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## Quantity over quality: light intensity, but not red/far-red ratio, affects extrafloral nectar production in *Senna mexicana* var. *chapmanii*

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### Keywords

Extrafloral nectar, Fabaceae, plant defenses, resource allocation, *Senna mexicana* var. *chapmanii*.

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### Abstract

Extrafloral nectar (EFN) mediates food-for-protection mutualisms between plants and insects and provides plants with a form of indirect defense against herbivory. Understanding sources of variation in EFN production is important because such variations affect the number and identity of insect visitors and the effectiveness of plant defense. Light represents a potentially crucial tool for regulating resource allocation to defense, as it not only contributes energy but may help plants to anticipate future conditions. Low red/far-red (R/FR) light ratios can act as a signal of the proximity of competing plants. Exposure to such light ratios has been shown to promote competitive behaviors that coincide with reduced resource allocation to direct chemical defenses. Little is known, however, about how such informational light signals might affect indirect defenses such as EFN, and the interactions that they mediate. Through controlled glass-house experiments, we investigated the effects of light intensity, and R/FR light ratios, on EFN production in *Senna mexicana* var. *chapmanii*. Plants in light-limited conditions produced significantly less EFN, and leaf damage elicited increased EFN production regardless of light conditions. Ratios of R/FR light, however, did not appear to affect EFN production in either damaged or undamaged plants. Understanding the effects of light on indirect defenses is of particular importance for plants in the threatened pine rockland habitats of south Florida, where light conditions are changing in predictable ways following extensive fragmentation and subsequent mismanagement. Around 27% of species in these habitats produce EFN and may rely on insect communities for defense.

### Introduction

Extrafloral nectaries (EFNs) are nectar-secreting glands located outside of flowers and have been observed on a huge diversity of species, spanning over 93 families and 332 genera (Koptur 1992a,b; Marazzi et al. 2013). These nectaries may serve diverse ecological functions (Baker et al. 1978; Becerra and Venable 1989; Wagner and Kay 2002; Heil 2011), but primarily they are known to provide indirect defense against herbivores by attracting predatory insects, predominantly ants (Bentley 1977; Koptur 1992a,b; Rosumek et al. 2009; Heil 2015). Despite their unquestionable importance, relatively little is known about the factors that regulate EFN production. Uncovering these factors can help us understand how plants

regulate their investment in defense, and how they manage and maintain interactions with beneficial insects.

Light conditions are likely to be particularly influential in controlling the expression of plant defensive traits, as light not only represents a crucial aspect of resource availability, but may also serve as an indicator of insect activity (Karban et al. 1999), or future competition (Izaguirre et al. 2006). Plants are well known to sense changes in spectral signals (e.g., Weller et al. 1997; Adams et al. 2001). Far-red light, for example, is a component of the solar spectrum (710–850 nm) that is heavily reflected by plant tissues (Izaguirre et al. 2006). Increases in far-red radiation, relative to the red portion of sunlight (620–750 nm), can be detected through the photoreceptor, phytochrome B (Ballare et al. 1990; Ballare 2014). A low red/far-red (R/FR) light ratio is

known to indicate the close proximity of competitors for many plants (Ballare 1999, 2014).

Plants exposed to low R/FR light conditions often express a suite of competition-focused traits collectively known as the shade-avoidance syndrome (Ballare 1999, 2014; Pierik et al. 2013). Responses associated with the shade-avoidance syndrome include increased stem elongation, reduced lateral branching, and a reduction in resource allocation to defensive traits (Izaguirre et al. 2006). The expression of several direct plant defenses such as phenolic compounds (Moreno et al. 2009), and latex (Rasmann et al. 2009; Agrawal et al. 2012), is known to be reduced in low R/FR light.

