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# Light reduction predicts widespread patterns of dominance between asters and goldenrods

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**Abstract** Here we investigate the long-cited pattern that throughout the eastern United States, *Solidago* species (goldenrods), and in particular *S. canadensis* displace *Aster* species and dominate old-field communities. Theory predicts that such a ubiquitous pattern of repeated dominance should be linked to competitive ability for a limiting resource. However, no one has investigated this possibility in old-fields, representing a potentially significant gap in our understanding of a common human-altered environment. We tested the hypothesis that *S. canadensis* is the superior competitor for light compared to other common co-occurring goldenrod species, and that the goldenrods in general are the superior competitors for light compared to coexisting aster species, which are typically less abundant. We tested this hypothesis by comparing the light attenuation abilities of four goldenrod species, *S. canadensis, S. rugosa*, *S. gigantea*, and *Euthamia graminifolia*, and three aster species, *Aster novae-angliae*, *A. pilosus*, and *A. prenanthoides*. Consistent with our hypothesis, *S. canadensis* had a greater ability to attenuate light than any of the other goldenrods at higher densities, and the goldenrods overall had a greater ability to attenuate light than the asters. By conducting a census in our study area, we verified that *S. canadensis* is locally the most abundant goldenrod and that goldenrods are more locally abundant than asters. Furthermore, by conducting a literature survey we found evidence that *S. canadensis* replaces *A. pilosus* through time. Thus we found a close correspondence between relative abundance in the field and light attenuation ability in field experiments. These results are consistent with theory predicting that competition for limiting resources, in this case light, explains patterns of dominance and relative abundance in old-field plant communities.

**Keywords** Resource reduction competition · Light competition · Old-fields · Goldenrod · Aster · Forb · *Solidago canadensis* · *Solidago gigantea* · *Solidago rugosa* · *Euthamia graminifolia* · *Aster novae-angliae* · *Aster pilosus* · *Aster prenanthoides*

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## Introduction

Predicting dominance in species assemblages is a central goal of community ecology. Some of our most long-standing patterns come from studies of succession, and yet experimental tests of mechanisms contributing to dominance in successional sequences are few (e.g., Keever 1950; Tilman 1988; Bazzaz 1996). Here we examined a classic turnover from asters to goldenrods (Bazzaz 1996), and we show that a species' light reduction capacity predicts its eventual dominance during this successional turnover.

Numerous studies in a variety of systems have investigated competition for below-ground resources (e.g., Tilman 1982, 1988; Schmid and Bazzaz 1992; Keddy et al. 1994; Miller et al. 2005; Harpole and Tilman 2006), and a few studies have experimentally linked the competitive ability of a species for this resource to its relative abundance (e.g., Tilman 1982; Keddy et al. 1994; Harpole and Tilman 2006). However, the role of competition for light in structuring plant communities has rarely been tested (Huisman 1999). Furthermore, there have been no empirical examinations of the role of light competition in structuring terrestrial old-field communities, despite the ubiquity of these environments in human-altered landscapes and speculation that light competition influences their structure (Carson and Root 2000; Walck et al. 2001). Understanding the competitive dynamics of old-fields is urgent, because North American goldenrods from these communities are invasive in Europe (Sheppard et al. 2006), and because so many invasive species become established in early stages of succession in environments like old-fields (Rejmánek 1989).

We examined if differences in the relative abundance of common species in old-field communities are consistent with interspecific differences in the ability of these species to cast shade. In old-fields throughout the Midwestern and eastern United States, goldenrods are typically the dominant herbaceous species and can form dense canopies of interconnected ramets that cast deep shade and reduce the abundance of coexisting species (Carson and Pickett 1990; Carson and Root 2000). *Solidago canadensis* is typically the most abundant of these co-occurring goldenrods and is known to form dense, low diversity communities (Werner et al. 1980; Hartnett and Bazzaz 1985; Carson and Pickett 1990; Vankat and Snyder 1991; Walck et al. 2001). Carson and Root (2000) demonstrated experimentally that insect herbivores were keystone species in old-fields because herbivore damage prevented *S. canadensis* from casting deep shade and thereby excluding species that were inferior competitors for light. Taken together, these findings suggest that competition for light is important in goldenrod-dominated communities, and that *S. canadensis* should be a superior light competitor allowing it to dominate old-fields. We operationally define a species as a superior light competitor if, on a per capita or per stand basis, it attenuates more light than a coexisting species.

Asters are subdominant in old-fields, and while they are similar in stature to goldenrods, they form relatively open canopies that are vulnerable to goldenrod invasion (Schmid and Bazzaz 1990; 1994). Asters typically colonize old-fields sooner than goldenrods but during early succession aster abundance declines while goldenrod abundance increases (Bazzaz 1996), suggesting that asters are inferior resource competitors compared to the goldenrods. We hypothesize that goldenrods displace asters at least in part because goldenrods are superior competitors for light.

We quantified the abilities of goldenrods and asters to attenuate light, across a range of monospecific stand densities, in two separate experiments at separate field sites. Our first experiment compared light attenuation abilities among four co-occurring goldenrods, *S. canadensis*, *S. gigantea*, *S. rugosa*, and *Euthamia graminifolia*. Our second experiment compared the light attenuation abilities of two goldenrods (*E. graminifolia* and *S. rugosa*) and three asters (*Aster novae-angliae*, *A. pilosus*, and *A. prenanthoides*). We examined the ability to attenuate light for each species across a range of monospecific densities, rather than only at a particular density, in order to examine if highly abundant species were superior light competitors across a wide range of stand densities as compared to less abundant species.

In order to verify that *S. canadensis* is naturally more abundant than other goldenrods, and that goldenrods are naturally more abundant than asters and replace them through time, we also performed a survey of our study species' local abundances and a quantitative literature survey of our species' abundances throughout the midwestern and eastern US.

