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Partial compensation in *Psychotria marginata* (Rubiaceae) after simulated defoliation increases photon capture and photosynthesis

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Abstract

We used Y-plant, a computer-based model of plant crown architecture analysis, to simulate effects of defoliation on daily canopy carbon gain in *Psychotria marginata* (Rubiaceae) plants under two contrasting irradiances. Five levels of defoliation were simulated using two different types of leaf blade damage. Compensatory increases in photon-saturated photosynthetic capacity ($P_{\max}$) of 25, 50, and 100 % defoliation were also simulated. In all simulations daily photon capture and CO_2 assimilation increased with defoliation. However, without a compensatory response, daily canopy carbon gain also decreased with defoliation. Under high irradiance, reduction in daily canopy carbon gain was less than what would be expected if the response was proportional to leaf area reduction. Thus, 25 and 50 % defoliation resulted in only 20 and 41 % of daily canopy carbon gain reduction, respectively. In the scenario where 25 % of the leaf area was removed, if the $P_{\max}$ value was increased by 25 %, the remaining leaves compensated for 94 % of the daily canopy carbon relative to an undamaged non-compensated plant. At the same defoliation level, incrementing $P_{\max}$ values by 50 and 100 % resulted in overcompensation. Hence, because the increment of daily photon capture and CO_2 assimilation after defoliation was more a passive consequence of the reduction in leaf area than an active response, under the conditions tested photosynthetic compensation could be only possible through an active mechanism such as the increment of $P_{\max}$ values.

Additional key words: computer modelling; daily carbon gain; photon capture.

Introduction

Compensatory photosynthesis and the resulting compensatory growth after defoliation have been broadly reported for more than three decades (Gifford and Marshall 1973, Belsky 1986, Wallace 1990, Senock *et al.* 1991, Morrison and Reekie 1995, Thomson *et al.* 2002). Both are proposed, among many other responses, as explanations for increases in plant fitness after defoliation events (Mabry and Wayne 1997, Paige 1999, Agrawal 2000, Parmesan 2000). These reports have fuelled a debate on the more complex question of whether herbivory can be benefical (Dyer 1975, Paige and Whitham 1987, Vail 1992, Bonser and Reader 1995, Lennartsoon *et al.* 1997, Paige 1999, Agrawal 2000) or is simple detrimental (Levin 1976, Prins *et al.* 1989, Bergelson and Crawley 1992, Painter and Belsky 1993, Aarssen 1995, Larson 1998).

Many responses and relationships have been proposed as an explanation for changes in plant fitness or growth rate after a defoliation event. These responses modify survivorship and reproduction (Paige and Whitham 1987, Mabry and Wayne 1997, McIntire and Hik 2002, Anten *et al.* 2003), evolutionary mechanisms (Vail 1992), plant physiology (Gifford and Marshall 1973, McNaughton and Chapin 1985, Prins *et al.* 1989, Anten and Ackerly 2001), and plant morphology (Bonser and Reader 1995, Meyer 1998, Chen *et al.* 2002). However, measurements of the changes in the internal irradiance of plant crown have received much less attention (Lee and Bazzaz 1980,

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Abbreviations: BCI: Barro Colorado Island; $P_{\max}$: photon-saturated photosynthetic capacity; PAR: photosynthetically active radiation; PFD: photon flux density; R_D: dark respiration rate.

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Nowak and Caldwell 1984, Gold and Caldwell 1990).

Much of our knowledge of plant responses to herbivory is based on grasses growing in high irradiances where photon availability was not a limiting resource that could compromise the production of new tissue after defoliation. However, for plants growing in dark tropical forest understory, photon capture becomes the most important factor for plant survival, photosynthesis, growth, and reproduction (Caldwell and Pearcy 1994, Montgomery and Chazdon 2002). Photon capture in any given micro-site is regulated by the spatial position of leaf blades (Chazdon 1985, Ackerly and Bazzaz 1995, Pearcy and Yang 1998, Valladares and Pearcy 1999, Muraoka *et al.* 2003). Changes in whole plant canopy architecture and its role in photon capture and total carbon (C) gain has been examined in few studies (Valladares and Pearcy 1998, Gálvez and Pearcy 2003) and the implication of defoliation on these factors has received even less attention (Anten and Ackerly 2001, Anten *et al.* 2003).

