

# Conditional allelopathic potential of temperate lianas

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**Abstract** Allelopathy is often treated as an innate characteristic of a species rather than a phenotypically plastic trait that can vary with environmental conditions. Lianas are a highly competitive, phenotypically plastic life form that typically occur in both shaded and unshaded environments. As such, we hypothesized that temperate lianas may conditionally change allocation to allelopathic chemicals in response to light availability though the expected direction of change is unclear. Shading may reduce resource availability and therefore reduce allocation to allelochemicals, induce allelopathy as a competitive mechanism, or may not be related to allelopathy. To test the conditionality of allelopathy, sun and shade leaves of five common liana species (*Toxicodendron radicans*, *Parthenocissus quinquefolia*, *Celastrus orbiculatus*, *Lonicera*

*japonica*, and *Vitis vulpina*) were collected from a young deciduous forest in New Jersey, USA, and tested with laboratory bioassays to detect allelopathic potential. All liana species showed allelopathic potential, and three species exhibited induction of increased allelopathic potential in shaded environments. The two species that were not shade induced are late successional lianas that persist for long periods in forest canopies. In contrast, the inducible lianas were early successional species that typically decline with canopy closure. This research indicates that lianas have the potential to be allelopathic and allelopathic potential conditionally responds to shading only for species that would normally be excluded from the forest canopy. As early successional lianas are present throughout forest regeneration in a range of light environments, allelopathic plasticity may increase their success by differentially allocating resources based on environmental conditions.

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## Introduction

Lianas (woody vines) are strong competitors with trees, frequently overtopping and shading forest canopies (Avalos and Mulkey 1999; Perez-Salicrup 2001; Avalos et al. 2007). Lianas can also injure trunks, break branches, and lower the flexibility of

woody species (Lutz 1943; Siccama et al. 1976; Putz 1984). The effects of the above and belowground competition by lianas can lead to slower growth, lower fecundity, and early mortality of trees that host lianas (Stevens 1987; Dillenburg et al. 1993; Schnitzer et al. 2005; Ladwig and Meiners 2009; Ingwell et al. 2010). Because of these effects, lianas have become problematic in many systems, often requiring costly eradication or resulting in economic loss if left unmanaged (Gerwing 2001; Perez-Salicrup et al. 2001). The opportunistic strategies of lianas also cause many species to become important invaders worldwide (Robertson et al. 1994; Fike and Niering 1999; Csiszár 2009). Although direct competition between lianas and trees has been documented, the role of chemical interactions, including allelopathy, remains unclear.

Plant allelochemicals disperse into the environment and may inhibit growth and nutrient uptake of neighboring plants, prevent seedling establishment, or decrease community diversity (Inderjit and Dakshini 1995; Inderjit 1996; El-Khatib 2000; Abhilasha et al. 2008). Allelochemicals enter surrounding communities via leachates and volatiles from live or dead plant material (Jackson and Willemsen 1976; Rice 1984; Inderjit and Dakshini 1994; Inderjit 1996). Interest in the ecology of allelochemicals has grown substantially in recent years, particularly focusing on the role of allelopathy in invasion (Callaway and Aschehoug 2000; Inderjit et al. 2008; Pisula and Meiners 2010b; Kim and Lee 2011). Several reviews discuss the diversity of phytochemicals and the advancement of allelochemistry as a field (e.g., Macias et al. 2007; Duke 2010). Within lianas, several species contain allelopathic compounds though surveys have not been exhaustive (Csiszár 2009; Pisula and Meiners 2010a; Rashid et al. 2010).

The relationship between resource availability and allelopathic potential in natural communities is of increasing interest (Nilsson 1994; Karageorgou et al. 2002; Kong et al. 2004) as it could differentially influence plant growth in heterogeneous environments (San Emeterio et al. 2007; Ormeño et al. 2008). As resources change within a community, the role of allelopathy may also change. Allelopathic intensity presumably varies with changing resource availability, but the extent of this relationship is not fully understood (Karageorgou et al. 2002). For example, competition can both increase (Kong et al. 2004) and

decrease (Rivoal et al. 2011) allelochemical production and allelochemical composition can change with plant age and successional stage (Fernandez et al. 2009). This variation in the linkage between the environment and allelopathy makes prediction of directionality difficult. Reduced resource availability from competition may reduce the ability of a plant to produce allelochemicals or may induce the production of allelochemicals as a defense against competition.

