No time for candy: passionfruit (*Passiflora edulis)* plants down-regulate damage-induced extra floral nectar production in response to light signals of competition

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Abstract Plant fitness is often defined by the combined effects of herbivory and competition, and plants must strike a delicate balance between their ability to capture limiting resources and defend against herbivore attack. Many plants use indirect defenses, such as volatile compounds and extrafloral nectaries (EFN), to attract canopy arthropods that are natural enemies of herbivorous organisms. While recent evidence suggests that upon perception of low red to far-red (R:FR) ratios, which signal the proximity of competitors, plants down-regulate resource allocation to direct chemical defenses, it is unknown if a similar phytochrome-mediated response occurs for indirect defenses. We evaluated the interactive effects of R:FR ratio and simulated herbivory on nectar production by EFNs of passionfruit (*Passiflora edulis* f. *flavicarpa*). The activity of petiolar EFNs dramatically increased in response to simulated herbivory and hormonal treatment with methyl jasmonate (MeJA). Low R:FR ratios, which induced a classic "shade-avoidance" repertoire of increased stem elongation in *P. edulis*, strongly suppressed the EFN response triggered by simulated herbivory or MeJA application. Strikingly, the EFN response to wounding and light quality was localized to the branches that received the treatments. In vines like *P. edulis*, a local response would allow the plants to precisely adjust their light harvesting and defense phenotypes to the local conditions encountered by individual branches when foraging for resources in patchy canopies. Consistent with the emerging paradigm that phytochrome regulation of jasmonate signaling is a central modulator of adaptive phenotypic plasticity, our results demonstrate that light quality is a strong regulator of indirect defenses.

Keywords Indirect defenses · Herbivory · Extrafloral nectaries · Jasmonate · Phytochrome · *Passiflora*

Introduction

Plant defenses include a range of strategies to minimize the effects of herbivorous organisms, and these defenses can be direct and indirect. Direct defenses are those that act directly on the herbivore, such as feeding deterrents and toxins. Indirect defenses involve a third trophic level, and are based on the production by the plant of specific structures or chemical compounds that attract natural enemies of the herbivores, such as carnivorous organisms and parasitoids (Karban and Baldwin 1997; Schoonhoven et al. 2005). A well-known example of indirect defenses is the production of nectar by nectaries located outside the floral structures (extrafloral nectaries, EFNs). EFNs attract ants, parasitoids, and generalist predators, which provide indirect defense against herbivorous arthropods for over 100 plant families (Bentley 1977; Stephenson 1982; for recent reviews, see Schoonhoven et al. 2005; Heil 2008, 2011).

The role of EFNs as a factor that increases plant fitness by acting as an effective anti-herbivore defense mechanism

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is now well established (Chamberlain and Holland 2009). Surprisingly, however, very little is known about the factors that modulate nectar production and secretion. In fact, the demonstration that extrafloral nectar secretion can be regarded as an inducible response, connected with the mainstream signal-transduction cascades of defense activation, is a relatively recent advance. Heil et al. (2001) showed that extrafloral nectar secretion can be promoted by herbivory, mechanical damage, and treatment with methyl jasmonate (MeJA) in the myrmecophilic plant *Macaranga tanarius*. More recent work in other systems has demonstrated that different species within the same genus (*Populus*) can display contrasting patterns of EFN activity (e.g., constitutive or inducible) (Escalante-Pérez et al. 2012).

The expression of direct defenses is often regulated by environmental factors, including, for example, nutrient supply (Held and Baldwin 2005), light (Roberts and Paul 2006; Ballaré et al. 2012), and temperature (De Lucia et al. 2012). Regulation of the plant's immune system by environmental cues is thought to be important for optimizing the allocation of limited resources to different metabolic activities and is receiving considerable attention in ecological and physiological studies of plant defense (Ballaré 2009; Heil 2010). An important signal in the regulation of direct defenses is light quality (reviewed in Ballaré 2011). Low red:far-red (R:FR) ratios, perceived by the plant photoreceptor phytochrome B (phyB), indicate the proximity of potential competitors and trigger the expression of a suite of growth-related changes collectively known as the shade-avoidance syndrome (SAS) (Ballaré 1999; Casal 2012; Ruberti et al. 2012; Pierik et al. 2013). Recent work has shown that plants exposed to low R:FR ratios, mimicking a competition scenario, express a weak defense phenotype in insect growth bioassays (Izaguirre et al. 2006; Moreno et al. 2009). Increased insect growth in bioassays has been attributed to the effect of low R:FR reducing the expression of several direct defenses, including phenolic compounds (Izaguirre et al. 2006; Moreno et al. 2009) and latex (Agrawal et al. 2012). A similar effect (attenuation of plant defense as measured in insect growth bioassays) has been demonstrated in studies with various species in which the phyB photoreceptor was inactivated by mutation (McGuire and Agrawal 2005; Izaguirre et al. 2006). Work in the reference plant *Arabidopsis thaliana* revealed that the expression of large numbers of defense-related genes is down-regulated by low R:FR ratios (Moreno et al. 2009; Cerrudo et al. 2012; De Wit et al. 2013).

