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Spatially Disjunct Effects of Co-occurring Competition and Facilitation

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Abstract

Little is known of the co-occurrence and implications of competitive and facilitative interactions within sites. Here we show spatially disjunct competition and facilitation at forest edges, with beneficial influences of trees on seedling growth via increased ectomycorrhizal infection apparent from 12 to 20 m while closer to trees seedling growth is negatively correlated with canopy closure. As a result, seedling growth is maximized at intermediate distances. Facilitative interactions were nonlinear: being within 15.7 m of a tree maximized

seedling mycorrhizal infection; while competitive effects were correlated with canopy closure, which was related to distance and generally scales with density. These patterns result in a positive correlation of tree density and seedling growth at low densities of trees, and negative correlation at higher densities because of competition. A spatial model suggests that plant communities are a mosaic of positive and negative interactions, which may contribute to population homeostasis and plant diversity.

Introduction

The establishment of seedlings may be both inhibited and facilitated by established plants (**Connell & Slatyer 1977**; **Callaway & Walker 1997**). Facilitation may occur where established plants increase the availability of otherwise limiting symbionts, provide increased water or nutrients or ameliorate harsh environmental conditions (**Callaway 1995**; **Bruno et al. 2003**). At the same time, established plants may inhibit the establishment of seedlings through competition, allelopathy, or by increasing populations of herbivores and pathogens (**Tilman 1982**; **Packer & Clay 2003**). Positive and negative interactions between established plants and seedlings are believed to influence plant succession (**Pickett et al. 1987**), invasion (**Callaway et al. 2004**; **Reinhart & Callaway 2004**), diversity (**Janzen 1970**; **Bever et al. 1997**; **Hacker & Gaines 1997**), and ecosystem resilience and stability (**Perry et al. 1989**). There has therefore been a great deal of interest in competition and facilitation and the environmental factors that regulate the balance between these positive and negative interactions (**Berkowitz et al. 1995**; **Holmgren et al. 1997**; **Brooker & Callaghan 1998**; **Maestre et al. 2005**). Nonetheless, most researchers have focused on between-site differences, particularly along stress gradients (**Callaway & Walker 1997**; **Pugnaire & Luque 2001**; **Callaway et al. 2002**). While it has been recognized that competition and facilitation commonly co-occur within sites, the net effect has generally been assumed to be spatially uniform (**Callaway et al. 1991**; **Callaway 1995**). Currently, there is only limited understanding of how net competition and facilitation might spatially co-occur within sites, potentially including both competition and facilitation from the same source to the same recipient.

One system where spatial co-occurrence of net competition and facilitation might be particularly likely is where established plants facilitate the establishment of seedlings by providing increased populations of root symbionts. Increased symbiotic infection of seedlings by established plants has been shown for ectomycorrhiza (**Baylis 1980**; **Perry et al. 1989**; **Dickie et al. 2002**; **Dickie & Reich 2005**), arbuscular mycorrhiza (**Weber et al. 2005**), *Frankia* (**Zimpfer et al. 1999**) and to a lesser degree for Rhizobium (reviewed by **Richardson et al. 2000**). As more than 80% of plants associate with at least one type of root symbiont, interactions between established plants and seedling via symbionts might have substantial ecological importance. We would expect that these interactions might occur in spatially complex mosaics because (i) plant roots and their associated symbionts may spread beyond the extent of the canopy, potentially resulting in the spatial decoupling of root and shoot effects of trees on seedlings, and (ii) the benefits of growing near an established plant may depend primarily on the presence of its associated symbionts and therefore be a function of the presence or absence (as opposed to density) of plants within some threshold distance, while competitive interactions are more likely to scale as a function of neighbouring plant density or biomass (**Dickie et al. 2002**).

Here we examine the interactions between established plants and seedlings during seedling establishment, particularly focusing on facilitation via shared ectomycorrhizal symbionts. To manipulate proximity to established trees, we planted seedlings at varying distances from an established forest edge. First-year results showed that ectomycorrhizal infection of seedlings increased as a nonlinear function with proximity to trees, being low distant from established trees and rapidly increasing where seedlings contacted the root zone and associated mycorrhizal fungi of established trees (**Dickie & Reich 2005**). In the present study we test the effects of this initial increase in ectomycorrhizal infection on seedling nutrient uptake and growth over 3 years. We hypothesized that:

1 Nitrogen uptake and growth of seedlings would increase with proximity to established trees as a result of increased mycorrhizal infection.

2 The increase in growth of seedlings with proximity to trees would occur only up to an intermediate distance as a result of facilitation via shared symbionts, after which seedling growth would decline as a result of competition with trees for light or other resources.

We then use the data collected in the field to build a spatially explicit model to extend our results to forest stands to test the hypothesis:

3 As a result of the linkage between nearest-neighbour distance and density, the net influence of trees on seedlings will be positively correlated with increasing tree density at relatively low densities of trees, but negatively correlated at higher densities of trees (as suggested in **Dickie *et al.* 2002**).

