Functional correlates of allelopathic potential in a successional plant community

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Abstract Allelopathy, plant–plant interactions mediated through chemical production, is an active area of ecological research. Despite this widespread interest, we still lack community scale information on the prevalence of this interaction and the types of species that may be expected to be allelopathic. To address this research need, the allelopathic potential of 65 plant species from all stages of succession in the Piedmont region of New Jersey, USA, was determined with laboratory bioassays. The strength of each species' allelopathic activity was then related to life form, origin, and fundamental plant traits. The vast majority of species tested exhibited significant allelopathic effects in the bioassays, with many of these having fairly strong effects. Overall, the allelopathic potential of species decreased with life span, roughly following the successional transitions from short-lived to long-lived herbs and to woody species. Herbaceous species on average were more allelopathic than woody species, but there was no difference between native and non-native species once life form was accounted for. In a principal components analysis, allelopathy was associated with other plant traits, but these relationships differed between woody and herbaceous species.

Allelopathic potential was positively associated with plant height in herbaceous species, but negatively associated with height, leaf mass, and seed mass in woody species. These results indicate that allelopathy may be a quite common ecological strategy in plants and is equally common in both native and non-native species. The linkage of allelopathy with other plant functional traits suggests that allelopathy can and should be integrated into the broader suite of plant strategies that are studied.

Keywords Allelopathy · Biological invasions · Functional traits · Life history · Plant strategies · Succession

Introduction

Allelopathy, plant–plant interactions mediated through chemicals released into the environment (Rice 1974), has been investigated in an ecological context for decades. Studies of allelopathy typically focus on identifying the mode and strength of the interaction between the allelopathy and one or more target species. These studies have identified a wide array of chemicals responsible for allelopathic interactions (e.g., Duke and Dayan 2006; Mallik et al. 2008; Kim and Lee 2011). Allelochemicals may have direct effects on neighboring species (Abhilasha et al. 2008; Thorpe et al. 2009; Kong 2010; Uesugi and Kessler 2013), or may indirectly influence growth by altering soil microbial

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communities (Lankau 2010a) or mutualisms associated with the target species (Roberts and Anderson 2005; Zhang et al. 2007; Hale et al. 2011). Allelopathic interactions may be quite complex (Koocheki et al. 2013), as they may be contingent on soil microbial communities (Lankau 2010b; Cipollini et al. 2012), the conditions under which the allelopathic plant is growing (Stowe 1979; Kong et al. 2002, 2004; Thelen et al. 2005; Rivoal et al. 2011; Uesugi and Kessler 2013), and on the evolutionary experience of the target species (Siemens et al. 2002; Callaway et al. 2005; Thorpe et al. 2009). Despite this complexity, allelopathy has been thought to play a role in plant–plant competition, plant invasions, and ecosystem processes (Wardle et al. 1998; Abhilasha et al. 2008; Inderjit et al. 2008; Mallik et al. 2008; Bertholdsson 2011; Inderjit et al. 2011Kim and Lee 2011; Lorenzo et al. 2013). Because of its potentially strong linkage with interaction outcomes, allelopathy may be an important plant functional trait for understanding community dynamics.

While the focus of allelopathic studies on the autecology of species provides detailed information on the chemicals produced and their modes of effect, scaling these studies to the community level is problematic. Most importantly, species selected for study are typically thought to be allelopathic based on field observations. This bias in species selection makes it impossible to determine the prevalence of allelopathy in plant communities from individual studies (Meiners et al. 2012). Similarly, the differences in the allelopathic chemicals produced across plant taxa, and differences in research methodologies create difficulties in assessing the magnitude of allelopathic effects and in comparing species. To understand the functional role of allelopathy at a community scale, a comparable measure of allelopathic activity is necessary to compare species and identify the ecological correlates that determine which species are likely to be allelopathic within plant communities. As with other plant functional traits such as chemical herbivore defenses, chemical defenses associated with competition are expected to be associated with other plant characteristics (Lankau 2008). Determining the prevalence and patterns across species will be necessary to fully develop a realistic perspective on allelopathy in plant communities.

In contrast to the detail of the chemically-focused autecological approach, bioassays provide a much broader view of allelopathic potential, reflecting the entire suite of chemicals produced by a plant species.

