



Canopy gaps are sites of reduced belowground plant competition in a productive old field

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Abstract

Whether small gaps in the aboveground vegetation of productive old fields correspond to gaps in belowground plant biomass, and whether such “root gaps” result in a reduction of competition for soil resources is not known. Our study in an abandoned hayfield shows that root biomass within small gaps (< 0.50 m diam) is 20% of that found within intact vegetation, similar to the findings for shoot biomass. Associated with the decrease in root biomass was a 25% reduction in the intensity of belowground competition within gaps compared to the surrounding matrix vegetation. These differences could not be attributed to variation in soil properties, as gap and matrix soils did not differ in any of the physical or chemical properties measured. These results indicate that the increased plant growth commonly observed within gaps may be partly due to reduced belowground competition, independent of any advantage gained from increased light availability. By providing areas of low belowground competitive intensity, gaps in this field could allow poor belowground competitors to exist with in old fields, thus increasing community diversity.

Introduction

In plant communities, local areas of reduced plant biomass (gaps) are common, and are important in community dynamics (Pickett and White 1985). The scale of these gaps can vary dramatically between and within communities, ranging from less than an individual plant to the size of an entire watershed (Pickett and White 1985). In productive herbaceous communities, gaps less than 50 cm diameter are most common (Platt 1975; Goldberg and Gross 1988), with gaps not only areas of bare ground, but generally containing some reduced level of plant cover (e.g., Bradshaw and Goldberg (1989)). Many species grow or survive better in gaps than within the surrounding matrix vegetation (Gross and Werner 1982; Hobbs and Mooney 1985; Aguilera and Lauenroth 1995; Morgan 1998), and gaps often have a species composition different from that of the matrix vegetation (Platt 1975; King 1977; Hobbs and Mooney 1985;

English and Bowers 1994; McIntyre et al. 1995). Growth benefits from gaps have generally been attributed to increased light availability (Goldberg and Werner 1983; Morgan 1998).

The study of gap dynamics has historically been from a canopy perspective, and only recently have researchers attempted to determine if gaps in the aboveground vegetation correspond to gaps in belowground biomass (Sanford 1990; Silver and Vogt 1993; Wilczynski and Pickett 1993; Campbell et al. 1998; Denslow et al. 1998; Ostertag 1998), and to a lesser extent, what effects gaps in root distributions may have on belowground interactions between plants (Aguilera and Lauenroth 1993, 1995; Ostertag 1998). However, the vast majority of this work has been conducted in forests (e.g., Whendee and Vogt (1993); Campbell et al. (1998); Denslow et al. (1998); Ostertag (1998)) and semi-arid grasslands (e.g., Coffin and Lauenroth (1998); Aguilera and Lauenroth (1995)). As plant-soil interactions in dry grasslands are funda-

mentally different than those in wetter communities (Burke et al. 1998), it is unclear to what extent we can extrapolate these prior findings to other grass-dominated communities. In particular, the below-ground gap dynamics of productive herbaceous communities are poorly understood, despite the fact that root competition can be very intense in herbaceous communities, often stronger than aboveground competition (Wilson 1988; Casper and Jackson 1997). If gaps in aboveground biomass correspond to gaps in belowground biomass, root competition may be reduced, independent of any benefit derived from increased light availability. Prior work demonstrating that small variations in root biomass can result in large variations in the intensity of belowground competition (Cahill and Casper 2000) suggests that even a modest reduction in neighbor root biomass within gaps may significantly reduce the importance of competition belowground.

Small gaps above- and belowground may be created through a variety of processes, including (1) variation in the underlying soil volume, (2) reduced soil nutrient availability, (3) plant death, and (4) fossorial mammal activity. Despite the fact that all of these potential causes of gap formation could result in gaps both above- and belowground, few studies have compared soil resource levels and root biomass inside vs. outside of small gaps in herbaceous communities (e.g., Koide et al. (1987); Bradshaw and Goldberg (1989)). It is important to note that although the majority of studies addressing gaps in herbaceous communities have focused on differences between “gaps” and “matrix” (including this one), these categories do in fact just represent two extremes of a continuous variable. A field experiment was conducted to address two main questions: (1) Do soil resources and plant biomass differ between small gaps and the matrix vegetation, and (2) Are the negative effects of root competition on plant growth lower in small gaps than within the surrounding matrix vegetation?

