

Kevin R. Kosola · Katherine L. Gross

Resource competition and suppression of plants colonizing early successional old fields

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Abstract Early colonizing annual plants are rapidly suppressed in secondary succession on fertile midwestern old fields, while later colonizing perennials persist. Differences in competitive ability for above- and belowground resources may be partly responsible for differences in species persistence during succession, as both light and nutrient availability may change rapidly. We found that, although both above- and belowground competition suppress growth of colonizing plants, belowground competition was the dominant factor in the suppression of the annual *Ambrosia artemisiifolia* in 2nd-year-old fields near the W.K. Kellogg Biological Station in southwestern Michigan. Despite an ability to persist in later successional fields, seedling transplants of the perennial *Achillea millefolium* were also suppressed by above- and belowground competition, with belowground competition having the strongest effect. As in many old fields, nitrogen availability is the primary factor limiting plant productivity. There was no clear difference between the species in ability to compete for ^{15}N from an enriched patch, although there was an indication of greater precision of foraging by *Achillea*. Life history differences between these species and consequent differences in the phenology of root growth relative to other old-field plants are likely to play a large role in the persistence of *Achillea* in successional fields where *Ambrosia* is suppressed.

Key words *Achillea millefolium* · *Ambrosia artemisiifolia* · Belowground competition · Nitrogen acquisition · Old-field succession

Introduction

Suppression of early colonizing plant species by later colonists is presumed to be one of the primary mechanisms driving secondary succession in old-field plant communities (Connell and Slatyer 1977; Pickett et al. 1987; Tilman 1988). Later colonizing species may suppress earlier colonizing species by competition for light or soil resources. Experimental studies in successional fields have demonstrated that both light and soil resources can limit plant growth in both low- (Wilson and Tilman 1991, 1993; Foster and Gross 1997) and higher-productivity sites (Raynal and Bazzaz 1975).

Light and nutrient availability can change dramatically during old-field succession. Consequently, early and later colonizing species may experience different competitive regimes and differ in their competitive ability for above- and belowground resources (Tilman 1993; Bazzaz 1996). Light levels typically decline during secondary succession, especially in high-fertility sites (Tilman 1988; Bazzaz 1996), so competition for light is expected to be important in determining species replacement patterns in such sites. However, soil nutrient levels may also be low in fertile sites with high plant productivity, as a consequence of plant uptake, making competition for soil nutrients important in these sites. Thus both above- and belowground competition may be important in determining species replacement patterns and successional dynamics in high-fertility sites.

Soils at the W.K. Kellogg Biological Station (KBS) in southwestern Michigan are relatively fertile, so plant production and cover is high and light levels are rapidly reduced in newly abandoned fields (Huberty et al. 1998; K.L. Gross, unpublished data). Soil nitrogen levels can also change dramatically within the first years following abandonment: total extractable N can decline by as much as a factor of ten over the first 2 years following abandonment (Huberty et al. 1998; see also Methods). Annuals are generally excluded from successional fields

K.R. Kosola (✉) · K.L. Gross
W.K. Kellogg Biological Station,
Botany and Plant Pathology Department,
Michigan State University,
3700 E. Gull Lake Drive,
Hickory Corners, MI 49060, USA
e-mail: kosola@kbs.msu.edu, Fax: +1-616-6712104

at KBS within 1–2 years following abandonment (Huberty et al. 1998); they are replaced by herbaceous perennials that can persist for decades (Gross and Werner 1982; Huberty et al. 1998). However, whether the exclusion of annuals from early successional sites is due to above- or belowground competition has not been established and has rarely been measured in the field, although the work of Raynal and Bazzaz (1975) indicated both could be important.

In this paper we report the results of experiments examining the importance of above- and belowground competition in the rapid exclusion of the early colonizing annual species *Ambrosia artemisiifolia* (ragweed) from successional fields at KBS. Annual seedlings colonize gaps in the established perennial and biennial vegetation for several years following abandonment. In these gaps, light is unlikely to be limiting; nevertheless, the annual plants growing there are strongly suppressed. This led us to hypothesize that belowground competition may be more important than aboveground competition in the exclusion of annuals such as *Ambrosia* from early successional old fields.