Testing the allelopathic potential of individuals under different resource levels allows for the quantification of the relationship between resource availability and chemical interactions. The research presented here focuses on the influence of light availability on allelopathic potential. Chemical composition often varies between sun and shade leaves with sun leaves containing higher concentrations of phenolics and alkaloids (Islam et al. 2003; Guerra et al. 2010; Ingersoll et al. 2010). Light availability frequently varies spatially and temporally throughout the lifespan of long-lived individuals; therefore, allelopathic potential related to light availability would also presumably vary across space and time. Changing light levels may shape community composition directly through physiological limitations and also indirectly through the alteration of allelopathic interactions. Understanding how allelopathic potential varies with light availability could help in explaining the dynamic role of allelochemicals in plant communities.

Lianas are an ideal life form for studying the influence of light availability on allelopathic potential because lianas naturally occur in a wide range of environments. Lianas can grow in deep understory shade and in full sun in the uppermost layers of the canopy and also respond quickly to changing light conditions (Carter and Teramura 1988; Baars and Kelly 1996; Avalos and Mulkey 1999; Greenberg et al. 2002; Leicht and Silander 2006). The success of lianas under various light conditions allows for the examination of the relationship between light availability and allelopathic potential along a naturally occurring light gradient. Given the competitive advantage that lianas frequently exhibit, we first hypothesized that lianas would express some degree of allelopathic potential. Second, given the highly plastic nature of lianas, we hypothesized that allelopathic potential would be conditionally based on light availability. We tested these hypotheses by assessing the allelopathic

potentials of five liana species which naturally occurred in high light and shaded environments.

## Materials and methods

### Study site

Plant material was collected in New Jersey, USA, at the Hutcheson Memorial Forest, the site of the Buell-Small Succession Study (BSS; 40.30'N, 74.34'W). The BSS consists of ten-old fields, where agriculture was experimentally halted between 1958 and 1966 to examine vegetation dynamics during old-field succession (Pickett 1982; Cadenasso et al. 2009). The experimental BSS fields border an old-growth oak-hickory forest that served as a seed source for forest regeneration in the fields (Monk 1961; Buell et al. 1971). The fields have been abandoned for over 50 years and currently represent young, closed canopy forests (Ladwig and Meiners 2010a). Mean annual precipitation is 116.1 cm evenly distributed throughout the year, and mean monthly temperatures range from  $-1.6$  °C in January to  $22.4$  °C in August (New Jersey State Climatologist; National Climate Data Center). Based on the long-term data, the temporal dynamics of lianas are well characterized for the site (Ladwig and Meiners 2010b).

### Study species

We assessed the allelopathic potential of the five most abundant lianas at the BSS site: *Celastrus orbiculatus* (oriental bittersweet; Celastraceae), *Lonicera japonica* (Japanese honeysuckle; Caprifoliaceae), *Parthenocissus quinquefolia* (Virginia creeper; Vitaceae), *Toxicodendron radicans* (poison ivy; Anacardiaceae), and *Vitis vulpina* (fox grape; Vitaceae). The five species vary in geographic origin, climbing mechanism, and invasiveness, but share fundamental characteristics of lianas (Gleason and Cronquist 1991). All species were commonly found in the understory and canopy at the BSS (Ladwig and Meiners 2010b). In the understory, some lianas grew mainly as a ground cover (*P. quinquefolia*, *T. radicans*), while others more commonly covered small, understory trees and shrubs (*C. orbiculatus*, *V. vulpina*). *L. japonica* frequently occurred as both growth habits within the understory.