In this study, we used Y-plant, a three-dimensional computer based model that reconstructs whole plant canopy geometry and simulates photon capture, CO_2 assimilation, and C gain (Pearcy and Yang 1996). To our knowledge, this is the first study to examine the effects of multiple levels of simulated defoliation, two types of herbivore patterns, changes in photon-saturated photosynthetic capacity (P_{max}), and increasing self-shading on a tropical understory woody species under two contrasting irradiances, made on the basis of daily whole-canopy carbon gain consequences rather than only in the photon interception consequences resulting from the physical removal of leaf tissue.

Materials and methods

Field site and plants: Plant architectural data was based on *Psychotria marginata* plants growing in a forest understory that has been largely undisturbed for at least 50 years in the Smithsonian Tropical Research Institute field station, Barro Colorado Island (BCI). The island is part of the Barro Colorado Natural Monument (BCNM), Panama (9º10´N, 79º51´W). BCI receives 2 650 mm of precipitation per year and has a strong, well-defined dry season typically lasting from December to April.

P. marginata Sw. (Rubiaceae) is an evergreen shrub species with opposite-oblanceolate leaves commonly found in the BCNM area. *P. marginata* plants have a moderate branching frequency with asymmetric vertical and lateral axes (Pearcy *et al.* 2004). It is locally abundant in deeply shaded understories but is also found in small tree-fall gaps to dry forest.

Plant 3-dimensional reconstruction: In order to reconstruct the *P. marginata* plants used in the simulations, the leaf lengths, azimuth, and angle of the normal to the surface, the azimuth of the midrib axis and the azimuth, and angle of the petioles and internodes of five wild plants growing in understory and gap photon environments on Buena Vista Peninsula were recorded to specify their positions in space. Diameters of the stem, branch segments, and petioles were also recorded (see Pearcy and Yang 1996 and Pearcy *et al.* 2004 for complete procedure). Hemispherical photography (Pearcy 1989, Rich 1990) was used to characterize the irradiance environment of each wild plant used to generate the 3-D reconstructions. This technique is well suited for comparisons among a relatively large number of sites and is especially well suited for the understory of BCI (Engelbrecht and Herz 2001). According to the standard protocol of this technique (Pearcy *et al.* 2004) photos were taken over each plant with a *Nikon* model *FM* 35 mm single lens reflex camera and *Nikkor* 8 mm fisheye lens. The photos were analyzed with the program *HemiView* (version *2.1*, *Delta-T Instruments*, Cambridge, UK) to determine the angular and azimuthal distribution of gap fraction in the overstory canopy above each plant, and the gap distribution along solar tracks for specific data as required for Y-plant. Leaf physiological parameters that are also required to parameterize Y-plant were determined from irradiance response curves measured on other *P. marginata* plants growing nearby in understory and gap environments on Buena Vista Peninsula. The irradiance response curves were constructed with a *Li-Cor 6400* (*Li-Cor*, Lincoln, NE, USA) photosynthesis system. PFD values inside the leaf cuvette were increased to saturating ones and waiting for full induction before decreasing the PFD in steps to darkness. Measurements were made on the most recently fully expanded leaves of three plants and values of PFD-saturated CO_2 assimilation rates (P_{max}), the apparent quantum yield, and the dark respiration rate (R_D) were determined by least squares curve fitting to a non-rectangular hyperbola irradiance-response model (Pearcy and Yang 1996). The mean values of P_{max}, R_D, quantum yield for CO_2 assimilation, and the curvature factor for the transition from PAR limitation to saturation from the three curve fits were then used as inputs into Y-plant (Table 1).

Types and levels of simulated defoliation: Two different types of herbivory damage were simulated using Y-plant (Pearcy and Yang 1996): The first is *bite* type damage (BD) where the leaf tissue was removed from the tip to the leaf-blade base, and the second is *edge* type damage (ED) where leaf tissue was removed from both leaf-blade margins to the centre, parallel to the midrib (Fig. 1). In nature, BD is a common result of mammal foraging and ED is characteristic of some caterpillar attacks (Coley, personal communication). Five different levels (0, 10, 25, 50, and 75 % leaf area reduction) of each type damages were simulated by combining these leaves with shoot architecture of five reconstructed plants in Y-plant. These reconstructions were used to perform simulations under high-PFD and low-PFD in order to estimate the effect of different types of defoliation on photon capture, CO_2 assimilation, and daily canopy carbon gain.