Further, we hypothesized that later colonizing species would be better belowground competitors than early colonizing species, because soil nutrient levels can be lower and more heterogeneous in later successional fields (Gross et al. 1995). Specifically, we predicted that the later colonizing herbaceous perennial, *Achillea millefolium* (yarrow), would be better able to exploit soil resources from patches than *Ambrosia*. *Achillea* persists in successional fields at KBS where *Ambrosia* is excluded (Goldberg 1987, Huberty et al. 1998). To test this hypothesis, we compared the abilities of these species to acquire nitrogen from enriched patches created with ^{15}N -labeled NH_4^+ , in the presence and absence of above- and belowground competition.

Materials and methods

Site description

We conducted this experiment in 1994 in a 2nd-year-old field at the W.K. Kellogg Biological Station of Michigan State University (KBS; see Gross et al. 1995 for a description). The field had been plowed and abandoned in the spring of 1993. Total extractable N was $0.81 \mu\text{g N/g}$ dry soil in our study site, compared to about $6 \mu\text{g N/g}$ dry soil in an adjacent 1st year-old field (Huberty 1994). The site was dominated by winter annuals and perennials. Plant cover was patchy, especially early in the spring. Gaps in the plant canopy were areas of soil (mean size $0.3 \pm 0.03 \text{ m}^2$) surrounded by established vegetation (Goldberg and Gross 1988); annual seedlings were common here (mean of 11 ± 0.8 *Ambrosia* seedlings per opening). Early in the growing season, light availability in these gaps was about threefold higher than under the surrounding canopy (midday light transmission within openings = $58 \pm 6\%$; under canopy = $18 \pm 5\%$ on 22 May 1994).

Species descriptions

The two species chosen for these experiments, *A. artemisiifolia* and *A. millefolium*, are both in the family Compositae. They have

similar seedling morphology, although they differ in later growth form. *A. artemisiifolia* is an annual with an erect growth form; it is frequently dominant in 1st-year successional old fields in the mid-west (Miller 1985; Goldberg and Miller 1990; Bazzaz 1996). *A. millefolium* is a later successional perennial with a rosette juvenile growth form and an erect flowering stem. *A. millefolium* is common throughout the midwestern U.S. in later successional old fields, where *Ambrosia* is absent. *Achillea* can persist in fields that have been abandoned for up to 50 years (Gross and Werner 1982; Goldberg 1987). Besides providing a contrast between an early and later colonizing species, we expected that these species would differ in their ability to acquire soil nitrogen; prior greenhouse work showed differences in their response to nutrient-enriched patches in soil (Gross et al. 1993).

Experimental design

To examine the effects of competition from established vegetation on growth of *Ambrosia* and *Achillea*, we established experimental treatments that manipulated exposure to aboveground and belowground competition in a factorial design. There were ten treatments: two species and all four combinations of above- (a) and belowground (b) competition: $a + b +$, $a + b -$, $a - b +$, $a - b -$, as well as a trenching treatment for each species.

We set up eight replicate blocks of the experiment on 15 June 1994. The blocks were arranged in a 4×2 array; each individual block was 5 m by 9 m, with the long axis running parallel to the contour of a slight north-to-south slope in the field. Within each block, we established ten 15-cm-diameter experimental plots in the center of haphazardly chosen gaps in the vegetation. Two seedlings of either *Ambrosia* or *Achillea* were transplanted into the center of each plot, except where *Ambrosia* seedlings were already present near the plot center; in this case, the existing *Ambrosia* plants were thinned to two seedlings per gap. Seedlings of each species were grown in flats of field soil in a greenhouse; all seeds were collected from local fields. They were transplanted into the field after about 6 weeks of growth. Seedlings of *Ambrosia* already present in many of the gaps were similar in size and developmental stage to the greenhouse-grown seedlings. Plants that died for any reason were replaced until the 3rd week of the experiment (July 9).

