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Effects of Distance to Juniperus virginiana on the Establishment of Fraxinus and Acer Seedlings in Old Fields

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ABSTRACT.—It has been hypothesized that *Juniperus virginiana* facilitates tree seedling establishment in secondary succession. To test this hypothesis, we sampled four old fields in southwestern Ohio and monitored experimentally planted seeds and seedlings of *Acer saccharum* and *Fraxinus americana* for two years. Seeds and seedlings were placed into herbivore exclosures placed 0.3 and 3.0 m from *J. virginiana* trees in an old field in Ohio. We found a significant positive spatial association between *Juniperus virginiana* and tree seedling densities in all four old fields. Soil temperature, soil moisture, evaporative demand and light level in the 0.3 m treatment were significantly reduced, whereas litter depth was increased. Germination of *A. saccharum*, but not *F. americana*, was reduced in the 0.3 m treatment, whereas seedling survival was unaffected in either species. Growth of *F. americana* seedlings was reduced by proximity to *J. virginiana* but *A. saccharum* growth was not affected. Stomatal conductance was reduced in the 0.3 m treatment for *F. americana* but unaffected in *A. saccharum*. Although there was a positive spatial association between *J. virginiana* and tree seedlings in the old fields sampled, experimental seedlings did not exhibit an early demographic response that indicated facilitation.

INTRODUCTION

The successful establishment of seedlings is an important element in the colonization of old fields by woody species. As most mortality of seedlings occurs within one year of germination (De Steven, 1991; Gill and Marks, 1991), factors affecting establishment are of extreme importance. Such diverse factors as moisture, light (Burton and Bazzaz, 1991), temperature (Burton and Bazzaz, 1991), soil resources (Kelly and Canham, 1992), predation (De Steven, 1991; Gill and Marks, 1991; Myster and Pickett, 1993), competition (Kolb *et al.*, 1990) and allelopathy (Fisher *et al.*, 1978) may limit the colonization of old fields by trees.

Seedling establishment may be affected by proximity to established trees. Shrubs and trees have dramatic effects on local microhabitat through soil improvement (Joffre and Rambal, 1993), soil temperature reduction and hydraulic lift (Dawson, 1993). At the same time, woody plants in many communities enhance establishment of other woody species, often through effects on microclimate (Petranka and McPherson, 1979; Callaway, 1992; De Pietri, 1992; Padien and Lajtha, 1992). These are often referred to as nurse plant associations. The increases in establishment associated with these woody species are examples of the facilitation mechanism of succession (Connell and Slatyer, 1977), where earlier successional species improve conditions for later successional species.

Within old fields, *Juniperus virginiana* (L.) may alter microhabitat conditions, affecting the establishment of tree seedlings. *Juniperus virginiana* is a bird-dispersed coniferous tree which characteristically invades old fields in eastern North America (Bard, 1952) and is well adapted to the high light and low soil moisture conditions of early successional habitats (Ormsbee *et al.*, 1976). *Juniperus virginiana* may enhance tree establishment through ame-

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lioration of microclimate (Bard, 1952; Yarranton and Morrison, 1974; Joy and Young, 1996), soil improvement (Yarranton and Morrison, 1974; Joy and Young, 1996), and protection from herbivores in pastures (Whitford and Whitford, 1988). The purpose of this study is to determine if a spatial association exists between *J. virginiana* and tree seedlings and to experimentally test the effects of *J. virginiana* on tree seedling establishment in old fields.

We hypothesized that the presence of *Juniperus virginiana* increases the establishment and/or growth of tree seedlings in old fields. To determine the effects of *J. virginiana* on seedling establishment, an experiment incorporating microenvironmental, demographic and physiological measurements was conducted using seeds and seedlings of *F. americana* and *A. saccharum* planted under and outside *Juniperus virginiana* canopies.

MATERIALS AND METHODS

Study species.—*Acer saccharum* Marsh. and *Fraxinus americana* L. are common deciduous tree species with wind-dispersed seeds. Physiologically, the species are very dissimilar. Photosynthetic response curves show that *A. saccharum* becomes saturated at very low light levels, while *F. americana* can exploit much higher levels of light and has a higher growth rate than *A. saccharum* (Bazzaz and Carlson, 1982). *Fraxinus americana* has stomata which open in the early morning when water stress is lowest (Tobiessen, 1982). When subjected to drought, carboxylation efficiencies of *A. saccharum* decline and stomatal reopening is limited (Davies and Kozlowski, 1977; Ni and Pallardy, 1992). These physiological traits may prevent *A. saccharum* from establishing on drier sites.