## Materials and methods

### Field sites and experimental designs

We studied native, herbaceous, clonal perennials in the Asteraceae family (Werner et al. 1980; Zhang et al. 1999; Chmielewski and Semple 2001, 2003), using two field sites within Crawford County in northwestern Pennsylvania, USA (for details see Stevens et al. 2004). One site (Beagle Road) was an old-field that was plowed and left fallow in 1995. It naturally contained high densities of goldenrod species, which we used to compare the light attenuation abilities of goldenrods across a range of monospecific densities. The other site (Ernst) was 10 km from Beagle Road. Obtaining estimates of light attenuation ability for species that do not naturally occur in dense stands or are uncommon is challenging. To overcome this challenge, we used established monocultures of target native species that were being cultivated by the Ernst Conservation Seeds Company (Meadville, PA). They cultivate native vegetation, not cultivars, to supply seeds for re-vegetation projects and ecologically appropriate landscaping. The plants are grown from multiple local parents to ensure a diverse genetic stock. Our plots at Ernst contained high-density, cultivated crop rows of native asters and goldenrods, which we used to compare the light attenuation abilities of goldenrods to those of asters across a similar range of monospecific densities.

At Beagle Road, we created monocultures of four naturally occurring goldenrod species *(Solidago canadensis, S. gigantea, S. rugosa, and Euthamia graminifolia*) by selecting areas where sufficiently dense quantities of the target species were located, and removing other species in 71 × 71 cm plots. In mid-June 2000, we created a density gradient by randomly assigning and then thinning plots of each species to densities of 2, 4, 8, 16, and 32 ramets/plot (corresponding to 4, 8, 32, and 64 stems/m$^2$, respectively). We defined a ramet as a stem that protruded separately from the soil surface. To achieve the target densities, we selected the *n* tallest ramets within each plot, where *n* is the target density, and thinned all others. Each treatment was replicated from five to nine times, depending on the abundance of the target species. In early August 2000, we quantified the proportion of photosynthetically active radiation (PPAR) that penetrated through each canopy in each plot by placing a 1-m line Quantum sensor through both diagonals (forming an X) at the soil surface. We cleared vegetation around the plots so that no shade was created besides that of the plants of interest, and we took light readings within 2 h of noon. To obtain ambient light levels, we placed a quantum point sensor above the canopy (LiCorr, Inc., Lincoln, NE). We used a LiCorr Data-Logger to take simultaneous readings from the line sensor and the point sensor. We took two readings from each diagonal, giving us a total of four paired readings (line sensor and point sensor) per plot. We estimated PPAR for each plot by dividing each line sensor reading by the corresponding point sensor reading and averaging these four proportions.

At Ernst we used cultivated monocultures of *Aster novae-angliae, A. pilosus*, and *A. prenanthoides* to quantify the abilities of uncommon species to attenuate light when grown at higher densities than they typically occur naturally. In other words, we examined how well these sub-dominant species would attenuate light if they became abundant. We also used cultivated monocultures of two goldenrods, *E. graminifolia* and *S. rugosa*. Because these monocultures were growing in relatively small clusters in rows, we reduced our plot size to 40 × 40 cm. We selected the tallest ramets within each plot and thinned all others, in order to create the following density gradients: *E. graminifolia*, 1, 4, and 12 stems/plot (6.25, 25, and 75 stems/m$^2$); *S. rugosa*, 1, 2, 4, 8, and 16 stems/plot (6.25, 12.5, 25, 50, and 100 stems/m$^2$); *A. novae-angliae*, 1, 2, 4, 8, and 20 stems/plot (6.25, 12.5, 25, 50, and 125 stems/m$^2$); *A. pilosus*, 1, 2, 4, 8, 16, and 32 stems/plot (6.25, 12.5, 25, 50, 100, and 200 stems/m$^2$); *A. prenanthoides*, 1, 2, 4, 8, 16, and 32 stems/plot (6.25, 12.5, 25, 50, 100, and 200 stems/m$^2$). The number of replicates of each species-density combination ranged from 9 to 16, depending on the species. We thinned the species to different sets of densities because the size of the crop rows, and the density of the plants, available to us were different for the different species. Our goal was to sample as a broad density gradient as possible for each species, so we could quantify the relationship between density and light attenuation, rather than to thin all species down to a more restricted, common set of densities.

As mentioned above, we thinned to the target densities by selecting the tallest individuals within each plot, regardless of their positions within the plot. The light attenuation readings for each plot therefore represent different spatial distributions of plants. We believe this is appropriate, because thinning for a particular spatial distribution of plants would have biased the results; this is especially true for the lowest density plots. With our approach, different spatial configurations should average each other out in the analyses, thereby allowing us to examine the average effect of a particular density of ramets regardless of their spatial distribution. Such an approach also mitigates the problem of edge effects, because there is no “edge” that is consistently defined by any sort of biased spatial configuration; the density of plants in the center of the plots will not systematically differ from that of plants toward the periphery.

The smaller plot size at Ernst precluded using the 1-m long line quantum sensor. We instead used two quantum point sensors and took 16 paired readings for a lattice of locations under the monoculture in each plot. In order to overcome the problem of shading from neighboring plots in the crowded crop rows, we used two 1-m-tall boxes constructed out of shade cloth on PVC scaffolding, with the top and bottom open. We placed one box over the plot of interest, so shade from the neighboring plots was blocked. We placed the other box away from the plot and the crop rows, parallel to the other box, so that the patterns of self-shading by the boxes themselves were the same. We placed one point sensor at the soil surface in the box containing the plot, to measure the photosynthetically active radiation (PAR) transmitted to the soil surface. We placed the other point sensor in the corresponding location in the other (empty) box, to measure ambient PAR and to account for self-shading by the boxes at that location. We took the light readings within 2 h of noon. In order to estimate PPAR for each plot, we divided each measurement of the PAR transmitted to the soil surface by the paired ambient PAR measurement and then averaged these 16 proportions within each plot.

