

SOIL PATHOGENS AND *PRUNUS SEROTINA* SEEDLING AND SAPLING GROWTH NEAR CONSPECIFIC TREES

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Abstract. Soil pathogens close to mature *Prunus serotina* trees reduce the survival of conspecific seedlings. We examined whether the soil community associated with *P. serotina* trees has continued negative effects on seedling growth. *P. serotina* seedlings and saplings were harvested after being followed for 1–3 years in the field, and above- and belowground biomasses were measured. Linear regression models including distance to adult *P. serotina* tree, conspecific seedling density, and seedling age explained 13.9% of the variation in biomass. Distance and age were positively correlated with total biomass, while density was negatively correlated with total biomass. A similar model for saplings established prior to the beginning of the study, and of unknown age, predicted 11.3% of the variation in total biomass, with distance to adult positively correlated with biomass.

To separate the effects of distance from density and remove confounding environmental factors, seedlings were grown in the greenhouse at high or low density in soil collected 0–5 m or 25–30 m from adult *P. serotina* trees. Half of the soil collected at each distance was sterilized by autoclaving. The experiment was repeated in 1998 and 1999, and in both years there was a significant sterilization-by-distance interaction. Sterilization of soil collected close to the tree resulted in higher root:shoot ratios, while sterilization of soil collected away from the tree resulted in lower root:shoot ratios. This suggests that soil biota vary with distance to adults and that elimination of soil biota changes plant allocation patterns differentially with distance.

Distance-dependent effects of soilborne pathogens may continue beyond seedling mortality and suppress juvenile growth. Reduced growth could increase an individual's chance of later mortality, suggesting that initial escape from damping-off pathogens close to parental trees does not ensure longer-term survival.

Key words: distance-dependent growth; Lake Griffy Nature Preserve, Indiana (USA); negative feedback; *Prunus serotina*; *Pythium*; root:shoot ratio; seedling and sapling growth; soil pathogens.

INTRODUCTION

Characteristics of the site into which a seed disperses affect germination, seedling growth, and survival. The effects of site on plant fitness are due in part to local vegetation. Dominant plants define the microhabitat characteristics for plants growing near them (termed autogenic habitat heterogeneity by Fox, 1977). Species-specific alteration of chemical or physical soil properties has frequently been documented (Mergen and Malcolm 1955, Zinke 1962, Challinor 1968, Boettcher and Kalisz 1990). Soil alteration may result from interspecific differences in patterns of nutrient acquisition and use (Hobbie 1992), modification of moisture and temperature (Burton and Bazzaz 1991), or litter production and quality (Finzi et al. 1998). As a result, the forest floor may be a mosaic landscape corresponding to the dominant plants above, and microsite quality may vary at the scale of individual trees.

Plant species can also differ in the microbial soil communities they host (Chanway et al. 1991, Bever et al. 1996, Westover et al. 1997). When soil microor-

ganisms are dependent on host plant composition, variation in plant species abundance and composition can result in different soil communities. Host-dependent sporulation resulted in differentiation of the mycorrhizal communities in a microcosm experiment (Bever et al. 1996), and species composition of mycorrhizal fungal communities in the field were associated with particular plant species (Bever et al. 1996, Eom et al. 2000). Soilborne pathogen communities can also vary depending on the plant community. Mills and Bever (1998) found differences in *Pythium* accumulation with plant species, potentially allowing for species coexistence. Van der Putten and Troelstra (1990) demonstrated that the decline of *Ammophila arenaria* in successional dune communities was due to an accumulation of species-specific soilborne pathogens that reduced the competitive ability of *A. arenaria*, allowing it to be replaced by *Festuca rubra*, a species relatively unaffected by the pathogens of *A. arenaria* (van der Putten and Peters 1997).

It has been proposed that plant modification of the biotic soil community be examined using the theoretical framework of feedback (Bever 1994, Bever et al. 1997). Positive feedback occurs when the presence of a plant or plant population makes conditions more fa-

Manuscript received 26 November 2001; revised 23 May 2002; accepted 28 May 2002. Corresponding Editor: M. Parker.

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avorable for individuals of the same species, e.g., symbiotic associations with rhizobia or mycorrhizal fungi. In contrast, negative feedback occurs when the presence of a plant causes conditions to be less hospitable for individuals of the same species. Evidence of negative feedback between plants and soil microorganisms is abundant in the agricultural literature (e.g., Shipton 1977, Bruehl 1987). For example, negative feedback in apple orchards leads to apple replant disorder (Mazzola 1998). It was believed that replant disease only occurred after sites were cultivated with apple for long periods of time, but Mazzola (1999) found that soil-borne fungi involved in replant disorder developed quickly in response to the presence of apple hosts. Several recent studies have also demonstrated negative feedback in natural communities (e.g., van der Putten et al. 1993, Bever 1994, Packer and Clay 2000).

Seeds that are dispersed further from their maternal parent may "escape" their native soil pathogens, provided they are not dispersed beneath another conspecific tree. Janzen (1970) and Connell (1971) hypothesized that seed and/or seedling mortality close to conspecific trees caused by host-specific natural enemies maintains high levels of tree diversity in tropical forests by creating an environment in which heterospecific seedling recruitment is favored. Seed predators and herbivores have been the primary focus of tests of the Janzen-Connell hypothesis, but pathogens can create similar patterns of distance- and/or density-dependent mortality (Augspurger 1983a, b, 1984, Augspurger and Kelly 1984, Gilbert et al. 1994).