Documentation of spatial pattern.—To determine if there is a spatial association between *Juniperus virginiana* and tree seedling density, sampling was conducted in four old fields dominated by *J. virginiana* near Oxford, Ohio in June 1993. All of the sites were previously cultivated fields or pastures and ranged in age from 25–35 years since abandonment. Within each old field we sampled 8–11 *Juniperus virginiana* trees ≥2 m in height, ≥3 m from other large trees. Circular plots with 2 m radii were centered at each *J. virginiana* tree. For each woody seedling ≥10 cm in height we recorded distance and direction from the *J. virginiana* tree. *Juniperus virginiana* seedlings were not included in the survey. Because of the high density of seedlings in site #1, only those ≥20 cm in height were recorded. Data were divided into two subsamples, 0–1 and 1–2 m from the focal tree, and densities were calculated for each. Density of tree seedlings was analyzed by ANOVA (Proc GLM, SAS Institute Inc., 1989) and was log-transformed to conform to assumptions of normality.

Experimental study.—The experimental work was carried out in site 4 of the spatial pattern analysis. This field (~1.0 ha) was the dry top of a large hill and was level over the majority of the area. The site was abandoned in the late 1960s following row crop agriculture. The herbaceous vegetation of the site was dominated by *Schizachyrium scoparium* with patches of *Solidago* spp. and *Aster* spp. The woody vegetation of the site was dominated by *Juniperus virginiana* with *Cornus racemosa, Fraxinus americana, Lonicera maackii,* and scattered small individuals of several other species (including *Acer saccharum*).

Fruits of *A. saccharum* and *F. americana* were collected in October 1992 from the campus of Miami University, Oxford, Ohio and stratified according to their specific requirements (Young and Young, 1992). Seeds of *A. saccharum* were placed in moist *Sphagnum* moss and cold-stratified at 5 C for 90 days. *Fraxinus americana* seeds were warm-stratified for 30 days at 25 C then cold-stratified at 5 C for 60 days. Empty or insect damaged fruits were discarded before stratification.

The planting experiment was structured as a 4 × 2 factorial design, with direction (north, south, east and west), and distance from focal *J. virginiana* trees (0.3 and 3.0 m) as treatments. This design was replicated for both seeds and greenhouse-germinated seedlings of

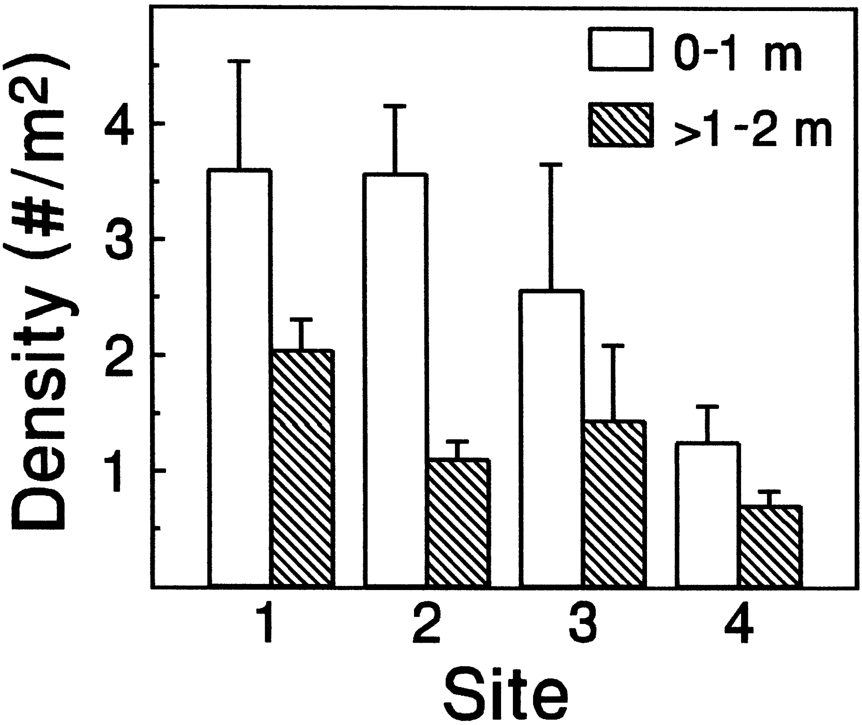

FIG. 1.—Mean density of woody seedlings at distances of 0–1 and >1–2 m from *Juniperus virginiana* trees for four sites in southwestern Ohio. Bars represent mean values ±1 SE

A. saccharum and *F. americana.* The plantings were centered at 25 *J. virginiana* trees ≥2 m in height and ≥5 m from other *J. virginiana.* The mean height of the experimental *J. virginiana* was 3.1 m with branches extending an average of 0.55 m, placing the 0.3 m plots directly under the canopy of the cedar and the 3.0 m plots outside the canopy.