Belowground competition was eliminated in half the plots by driving 15-cm-diameter PVC pipe root exclosures 20 cm into the ground (Fig. 1). The pipes had ten 6.35-cm-diameter circular openings distributed evenly around the pipe that were covered with 35- μm nylon mesh (Nitex mesh, Tetko, Briarcliff Manor, N.Y.) attached to the outside of the PVC pipe with PVC cement. This mesh size is small enough to prevent plant roots from growing into or out of the exclosure, but large enough to allow movement of water, nutrients, and mycorrhizal hyphae in and out of the root exclosure (Johansen et al. 1994). Root exclosures were installed in the field 4 days before transplanting seedlings into the plots. Because many previous studies have used trenching to exclude belowground competition, we also included a set of plots trenched to 20 cm depth with a shovel for a comparison to these studies. Trenching was performed once, 4 days before transplanting seedlings into the plots. To remove aboveground competition in half the plots, we placed cone-shaped wire mesh collars around the 15-cm plots; these held the shoots of surrounding vegetation away from the target seedlings (Fig. 1). Vegetation which grew through the mesh into the plot was pulled back every week. The collars were installed in late June, after transplanted seedlings were established, and left in place until the end of the experiment (late August).

In early July, we noticed that about 25% of the *Achillea* seedlings had been damaged by small mammals, probably mice. To prevent further damage to the seedlings, we enclosed the *Achillea* seedlings with an open-topped wire mesh cylinder (15 cm high and 15 cm diameter, constructed out of 0.6-cm 2 mesh hardware cloth) for the remainder of the experiment. We observed no evidence of mouse grazing on *Ambrosia* seedlings, and did not install animal exclosures around these plants. We dusted all seedlings with Sevin

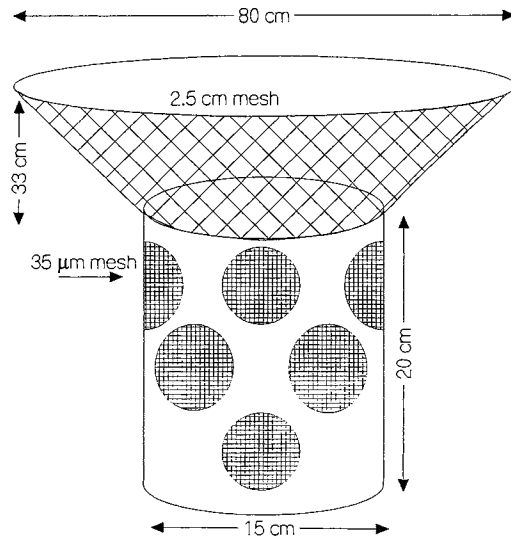


Fig. 1 Schematic of root and shoot exclosures

(Ortho Chemicals, San Ramon, Calif.) and sprayed with *Bacillus thuringiensis* (Ortho Chemicals) once in early July to prevent beetle and caterpillar herbivory.

Final plant biomass

We harvested the plants in late August after about 2 months of growth; *Ambrosia* plants were just beginning to flower at this time. Plots were harvested and processed in sets of two blocks per day. We clipped shoots of the experimental plants at ground level and placed them in paper bags for drying. We also collected shoots of neighboring vegetation in two concentric rings of 30 cm diameter and 40 cm diameter centered on the plot. Roots from plots with belowground exclosures were harvested by pulling out the exclosure and contained soil, and then washing roots free of soil on a 6-mm screen. Roots from plots without belowground exclosures were harvested from 15-cm-diameter 15-cm-deep soil cores, as the soil was too dry at the time of harvest to drive soil cores to 20 cm. We recovered most roots from the top 10 cm of the cores, and so assumed that the errors introduced by slightly different soil core sizes would be negligible compared to unavoidable variation in total root recovery.

All plant material was dried immediately after harvesting at 70 °C for at least 72 h and stored at room temperature pending further processing. Stored samples were subsequently dried for a further 24 h immediately prior to weighing and grinding.