Testing the consequences of compensatory photosynthesis: After parameterization, Y-plant was used to reconstruct the 3-dimensional architecture of plants with different types and levels of herbivory damage. These were used to calculate the absorbed PFD, photosynthetic rate of each leaf, and by summation over all leaves, the whole plant photon absorption and photosynthetic rate. Regardless of the level of herbivory simulated, Y-plant simulation of each plant in the understory was run using the hemispherical photographs taken over the natural plant and used to generate the reconstructed versions. For simulations under high PFD, we used hemispherical photographs taken in a range of medium-size gaps located nearby at Buena Vista Peninsula. The average daily integrated PFD in the understory was 1.2 mol m^{-2} d^{-1} and in gaps 7.30 mol m^{-2} d^{-1}. Because no significant differences among the herbivory types BD and ED were observed, all subsequent simulations were done using only plants with BD. Photon capture, CO_2 assimilation, and daily canopy carbon gain simulations were run under gap and understory environments for all herbivory levels.

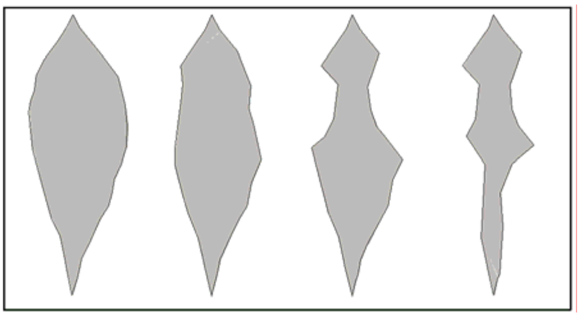

Fig. 1. Simulated leaf damage reconstruction by Y-plant. The series shows *Psychotia marginata* leaves with 0, 10, 25, and 50 % of leaf area reduction by edge type damage.

Table 1. Photosynthetic characteristics of *Psychotria marginata* wild leaves from understory and gap irradiance environments on Buena Vista Peninsula. The values are from a least squares fitting of the rectangular hyperbolic model (see Pearcy and Yang 1996).

	P_{max} [μmol m^{-2} s^{-1}]	Quantum yield [mol(CO_2) mol^{-1}(photon)]	Curvature [relative]	Dark respiration [μmol m^{-2} s^{-1}]
Gap	8.410 ± 0.92	0.060 ± 0.007	0.540 ± 0.230	-0.320
Understory	3.820 ± 0.45	0.026 ± 0.005	0.920 ± 0.051	-0.170

Increases in P_{max} after defoliation: After defoliation, the plant may respond through compensatory increases in photosynthetic capacity of the remaining leaves (Anten *et al.* 2003). To examine this scenario, we simulated 0, 25, 50, and 75 % leaf area defoliation combined with increases in P_{max} by 25, 50, and 100 %. Different post-defoliation increases in P_{max} have been reported in nature, ranging from 12 % (Doescher *et al.* 1997) to 62 % (Larson 1998). All combinations of defoliation and compensatory photosynthesis were simulated under the low and high PFD already described. We compared the CO_2 assimilation and daily canopy carbon gain obtained from these simulations with the values of the same plants with no defoliation and no increase in P_{max} (control plants). Daily canopy carbon gain expressed relative to the control values was used as a measure of compensation. Relative values <1 were interpreted as below full compensation, whereas values >1 indicated that full compensation for herbivory had occurred.