Methods

Study sites and experimental design

We used two fields, field 56 and field 57, abandoned from agriculture in 1958 and 1943, respectively, at the Cedar Creek Natural History Area and Long Term Ecological Research site of the University of Minnesota, located in Anoka County, MN, USA (see **Dickie & Reich 2005**). Old fields at this site are highly N limited and have very slow rates of succession to woody vegetation (**Inouye *et al.* 1994**; **Lawson *et al.* 1999**). Herbaceous vegetation in field 56 was dominated by *Poa* spp., *Bromus* spp., *Panicum* sp., *Ambrosia* sp. and *Equisetum* sp. (in decreasing order of dominance), while field 57 was dominated by *Poa* spp., *Ambrosia* sp. and *Agropyron* sp. The northern edge of both fields border established oak woodlands with a relatively straight edge between the two habitats, running east–west. Oak grubs (multi-stemmed shrub-like oaks resulting from repeated die back) were common near the forest edge (0.7–1.6 grubs m^{-2}) but were largely absent beyond 12 m from the forest edge. Prior to European settlement these sites were *Quercus macrocarpa* dominated savanna with tree densities of 14–35 trees ha^{-1} (**Bray 1955**). Fire suppression since 1938 has led to canopy closure with in-growth of *Quercus ellipsoidalis* and gradual succession to more shade tolerant tree species, although large open-grown *Q. macrocarpa* are still present (**Peterson & Reich 2001**; **Reich *et al.* 2001**). The forest north of field 56 had 429 ± 83 trees ha^{-1} (> 10 cm diameter) with a basal area (BA) of 14.7 ± 1.6 m^2 ha^{-1} comprising 97% *Q. ellipsoidalis* and 3% *Q. macrocarpa* (by BA), while the forest north of field 57 had 495 ± 57 trees ha^{-1} with a BA of 34.7 ± 0.7 m^2 ha^{-1} comprising 85% *Q. ellipsoidalis*, 13% *Q. macrocarpa* and 2% other tree species. The soils were flat, very sandy, excessively drained Typic Udipsamment, Nymore series soils (94% sand, 5% silt, 1% clay). The fields are separated by about 420 m distance.

In each of the two fields we established four transects running from the forest edge into the field with plots at 0, 4, 8, 12, 16 and 20 m from a point approximately 1 m from the base of an established *Q. ellipsoidalis* tree (focal tree). Although focal trees were *Q. ellipsoidalis* and planted acorns were *Q. macrocarpa*, both species occurred in the forest and roots, shading and litter from both species are likely to have influenced seedlings. Prior experience suggested that *Q. macrocarpa* seedlings would have higher growth rates than *Q. ellipsoidalis* seedlings in our sites (**Davis *et al.* 1999**), and might therefore be more likely to show significant growth responses. The choice of *Q. ellipsoidalis* for focal trees was pragmatic: there were too few *Q. macrocarpa* at the forest edge to permit sufficient replicate transects. As host specificity of mycorrhizal fungi is typically at the genus, not species, level (**Molina *et al.* 1992**), we expect that mycorrhizal interactions would be similar between conspecific and congeneric tree seedling pairs. Focal trees were 17–26 cm diameter at breast height (DBH) in field 56, and 28–46 cm DBH in field 57. Based on tree diameter–age correlations for oak

woodlands at Cedar Creek (P.B. Reich, unpublished data), these trees were likely between 40–60 and 60–100 years old for fields 56 and 57, respectively, and therefore were likely to have established at or before the time when the fields were abandoned from agriculture. All transects ran approximately due south from the north edge of fields.

Site variables

At each plot we measured canopy openness (diffuse non-interceptance; DIFN), soil pH, the N concentration of herbaceous plants, the community composition of herbaceous vegetation, and the biomass of oak litter, herbaceous litter and living herbaceous biomass. Canopy openness was measured between first light and sunrise on a midsummer day in 2004 with a Licor LAI 2000 (Li-cor Biosciences, Lincoln, NE, USA) with a 90 ° sensor cover oriented so as to measure DIFN over the southern quarter sphere of each plot. Soil pH was measured from a homogenized soil core (0–20 cm depth, 2.5 cm diameter) with a 1 : 2, soil : water (by volume) extract. To obtain an indication of plant-available inorganic N independent of ectomycorrhiza, we collected fully expanded shoots of two common arbuscular mycorrhizal species: *Ambrosia artemisiifolia* (a weedy annual common in both fields), and *Poa pratensis* (a grass, dominant in both fields) and analysed foliar N concentrations on an ECS 4010 element analyzer (Costech Analytical, Valencia, CA, USA) at the University of Nebraska. We were able to collect *Poa* from all but one plot ($n = 47$), and *Ambrosia* from 37 of the 48 total plots. Community composition of herbaceous plants was measured by visual estimation in 1 m^2 plots adjacent to the experimental plots, with analyses performed on midpoints of Daubenmire cover classes. In August 2004, we collected all live and dead biomass from a 0.125 m^2 plot adjacent to each experimental plot, and measured dry mass of oak litter, living herbaceous biomass and dead herbaceous biomass.

Seedlings

We planted each plot with four bur oak (*Q. macrocarpa*) acorns collected from local seed sources in the autumn of 2001, stored for approximately 3 weeks under refrigeration, and planted in late September. We placed a 30-cm diameter, 60-cm tall cylindrical cage of 1.25 cm mesh galvanized 'hardware cloth' over seedlings to protect them from non-fossorial mammalian herbivory. Although protecting seedlings from herbivory does remove one potential tree–seedling interaction (**Booth 2004**), we decided that the potential increase in variance associated with deer browse was not compatible with other constraints on replication in this study. In September 2002, we harvested one seedling from each of a total of 40 plots for measurement of ectomycorrhizal infection, biomass and nutrients (four plots had no surviving seedlings, and an additional four had only one seedling which was left for future measurement of growth and nutrient concentration). In September 2003 we measured the height and leaf numbers of the remaining seedlings, and removed a 17-mm diameter leaf punch from adjacent to the midrib at the middle of the largest leaf on each seedling to measure nutrient concentrations but did not harvest whole plants. In September 2004 we harvested the remaining seedlings.