At both sites the target densities were maintained from the time of thinning until we took the light measurements, which was approximately at the beginning of flowering, although floral display was minor. The plants were grown at high densities before thinning to the target densities. Consequently one might argue that, had the plants been grown throughout the season at the lower densities to which they were eventually thinned, they would have had a different phenotype (e.g., a different stem architecture and overall size) and therefore different light attenuation abilities. Low-density communities, however, do not exist in these goldenrod-dominated old-fields, and thus would not reflect natural habitats. Uniquely, our approach allows us to measure the marginal affect of additional ramets of a particular species, with ecologically realistic high-density phenotypes, on light attenuation.

### Data analysis

Because the two field sites were different (an old-field versus an active agricultural field), we analyzed the Beagle Road and Ernst sites separately and only made comparisons within a site. Using analyses of covariance (ANCOVAs) in R version 2.5.0 (R Development Core Team 2007), we modeled PPAR as a function of: species, density ($\log_{10}$-transformed and measured in stems/m$^2$), and their interaction. We checked the residuals from each analysis for equal variance and platykutrosis. At Ernst, a square-root-transformation of PPAR was necessary to satisfy the assumptions of the ANCOVA (Sokal and Rohlf 1995).

### Old-fields natural survey

We surveyed the naturally occurring abundances of the goldenrods and asters used in our experiments (*S. canadensis*, *S. gigantea*, *S. rugosa*, *E. graminifolia*, *A. novae-angliae*, *A. pilosus*, *A. prenanthoides*) in eight old-fields within a 20-mile radius of the University of Pittsburgh Pymatuning Laboratory of Ecology (Linesville, PA, USA) ranging in age from 3 to 20 years since agricultural abandonment.

To sample each old-field, we randomly placed 2 × 2 m quadrats along linear transects. The number of transects varied based upon the field size in an attempt to equalize sampling effort between old-fields. Within each quadrat we recorded the percent cover of each of the 10 focal species if present. We averaged the percent cover over all quadrats for each species at each old-field.

We performed a one-way analysis of variance (ANOVA) of percent cover ($\log_{10}$-transformed to normalize the residuals) as a function of species. We performed multiple comparisons between species using planned least squares means contrasts (Sokal and Rohlf 1995). Specifically, we tested if *S. canadensis* was more abundant than the other goldenrods, and if the goldenrods were more abundant than the asters. Furthermore, in order to match the survey results to Ernst more precisely, we also tested if *E. graminifolia* and *S. rugosa* (but not *S. canadensis*) were more abundant than the asters, since we only examined those particular goldenrods at Ernst. Analyses were performed using JMP IN 5.1 (SAS Institute, Inc. 2003).

### Quantitative literature survey

We conducted a literature search of the goldenrods and asters used in our experiments using the Web of Science (ISI) electronic bibliographic database (1900–2003). Our keyword searches included different combinations of "old field," "old-field," and focal species names (e.g., "*Aster prenanthoides*"). Additionally, we searched North American references in Rejmánek and Katwyk's *Old-field succession: a bibliographic review 1901–1991* (botanika.bf.jcu.cz/suspa/pdf/BiblioOF.pdf) for appropriate articles. Titles and abstracts were surveyed for publications that were likely to contain measures of relative abundance of old-field species. Our criteria for acceptable studies were publications that reported the biomass or percent cover of at least two of our focal species from North American fields at least 3 years since abandonment or mowing. Associated but unpublished data discussed in two publications (Carson and Barrett 1988; Carson and Root 2000) were also incorporated, as well as data from a doctoral dissertation. There were ultimately 11 studies that met our criteria, and they contained a total of 22 old-fields ranging in age from 3 to 50 years since agricultural abandonment or mowing (Table 1). We recorded relative abundance (species abundance measure divided by the sum of abundances of all species), measurement type (cover or biomass), and old-field age.

Using ANCOVA, we modeled relative abundance (square-root transformed to normalize residuals) as a function of: measurement type, species, years since old-field abandonment or mowing ($\log_{10}$-transformed), and species × years. We performed multiple comparisons between species using the same planned least squares means contrasts as for the old-fields natural survey, and likewise used the statistical software JMP IN.

## Results

### Field experiments

The main effects and the interaction effects were significant at both sites. Increases in stem densities caused decreases in the proportion of photosynthetically active radiation transmitted to the soil surface (PPAR), but the effect of density varied among species.

At Beagle Road, species cast similar amounts of shade at low density (4 stems/m$^2$) but at higher densities (16 and 64 stems/m$^2$) *Solidago canadensis* cast deeper shade than any other species and *S. gigantea* cast deeper shade than *Euthamia graminifolia* (Fig. 1a). At Ernst, the goldenrods cast deeper shade than the asters at lower densities, but all asters cast similar amounts of shade. At higher densities, the goldenrods still cast deeper shade than the asters, and *Aster pilosus* cast significantly less shade than the other asters, which cast similar amounts of shade (Fig. 1b).

At Beagle Road, we found a steeper slope of PPAR as a function of density for *S. canadensis* as compared to the other goldenrods (Fig. 2a). At Ernst, we found similar slopes of PPAR as a function of density (Fig. 2b) for *E. graminifolia*, *S. rugosa*, *A. novae-angliae*, and *A. prenanthoides*, indicating that the relationship between light attenuation and density as density increases is similar among these species even though they cast different amounts of shade at the same density. *A. pilosus* had a shallower slope than the other species as density increased. These differences in slopes at both sites were corroborated by the significant species × density interaction in the ANCOVAs (Table 2).