### Field sampling

Leaves from the five liana species were collected from shade and sun locations in late July 2009. Only fully developed, healthy leaves without visual damage or stress were collected to reduce the influence of other induced or developmental responses. The study species were all deciduous, therefore all leaf tissue was roughly the same age. Sun leaves were collected from locations with full exposure to sunlight, and shade leaves were collected from plants in the understory receiving only occasional sunflecks. Light transmittance in the understory of the BSS ranged from 2.6 to 17.2 % on average (unpublished data). Sun and shade collections were often in close proximity, minimizing the potential influence of other factors on allelopathic potential. For each liana species  $\times$  light combination, 80 g (fresh weight) was collected from at least ten different individuals and mixed. To document the morphological variation between sun and shade leaves, area and fresh mass were recorded for 20 random sun and shade leaves of each species. Leaf area and density (dry mass per unit area;  $\text{g}/\text{cm}^2$ ) were compared between sun and shade leaves with a separate ANOVA for each species. Leaf density was used instead of specific leaf area as it captures the same allocation pattern, but is less variable and has better statistical properties (Wilson et al. 1999). Leaves were dried at  $60$  °C for 2 days in preparation for laboratory bioassays.

### Laboratory bioassays

Allelopathic potential is often tested through bioassays, typically by assessing the effects of plant tissue extracts on the germination of a target species (Inderjit and Dakshini 1995). Though there are limitations associated with using bioassays to determine allelopathic potential (Inderjit and Dakshini 1995; Gibson 2002), the bioassay approach allowed us to evaluate and compare taxonomically unrelated species with widely differing chemistries. The allelopathic potential of sun and shade leaves was assessed following the bioassay methods of Butcko and Jensen (2002) as modified by Pisula and Meiners (2010a). We used radish (*Raphanus sativus* L. 'Early Scarlet Globe': Bay Farm Services, Inc., Bay City, MI) as the target species in all trials. Radish was used to indicate allelopathic potential because it germinates quickly, it

is commonly used in allelopathic studies, it is sensitive to allelopathic inhibition, and it responds to differences among species' extracts (Butcko and Jensen 2002; Pisula and Meiners 2010a, b). For each liana species  $\times$  light combination, extracts were made from 12.5 g of dried leaf tissue in 500 ml of deionized water. This ratio of plant biomass to water generates plant extracts that affect germination of target species and allows for differentiation among species (Butcko and Jensen 2002; Pisula and Meiners 2010a). The mixture was placed on a magnetic stirrer for 24 h at room temperature and strained through cheesecloth to remove particulate plant material. The chemical composition of the leachate was unknown. Dilutions of each extract were made in 10 % increments ranging from 0 to 100 % of the extract. This dilution range represented a gradient of plant extracts from 0 to 2.5 % w/w. Filter paper was placed in 90-mm petri plates with 20 seeds of the target species.