We washed harvested roots under running water over a wire screen and then stored roots in water under refrigeration for no more than 21 days before measurement of mycorrhizal infection. No visible degradation of roots occurred during storage. Fine roots were cut into 1–3 cm sections and a random sample of at least 100 root tips per seedling were examined. On each root fragment we counted all ectomycorrhiza as the number of root tips infected, regardless of whether tips were individual monopoid mycorrhizas or part of a larger cluster of ectomycorrhizal roots. Mycorrhizal collections in 2002 were identified and are described in **Dickie & Reich (2005)**. Mycorrhizal infection in 2004 was quantified but species were not identified. Foliar N concentrations were obtained from harvested leaves (pooling all leaves from each seedling) in 2002 and 2004, and from leaf punches from 2003. Biomass was measured on an aboveground basis only, as our harvests did not obtain 100% of root tissue.

Statistics and model

Seedling mycorrhizal infection, nitrogen concentration and growth data were analysed using mixed effects models with random effects for transect within field using the lme procedure of R (2.0.1; R Foundation for Statistical Computing, Vienna, Austria). We tested significance of a 'Field' term and Field by Distance interactions using maximum likelihood methods and selecting the model with the lowest AIC values (**Venables & Ripley 2002**). Where appropriate, we ran regressions as quadratic functions, removing the quadratic effect if not significant. *P*-values for fixed terms are for a full model with random terms for 'Field' and 'Transect'. Correlations between variables other than distance effects were tested as linear models without incorporating random terms, largely for ease of presentation and interpretation. In no case did the simpler model result in a qualitative change in significance when compared with a mixed effects model approach.

Using regression equations generated from our data and data from a previous study on the same research area relating canopy openness to tree density (**Peterson 1998**), we developed a spatially explicit model of tree–seedling interactions to model the average influence of trees on seedlings as a function of tree density. The model was programmed in R on a 250 × 250 m landscape and run with absorbing edges under Mac OSX version 10.3.8. Model output is from 26 runs of the model with a range of densities, normally distributed tree diameters around the average of 20.8 cm (from **Peterson & Reich 2001**), and the assumption of randomly distributed trees and seedlings on the landscape.

Results

Site variables

There was a strong gradient in canopy openness from 0 to 8 m distance from the forest edge (**Fig. 1**). There were also significant increases in the mass of herbaceous biomass and litter, and significant decreases in oak leaf litter with increasing distance from the forest edge (**Table 1**). No other site variable showed strong or consistent distance effects. There were significant field effects on a number of variables, generally reflecting more fertile and slightly less acidic conditions in field 57 than in field 56, including greater oak and herbaceous litter mass, increased N content of *Poa pratensis* and *Ambrosia artemisiifolia* foliage (**Table 1**), and slightly less acidic soil pH (mean ± SE; 5.39 ± 0.06 and 5.42 ± 0.03 in field 56 and 57, respectively; *P* = 0.042). Multivariate analyses of vegetation composition revealed complete separation of the two fields, but no clear effect of distance in either field (not shown).
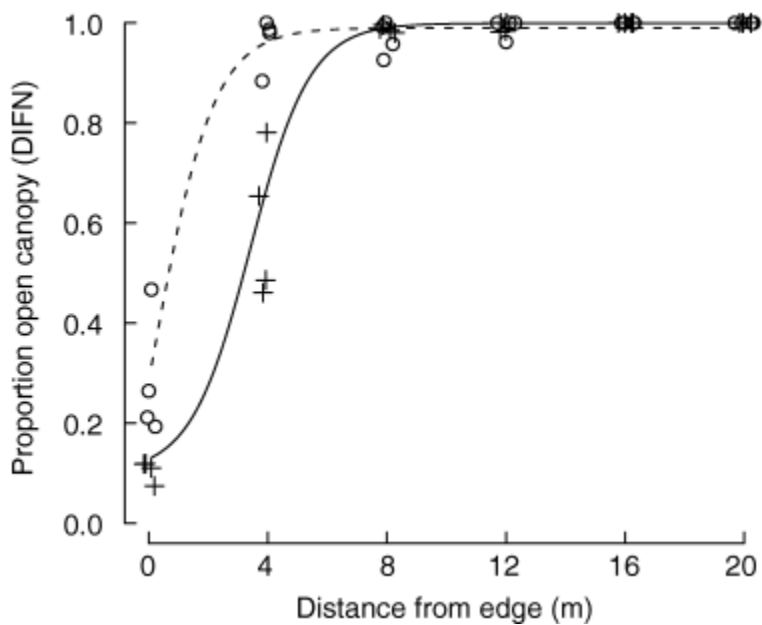
Figure 1

Canopy openness over the southern quarter sphere of plots (LAI 2000 measure of DIFN with a 180 ° lens cover) as a function of distance from the edge in field 56 (dashed line, circles) and field 57 (solid line, crosses). A small amount of noise has been added to the measurement of 'Distance' to separate overlapping data points, all points actually fell on the distances indicated on the *x*-axis. Lines are four-parameter logistic functions fit independently to data from each field.

Table 1. Environmental variables as a function of field and distance

	Distance from forest edge (m)						Field* (P-value)	Model†	Significant fixed terms
	0	4	8	12	16	20			
Ambrosia artemisiifolia leaf N concentration (%)									
Field 56	2.31 ± 0.27	2.38 ± 0.16	2.63 ± 0.15	2.35 ± 0.18	2.34 ± 0.19	2.11 ± 0.35	0.041	*D:F*	*D:F*
Field 57	2.09 ± 0.39	2.71 ± 0.49	2.59 ± 0.09	2.97 ± 0.16	2.97 ± 0.24	2.89 ± 0.24			(*P* = 0.001)
Poa pratensis leaf N concentration (%)									
Field 56	1.26 ± 0.07	1.21 ± 0.05	1.21 ± 0.05	1.20 ± 0.07	1.17 ± 0.04	1.22 ± 0.08	< 0.001	NA‡	None
Field 57	1.74 ± 0.08	1.64 ± 0.16	1.46 ± 0.13	1.57 ± 0.08	1.89 ± 0.45	1.61 ± 0.17			
Herbaceous live aboveground biomass (g m^{-2})									
Field 56	131 ± 21	108 ± 31	111 ± 28	147 ± 16	202 ± 45	179 ± 6	0.16	*D*	*D* (*P* < 0.001)
Field 57	52 ± 16	114 ± 32	94 ± 29	126 ± 12	141 ± 19	158 ± 15			