Negative feedback has also been proposed as a mechanism that promotes species coexistence in temperate forests. It has been suggested that "reciprocal replacement" (Woods 1979), also termed "natural rotation" (Ammon 1951, cited in Florence 1965) and "alternation of species" (Schaeffer and Moreau 1958, cited in Fox 1977), allows for species coexistence. For example, Woods (1979, 1984) and Fox (1977) found the greatest abundance of beech seedlings beneath maple canopies, and the greatest abundance of maple seedlings beneath beech canopies (but see Poulson and Platt 1996). Further, Fox (1977) found that within patches with particularly high aggregations of conspecific trees, there was an even stronger tendency for alternation (i.e., higher abundances of heterospecific saplings were found). It would be expected that the density of conspecific seeds and seedlings should be highest beneath monospecific aggregations of adult trees. Woods (1979, 1984) and Fox (1977) suggested that the inability of seedlings to establish beneath conspecific canopies could be due to root pathogens, but this hypothesis was not tested. In a temperate floodplain forest, negative correlations between seedling survival and proximity to a conspecific adult tree and basal area of conspecific trees were detected, but the causes of seedling mortality were not conclusively determined (Streng et al. 1989, Jones et al. 1994).

The goal of this research was to determine whether negative plant-soil feedback affects growth of black cherry (*Prunus serotina*) seedlings near mature black cherry trees. Field studies of black cherry seedling survival provided evidence that seedling mortality close to the parental tree was due to soil pathogens (Packer and Clay 2000). Here we present results from field and greenhouse experiments examining whether seedling and sapling growth exhibit distance and/or density dependence. Previous studies of temperate trees have shown that growth and mortality rates of individuals tend to be negatively correlated within a species (e.g., Coyea and Margolis 1994, Ward and Stephen 1997). If black cherry seedlings and saplings suffer from distance- or density-dependent reductions in growth, it could increase their mortality at later stages, suggesting that future community composition cannot be predicted based on patterns of early seedling survival.

METHODS

Study system

Plant.—Black cherry (*Prunus serotina* Ehrh.) occurs commonly in forests, old fields, fencerows, and pastures throughout eastern North America, and is generally thought to be shade intolerant (Deam 1940, Baker 1949 and Hough 1960, cited in Auclair and Cottam 1971). *Prunus* trees may begin producing fruit while still small, and continue producing seeds every year. Large fruit crops typically occur every 3–4 yr (Morden-Moore and Willson 1982). Birds disperse large numbers of these fruits, but many are left uneaten and fall to the ground (A. Packer and K. Clay, *personal observation*). Seeds germinate in the spring, often forming dense seedling mats.

Fungi.—*Pythium* species, pathogenic oomycetes, live as saprophytes on dead plant and animal matter, or as parasites on plant roots. Members of this genus are typically assumed to be host generalists (Carlile and Watkinson 1994). *Pythium* spp. may encounter host tissue either by chance, or as a result of plant exudates that stimulate zoospore germination or mycelial growth (Martin and Loper 1999). Once the pathogen and host come into contact, the fungal mycelium invades epidermal or cortical cells at or below the soil line, often causing damping-off epidemics (Hendrix and Campbell 1973).

Pythium can affect plants of any age, although it tends to inflict the greatest damage during germination and early seedling growth (Martin and Loper 1999). As seedlings mature, they become less likely to die as a result of damping-off infections. Infection of older plants is often limited to fine roots. When fine roots are damaged or killed, aboveground plant parts are often stunted or killed (Hendrix and Campbell 1973, Agrios 1988). Severity of fungal infection is largely influenced by interactions among environmental conditions, host plant growth, and pathogen growth. *Pyth-*

ium infections can cause substantial damage when soil water content is high (Stanghellini and Burr 1973, Stanghellini 1974). Other environmental factors that influence disease severity include nitrogen availability, temperature, and previous land use practices (Agrios 1988).

Field censuses

Censuses were conducted at Lake Griffy Nature Preserve, Bloomington, Monroe County, Indiana, USA. The soils are classified as Burk's silt loam (on slopes) and Hagerstown silt loam (on ridge tops) (USDA 1981). The forest community is at least 70 yr old and consists of a diverse mix of hardwood species, with many individuals >50 cm dbh. Arcs (30 degrees wide, extending 30 m) were established beneath six large black cherry trees, with each tree at the apex. Three arcs were initiated in 1996 and three in 1997. Black cherry seedlings and saplings within the arcs were tagged and their *X*-*Y* coordinates were recorded. The tree at the arc apex is referred to as the parental tree, although some seeds may have been dispersed into the arc from elsewhere. Two cohorts of germinating seedlings were followed beneath each parental tree (i.e., for trees first censused in 1996, the 1996 and 1997 cohorts were followed, and for trees first censused in 1997, the 1997 and 1998 cohorts were followed). Individuals established before the beginning of the study (referred to hereafter as saplings) were also censused. These saplings, which were a minimum of one year old, ranged in height from ~2 cm to 2 m. Thus, there were a total of six sapling cohorts (one per tree) and 12 seedling cohorts (two per tree; three from 1996, six from 1997, and three from 1998). Individuals were censused in late spring and again in early fall through 1998, at which time survival was noted. Seedling and sapling distances to parent and distances to all other black cherry seedlings and saplings were calculated using *X*-*Y* coordinates.

Neighborhood density was defined as the number of conspecific seedlings or saplings within a 20-cm radius. Most seeds typically fall close to the parent trees, generating a negative correlation between distance and seedling density. Neighborhood density was estimated for individuals within 20 cm of the arc's edge by projecting a mirror image of seedling distribution beyond both edges of the arc.

Fifty seedlings and 50 saplings from each adult tree were randomly selected and harvested. Stem length and mass, root mass, tap root length, and total seedling biomass were determined, and root:shoot ratios were calculated. All data were transformed to meet assumptions of normality. The effects of distance to parent and density on survival through fall 1998 were analyzed using logistic regression analyses and reported in Packer and Clay (2000).

We examined the relationship between plant growth and distance to parent, neighborhood density, and seed-

ling age. All seedlings that germinated during the course of the study were grouped together by cohort, and their growth was analyzed using multiple linear regression models. Specifically, models were created for stem length, tap root length, total biomass, and root:shoot ratio. Distance to parent, neighborhood density, and seedling age were included in all models as independent variables. While we expected distance and density to be negatively correlated due to the nature of the seed shadow, distance to parent was not a reliable predictor of neighborhood density for germinating seedlings ($P = 0.223$, $r^2 = 0.004$) but explained 17.4% of the variation in neighborhood density for saplings ($P < 0.001$). The correlation varied among individual trees, with significant negative correlations found for seedlings beneath trees 4 and 5, and saplings beneath trees 3, 4, 5, and 6. In general, neighborhood density was more strongly negatively correlated with distance to parent for older age classes.