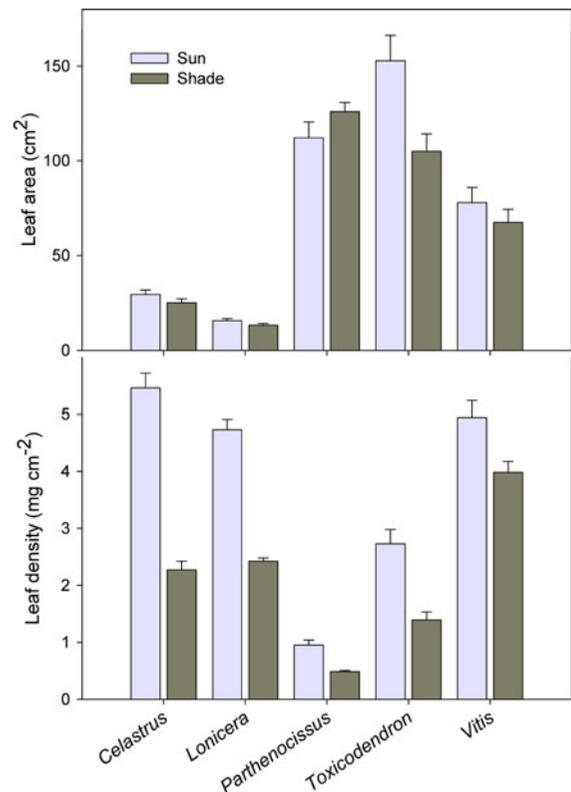
Five trials were run at each dilution for each liana species  $\times$  light condition tested. Four millilitre of extract was added to each plate and incubated at 25 °C for a 12/12 h light/dark cycle. Petri plates were placed in sealed plastic bags to retain moisture. After 4 days, germinated seeds were counted. Data were analyzed in three ways. Germination as a function of extract concentration and light level was evaluated for each species with a logistic analysis using extract concentration as a continuous variable and light as categorical. This analysis specifically tested for shifts in potential allelopathy between light conditions through the significance of the light  $\times$  concentration interaction. We used this analysis as our primary hypothesis test. This analysis was followed by individual logistic regressions to quantify the germination response for each plant extract. This analysis was used to visualize differences between sun and shade allelopathic potential. Finally, to determine the threshold concentration at which allelopathic potential was noted, Tukey's post hoc tests from separate ANOVAs for each species by light combination were used to determine the lowest extract concentration that differed from the control.

## Results

Light conditions altered leaf morphology, particularly leaf density, in all the liana species studied. Leaf area was not uniformly influenced by light environment,

and for most species, sun and shade leaves had the same area with the exception of the significantly larger sun leaves of *T. radicans* ( $p = 0.0057$ ,  $F_{1,38} = 8.6$ ; Fig. 1). Leaf density was significantly greater for sun leaves than shade leaves in all species (*V. vulpina*,  $p = 0.0105$ ; all other species  $p < 0.0001$ ; Fig. 1). For *C. orbiculata*, *L. japonica*, *P. quinquefolia*, and *T. radicans*, leaf density in the shade was at most half of that of plants from full sun environments. The shade effect was much less pronounced in *V. vulpina*.

All lianas expressed allelopathic potential, but intensity varied among species. In general, the most allelopathic lianas were *P. quinquefolia* and *C. orbiculatus*, as germination inhibition continually increased with increasing extract concentration (Fig. 2). However, the greatest germination inhibition occurred with full strength extract from *L. japonica*, but the response



**Fig. 1** Top—Leaf area of sun (light bars) and shade (dark bars) leaves. *Toxicodnedron radicans* sun leaves were significantly larger than shade leaves ( $p = 0.0057$ ), all other species were not significantly different. Bottom—Leaf densities of sun and shade leaves. For all species, sun leaves had significantly greater density than shade leaves at an  $\alpha = 0.05$ , Error bars indicate  $\pm 1$  SE

at this concentration was a large departure from inhibition at other extract concentrations. *T. radicans* and *V. vulpina* expressed the lowest allelopathic potential. The allelopathic potentials of *C. orbiculatus* and *L. japonica* corresponded to previously recorded levels (Pisula and Meiners 2010b).