Methods

Study site and target species

Fieldwork was conducted in a 2.5 ha area within the Laurels Conservation Preserve, Chester County, Pennsylvania. The field was cultivated for hay for more than 20 years, and last cut for hay in 1994, two

years before this study. At the time of the study, the vegetation was primarily herbaceous, dominated by grasses (e.g., *Festuca spp.*, *Dactylis glomerata*) and Canada thistle (*Cirsium arvense*). Rooting depth is shallow, with most roots located in the upper 15 cm of soil (Cahill 1999). Plant growth is both nutrient and light limited, with growth responses occurring with either NPK fertilization or elimination of root or shoot competition (Cahill 1997, 1999).

Abutilon theophrasti

Medic., an annual originally from Asia (Spencer 1984), was chosen as the target species in this study for several reasons. It is a common weed throughout the northeastern United States, often found in disturbed habitats and agricultural systems including the Laurels Preserve. This species has previously been shown to be a poor competitor belowground (Cahill 1999). Therefore, if these small gaps are areas of reduced root competition, they would most likely be relevant to the growth of species such as *A. theophrasti*. Additionally, the seeds of this species germinate rapidly in the field, avoiding the need to transplant seedlings into experimental plots.

Gap Selection

Newly created gaps are rare in old fields, and most gaps are more than 1-y old (Goldberg and Gross 1988). Soon after gaps are created, they begin to be filled from the germination of new propagules and from encroachment by the existing vegetation on the gap edge. Only the rare, newly created gaps contain absolutely no aboveground plant biomass. We were unable to find sufficient numbers of new gaps for use in this study, and thus older gaps were included. Since fresh gaps may be home to resident mammals, it is likely that soil and plant processes within new gaps may be different from those processes within older gaps. Therefore, gaps were chosen only if it was clear that there was no current mammal activity. As a result, gaps in this study were not devoid of vegetation, but did contain visibly reduced aboveground biomass (35% of that found in the matrix plots; Table 1). Because of these choices, any differences between gaps and the matrix vegetation in any of the variables measured are likely underestimates of what would be found had we exclusively used “new” gaps. It is important to note that the exact mechanism(s) which generated the gaps used in this study are unknown.

Table 1. Soil nutrient and plant biomass levels as measured within gaps and the surrounding matrix vegetation. There were 10 replicates for all measures, except root biomass, for which there were eight. Only shoot and root biomass differed significantly between the gap and matrix locations, as represented in the table by * = $P < 0.05$ (See Table 2 for ANOVA details).

	Shoot biomass g/m ² (SD)	Root biomass g/m ² (SD)	Soil mass kg/m ² (SD)	Rock mass kg/m ² (SD)	pH (SD)	P ppm (SD)	K ppm (SD)	Mg ppm (SD)	Ca ppm (SD)
Gap	160.6* (96.6)	98.7* (49.3)	128.2 (32.0)	41.1 (25.0)	5.88 (0.42)	21.28 (5.93)	86.67 (22.21)	174.67 (90.02)	660 (196)
Matrix	456.1 (221.5)	498.3 (197.4)	127.1 (34.2)	44.0 (24.4)	5.92 (0.32)	24.50 (15.46)	124.37 (95.86)	164.00 (65.18)	598 (120)