### Old-fields natural survey

In our survey of local old-fields, some species were consistently more abundant than others (model

**Table 1** A summary of the publications included in the quantitative literature survey of the natural abundances of our study species

| Publication | No. of old-fields | Old-field ages (years) | Location | Measurement type | Relevant species |
|---|---|---|---|---|---|
| Armesto and Picket (1985) | 1 | 7 | New Jersey | % Cover | *E. gramifolia, S. canadensis, S. rugosa, A. pilosus* |
| Bakelaar and Odum (1978) | 1 | 7 | Georgia | Biomass | *S. canadensis, A. pilosus* |
| Bazzaz (1968) | 11 | 3–40 | Illinois | % Cover | *S. canadensis, A. pilosus* |
| Bowers (1993) | 1 | 3 | Virginia | % Cover | *A. pilosus, S. candensis* |
| Carson and Barret (1988) | 2 | 3–6 | Ohio | Biomass | *E. gramifolia, S. canadensis, S. rugosa, S. gigantea, A. novae-angliae, A. pilosus, A. prenanthoides* |
| Carson and Peterson (1990) | 1 | 14 | New Jersey | Biomass | *S. canadensis, S. rugosa* |
| Carson and Root (2000) | 1 | 17 | New York | Biomass | *E. gramifolia, S. canadensis, S. rugosa, S. gigantea, A. novae-angliae, A. pilosus, A. prenanthoides* |
| Mellinger and McNaughton (1975) | 5 | 5–36 | New York | Biomass | *E. gramifolia, S. canadensis, S. rugosa, S. gigantea, A. novae-angliae, A. pilosus, A. prenanthoides* |
| Stevens (1999) | 1 | 4 | Pennsylvania | % Cover | *E. gramifolia, S. canadensis, S. rugosa, S. gigantea, A. novae-angliae, A. pilosus, A. prenanthoides* |
| Tramer (1975) | 2 | 3–4 | Ohio | Biomass | *A. pilosus, S. candensis* |
| Vankat and Carson (1991) | 2 | 10–50 | Ohio | % Cover | *E. gramifolia, S. canadensis, S. rugosa, S. gigantea, A. novae-angliae, A. pilosus, A. prenanthoides* |

The number of old-fields reported and their ages, the location, the type of measurement used to assess abundance, and the relevant species reported are presented

$R^2 = 0.52$; df $= 6$; MS $= 1.00$; $F$-ratio $= 8.92$; $P < 0.001$). Furthermore, the planned least squares means contrasts revealed that *S. canadensis* was significantly more abundant than the other goldenrods (*S. canadensis* versus *S. gigantea*, *S. rugosa*, and *E. graminifolia*: $P < 0.001$) and that the goldenrods as a group were significantly more abundant than the asters regardless of whether all of the goldenrods or only *E. graminifolia* and *S. rugosa* were compared to the asters (*S. canadensis*, *S. gigantea*, *S. rugosa*, and *E. graminifolia* versus *A. novae-angliae*, *A. pilosus*, and *A. prenanthoides*: $P < 0.001$; *S. rugosa* and *E. graminifolia* versus *A. novae-angliae*, *A. pilosus*, and *A. prenanthoides*: $P < 0.001$).

## Quantitative literature survey

The effect of species and the species × years interaction on relative abundance were significant, whereas the effects of measurement type and year were not (Table 3). The species × years interaction indicated that the rate of change in relative abundance through time differed among species. The planned least squares means contrasts revealed that *S. canadensis* was significantly more abundant than the other goldenrods (*S. canadensis* versus *S. gigantea*, *S. rugosa*, and *E. graminifolia*: $P < 0.001$) and that the goldenrods as a group were significantly more abundant than the asters (*S. canadensis*, *S. gigantea*, *S. rugosa*, and *E. graminifolia* versus *A. novae-angliae*, *A. pilosus*, and *A. prenanthoides*: $P = 0.0161$). However, when only *E. graminifolia* and *S. rugosa* were compared to the asters, the contrast was not significant (*S. rugosa* and *E. graminifolia* versus *A. novae-angliae*, *A. pilosus*, and *A. prenanthoides*: $P = 0.443$).

We found that most species did not change significantly in abundance depending on the years since old-field disturbance (Fig. 3). However, *S. canadensis* increased, and *A. pilosus* decreased, markedly in abundance with time. The difference in the slopes between *S. canadensis* and *A. pilosus* likely drives the significant species × years interaction in the ANCOVA (Table 3).