In contrast to the work on direct defenses, little is known about how indirect defenses are regulated by environmental cues. In some species, competition and resource availability have been reported to affect the emission of volatile compounds, some of which could be involved in indirect defense mechanisms (Kegge and Pierik 2010; Kigathi

et al. 2013). In the case of EFNs, information on regulation by competition signals is even more limited. Evidence from field studies indicates that nectar production can vary between the gaps and the understory. For example, studies in species of the genus *Inga* indicated greater nectar production in gaps (Bixenmann et al. 2011). However, in those field studies, the environmental variables controlling nectar production were not identified. On the other hand, laboratory studies with lima bean (*Phaseolus lunatus*) have shown that EFN activity is promoted by light (compared to darkness), with the light environment modulating the plant's response to jasmonates (JAs) as well as the biosynthesis of bioactive JA (Radhika et al. 2010). The light treatments used in those laboratory experiments were not specifically designed to mimic the canopy light environment, as plants were exposed to prolonged light treatments with combinations of nearly monochromatic light sources. Therefore, whether or not EFNs are regulated by informational light signals typical of plant canopies remains an open question.

In order to gain insight into the regulation of EFN activity, we used passionfruit (*Passiflora edulis* f. *flavicarpa*) as a model system. *Passiflora* is a pantropical genus, with c. 450 species of which approximately 120 are present in tropical and sub-tropical areas of the Americas (Deginani 2001). *P. edulis* produces abundant nectar in EFNs located in the petioles, leaf margins, and the outer side of the sepals (Fig. 1).

We first used a manipulative experiment to test the effectiveness of *P. edulis* EFNs in attracting predatory ants, because ants have been shown to provide protection against herbivorous insects in other species of the genus *Passiflora* (McLain 1983; Smiley 1986; Xu and Chen 2010). After testing for ant attraction, we studied the effects of simulated herbivory and JA on extrafloral nectar production. We were particularly interested in testing the influence of light signals of competition (low R:FR ratio) on EFN activity and EFN responses to herbivory cues. To this end, we exposed plants grown under full sunlight to lateral illumination with FR radiation, which reduced the R:FR mimicking the proximity of other plants (Izaguirre et al. 2006). Previous attempts to study the interplay between light quality and herbivory signals on defense induction have been carried out using the whole plant as the unit of response. However, plants have a modular structure (Harper 1977; De Kroon et al. 2009), and different parts (modules) of the plant can be exposed to very different environmental conditions and may present specific responses to their local environment. This is particularly true in vines like *Passiflora*, where a single genet can cover dozens of square meters of patchy canopy environments. Therefore, we also tested how EFN activity is regulated at the modular (branch) level when different parts of the same plant receive contrasting signals of herbivory and competition.
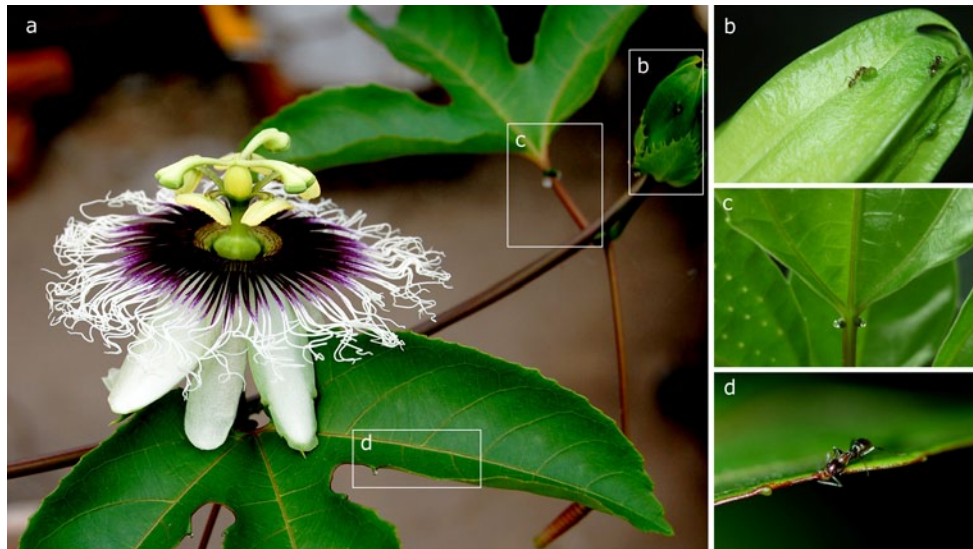
Fig. 1 EFNs in *Passiflora edulis* f. *flavicarpa*. *a* View of the *P. edulis* plant and flower, and close-ups of different types of EFNs. *b* EFNs in sepals in a closed flower (note the ants feeding on active EFNs). *c* Petiolar EFNs, showing nectar accumulation and the light damage inflicted to the leaf tissue using a fabric pattern wheel (simulated herbivory). *d* EFN located in the leaf margin with an ant feeding on nectar