To test for an interaction between distance and density, such as a greater effect of density close to the parent, the products of these two independent variables were computed and entered into linear regression models. Generally, the overall model fit was reduced when the interaction term was included in the model, and the partial regression coefficient associated with the interaction term was not significant. These interactions were therefore not included in any of the final linear regression models. The same procedures were repeated to examine growth of saplings present prior to the establishment of our arcs. However, the ages of these saplings were unknown, so age was not included as an independent variable in these models. Growth of seedlings and saplings was also modeled separately beneath individual trees.

Greenhouse experiment

To evaluate the role of soil pathogens in distance- and density-dependent growth, a greenhouse experiment was conducted using field soil. Experimental treatments were (1) soil collection distance (0–5 m or 25–30 m from the adult *Prunus* tree), (2) seedling density (one or three seeds planted per pot), and (3) soil sterilization (sterilized or not sterilized). Fruits were collected from trees throughout Bloomington, Indiana, during fall 1997 and 1998. Fruit tissue was removed and seeds were surface sterilized. Seeds were planted in plastic boxes filled with sterile moistened sand and left at 4°C for 5 to 6 mo to break seed dormancy. Seeds began to germinate in February.

Soil was collected in either late February (1998) or early March (1999) from both 0–5 m and 25–30 m from three of the adult black cherry trees used in the field censuses. Field soil was sieved and root material was cut into 1-cm pieces and returned to the soil. All soil treatments were diluted 1:1 with Metro-Mix (Scotts Company, Marysville, Ohio, USA) and thoroughly mixed. One half of both the near and distant soil was

autoclaved for 5 h at 211°C. We tested soil from the same sites for nutrients at a later date in order to determine whether sterilization could increase nutrient availability (Maine Soil Testing Service, Orono, Maine, USA). NPK concentrations were very similar in close and far field soils (data not shown), suggesting that nutrient availability was not distance dependent. We found that sterilized soil had increased ammonium nitrate, potassium, and phosphorus relative to unsterilized soil, but the proportional increase in nutrient levels was similar at both distances.

In 1998, seedlings were planted during the last week in February in 4 × 4 cm cells, with all cells of a given soil treatment in the same flat to prevent cross-contamination. Seedling density was either one or three per cell. Flats were rotated on greenhouse benches weekly. Each combination including sterilized soil had 12 replicates, while each combination including unsterilized soil had 18 replicates, due to a shortage of germinating seedlings that was not detected until after all unsterilized treatments were planted. Seedling survival was monitored twice a week for ~10 wk. Surviving seedlings were harvested the first week in May. Leaf number and leaf, root, and stem dry masses were determined, and root:shoot ratios were calculated. All data were transformed to meet assumptions of normality.

A replicate experiment was conducted in spring 1999 with minor modifications. Seedlings were planted in mid-March, in individual 6.5-cm pots that were randomly located beneath lighted shelves. Soil was treated as in the 1998 experiment. There were 16 replicates of each treatment combination. Mortality was monitored twice a week through mid-April, when survivors were harvested. Some seedlings in the 1999 experiment became infested by thrips, and therefore leaf masses were not taken due to tissue damage. Thrips occurred only on leaf tissue, and should not have transferred soil fungi to sterile treatments. Other variables were recorded as before, and all data were transformed to meet assumptions of normality.

There were no significant differences in survival between years, so data from 1998 and 1999 were combined and analyzed using backward conditional logistic regression (Packer and Clay 2000). For growth data, there were significant interactions between year and other factors; therefore, data from 1998 and 1999 were analyzed separately. In low-density treatments, only one seedling was ever present, while in high-density treatments the surviving individuals grew with two other seedlings during at least some portion of the study. Therefore, low-density and high-density treatments were also analyzed separately, and the number of surviving seedlings in the pot (1, 2, or 3) was entered as a covariate for high-density seedlings. Root:shoot ratios were analyzed using univariate ANOVA with plant biomass as a covariate. Leaf number, stem mass, and root mass were analyzed using MANOVA with distance and sterilization as fixed factors. Multivariate dif-

ferences were assessed using Pillai's Trace. While there are several similar test statistics, Pillai's Trace has been found to be the most robust for general use (Olson 1974, 1976, 1979, cited in Zar 1999).

Pathogen inoculation experiment

Upon seedling death in unsterilized field soil in the greenhouse experiment, root tissue from the leading edge of the disease lesion was plated to isolate the causal agent. Roots were surface sterilized, and then cut in thin cross-sections and placed on corn meal agar plates. The three most common isolates obtained were used to create inocula. Over 80% of all isolates were one of these three (distinguished based on growth rate; color and texture were similar). Karen Rane, Plant and Pest Diagnostic Laboratory at Purdue University (West Lafayette, Indiana, USA) identified the three isolates as *Pythium* spp. One isolate has since been tentatively identified as *Pythium* AP1 (aff. *intermedium*) by André Lévesque, Agriculture and Agri-food Canada (Ottawa, Ontario, Canada). Isolates were cultured in vermiculite amended with cornmeal and V-8 (mixed-vegetable juice) broth (Martin 1992). When fungal hyphae had grown throughout the media, 15 mL of medium were added to 6.5-cm pots filled with Metro-Mix. Inoculation treatments are referred to as P1, P2, and P3, corresponding to each isolate. Two controls were included: control 1, Metro-Mix only (the background soil in the pathogen inoculation treatments); and control 2, sterile vermiculite/cornmeal/V-8 medium and Metro-Mix (the medium in which the fungal isolates were grown together with the background soil). There were 40 replicates of each treatment and control, with one seedling per pot. The null hypothesis that survival was independent of treatment was tested using the χ^2 test statistic. Leaf number and leaf, stem, and root masses were measured for surviving seedlings. Data were transformed when necessary, and tested using ANOVA. Given the relatively low survival of seedlings in each pathogen inoculation treatment, surviving seedlings were combined to analyze the effect of pathogen inoculation on growth characteristics.