As an effect-based measure of allelopathic potential, species with differing chemistries can be compared on an equivalent basis—an important characteristic of any functional trait. By using controlled germination conditions, the species- and system-specific contingencies that mitigate allelochemical interactions with the physical structure and microbial composition of soils are dramatically reduced. The bioassay approach is also logistically simpler, allowing functional characterization of the broad suite of species necessary to assess allelopathy at the community scale. To verify the allelopathic activity of individual plant species, more traditional ecological approaches will still be necessary, including interactions with soil microbes, commonly associated plant species, and multiple plant tissues. While the limitations imposed by such a simple approach have been pointed out many times (e.g., Inderjit and Dakshini 1995; Gibson 2002), bioassays provide useful estimates of the functional characteristics of species. For example, the bioassay approach is analogous to glasshouse studies where plant relative growth rate (RGR) is determined. RGR under such artificial conditions is clearly different than would be seen in the field, but still yields useful information on the functional characteristics of species.

To understand the community ecology of allelopathy, a bioassay approach was used to characterize the allelopathic potential of 65 species representing all successional stages of a diverse plant community. These data were combined with traditional plant functional traits to address the following community level questions: (1) What is the prevalence and range of magnitude of allelopathic potential in the species pool? (2) What are the primary sources of variation in allelopathic potential among species? (3) Can allelopathy be integrated with other functional traits to inform plant strategies? As allelopathy is thought to increase a species' competitive ability, it should be associated with other competitive traits. The overarching goal of this work is to provide an ecological context for plant–plant chemical interactions in communities.

Materials and methods

BSS study and site

This research uses as its ecological context a long-term study of old field succession—the Buell-Small

Succession Study (BSS). The site is located in the Piedmont region of New Jersey, USA, at the Hutcheson Memorial Forest Center (HMFC; 40.300N, 74.340W). The BSS consists of ten old fields, where agriculture was experimentally halted between 1958 and 1966 following a diversity of pre-abandonment conditions to document the dynamics of old field succession (Pickett 1982; Cadenasso et al. 2009). The experimental BSS fields border an old-growth oak-hickory (*Quercus-Carya*) forest that served as a seed source for forest regeneration in the fields (Monk 1961; Buell et al. 1971). Mean annual precipitation is 116.1 cm which is evenly distributed throughout the year, and mean monthly temperatures range from -0.6 °C in January to 22.4 °C in August (New Jersey State Climatologist; National Climate Data Center). All plant materials were collected from the HMFC or in adjacent areas to maintain the same soil and climatic conditions among species.

Species collection and trait data

The 65 species selected for the survey were specifically chosen from the BSS species pool to reflect dominant species across successional stages (Meiners 2007), represent a range of species origins (native and non-native) and life forms (annual, perennial, liana, etc.), or to represent species likely to expand as the forest community further develops (see Table 3 in Appendix). These represent most of the species currently abundant enough to collect sufficient leaf material. Care was also taken to examine as broad of suite of taxa as possible. Leaf tissues were collected from several healthy and vigorous individuals of each species. In the majority of cases, leaf tissues were collected from 10 or more individuals to capture any variation among individuals in allelopathic activity. Because of their small size, the number of individuals collected from many of the herbaceous species was much larger to provide sufficient leaf material. Collected leaf material was placed in paper bags and immediately dried at 60 °C to prevent microbial breakdown of tissues.

As part of the larger project, plant trait data have been collected for many species in the BSS. Methods for trait collection follow recommendations in Cornelissen et al. (2003). Potential plant height and seed mass were determined from published and online sources (e.g., Gleason and Cronquist 1991) and supplemented with data collection when necessary.

Leaf physical and nutrient characteristics were determined from 10 or more individuals from HMFC whenever possible. Leaf nutrient analyses were conducted by the University of Georgia's Stable Isotope/Soil Biology Laboratory (www.swpa.uga.edu) following standard protocols.

Allelopathy bioassays

The allelopathic potential of each plant species 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 quantify allelopathic potential because it germinates quickly, it is sensitive to allelopathic inhibition, and it can differentiate among species (Butcko and Jensen 2002; Pisula and Meiners 2010a, b) or between species growing under different environmental conditions (Ladwig et al. 2012). For each species, extracts were made from 12.5 g of dried leaf tissue in 500 ml of deionized water. The mixture was placed on a magnetic stirrer for 24 h at room temperature and strained through cheesecloth to remove particulate plant material. A single target species and leaf tissues were used for logistical reasons to allow for the comparison of the large number of plant species here.