Nitrogen acquisition

To test the hypothesis that later successional species are better at acquiring resources from patches than early successional species, we created a nitrogen-enriched patch in each plot 1 month after the initial transplant date (see Knowles and Blackburn 1993, for discussion of use of ^{15}N as a tracer). The patch was created by injecting 1 ml of 88.5 mM 25% enriched ^{15}N NH_4Cl , followed by 1 ml of distilled, deionized water 4 cm deep in the soil. Based on prior soil analyses, this was sufficient to give an approximately fivefold increase in available N within the labeled soil volume, a roughly spherical volume about 2 cm in diameter. We estimated the labeled volume in laboratory studies of water distribution in intact cores using the iodine tracer method of van Ommen et al. (1988). The enriched patch was placed midway between the two plants in

each plot, approximately 4 cm from the base of the shoots. All plants were large enough to have lateral roots reaching into the labeled volume at time of labeling.

Plants grew for about 40 days between soil labeling and harvest. Analysis of acquisition of applied ^{15}N was carried out for all plots, based on total plant biomass in the plot for target plants and on shoot biomass for neighboring plants. In addition, ^{15}N enrichment of plant nitrogen provided an index of the proportion of total plant N which was acquired from the labeled patch. We measured ^{15}N content in combined shoots and roots of individual plants from the experimental treatments and in shoots of neighboring plants. All plant tissue was coarsely ground in a centrifugal mill (Tecator Cyclotec, Tecator, Sweden). Subsamples of the coarse-ground material were ground further in a miniature ball mill (Wigg-L-Bug, Crescent Dental, Lyons, Ill.) to the flour-like consistency required for accurate mass spectrometer analysis. We took 15-cm-deep 2.5-cm-diameter soil cores centered on the ^{15}N injection site from each plot for estimates of soil nitrogen pools, and analyzed several for extractable inorganic ^{15}N and microbial biomass ^{15}N using the fumigation-extraction method for microbial biomass nitrogen (Paul et al. 1998) and the diffusion method for analysis of extracted ^{15}N (Brooks et al. 1989). All ^{15}N analyses were run on an ANCA-MS system (Harris and Paul 1989).

Statistical analysis

All statistical analyses were done using the SAS GLM program (Freund et al. 1986). Plot-mean final plant biomass data were log-transformed before ANOVA to correct for heteroscedasticity. Growing two plants per plot and analyzing mean plant biomass reduced the effect of plant-to-plant variation without requiring an increase in replication. Plots with single surviving plants were excluded from this analysis, as they grew slightly larger than plants from equivalent treatment plots containing two plants. We carried out comparisons of species and treatment effects using a mixed-model ANOVA, with blocks as a random effect and competition treatments as fixed effects; trenching was excluded from this model. Effects of trenching on final plant biomass were analyzed with a separate one-way ANOVA.

Results

Competition and plant growth

Both aboveground and belowground competition significantly depressed the final dry weight of both *Ambrosia* and *Achillea*; exclusion of either neighboring shoots, neighboring roots, or both roots and shoots increased growth in both species (Table 1, Fig. 2). Removing belowground competition by excluding neighboring roots increased growth of both species more than removing aboveground competition by excluding neighboring shoots (Fig. 2). We observed no significant growth differences between transplanted and untransplanted *Ambrosia* (data not shown).

For both species, plants from the trenched plots were intermediate in size between plants with and without root exclosures (Fig. 2). Plants grown in trenched plots without root exclusion were significantly larger than plants in untrenched plots, but significantly smaller than plants grown in root exclosures ($P < 0.05$). Trenching therefore partially reduced belowground competition.

Table 1 Plant growth. ANOVA table for the effects of above- (a) and belowground (b) competition on final dry weight of *Ambrosia artemisiifolia* and *Achillea millefolium*

Effect	df	F
Block	7	1.38
Species	1	22.0***
a	1	19.19***
b	1	152.05***
Species × a	1	2.21
Species × b	1	0.11
a × b	1	0.99
a × b × species	1	1.08
Error	32	