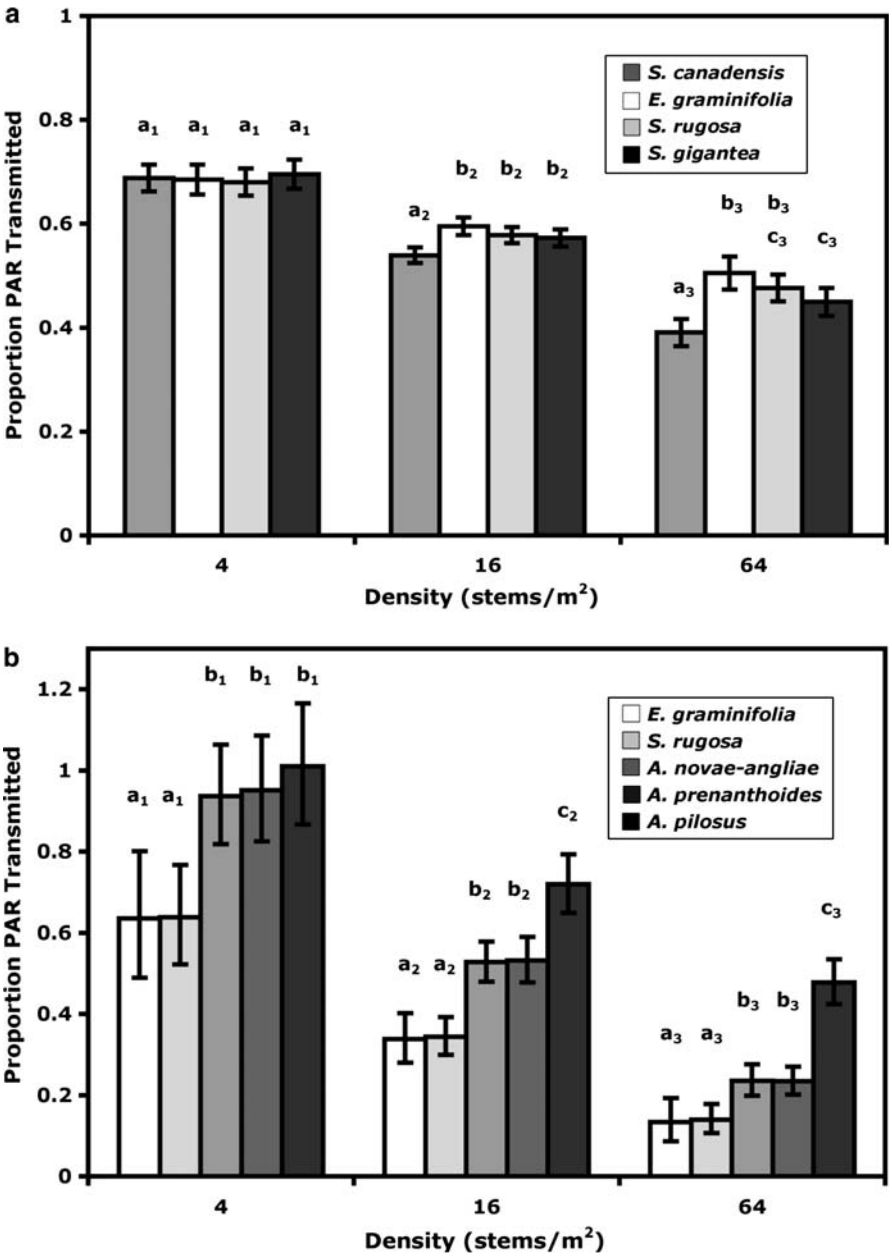

**Fig. 1** Least squares mean values, from the analyses of covariance, of the proportion of PAR transmitted to the soil surface for (**a**) Beagle Road and (**b**) Ernst at three different densities. The error bars represent 95% confidence limits. Species not connected by the same letter within a density are significantly different at $\alpha = 0.05$, using Dunn–Šidák-corrected $\alpha$ values of 0.0085 and 0.0051 for Beagle Road and Ernst, respectively

## Discussion

### Is competition for light consistent with patterns of species dominance in old-fields?

Light is a key limiting resource for many species in non-arid terrestrial plant communities from herbaceous old-fields to tropical forests (Cannell and Grace 1993; Hubbell et al. 1999; Carson and Root 2000; Wright 2002). While the status of light as a key limiting resource is recognized, studies testing if differences in the ability to compete for light map on to well-documented differences in relative abundance in terrestrial plant communities are rare. Especially surprising is the lack of previous investigation into this hypothesis in old-fields, which are so prevalent in human-altered landscapes. We found that, indeed, the hierarchy of light attenuation abilities of our study species matched their natural abundances in surrounding old-fields. This is consistent with the