Dilutions of each extract were made in 10 % increments ranging from 0 to 100 % of the original extract concentration, representing a gradient of plant extracts from 0 to 2.5 % w/w. Filter paper was placed in 90-mm petri dishes with 20 seeds of the target species. Five trials were run at each dilution for each plant species tested. Four mL of extract was added to each plate and incubated at 25 °C under a 12/12 h light/dark cycle. Petri dishes were placed in sealed plastic bags to retain moisture. After 4 days, germinated seeds were counted.

Statistical analyses

To quantify the strength of inhibition for each species, the data were analyzed with a logistic regression using count data from each dish individually as a function of extract concentration. The coefficient from this analysis was used as the metric for allelopathic potential and was always at least slightly negative. For simplicity of presentation, the absolute value of these coefficients

was taken so that greater values represent greater inhibition of germination. These coefficients were then used in subsequent analyses to determine patterns in toxicity across the plant community.

To assess variation in allelopathic potential based on life form, species were separated into annual, biennial/short-lived perennials, and perennial species for herbaceous groups and shrubs, lianas, and trees for woody taxa following Gleason and Cronquist (1991). This transition in life forms also represents the order of dominance of each group during succession within the BSS (Pickett et al. 2013), so patterns among life forms can also be used to broadly represent successional trajectories in allelopathy. To determine associations between allelopathic potential and non-native species invasions, species life forms were combined into woody and herbaceous species because of limited replication in life forms. Finally, for those plant families with three or more representatives in the survey, systematic variation among families was also tested. All categorical analyses utilized ANOVA and the measure of allelopathic potential did not require transformation.

To relate allelopathy to other plant traits, principal components analyses (PCA) were used to determine the underlying axes of variation among plant traits. Log values were used for height, leaf mass, water content, SLA, and seed mass as is typically done in trait analyses (e.g., Westoby and Wright 2006). Because of the large shift in strategies between woody and herbaceous species, separate analyses were conducted for each group using a correlation matrix. Associations between the individual plant traits and the PCA axes were evaluated with Pearson correlations with a Dunn-Šidák correction for multiple comparisons.

Results

The vast majority of species (91.8 %) showed some allelopathic activity in the bioassays with only six woody species (*Acer rubrum* L., *A. saccharum* Marshall, *A. negundo* L., *Elaeagnus angustifolia* L., *Juglans nigra* L., and *Quercus rubra* L.) not generating a statistically significant depression in germination. Together, the data reveal a gradient of inhibitory effects ranging from effectively no effects to fairly strong inhibition (Fig. 1.). Most species generated slight to moderate effects on germination, though 21.5 % of the
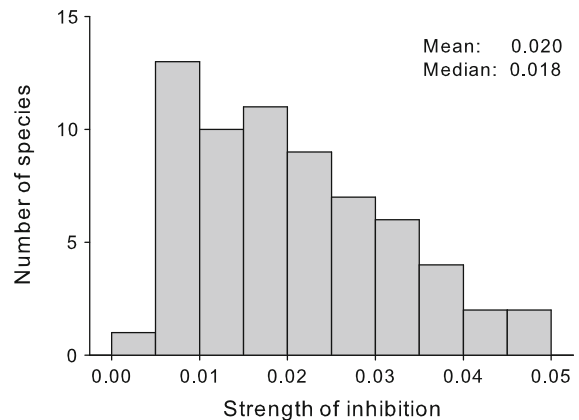

Fig. 1 Frequency distribution of allelopathic potential among the 65 species used in this survey. Total range was 0.001 for *Acer rubrum* to 0.0485 for *Daucus carota*. Strength of inhibition measured as the absolute value of the regression coefficient from a logistic regression for germination in each species
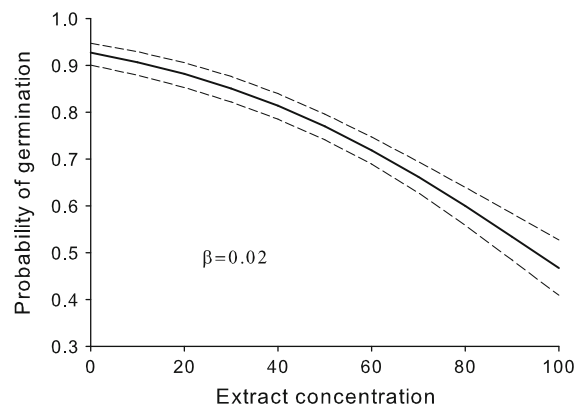