Oak leaf litter (g m⁻²)§									
Field 56	379 ± 94	76 ± 17	43 ± 19	26 ± 11	12 ± 1	8 ± 3	< 0.001	D + D²	D (P < 0.001),
Field 57	840 ± 306	302 ± 84	149 ± 31	44 ± 5	40 ± 7	14 ± 2			D² (P = 0.010)
Herbaceous litter (g m⁻²)									
Field 56	115 ± 6	116 ± 24	112 ± 32	199 ± 9	159 ± 37	178 ± 39	0.015	D	D (P = 0.015)
Field 57	151 ± 77	184 ± 66	201 ± 24	219 ± 24	267 ± 61	212 ± 48			

*Significance of Field random effect (*P*-value from ANOVA of model including random term for field vs. model without field term).

†All response variables were tested with quadratic ($D + D^2$) and linear models (*D*), and with and without interaction terms with Field (*D:F*) effects. The best model is indicated and significant *P*-values for fixed terms given.

‡No model tested had significant fixed terms. Significance of random term for field is from quadratic model.

§Oak leaf mass was log-transformed for statistical modelling; mean and SE are for untransformed data, *P*-values are for transformed data.

Seedling responses to distance from trees

There were strongly nonlinear responses of ectomycorrhizal infection to distance at one and three growing seasons (**Fig. 2**), which we described as a four-parameter logistic model:

$$E = \alpha + \frac{\beta - \alpha}{1 + e^{[(D-\lambda)/\theta]}} \quad (1)$$

$$E = \alpha + \frac{\beta - \alpha}{1 + e^{[(D-\lambda)/\theta]}}$$

where *E* is the ectomycorrhizal infection (0–100%); *D*, distance from trees (0–20 m in our data); *α*, infection distant from trees (the right asymptote); *β*, infection near trees (the left asymptote); *λ*, distance where ectomycorrhizal infection is halfway between *α* and *β*; and θ determines the slope (Venables & Ripley 2002). Ectomycorrhizal infection after one growing season (Fig. 2a) was high near trees (*β* =76.5 ± 5.0%, estimate and SE), and showed an abrupt decline at *c.* 15.7 m (*λ* = 14.7 ± 1.1, +1 m to account for offset of 0 m plot from trees) from the base of trees to very low levels (*α* = 8.6 ± 11%).
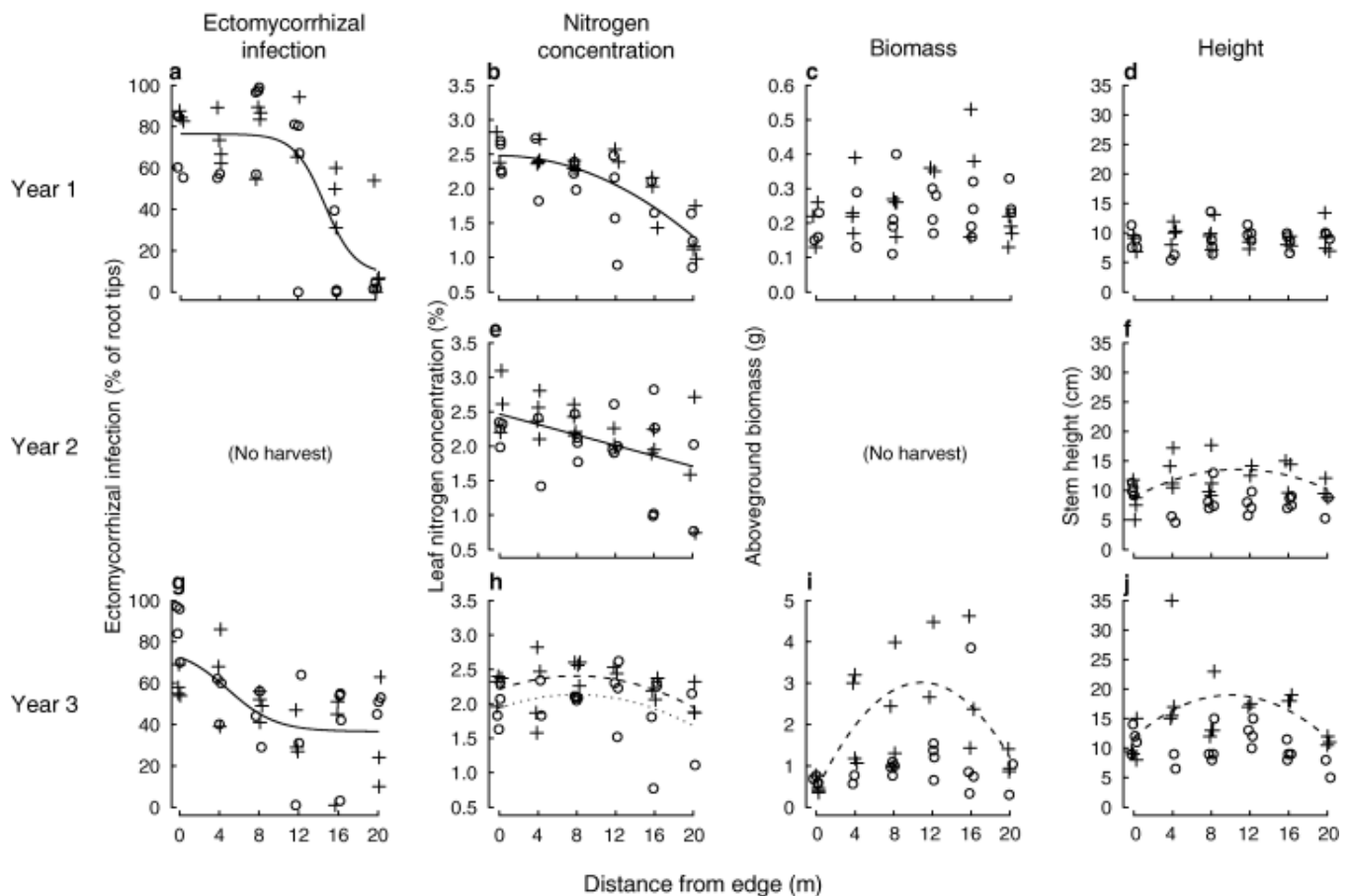
Figure 2
Response of seedling mycorrhizal infection (a, g), leaf N concentration (b, e, h), aboveground biomass (c, i), and height (d, f, j) to distance from the forest edge at year 1 (a–d), 2 (e, f) and 3 (g–j). Circles indicate data from field 56, crosses indicate data points from field 57. Solid lines indicate overall significant effect of distance with no significant field effect. N concentration in year 3 had a significant field effect (h), lines indicate main effect of distance in field 56 (dotted) and field 57 (dashed). In (f), (i) and (j) there were significant differences between fields. We therefore analysed the data separately from each field. Dashed lines indicate significant effects of distance in field 57, there were no significant effects of distance on mass or height in field 56.