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$

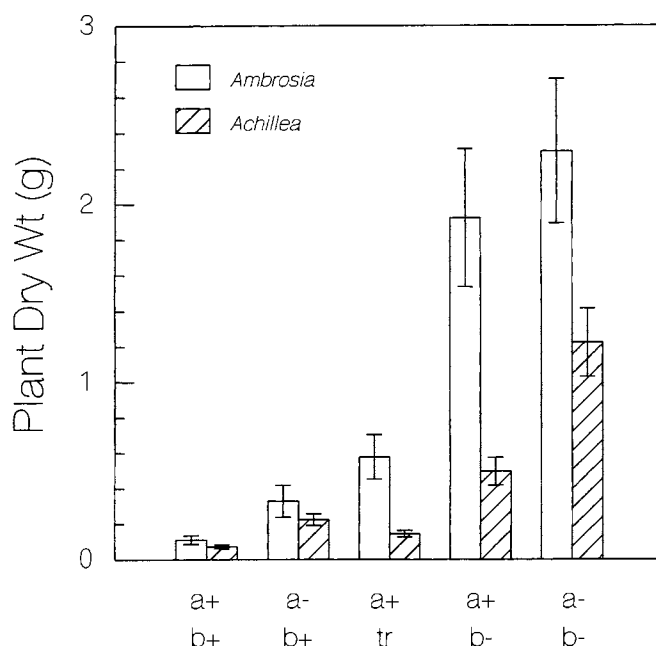


Fig. 2 Mean total plant dry weight (g) of plants in each of the experimental treatments. Labels along x-axis list treatment combinations: a aboveground competition from neighbors, b belowground competition from neighbors, tr trenching to 20 cm; + signifies presence of competition, - indicates experimental exclusion of competition. Error bars for this and following figures are \pm SE of the mean. Growth increase after removing aboveground competition $[(a-b+) - (a+b+)]/(a+b+) = 1.5$ for *Ambrosia* and 1.6 for *Achillea*; growth increase after removing belowground competition $[(a+b-) - (a+b+)]/(a+b+) = 11.5$ for *Ambrosia* and 7.5 for *Achillea*

Ambrosia had a significantly lower root/shoot biomass ratio than *Achillea* ($P < 0.0001$; Fig. 3). Belowground competition had a significant effect on the root/shoot ratio for both species ($P < 0.05$ for 2-way ANOVA, Fig. 3). *Achillea* plants were generally smaller than *Ambrosia* plants in equivalent treatments (Fig. 2), but had a greater root/shoot ratio (Fig. 3); consequently, root weights (excluding *Ambrosia* tap roots) and estimated root lengths for the two species (based on specific root length of greenhouse-grown plants for the two species; unpublished data) were not significantly different within each treatment (data not shown).

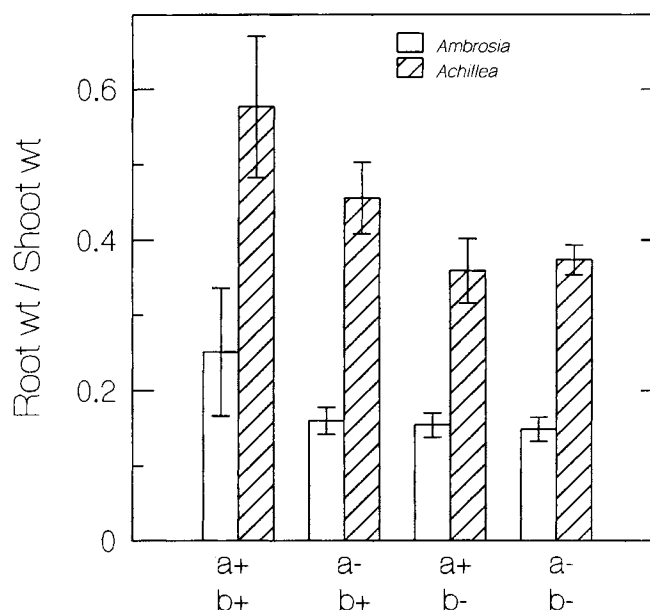


Fig. 3 Mean root weight/shoot weight ratio of plants in each of the experimental treatments. Labels and error bars as in Fig. 2

Table 2 ^{15}N enrichment of plant nitrogen pools ((atom % ^{15}N)-(natural abundance % ^{15}N) w/w) \pm SE

Treatment	<i>Ambrosia</i> % ^{15}N	<i>Achillea</i> % ^{15}N
a + b +	2.48 \pm 0.55	4.35 \pm 1.80
a - b +	3.99 \pm 0.93	3.22 \pm 0.64
a + b -	3.27 \pm 0.56	8.69 \pm 3.33
a - b -	2.97 \pm 0.70	5.72 \pm 1.21