At each of the experimental trees, one seed and one seedling of each species were planted for each direction × distance combination. Seeds were pressed into the soil surface beneath leaf litter and seedlings were installed with a planting bar. Total sample size was 200 seeds and 176 seedlings of *F. americana* and 176 seeds and 200 seedlings of *A. saccharum.* Because of fungal attack on the *A. saccharum* fruits and low germination of *F. americana* in the

TABLE 1.—ANOVA of density of tree seedlings located at two distances (0–1 and >1–2 m) from focal *Juniperus virginiana* trees across four sites in southwestern Ohio. Data were log-transformed before analysis

Source	df	MS	F	P
Site	3	1.42	5.30	0.0024
Distance	1	2.68	10.02	0.0023
Site*Distance	3	0.22	0.85	0.4740
Error	68	0.27		

TABLE 2.—Effects of distance from *Juniperus virginiana* trees on the microhabitat of tree seedlings. Results are reported as mean ± 1 SE. Environmental variables are reported from July, except for throughfall, which was measured in August. Bonferroni-adjusted significance criteria for multiple comparisons is P = 0.004, for an overall α = 0.05. * = significant; NS = nonsignificant

	Distance treatment		
	0.3 m	3.0 m	t-test
Environmental variables			
Soil temperature (C)	26.34 ± 0.26	31.47 ± 0.29	*
Throughfall (mm)	0.99 ± 0.13	3.60 ± 0.22	*
Soil moisture (%)	44.4 ± 4.2	69.2 ± 4.0	*
Evaporative demand (g H_2O lost)	0.54 ± 0.02	0.84 ± 0.03	*
Quantum flux (μmol/m^2·s)	90 ± 10	263 ± 26	*
Soil variables			
Litter depth (cm)	7.40 ± 0.20	5.74 ± 0.33	*
Organic matter (%)	3.0 ± 0.2	2.5 ± 0.1	NS
pH	5.6 ± 0.1	5.6 ± 0.1	NS
Phosphorus (g/m^2)	0.5 ± 0.2	0.3 ± 0.1	NS
Potassium (g/m^2)	27.1 ± 1.5	26.5 ± 1.5	NS
Calcium (g/m^2)	268.5 ± 24.1	253.4 ± 22.2	NS
Magnesium (g/m^2)	74.3 ± 7.0	73.4 ± 6.9	NS

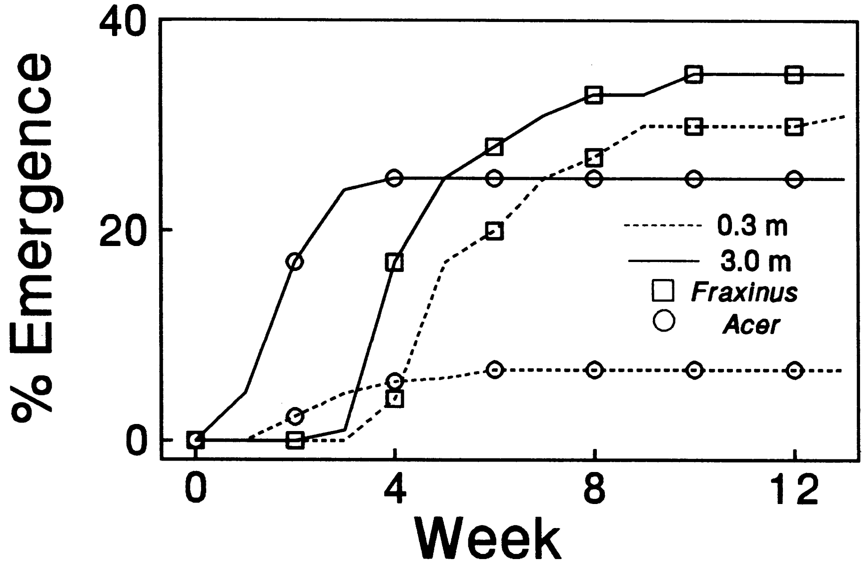

FIG. 2.—Cumulative emergence of *Fraxinus americana* (boxes) and *Acer saccharum* (circles) seedlings planted April 1993. Data represent two distance treatments, 0.3 m (dashed lines) and 3.0 m (solid lines) from focal *Juniperus virginiana* trees. Week 0 = April 10, 1993

