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Allelopathic Effects of Goldenrod Species on Turnover in Successional Communities

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ABSTRACT.—While goldenrod species are often found to be allelopathic in laboratory settings, its importance in controlling plant community dynamics has been much more difficult to assess. We designed a study to determine whether allelopathy is related to the success of goldenrods in abandoned agricultural land. To accomplish this, we conducted laboratory bioassays for six co-occurring goldenrod species and compared these results to the cover and impacts of these species in the field. We determined the germination responses of two target species to a gradient of leaf extract concentrations to assess the allelopathic potential of these goldenrods. We also used long-term successional data to determine the influence of each goldenrod species on community turnover. Germination percentages in the lab were reduced by leaf extracts for most goldenrod species and varied dramatically among species. In the field, influences of goldenrods on their associated communities were weak and opposite expected allelopathic effects, as the number of associated species generally increased with goldenrod cover. The relative strength of allelopathy among goldenrods was not related to the abundance achieved during succession. In this system, we documented the potential for goldenrods to exhibit allelopathic interactions in a controlled situation. However, these effects were not strong enough to alter community structure and turnover.

INTRODUCTION

Goldenrods (largely *Solidago* spp.) are herbaceous perennials commonly found in meadows, prairies, roadsides and abandoned agricultural land in eastern North America. They are self-incompatible, produce numerous wind-dispersed seeds and germinate easily on a wide range of soils (Weber, 2001). Once a population is established through seed establishment, energy allocation shifts to vegetative growth (Hartnett & Bazzaz, 1985; Bazzaz, 1996; Meyer and Schmid, 1999; Weber, 2001) leading to genetically uniform clonal patches of goldenrods. Vegetative propagation is important as a competitive mechanism for gaining territory for expansion (Salisbury, 1942; Werner, 1976; Grime, 2001) and is an important process in successional systems (Grime, 2001). Together, these two modes of reproduction are important in determining the competitive success and impacts of goldenrods in successional systems (Hartnett and Bazzaz, 1985; Myster and Pickett, 1992; Long *et al.*, 2003). This competitive ability has contributed to their invasiveness in Europe where they are not attacked by herbivores (Weber, 2001).

Beyond direct competitive interactions, goldenrods have the potential to interact indirectly with their neighbors through allelopathy. Allelopathy has generally come to mean the deleterious effect that one plant has on another through the production of chemical retardants (Martin and Rademacher, 1960; Muller, 1965; Jackson and Willemsen, 1976). However, this process is more complex because allelopathic plants are also capable of stimulatory effects (Jackson and Willemsen, 1976). The chemical producing plant may also inhibit itself with the same chemicals that inhibit its neighbors (Kumari and Kohli, 1987).

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Previous studies have tested *Solidago* species for allelopathic inhibition of germination and have found varying results. For example, Fisher *et al.* (1977) found that goldenrods reduced the germination and growth of maples even in the absence of competing vegetation. Bing-yao *et al.* (2006) observed both inhibitory and stimulatory effects of *S. canadensis* against several target species. However, in higher chemical concentrations the interactions were predominantly inhibitory. In another study, *Euthamia graminifolia* and *S. canadensis* reduced germination of seeds in target species, but inhibition was tissue-specific, only occurring with leachates of leaves (Butcko and Jensen, 2002).

The effect of allelopathic chemicals is often tested through bioassays, typically by testing the effects of plant tissue extracts on the germination of seeds. However, there are issues in relating laboratory bioassays to allelopathic interactions in the field. The few studies that examine both find a conflict between lab and field data where allelopathy in the laboratory is not always demonstrated in the field (Keever, 1950; Muller and Muller, 1956; Jameson, 1970; del Moral and Cates, 1971; Neill and Rice, 1971; Stowe, 1979). This difficulty may relate to low concentrations of the allelopathic agent or fluctuations in toxicity in time and space, or be a sign that chemical interactions are offset by other processes. In spite of these limitations, laboratory bioassays are useful for identifying potential allelopathic interactions that must be then verified in the field.