Materials and methods

Plant material and study site

Mature fruits of *Passiflora edulis* f. *flavicarpa* were obtained in a local market in Buenos Aires, Argentina. Seeds were extracted and cleaned with tap water, dried, and stored at 4 ºC until use. Seeds were germinated in darkness, in plastic boxes containing wet filter paper at ambient temperature. When the radicle was visible, seedlings were transplanted to individual pots containing a 1:1:1 vermiculite:perlite:peat mixture and watered with Hakaphos Rojo 18-18-18 (Compo, Spain). For the physiological experiments, plants were cultivated in a greenhouse under ambient sunlight (peak photosynthetically active radiation, PAR, >1,400 μmol m^{-2} s^{-1}), and exposed in the same greenhouse to the various treatments, as described below. For the ant visitation studies, plants were initially cultivated in a greenhouse and then transferred to the field for evaluation of ant responses to EFN manipulations.

Ant visitation

The effectiveness of *P. edulis* EFNs in attracting predatory ants in our field site was tested using a manipulative experiment. Plants were grown in the greenhouse until they had eight leaves, when they were divided into three groups of 18 plants each, which received one of the following treatments: (1) no treatment (intact plants); (2) ablation of both petiolar EFNs of each leaf; or (3) wounding of the petiole but without affecting EFNs. Petiole ablation was performed with a scalpel; it caused a lignified scar and stopped nectar secretion. The third treatment (petiole wounding) was intended as a control for mechanical damage: the petiole was damaged with scalpel, simulating EFN ablation but without actually damaging the EFNs. After application of these treatments, plants were transferred to an old field in the experimental grounds of the School of Agronomy (University of Buenos Aires) (34°35′S, 58°29′W), Buenos Aires. The pots were sunk in the soil, leaving the base of the stem at the level of the ground surface. In the field, plants were exposed to diffuse summertime solar radiation, protected from direct sunlight by nearby trees. The experiment was carried out during the spring, when ant activity at the site is high. The number of ants that visited each plant was evaluated at noon for 10 days. In our experiment, the more frequent ant visitor of *P. edulis* EFNs was the aggressive Argentine ant (*Linepithema humile*, formerly *Iridomyrmex humilis*).

Light treatments

For the EFN activity experiments, plants with six leaves growing in a greenhouse under full sunlight were placed in front of banks of incandescent lamps that were either covered with opaque screens (Ambient treatment) or FR-transmitting filters (FR treatment). In both cases, water filters were interposed between the light sources and the plants to remove the heat produced by the incandescent lamps. The

experimental setup for light treatments was as described previously (Izaguirre et al. 2006). Individual plants were irradiated from 1000 to 1900 hours every day. The FR treatment simulated the effect of neighbor proximity in a canopy of leaf area index = 0.5 (R:FR of horizontally-propagated radiation = 0.55), where mutual shading among neighbors is negligible (Ballaré 1999). Neither air temperature nor the PAR received by the plants were affected by the FR treatment.

Morphology

Petiole and internode length, plant height, and lamina length and width were measured for each plant before placing them in front of the lamps. These measures were repeated periodically to evaluate SAS expression and growth.

Plant defense elicitation

EFN activity was measured in 5-week old plants with eight leaves and nectar production measurements correspond to petiolar EFNs (Fig. 1c). Before the elicitation treatment, petiolar EFNs were washed with distilled water to remove existing nectar. Herbivory was simulated by gently damaging the leaves using a fabric pattern wheel. This treatment causes small punctures in the lamina without affecting vascular connections (see detail in Fig. 1c). In plants assigned to this treatment (simulated herbivory), four rows of punctures were applied on each side of the mid-vein in three fully expanded leaves (as described in Izaguirre et al. 2003). Control plants received no treatment. For chemical elicitation, plants were sprayed with an aqueous solution of 0, 150, and 450 μM MeJA (Sigma) until runoff. Nectar production was measured 2 days after elicitation; during this period, plants remained under solar radiation in the greenhouse, in front of the light sources. In the experiments that tested the effects of FR supplementation on EFN activity, plants were exposed to the light treatments for 2 weeks before they were used in the defense elicitation experiments.