Far less is known about the effects of light conditions on the expression of indirect plant defenses such as EFN. Light intensity is known to affect trade-offs between indirect defenses in *Mallotus japonicus* (Yamawo and Hada 2010); however, only the effects of light intensity, and not light quality, were observed and so we know little about how these plants may respond to informational light signals. In lima beans (*Phaseolus lunatus*), the induction of EFN production with jasmonic acid (JA) has been shown to be dependent on light intensity, and on the ratio of R/FR wavelengths (Radhika et al. 2010). Izaguirre et al. (2013) also observed EFN production in passion fruit (*Passiflora edulis*) in carefully manipulated light conditions. Plants (and plant parts) exposed to low R/FR light conditions exhibited reduced EFN production, compared to those exposed to higher R/FR light ratios, particularly in response to simulated herbivory.

Pine rockland habitats contain a high proportion of EFN-bearing plants (27%) (Koptur 1992a,b), but the dynamics of EFN production in these species have rarely been studied (but see Rutter and Rausher 2004; Jones and Koptur 2015). *Senna mexicana* var. *chapmanii* (hereafter referred to as *Senna chapmanii*) is an herbaceous legume native to the pine rocklands of south Florida and the Caribbean. We have already shown that *S. chapmanii* plants produce more EFN in response to leaf damage (Jones and Koptur 2015). We have also observed that plants in shady conditions are less well defended by ants than those in direct sunlight (I. M. Jones, S. Koptur, J. Tardanico, H. Gallegos and P. Trainer, unpubl. data).

In this study, we investigated the effects of light intensity and R/FR light ratio on EFN production in *S. chapmanii*. Both artificially defoliated and undamaged plants were tested. We expected EFN production would be increased in response to leaf damage and high light intensity, but reduced in response to low R/FR light ratios. Understanding the factors that control EFN production is important, because such variations affect the number and identity of insect visitors, and the effectiveness of plant defense (Fig. 1).