The primary interest of this study was the potential for allelopathic interactions of plants and their importance in shaping the surrounding plant community. Goldenrods were chosen as the focus for this study because they are documented as being allelopathic, they are important in successional systems, and they are becoming invasive worldwide. We addressed the primary question, the importance of allelopathy in determining the success of and impact of goldenrods in old field succession, in two ways. First, we experimentally assessed the allelopathic potential of each goldenrod species in the lab. Second, we used long-term vegetation data to determine the influence of goldenrods on the surrounding community. Finally, we related these two data sets to determine whether allelopathic interactions could explain vegetation patterns seen in the field.

MATERIALS AND METHODS

Six species of goldenrods were included in this study: *Euthamia graminifolia* Nutt. (formerly *Solidago graminifolia*), *S. canadensis* L. (synonymous with *S. altissima*), *S. gigantea* Aiton., *S. juncea* Aiton, *S. nemoralis* Aiton. and *S. rugosa* Miller. Although closely related species, they vary considerably in morphology, habitat selectivity and invasiveness. Two of the species, *S. juncea* and *S. nemoralis*, produce basal rosettes of leaves whereas the other species produce upright stems. All species reproduce clonally; however, *S. canadensis* and *S. rugosa* are the most aggressive vegetative spreaders (Gleason and Cronquist, 1991). *Solidago gigantea* allocates most of its energy into sexual reproduction and produces large flower heads and achenes, contributing to its invasiveness (Abrahamson *et al.*, 2005). Species also vary in their niche preferences. *Euthamia graminifolia* and *S. gigantea* are often associated with more mesic conditions, contrasting with *S. juncea* and *S. nemoralis* which occur in drier areas (Abrahamson and Gadgil, 1973; Werner and Platt, 1976). *Solidago canadensis* and *S. rugosa* prefer intermediate conditions (Abrahamson and Gadgil, 1973; Werner and Platt, 1976). Additionally, *E. graminifolia* and *S. rugosa* have higher abundances on acidic soils (Abrahamson *et al.*, 2005). At least three goldenrod species, *E. graminifolia*, *S. canadensis* and *S. gigantea* have been observed to be invasive in Europe (Abrahamson *et al.*, 2005).

ALLELOPATHIC TESTING

To assess allelopathic potential, all six goldenrods were tested with laboratory bioassays following Butcko and Jensen (2002). Leaf samples were collected from the Hutcheson Memorial Forest in Jul. 2007. For each species, leaves from at least 20 plants were collected and air dried for 2 d. Extracts were made from 12.5 g of dried leaf tissue placed in 500 ml of distilled water. The mixture was placed on a magnetic stirrer for 24 h at room temperature and was strained through cheesecloth to remove particulate plant material. Dilutions of each extract, ranging from 0% to 100% in 10% increments were made. Filter paper was placed in 90 mm petri plates with 20 seeds of the target species. Five trials were run for each dilution for each goldenrod species tested. We used two target species, lettuce (*Lactuca sativa* L., 'Black Seed Simpson') and radish (*Raphanus sativus* L., 'Early Scarlet Globe': Bay Farm Services, Inc., Bay City, MI). Lettuce and radish seeds were selected because they are commonly used in allelopathic testing. Four mL of extract was added to each plate and incubated at 25 C for a 12/12 h light/dark cycle. The plates were removed after 4 d and germinated seeds were counted.

The proportion of seeds that germinated in each dish was analyzed in two ways. First, an ANCOVA of goldenrod species and extract concentration was run to determine overall effects in both target species. This analysis was followed by a separate regression analysis for each goldenrod to quantify the slope of the inhibition response. Pair-wise differences between species were determined using *t*-tests with Bonferroni correction for multiple comparisons. All statistical analyses were conducted using SPSS 15.0 (SPSS Inc., Chicago Illinois).

FIELD DATA

Field data were obtained from the Buell-Small Successional Study (BSS), a long-term study of old field successional dynamics. The study is located within the Hutcheson Memorial Forest on former agricultural land in the Piedmont region of New Jersey, (40°30′ N, 74°34′ W). The BSS contains 10 replicated fields each having 48 permanently marked plots (0.5 × 2.0 m). Fields were abandoned in pairs from 1958–1966. The identity and percent cover of all species present in each plot were recorded for each year (alternate years since 1979).