Nectar quantification

Due to its high viscosity, which does not allow collection with a pipette, nectar volume was calculated from photographs of the petioles taken 2 days after the elicitation treatments. The drop radius and the petiole width were measured on each photograph in pixel units using Adobe Photoshop. In addition, when the pictures were taken, the actual width of each petiole was measured with a digital caliper and used as a reference to convert pixels into millimeters when the photographs were analyzed. Drop

volume was estimated from the radius data using a spherical or hemi-spherical model for the drop shape. After taking the pictures, all the nectar from each EFN was collected using a small spatula. The nectar obtained from all the petiolar EFNs of each plant was pooled and diluted in 100 μL distilled water, in order to measure the concentration of soluble solids using a digital temperature-compensating refractometer Pal-1 ATAGO.

Modular assays

These experiments were designed to find out whether the control of EFN activity by light and simulated herbivory signals occurs locally at the level of individual branches. Passionfruit plants present a remarkable apical dominance and do not develop branches until the apical bud is removed. To obtain plants with two branches, plants were grown under the same greenhouse conditions described above. When plants had five true leaves they were decapitated. The stem was gently bent 90° (from vertical to horizontal) and allowed to re-sprout from its axillary buds. Plants normally developed two branches; when each of these branches had five or six leaves, they were placed in front of the light sources to expose each branch to either the Ambient or FR light treatments (Fig. 2). Plants remained in the light treatment for 2 weeks. After this period, the
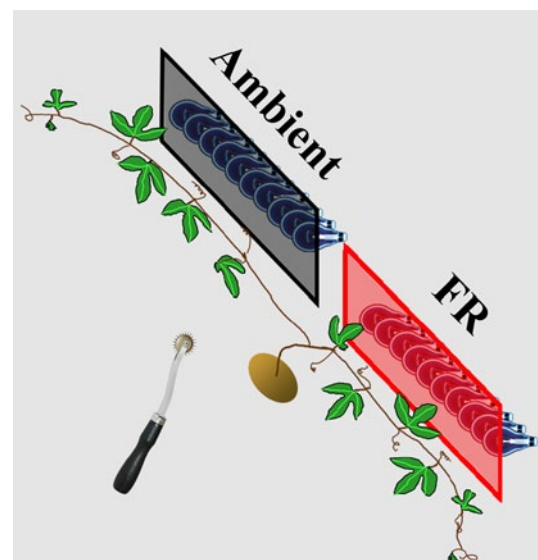
Fig. 2 Schematic diagram of the experiment designed to test for local responses. Two-branched plants were placed in front of lamp banks bearing FR-transmitting filters (FR treatment, low R:FR ratio) or opaque screens (Ambient treatment), in order to apply local light treatments in different parts of the same plant. Two weeks after placing the plants in front of the light sources, two levels of simulated herbivory (control and wounding with a fabric pattern wheel) were locally applied to the branches in factorial combination with the light conditions

branches received a simulated herbivory treatment (wounding with a fabric pattern wheel or left unwounded, as described before) in factorial combination with the lateral light treatments. After two more days in front of the lamps, nectar quantification was performed as described above. There were between three and five replicates of each combination of light and simulated herbivory treatments.

Data analysis

Statistical analyses of data presented in Figs. 4, 5, 6, 7, and 8 (below) and sugar concentration were performed using PROC GLM in the SAS v.8.0 package (SAS Institute, Cary, NC, USA). Appropriate transformations of the primary data were used when needed to meet the assumptions of the analysis of variance (cube root for data presented in Figs. 4, 5, 6a, 7; square root for data displayed in Fig. 8). Ant visitation data (Fig. 3) were analyzed with repeated measurements ANOVA, followed with a Tukey's test for differences among treatments on each day. A paired Student's t test was performed for comparing nectar volume in two branches of same plant in the assays for local responses (Fig. 9).

Results

EFNs attract predatory ants

P. edulis plants had highly active EFNs, which were visited by several species of canopy arthropods, particularly Argentine ants (*Linepithema humile*). Removal of the petiolar EFNs drastically reduced the number of ants patrolling the plants (Fig. 3a), demonstrating a strong effect of the presence of active EFNs on ant visitation. In contrast, mechanical damage to the petiole, which simulated EFN ablation without affecting extrafloral nectar production, did not affect ant visitation (Fig. 3a). The effect of EFN ablation reducing ant numbers persisted for several days after the beginning of treatments (Fig. 3b), even though, during that period, the plants produced new leaves bearing petiolar EFNs, which were not experimentally manipulated. Argentine ants are well-known predators of herbivorous insects (Koptur 1974; Bernays and Cornelius 1989; Cornelius and Bernays 1995; Way et al. 1999), and can prey on a wide range of lepidopteran larvae.