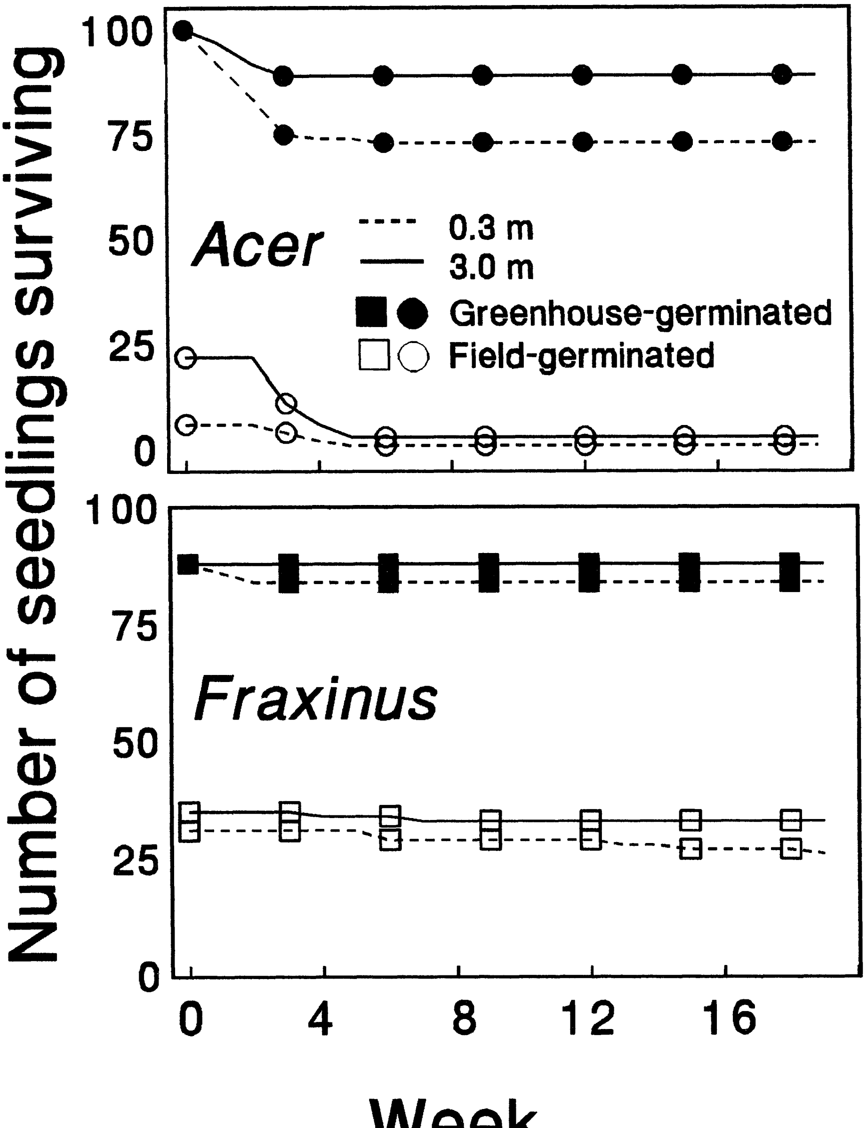

FIG. 3.—Survival curves for field-germinated (open symbols) and greenhouse-germinated (closed symbols) seedlings of *Acer saccharum* and *Fraxinus americana* from May 1993 to August 1993. Data represent two distance treatments, 0.3 m and 3.0 m from focal *Juniperus virginiana* trees

greenhouse, only 176 of these (complete plantings at 22 focal trees) could be used in the experiment. Hardware cloth exclosures 30 cm tall and 25 cm in diameter were placed around all seeds and seedlings to prevent predation by mammals. As the lower portions of *J. virginiana* trees are frequently browsed in the experimental area (pers. observ.), they would offer little protection to seedlings from deer, and would provide no protection from