To determine the population dynamics of each goldenrod species during succession, percent plot cover and frequency were calculated for each species in all 10 fields (C3, C4, C5, C6, C7, D1, D2, D3, E1 and E2 named for their position in the field). From the original six species, four that attained a minimum of 3.5% cover per plot were selected for further analysis: *Euthamia graminifolia*, *Solidago canadensis*, *S. juncea* and *S. rugosa*. The remaining species were too infrequent for analysis. Cover of goldenrods varied among fields and was examined using an ANOVA for each of the four selected species using plot data. Correlation analyses were also run to test for associations among goldenrod species.

COMMUNITY EFFECTS OF GOLDENROD

To document the influence of goldenrod species on plant community structure, the effect of goldenrods on species richness during peak cover was analyzed. Years 23 and 24 post abandonment were chosen for this analysis because all goldenrods were abundant during this time period. Because fields were sampled in alternate years, both years were used to include data from all 10 fields. Since fields varied dramatically in cover for goldenrod species, a subset of fields was selected for each species based on average plot cover. Fields which did not achieve an average percent cover of at least 3.5% in years 23/24 for a species

TABLE 1.—Influence of goldenrod species identity and extract concentration on the germination of radish and lettuce seeds. Significant values are indicated by bolding

Source	df	MS	F	P
Radish				
Species	5	43.27	0.331	0.896
Concentration	1	80,561.52	609.69	**<0.001**
Species × Concentration	5	1907.52	14.44	**<0.001**
R^2	0.72			
Lettuce				
Species	5	428.97	2.01	0.076
Concentration	1	33,509.33	157.32	**<0.001**
Species × Concentration	5	4827.06	22.66	**<0.001**
R^2	0.57			

were excluded from analysis in order to prevent bias from poorly colonized fields. The influence of plot goldenrod cover (continuous) and field identity (categorical) on species richness was analyzed with an ANCOVA. Pearson correlations between species richness and goldenrod cover were calculated for each field to assess variation among fields and to interpret ANCOVA interactions. To assess goldenrod impacts on individual species, the percent cover of the four most abundant resident species, *Centaurea dubia* Suter., *Fragaria virginiana* Duchesne., *Hieracium caespitosum* Dumort. and *Poa compressa* L., was correlated with percent cover of each goldenrod species.

To determine the underlying dynamics which generated goldenrod effects on associated species richness, colonization and extinction rates were also calculated. These rates were calculated for the periods of 23–25 and 24–26 y for all fields which met abundance criteria. Data collection in alternate years set a minimum interval of 2 y for this analysis. Rates were calculated as the number of species which appeared or disappeared from each plot during the interval. Colonization and extinction rates were analyzed via ANCOVA as above. Pearson correlations were conducted for species gain/loss in each field to assess variation among fields and to interpret interactions between goldenrod cover and turnover.

RESULTS

ALLELOPATHY DATA

Allelopathic effects were seen in all goldenrod species through reduced seed germination in lettuce and radish. There was significant variation among goldenrod species in toxicity and separation between target species in their susceptibility to allelochemicals (Table 1; Fig. 1). Radish seeds showed more separation among goldenrod species compared to lettuce seeds. In lettuce, the most toxic species were *Euthamia graminifolia* and *Solidago juncea*, whereas the weakest inhibitors were *S. canadensis* and *S. gigantea*. Radish yielded different species in terms of strongest (*E. graminifolia* and *S. canadensis*) and weakest (*S. gigantea* and *S. nemoralis*) germination inhibitors.

FIELD DATA

Goldenrod cover was generally low in early succession and rapidly increased at mid-succession (years 10–20; Fig. 2). In late succession (years 30–40), the cover and frequency of goldenrods decreased for all species. However, two species, *Solidago gigantea* and *S. nemoralis*,