EFNs are inducible by mechanical damage and MeJA

We tested whether EFN activity can be stimulated by simulated herbivory to the leaves and hormonal elicitation with MeJA. Mechanical damage to the leaf using a fabric pattern wheel, which caused minimal damage to the vasculature, strongly increased nectar secretion from the petiolar
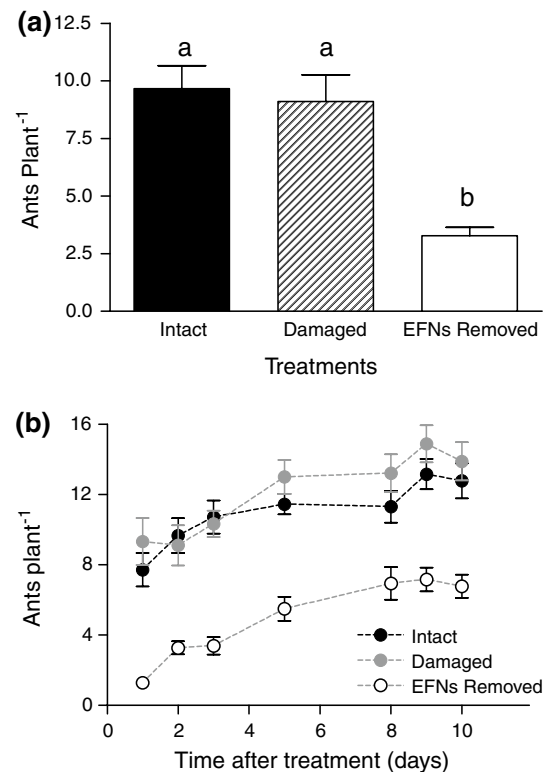

Fig. 3 *P. edulis* EFNs are very effective in attracting ants. **a** Ant visitation of intact plants (*black bar*), plants with damaged petioles as a control for EFNs removal (*hatched bar*), and plants with petiolar EFNs removed (*white bar*). Data were recorded at 1200 hours 2 days after the EFN removal treatment under natural conditions. *Error bars* 1 SEM ($n = 18$). *Different letters* indicate statistical differences at $P = 0.0001$ (Tukey). **b** Time-course of ant numbers per plant during 10 days following the EFN manipulation treatments. *P* values (repeated-measurements ANOVA) were as follows. Time effect: 0.0001; treatment effect: 0.0001; time × treatment effect: 0.87. For each sampling date, there was a significant difference in ant visitation between plants with EFN removed and either intact plants or plants with damaged petioles ($P < 0.01$), whereas no differences were found between intact plants or plants with damaged petioles ($P > 0.15$) (Tukey)

EFNs within 2 days (Fig. 4). Similarly, treatment of the plants with MeJA caused a rapid increase in nectar secretion (Fig. 5). Sugar concentration in the nectar was not affected by mechanical damage ($P = 0.76$) or MeJA treatment ($P = 0.75$).

Low R:FR ratios induce typical SAS responses in Passiflora

Having demonstrated that EFNs in *P. edulis* are functional in attracting predatory ants and that their activity can be induced by simulated herbivory and MeJA treatment, we wanted to study the effects of light quality on nectar production. Because virtually nothing was known about *Passiflora* responses to light quality, we first measured the
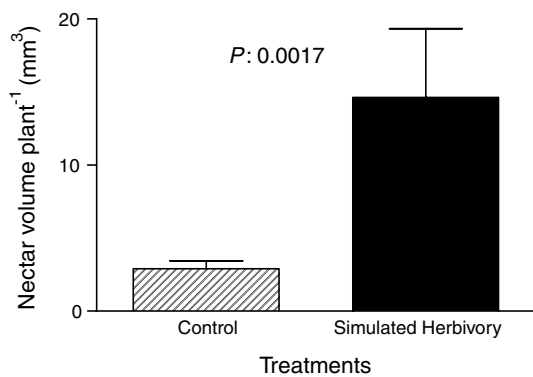
Fig. 4 Simulated herbivory induces extrafloral nectar production. Leaves were damaged with a fabric pattern wheel (*black bar*, see Fig. 1c) or left undamaged (Control; *hatched bar*). Nectar volume was quantified 2 days after elicitation. *Error bars* 1 SEM (*n* = 6). The *P* value indicates the level of significance of the difference between treatments (one-way ANOVA)
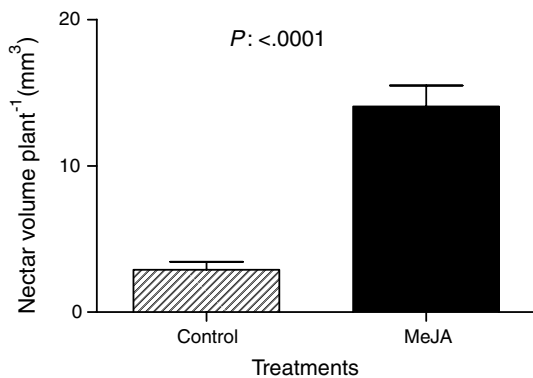
Fig. 5 Exogenous application of MeJA induces extrafloral nectar production. Leaves were sprayed with 150 μM MeJA (*black bar*) or with a mock solution [distilled water supplemented with ethanol in the same proportion (0.04 ‰) as that used to dissolve MeJA in the solutions used for the JA treatment] (Control; *hatched bar*). Two days after elicitation nectar volume was quantified. *Error bars* 1 SEM (*n* = 6). The *P* value indicates the level of significance of the difference between treatments (one-way ANOVA)