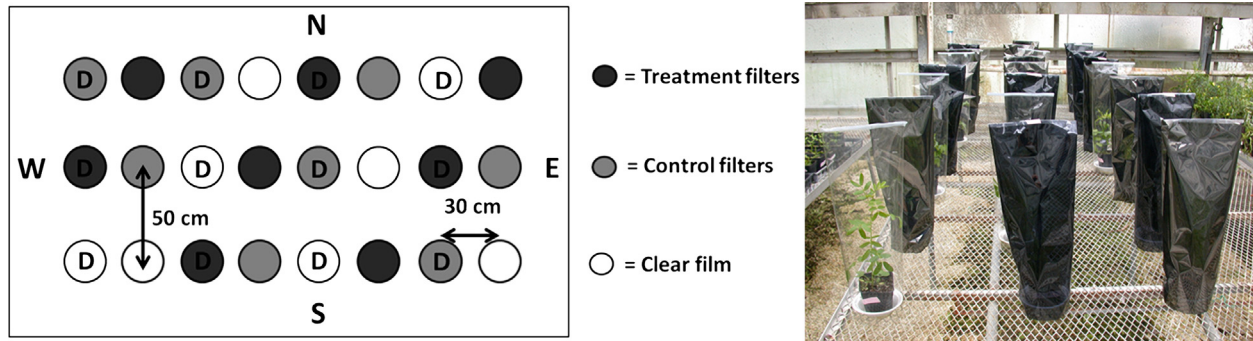


**Figure 1.** Extrafloral nectary on the leaf rachis of *Senna mexicana* var. *chapmanii*. Photograph by Ian Jones.

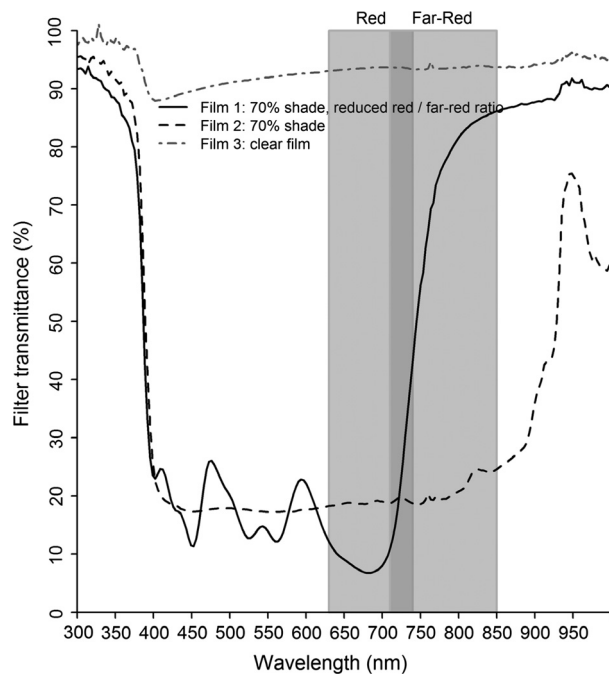
## Methods

To control *S. chapmanii* light environments, film cylinders (50 cm in circumference and 60 cm in height) were constructed using three calibrated light filtration films. Film 1 (treatment film) was a metal sputter-coated film designed to mimic shading by other plants by reducing photosynthetically active radiation (PAR) by approximately 80%, and reducing the ratio of R/FR light. Film 2 (control film), a dye-impregnated film, was designed to reduce PAR by approximately 80%, but without impacting R:FR light ratio. Films 1 and 2 were supplied by the 3M Corporation (St. Paul, MN, 55144, USA) and have been used previously to test the effects of irradiance and spectral quality on forest tree seedling development (Lee et al. 1996). Film 3 was a clear acetate film which allowed approximately 90% PAR transmission and had no impact on R:FR light ratio. Film 3 was supplied by BLICK art materials (Galesburg, IL, 61402, USA), and controlled for the effects of the cylinders themselves. Twenty-four film cylinders (8 of each type) were placed on a glasshouse bench. The open bottom of each cylinder was placed around the plant pot, and the top end was sealed closed using clear tape. Cylinders composed of the three film types were placed alternately in three rows running east to west (Fig. 2).

To determine the actual light environments within the film cylinders, the intensity and spectral distribution of light within the glasshouse were measured using a radiospectrometer (Unispec-DC, PP SYSTEMS, Amesbury, MA, USA). These measurements were then compared with measurements taken inside the film cylinders 1, 2, and 3. Percentage transmittance of light through each film type, at a range of wavelengths (300–1000 nm), was then calculated. Three of each filter type were tested (Fig. 3).



**Figure 2.** Light filter cylinder arrangement. The letter D indicates plants subjected to leaf damage.



**Figure 3.** Mean percentage of light of different wavelengths (300–1000 nm) transmitted through the three filter types. Light gray bands indicate red and far-red light wavelengths, while the dark gray band indicates crossover between the two. The sharp rise in percentage light transmission in film 1, starting at around 710 nm, indicates the desired increase in R:FR light ratio within film 1 cylinders.

*Senna chapmanii* was grown from seeds in the glasshouse on the Modesto Maidique campus at Florida International University. After 3 weeks, seedlings were transplanted into 0.6-L pots, and 1.5 g of slow release fertilizer (Nutricote NPK; Florikan, Sarasota, FL, USA) was added to each plant. Plants were maintained in the glasshouse until they had at least 10 mature leaves. Experiments were conducted from June to August 2014.

Twenty-four plants were placed randomly in the cylinders (Fig. 2). After 48 h inside the cylinders, 12

plants (4 from each cylinder type) were subjected to 50% leaf damage. Leaf damage was inflicted by removing 50% of each leaflet using scissors. The same damage treatments were used in a previous study (Jones and Koptur 2015) and induced a highly significant increase in EFN production in *S. chapmanii*. The remaining 12 plants were left undamaged. The experiment therefore had two independent variables, light quality and leaf damage.