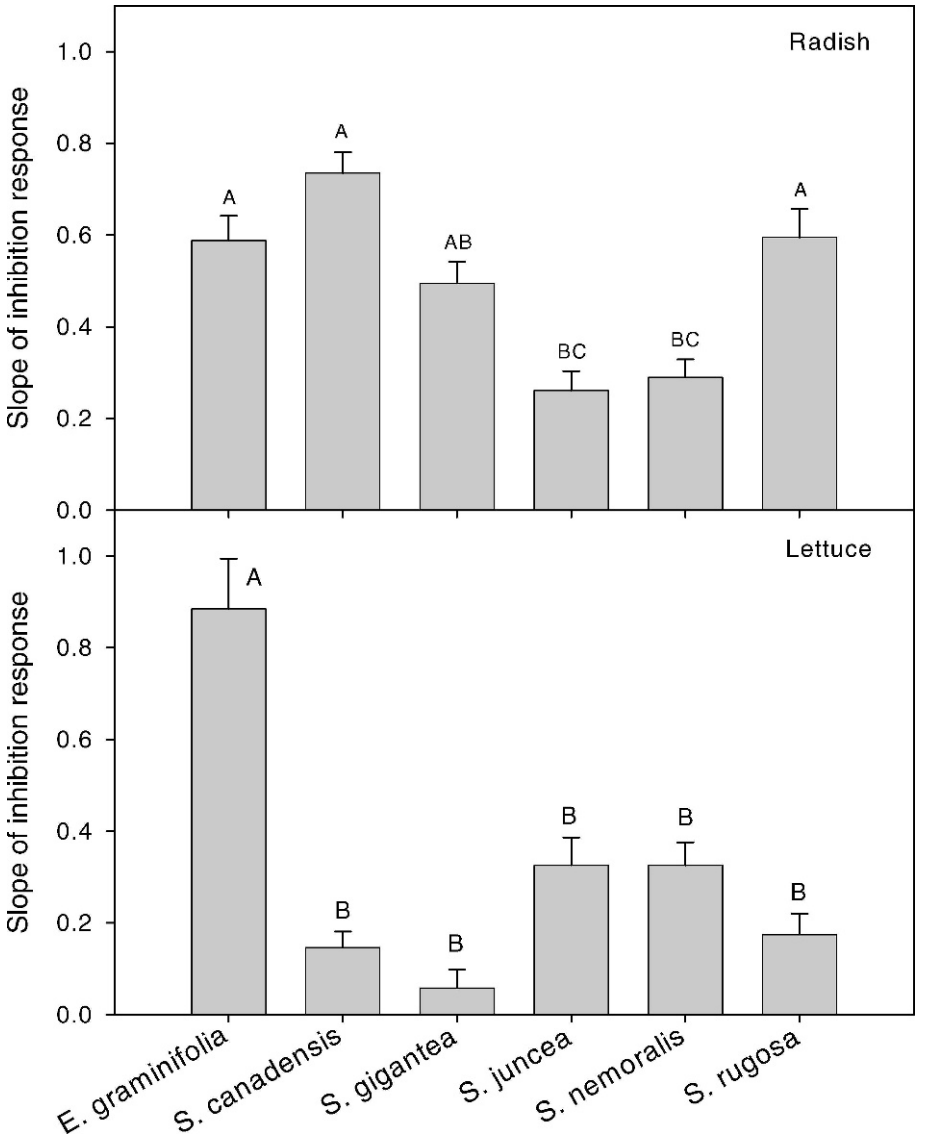

FIG. 1.—Comparison of the strength of allelopathic response between extract concentration and germination response for each of the six goldenrod species. Values plotted are the absolute value of regression coefficients for each species. Letters represent significant pair-wise differences

remained at a relatively consistent, but low cover throughout succession. These two species were dropped and only the four most abundant species were analyzed further.

There was dramatic variation among fields in goldenrod cover (Fig. 3). *Euthamia graminifolia* ($F_{9,470} = 4.39$, $P < 0.001$), *S. canadensis* ($F_{9,470} = 2.79$, $P = 0.003$), *S. juncea* ($F_{9,470} = 20.2$, $P < 0.001$) and *S. rugosa* ($F_{9,470} = 9.26$, $P < 0.001$) all had significant variation