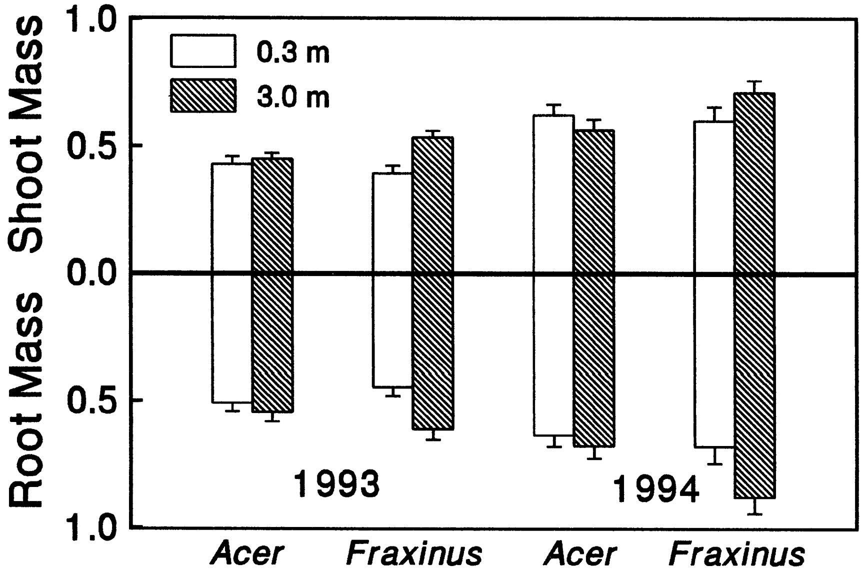

FIG. 4.—Root and shoot growth of greenhouse-germinated *Acer saccharum* and *Fraxinus americana* seedlings in the two distance treatments for harvests at the end of the 1993 and 1994 growing seasons. Treatments are 0.3 m (open bars) and 3.0 m (hatched bars). Bars represent mean values ±1 SE

small mammals. The lack of *Juniperus virginiana* cover close to the ground would allow herbivores equal access to all seedlings in the site, regardless of proximity to *J. virginiana*. For this reason, spatial patterns were not thought to be determined by mammalian herbivory and so it was excluded to preserve sample size.

Stratified seeds and seedlings were planted 10 April and 14 May 1993, respectively. The seedlings were from fruits planted in the greenhouse six weeks earlier for *F. americana* and four weeks earlier for *A. saccharum* and were 10–15 cm tall. Seeds and seedlings were monitored weekly through June and biweekly through September for emergence (seeds) and survival (both cohorts). Count data of emergence and survival were compared using Fisher's Exact test (Proc FREQ, SAS Institute Inc., 1989).

Half of the seedlings (12 of 25 arrays) were excavated at the end of the first growing season (22–24 September 1993). These seedlings were washed, divided into root and shoot portions, and dried. The remaining seedlings were left to overwinter in the field and were harvested at the end of the second growing season (17–18 August 1994). Growth and root: shoot ratio data for each species were analyzed with ANOVA (Proc GLM, SAS Institute Inc., 1989). Data were log-transformed when necessary to meet normality assumptions of ANOVA.

Environmental measurements.—Measurements of the microhabitat within the experimental exclosures were taken monthly throughout the 1993 growing season. All distance and direction combinations were sampled except for soil moisture and throughfall, which were measured at only one direction. Quantum flux, evaporative demand and soil temperature were measured on clear, sunny days between 12:00 and 4:00 PM. Relative soil moisture was measured with gypsum resistance blocks buried at a depth of 10 cm, 0.3 and 3.0 m from experimental *Juniperus virginiana* trees. Quantum flux at the position of the tree seedlings was measured with a quantum sensor (Li-Cor Inc., Lincoln, Nebraska). Evaporative demand

TABLE 3.—ANOVA of the effects of *Juniperus virginiana* on the growth of greenhouse-germinated *Acer saccharum* and *Fraxinus americana* seedlings harvested in 1993 and 1994. Significant terms are indicated in boldface

	Source	df	MS	F	P
1993					
Acer saccharum	Tree	11	0.1120	0.82	0.6209
	Distance	1	0.0905	0.66	0.4192
	Direction	3	0.3306	2.42	0.0754
	Direction*Distance	3	0.0574	0.42	0.7392
	Error	58	0.1367		
Fraxinus americana	Tree	10	0.1702	0.99	0.4606
	Distance	1	2.0239	11.77	**0.0010**
	Direction	3	0.2044	1.19	0.3204
	Direction*Distance	3	0.1972	1.15	0.3362
	Error	69	0.1719		
1994					
Acer saccharum	Tree	12	0.4750	1.92	**0.0486**
	Distance	1	0.0103	0.04	0.8385
	Direction	3	0.1196	0.48	0.6942
	Direction*Distance	3	0.3975	1.61	0.1961
	Error	61	0.2468		
Fraxinus americana	Tree	10	0.0425	1.08	0.3910
	Distance	1	0.2768	7.04	**0.0101**
	Direction	3	0.0272	0.69	0.5600
	Direction*Distance	3	0.1087	2.77	**0.0493**
	Error	62	0.0393		