Extrafloral nectar production, by each plant, was measured 12 and 24 h after leaf damage as the increase in EFN production by *S. chapmanii* in response to leaf damage has been shown to be greatest during this period (Jones and Koptur 2015). Leaf damage was inflicted at 7 am, so nectar measurements took place at 7 pm on the day of leaf damage, and at 7 am the following morning. Taking measurements in the morning, and at night, allowed us to calculate a mean EFN production for each plant, controlling for natural diurnal variations in EFN production. Nectar volume was measured using 1, 2, and 10  $\mu$ L micropipettes, and its concentration determined using a handheld refractometer. Total sugar production by each plant was then calculated as described by Jones and Koptur (2015). The experiment was repeated 6 times, using a total of 144 plants.

We report EFN production as the mean mass of sugar (mg) produced by each plant, as this provides the best representation of defensive investment. Previous studies have often reported only nectar volume or concentration, both of which are affected by environmental factors such as temperature and humidity. Where we refer to EFN production in the discussion, we refer to mean sugar production.

### Statistical analysis

Kruskal–Wallis H-tests were used to compare EFN production between the three light treatments in damaged and undamaged plants. Post hoc comparisons between pairs of light treatments were then conducted separately

using Mann–Whitney *U*-tests. Holm's sequential Bonferroni adjustments were applied to control for type 1 errors. Damaged and undamaged plants within each light treatment were compared using Mann–Whitney *U*-tests.

## Results

Radiospectrometer readings confirmed that light conditions inside the cylinders were as expected (Fig. 3). Film 1 admitted between 10% and 30% of light in photosynthetically active wavelengths, but transmittance rose to almost 90% in the far-red wavelength band. Film 1 therefore adequately mimicked shading by other plants, as compared to film 2, which admitted around 20% of light in photosynthetically active wavelengths, with transmittance rising only slightly in the far-red band. Film 3, the clear film, admitted around 90% of light across all wavelengths (Fig. 3).

In all three light treatments, damaged plants produced more EFN than undamaged plants (Film 1:  $z = -2.492$ ,  $df = 46$ ,  $P = 0.013$ ; Film 2:  $z = -2.474$ ,  $df = 46$ ,  $P = 0.013$ ; Film 3:  $z = -2.062$ ,  $df = 46$ ,  $P = 0.039$ ). Light treatments significantly affected EFN production in both damaged ( $\chi^2 = 18.355$ ,  $df = 2$ ,  $P < 0.001$ ) and undamaged plants ( $\chi^2 = 23.014$ ,  $df = 2$ ,  $P < 0.001$ ) (Fig. 4).

Among damaged plants, those in clear tubes (film 3) produced significantly more EFN than those in 70% shade with reduced R/FR light ratio ( $z = -3.843$ ,  $df = 46$ ,  $P < 0.001$ ), and those in 70% shade ( $z = -3.350$ ,  $df = 46$ ,  $P = 0.001$ ). There was no difference in sugar production between plants in 70% shade with reduced R/FR light ratio, and those in 70% shade ( $z = -1.012$ ,  $df = 46$ ,  $P = 0.311$ ) (Fig. 4).

Among undamaged plants, those in clear tubes (film 3) produced significantly more EFN than those in 70% shade

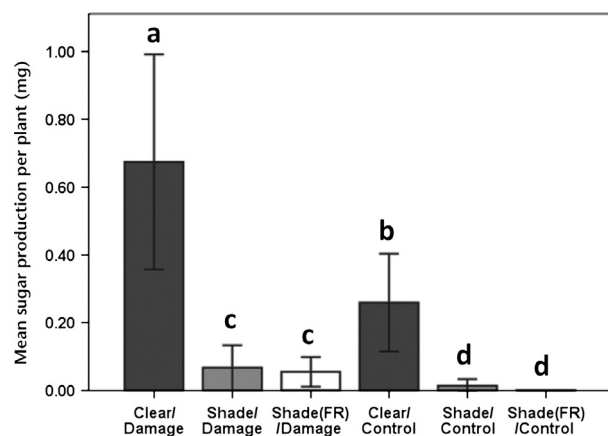
with reduced R/FR light ratio ( $z = -4.245$ ,  $df = 46$ ,  $P < 0.001$ ), and those in 70% shade ( $z = -3.343$ ,  $df = 46$ ,  $P = 0.001$ ). There was no difference in sugar production between plants in 70% shade with reduced R/FR light ratio, and those in 70% shade ( $z = -1.343$ ,  $df = 46$ ,  $P = 0.179$ ) (Fig. 4).