Calculation of relative fitness at increasing distances

The resulting logistic regression equations from seedling and sapling survival analyses were used to predict survival from 0–30 m from the parental tree at 1-m intervals. For this purpose, the number of neighbors within 20 cm was held constant at 0. Similarly, the multiple linear regression equations from analyses of seedling and sapling growth in the field were used to calculate predicted total biomass at 0–30 m from the parental tree at 1-m intervals, with neighborhood density within 20 cm again held constant at 0. Survival and biomass values were multiplied together to determine how relative fitness is related to distance to parent. Because all individuals were pre-reproductive, we used biomass as a surrogate for reproduction.

TABLE 1. Multiple linear regression models examining how much variation in seedling stem length, tap root length, total biomass, and root:shoot (R:S) ratio is explained by distance to parent and neighborhood density.

Response variable	R^2	Model P value	Variables included in model			
			Distance (β , P)		Density (β , P)	
Seedlings ($N = 358$)						
Stem length	0.012	0.222	0.023, 0.669	0.090, 0.102	0.089, 0.106	
Tap root length	0.081	<0.001	0.149, 0.004	-0.047, 0.377	0.216, <0.001	
Total biomass	0.139	<0.001	0.107, 0.032	-0.109, 0.035	0.307, <0.001	
R:S ratio	0.080	<0.001	0.109, 0.035	-0.118, 0.026	0.196, <0.001	
Saplings ($N = 274$)						
Stem length	0.053	<0.001	0.242, <0.001	0.036, 0.580	N/A	
Tap root length	0.019	0.078	0.128, 0.055	-0.019, 0.778	N/A	
Total biomass	0.113	<0.001	0.322, <0.001	-0.485, 0.628	N/A	
R:S ratio	0.011	0.209	0.070, 0.295	-0.057, 0.389	N/A	

Notes: Transformed data from all germinating seedlings were analyzed together by pooling seedlings located at six parent trees. These models include seedling age as an independent variable. Data from all seedlings established prior to arc establishment are also analyzed together without age. Betas (β) are partial regression coefficients expressed in standardized form for independent variables. Values of $P < 0.05$ are in bold.

RESULTS

Field censuses

Seedling survival and growth.—Survival of seedlings increases with distance to parent and decreases with conspecific seedling density (Packer and Clay 2000), but distance and density effects extended beyond early seedling mortality. Linear regression models that included distance, density, and seedling age explained 13.9% of the variation in total biomass and 8.0% of the variation in root : shoot ratio of surviving seedlings. All three independent variables had significant partial regression coefficients. Total biomass and root:shoot ratio were positively correlated with distance to parent and seedling age, and negatively correlated with density (Table 1). Tap root length increased with increasing distance to parent, as well as with increasing seedling age. Linear regression models explained 8.1% of the variation in tap root length, with distance and age having significant partial regression coefficients (Table 1).

Sapling survival and growth.—There were pronounced outward shifts in mean distance to parent of surviving saplings (Packer and Clay 2000). Size of surviving saplings was also distance dependent. The regression model including distance and density explained 11.3% of the variation in total biomass, with only the partial regression coefficient associated with distance being significant (Table 1). The same model explained 5.3% of the variation in stem length of saplings, and again only the partial regression coefficient associated with distance was significant.

Variation among trees in seedling growth.—Individual trees differed in the strength of distance, density, and seedling age effects on growth. Linear regression models, including distance, density, and seedling age, significantly predicted some aspects of seedling growth beneath individual trees 1, 4, and 5. The models best

explained variation in seedling biomass (20–24% variation explained), with distance and age positively correlated with total biomass, and density negatively correlated with total biomass beneath tree 1 (Table 2). For tree 1, regression models also explained 12.9% of the variation in stem length and 16.6% of the variation in tap root length (Table 2). Only partial coefficients for distance and age were significant. Regression models explained a significant portion (ranging from 9.3% to 24.4%) of the variation in all measured variables for seedlings beneath tree 4. Beneath tree 5, the model explained 21.1% of the variation in total biomass, with distance and age positively correlated with biomass (Table 2). However, models poorly predicted seedling growth beneath trees 2 and 3. It should be noted that trees 2 and 3 had the fewest numbers of seedlings compared to the other trees (Table 2). Tree 2 was also the smallest tree (mean: 25 cm dbh vs. 44 cm dbh).

Saplings beneath individual trees.—In general, regression models were weaker for saplings than for seedlings. However, distance was a significant predictor of total biomass for previously established saplings beneath trees 4, 5, and 6 (Table 3), explaining between 13.4% and 25.5% of the variation in total biomass. Partial regression coefficients associated with both distance and density for tree 6 were significant in the regression model (Table 3). The regression model explained 27.5% of the variation in stem length of individuals harvested beneath tree 1, with the partial regression coefficient associated with distance being significant (Table 3). Linear regression models did not predict the biomass of saplings beneath trees 2 and 3. It should be noted that biomass is not equivalent to growth, because sapling age is likely to be correlated with distance due to distance-dependent mortality.

Survival and growth of seedlings in the greenhouse

We found that sterilization of soil collected beneath *Prunus* trees greatly improved the survival of seedlings

TABLE 2. Multiple linear regression models examining how much variation in seedling stem length, tap root length, total biomass, and root:shoot (R:S) ratio is explained by distance to parent, neighborhood density, and seedling age.