response of *P. edulis* shoots to low R:FR. Plants grown in a glasshouse and supplemented with lateral FR radiation to mimic the proximity of neighboring plants presented typical SAS responses, including increased internode and petiole elongation (Fig. 6).

Low R:FR ratios repress the EFN response triggered by simulated herbivory and MeJA

Because *P. edulis* was shown to be sensitive to light treatments that signal the proximity of competitors, we investigated the effects of supplemental FR radiation on EFN activity. Lowering the R:FR ratio by adding FR to the

sunlight received by plants in the greenhouse strongly reduced the nectar response to simulated herbivory and MeJA, even at the highest doses of MeJA tested in the present experiments (Figs. 7, 8).

**EFN activity is controlled by herbivory and light signals at the modular level**

To test the effect of local versus systemic conditions on EFN activity, *P. edulis* plants were pruned to obtain individuals with two branches. The two branches of each plant received all possible combinations of FR supplementation and simulated herbivory treatments. (Fig. 2; see "Materials and methods" for details). For each focal branch, the variables that explained local nectar production were the local herbivory treatment (i.e. damaged or not damaged) and the local light conditions (i.e. Ambient or FR radiation). Thus, if a branch was exposed to simulated herbivory, extrafloral nectar production in that branch increased, regardless of the treatment received by the other branch. Furthermore, if the light environment of the wounded branch was enriched in FR radiation, the local EFN response to wounding was completely canceled (Fig. 9).
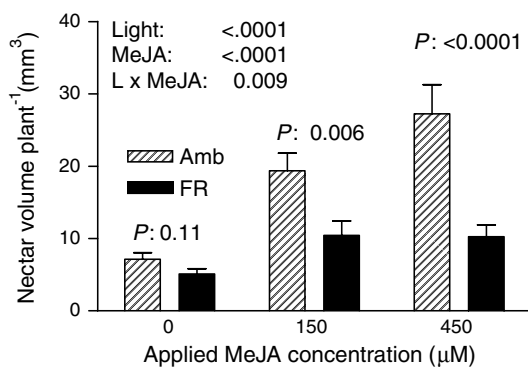
Discussion

Growing evidence from physiological studies demonstrates that plants down-regulate the expression of direct defenses against herbivores and pathogens in response to light signals that indicate an increased level of actual or future competition (such as low R:FR ratios and reduced levels of UV radiation) (Ballaré 2009; Kazan and Manners 2011; Ballaré et al. 2012). Our experiments demonstrate a similar pattern of down-regulation for an indirect defense, extrafloral nectar production. In addition, our experiments suggest that a conserved mechanism, based on down-regulation of JA response, can account for the effects of low R:FR ratios on both types of defenses. Taken together, these results suggest that repression of inducible anti-herbivore defenses by low R:FR ratios is a very general phenomenon, which is likely to play a central role regulating the allocation of limited resources between growth and defense in shade-intolerant plants.

The EFN system of *P. edulis* is highly effective in attracting predatory ants (Fig. 3), and ants have been shown to provide protection from insect herbivores in other species of the genus *Passiflora* (McLain 1983; Smiley 1986; Xu and Chen 2010). Our observations in *P. edulis* indicated that Argentine ants, which were continuously patrolling the branches and feeding on extrafloral nectar, were aggressive toward larvae of *Agraulis vanillae* (gulf fritillary), a herbivore that specializes in plants of the genus *Passiflora*.