By the end of the third growing season, the pattern of ectomycorrhizal infection of seedlings had changed (**Fig. 2g**). Mycorrhizal infection remained high near trees (β = 77.2 ± 19.0), but had increased distant from trees (α = 36.6 ± 5.4), although four plots, all beyond 8 m from the edge, continued to have < 20% of root tips infected. Although mycorrhizal infection again varied as a logistic function of distance, the increase in seedling infection occurred substantially closer to the edge than in year 1 (5.9 m ± 3.3), which is approximately at the edge of the canopy. This led us to suspect that shading might be an important factor, which was supported by a significant correlation of year 3 infection with percent open canopy in plots from 0 to 8 m (P = 0.008, r^2 = 0.27; not shown).

Leaf nitrogen concentration of oak seedlings declined sharply with distance from the edge after 1 year (quadratic term significant, P = 0.045) and somewhat less sharply after 2 years (linear P = 0.0021). Third year leaf N showed a humped pattern, with an increase in leaf N from 0 to *c.* 8 m, and a decline in leaf N from 8 m to 20 m (quadratic term significant, P = 0.042), and a significant effect of field (P = 0.049), with higher leaf N in field 57 than in field 56.

First year mycorrhizal infection was a strong predictor of leaf N at 1 year ($P < 0.001$, $r^2 = 0.60$) and 2 years ($P < 0.001$, $r^2 = 0.35$), but not at 3 years ($P = 0.19$). Third year mycorrhizal infection was not correlated with third year leaf N ($P = 0.17$).

At year 1, there was no significant effect of distance or field on seedling height or mass. In years 2 and 3 there were very strong field effects on height and mass with generally greater and more variable growth in field 57 than in field 56. We therefore divided the data by field and analysed each field individually. This greatly aided in interpretation of the results, but did not fundamentally change any outcome when compared with analysis of the full data set. In the second growing season, there were significant linear and quadratic effects of distance ($P = 0.019$ and $P = 0.025$, respectively) on the height of seedlings in field 57 but not in field 56. After three growing seasons, both mass and height showed strongly humped patterns in field 57 (mass: linear term $P = 0.0003$ and quadratic term $P = 0.0005$; height: linear term $P = 0.039$ and quadratic term $P = 0.034$), but again there was no significant effect of distance on mass or height in field 56.