## Discussion

Extrafloral nectar is an extremely widespread, often inducible trait that mediates food-for-protection interactions between plants and ants. Although the ecological role of EFN is well established (Bentley 1977; Koptur 1992a,b; Rosumek et al. 2009), far less is known about how changes in environmental conditions, even over small scales, may affect its production and, therefore, the outcomes of the interactions it mediates.

Plants in all three light treatments produced more EFN in response to leaf damage. Inducible EFN nectar production has been reported in many species (Stephenson 1982; Koptur 1989; Agrawal and Rutter 1998; Engel et al. 2001; Heil et al. 2001; Mondor and Addicott 2003; Choh and Takabayashi 2006; Lach et al. 2009; Heil 2015). Indeed, increased EFN production in response to leaf damage has been observed previously in *S. chapmanii* (Jones and Koptur 2015). We observe for the first time, however, that this induced response is maintained in light-limited conditions, albeit at a lower level. It should be noted that, in the present study, we observed the effects of mechanical leaf damage and not true herbivory. Plants have been observed to respond to the oral secretions of specific herbivores (Kessler et al. 2010), and responses to damage have been shown to vary based on herbivore feeding guild (Schmidt et al. 2009; Sotelo et al. 2014). Future work therefore should focus on the effects of damage inflicted by key herbivores.

Light intensity had a significant impact on EFN production, as both damaged and undamaged plants produced more EFN at high light intensities. It might seem intuitive that a reduction in the availability of photosynthetically active light would reduce the level of resources available for defense. Indeed, some so-called green nectaries may be isolated from phloem tissue and produce nectar only at a rate that can be supported by their own photosynthesis (Lüttge 2013). The resource availability hypothesis (RAH), however, suggests that low-nutrient environments may promote greater investment in defensive traits, compared to nutrient-rich environments where plants must grow quickly in order to compete (Coley et al. 1985; Endara and Coley 2011). The relationship between nutrient availability and defense is therefore complex, and assumptions that increased resources should lead to a greater investment in defense may be misplaced.



**Figure 4.** Mean sugar production (mg) by damaged and undamaged plants subjected to three light treatments. Error bars indicate standard error. Letters indicate significant differences.

The carbon–nutrient balance hypothesis (CNBH) suggests that when a given resource limits plant growth, other resources, found in relative excess, may be allocated toward defenses (Bryant et al. 1983). For example, in light-rich and nutrient-poor conditions, plants are expected to invest in carbon-based defenses, while in shaded but nutrient-rich conditions, plants should invest more heavily in nitrogen-based defenses (Lerdau and Coley 2002). Yamawo and Hada (2010) found that light intensity affected the trade-off between two indirect defenses in *Mallotus japonicus*. In low light conditions, both the size and the productivity of EFNs were reduced, but the production of pearl bodies was increased. These results seem to support CNBH, as pearl bodies are rich in protein and represent a significant nitrogen investment (Heil et al. 2004). Our observations that EFN production in *S. chapmanii* is reduced in low light conditions seem to reflect resource availability and contradict RAH. However, it remains possible that reduced EFN production may coincide with an increased investment in nitrogen-based defensive compounds such as alkaloids. Future studies should seek to understand these dynamics, in *S. chapmanii* and other species.

The simplest and most elegant explanation for the observed pattern of EFN production may come from Millán-Cañongo et al. (2014), who observed reduced EFN production in shaded leaves of *Ricinus communis*. Changes in EFN production were shown to be mediated by cell wall invertase, an enzyme involved in the unloading of sucrose from the phloem into the nectary. Light conditions did not appear to affect cell wall invertase activity, so it was suggested that reduced EFN production was a result of lower sucrose content available in the phloem (Millán-Cañongo et al. 2014).