Results

Types and levels of simulated defoliation: After all Y-plant simulations were run, defoliated plants, regardless of herbivory type or level simulated, showed an increase in photon capture and net photosynthesis per unit area (hereafter CO_2 assimilation) relative to undamaged plants (Fig. 2). This increase was positively correlated (Pearson $r^2 = 0.762$) but not proportional to the percent of leaf area reduction. Daily canopy carbon gain values, however, showed a decrease relative to undamaged plants. This decrease was also positively correlated (Pearson $r^2 = 0.74$) with the percentage of leaf area reduction. Thus while defoliation caused an increase in photon capture and hence CO_2 assimilation of the remaining leaf area, at the whole crown level it did not compensate for the lost leaf area. No significant differences associated with the defoliation type were obtained in either gap or understory conditions (ANOVA $p>0.05$) (Fig. 2).

Testing the consequences of compensatory photosynthesis: Using simulations under high-PFD, the percent increase in photon capture resulted in an almost identical increase in CO_2 assimilation. Nevertheless, these increases were not proportional to the decrease in leaf area, thus while a 10 % leaf area reduction resulted in

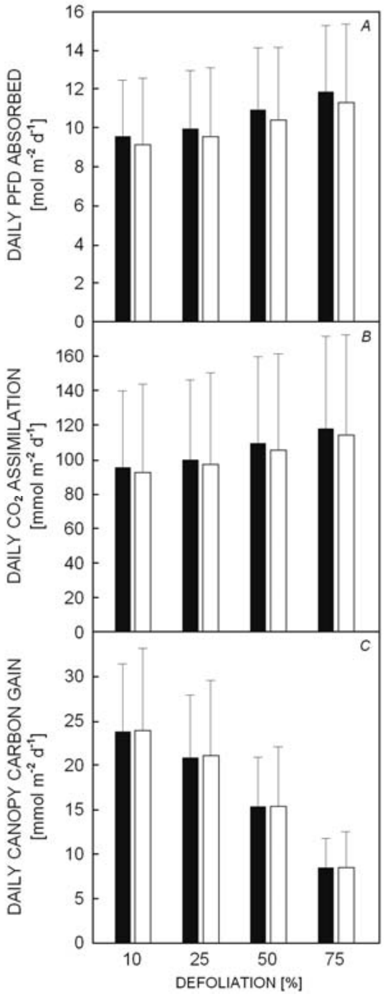

Fig. 2. Modelled daily PFD (*A*), CO$_2$ assimilation (*B*), and daily canopy carbon gain (*C*) of simulated *Psychotria marginata* plants growing under gap irradiance environment after bite defoliation type (*black bars*) and edge defoliation type (*white bars*). *Each bar* gives the mean and SD of five model runs.

only a 3 % increase in photon capture and CO$_2$ assimilation, a 75 % leaf area reduction increased photon capture by 28 % and CO$_2$ assimilation by 27 % above that of undamaged plants (Fig. 3*A*). Understory simulations showed that after defoliation, as a result of the increased PAR penetration across the canopy, the percent of increase in CO$_2$ assimilation could be two to three times greater than the percentage of increase in photon capture (Fig. 3*B*). In spite of increases in CO$_2$ assimilation, daily whole canopy carbon gain decreased as direct response to leaf area reduction. This was true for both gap and understory irradiance.

Increases in P_{max} after defoliation: Simulation under high-PFD showed a complex trade-off between reduction of leaf area and daily canopy carbon gain of the remaining leaves when P_{max} values were increased by 25, 50, and 100 %. Plants with 25 % leaf area reduction were able to compensate for 94 % of the leaf area lost if the P_{max} value of remaining leaves increased by 25 %. With a P_{max} increase of 50 and 100 %, the simulations showed that the plants were able to fully compensate and overcompensate the leaf area lost. Plants with 50 % leaf area reduction were able to compensate for 80 and 98 % of leaf area lost if the P_{max} value of remaining leaves increased by 50 and 100 %, respectively (Fig. 4*A*). None of the simulations made under low PAR showed full compensation (Fig. 4*B*).