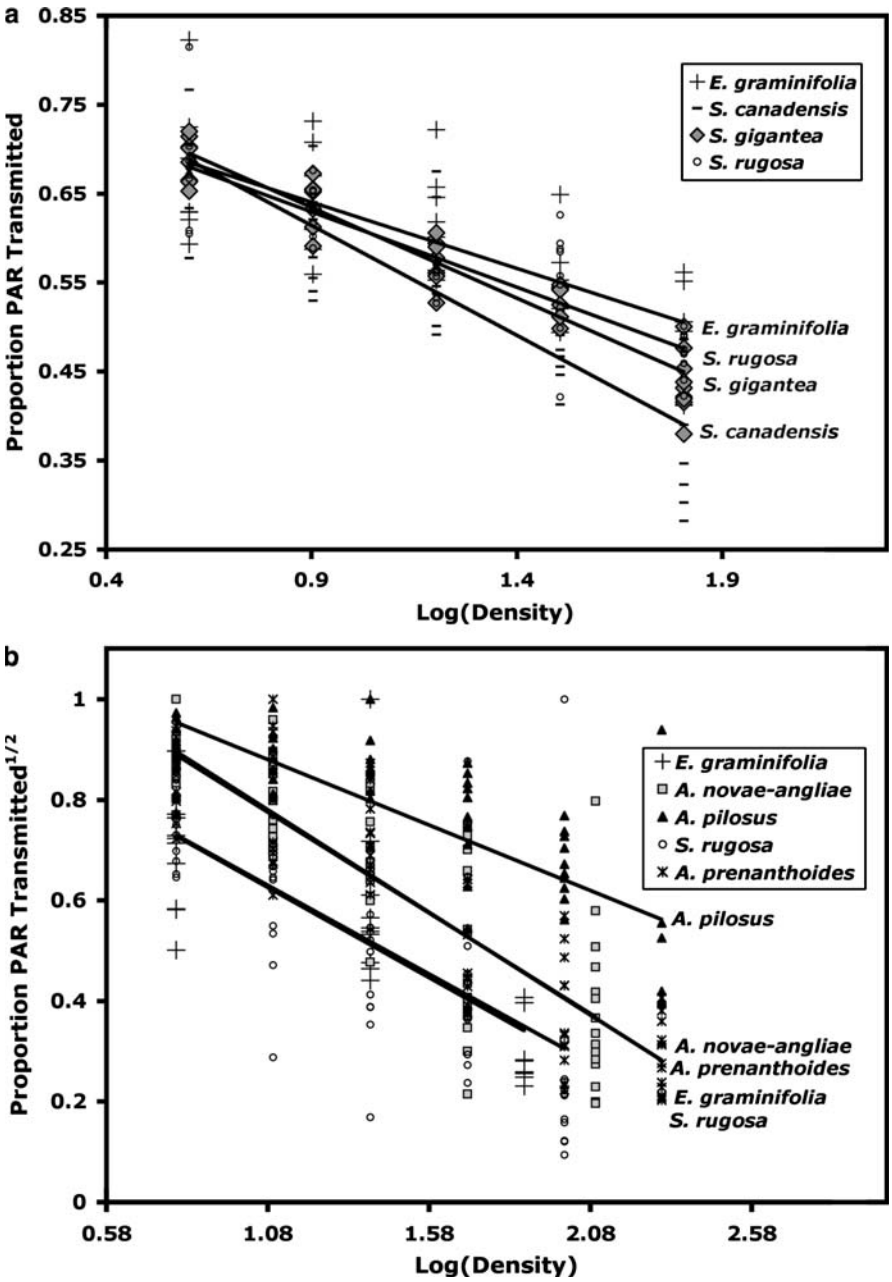

**Fig. 2** Proportion of photosynthetically active radiation transmitted to the soil surface (PPAR) as a function of log(density) for (**a**) Beagle Road and (**b**) Ernst. Density is measured in stems/m$^2$. The lines are best-fit linear regression lines. PPAR$^{1/2}$ is used for Ernst to make the figure congruent with the corresponding ANCOVA

hypothesis that the dominant species, in this case goldenrods and in particular *S. canadensis*, were able to achieve the greatest abundance because they were the best competitors for the limiting resource, in this case light.

An alternative interpretation of our data is that patterns of species abundance are determined not by light attenuation ability but by the ability to compete for some other resource correlated with it. If competition for belowground resources were actually the predominant process in these communities, and larger plants were better able to compete for belowground resources, then (assuming larger plants cast more shade) this could result in a non-causal association between light attenuation and abundance. While we did not account for belowground competition, we think this scenario is less likely. Because old-fields support very high density and biomass of

**Table 2** Analyses of covariance for the proportion of photosynthetically active radiation transmitted to the soil surface (PPAR) for the Beagle Road and Ernst sites, separately

| | Beagle Road | | | | Ernst | | | |
|---|---|---|---|---|---|---|---|---|
| | df | SS | MS | *F* | df | SS | MS | *F* |
| Log(density) | 1 | 1.14 | 1.14 | 452.58*** | 1 | 7.65 | 7.65 | 421.42*** |
| Species | 3 | 0.063 | 0.021 | 8.31*** | 4 | 3.02 | 0.75 | 41.55*** |
| Species × Log(density) | 3 | 0.040 | 0.013 | 5.32** | 4 | 0.22 | 0.055 | 3.02* |
| Error | 152 | 0.38 | 0.0025 | | 283 | 5.14 | 0.018 | |

The multiple $R^2$ values for the models are presented, as well as sums of squares (SS), mean squares (MS), F statistics (*F*), and significances for the individual factors (rows)

* $P < 0.01$; ** $P < 0.01$; *** $P < 0.001$

Beagle Road Model $R^2 = 0.76$; Ernst Model $R^2 = 0.68$

**Table 3** Analysis of covariance for the relative abundance of the species in our study, according to a quantitative literature survey

| | df | SS | MS | *F* |
|---|---|---|---|---|
| Measurement type | 1 | 0.042 | 0.042 | 1.56 |
| Log(years since abandonment or mowing) | 1 | 0.0061 | 0.0061 | 0.23 |
| Species | 6 | 1.89 | 0.31 | 11.69** |
| Species × Log(years) | 6 | 0.66 | 0.11 | 4.09* |
| Error | 86 | 2.31 | 0.027 | |

* $P < 0.01$; ** $P < 0.001$

Model $R^2 = 0.52$

vegetation, it is reasonable to assume that they contain high levels of soil nutrients. Therefore, it seems much more likely that competition would be predominantly aboveground, where light is scarce. Furthermore, we found that plants from Beagle Road showed only an extremely weak negative relationship between monoculture height and light attenuation ($R^2 = 0.028$, $P = 0.033$), and that plants from Ernst showed only a moderate negative relationship ($R^2 = 0.19$, $P < 0.001$), suggesting that larger plants do not necessarily cast more shade than smaller ones. It seems likely that some other aspects of the phenotype, perhaps stem architecture and leaf density distribution (Schmid and Bazzaz 1990, 1994), are accounting for much interspecific variation in light attenuation ability. An important extension to our work would be to study above- and belowground competition simultaneously to determine the relative importance of these processes in old-fields.

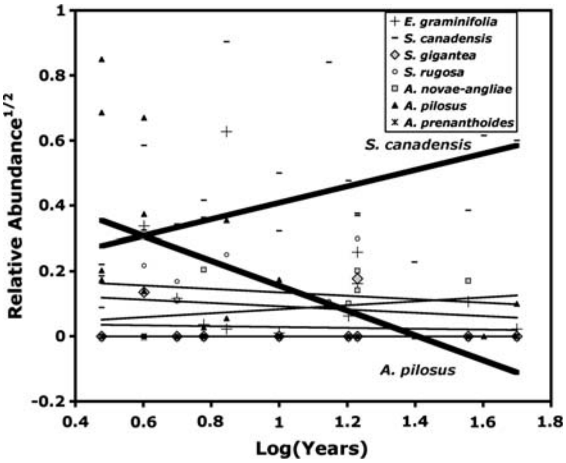

**Fig. 3** Relative abundance$^{1/2}$ of our study species as a function of log(years since old-field abandonment or mowing) according to a quantitative literature survey. The lines are best-fit linear regression lines. The bold lines highlight the best-fit linear regression lines for *S. canadensis* and *A. pilosus*. Relative abundance$^{1/2}$ is used to make the figure congruent with the corresponding ANCOVA

It would be interesting to investigate the stage at which light competition occurs in old-fields. For instance, it could be that it is most important in the establishment phase, with young goldenrod seedlings and ramets better able to tolerate the shade levels under asters than vice versa, rather than among mature individuals. To address this hypothesis, future studies should integrate the competition process over the entire season and establishment phase.