was estimated by the loss of water from polyester sponges placed at the soil surface for 2–4 h (Meiners, 1994). Soil temperature was measured using soil thermometers at a depth of 2 cm. Throughfall data were collected in late summer (25 August–14 September) with rain gauges 30 mm in diameter placed 5 cm above the soil surface. Soil cores 10 cm deep were taken from each focal tree at distances of 0.3 and 3.0 m in one randomly determined direction. Soil samples were sent to Ohio State University's Research Extension Analytical Laboratory for analysis. The following tests were done on each sample: organic matter (Walkley-Black method), pH (pH electrode), P (ascorbic acid method), K, Ca, and Mg (by atomic absorption). For brevity, environmental data are presented for July only (except throughfall for 25 August) and analyses are restricted to comparisons between distance treatments. Results were qualitatively similar in other months with similar statistical results.

Physiological measurements.—Leaf temperature and stomatal conductance were measured with a Li-Cor steady-state porometer (LI1600c, Li-Cor Inc., Lincoln, Nebraska). Measurements on the surviving seedlings of 3–6 focal *J. virginiana* trees were taken monthly from 12:00–3:00 PM (EST) on clear sunny days. Data are presented for the July sampling only, which were qualitatively similar to other months.

RESULTS

Spatial pattern of seedlings.—A total of 840 seedlings were sampled at the four sites. The majority of seedlings recorded were of wind-dispersed species (66%), of which *Fraxinus*

TABLE 4.—ANOVA of the effects of *Juniperus virginiana* on the root:shoot ratios of greenhouse-germinated *Acer saccharum* and *Fraxinus americana* seedlings harvested in 1993 and 1994. Significant terms are indicated in boldface

	Source	df	MS	F	P
1993					
Acer saccharum	Tree	11	0.1764	1.32	0.2348
	Distance	1	0.0448	0.34	0.5644
	Direction	3	0.0586	0.44	0.7252
	Direction*Distance	3	0.1789	1.34	0.2693
	Error	58	0.1332		
Fraxinus americana	Tree	10	0.1695	1.97	0.0507
	Distance	1	0.0052	0.06	0.8076
	Direction	3	0.0472	0.55	0.6514
	Direction*Distance	3	0.0318	0.37	0.7755
	Error	69	0.0862		
1994					
Acer saccharum	Tree	12	0.0663	0.51	0.9011
	Distance	1	0.5615	4.31	**0.0421**
	Direction	3	0.0542	0.42	0.7422
	Direction*Distance	3	0.0234	0.18	0.9097
	Error	61	0.1302		
Fraxinus americana	Tree	10	0.1184	1.47	0.1740
	Distance	1	0.1943	2.40	0.1260
	Direction	3	0.0739	0.91	0.4390
	Direction*Distance	3	0.2652	3.28	**0.0266**
	Error	62	0.0808		

americana was the most common. Woody seedling density decreased with distance from the focal *J. virginiana* trees in all four old fields (Fig. 1). Analysis of variance shows a significant effect of both site and distance from focal tree (ANOVA overall $R^2 = 0.29$; Table 1) with an insignificant interaction term.

Seedling microhabitat.—The microhabitat was significantly altered near focal *J. virginiana* trees for all environmental factors measured (Table 2). Seedlings in the 0.3 m treatment were exposed to reductions in temperature, relative soil moisture, throughfall, evaporative demand and light level but had a greater litter depth. Soil nutrient levels did not differ between distance treatments.

Seedling performance.—*Fraxinus americana* emergence did not differ between distance treatments with 31% and 35% germinating in the 0.3 and 3.0 m treatments, respectively (Fisher's exact test, $P = 0.652$, Fig. 2). Emergence in *A. saccharum* was significantly reduced ($P = 0.002$) from 25% at 3.0 m to 7% at 0.3 m. Of the emerged seedlings, 86% of *A. saccharum* and 11% of *F. americana* died during the first growing season (Fig. 3). No differences in survival were found between distance treatments, though sample size was too small in *A. saccharum* for statistical testing.