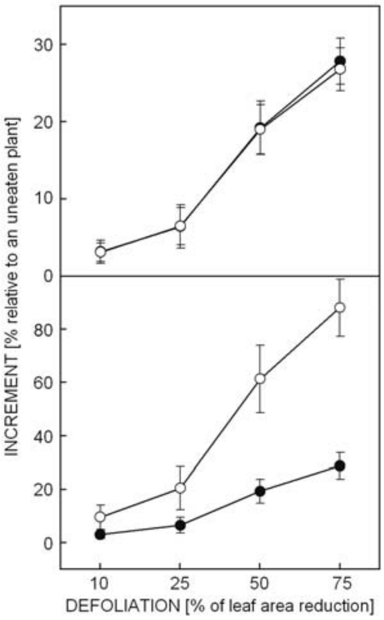

Fig. 3. Percentage of daily photon capture (●) and CO$_2$ assimilation (○) increases of modelled *P. marginata* plants growing in gaps (*A*) and understory (*B*) under different levels of defoliation. Herbivory type in all the plants shown is bite type. *Each bar* gives the mean and SD of five model runs.

Discussion

During recent years, new tools for compensatory photosynthesis analysis after defoliation have been developed adding an important theoretical framework (Anten and Ackerly 2001, Anten *et al.* 2003). A critical element introduced to this kind of analysis is a reframing of the traditional null model. In almost every experiment on compensatory photosynthesis, defoliated plants have been compared to undamaged plants: this evaluates the net impact of defoliation but does not directly assess the functional role of compensatory photosynthesis. To solve this problem, Anten and Ackerly (2001) and Anten *et al.* (2003) proposed the use of a hypothetical plant that is defoliated but does not posses any mechanisms for compensation. As none of the plant physiological parameters (*i.e.*

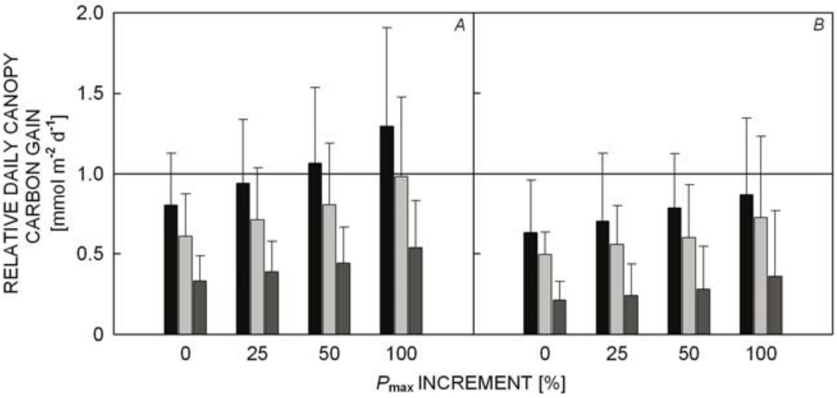

Fig. 4. Daily canopy carbon gain of modelled *P. marginata* plants in gap (*A*) and understory (*B*) irradiance with different levels of defoliation and increases in P_{max} values relative to undamaged plants with no increase in P_{max}. *Black bars* denote 25 % defoliation, *light gray* 50 %, and *dark gray* 75 %. *Each bar* gives the mean and SD of five model runs.

P_{max} or R_D) used by Y-plant simulations change after defoliation, our plant-sets fulfil this requirement.

Types and levels of simulated defoliation: The importance of herbivore damage type or pattern has been analyzed using many different elements including degrees of herbivory, defined as the amount of leaf tissue removed by an herbivore (Prins *et al.* 1989), spatial pattern of defoliation where the uppermost or the lowest leaf blades were removed (Gold and Caldwell 1990), natural defoliation *versus* artificial clipping (Wallace 1990, Chen *et al.* 2002), concentrated *versus* disperse damage (Meyer 1998), and pattern of defoliation where different portions of leaf blades (the tip, one or two edges, and perforations) were removed (Morrison and Reekie 1995). Using this terminology, our study simulated five levels (0, 10, 25, 50, and 75 % of leaf area removed) and two patterns (bite and edge) of defoliation.

We found that for *P. marginata* plants, regardless the defoliation type (bite or edge), leaf area reduction had a consistent effect on photon capture and daily carbon gain, but we found no evidence of effects specifically associated with any of the two defoliation types.

Testing the consequences of compensatory photosynthesis: Most studies of plant crown architecture and leaf display have been focused on photon capture efficiency or capacity, but not on their implications for CO_2 assimilation. Nevertheless, the evaluation of herbivory could be expressed on the basis of photosynthetic consequences rather than PAR interception.