Changes in R/FR light ratio had no effect on EFN production in *S. chapmanii*. Plants exposed to low R/FR light ratios produced slightly less EFN in both damaged and undamaged plants, but the differences were not significant. These results were surprising as light spectral quality has been observed to affect EFN production significantly in both lima beans (Radhika et al. 2010) and passion fruit (Izaguirre et al. 2013). It is possible that our shade treatments reduced overall light intensity to such an extent that the effects of light spectral quality were tempered. This seems unlikely, however, as Radhika et al. (2010) showed that R/FR light ratio affected JA-induced EFN production even at low light intensities. Our results suggest that *S. chapmanii* downregulates indirect defenses in response to shade, but that it does not do so in response to specific spectral signals that indicate competition.

This study contributes to an improved understanding of plant resource allocation, and the dynamics of defensive traits. Spatiotemporal patterns of EFN production are often

adapted to optimize plant defense (Tilman 1978; Heil 2015). These patterns, however, are driven by simple physiological mechanisms that respond to environmental conditions (Heil 2015). We add to a growing understanding of how changing environmental conditions affect indirect plant defenses, and the interactions that they support.

Understanding how EFN production responds to changing light conditions is of particular importance in pine rockland habitats, where roughly 27% of plants bear EFNs (Koptur 1992b). Over the last century, roughly 98% of pine rockland habitat in south Florida (with the exception of Everglades National Park) has been destroyed for agriculture and urban development (Barrios et al. 2011). Due to their close proximity to dense human populations, the remaining fragments are frequently mismanaged. In particular, the fires that are necessary to maintain healthy pine rocklands are often suppressed (Possley et al. 2008). Pine rockland habitats are characterized by an open canopy, with high levels of light reaching the species-rich herb layer. In the absence of fire, trees and shrubs quickly become overgrown, and understory plants are shaded. With this experiment, we hoped to create a clearer understanding of how changing light conditions in the pine rocklands might affect insect–plant interactions, and the fitness of plants that rely on these interactions for defense.

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## Conflict of Interest

None declared.

## References

- Adams, S. R., S. Pearson, and P. Hadley. 2001. Improving quantitative flowering models through a better understanding of the phases of photoperiod sensitivity. *J. Exp. Bot.* 52:655–662.