Gap characterization

To determine whether soil and vegetation properties differed between gap and matrix locations, ten gaps (< 60 cm diameter) were randomly chosen within the field in mid-June 1995. Each gap was paired with a plot located in the surrounding matrix vegetation 65 cm from the gap edge in a randomly chosen direction. The living aboveground vegetation within a 40 cm diameter circle in the center of each plot was cut at the soil surface, dried at 70°C for 48 hours, and weighed. To estimate root biomass and to collect soil for nutrient analyses, a single soil core (5 × 15 cm) was taken in the center of each plot. Over 80% of the root biomass found in the upper 30 cm of soil in this system occurs in the first 15 cm of soil (Cahill 1999), and thus this sampling depth is appropriate for determining effects of gaps on plant growth, rather than a full characterization of gap soil properties. Soil cores were passed through a 2 mm sieve with the roots and rocks separated from the soil, dried at 70 °C for 48 hours and weighed. Roots were not separated into living and dead components. Although direct measures of living roots would be informative, gross level measures of root biomass such as those collected here, are a strong correlate of the strength of root competition in this field (Cahill and Casper 2000). The sieved soil was air dried and a sub-sample was sent to Penn State Analytical Services (State College, PA) for analyses of extractable P, K, Mg, Ca, and pH. N was not determined in this study, however, prior work in this field has shown mineralizable N to be strongly correlated with P and K availability (Cahill 1997).

Root competition

On 6 April 1996, 38 randomly chosen gaps (20 cm < canopy gap diameter < 60 cm) were marked along a 200 m transect in the field. Plots were designated as gaps based solely upon the subjective visual criteria that the plot appeared to have substantially less aboveground cover than the surrounding area. As in the gap characterization study, gaps with current mammal activity were not used. Each gap was paired with a second plot centered within the matrix vegetation one meter from the gap center in a randomly determined direction. Each pair of gap-matrix plots is herein referred to as a block, and there were a total of 76 plots within 38 blocks. To be sure that the initial subjective characterization of gaps corresponded to actual differences in light availability, PAR ($\mu\text{M}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$) was measured at ground level in each of the 76 plots using a Li-Cor 1000 Datalogger with a LI-190SA Quantum Sensor. Light levels were recorded within 1 h of solar noon on 5–6 May 1996, both cloudless days. On average, a greater proportion of available light reached the soil surface in the center of gaps than within the matrix vegetation (Mean proportion of light reaching the soil surface (SD): Gap 0.506 ±0.27, Intact Vegetation 0.079 ±0.10). However, less light reached the soil surface in the gaps than within the paired matrix vegetation in two of the 38 blocks. Since our initial characterization of gap and matrix was based on subjective criteria, it is likely we inaccurately assigned these plots to “gap” and “matrix” classifications. These two blocks were eliminated from the study, resulting in 36 rather than 38 blocks used in the experiment.

Each of the 36 blocks was then assigned one of two possible belowground competition treatments: (1) neighbor roots excluded, or (2) neighbor roots accessible. To minimize any potentially confounding ef-

fect of changes in plant species composition or soil resource levels along the transect, a stratified random design was used to assign the belowground competition treatments. Adjacent blocks were paired, randomly assigning one belowground competition treatment to one block with the second block receiving the alternative belowground treatment.

To install the belowground treatments into the 72 plots, a 15 cm (diameter) × 25 cm (deep) hole was drilled with a gas powered auger in the center of each plot. Large rocks and roots were removed by hand from the excavated soil. The root exclusion treatments were installed in one-half of the plots by inserting a 10 cm diam × 25 cm piece of PVC pipe into the hole and then filling the pipe with the soil removed by the auger. The root accessible treatment was constructed by refilling the holes with the soil removed by the auger, without inserting any PVC. Soil was not mixed within or between blocks.

After the belowground treatments were installed, the aboveground vegetation of the neighboring plants around each plot was tied back using thin netting (2 × 2 cm squares 1 mm thick netting), forcing any target-neighbor interactions to be belowground. The netting used is similar in diameter to fishing line, and its shading effects are negligible – allowing approximately 93% light penetration. Similar netting has been used in other studies without adverse effects on the neighboring vegetation (Wilson and Tilman 1991; Twolan-Strutt and Keddy 1996; Cahill 1999). To tie back the neighboring vegetation, a 50 × 50 cm square of netting was placed over the center of each plot, anchored flush with the soil surface immediately around the plot. The four corners of the netting were each raised approximately 20 cm above the soil surface.