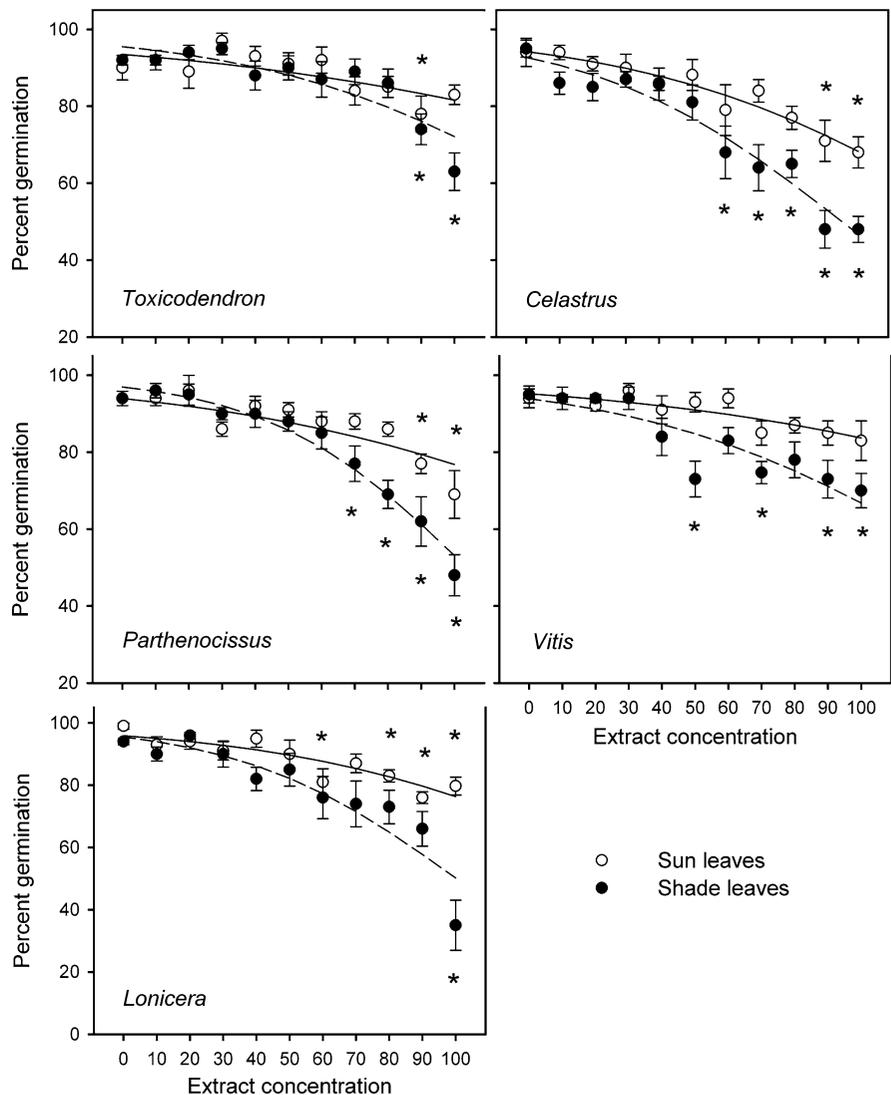
The interaction between extract concentration and light level was significant for three of the species (*L. japonica*, *T. radicans*, and *P. quinquefolia*), indicating that there was increased germination inhibition under shade conditions (Table 1). Individual logistic regressions of percentage germination as a function of extract concentration were performed for each species (Table 2). Coefficients ( $\beta$  values) from these regressions were used to compare the relative strength of plant

extracts on seed germination. Lower  $\beta$  values for shade leaves of all species indicated greater germination inhibition and allelopathic toxicity (Table 2). The size of the shade effect varied among species, with *C. orbiculata* showing the smallest increase in  $\beta$  (32%), *V. vulpina* and *L. japonica* moderate increases (51 and 54%) and the  $\beta$  of *T. radicans* and *P. quinquefolia* increasing the most (76 and 115%).

### Discussion

All liana species responded morphologically to shade as expected, producing thinner leaves in shaded environments. Morphological plasticity of leaves with

**Fig. 2** Allelopathic effects of plant extract concentrations from sun and shade environments on radish seed percent germination (vertical axis). The extract concentration range represented a gradient of plant extracts from 0 to 2.5 % w/w. Inducible lianas are shown on the left and non-inducible lianas on the right. Lines are predicted germination percentages from separate logistic regressions for sun (solid line) and shade (dashed line) plants. Stars indicate germination rates that were significantly different than the pure water control. Points are the average germination of the five trials at each extract concentration  $\pm 1$  SE