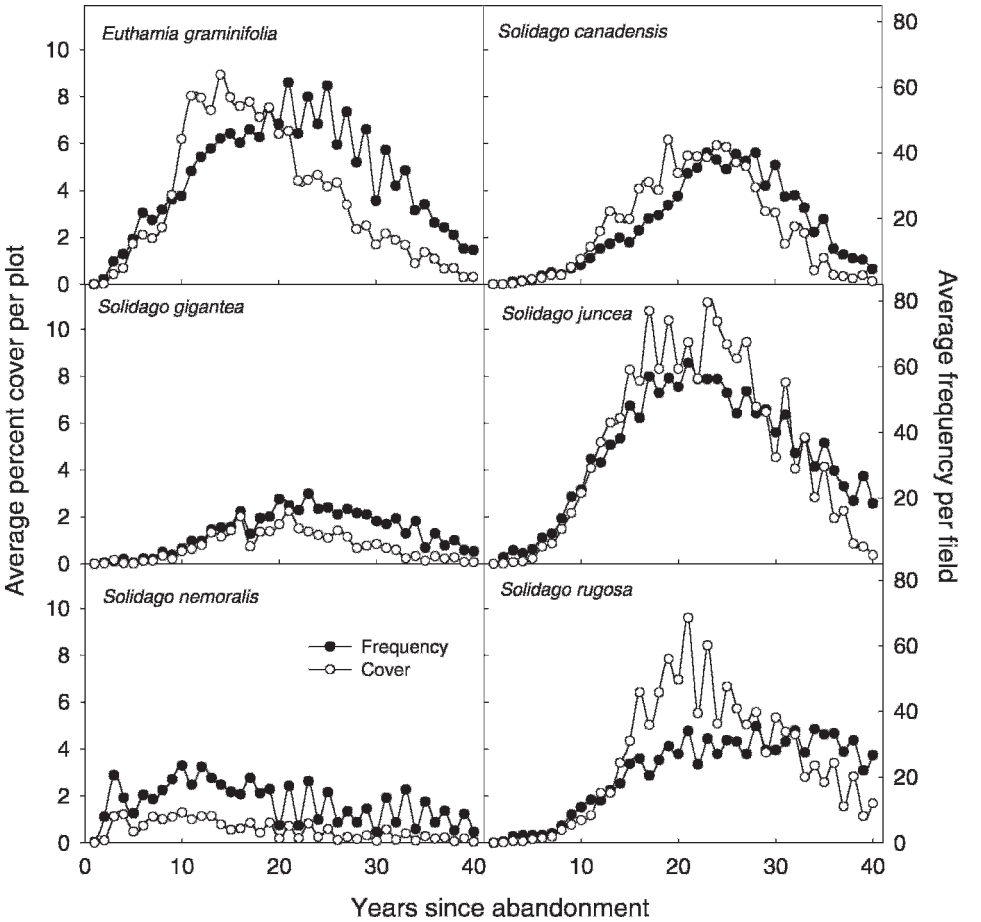

FIG. 2.—Cover and frequency of six common goldenrod species among the 10 Buell-Small Succession fields during the first 40 y of succession. Data are from Jul. sampling dates

among fields in plot cover. Interestingly, these species also showed some spatial segregation within the fields. *Solidago juncea* was negatively correlated with both *S. canadensis* and *S. rugosa* ($R = -0.143$, $P = 0.002$ and $R = -0.178$; $P < 0.001$ respectively). Although most fields had a single dominant goldenrod, all species were present in most fields (Fig 3.)

COMMUNITY EFFECTS OF GOLDENROD

Species richness was influenced by either cover or the cover × field interaction for three of the four goldenrod species tested (Table 2). Species richness was overall positively associated with *Solidago juncea* cover, but this association varied among fields. *Solidago juncea* was positively correlated with richness only in fields C5 ($R = 0.450$, $P = 0.001$), D2 ($R = 0.428$, $P = 0.002$) and E2 ($R = 0.480$, $P = 0.001$), whereas cover in the other fields was not correlated with species richness. The only significant model term for *Euthamia graminifolia* was a field effect on species richness. For *S. rugosa*, the only significant effect on richness was the cover × field interaction. The only field where cover of *S. rugosa* was associated with