Due to its crown architecture, small *P. marginata* plants with mono-axial stems or just few branches and opposite-decussate leaves inevitably self-shade their older leaves during plant growth (Yamada *et al.* 2000). This is because the position of leaf lamina repeats with every other pair. This crown structure causes any reduction of leaf lamina on the distal and medium section of the plant, to increase PAR penetration across the plant crown. But due to non-linear responses to PAR, maximizing PAR interception and maximizing photosynthesis is not necessarily the same. Increasing photon capture represents a major advantage only for direct photon capture during the day when the solar disc is near the plant's top but not during morning and afternoon periods.

In general terms, all simulation outputs of this experiment reflect a cascade of responses occurring after a defoliation event: (*a*) defoliation decreases leaf area and increases photon penetration, (*b*) photon capture increases, but not proportionally to defoliation level, (*c*) since the PFD remains below saturation values, CO_2 assimilation also increases proportionally to photon capture, and (*d*) because the leaf area reduction is higher than CO_2 increment, daily canopy carbon gain decreases with defoliation (Fig. 2). After absolute values were transformed to percentage relative to undamaged plants, the relationship between irradiance and % defoliation becomes more evident. For gap plants, growing in an environment where photon availability is not a limiting factor, the increase in daily PFD after defoliation results in an almost identical increase in CO_2 assimilation (Fig. 3*A*). On the other hand, in understory environments, where natural selection pressure favours strategies that maximize photon use efficiency, 10 % of leaf area reduction results in a 3 % increase in daily photon uptake and a 9 % increase in CO_2 assimilation. Nevertheless, a 75 % leaf area reduction results in a 29 % increase in daily PFD and an 88 % increase in CO_2 assimilation. These outputs could be linked to more complex problems related with natural selection forces in environments with limiting resources as presented in the resource availability hypothesis (Coley *et al.* 1985). Following the predictions of this hypothesis, our results show that on a daily canopy carbon gain basis, defoliation has a much higher impact in understory plants than in gap plants. For gap plants, 25 and 50 % defoliation results in 20 and 41 % of daily canopy carbon gain reduction, respectively, but for understory plants the same defoliation level represents 42 and 84 % of daily carbon gain reduction. Our results show that the increases in photon capture due to leaf area reduction could not increase CO_2 assimilation of the remaining leaves to fully compensate for the leaf area lost.

Increase in P_{max} after defoliation has been reported as a common response (Prins *et al.* 1989, Larson 1998, Anten and Ackerly 2001) due to improved water relations (Fay *et al.* 1993), changes in the source-sink ratio after a defoliation event (McNaughton 1983), improved photon penetration in the canopy (Anten and Ackerly 2001), and hormone supply by roots (Trumble *et al.* 1993). Our results show that without a compensatory mechanism, the increase in daily PFD and CO_2 assimilation does not fully compensate for leaf area reduction. Nevertheless, simulations for gap plants predict that if a plant that has been 25 % defoliated, increases in P_{max} of the remaining leaves by 25 % could compensate for 94 % of the daily canopy carbon gain relative to undamaged non-compensating plant (Fig. 4*A*). The scenario simulated above is similar to natural defoliation of *P. marginata* (Coley, personal communication) and the increase in photosynthetic rate found in the remaining leaves of *Solidago altissima* after a 50 % leaf area reduction (Meyer 1998). In a scenario where the same plant increases the P_{max} value of the remaining leaves by 50 or 100 %, a full compensation and overcompensation is possible, however, an increase of this magnitude has not been reported under natural conditions.

In a scenario where the plant suffers by 50 % leaf area reduction, partial compensation would occur only if the P_{max} value of the remaining leaves was increased by 50 or 100 % (Fig. 4*A*). Simulations for understory plants showed that this compensation is not possible even in a scenario where post-defoliation increases in P_{max} are 100 % (Fig. 4*B*).

We conclude that the increase in photon capture and CO_2 assimilation resulting from herbivory could only partially contribute to post-defoliation compensation of daily canopy carbon gain. Because the increase of these two factors is a passive consequence of the reduction in leaf area instead of an active response, under the conditions presented here, photosynthetic compensation could be only possible through an active mechanism such as the increment of P_{max} values.

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