Competition vs. facilitation

The humped pattern in the biomass data for field 57 suggested that different factors might influence seedling growth near and distant from trees. From 0 to 8 m there were strong gradients in canopy openness and uniformly high first year mycorrhizal infection, suggesting that competition via shading would be most apparent at these distances; while from 12 to 20 m there was a strong gradient in first year mycorrhizal infection but uniformly high canopy openness, suggesting that facilitation would be most apparent at these distances. We therefore further divided the data into two parts: plots 0–8 m from the base of trees, and plots 12–20 m from the base of trees. From 0 to 8 m there was a negative correlation of third-year biomass with canopy openness in field 57 (**Fig. 4a**; $P = 0.040$, $r^2 = 0.30$) and in field 56 (**Fig. 4b**; $P = 0.053$, $r^2 = 0.31$). We also observed etiolation of seedlings in shaded plots, reflected in a significant correlation of the third year height to biomass ratio of seedlings with canopy openness (not shown, $P < 0.0001$, $r^2 = 0.67$). From 12 to 20 m there was a positive correlation of third year biomass with mycorrhizal infection in both field 56 (**Fig. 4c**; $P = 0.0038$, $r^2 = 0.68$) and field 57 (**Fig. 4d**; $P = 0.033$, $r^2 = 0.55$). There was no significant correlation of growth with ectomycorrhizal infection from 0 to 8 m ($P = 0.16$) or canopy closure from 12 to 20 m ($P = 0.98$).
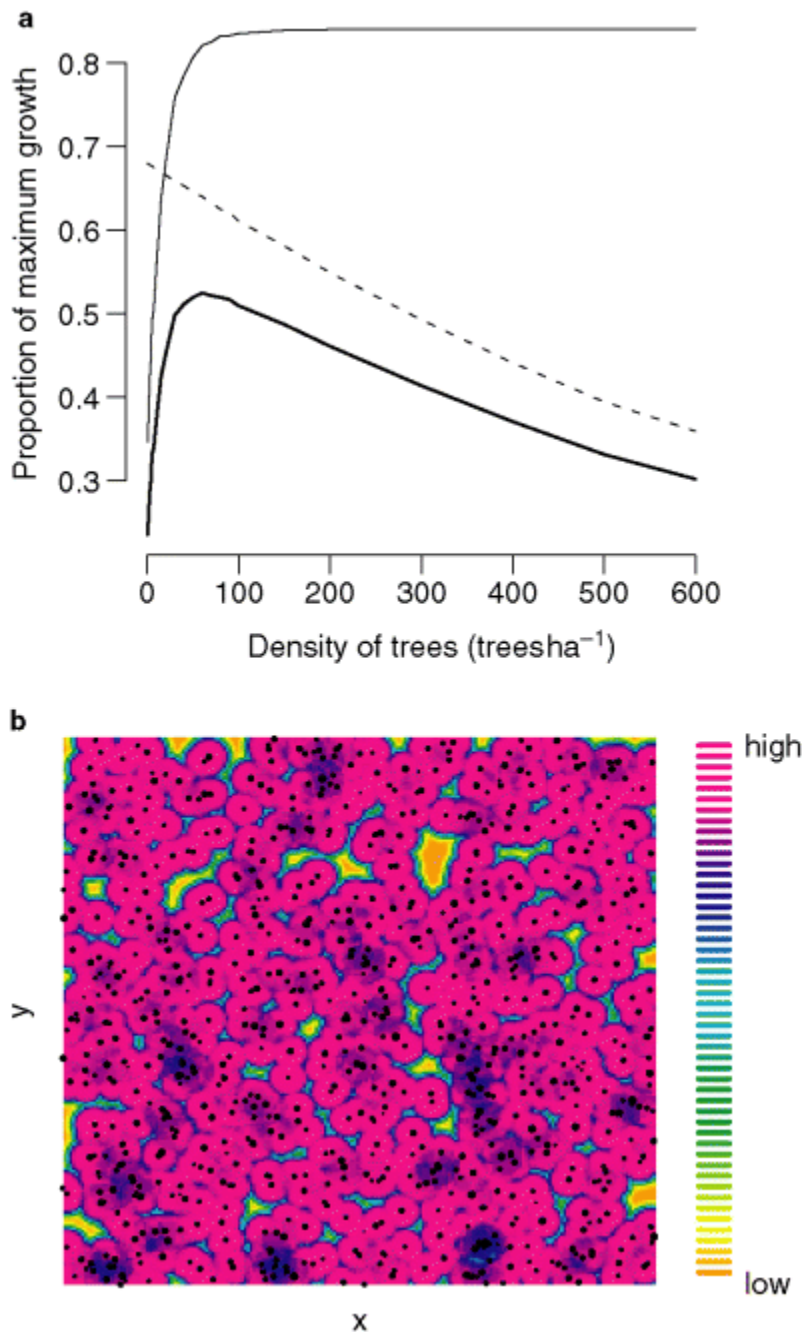
Figure 4

Effect of density of trees on the growth of seedlings in simulation model based on data from **Figs 1, 2a and 3**, showing average effects on seedlings (a) via mycorrhiza (thin line), shading (dashed line), and the net effect (heavy line) coand spatial distribution of positive and negative effects on a simulated landscape with randomly distributed trees (b). Lines follow actual output of model and are not averaged or smoothed (i.e. variance was very low). (b) The landscape with seedling growth from high (red) to low (orange) with trees indicated by black points for model run with 50 trees ha^{-1}. There are large areas of favourable conditions (red) with frequent denser clusters of trees causing minor growth reductions (shading from red to dark blue), and infrequent large openings where seedlings are severely growth limited by a lack of mycorrhiza (shading to orange). Relative tree diameters indicated by diameter of points, not drawn to same scale as axes.