Approximately 20 seeds of *A. theophrasti* (purchased from Valley Seed Service, Fresno, CA) were sown in the center of each plot on 9 June, 1996, and following germination, seedlings were thinned to one per plot. After two weeks, all of the plants were sprayed with ISOTOX, a generalist insecticide. There is some evidence that this insecticide may have a modest fertilization effect for this species (Cahill 1997), but since all plants of all treatments were given an identical dose, there should be no bias due to its use. On 10 Aug. 1996, all plants were cut at the soil surface, dried at 70 °C for 24 h, and weighed. Shoot biomass (excluding reproductive structures) is a good correlate of reproductive biomass in this species (Casper and Cahill 1996), thus the assumption being

made is that changes in plant biomass in response to the treatments imposed is indicative of the overall performance of this species in this community. Howard and Goldberg (2001) provide support for such an assumption, where they found that the strength of competition measured as changes in seedling shoot biomass to be a good correlate of a species relative abundance in the field.

Statistical analyses

To determine whether there are soil chemical or physical differences between gaps and the matrix vegetation, separate two-way ANOVA were conducted for each of the measured soil properties (e.g., P, K, rock mass, etc.) and plant biomass (above- and belowground). Root and shoot biomass were ln-transformed to achieve normally distributed data, and satisfy the assumptions of ANOVA. In each analysis, location (gap vs. matrix) and block (each gap-matrix pair) served as the two independent variables. Since gaps were chosen randomly within the field, block was treated as a random effect in the ANOVA model, and location MS were tested over the block MS. As there was no replication within a block, location × block interactions could not be determined.

To determine the effects of root competition and planting location on target plant growth, a three-way mixed model nested ANOVA was performed. Block, plant location (gap vs. matrix), and belowground treatment (+PVC vs. -PVC) served as the three independent variables. Since both plots in a given block received the same belowground treatment, block was treated as a random variable nested within the belowground treatment. Final dry aboveground biomass of *Abutilon* served as the dependent variable, Ln transformed to achieve normality and homogeneity of variances. Two *a priori* planned comparisons (linear contrasts) were conducted. The first contrasted target plant biomass in gaps vs. matrix vegetation when belowground interactions are excluded (+PVC). A significant contrast would suggest differences in factors other than the intensity of belowground plant interactions (such as soil resource levels) between gaps and intact vegetation are strong enough to affect plant growth. The second planned comparison contrasted gaps vs. matrix vegetation only in the presence of belowground interactions with neighbors (-PVC). A significant contrast would suggest the strength of belowground interactions differs between planting locations.

Table 2. ANOVA results for the test of whether soil nutrient and plant biomass varied between gaps and the surrounding vegetation. Each soil or vegetation property was the dependent variable in a separate ANOVA in which location and plot (random) served as the two dependent variables. For each response variable, the location MS was tested over the block MS (df location = 1; df block = 9).

Response Variable	Location MS	F	p
Shoot	7.173	19.808	0.002
Root	15.434	67.846	< 0.001
Soil	24.575	0.025	0.877
Rock	171.112	0.270	0.616
pH	0.009	0.215	0.655
P	46.722	0.452	0.520
K	6395.805	1.421	0.267
Mg	512.000	0.308	0.594
Ca	17422.222	1.574	0.245

During the course of the experiment 19 of the target plants experienced severe herbivory from the common woodchuck, *Marmota monax*. Since the design of this experiment was based upon pairing gap-matrix plots, when one plant in a block was killed, the other plant in the block was also excluded from all analyses. This resulted in the elimination of 13 of the 36 blocks from the analyses.

Results

Gap characterization

Plots located within the matrix vegetation contained nearly three times as much aboveground biomass as did plots centered on a gap (Tables 1 and 2). This is not particularly surprising as gaps were chosen based upon the observation that vegetative biomass appeared low. However, gaps were even more distinct belowground, with five times as much root biomass under intact vegetation than within a gap (Tables 1 and 2). Differences in biomass between gaps and matrix vegetation can not be attributed to small-scale variation in rock abundance or soil bulk density, as measured rock and soil mass did not differ as a function of location (Tables 1 and 2). Soil resource levels did not differ between the gap and matrix locations for any of the measured resources (Tables 1 and 2).

