on $J$ and $A_n$ are consistent with numerous studies showing a negative feedback effect of carbohydrate accumulation on leaf photosynthesis (Azcon-Bieto 1983, Foyer 1988, Koch 1996, Paul and Foyer 2001, Paul and Pellny 2003). Notably, the increases in $A_n$ and $J$ observed immediately after the appearance of inflorescences were not associated with decreases in leaf carbohydrate concentration during the first month following the onset of flowering, suggesting that there are carbohydrate-dependent and carbohydrate-independent mechanisms of sink regulation of photosynthesis. In response to girdling, leaf nitrogen concentration decreased progressively over a period of about 40 days. The decrease in leaf nitrogen concentration indicates that, in addition to the negative effects of girdling on $J$ and $A_n$ mediated by carbohydrate accumulation, girdling may have negative long-term effects on photosynthetic capacity.

### *Effect of girdling on photoinhibition*

Increased photoinhibition has been found in association with low sink demand (Buwalda and Noga 1994, Myers et al. 1999) and in the presence of carbohydrate accumulation (Roden and Ball 1996). Wingler et al. (2004) observed that, on parts of senescent *Arabidopsis* rosette leaves that had not yet lost their chlorophyll, decreases in $F_v/F_m$ were caused by greatly increased $F_0$ in combination with reduced $F_m$. Increased $F_0$ may be caused by the release of free chlorophyll from protein–pigment complexes, whereas decreased $F_m$ reflects sustained engagement of zeaxanthin in a state primed for energy dissipa-

tion. By contrast with the observations of Wingler et al. (2004), the decrease in $F_v/F_m$ in G leaves was caused by decreased $F_m$ only, indicating that that girdling did not trigger the same responses as senescence. The observed decreases in $A_n$ and $J$, and the moderate decreases in $F_v/F_m$ and $\alpha$ are characteristic features of moderate photoinhibition (Adams et al. 2005). The decrease in predawn $F_v/F_m$ in G leaves may be interpreted to reflect sustained engagement of zeaxanthin in photoprotective energy dissipation. It may be argued that decreases in $J$ lower the risk of electrons reducing $O_2$ to anion superoxide $O_2^-$, whereas sustained zeaxanthin-dependent energy dissipation reduces the risk of formation of singlet oxygen $^1O_2$ (Adams et al. 2005). Based on our results and previous studies, we conclude that the photosynthetic system was maintained in a highly photoprotected state in G leaves, which explains the vigorous recovery observed immediately after the appearance of inflorescences.

### *Modeling the effect of girdling and leaf starch concentration on net photosynthesis*

Net photosynthetic rate decreased in G leaves as a consequence of the negative effect of girdling on $J$. The decrease in $J$ is partially attributable to lower $N_a$ and $\alpha$ values. For simplicity, we decided to focus on the effect of girdling on $J$ independently from its effect on leaf nitrogen concentration. Introduction of a global correction factor for $J$ in the biochemical model of leaf net photosynthesis has the merit of simplicity because it takes into account in a single formula all of the negative effects of girdling on $J$ and thus $A_n$. However, this correction factor does not apply in the presence of sink activity because then $\alpha$ is unaffected. A new correction factor was therefore calculated to deal with the case of starch accumulation in the presence of sink activity. The principle of integrating the effect of starch accumulation in the model of leaf photosynthesis of Farquhar et al. (1980) proved effective. A further step in modeling would consist in representing the decrease in $N_a$ triggered by girdling.

In conclusion, the major effect of girdling is a dramatic increase in leaf carbohydrate concentration and concomitant decreases in photosynthetic electron transport and net photosynthesis. The decrease in photosynthetic electron transport and the sustained engagement of zeaxanthin in photoprotective energy dissipation (reflected by the decrease in predawn $F_v/F_m$) provided the photosynthetic system of G leaves with effective protection from photodamage. Apart from the negative effect of girdling on the carbon budget of mango trees, girdling appears harmless in the short term; however, the decrease in leaf nitrogen concentration indicates that there may be long-term negative effects of girdling on photosynthetic capacity. We demonstrated that the effect of carbohydrate accumulation on photosynthesis is mediated by sink activity. This observation has immediate applications in modeling studies, making it necessary to differentiate between sink activity and carbohydrate accumulation. Further studies are needed to determine the roles played by sink activity and carbohydrate accumulation in sink regulation of photosynthesis.

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