Fig. 2 Example logistic regression showing the magnitude of the germination response to a species with the survey average $\beta = 0.02$

species tested generated fairly large effects with regression coefficients of 0.03 or higher. To place this into context, the average strength of inhibition for the species tested, $\beta = 0.020$, would generate a decrease in germination of approximately 50 % at the highest leaf extract concentration in the bioassays (Fig 2.). The species with the greatest strength of inhibition were *Daucus carota* ($\beta = 0.0485$), *Centaurea dubia* ($\beta = 0.0455$), *Ambrosia artemisiifolia* ($\beta = 0.0412$), and *Bromus racemosus* ($\beta = 0.0404$). Overall, plants with a moderate or greater allelopathic potential appear to be fairly common within the community.
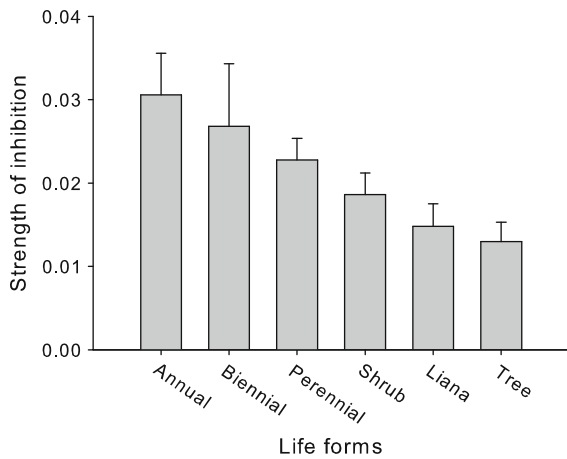
Fig. 3 Influence of life form on allelopathic potential. Life forms are ordered by their dominance in succession within the BSS from earliest to latest. Data plotted are means ± 1 SE

Table 1 Influence of life form (herbaceous vs. woody) and species origin (native vs. non-native) on the allelopathic potential of species in a successional community

Source	df	MS	F	P
Life form	1	0.00099	9.42	0.0082
Origin	1	0.00005	0.40	0.5273
Form × Origin	1	0.00005	0.49	0.4868
Error	61	0.00011		

Overall model: $F_{3,61} = 4.44$; $P = 0.0069$; $R^2 = 0.179$

Strength of inhibition was significantly associated with plant life form (ANOVA: $F_{5,59} = 3.61$, $P = 0.0065$, $R^2 = 0.234$). Allelopathic potential was the greatest in annuals and biennials (Fig. 3), and lowest in lianas and trees. Overall, allelopathic potential declined with the successional peak of each life form, with the later successional forms exhibiting lower strength of inhibition. However, there was sufficient variation within life forms so that the only significant post hoc comparison was between annuals and trees. As there was a strong dichotomy between the allelopathic potential of herbaceous and woody species, these groups were separated in an ANOVA to determine whether native and non-native species differed in allelopathic potential. Though the overall model was significant, only plant form significantly influenced allelopathic potential, while species origin had no effect (Table 1; Fig. 4).
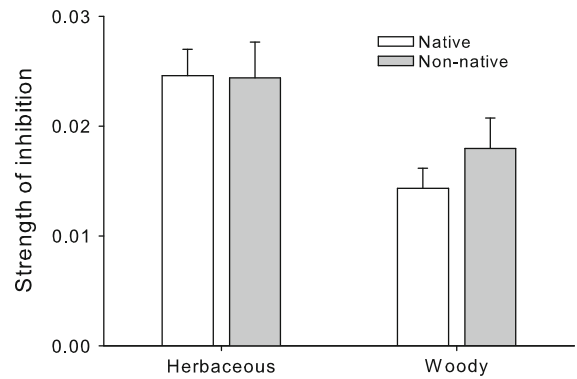