Spatially explicit model of competition and facilitation vs. density

We used a spatially explicit model parameterized with field data to assess how tree–seedling interactions might change as a function of tree density, ranging from open fields to closed canopy forest. In order to combine data from both fields we first scaled growth as a proportion of the growth of the largest seedling in each field, after which there was no longer a significant field effect. To model facilitation, we derived equations for growth as a function of first year mycorrhiza (proportion of maximum growth $=0.27 + 0.74(ECM)$, where ECM is first year mycorrhizal infection, see **Fig. 3b,d**); and mycorrhizal infection as a function of proximity to trees (see **eqn 1**, above). To model competition, we took proportion of maximum growth as a function of canopy openness measured as DIFN (proportion of maximum growth $= 0.25 + 0.47(DIFN)$; see **Fig. 3a,c**), and reanalysed data from a prior study in the same research area (**Peterson 1998**) on canopy openness (DIFN) as a function of tree BA in oak savanna (DIFN $=0.92-0.045(BA) + 0.00053(BA)^2$; $P < 0.001$, $r^2 = 0.78$). The resulting seedling growth potential is calculated as the product of the two functions. We then generated a spatially explicit model with varying densities of trees on a 250×250 m landscape and ran the model at 26 densities ranging from 0.1 to 600 trees ha^{-1} to determine the effect of tree density on facilitation and competition of seedling establishment by trees.
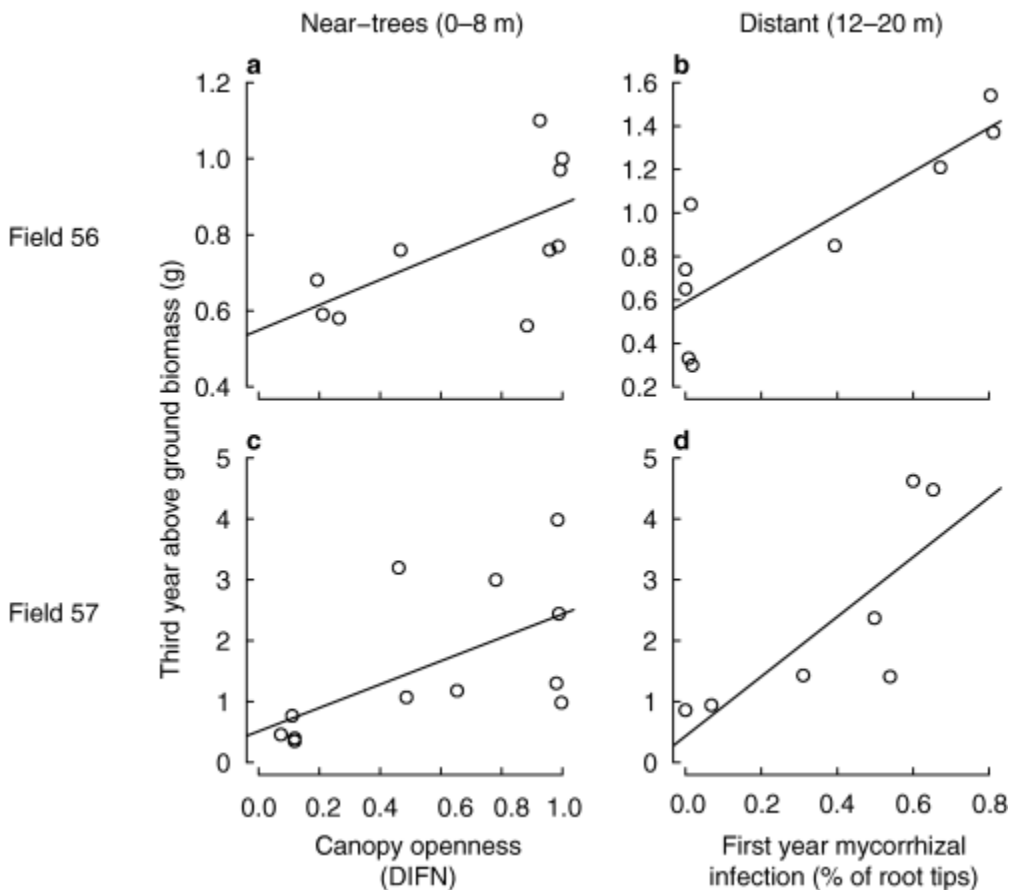

Figure 3

Correlations between final (third year) aboveground biomass and canopy openness near trees (a, c) and between biomass and mycorrhizal infection distant from trees (b, d) for field 56 (a, b) and field 57 (c, d). Correlations were significant ($P < 0.05$) for all except the correlation of DIFN and biomass in field 56 (a), for which $P = 0.053$.

With increasing density of trees there is a benefit to seedlings because of increased ectomycorrhizal infection (thin solid line in **Fig. 4a**) which rapidly asymptotes. Increasing density of trees has concomitant negative

influences on seedlings because of increased canopy closure, which scale as a near-linear function of local BA (dashed line). Combining both influences (thicker solid line) there is a 'zone of net facilitation' up to a relatively low density of trees, followed by a 'zone of net inhibition' of seedling growth with further increases in tree density.

Although discussion of average effects is informative, it is important to look at how positive and negative effects co-occurred on the landscape (**Fig. 4b**). At densities of trees of *c.* 50   trees   ha^{-1} (e.g. an open oak savanna with an average 14.1   m distance between trees), where average seedling growth was the greatest, our model landscape showed generally high levels of growth with a few pockets of severe growth limitation. Relatively frequent randomly occurring denser patches of trees on the landscape were associated with small reductions in seedling growth. Much more dramatic declines in seedling growth were observed in the more infrequent 'openings' where seedlings would be limited by very low levels of mycorrhizal infection.

Discussion

Trees both facilitated and inhibited the establishment of seedlings at forest edges. Seedlings germinating within *c.* 15.7   m of trees had increased mycorrhizal infection, resulting in increased nitrogen uptake and ultimately increased growth. These distances are consistent with the known root distributions of mature oak trees (**Weaver & Kramer 1932**; **Lyford 1980**), suggesting that being in the root zone of established trees was responsible for the sharp increase in seedling mycorrhizal infection. In contrast, the negative effects of proximity to trees appeared to be strongly correlated with canopy openness and the horizontal spread of the canopy of *c.* 8   m. As competition and facilitation had disjunct spatial patterns of occurrence, they did not simply cancel each other. Instead, net positive and negative interactions co-occurred at forest edges, with maximal seedling growth at intermediate distances in field 57. In field 56 the growth response was not observed, however the same underlying processes were apparent. A related although opposite pattern has been observed in dry habitats where positive shoot effects via shading are counterbalanced by negative influences of root competition (**Callaway *et al.* 1991**); whether differential root and shoot effects led to spatially disjunct competition and facilitation has not been explicitly investigated in previous studies.

The positive effect of being near trees for mycorrhizal infection is a nonlinear and non-additive function (being within a critical distance of a single tree provides most or all of the benefit, with no further benefit because of increased proximity or density of trees), while competition is a largely linear process with increasing shading resulting in continued decreases in seedling growth. The increase in ectomycorrhizal infection of first-year seedlings close to established trees was so large (from 9% to 77% of root tips) that any further linear increase would be mathematically impossible. Similarly large effects of proximity to a single tree on mycorrhizal infection of seedlings have been observed in other studies (**Borchers & Perry 1990**; **Kranabetter 1999**; **Dickie *et al.* 2002**), suggesting that non-additive facilitation may be common.