Nitrogen acquisition

^{15}N enrichment of plant nitrogen pools ((atom % ^{15}N)-(natural abundance % ^{15}N)) was greater for *Achillea* tissue than *Ambrosia* (Table 2; $P \leq 0.05$), indicating that *Achillea* obtained a greater proportion of its nitrogen from the ^{15}N -labeled patch of NH_4^+ than did *Ambrosia*. There was no significant difference between the two species in total ^{15}N acquired (Table 3). There were significant competition treatment effects on ^{15}N acquisition and a significant interaction between above- and belowground competition treatments (Table 3). Aboveground competition only affected ^{15}N acquisition for plants grown without belowground competition ($P < 0.05$, Tukey's HSD for one-way ANOVA of simple effects of each combination of above- and belowground competition). ^{15}N acquisition from the labeled patch was linearly proportional to the log of plant biomass for both *Achillea* and *Ambrosia* (Fig. 4a). For both species, the highest ^{15}N acquisition was in the plots with both above- and belowground competition excluded, where the plants were largest. ^{15}N acquisition by each species was linearly proportional to root weight (excluding the central tap root of *Ambrosia*, Fig. 4b).

Table 3 ^{15}N acquisition. ANOVA table for the effects of above-ground and belowground competition on acquisition of ^{15}N -labeled nitrogen by *Ambrosia artemisiifolia* and *Achillea millefolium*. Treatment codes as in Table 1

Effect	df	F
Block	7	1.53
Species	1	0.10
a	1	21.27***
b	1	118.78***
Species \times a	1	0.33
Species \times b	1	0.00
a \times b	1	5.92*
a \times b \times species	1	1.37
Error	42	

* $P \leq 0.05$; *** $P \leq 0.001$

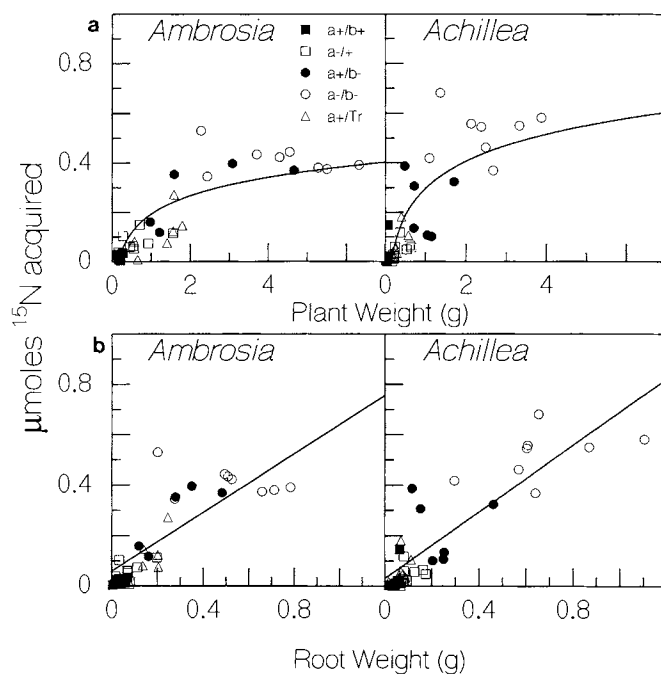


Fig. 4 **a** ^{15}N acquired by individual plants as a function of plot total plant dry weight (g). Regression equations: *Ambrosia* ^{15}N acquired = $0.19 + 0.11(\ln \text{ dry weight})$, $r^2 = 0.73$, $P < 0.0001$; *Achillea* ^{15}N acquired = $0.30 + 0.16(\ln \text{ dry weight})$, $r^2 = 0.71$, $P < 0.0001$. **b** ^{15}N acquired recovered by individual plants as a function of plot total root dry weight (g). Regression equations: *Ambrosia*: ^{15}N acquired = $0.06 + 0.58(\text{root dry weight})$, $r^2 = 0.50$, $P < 0.0001$; *Achillea*: ^{15}N acquired = $0.03 + 0.66(\text{root dry weight})$, $r^2 = 0.71$, $P < 0.0001$

There was no significant effect of species on proportional acquisition of ^{15}N by neighboring plants [^{15}N in neighbors/total ^{15}N (neighbors + target plants)] (Table 4), but there was a significant effect of both above- and belowground competition ($P < 0.05$) and a significant interaction term ($P < 0.05$, Tukey's HSD for one-way ANOVA of simple effects of each combination of above- and belowground competition). Aboveground competition only had an effect on ^{15}N acquisition by neighbors in the presence of belowground competition.