**Table 1** Logistic regression analysis of the influence of light environment (categorical) on plant extract's toxicity

	Model term	df	Wald $\chi^2$	<i>p</i>
<i>Celastrus orbiculatus</i>	Concentration	1	150.76	< <b>0.0001</b>
	Light	1	0.91	0.3412
	Conc. × light	1	2.85	0.0911
<i>Lonicera japonica</i>	Concentration	1	134.44	< <b>0.0001</b>
	Light	1	0.10	0.7504
	Conc. × light	1	6.08	<b>0.0137</b>
<i>Parthenocissus quinquefolia</i>	Concentration	1	127.38	< <b>0.0001</b>
	Light	1	5.44	<b>0.0196</b>
	Conc. × light	1	17.07	< <b>0.0001</b>
<i>Toxicodendron radicans</i>	Concentration	1	56.60	< <b>0.0001</b>
	Light	1	1.43	0.2311
	Conc. × light	1	4.34	<b>0.0372</b>
<i>Vitis vulpina</i>	Concentration	1	59.22	< <b>0.0001</b>
	Light	1	0.67	0.4138
	Conc. × light	1	2.48	0.1154

*Bold* indicates a significant *p* value at  $\alpha = 0.05$

regard to light availability typically relates to maintaining a positive energy balance in leaves regardless of local light environment (Valladares and Niinemets 2008). Sun exposed leaves are typically thicker, and therefore more dense, to take photosynthetic advantage of higher light intensities. In contrast, leaves in shaded environments can be larger to access more light with fewer transpirational costs, but must also have thinner photosynthetic tissues (Carpenter and Smith 1981; Abrams and Kubiske 1990; Sack et al. 2003). The direction of morphological changes in the study species confirmed that the sun and shade leaves were physiologically and developmentally responding to local light conditions. Differences in leaf morphology strongly suggest that shading was the primary difference between collections, and therefore responsible for the observed variation in allelopathic potential.

Liana species also varied in the strength of their allelopathic potentials though all species generated significant germination inhibition responses in bioassays. In sun environments, the two non-native lianas (*L. japonica* and *C. orbiculata*) had the greatest allelopathic potential. This pattern suggests that invasiveness in these two species may be linked with their ability to produce allelochemicals. *T. radicans* and *V. vulpina* consistently expressed the weakest effects on germination in the bioassays. Of the natives, other *Vitis* species and *P. quinquefolia* were allelopathic in

Eurasia, where they are invasive (Lambdon et al. 2008; Csiszár 2009). For this reason, it is difficult to separate whether allelopathy is more associated with invasion or with liana species in general.

Separate to the issue of overall allelopathic potential is our original question, whether allelopathy is a plastic response to resource availability. In this study, the allelopathic potential of three species—*L. japonica*, *P. quinquefolia*, and *T. radicans*—was conditional with light level. *L. japonica* and *P. quinquefolia* became the most allelopathic species when grown in the shade, reversing the ranking of allelopathic potentials based on sun leaves for the top three species. *T. radicans* was consistently the least allelopathic species in both environments, yet it still showed a significant induction of allelopathic potential in shade. Patterns of allelopathic induction appear separate to the induction of shade morphology, as *C. orbiculatus* had very strong morphological responses to shading, but no allelopathic response.

A potential explanation for the difference between inducible and non-inducible liana species may lay in their ecology. The two species with allelopathic potentials independent from light availability occupy a different successional niche than the other three lianas. *C. orbiculatus* and *Vitis* species both occur later in succession and maintain high abundance following canopy closure (Ladwig and Meiners 2010b). In

**Table 2** Regression coefficients ( $\beta \pm$  standard error) of the relationship between plant extract concentration and percent germination to quantify the strength of allelopathy for each liana species