Survival of greenhouse-germinated *F. americana* seedlings over the first growing season was not significantly affected by distance (Fisher's exact test, $P = 0.121$) with mortality below 5% at both distances (Fig. 3). For greenhouse-germinated *A. saccharum*, first year mortality was significantly higher ($P = 0.006$) at 0.3 m (27.0%) than at 3.0 m (11.0%; Fig. 3). Most

TABLE 5.—Effects of distance and direction from *Juniperus virginiana* trees on physiological characteristics of greenhouse-germinated *Acer saccharum* and *Fraxinus americana* tree seedlings. Significant terms are indicated in boldface

	Source	df	MS	F	P
Leaf temperature					
Acer saccharum	Distance	1	8.9192	18.30	**0.0003**
	Direction	3	1.7814	3.65	**0.0273**
	Direction*Distance	3	0.5121	1.05	0.3891
	Error	23	0.4874		
Fraxinus americana	Distance	1	6.0877	6.58	**0.0146**
	Direction	3	0.4824	0.52	0.6702
	Direction*Distance	3	0.7495	0.81	0.4965
	Error	36	0.9249		
Stomatal conductance					
Acer saccharum	Distance	1	37.28	0.02	0.8985
	Direction	3	2620.89	1.17	0.3431
	Direction*Distance	3	2141.59	0.96	0.4305
	Error	23	2241.80		
Fraxinus americana	Distance	1	24,038.05	4.12	**0.0498**
	Direction	3	16,648.77	2.85	0.0506
	Direction*Distance	3	10,373.34	1.78	0.1687
	Error	36	5832.20		

mortality occurred within the first 3 weeks of the experiment. Few seedlings died in the second year of the experiment with no difference between distance treatments.

In both the 1993 and 1994 harvests, growth of greenhouse-germinated *F. americana* seedlings was significantly reduced at 0.3 m (Fig. 4; Table 3). *Acer saccharum* growth was unaffected by distance treatment in both years. Root:shoot ratios did not differ among treatments for either species in 1993 (Table 4). In 1994, *A. saccharum* seedlings had reduced root:shoot ratios at 0.3 m. The distance*direction interaction was significant for *F. americana* in 1994. This interaction resulted from a reduction in root:shoot ratio in seedlings planted at 0.3 m to the north of the focal *J. virginiana* tree.

Seedling physiological responses.—The distance and direction of tree seedlings from *J. virginiana* significantly altered their physiological characteristics (Table 5). The seedlings of both *A. saccharum* and *F. americana* had lower midday leaf temperatures at 0.3 m (Fig. 5). In general, stomatal conductance was reduced at 0.3 m for *F. americana* seedlings, whereas distance had no effect on the stomatal conductance of *A. saccharum* seedlings (Fig. 5).

DISCUSSION

The reduction in seedling emergence in *A. saccharum* at the 0.3 m treatment could result from either the deeper litter or lower soil temperature. Both of these factors could slow emergence, prolonging the period when seedlings would be susceptible to pathogens and invertebrate herbivory within the litter. A similar depression of seedling emergence by a nurse plant was found in *Quercus* seed located beneath shrubs (Callaway, 1992) and was attributed to temperature reduction.

Essentially all mortality of the greenhouse-germinated seedlings occurred within 3 wk of planting. For this reason we attribute the mortality to transplant shock. Greater mortality