Response variable	R ²	Model P value	Variables included in model		
			Distance (β , <i>P</i>)	Density (β , <i>P</i>)	Age (β , <i>P</i>)
Tree 1 (<i>N</i> = 89)					
Stem length	0.129	0.009	0.274, 0.009	0.022, 0.830	0.209, 0.046
Tap root length	0.166	0.002	0.300, 0.004	-0.148, 0.146	0.196, 0.056
Total biomass	0.201	< 0.001	0.209, 0.037	-0.200, 0.045	0.307, 0.003
R:S ratio	0.022	0.605			
Tree 2 (<i>N</i> = 22)					
Stem length	0.044	0.840			
Tap root length	0.223	0.199			
Total biomass	0.054	0.793			
R:S ratio	0.109	0.545			
Tree 3 (<i>N</i> = 32)					
Stem length	0.065	0.593			
Tap root length	0.048	0.708			
Total biomass	0.064	0.598			
R:S ratio	0.028	0.851			
Tree 4 (<i>N</i> = 91)					
Stem length	0.107	0.019	0.189, 0.098	0.169, 0.135	0.272, 0.010
Tap root length	0.098	0.029	0.276, 0.017	0.066, 0.561	0.224, 0.033
Total biomass	0.244	< 0.001	0.330, 0.002	-0.011, 0.916	0.428, < 0.001
R:S ratio	0.093	0.037	0.172, 0.134	-0.157, 0.169	0.191, 0.070
Tree 5 (<i>N</i> = 67)					
Stem length	0.058	0.282			
Tap root length	0.018	0.768			
Total biomass	0.211	0.002	0.308, 0.058	-0.263, 0.116	0.414, 0.007
R:S ratio	0.071	0.195			
Tree 6 (<i>N</i> = 56)					
Stem length	0.027	0.698			
Tap root length	0.135	0.054	-0.291, 0.039	0.054, 0.689	0.142, 0.290
Total biomass	0.051	0.428			
R:S ratio	0.026	0.710			

Notes: Transformed data are presented separately for each of the parent trees. Betas (β) represent partial regression coefficients expressed in standardized form for independent variables. Values of $P < 0.05$ are in bold. Empty cells indicate nonsignificant results.

planted at high density in the greenhouse, while sterilization of soil collected 25–30 m from adults did not affect survival (Packer and Clay 2000). Growth of surviving seedlings was also affected by distance and sterilization. For low-density treatments, only sterilization significantly affected growth variables in the 1998 experiment (Pillai's trace = 0.199, *df* = 3, 53, $F = 4.40$, $P = 0.008$). Stem masses and root masses were higher in sterilized soil, regardless of distance (*df* = 1, 110, $F = 7.517$, $P = 0.008$ and *df* = 1, 110, $F = 13.454$, $P = 0.001$, respectively). In 1999 there were no significant effects of distance, sterilization, or their interaction on measured variables. In both years, there was a significant interaction between distance and sterilization on root:shoot ratios of plants in low-density treatments (*df* = 1, 54, $F = 5.28$, $P = 0.025$ and *df* = 1, 45, $F = 4.62$, $P = 0.037$, for 1998 and 1999, respectively; Fig. 1a, b). The covariate (plant biomass) was not significant in either year. Sterilization increased mean root:shoot ratio in soil collected close to the tree, while it decreased the mean root:shoot ratio in soil collected far from the tree (Fig. 1a, b).

For high-density treatments there were no significant effects of distance, sterilization, or number of surviving seedlings on growth variables in 1998, but in 1999 there was a significant effect of distance (Pillai's Trace = 0.162, *df* = 3, 45, $F = 2.91$, $P = 0.045$). Leaf number was higher in distant soil relative to close soil (*df* = 1, 47, $F = 7.298$, $P = 0.010$).

Survival and growth of seedlings from pathogen inoculation experiment

Seedling survival was reduced by an average of 65% in inoculation treatments (Packer and Clay 2000). The biomass of survivors from pathogen inoculation treatments was compared to that of the surviving seedlings in both the Metro-Mix and vermiculite controls. All biomass measures were highly correlated (data not shown), so only the effect of treatment on total biomass was analyzed. There was a nonsignificant trend ($P = 0.33$) for seedlings grown in pathogen-inoculated soil to have lower biomass than seedlings grown in Metro-Mix control soil (Fig. 2). The mean biomass of seed-

TABLE 3. Multiple linear regression models examining how much variation in sapling stem length, tap root length, total biomass, and root:shoot (R:S) ratio is explained by distance to parent and neighborhood density.

Response variable	R^2	Model P value	Variables included in model	
			Distance (β , P)	Density (β , P)
Tree 1 ($N = 42$)				
Stem length	0.275	0.002	0.496, 0.001	-0.158, 0.253
Tap root length	0.008	0.858		
Total biomass	0.062	0.289		
R:S ratio	0.022	0.654		
Tree 2 ($N = 37$)				
Stem length	0.001	0.986		
Tap root length	0.007	0.888		
Total biomass	0.009	0.852		
R:S ratio	0.056	0.376		
Tree 3 ($N = 49$)				
Stem length	0.013	0.749		
Tap root length	0.012	0.750		
Total biomass	0.026	0.547		
R:S ratio	0.008	0.838		
Tree 4 ($N = 46$)				
Stem length	0.081	0.164		
Tap root length	0.082	0.160		
Total biomass	0.134	0.046	0.373, 0.039	0.045, 0.940
R:S ratio	0.008	0.839		
Tree 5 ($N = 50$)				
Stem length	0.010	0.796		
Tap root length	0.090	0.109	0.375, 0.041	0.167, 0.355
Total biomass	0.169	0.013	0.333, 0.057	-0.112, 0.516
R:S ratio	0.059	0.242		
Tree 6 ($N = 51$)				
Stem length	0.054	0.274		
Tap root length	0.088	0.115	-0.049, 0.757	-0.315, 0.049
Total biomass	0.255	0.001	0.322, 0.027	-0.272, 0.059
R:S ratio	0.090	0.109	0.018, 0.907	-0.292, 0.067

Notes: Transformed data from saplings are analyzed separately for each of the parent trees. Betas (β) are partial regression coefficients expressed in standardized form for independent variables. Values of $P < 0.05$ are in bold. Empty cells indicate nonsignificant results.

lings grown in the vermiculite control treatment was intermediate.