- Agrawal, A. A., and M. T. Rutter. 1998. Dynamic anti-herbivore defense in ant-plants: the role of induced responses. *Oikos* 83:227–236.
- Agrawal, A., E. Kearney, A. Hastings, and T. Ramsey. 2012. Attenuation of the jasmonate burst, plant defensive traits, and resistance to specialist monarch caterpillars on shaded common milkweed (*Asclepias syriaca*). *J. Chem. Ecol.* 38:893–901.
- Baker, D. A., L. J. Hall, and J. R. Thorpe. 1978. A study of the extrafloral nectaries of *Ricinus communis*. *New Phytol.* 81:129–137.
- Ballare, C. L. 1999. Keeping up with the neighbours: phytochrome sensing and other signalling mechanisms. *Trends Plant Sci.* 4:97–102.
- Ballare, C. L. 2014. Light regulation of plant defense. *Annu. Rev. Plant Biol.* 65:335–363.
- Ballare, C. L., A. L. Scopel, and R. A. Sanchez. 1990. Far-red radiation reflected from adjacent leaves— an early signal of competition in plant canopies. *Science* 247:329–332.
- Barrios, B., G. Arellano, and S. Koptur. 2011. The effects of fire and fragmentation on occurrence and flowering of a rare perennial plant. *Plant Ecol.* 212:1057–1067.
- Becerra, J. X. I., and D. L. Venable. 1989. Extrafloral nectaries: a defence against ant–Homoptera mutualisms? *Oikos* 55:276–280.
- Bentley, B. L. 1977. The protective function of ants visiting the extrafloral nectaries of *Bixa orellana* (Bixaceae). *J. Ecol.* 65:27.
- Bryant, J. P., F. S. III Chapin, and D. R. Klein. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos* 40:257–368.
- Choh, Y., and J. Takabayashi. 2006. Herbivore-induced extrafloral nectar production in lima bean plants enhanced by previous exposure to volatiles from infested conspecifics. *J. Chem. Ecol.*, 32:2073–2077.
- Coley, D. P., J. P. Bryant, and S. Chapin. 1985. Resource availability and plant anti-herbivore defense. *Science* 230:895–899.
- Endara, M. J., and P. D. Coley. 2011. The resource availability hypothesis revisited: a meta-analysis. *Funct. Ecol.* 25:389–398.
- Engel, V., M. K. Fischer, F. L. Wackers, and W. Volkl. 2001. Interactions between extrafloral nectaries, aphids and ants: are there competition effects between plant and homopteran sugar sources? *Oecologia* 129:577–584.
- Heil, M. 2011. Nectar: generation, regulation and ecological functions. *Trends Plant Sci.* 16:191–200.
- Heil, M. 2015. Extrafloral nectar at the plant-insect interface: a spotlight on chemical ecology, phenotypic plasticity, and food webs. *Annu. Rev. Entomol.* 60:213–232.
- Heil, M., T. Koch, A. Hilpert, B. Fiala, W. Boland, and K. E. Linsenmair. 2001. Extrafloral nectar production of the ant-associated plant, *Macaranga tanarius*, is an induced, indirect, defensive response elicited by jasmonic acid. *Proc. Natl. Acad. Sci. USA* 98:1083–1088.
- Heil, M., B. Baumann, R. Krüger, and K. E. Linsenmair. 2004. Main nutrient compounds in food bodies of Mexican *Acacia* ant-plants. *Chemoeology* 14:45–52.
- Izaguirre, M. M., C. A. Mazza, M. Biondini, I. T. Baldwin, and C. L. Ballare. 2006. Remote sensing of future competitors: impacts on plant defenses. *Proc. Natl. Acad. Sci. USA* 103:7170–7174.
- Izaguirre, M. M., C. A. Mazza, M. S. Astigueta, A. M. Ciarla, and C. L. Ballare. 2013. No time for candy: passion fruit (*Passiflora edulis*) plants down-regulate damage-induced extra floral nectar production in response to light signals of competition. *Oecologia* 173:213–221.
- Jones, I. M., and S. Koptur. 2015. Dynamic extrafloral nectar production: the timing of leaf damage affects the defensive response in *Senna mexicana* var. *chapmanii* (Fabaceae). *Am. J. Bot.* 102:58–66.
- Karban, R., A. A. Agrawal, J. S. Thaler, and L. S. Adler. 1999. Induced plant responses and information content about risk of herbivory. *Trends Ecol. Evol.* 14:443–447.
- Kessler, D., D. Diezel, and I. T. Baldwin. 2010. Changing pollinators as a means of escaping herbivores. *Curr. Biol.* 20:237–242.
- Koptur, S. 1989. Is extrafloral nectar production an inducible defence? Pp. 323–339 in J. Bock and Y. Linhart, eds. *Evolutionary ecology of plants*. Westview Press, Boulder, CO.
- Koptur, S. 1992a. Extrafloral nectary-mediated interactions between insects and plants. Pp. 81–129 in E. A. Bernays, ed. *Insect-plant interactions*. Vol IV. CRC Press, Boca Raton.
- Koptur, S. 1992b. Plants with extrafloral nectaries and ants in everglades habitats. *Fla. Entomol.* 75:38–50.
- Lach, L., R. J. Hobbs, and J. D. Majer. 2009. Herbivory-induced extrafloral nectar increases native and invasive ant worker survival. *Popul. Ecol.* 51:237–243.
- Lee, D. W., K. Baskaran, M. Mansor, H. Mohamad, and S. K. Yap. 1996. Irradiance and spectral quality affect Asian tropical rain forest tree seedling development. *Ecology* 77:568–580.
- Lerdau, M., and P. Coley. 2002. Benefits of the carbon-nutrient balance hypothesis. *Oikos* 98:534–536.
- Lüttge, U. 2013. Green nectaries: the role of photosynthesis in secretion. *Bot. J. Linn. Soc.* 173:1–11.
- Marazzi, B., J. L. Bronstein, and S. Koptur. 2013. The diversity, ecology and evolution of extrafloral nectaries: current perspectives and future challenges. *Ann. Bot.* 111:1243–1250.
- Millán-Cañongo, C., D. Orona-Tamayo, and M. Heil. 2014. Phloem sugar flux and jasmonic acid-responsive cell wall invertase control extrafloral nectar secretion in *Ricinus communis*. *J. Chem. Ecol.* 40:760–769.
- Mondor, E. B., and J. F. Addicott. 2003. Conspicuous extra-floral nectaries are inducible in *Vicia faba*. *Ecol. Lett.* 6:495–497.
- Moreno, J. E., Y. Tao, J. Chory, and C. L. Ballare. 2009. Ecological modulation of plant defense via phytochrome