The literature survey suggested that increased abundance of goldenrods as compared to asters is driven almost entirely by an increase in the abundance of *S. canadensis* and a decrease in the abundance of *A. pilosus* through time. We cannot make light attenuation comparisons directly between *S. canadensis* and *A. pilosus*, because we sampled one species in an old-field and the other in an agricultural monoculture. Nonetheless we found that *A. pilosus* intercepted less light, and *S. canadensis* intercepted more light, than any other co-occuring species. The fact that *S. canadensis* has a good ability to cast shade and also increases in abundance through time, whereas *A. pilosus* has a poor ability to cast shade and decreases in abundance through time, is consistent with the hypothesis that *S. canadensis* displaces *A. pilosus* because it is a better competitor for light.

While we observed that only *S. canadensis* and *A. pilosus* change in abundance through time, this differs from the conventional view that goldenrods generally displace asters regardless of the specific species (Baskin and Baskin 1979; Armesto and Pickett 1985; Bazzaz 1996; Leck and Leck 1998). We cannot offer a definitive explanation for this discrepancy. One possibility, however, is that limited sampling influenced our survey because we only had 11 studies that met our criteria, and they represented only nine different localized areas of the US. In contrast to our survey, the five-decades-long Buell-Small succession study supports the conventional view, showing a much more general pattern of goldenrods replacing asters through time and showing unimodal temporal distributions in abundance that are expected during succession (Meiners et al. unpublished; Fig. 4).

## Competition for light in other terrestrial plant communities

While our results suggest that light is important in structuring old-field plant communities, the importance of light competition depends on the particular community being examined. For example, Canham et al. (1994) analyzed light attenuation beneath the canopies of nine coniferous and deciduous canopy tree species of southern New England. As with our study, they found that the most abundant species in the oldest stands were the ones that cast the most shade; tree species that were abundant in younger stands cast less shade and were apparently displaced in older stands. They interpreted their results as suggesting that light competition was important in structuring those communities. Representing another aspect of light competition (light use efficiency, rather than light use preemption), Pattison et al. (1998) and Durand and Goldstein (2001) found that several invasive plant species in Hawaiian rainforests were more efficient with light resources under shaded, and presumably more light-limited, conditions than their native counterparts. This implies that light competition could be important in accounting for the displacement of native species in that system. On the other hand, Seabloom et al. (2003) found that light competition was not important in structuring a semi-arid grassland in California. Exotic annuals had an inferior ability to attenuate light versus native perennials, even though the exotic annuals were far more abundant, perhaps reflecting an increased role of belowground competition. We believe more empirical research on the importance of light competition is warranted in a larger variety of terrestrial plant communities.

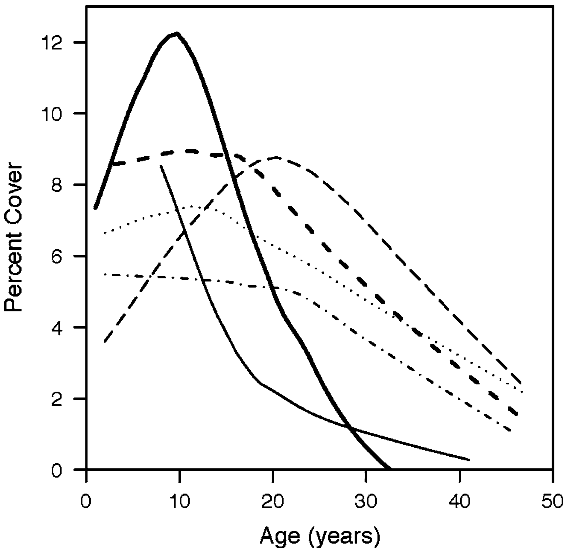

**Fig. 4** Percent cover as a function of the time since old-field abandonment. Data is from the ongoing Buell–Small Succession Study begun in 1958 in Somerset County, New Jersey, USA, and is based on more than 15,000 observations of 0.5 × 2 m plots distributed across 10 fields which entered secondary succession in different years (Meiners et al. unpublished; see http://www.ecostudies.org/bss/ for more information). Lines were fit with local polynomial regression. The solid lines are asters and the dashed or dotted lines are goldenrods. The thick solid line is *A. pilosus*, the thin solid is *A. novae-angliae*, the thick dashed is *S. canadensis*, the thin dotted is *E. graminifolia*, the thin dot-dash is *S. gigantea*, and the thin dash is *S. rugosa*

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## References

Armesto JJ, Pickett STA (1985) Experiments on disturbance in old-field plant communities: impact on species richness and abundance. Ecology 66:230–240

Bakelaar RG, Odum EP (1978) Community and population level responses to fertilization in an old-field ecosystem. Ecology 59:660–665

Baskin JM, Baskin CC (1979) Germination strategy of oldfield aster (*Aster pilosus*). Am J Bot 66:1–5

Bazzaz FA (1968) Succession on abandoned fields in the Shawnee Hills, southern Illinois. Ecology 49:924–936

Bazzaz FA (1996) Plants in a changing environment. Cambridge University Press, Cambridge

Bowers MA (1993) Influence of herbivorous mammals on an old-field plant community: years 1–4 after disturbance. Oikos 67:129–141

Canham CD, Finzi AC, Pacala SW, Burbank DH (1994) Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. Can J For Res 24:337–349

Cannell MGR, Grace J (1993) Competition for light: detection, measurement, and quantification. Can J For Res 23:1969–1979

Carson WP, Barrett GW (1988) Succession in old-field plant communities: effects of contrasting types of nutrient enrichment. Ecology 69:984–994