Relative fitness at increasing distances

Predicted relative fitness of seedlings and saplings increased with distance from the parental tree. The increase for seedlings was linear, with relative fitness at 25 m being double that at 5 m (Fig. 3). Relative fitness of saplings at 25 m was over three times higher than at 5 m (Fig. 3). These results are conservative estimates of relative fitness because we assumed constant density with distance for simplicity when actually density is correlated with distance.

DISCUSSION

Our results suggest that seedlings growing close to parental trees do not escape pathogen attack despite surviving periods of high mortality. In the field, seedlings near conspecific trees suffered from reduced growth relative to seedlings farther from adult trees. Total biomass and root:shoot ratios of seedlings increased with increasing distance from the adult tree

and decreased when conspecific seedling densities were high. Tap root length also increased with distance from the adult tree, consistent with the hypothesis that host-specific soil pathogens are concentrated around the parental tree. Sapling stem length and total biomass were also positively correlated with distance to parent. While growth variation could reflect competition with the parent tree, there were many large trees of other species within the arcs (A. Packer and K. Clay, *personal observation*), which should weaken correlations between distance and biomass. The greenhouse experiments designed to isolate the effect of soil pathogens were consistent with, but weaker than, field results, suggesting that environmental conditions in the field (i.e., shading) may exacerbate pathogen effects.

Despite the strength of distance and density effects on plant growth, there was variation in relative performance of seedlings and saplings among individual trees. The variation observed may reflect spatial variation in pathogen and/or seedling densities, genetic variation in those populations, or differences in their abiotic environment. It is noteworthy that trees showing

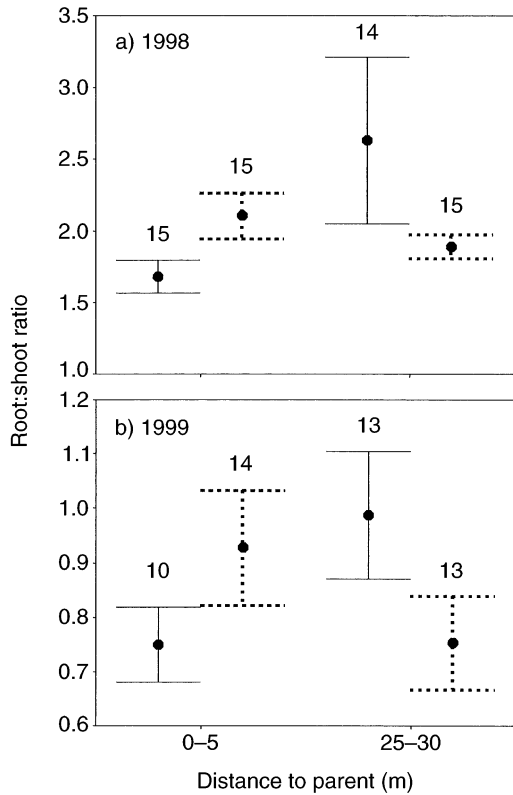


FIG. 1. Mean root:shoot ratio of low density black cherry seedlings in (a) 1998 and (b) 1999. Solid lines represent unsterile soil, and dashed lines represent sterile soil. Means \pm 1 SE are presented.

no effects of distance or density on seedling growth also showed no effect on sapling growth, suggesting that differences are consistent over time. Understanding the basis for this variation may provide insights into the underlying mechanisms generating distance-dependent and density-dependent growth.

Previously reported effects on survival, together with the present results on growth patterns, suggest black cherry is more likely to reach the canopy only at some distance from conspecific adults. Censuses beneath three adult trees with high densities of black cherry seedlings revealed only four black cherry saplings over 0.5 m high within 10 m (Packer and Clay 2000). When logistic and linear regression models for survival and growth were combined to predict relative fitness, we found dramatic declines in fitness with increasing proximity to the parental tree. Sapling fitness was more negatively affected by proximity than was seedling fitness. Because survival is decreased beneath the parental tree, saplings in that area are likely to be younger than saplings farther from the parental tree. The negative relationship between sapling growth and distance to parent may therefore reflect the effects of distance on both growth and the age of saplings.

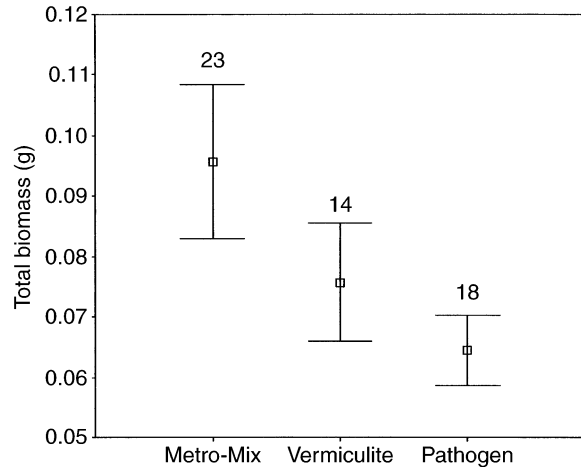


FIG. 2. Mean biomass (g) of plants from pathogen inoculation experiment (\pm 1 SE).