Fig. 4 Influence of life form and species origin on allelopathic potential. Data plotted are mean ± 1 SE
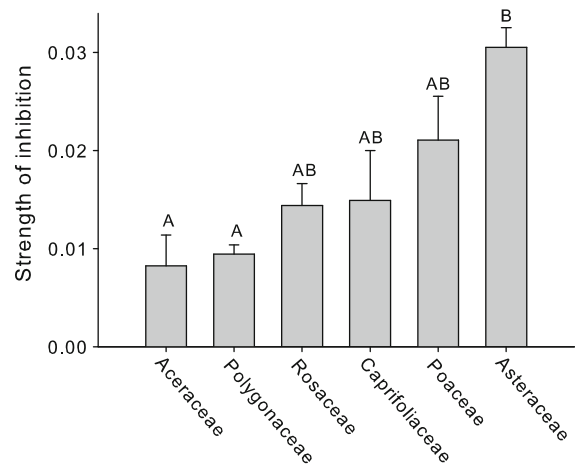
Fig. 5 Taxonomic patterns in allelopathic potential. Data include all plant families with at least three representative species. Data plotted are mean ± 1 SE and means with the same letters are not distinguishable with a Tukey's post hoc test

There was also a strong taxonomic pattern in allelopathic potential in those families represented by three or more species (Fig. 5). Species in the Asteraceae consistently had the greatest inhibition of germination in the bioassays, followed by the grasses (Poaceae). The consistently weakest effects were seen in the trees of the Aceraceae and the herbs of the Polygonaceae (ANOVA: $F_{5,32} = 8.43$, $P < 0.0001$, $R^2 = 0.57$).

Allelopathy was related to a suite of other plant functional traits which differed between woody and herbaceous taxa (Table 2). In the principal components analysis of herbaceous species, allelopathic potential was associated with the third PCA axis,

Table 2 Principal components analyses of allelopathic potential and other plant functional traits for herbaceous ($n = 34$) and woody ($n = 28$) species

	Herbaceous species			Woody species		
	PCA 1	PCA 2	PCA 3	PCA 1	PCA 2	PCA 3
Variation explained	31.0 %	17.7 %	16.1 %	29.7 %	25.6 %	14.0 %
Traits Allelopathy	0.198	−0.296	**0.568**	0.412	**−0.523**	−0.256
Log height	−0.095	0.012	**0.841**	0.275	**0.706**	0.036
Log leaf mass	−0.132	**0.893**	0.188	**0.433**	**0.578**	−0.085
Log WC	**0.685**	0.039	−0.350	0.404	−0.486	**0.625**
Log SLA	**0.756**	−0.331	−0.011	**0.632**	−0.018	**0.626**
Log seed mass	0.368	**0.631**	−0.045	0.330	**0.740**	0.036
Leaf P content	**0.781**	0.128	0.013	**0.655**	−0.393	−0.446
Leaf C:N ratio	**−0.793**	−0.087	−0.312	**−0.917**	0.009	0.254

Values presented are pearson correlation coefficients of the individual trait with the PCA axis. Values in bold were significant at $\alpha = 0.05$ following Dunn-Sidák correction for multiple comparisons

which explained 16.1 % of the variation in plant traits among species. Allelopathic potential loaded positively along with plant height, suggesting that taller herbs were more allelopathic than shorter ones. Allelopathic potential was associated with the second PCA axis in woody species, which explained 25.6 % of the variation in trait data. Allelopathic potential loaded negatively on this PCA axis, opposite to plant height, leaf mass, and seed mass which were negatively associated. Allelopathic potential was statistically independent of the plant traits, leaf C:N ratio, leaf P, specific leaf area, and leaf water content in both woody and herbaceous species.

Discussion

Allelopathy appears to be a common characteristic of species in this successional system with the vast majority having at least some allelopathic activity in the bioassays. Perhaps more surprising was the number of species in this survey which showed activity that may be sufficient to influence interactions with other species. The prevalence of allelopathy in this survey is consistent with early surveys of allelopathy which found many plant species to be allelopathic (e.g., Del Moral and Cates 1971; Jackson and Willemsen 1976). The bioassay results presented here are also consistent with other analyses of a great

number of the species in the survey that also found allelopathic effects (e.g., McCarthy and Hanson 1998; Skulman et al. 2004; Wang et al. 2005; Abhilasha et al. 2008; Gómez-Aparicio and Canham 2008).