Carson WP, Peterson CJ (1990) The role of litter in an old-field community: impact of litter quantity in different seasons on plant species richness and abundance. Oecologia 85:8–13

Carson WP, Pickett STA (1990) Role of resources and disturbance in the organization of an old-field plant community. Ecology 71:226–238

Carson WP, Root RB (2000) Herbivory and plant species coexistence: community regulation by an outbreaking phytophagus insect. Ecol Monogr 70:73–99

Chmielewski JG, Semple JC (2001) The biology of Canadian weeds. 114. *Symphyotrichum pilosum* (Willd.) Nesom (*Aster pilosus* Willd.). Can J Plant Sci 81:851–865

Chmielewski JG, Semple JC (2003) The biology of Canadian weeds. 125. *Symphyotrichum ericoides* (L.) Nesom (*Aster ericoides* L.) and *S. novae-angliae* (L.) Nesom (*A-novae-angliae* L.). Can J Plant Sci 83:1017–1037

Durand LZ, Goldstein G (2001) Photosynthesis, photoinhibition, and nitrogen use efficiency in native and invasive tree ferns in Hawaii. Oecologia 126:345–354

Harpole WS, Tilman D (2006) Non-neutral patterns of species abundance in grassland communities. Ecol Lett 9:15–23

Hartnett DC, Bazzaz FA (1985) The integration of neighborhood effects by clonal genets in *Solidago canadensis*. J Ecol 73:415–427

Hubbell SP, Foster RB, O'Brien ST, Harms KE, Condit R, Wechsler B, Wright SJ, Loo de Lao S (1999) Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. Science 283:554–557

Huisman J (1999) Population dynamics of light-limited phytoplankton: microcosm experiments. Ecology 80: 202–210

Keddy PA, Twolan SL, Wisheu IC (1994) Competitive effect and response rankings in 20 wetland plants: are they consistent across three environments? J Ecol 82:635–643

Keever C (1950) Mechanisms of plant succession on old fields of Lancaster County, Pennsylvania. Bull Torrey Bot Club 106:299–308

Leck MA, Leck CF (1998) A ten-year seed bank study of old field succession in central New Jersey. J Torrey Bot Soc 125:11–32

Mellinger MV, McNaughton SJ (1975) Structure and function of successional vascular plant communities in central New-York. Ecol Monogr 45:161–182

Miller TE, Burns JH, Munguia P, Walters EL, Kneitel JM, Richards PM, Mouquet N, Buckley HL (2005) A critical review of twenty years' use of the resource-ratio theory. Am Nat 165:439–448

Pattison RR, Goldstein G, Ares A (1998) Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. Oecologia 117:449–459

R Development Core Team (2007) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org. Accessed on October 14, 2007

Rejmánek M (1989) Invasibility of plant communities. In: Mooney HA, DiCastri F, Groves RH, Kruger FJ, Rejmánek M, Williamson M (eds) Biological invasions: a global perspective. John Wiley & Sons, Chichester, UK, pp 369–377

SAS Institute, Inc (2003) JMP IN version 5.1. Cary

Schmid B, Bazzaz FA (1990) Plasticity in plant size and architechture in rhizome-derived *Solidago* and *Aster*. Ecology 71:523–535

Schmid B, Bazzaz FA (1992) Growth responses of rhizomatous plants to fertilizer application and interference. Oikos 65:13–24

Schmid B, Bazzaz FA (1994) Crown construction, leaf dynamics, and carbon gain in two perennials with contrasting architechture. Ecol Appl 64:177–203

Seabloom EW, Harpole WS, Reichman OJ, Tilman D (2003) Invasion, competitive dominance, and resource use by exotic and native California grassland species. Proc Natl Acad Sci USA 100:13384–13389

Sheppard AW, Shaw RH, Sforza R (2006) Top 20 environmental weeds for classical biological control in Europe: a review of opportunities, regulations and other barriers to adoption. Weed Res 46:93–117

Sokal RR, Rohlf FJ (1995) Biometry: the principles and practice of statistics in biological research. W.H. Freeman and Company, New York

Stevens MH (1999) Ph.D Dissertation

Stevens MHH, Bunker DE, Schnitzer SA, Carson WP (2004) Establishment limitation reduces species recruitment and species richness as soil resources rise. J Ecol 92:339–347

Tilman D (1982) Resource competition theory and community structure. Princeton University Press, NJ

Tilman D (1988) Dynamics and structure of plant communities. Princeton University Press, NJ

Tramer EJ (1975) The regulation of plant species diversity on an early successional old-field. Ecology 56:905–914

Vankat JL, Carson WP (1991) Floristics of a chronosequence corresponding to old field deciduous forest succession in southwestern Ohio. III. Post-disturbance vegetation. Bull Torrey Bot Club 118:385–391

Vankat JL, Snyder GW (1991) Floristics of a chronosequence corresponding to old field deciduous forest succession in southwestern Ohio. 1. Undisturbed vegetation. Bull Torrey Bot Club 118:365–376

Walck JL, Baskin JM, Baskin CC (2001) Why is *Solidago shortii* narrowly endemic and *S. altissima* geographically widespread? A comprehensive comparative study of biological traits. J Biogeogr 28:1221–1237

Werner PA, Bradbury IK, Gross RS (1980) The biology of Canadian weeds. 45. *Solidago canadensis* L. Can J Plant Sci 60:1393–1409

Wright SJ (2002) Plant diversity in tropical forests: a review of mechanisms of species coexistence. Oecologia 130:1–14

Zhang JJ, Stephenson DE, Semple JC, Oldham MJ (1999) COSEWIC status report on the crooked-stem aster *Symphyotrichum prenanthoides*. In: COSEWIC assessment and status report on the crooked-stem aster *Symphyotrichum prenanthoides* in Canada. Committee on the Status of Endangered Wildlife in Canada, pp 1–16