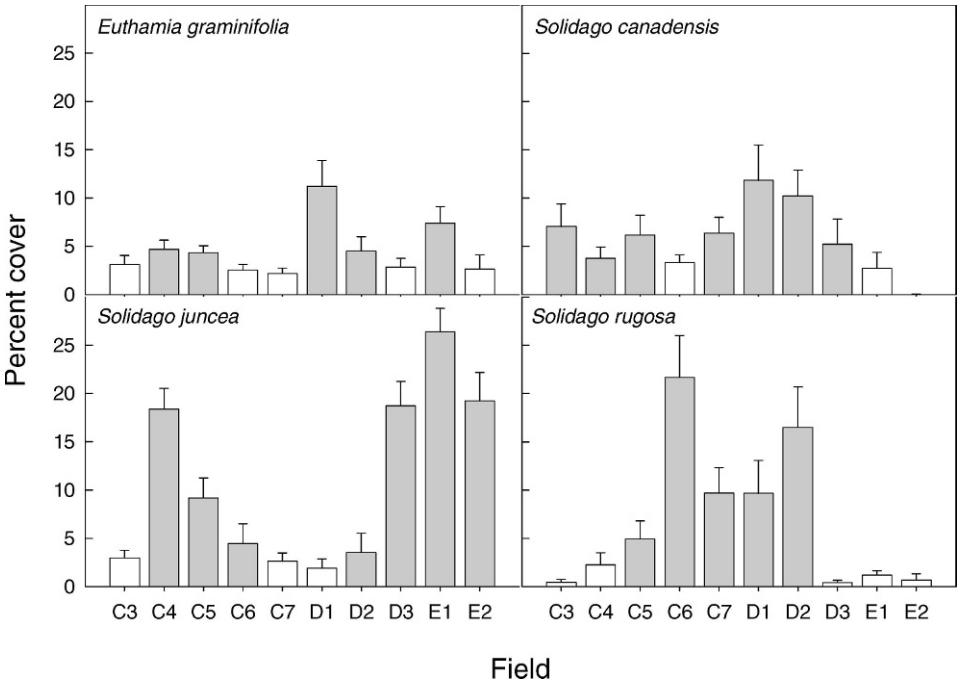

FIG. 3.—Variation in cover of the four common goldenrod species among the 10 Buell-Small Succession fields for years 23 and 24. Grey denotes the fields used in analysis of community impacts

TABLE 2.—Influence of goldenrod cover and field identity on local (plot scale) species richness using analysis of covariance of the four most abundant goldenrods within the BSS data. Significant values are indicated by bolding

Source	df	MS	F	R^2	P
E. graminifolia					
Field	4	397.81	21.37	0.33	**<0.001**
Cover	1	1.13	0.06		0.806
Field × Cover	4	21.37	1.15		0.335
S. canadensis					
Field	6	315.29	14.85	0.09	**<0.001**
Cover	1	0.04	0.00		0.966
Field × Cover	6	47.94	2.26		**0.038**
S. juncea					
Field	6	187.40	10.32	0.35	**<0.001**
Cover	1	466.64	25.70		**<0.001**
Field × Cover	6	38.51	2.12		0.051
S. rugosa					
Field	4	47.55	2.27	0.27	0.062
Cover	1	3.27	0.16		0.693
Field × Cover	4	57.01	2.73		**0.030**

TABLE 3.—Correlations of the four most common associated species in relation to goldenrod cover within the BSS data. Values reported are Pearson correlation coefficients (p-value). Significant values are indicated by bolding

	Centaurea dubia	*Fragaria virginana*	*Hieracium caespitosum*	*Poa compressa*
E. graminifolia	−0.03 (0.619)	**0.17 (0.009)**	0.00 (0.947)	**0.21 (<0.001)**
S. canadensis	−0.01 (0.911)	0.06 (0.305)	**0.17 (0.002)**	**0.14 (0.010)**
S. juncea	−0.05 (0.345)	**0.29 (<0.001)**	**0.29 (<0.001)**	−0.05 (0.340)
S. rugosa	−0.09 (0.151)	−0.05 (0.476)	−0.02 (0.788)	**0.16 (0.014)**

richness was field C7 (R = 0.348; P = 0.015); all other fields were non-significant. *Solidago canadensis* was similar to *S. rugosa* in that there was a significant cover × field interaction, although the field term was also significant. The relationship between *S. canadensis* and species richness varied across fields with field C5 (R = −0.313, P = 0.030) negatively correlated and field D2 (R = 0.323; P = 0.025) positively correlated.