In many species survival is positively correlated with size and/or growth rate (e.g., Streg et al. 1989, Jones and Sharitz 1998, Lawson et al. 1999). For example, Aizen and Woodcock (1996) found that overwintering mortality in oaks was negatively associated with seedling size, and Walters and Reich (2000) found that sur-

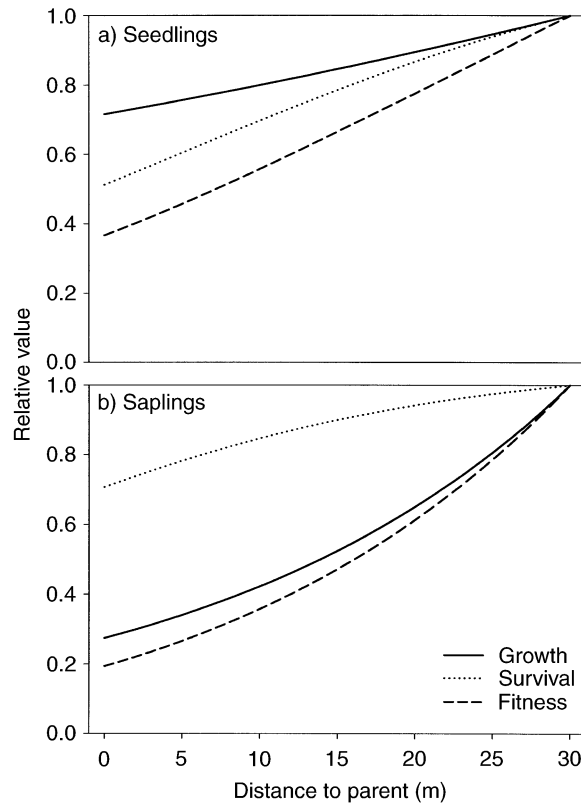


FIG. 3. Relative growth, survival, and fitness estimates of seedlings and saplings at increasing distances to the adult black cherry tree (see *Methods* for calculation of relative fitness).

vival of several North American tree species was strongly related to their relative growth rate. If similar correlations occur in black cherry, reduced seedling and sapling growth close to the parental tree will lead to continued distance-dependent mortality, stressing the importance of long-term studies that examine effects of host-specific natural enemies on the spatial distribution of tree species.

An important question is whether heterospecific seedlings also exhibit decreased growth or survival close to black cherry trees. Data on heterospecific and conspecific sapling sizes suggest that heterospecific seedlings experience less severe negative effects in soil beneath black cherry trees. Packer and Clay (2000) found 10-fold higher density of heterospecific saplings (>0.5 m tall) than conspecific saplings under black cherry trees, despite the high density of black cherry seeds and seedlings. Conspecific saplings were also smaller than heterospecific saplings, suggesting that other species are more likely to replace mature black cherry trees in the forest canopy.

Nature of distance-dependent effects

The relationship between distance to parent and growth of seedlings and saplings in the field could result from factors other than soil pathogens, such as competition with the parental tree or soil nutrient differences. However, our experimental approaches allowed us to specifically evaluate the effects of soilborne pathogens. Greenhouse studies using field-collected soil removed potential confounding effects of vegetation on seedling and sapling growth, and soil sterilization was used to further separate biotic vs. abiotic soil factors. We recognize that autoclaving soil has a variety of effects besides eliminating pathogens (i.e., elimination of mycorrhizal fungi [Bever 1994, Wilson and Hartnett 1997] and nutrient release from microbial biomass [Troelstra et al. 2001]), and soil sterilization alone cannot be viewed as reflecting the effect of soil pathogens. The use of pure fungal cultures to inoculate sterile soil in seedling growth experiments allowed us to directly examine the effect of soilborne pathogens.

Studies using sterilization treatments have found both increases and decreases in plant biomass. Van der Putten et al. (1993) found that the productivity of the sand dune grass *Ammophila arenaria* improved when soil previously cultured by *A. arenaria* was sterilized. The same effect was not observed when beach sand was sterilized, suggesting negative effects of the native soil community on *A. arenaria* growth. Similarly, blackbutt (*Eucalyptus pilularis*) seedlings were severely inhibited in blackbutt forest soil, but this inhibition was overcome by gamma irradiation of the soil (Florence and Crocker 1962). Apple trees, which commonly suffer poor survival and/or growth when grown on sites previously planted with apple, showed enhanced growth when orchard soils were sterilized (Mazzola 1998). Removal of soil biota has also been

found to inhibit plant growth relative to unsterile field soil, suggesting an important role for soilborne microbial mutualists like mycorrhizal fungi (Bowman and Panton 1993, Ronsheim and Anderson 2001). In this study, we found that soil sterilization generally improved seedling growth, indicating that the detrimental effects of soil pathogens outweighed the effect of soil mutualists.

In experiments designed to separate distance and density effects, seedlings grown at high density in unsterilized soil collected close to parental trees had lower survival than seedlings in sterile soil (Packer and Clay 2000), suggesting that biotic sources of mortality were most effective at high host densities. Stem and root masses of low-density seedlings grown in unsterile soil were reduced relative to those in sterile soil in the 1998 experiment. Stem and root masses may have increased in sterile soil due to the elimination of pathogens, but there was no interaction between sterilization and distance as would be expected for pathogens concentrated close to the parental tree. Alternatively, biomass may have increased in response to nutrients released during soil sterilization (Troelstra et al. 2001). However, there was a significant distance by sterilization interaction effect on seedling root:shoot ratio. In both years, root:shoot ratio of *P. serotina* seedlings was lower in soil collected 0–5 m from mature black cherry trees than in soil collected 25–30 m away, consistent with the field study in which root:shoot ratio was positively correlated with distance to parent. In the greenhouse, the effect of sterilization depended on collection distance. Root:shoot ratio increased when soil collected near the parental tree was sterilized, while sterilization of soil collected further away led to a decreased root:shoot ratio. This suggests that the microbial soil community is causing changes in resource allocation in a distance-dependent manner.

The interaction between distance and sterilization found in our study may result in part from nutrient effects. Optimal partitioning theory predicts shifts in root:shoot ratios in order to compensate for the limiting resource (Chapin 1980). Plants generally allocate fewer resources to roots under high soil nutrient conditions, and instead allocate reserves to shoot growth, which lowers the root:shoot ratio. Because sterilization resulted in nutrient release, lower root:shoot ratios would be expected in sterilized soil. This was the relationship found for soil collected farther from parental trees. However, cherry seedlings had higher root:shoot ratios in sterile soil than in unsterile soil collected beneath parental trees. Close to cherry trees, root:shoot ratios could be reduced because soil pathogens destroy roots.