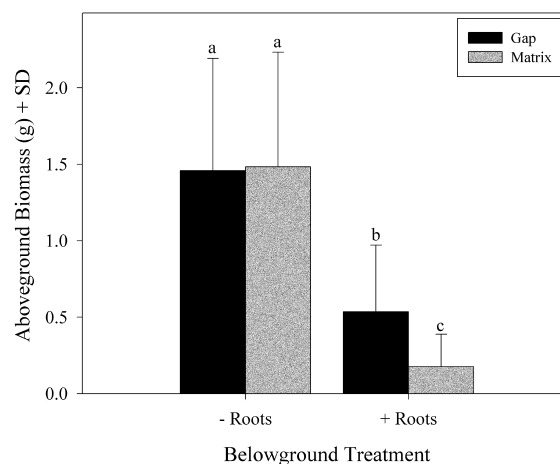


Figure 1. Mean aboveground target plant biomass as a function of belowground treatment and planting location. Error bars represent one standard deviation. Similar letters above the error bars correspond to non significant pair-wise contrasts ($p > 0.05$).

Table 3. ANOVA results for ln target shoot biomass. In the analysis, root treatment (presence or absence of PVC) and location (gap or matrix) served as fixed effects with block a random effect nested within the root treatment.

	Type III SS	df	MS	F	p
Root Treatment	42.507	1	42.507	47.590	< 0.001
Location	3.053	1	3.053	5.340	0.031
Block(TRT)	18.757	21	0.893	1.563	0.157
TRT * Location	3.597	1	3.597	6.293	0.020

Competition plots: target plant biomass

On average, *Abutilon theophrasti* target plants growing within gaps were larger than those growing within the surrounding matrix vegetation (Figure 1, Table 3). However, a significant belowground treatment x location interaction indicates that the effect of root exclusion is dependent upon planting location (Figure 1, Table 3). In the absence of interactions either above- or belowground between target plants and their neighbors, target plant biomass did not differ as a function of planting location (Planned Comparison: $F_{1,21} = 0.025$; $P > 0.85$). When target plants and neighbors could interact belowground, target plants were significantly larger when grown in gaps than when grown within the surrounding matrix vegetation (Planned Comparison: $F_{1,21} = 9.54$; $P < 0.01$).

Discussion

In the absence of light competition, differences in plant growth between gaps and matrix vegetation were due to differences in belowground competition rather than simple differences in gross nutrient supply or soil resource availability. This is supported by the facts that (1) plant growth did not differ between gaps and matrix vegetation in the absence of belowground interactions (Figure 1, Table 3), (2) the measured resource pools did not differ between gaps and intact vegetation (Tables 1 and 2), and (3) there was five times more root biomass under intact vegetation than in a gap (Tables 1 and 2).

Although gaps are recognized as important sites for plant establishment (Gross and Werner 1982; Hobbs and Mooney 1985; Goldberg 1987; Aguilera and Lauenroth 1993; Morgan 1998), and root competition is a prevalent form of plant interaction (Casper and Jackson 1997), little research has been directed at understanding how root competition may differ between gaps and matrix vegetation in productive habitats. Contrary to the standard assumption that plant benefit from gaps is only through increased light availability, this study demonstrates that even without aboveground interactions, gaps are important as areas of reduced belowground competition – at least for poor belowground competitors such as *A. theophrasti*. A likely mechanism for such a finding is the lower root biomass in gaps than in the surrounding vegetation (Table 1). Prior work in this field has shown that small changes in root biomass are associated with large changes in the strength of root competition (Cahill and Casper 2000).

The effects of large gaps on soil resources have been documented in forest systems, often finding increased soil moisture and N within the gaps compared to the surrounding canopy, generally attributed to decreased plant uptake and transpiration (e.g., Denslow et al. (1998)). In contrast, the work on small gaps in herbaceous communities suggests that reduced aboveground biomass in gaps can be detrimental to plant growth, due to increased water evaporation (Goldberg and Werner 1983; Goldberg 1987; Bradshaw and Goldberg 1989). Goldberg (1987) argued that there is a tradeoff in the costs and benefits of gaps to colonizing plants, with benefits arising from increased irradiance while plants could also potentially be harmed by decreased soil moisture. As a result, the net effects of gaps will vary among years.