Neighboring plants beyond 15 cm radius did not accumulate detectable levels of ^{15}N (data not shown).

Of the ^{15}N added to each plot (22.125 μmol), we recovered less than 4% in plant tissue in any plot. Some of the ^{15}N remained in the soil, or was immobilized by soil microbes; up to 6% of the applied ^{15}N was recovered in microbial biomass nitrogen and inorganic soil nitrogen from 15-cm-deep 2-cm-diameter soil cores centered on the injection site (data not shown).

Discussion

Competition and plant growth

Our results indicate that both above- and belowground competition suppress the growth of *Ambrosia* and *Achillea* plants colonizing this 2nd-year-old field. In both species, belowground competition had a much larger effect on growth than aboveground competition (Fig. 2, Table 1). *Ambrosia* has been shown to be strongly affected by belowground competition in greenhouse studies (Raynal and Bazzaz 1975; Crowell and Boerner 1988), but, to our knowledge, this is the first field measurement of the magnitude of suppression of *Ambrosia* by belowground competition. Canopy gaps do not correspond to root gaps, so seedlings that emerge in these openings experience strong belowground competition in 2nd-year-old fields. This is consistent with the results of Wilson and Tilman (1991, 1993) which showed that belowground competition was always a factor in determining plant performance of perennial grasses over a wide range of soil fertility. The strong influence of belowground competition on exclusion of *Ambrosia* is noteworthy, given the rapid decline in light availability seen during secondary succession in high-fertility sites (Tilman 1988, 1993; Bazzaz 1996).

Belowground competition has long been recognized as a significant factor in plant species interactions (Casper and Jackson 1997), and has often been demonstrated by measurement of growth increases in response to trenching around the target plant (e.g., Putz 1992; Riegel et al. 1995; Twolan-Strutt and Keddy 1996) or solid root exclosures (e.g., Cook and Ratcliff 1984; Reichenberger and Pyke 1990; Wilson and Tilman 1993; van Auken and Bush, 1997). Both trenching and root exclosures may introduce artifacts that would increase plant growth. For example, nitrogen availability may increase inside the experimental plots due to mineralization of roots left behind in both types of manipulation (Campbell et al. 1991b; Mclellan et al. 1995). Including trenched control plots for comparison with our other treatments allowed us to address this issue. Although trenched plots and plots with root exclosures both probably had similar amounts of decaying roots, the plants grown with root exclosures were much larger than plants in trenched plots (Fig. 2); therefore, any growth increase caused by increased nitrogen mineralization was much smaller than that due to release from belowground competition. This

Table 4 ^{15}N acquisition by target plants and neighboring vegetation, $\mu\text{mol } ^{15}\text{N}$. Proportional acquisition by neighbors = $(\text{neighbor}^{15}\text{N})/(\text{neighbor} + \text{target}^{15}\text{N})^{-1}$. Neighboring vegetation was collected from the perimeter of the plot (between 7.5 cm and

15 cm from the plot center). No ^{15}N was detected in samples collected between 15 cm and 22.5 cm from the plot center. Treatment codes as in Fig. 2