Fig. 6 SAS responses in *P. edulis*. Lateral supplementation with FR radiation (*black bars*) causes increases in internode (*left panel*) and petiole (*right panel*) elongation, which are typical morphological markers of the SAS response. *Error bars* 1 SEM (*n* = 20). The *P* value indicates the level of significance of the difference between treatments (one-way ANOVA)
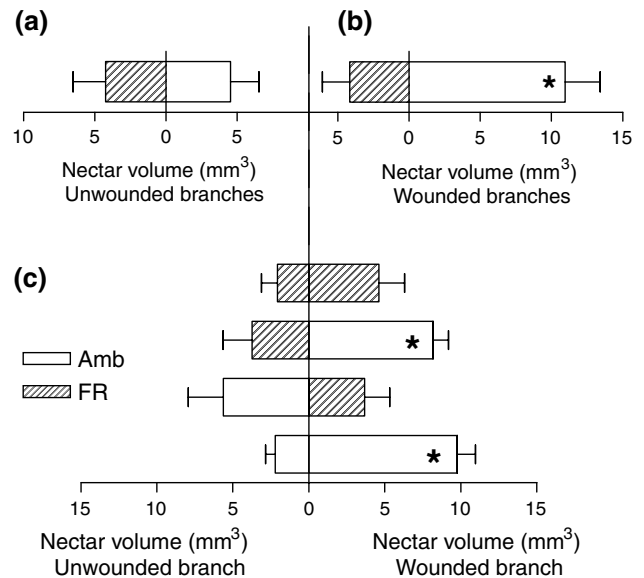

(a) Internode length

(b) Petiole length
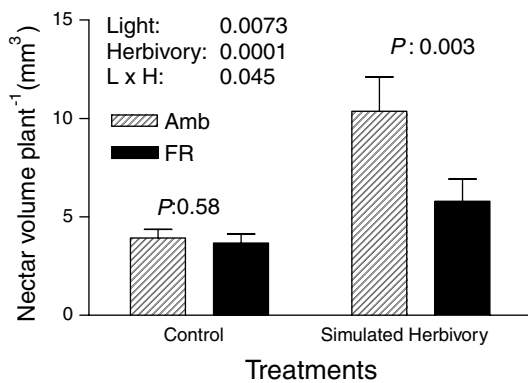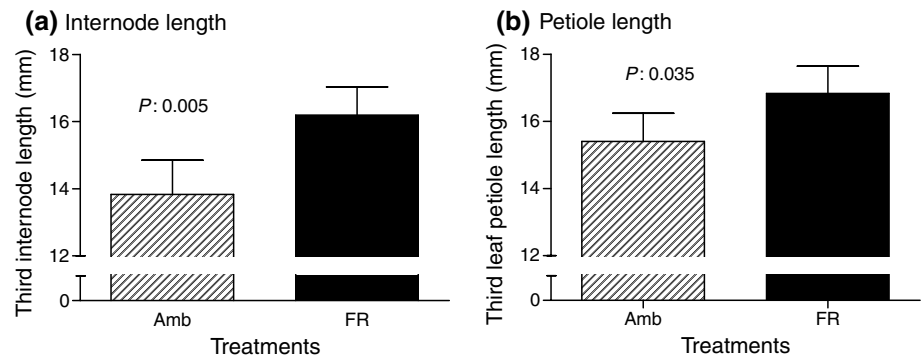
Fig. 7 FR supplementation represses damage-induced production of extrafloral nectar. Plants grown under Ambient (*hatched bars*) or FR-enriched (*black bars*) light environments were damaged with a fabric pattern wheel or left undamaged in a factorial design. Two days after elicitation nectar volume was quantified. *Error bars* represent 1 SEM (*n* = 20). *Numbers* indicate statistical significances (*P* values, two-way ANOVA) for main effects, interaction term, and specific comparisons

Thus, our results in *P. edulis* are consistent with the extensive body of literature demonstrating an important role for EFNs in indirect defense. Variation among species has been observed regarding whether EFNs are constitutively active or inducible (reviewed in Heil 2011). In our study, petiolar EFNs of *P. edulis* behaved as those of the ant-loving plant *Macaragna tanarius*, in terms of their inducibility by wounding and hormonal treatment (Heil et al. 2001). Regulation of EFN activity by JA therefore appears to be a general mechanism by which nectar secretion is connected to the signal transduction cascades that orchestrate defense

Fig. 8 FR supplementation represses MeJA-induced production of extrafloral nectar. Plants grown under Ambient (*hatched bars*) or FR-enriched light (*black bars*) environments were sprayed with MeJA solutions at the indicated concentrations. Two days after elicitation nectar volume was quantified. *Error bars* 1 SEM (*n* = 10 for each light × MeJA dose combination). *Numbers* indicate statistical significances (*P* values, two-way ANOVA) for main effects, interaction term, and specific comparisons