The prevalence of allelopathic potential in this survey has two implications for understanding the role of allelopathy in plant communities. First, allelopathy may be a quite common plant characteristic, much like anti-herbivore chemical defenses. If this is the case, then allelopathic interactions in diverse plant assemblages such as the one studied here are likely diffuse and it may be difficult to isolate the effects of individual species in the field. Analytical approaches that incorporate the allelopathic signature of the local assemblage may be better able to detect community level effects. Second, experimental field and greenhouse studies of allelopathic interactions often focus on one allelopathic species and one or more target species. If the target species are also allelopathic, the manipulation of allelopathic activity will affect both species. For example, activated charcoal is often used to effectively remove allelochemicals from the soil, resulting in treatments that can isolate the contribution of allelopathy to the competitive effect (e.g., Siemens et al. 2002; Zhang et al. 2007; Gómez-Aparicio and Canham 2008; Yuan et al. 2012). However, if both the trial and target species are allelopathic, then the treatments represent two species competing with and without allelochemicals. Given the frequency of

allelopathy in the herbaceous plants of this survey, selecting two plants with a moderate allelopathic potential would appear quite likely.

There was a strong taxonomic component to allelopathic activity in this survey. At least a portion of the allelopathic patterns seen may be driven by the composition of the community. The Asteraceae had consistently high allelopathic activity (Chon and Nelson 2010), with all but one of the 15 species with a β of greater than the community mean of 0.02. As species of the Asteraceae dominate early to mid-successional communities in the study region, a significant portion of the herbaceous communities' allelopathic potential comes from these species. Similarly, later successional trees of the Aceraceae and herbs of the Polygonaceae had consistently low allelopathic potentials. Related taxa may not only have similar allelopathic potentials, but also would likely produce a similar suite of chemicals (Chon and Nelson 2010; Kim and Lee 2011). Suites of related species with a range of allelopathic traits would provide a mechanism by which the evolution and function of allelopathy could be studied in the context of life history trade-offs.

Ecological role of allelopathy

Despite the limitations of such laboratory assays, there were clear patterns that emerged from the community-wide survey of allelopathic potential in this system. Allelopathy has been frequently invoked as a potential mechanism of succession (Wilson and Rice 1968; Rice 1972; Bazzaz 1975; Jackson and Willemsen 1976; Stowe 1979; Hils and Vankat 1982; Myster and Pickett 1992; Kaligarič et al. 2011) either in slowing or promoting compositional turnover. Though there was much variation, the allelopathic potential of life forms followed their patterns of dominance in old field succession. Annuals and biennials/short-lived perennials had the highest allelopathic potential, with decreased activity in herbaceous perennials. This ecological strategy is consistent with the short-time period during which an annual or other short-lived plant has to gather sufficient resources to reproduce. Allelopathy may allow short-lived plants to chemically protect their access to resources and increase fecundity. The short-lived forest understory herbs

Microstegium vimineum (annual) and *Alliaria petiolata* (biennial), both non-natives, also had high allelopathic potential, so the pattern was not purely a successional one. Woody species had a marked decrease in allelopathic activity relative to herbaceous species, with the more opportunistic shrub and liana species intermediate between canopy trees and herbaceous perennials. This does not mean that all canopy trees had low allelopathic potential. *Ailanthus altissima*, an invasive non-native species had high activity ($\beta = 0.0332$) relative to all the other trees in the survey and has shown allelopathic impacts in the field (Lawrence et al. 1991; Heisey 1996; Gómez-Aparicio and Canham 2008). In general, allelopathic potential decreased with succession, suggesting a shift in ecological strategy over time. Though a successional shift from soil resource limitation to light limitation has been suggested (Tilman 1985), allelopathic interactions may alter competitive interactions for either light or soil resources by reducing the recruitment of adjacent species. However, the pattern of shorter woody plants having greater allelopathic potential would be consistent with allelopathy being a response to light competition (Ladwig et al. 2012).

One of the primary motivations in contemporary allelopathy ecological research has been an interest in biological invasions. Studies of non-native plant invasions often invoke allelopathy as a mechanism behind the success and impacts of the invading species (Heisey 1996; Roberts and Anderson 2005; Abhilasha et al. 2008; Inderjit et al. 2008, 2011). As the invaded plant community may be evolutionarily naïve to the chemicals produced by an invader, the impacts of the chemicals may be greater (Callaway and Aschehoug 2000; Abhilasha et al. 2008; Thorpe et al. 2009; Kim and Lee 2011). However, this advantage may be short-lived as there can be rapid selection for resistance in native species' populations (Callaway et al. 2005). There may also be an evolutionary increase in allelopathic allocation in introduced populations or when herbivore pressure changes (Yuan et al. 2012; Uesugi and Kessler 2013). In a study that specifically focused on comparing the allelopathic effects of native and non-native species, there was a tendency for non-native species to be more allelopathic (Scharfy et al. 2011). However, this effect was primarily due to the large allelopathic effects of two