Treatment	Target plants		Neighboring plants		Proportional acquisition by neighbors (%)	
	<i>Ambrosia</i>	<i>Achillea</i>	With <i>Ambrosia</i>	With <i>Achillea</i>	With <i>Ambrosia</i>	With <i>Achillea</i>
a + b +	0.02 \pm 0.006	0.03 \pm 0.02	0.010 \pm 0.002	0.005 \pm 0.002	37.2 \pm 12.0	30.0 \pm 11.9
a - b +	0.07 \pm 0.01	0.05 \pm 0.01	0.004 \pm 0.002	0.010 \pm 0.003	4.8 \pm 2.1	21.6 \pm 5.8
a + trench	0.17 \pm 0.05	0.10 \pm 0.04	0.010 \pm 0.005	0.007 \pm 0.002	5.2 \pm 1.7	17.8 \pm 7.9
a + b -	0.18 \pm 0.09	0.23 \pm 0.06	0.0009 \pm 0.0006	0.003 \pm 0.002	0.5 \pm 0.4	1.6 \pm 1.0
a - b -	0.42 \pm 0.02	0.47 \pm 0.08	0.0003 \pm 0.0002	0.0005 \pm 0.0005	0.1 \pm 0.1	3.1 \pm 3.3

finding is consistent with the greenhouse experiments of Mclellan et al. (1995), where inclusion of decaying roots had little effect on plant growth. Roots from neighboring plants probably grew into the trenched plots, as shown by the similarity in ^{15}N recovered by neighboring plants in trenched plots and in plots with no exclusion of neighboring roots (Table 4). These data indicate that trenching once at the beginning of the season was not sufficient to completely exclude belowground competition. Consequently, measurements of belowground competition intensity derived from trenching studies (e.g., Twolan-Strutt and Keddy 1996) may underestimate the magnitude of belowground competition, depending upon the rate of root growth into the trenched plot during the experiment and the frequency of trenching.

Nitrogen acquisition from enriched patches

Nitrogen has previously been shown to be the primary limiting factor in growth of annual communities in 1st-year-old fields on our experimental site (Goldberg and Miller 1990). Given the decline in extractable soil nitrogen between the 1st and 2nd year of abandonment (Huberty et al. 1998; Huberty 1994), it is likely that competition for soil nitrogen is an important factor determining successional patterns at this site. Although competition for water may play a role in 2nd-year-old fields at our site in some years, we found no difference in soil water content among the plots in the last 3 weeks of the experiment (weekly TDR measurements, data not shown) or at the final harvest (gravimetric measurement, data not shown). Our ^{15}N acquisition data are consistent with strong competition for nitrogen among target plants and neighbors in our plots. Target plants acquired the most ^{15}N when neighboring shoots and roots were excluded (Table 4). When neighboring roots were present in the plot, neighboring plants acquired almost as much ^{15}N as target plants (Table 4). The lack of ^{15}N in shoots of neighboring plants beyond a radius of 15 cm from the plot center is consistent with the 20-cm neighborhood radius estimated by Pacala and Silander (1990) for competitive interaction among annuals in a newly abandoned field.

Is *Achillea* better at acquiring nitrogen from an enriched patch than *Ambrosia*? There was no significant difference between the species in the total amount of ^{15}N acquired in each treatment, nor was there a significant difference between the species in ^{15}N competition with neighboring plants (Table 4). ^{15}N acquisition was proportional to the log of plant weight, and linearly proportional to root weight (Fig. 4). This is consistent with models of plant nutrient acquisition which indicate that root growth is the dominant factor regulating plant acquisition of a relatively immobile nutrient such as NH_4^+ (Barber 1984, Casper and Jackson 1997). The only difference we observed between the species was in the proportion of plant ^{15}N acquired from the enriched patch, as indicated by plant ^{15}N enrichment. Because root weights and estimated root lengths (calculated from specific root length) for the two species were not significantly different within each treatment, there might be greater precision in nutrient foraging from an enriched patch by *Achillea* relative to *Ambrosia* (Campbell et al. 1991a). Further experiments including measurements of root distribution and activity are required to test this hypothesis.

In contrast to our hypothesis, our data indicated that growth of both *Ambrosia* and *Achillea* plants was suppressed to a similar extent by competition from established vegetation in 2nd-year-old fields. There was no clear difference between the species in ability to compete for ^{15}N from an enriched patch, although there was an indication of greater precision of foraging by *Achillea*. Life history differences between these species and consequent differences in the phenology of root growth relative to other old-field plants are likely to play a large role in the persistence of *Achillea* in later successional fields where *Ambrosia* is suppressed.

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