Fig. 9 EFN activity is locally controlled at the modular level. Two-branched plants were used in this experiment, and each branch received a particular combination of light environment (Ambient or FR-enriched) and simulated herbivory (wounded or unwounded) (see Fig. 2 for a schematic representation). **a, b** Results of experiments in which both branches received the same treatment of simulated herbivory (either unwounded or wounded); **c** results of experiments in which branches of the same plant received contrasting treatments of simulated herbivory. Significant differences (*P* < 0.05, paired Student's *t* test) are indicated with *asterisks*; *thin bars* indicate SE of mean differences (*n* = 3–5)

responses (this study; Heil et al. 2001; Radhika et al. 2010), although cases in which inducible EFNs are not stimulated by MeJA treatment have also been reported (Escalante-Pérez et al. 2012).

Decreased sensitivity of plant tissues to JA is the most plausible explanation for the repression of EFN activity caused by low R:FR ratios in our experiments. Alternative explanations for the effects of low R:FR on defense, such a diversion of an increased fraction of resources to growth (in detriment of defense), have been ruled out in other systems. For example, studies in *Arabidopsis* have shown that even mutants that fail to induce SAS (but have otherwise normal phytochrome responses), such as the *sav3* mutant (Tao et al. 2008), down-regulate the expression of their defense system when grown under low R:FR ratios (Moreno et al. 2009). Similarly, triggering plants to express a SAS phenotype by manipulation of other photoreceptors, such as the blue light photoreceptor cryptochrome 1, activates increased elongation responses (Keller et al. 2011), but does not result in a weak defense phenotype in infection bioassays (Cerrudo et al. 2012). Collectively, these previous results suggest that depression of plant defense by low R:FR ratio is not a simple by-product of increased resource allocation to SAS responses.

Reduction of JA response by phyB-mediated competition signals is a well-documented phenomenon in studies that measured defense using insect growth and pathogen infection bioassays (Moreno et al. 2009; Cerrudo et al. 2012; De Wit et al. 2013), accumulation of secondary metabolites (Izaguirre et al. 2006; Moreno et al. 2009; Cagnola et al. 2012), and expression of defense-related genes (Cerrudo et al. 2012; De Wit et al. 2013). It has also been shown that light environments rich in FR can depress JA accumulation (Radhika et al. 2010; Agrawal et al. 2012; Cagnola et al. 2012), which might also explain the decreased EFN activity under low R:FR ratios in *P. edulis*. We did not measure bioactive JAs in our system and, therefore, we cannot rule out effects of light on JA biosynthesis, but the responses to our treatments involving exogenous MeJA application clearly demonstrate that JA sensitivity is impaired in *P. edulis* exposed to low R:FR ratios (Fig. 8).

The vast majority of the experiments that have tested for light effects on sensitivity to defense hormones have been carried out using whole plants of *Arabidopsis thaliana* (reviewed in Ballaré et al. 2012). Whereas this approach is valid and informative to investigate mechanisms of signaling cross-talk, it does not provide much insight into the problem of signal integration in a modular organism. The modular architecture of plants may allow a spatially-defined control of adaptive plasticity (De Kroon et al. 2009). Vines in particular can continuously track resource availability in patchy canopies (e.g., Ray 1992) by directing new growth toward (and consolidating modules in) resource-rich patches. To optimize the deployment of modules in high-light patches, plants frequently rely on informational photoreceptors, such as phyB (Ballaré et al. 1995). Our data suggest that phyB can provide additional levels of regulation in the modular strategy, as they show that the suppression of defense responses by low R:FR ratios displays a significant level of local control (Fig. 9). An important implication of this local modulation is that the plant as a whole may be able to concentrate its limited defense resources in those modules located in high-quality microsites, while "sacrificing" those that met less promising conditions of light resource capture.

Within the framework of the dilemma of plants ("to grow or defend"; Herms and Mattson 1992), we postulate that local suppression of JA signaling is part of a mechanism that optimizes the distribution of resources as a function of the value of the branch, which the plant establishes using light signals perceived by phytochrome. In this context, light-guided distribution of the sensitivity to herbivory cues may represent a case of the strategy of "picking battles wisely" (Novoplansky 2009). Alternative explanations for the ecological benefit of down-regulating EFN activity in response to neighbor proximity signals may also be considered. For example, the probability of recruiting ants may increase with the number of contacts between the vine stems and other vegetation (Apple and Feener 2001; Di Giusto et al. 2001). Therefore, producing abundant extrafloral nectar to attract defenders may be less important for plants growing in a dense canopy than for those growing in open conditions. In either case, light quality will provide the plant with useful information to optimize the allocation of resources to defense.

Conflict of interest The authors declare no conflicts of interest.

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