annual non-native species. As annual plants in general have the highest allelopathic potential (this study), the trend may reflect the difference in life history rather than a functional shift between native and non-native species. The larger survey presented here contained a mix of life histories for both native and non-native groups and found no effect of species origin on allelopathic potential, despite the strong activity of some invasive non-native species. The discrepancy in results highlights the need to make sure that ecologically equivalent groups are being compared (van Kleunen et al. 2010). Allelopathy appears to be a plant trait common to both native and non-native species. As such, allelopathy should be thought of as a general mechanism of plant dominance in communities, rather than being unique to, or more prevalent in, non-native species.

Plant ecological strategies are generated by suites of associated functional traits. This survey found that allelopathic potential was associated with other plant functional traits, suggesting that it can and should be integrated into a broader functional view of plant strategies. In herbaceous species, allelopathic potential was positively associated with potential plant height. This suggests that tall herbs, those that have the potential to dominate local communities, are more likely to be allelopathic than shorter subordinate species such as *Fragaria virginiana* ($\beta = 0.007$) and *Rumex acetosella* ($\beta = 0.011$). Though allelopathy should be mechanistically related to resource acquisition (e.g., Callaway and Aschehoug 2000; Abhilasha et al. 2008), it was independent of herbaceous leaf traits related to light capture and utilization. In marked contrast to the herbs, allelopathic potential in woody species was negatively associated with plant height and seed mass. These associations suggest that allelopathy in woody plants may be most important in weedier species that have greater dispersal ability, but would ultimately be overtopped by others, (Weiher et al. 1999; Westoby and Wright 2006). In both woody and herbaceous species, allelopathy was associated with strategies that may allow the plant to maintain dominance. However, there was not a single, overall

strategy for both woody and herbaceous species, suggesting that the functional role of allelopathy may vary fundamentally with life form.

Conclusions

Despite the necessary constraints associated with the bioassay approach, it was able to identify ecologically relevant patterns in allelopathic potential in this successional community. Specifically, this survey generated the first real generalizations of the types of species that may be expected to be allelopathic within a plant community. Many species exhibited allelopathic activity that would appear to be sufficient to have impacts on other species. Herbaceous species, on average, exhibited a greater allelopathic potential than woody species. Within both woody and herbaceous species, allelopathic potential was associated with aggressive plant strategies—taller plants in herbaceous species and small-seeded shorter plants in woody species. These results suggest that allelopathy may play a role in determining the dominance of plant species, regardless of whether the species is non-native or native. Overall, it appears that allelopathy may be a quite common characteristic of plants and should be more fully integrated into plant functional strategies.

Appendix

See Table 3.