- control of jasmonate sensitivity. *Proc. Natl. Acad. Sci.* 106:4935–4940.
- Pierik, R., L. Mommer, and L. A. C. J. Voesenek. 2013. Molecular mechanisms of plant competition: neighbour detection and response strategies. *Funct. Ecol.* 27:841–853.
- Possley, J., S. W. Woodmansee, and J. Maschinski. 2008. Patterns of plant composition in fragments of globally imperiled pine rockland forest: effects of soil type, recent fire frequency, and fragment size. *Nat. Areas J.* 28:379–394.
- Radhika, V., C. Kost, A. Mithofer, and W. Boland. 2010. Regulation of extrafloral nectar secretion by jasmonates in lima bean is light dependent. *Proc. Natl. Acad. Sci. USA* 107:17228–17233.
- Rasmann, S., M. D. Johnson, and A. A. Agrawal. 2009. Induced responses to herbivory and jasmonate in three milkweed species. *J. Chem. Ecol.* 35:1326–1334.
- Rosumek, F. B., F. A. O. Silveira, F. D. Neves, N. P. D. Barbosa, L. Diniz, Y. Oki, et al. 2009. Ants on plants: a meta-analysis of the role of ants as plant biotic defenses. *Oecologia* 160:537–549.
- Rutter, M. T., and M. D. Rausher. 2004. Natural selection on extrafloral nectar production in *Chamaecrista fasciculata*: the costs and benefits of a mutualism trait. *Evolution* 58:2657–2668.
- Schmidt, L., U. Schurr, and U. S. R. Rose. 2009. Local and systemic effects of two herbivores with different feeding mechanisms on primary metabolism of cotton leaves. *Plant, Cell Environ.* 32:893–903.
- Sotelo, P., E. Perez, A. Najar-Rodriguez, A. Walter, and S. Dorn. 2014. *Brassica* plant responses to mild herbivore stress elicited by two specialist insects from different feeding guilds. *J. Chem. Ecol.* 40:136–149.
- Stephenson, A. G. 1982. Iridoid glycosides in the nectar of *Catalpa speciosa* are unpalatable to nectar thieves. *J. Chem. Ecol.* 8:1025–1034.
- Tilman, D. 1978. Cherries, ants and tent caterpillars: timing of nectar production in relation to susceptibility of caterpillars to ant predation. *Ecology* 59:686–692.
- Wagner, D., and A. Kay. 2002. Do extrafloral nectaries distract ants from visiting flowers? An experimental test of an overlooked hypothesis. *Evol. Ecol. Res.* 4:293–305.
- Weller, J. L., I. C. Murfet, and J. B. Reid. 1997. Pea mutants with reduced sensitivity to far-red light define an important role for phytochrome a in day-length detection. *Plant Physiol.* 114:1225–1236.
- Yamawo, A., and Y. Hada. 2010. Effects of light on direct and indirect defenses against herbivores of young plants of *Mallotus japonicus* demonstrate a trade-off between two indirect defence traits. *Ann. Bot.* 106:143–148.