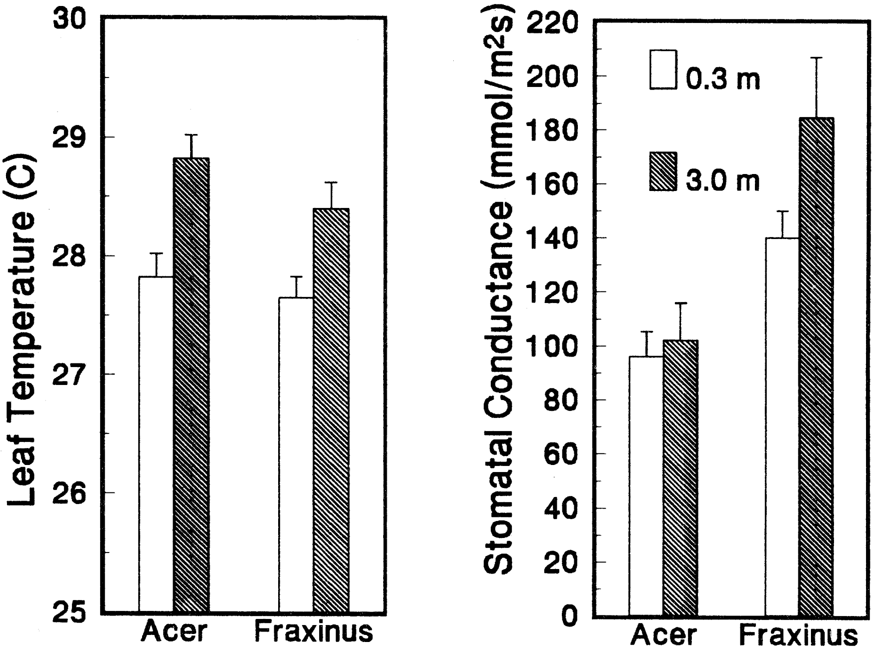

FIG. 5.—Physiological responses of *Acer saccharum* and *Fraxinus americana* seedlings to proximity to *Juniperus virginiana* trees. Treatments are 0.3 m (open bars) and 3.0 m (hatched bars). Bars represent mean values ±1 SE

of *A. saccharum* seedlings closer to the *J. virginiana* resulted probably from difficulties in planting seedlings into the dense root mass of the *J. virginiana.* After 3 wk, proximity to *J. virginiana* had no effect on tree seedling survivorship. For field-germinated *A. saccharum* seedlings, survivorship was very low. Many of these seedlings showed signs of invertebrate herbivory although it was not possible to determine the cause of mortality in most seedlings. This observation is interesting as most studies of tree seedlings do not show significant effects of invertebrate herbivory (but *see* Facelli, 1994).

Biomass of greenhouse-germinated *A. saccharum* seedlings was unaffected by distance. However, *F. americana* seedling biomass was reduced 0.3 m from *J. virginiana.* This difference is most likely the result of the ability of *F. americana* to use higher light levels and withstand drier conditions (Davies and Kozlowski, 1977; Bazzaz and Carlson, 1982). Both species exhibited lower root : shoot ratios closer to *J. virginiana.* For *F. americana* this only occurred to the north, where the environmental effects of *J. virginiana* are greatest (Meiners, 1994). *Fraxinus americana* seedlings consistently showed negative affects of proximity to *J. virginiana* through their reduction in stomatal conductance. This is in contrast to *Acer saccharum,* in which conductance was unaffected by the presence of *J. virginiana.*

Juniperus virginiana was found to 'nucleate' succession in sand dunes (Yarranton and Morrison, 1974) through soil improvement. In contrast, we found no differences in soil nutrient levels under *J. virginiana* canopies. Microclimate amelioration was also proposed as a contributing factor by both Yarranton and Morrison (1974) and Bard (1952). In this study, *J. virginiana* altered all microclimate variables measured. However, demographic and growth measurements over the two years of the experiment failed to show a positive response in seedlings closer to *J. virginiana.* It may be that periodic environmental stresses not occurring during the two years of this study would result in a facilitative interaction.

A third mechanism of facilitation is that *J. virginiana* protects seedlings from mammalian herbivory (Whitford and Whitford, 1988). We cannot rule out this possibility because exclosures protected seedlings from mammalian herbivory. The greater density of hardwood seedlings near *J. virginiana* in four old fields (Meiners, 1994) could result from reduced browsing, although the crowns of *J. virginiana* in the study did not extend low enough to exclude deer or other mammals. In Whitford and Whitford (1988) the facilitative interaction was found in a cattle pasture. This site would have extremely high herbivore pressure compared to an old field. Furthermore, deer will browse on *J. virginiana,* allowing them access to seedlings growing beneath them.

The positive spatial association between woody seedling densities and *Juniperus virginiana* trees found in the old fields is highly indicative of a facilitative interaction. The spatial relationship was consistent for both bird- and wind-dispersed species, indicating that the relationship is not dependent on dispersal mode (Meiners, 1994). This spatial pattern shows the potential for *J. virginiana* to enhance tree establishment in old fields. However, this study does not define the mechanism by which this positive spatial association between *Juniperus virginiana* and other species is maintained. The effects of *J. virginiana* on tree seedlings ranges from negative to neutral but not positive. It may be that periodic environmental stresses not occurring during this study would result in a facilitative interaction. Species interactions which affect the establishment of trees at early successional stages have the potential to affect community structure for long periods of time. To understand the dynamics of old field succession, the prevalence and importance of these early inter-species interactions must be determined.

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