Poor belowground competitors, such as *A. theophrasti*, do persist within this system, despite an 80% reduction in plant size due to belowground interactions. Variation in root biomass in plant communities may be an important factor in determining the species composition of early successional communities, as even small variations in root biomass can result in large changes in the strength of root competition (Cahill and Casper 2000). However, even in gaps target plant biomass was reduced by 60% compared to the no competition reference plots (Figure 1). Although these average levels of belowground competition were high, there was considerable variation in plant biomass when grown within gaps (Dry Plant Biomass Ranges: Neighbor roots excluded: 0.30 – 2.78 g; Neighbor roots accessible: 0.02 – 1.28 g). In contrast, for plants growing within the matrix vegetation, there was limited overlap in the ranges of plant biomass between the two belowground treatments (Ranges: Neighbor roots excluded: 0.48 – 2.82 g; Neighbor roots accessible: 0.04 – 0.58 g). If a plant is growing within the matrix vegetation, root competition is almost certainly going to limit its growth. However, if a plant is growing within a gap, there is some chance that root competition will not greatly reduce its growth.

Gap size can influence seedling emergence, survival, or reproductive output (e.g., Goldberg and Werner (1983); McConnaughay and Bazzaz (1987); Morgan (1998)). It is unclear to what extent such variation is attributable to variation in the size of the belowground gap, as that was not measured. Other work suggests the effects of belowground competition may be independent of gap size (Aguilera and Lauenroth 1993), or the effects of gaps on species turnover rates could be a function of both gap size, and the cause of the gap origin (Coffin and Lauenroth 1988).

Another factor determining the influence of belowground gaps in species establishment and persistence is how long individual root gaps persist. Although there is evidence to suggest that small shoot gaps generally last only a few years (Goldberg and Gross 1988), it is unclear whether the timing of the closure of the belowground gap is simultaneous to that of the aboveground gap. Depending upon the lateral spread of the plants in the community, it would be easy to see how belowground gaps could be either shorter, or longer lived. Unfortunately, not only do we have no information about the longevity of belowground gaps in these productive herbaceous communities, our knowledge of the structure of belowground neighbor-

hoods is also quite limited (but see Tilman (1989); Casper et al. (2001)).

The origin of the gaps used in this study was most likely due to a combination of past digging activity by mammals, and plant death. Gaps did not appear to arise due to locally depressed soil resource availability, or due to locally high levels of rocks (Tables 1 and 2). In other studies, animal activity often alters soil resource levels (King 1977; Koide et al. 1987; Bradshaw and Goldberg 1989). Since we excluded gaps which exhibited no signs of current animal activity it is not surprising that we found results different from these prior studies. However, this contrasting finding does suggest that the cause of gap formation could have differing effects on plant growth and community organization, as has been explicitly demonstrated in other systems (Coffin and Lauenroth 1988, 1998).

There was no evidence that the plants growing in the absence of belowground interactions with neighbors (+PVC) were restricted in their root growth. These plants were not significantly different in size from plants grown for a similar duration using larger root exclusion tubes (15 cm) in a separate experiment within the same field that year (Cahill 1999). The methods used in this study to separate root interactions may have resulted in root competition being overestimated as disturbing soil can stimulate new root growth (Joslin and Wolfe 1999), thereby increasing neighbor root biomass in the root accessibility treatments and thus the strength of root competition. PVC tubes may also alter hyphal growth and water drainage, with unknown consequences on target plant growth. However, in a different study run without target plants, I found no difference in soil moisture inside PVC tubes compared to tubes made of fabric (which allow water flow) and no tube controls (Cahill, unpublished data). Although these methodological issues could result in the observed measures of competitive intensity being different than that which actually occurs in non-experimental situations, there is no reason to suspect the differences observed between gaps and intact would be due to such an effect.

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