To understand these influences on species richness, cover of the four most abundant resident species was correlated with goldenrod cover (Table 3). These results were largely similar to the relationships with species richness in that positive associations were found. Each goldenrod had at least two positive associations with resident species, except for *S. rugosa* which had only one positive association (Table 3).

Colonization and extinction rates of associated species varied greatly among fields for all four goldenrod species. However, only *Solidago juncea* cover affected colonization rates (Table 4). As *S. juncea* showed a nearly significant cover × field interaction for colonization, Pearson correlations were used to identify which fields were associated with species turnover. Fields C6 (R = 0.335, P = 0.020), D2 (R = 0.311, P = 0.032), and E1 (R = 0.292, P = 0.044) showed positive associations of the species with colonization. Laboratory bioassay data did not predict cover of goldenrods in the field as correlations between the allelopathic toxicity and field cover were not significant for either target species (Fig. 4; both P ≥ 0.125).

DISCUSSION

Although laboratory bioassays confirmed the presence of at least some allelopathic capability for all of the goldenrod species tested, there was dramatic variation among

TABLE 4.—Influence of goldenrod cover and field identity on local (plot scale) colonization and extinction rates of the four most abundant goldenrods within the BSS data. Significant values are indicated by bolding

	E. graminifolia		*S. canadensis*		*S. juncea*		*S. rugosa*	
	F	P	F	P	F	P	F	P
Colonization								
Field	2.58	**0.038**	5.23	**<0.001**	2.86	**0.010**	3.92	**0.002**
Cover	0.03	0.854	0.93	0.336	8.78	**0.003**	0.03	0.861
Field × Cover	1.99	0.097	0.51	0.801	2.11	0.052	0.41	0.844
R^2	0.07		0.11		0.13		0.09	
Extinction								
Field	4.33	**0.002**	6.73	**<0.001**	3.26	**0.004**	3.43	**0.005**
Cover	1.19	0.276	0.32	0.570	0.22	0.638	1.24	0.267
Field × Cover	0.76	0.554	0.71	0.642	0.95	0.461	1.25	0.286
R^2	0.10		0.16		0.09		0.11	

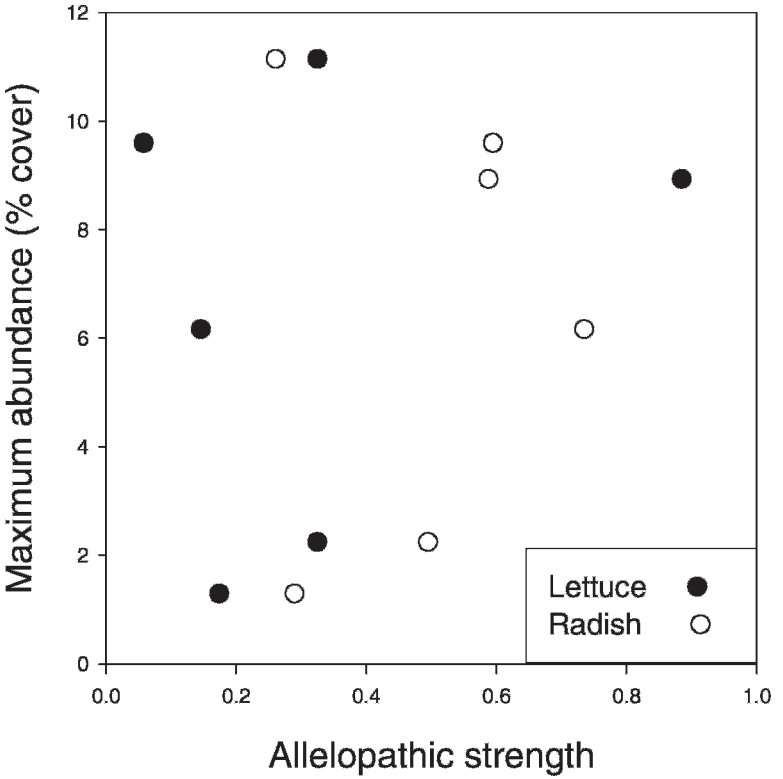

FIG. 4.—Correlation analysis between allelopathic strength of radish and lettuce species to the maximum percent cover of goldenrods during the first 40 y of succession. The results show no correlation