Pythium and plant performance

When *Pythium* spp. were isolated from dying seedlings and used to inoculate soil, seedlings exhibited significantly higher mortality than controls (Packer and Clay 2000). Here we found that there was a tendency for survivors to have reduced biomass in inoculated

soil as well, although differences in growth were not statistically significant ($P > 0.10$). Seedling biomass was lowest in the pathogen inoculation treatment, intermediate in the vermiculite treatment, and highest in the Metro-Mix control. The experimental seedlings used in the inoculation experiment were collected from the field, and although their roots were thoroughly rinsed clean of soil, it is likely that some microorganisms were still present. The nutrient-rich vermiculite medium may have provided environmental conditions conducive to the growth of various fungi. These results, together with growth data from the field studies, suggest that *Pythium* infection can reduce total plant biomass of black cherry without killing the plant. Several studies with other plant species have also demonstrated that *Pythium* can reduce root and shoot growth without causing mortality (Hancock 1985, 1991, Smither and Jones 1989, Larkin et al. 1995 and references cited therein).

Pathogens and plant community dynamics

We found that black cherry seedlings beneath conspecific trees were inhibited by disease, while seedlings of other species under cherry were apparently unaffected. This research focused on black cherry, and the survival and growth of other tree species was not monitored. If the pathogens attacking black cherry are not highly specialized, yet they cause differential mortality in the field, then the mechanisms by which other species escape *Pythium* attack are of particular interest. When fungal pathogens exhibit host specificity or have differential effects on host plant growth or survival, they may act to maintain greater species diversity in temperate forests. *Pythium* spp. are typically viewed as generalist pathogens (Hendrix and Campbell 1973, Carlisle and Watkinson 1994). However, differential responses of host species to *Pythium* inoculations have been observed (Neher et al. 1987, 1992). McCarter and Littrell (1970) reported that different host plants varied in their susceptibility to pre- and post-emergence damping off caused by *P. aphanidermatum* and *P. myriotylum*. Mills and Bever et al. (1997) also found that *Pythium* responded to host species identity by greater or lesser population growth.

Burton and Bazzaz (1991) found that *Prunus serotina* seeds had the highest emergence at low temperature and low moisture, although emergence was generally high across a wide range of temperatures if soil moisture was low. These conditions may be advantageous when soil pathogens are present since damping-off fungi thrive in warm, moist soil environments (Augspurger 1990 and references cited therein). While black cherry is often considered to be a relatively shade-intolerant species (Deam 1940, Baker 1949 and Hough 1960, cited in Auclair and Cottam 1971), Canham et al. (1999) found that light level had relatively little effect on black cherry seedling size, growth rate, biomass allocation, or survival. Similarly, Harrington et

al. (1989) found that aboveground growth rates of *P. serotina* were unaffected by light availability. However, they suggested that there was proportionally greater carbon allocation to belowground biomass in the open site relative to an understory environment. This could occur if soil pathogens in the understory environment were limiting development of belowground biomass. These findings, and our results, are consistent with the hypothesis that shade intolerance of black cherry is an indirect effect of greater pathogen attack under shaded conditions in moist, organic forest soils. Black cherry may thrive in early successional communities not because it requires high light, but because high light and low soil moisture inhibit damping-off fungi.

In the absence of soil pathogens, aggregated spatial distributions of adult black cherry trees in forests would be expected since many seeds fall beneath the maternal tree and under bird perches. Closely spaced adults are readily observed along fencerows and in early successional communities (A. Packer and K. Clay, *personal observation*). The occurrence of similarly aged adult cohorts with no recruitment has been documented in another Indiana woodland (B. Smith, *personal communication*). Similarly, Bonkoungou et al. (1983) reported that black cherry trees in a New York forest community were all ~50 yr old. Auclair and Cottam (1971) also found that 58% of 854 cherry cores indicated establishment between 1931 and 1941 in a Wisconsin forest, and suggested that this was due to an intense disturbance followed by episodic establishment without further recruitment. Hough and Forbes (1943) reported high black cherry seedling mortality except in forest openings. They reported that seedlings in moderate shade were capable of persisting "indefinitely" with little growth, and stated that it was not uncommon for black cherry juveniles ≤ 1 cm to be 20 yr old. In full sun, however, cherry seedlings can outgrow most co-occurring species (Hough and Forbes 1943, Husch 1954). Based on our results and these findings from other studies, we would predict that aggregations of adult black cherry trees in mature forests should be evenly aged, and that successful recruitment is possible only at some distance from these adult trees.

Conclusions

Pathogens that accumulate in the soil surrounding black cherry trees can influence the population dynamics and spatial distribution of black cherry seedlings. Negative interactions between plants and their associated soil biota may therefore have important implications for species coexistence and succession in temperate forests. In the short term, dispersal of black cherry fruits may provide an effective means for seedlings to escape natural enemies of their parents. However, the chance that seeds will be dispersed to a "safe site" (Harper 1977) decreases as black cherry becomes more common within the community. Within a mature community, these negative feedbacks may promote species

coexistence, as proposed for forests in which beech and maple trees tend to show reciprocal replacement (Fox 1977, Woods 1979, 1984). Our results suggest that plant modification of their microbial soil community affects offspring fitness through both survival and growth, and is an important determinant of temperate forest structure and dynamics.

ACKNOWLEDGMENTS

This research represents a portion of the dissertation submitted to Indiana University by A. Packer. We thank J. Bever, D. Parkhurst, J. C. Randolph, P. Schultz, M. Watson, and two anonymous reviewers for many helpful suggestions that greatly improved this manuscript. We thank the City of Bloomington, Dept. of Parks and Recreation for permission to conduct research at Lake Griffy Nature Preserve, Karen Rane, and André Lévesque for help with *Pythium* identification, as well as many undergraduate assistants who helped with fieldwork. This research was supported in part by the Bayerd Franklin Floyd Memorial Fellowship, the Indiana Academy of Sciences, and NSF DEB-0090056.

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