	Sun			Shade		
	$\beta$	SE	<i>p</i>	$\beta$	SE	<i>p</i>
<i>Celastrus orbiculatus</i>	−0.0203	0.0029	< <b>0.0001</b>	−0.0267	0.0025	< <b>0.0001</b>
<i>Lonicera japonica</i>	−0.0198	0.0033	< <b>0.0001</b>	−0.0305	0.0028	< <b>0.0001</b>
<i>Parthenocissus quinquefolia</i>	−0.0155	0.0030	< <b>0.0001</b>	−0.0334	0.0031	< <b>0.0001</b>
<i>Toxicodendron radicans</i>	−0.0120	0.0031	< <b>0.0001</b>	−0.0211	0.0031	< <b>0.0001</b>
<i>Vitis vulpina</i>	−0.0135	0.0033	< <b>0.0001</b>	−0.0204	0.0028	< <b>0.0001</b>

*Bold* indicates a significant *p* value

contrast, the other three lianas establish early in succession, peak at intermediate ages, and then decline following canopy closure. These three species also tend to form a persistent understory layer much more commonly than *C. orbiculatus* or *Vitis* species (LML personal observation). Conditional allelopathy in these taxa may, therefore, relate to successional status and the range of environmental conditions that an individual may experience over its lifetime. As late successional lianas tend to persist for long periods in full sun following canopy closure, resource variability may be less important to their long-term fitness.

The conditional allelopathy of lianas potentially influences communities both spatially and temporally. Spatially within the forest, lianas prefer edges and forest gaps (Londré and Schnitzer 2006), and these high light locations may foster less chemical inhibition from lianas. Many temperate lianas also show host tree preference (Talley et al. 1996; Ladwig and Meiners 2010a; Leicht-Young et al. 2010); thus, any chemical influence of lianas may follow the patterns of host tree distributions. Temporally throughout succession, trends of allelopathy could shift with changing resource availability. Lianas can enter an old-field community shortly after field abandonment and persist throughout forest regeneration (Ladwig and Meiners 2010b). Herbaceous plants within the high light conditions of early successional communities may not experience chemical inhibition from lianas. As succession progresses, canopy closure leads to decreased light levels, and lianas that find themselves in the understory may utilize allelochemicals, while those in the canopy remain less allelopathic.

The way in which allelopathic potential would respond to light availability was difficult to predict a priori. Resource limitation may have reduced the

ability of the plant to produce allelochemicals (Rivoal et al. 2011) or may have served as a signal to induce the production of allelochemicals (Kong et al. 2004). In this system, shading induced the species capable of plasticity in allelopathy to increase their allelopathic potential. This induction was independent from the morphological responses of species and from their overall effectiveness in the bioassays. This suggests that allelopathy in *L. japonica*, *P. quinquefolia*, and *T. radicans* is contingent on light availability and functions as a chemical defense against light competition.

Although these species exhibited conditional allelopathy in laboratory trials, it is unclear how strong these effects would be in the field. Inhibition of allelochemical in laboratory trials do not directly indicate ecological significance (Kaur et al. 2009). Many factors can interact with allelochemicals during their journey from leaving one plant to encountering the root of another. Within the soil there can be leaching, adsorption, or chemical alterations by abiotic or biotic forces, all of which could influence the impact of allelochemicals within the soil (Blum et al. 1999; Inderjit 2005; Barto et al. 2011). Although these aspects were not directly measured in this study, we still found that the potential for lianas to produce allelochemicals was conditional on light levels for some species.

Conditional allelopathy may be common in plant communities as a mechanism to more efficiently allocate resources. From an allocation perspective, producing allelochemicals only when in competition with other plants may increase fitness, analogous to inducible herbivore defenses (Harvell and Tollrian 1999). Plants grown in full sun or with sufficient soil resources may preferentially allocate resources to growth and reproduction rather than defensive

chemistry. Costs associated with allelochemical production (Lankau 2008) would only be incurred once resources became limiting. Data on the lianas in this system suggest that even inducible species maintain some allelopathic activity when in full sun, but increase allocation to allelochemicals when in competition. Unfortunately, it is difficult to assess how common conditional allelopathy is in plant communities because studies do not often explicitly study a range of environmental conditions. Plasticity in response to local environments may generate variability in allelopathic interactions across or even within habitats. Environmental variation will likely make it more difficult to understand the importance of allelopathy in structuring communities.

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