Positive feedback may reduce plant community diversity (**Bever *et al.* 1997**; **Reynolds *et al.* 2003**; but see **Molofsky *et al.* 2001**) and potentially contribute to monodominance in ectomycorrhizal trees (**Molofsky & Bever 2002**). However, current models of positive feedback have generally implicitly or explicitly assumed an additive process (**Bever *et al.* 1997**; **Brooker & Callaghan 1998**; **Molofsky & Bever 2002**). Our model suggests that non-additive facilitation, as observed in our data, may result in net facilitation at relatively low densities of plants, which would tend to increase populations, and net competitive interactions at higher densities, which would tend to reduce populations. This trade-off between facilitation and competition may therefore result in a degree of homeostasis and the moderation of dominance, potentially increasing plant diversity by preventing monodominance. Although our model is directly derived from field observations, it is limited in several respects; particularly the extension of one-dimensional transect data to a two-dimensional landscape, the assumption of random plant distributions and the lack of a dynamic component to account for temporal processes.

Nonetheless, given the difficulty of experimentally manipulating the density of mature trees on landscapes, we believe modelling is a tractable way of approaching these questions.

Our model also shows that spatial co-occurrence of competition and facilitation may create a complex spatial mosaic of patches where a species is either favoured or disfavoured in competitive interactions with other species. In the case of oak savanna, our model suggests that there may be pockets in the landscape where tree seedlings compete poorly because of a lack of mycorrhiza, and that areas of high density of adult trees are also associated with reduced growth of oak seedlings. This finding is similar to observations of persistent openings in oak savannas largely devoid of tree regeneration (**Bray 1955**), and a succession to more shade tolerant species in higher density closed-canopy oak woodlands (**Peterson & Reich 2001**). Whether savanna openings arise from random processes (as in our model) or other causes such as herbivory (**Rietkerk & van der Koppel 1997**), dispersal limitation (**Brown & Archer 1987**) or fire (**Peterson & Reich 2001**), a lack of mycorrhizal infection of tree seedlings may combine with other factors, such as herbivory (**Inouye *et al.* 1994**; **Lawson *et al.* 1999**) and low nitrogen supply in grass-dominated patches (**Reich *et al.* 2001**; **Dijkstra *et al.* 2005**), to delay the colonization of openings by trees, resulting in fine-grain interspersed alternative steady-state patches of grass or tree domination and an increase in total plant diversity.

The positive effect of trees on the mycorrhizal infection of seedlings was a somewhat transient effect: by the third year only four seedlings (all 12–20 m from the edge) had < 20% of root tips infected. Despite the transient effect on mycorrhizal infection, there were persistent correlations of first year mycorrhizal infection with seedling growth at least through the end of the third growing season. This may reflect a lag-time between the presence of mycorrhiza increasing nutrient uptake and the expression of plant growth responses to increased nutrients. It is possible that seedlings germinating distant from trees would eventually overcome an initial delay in mycorrhizal infection; however, it is also possible that these seedlings may be at a persistent disadvantage in having utilized a greater proportion of seed reserves for prolonged maintenance rather than growth. Transient benefits to seedlings may be of great importance to plant community dynamics, as early establishment is a period of very high mortality for tree seedlings, and mortality can be strongly affected by plant size (**Lawson *et al.* 1999**).

Our focus on shade and mycorrhiza as the two driving factors is largely based on correlations (mycorrhizal infection with N uptake and aboveground biomass; canopy closure with biomass and height : biomass ratios) and does not prove causation. There are numerous other factors that may have contributed to the observed growth patterns, including altered soil moisture through shading (**Davis *et al.* 1999**; **Danner & Knapp 2003**), root competition (**Anderson *et al.* 2001**) or hydraulic lift (**Caldwell *et al.* 1998**); increased pathogen load (**Packer & Clay 2003**), although no obvious evidence of pathogens was observed; interspecific competition for nutrients; or increased organic N near trees that may have been available to ectomycorrhizal plants but not to grasses and forbs (which showed no increase in foliar N content near the forest edge). There were also substantial changes in the community of ectomycorrhizal fungi infecting seedlings as a function of distance which have been previously described (**Dickie & Reich 2005**). At present we are not able to link these shifts in community with any effect on seedling growth; nonetheless, shifts in ectomycorrhizal communities are likely to influence seedlings. We have also assumed that facilitation will lead to positive feedback, which is only true if the net positive effect of trees on seedlings is greater than any positive effects of trees on potential competitors, which we did not measure.

The extent to which our results can be generalized beyond oak–ectomycorrhiza interactions may depend not only on what symbiont is considered but also the host species. For example, a lack of ectomycorrhiza appears to be a significant limitation for *Quercus* (**Dickie *et al.* 2002**) and *Nothofagus* seedlings (**Baylis 1980**) and in some Pinaceae (**Borchers & Perry 1990**). Nonetheless, some Pinaceae appear to be quite capable of regenerating distant from established trees (**Dovciak *et al.* 2005**), perhaps because of the apparent great longevity and

dispersal ability of *Rhizopogon* propagules (T.R. Horton, personal communication), an ectomycorrhizal fungus host-specific to the Pinaceae. Symbiont specificity may also play a role in other symbioses (**Richardson *et al.* 2000**).

Bruno *et al.* (2003) suggest that the integration of facilitation into ecological theory should be a priority for ecologists. We concur. Further, we suggest that this integration requires an understanding of the spatial mosaic of positive and negative interactions in communities, including those involving the same pairs of organisms, and an understanding and appreciation of additive and non-additive processes.

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