Table 3 Species used in the survey or allelopathy

Species	Life form	Origin	Family	β
Acer negundo L.	Tree	N	Aceraceae	0.0071
Acer platanoides L.	Tree	NN	Aceraceae	0.0163
Acer rubrum L.	Tree	N	Aceraceae	0.0010
Acer saccharum Marshall.	Tree	N	Aceraceae	0.0087
Achillea millefolium L.	Perennial	N	Asteraceae	0.0194
Agrostis stolonifera L.	Perennial	NN	Poaceae	0.0179
Ailanthus altissima Miller (Swingle).	Tree	NN	Simaroubaceae	0.0332
Alliaria petiolata (Bieb.) Cavara & Grande	Biennial	NN	Brassicaceae	0.0240
Ambrosia artemisiifolia L.	Annual	N	Asteraceae	0.0412
Apocynum cannabinum L.	Perennial	N	Apocynaceae	0.0175
Artemisia vulgaris L.	Perennial	NN	Asteraceae	0.0286
Asplenium platyneuron (L.) Oakes.	Perennial	N	Aspleniaceae	0.0179
Aster lanceolatus Willd.	Biennial	N	Asteraceae	0.0204
Bromus racemosus L.	Annual	NN	Poaceae	0.0404
Carex spp. L.	Perennial	N	Cyperacea	0.0068
Carya spp. Nutt.,	Tree	N	Juglandaceae	0.0146
Celastrus orbiculatus Thunb.	Liana	NN	Celastraceae	0.0222
Centaurea dubia Suter.	Perennial	N	Asteraceae	0.0455
Chrysanthemum leucanthemum L.	Perennial	NN	Asteraceae	0.0270
Circaea lutetiana L.	Perennial	N	Onagraceae	0.0205
Cirsium discolor (Muhl.) Sprengel.	Perennial	N	Asteraceae	0.0256
Conyza canadensis (L.) Cronquist	Annual	N	Asteraceae	0.0367
Cornus florida L.	Tree	N	Cornaceae	0.0172
Cornus racemosa Lam.	Shrub	N	Cornaceae	0.0214
Dactylis glomerata L.	Perennial	NN	Poaceae	0.0112
Daucus carota L.	Biennial	NN	Apiaceae	0.0485
Elaeagnus angustifolia L.	Shrub	NN	Elaeagnaceae	0.0065
Eupatorium rugosum Houttuyn.	Perennial	N	Asteraceae	0.0316
Euthamia graminifolia (L.) Nutt.	Perennial	N	Asteraceae	0.0330
Fragaria virginiana Duchesne.	Perennial	N	Rosaceae	0.0068
Fraxinus americana L.	Tree	N	Oleaceae	0.0099
Juglans nigra L.	Tree	N	Juglandaceae	0.0056
Juniperus virginiana L.	Tree	N	Cypressaceae	0.0137
Ligustrum vulgare L.	Shrub	NN	Oleaceae	0.0161
Lindera benzoin (L.) Blume.	Shrub	N	Lauraceae	0.0367
Lonicera japonica Thunb.	Liana	NN	Caprifoliaceae	0.0069
Lonicera maackii (Rupr.) Maxim.	Shrub	NN	Caprifoliaceae	0.0244
Microstegium vimineum (Trin.) A. Camus.	Annual	NN	Poaceae	0.0270
Oenothera biennis L.	Biennial	N	Onagraceae	0.0143
Parthenocissus quinquefolia (L.) Planchon.	Liana	N	Vitaceae	0.0196
Phytolacca americana L.	Perennial	N	Phytolaccaceae	0.0267
Plantago lanceolata L.	Perennial	NN	Plantaginaceae	0.0288
Poa compressa L.	Perennial	NN	Poaceae	0.0134
Polygonum pensylvanicum L.	Annual	N	Polygonaceae	0.0080
Prunus serotina Ehrh.	Tree	N	Rosaceae	0.0203

Table 3 continued

Species	Life form	Origin	Family	β
Quercus rubra L.	Tree	N	Fagaceae	0.0051
Rhus glabra L.	Shrub	N	Anacardiaceae	0.0272
Rosa multiflora Thunb.	Shrub	NN	Rosaceae	0.0177
Rubus allegheniensis Porter	Shrub	N	Rosaceae	0.0086
Rubus flagellaris Willd.	Shrub	N	Rosaceae	0.0147
Rubus phoenicolasius Maxim.	Shrub	NN	Rosaceae	0.0183
Rumex acetosella L.	Perennial	NN	Polygonaceae	0.0112
Rumex crispus L.	Perennial	NN	Polygonaceae	0.0091
Sassafras albidum (Nutt.) Nees.	Tree	N	Lauraceae	0.0163
Schizachyrium scoparium (Michx.) Nash	Perennial	N	Poaceae	0.0075
Setaria faberi R. Herrm.	Annual	NN	Poaceae	0.0301
Solanum carolinense L.	Perennial	N	Solanaceae	0.0368
Solidago canadensis L.	Perennial	N	Asteraceae	0.0389
Solidago gigantea Aiton.	Perennial	N	Asteraceae	0.0327
Solidago juncea Aiton.	Perennial	N	Asteraceae	0.0220
Solidago nemoralis Aiton.	Perennial	N	Asteraceae	0.0240
Solidago rugosa Miller.	Perennial	N	Asteraceae	0.0315
Toxicodendron radicans (L.) Kuntze.	Liana	N	Anacardiaceae	0.0120
Viburnum prunifolium L.	Shrub	N	Caprifoliaceae	0.0134
Vitis vulpina L.	Liana	N	Vitaceae	0.0135

Taxonomy, origin and life form follows Gleason and Cronquist (Gleason and Cronquist 1991). Allelopathic potential represented by the absolute value of the slope (β) from the logistic regression. Origin coded as non-native (NN), native (N)

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