species. Moreover, toxicity of goldenrod species varied between target species. This toxicity, however, was not consistent with the observed dynamics in the field. While some goldenrod species reached high cover in the field, we found no inhibitory effects of goldenrod cover on species richness or turnover. In contrast, the field data revealed a significant, but minor facilitative effect of goldenrods on other species. Finally, there was no correlation between allelopathic potential and the cover achieved by each species in the long-term data, suggesting that allelopathy is not an integral part of a goldenrod's success in its native range.

Our results are consistent with experimental work done at the BSS site. In a field experiment, Facelli and Pickett (1991) tested litter of three species: *Quercus alba* L., *Setaria faberii* Herrm. and *Solidago* spp. (mostly *S. canadensis*) for persistence and the ability to reduce total plant cover. They found that goldenrod litter was the most persistent of the three species tested, but had little impact on plant cover (Facelli and Picket, 1991). While Facelli and Pickett (1991) would have integrated both the physical and chemical influences of goldenrod litter, the lack of impacts suggests little direct influence of allelochemicals on the community.

Although it is evident that goldenrod species have allelopathic potential, it does not appear to be sufficiently strong to affect surrounding plants in this system. If allelochemicals primarily function as germination inhibitors, the total availability of seeds should determine the net

effect of allelopathy on the community. In this study, plant extracts reduced germination on average by 54.8% for lettuce seeds and 37.8% in radish seeds at full concentration. If the plant community was not seed limited (*i.e.*, if seed availability was high), then there may have been too many seeds present to reduce colonization rates. Therefore, the importance of allelopathy may vary along gradients of propagule pressure, with the greatest effects occurring in areas of low seed availability. As target species appear to vary greatly in their response to plant extracts, the diversity of seeds available in a habitat may include a mix of susceptible and resistant species, further reducing the observed impacts.

The rate at which allelochemicals are released and their concentration in the soil could be affected by several factors such as rainfall, concentration of chemicals produced in goldenrod tissues and decomposition rates. Once incorporated into the environment, allelochemicals may have been metabolized by soil organisms so rapidly that their concentration in the soil decreased and, therefore, their effect was minimized. As the allelochemicals that we investigated would typically be released into the environment upon leaf abscission, their effects would be mixed with other allelopathic old-field plants that may mask the community level influences of goldenrods (Keever, 1950; Jackson and Willemsen, 1976; Gómez-Aparicio and Canham, 2008).

Allelopathy is often thought to be an important mechanism in determining the success of non-native species in their introduced ranges (Inderjit *et al.*, 2008). In contrast to our results, allelopathy has been shown to be important in invasive *Solidago canadensis* populations in Europe (Abhilasha *et al.*, 2008). Nearly all of the native European species tested against *S. canadensis* showed reduced performance in the presence of allelochemicals. This result may be due to the lack of evolutionary exposure of plants in the introduced range to the novel chemicals produced by the invading species (Callaway and Aschehoug, 2000; Abhilasha *et al.*, 2008). Within their native range, herbivore pressure may ameliorate goldenrod effects on the community (Carson and Root, 2000). Insect herbivory on goldenrods can promote plant species richness and coexistence, primarily by augmenting light availability to suppressed understory species but also by increasing soil moisture and nitrogen levels in the soil (Carson and Root, 2000; Long *et al.*, 2003). However, herbivory may stimulate the production of allelochemicals (Thelen *et al.*, 2005; Abhilasha *et al.*, 2008), potentially mitigating these effects.

The contradiction between lab and field data suggests that allelopathy, although present, plays a minimal role in the success of goldenrods within their native range. Their dominance within successional systems appears primarily due to more direct competitive strategies. However, the contrast between allelopathy in native and introduced ranges indicates the potential for conditionality in allelopathy. The context-dependent nature of allelopathy in goldenrods makes them a useful model system to explore the range of allelopathic impacts seen in plant communities.

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