The Effects of Black Locust (*Robinia pseudoacacia* L.) on Species Diversity and Composition of Black Oak Savanna/ Woodland Communities

Robert L. Peloquin
Department of Biological Sciences
Purdue University Calumet
Hammond, IN 46323 USA

Ronald D. Hiebert
Midwest Regional Office
National Park Service
1709 Jackson Street, Omaha, NE 68102
USA

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ABSTRACT: Black locust (*Robinia pseudoacaciat* L.), a nitrogen-fixing tree species introduced to northern Indiana, is invading disturbed and native communities of the Indiana Dunes. This study investigated three *Quercus velutina* (black oak) savanna and woodland dune communities to determine the effects of black locust on species diversity and composition. Data revealed that the mean plot basal area and density of black locust were highest in plots containing older black locusts and decreased in outlying plots where the saplings often occurred in ramets. The lowest densities of black locust saplings existed under the oldest trees. At all sites the herbaceous species diversity was lowest in the older black locust stands and higher in the younger stands. Downy brome grass (*Bromus tectorum* L.), a nonindigenous grass species, was dominant under older black locust trees and decreased in mean cover toward the younger stands. In a black oak savanna, soils of the oldest black locust trees had higher concentrations of nitrate (3.3 ± SE 0.3 ppm) and ammonium (4.2 ± SE 0.7 ppm) than the control soils (nitrate 1.4 ± SE 0.1 ppm, ammonium 2.8 ± SE 0.25 ppm). The results suggest that (1) black locust tree shade significantly reduced the natural diversity of herbaceous species at these sites, and (2) increased soil nitrogen produced by black locust facilitates dominance by the nitrogen-responsive downy brome. Implications for management are discussed.

Index terms: black locust, dune communities, invading species, soil nitrogen, species diversity

INTRODUCTION

Invasions by plant species have severely impacted the structure and function of natural ecosystems worldwide by altering nutrient availability, causing species displacement or extinction, forming single-species stands, and changing the pattern and trajectory of ecological succession (Vitousek and Walker 1989, Cronk and Fuller 1995, Ruesink et al. 1995). Six hundred fifty three of these invasive plant species are woody (Binggeli 1996); 235 are invasive woody species in North America, and only 3% of these are listed as native to North America (Reichard 1994). *Populus* spp. and *Salix* spp. are examples of native, invasive woody species that have dominated a variety of landscape types following human disturbance in the United States (Palik and Pregitzer 1992, Johnson 1994, Choi and Wali 1995, Lapin and Barnes 1995). *Robinia pseudoacacia* L. (black locust), which is also endemic to the United States, is regarded as one of the world's most invasive woody species (Rejmanek and Richardson 1996) and is the subject of this study.

Black locust is classified as a shade-intolerant, early successional, nitrogen-fixing leguminous tree species, which, while capable of reproducing from seed, more commonly reproduces from root suckers under natural conditions (Fowells 1965, Burns and Honkala 1990, Mebrahtu and Hanover 1991). The eastern distribution of the black locust species section is centered on the Appalachian Mountains from central Pennsylvania to northern Alabama and Georgia; the western distribution includes the Ozark Plateau and the Ouachita Mountains of Missouri through Oklahoma. Outlying populations are naturally found in southern Illinois and southern Indiana. Due to its desirable wood and rapid growth properties, black locust has been planted widely and has become naturalized throughout the United States, southern Canada, and parts of Europe and Asia (Fowells 1965, Keresztesi 1988, Burns and Honkala 1990).

Several studies concluded that nitrogen is in short supply relative to other elements, particularly early in soil development, and that nitrogen fixers should therefore dominate during some stage of primary succession (Vitousek 1982, Walker et al. 1983, Vitousek and Walker 1989). Nitrogen often represents the limiting resource for major terrestrial habitats in early succession (Vitousek 1982, Tilman 1985). The elevation of available soil nitrogen by nitrogen-fixing species may have profound effects on associated species. Tilman (1987) indicated that where nitrogen limited primary production, added nitrogen (by fertilizer application) led to the dominance of one or a few nitrogen-response plant species as the result of competition between species. Such resource-based competition contributed to a decline of species richness and cover in nitrogen-enriched plots (Tilman 1982, 1987; Wedin and Tilman 1993).

Observations of an anthropogenically disturbed savanna at Miller Woods of Indiana Dunes National Lakeshore (INDU), in which black oak (*Quercus velutina* Lam.) was associated with the black locust, indicated there was a reduction in plant species richness (Peloquin 1989). Elevated soil nitrogen, as well as canopy shade, are primary factors that may explain the observed species reduction.

The objectives of this study were (1) to determine the effects of black locust trees on herbaceous species diversity and composition in anthropogenically disturbed black oak savanna and woodland communities at the Indiana Dunes, and (2) to evaluate the roles of shade and soil nitrogen in producing these vegetation effects.

METHODS

Study Areas and Sampling Procedures

Black locust is one of the most widespread of the nonindigenous plant species invading INDU (Klick et al. 1989, Hiebert 1990), which comprises much of the undeveloped Indiana Dunes along the southern shore of Lake Michigan in northwestern Indiana (Figure 1). We investigated three disturbed dune communities at INDU that contained established populations of black locust, including two Inland Marsh black oak savanna sites ("Inland Marsh East" and "Inland Marsh West," T37N, R7W), which represent the predominant ecosystem type in the western part of INDU, and a "Razed Homesite" (T37N, R6W), located within a more mesic, mixed species woodland. The woodland site is located 8 km east of the Inland Marsh savannas (Figure 1).

Inland Marsh East was severely disturbed by sand mining in the late 1930s. A razed homesite and gravel outcropping occur at the southern perimeter. Planted trees from a nearby homesite to the east appear to have provided the propagules to establish this black locust population. The distribution of large and small diameter trees at the Inland Marsh East site is centric, with increasingly smaller trees occurring at greater distances from the established population center.

The Inland Marsh West site lies at the western edge of the large sand-mined section on a four-sided black oak savanna dune ridge. The largest black locust trees grow on the steep eastern slope that was created by the mining. Four small black locust trees, all barely tree-sized (≥ 2.5 cm at dbh), grow at the periphery of the black locust population within the oak savanna.

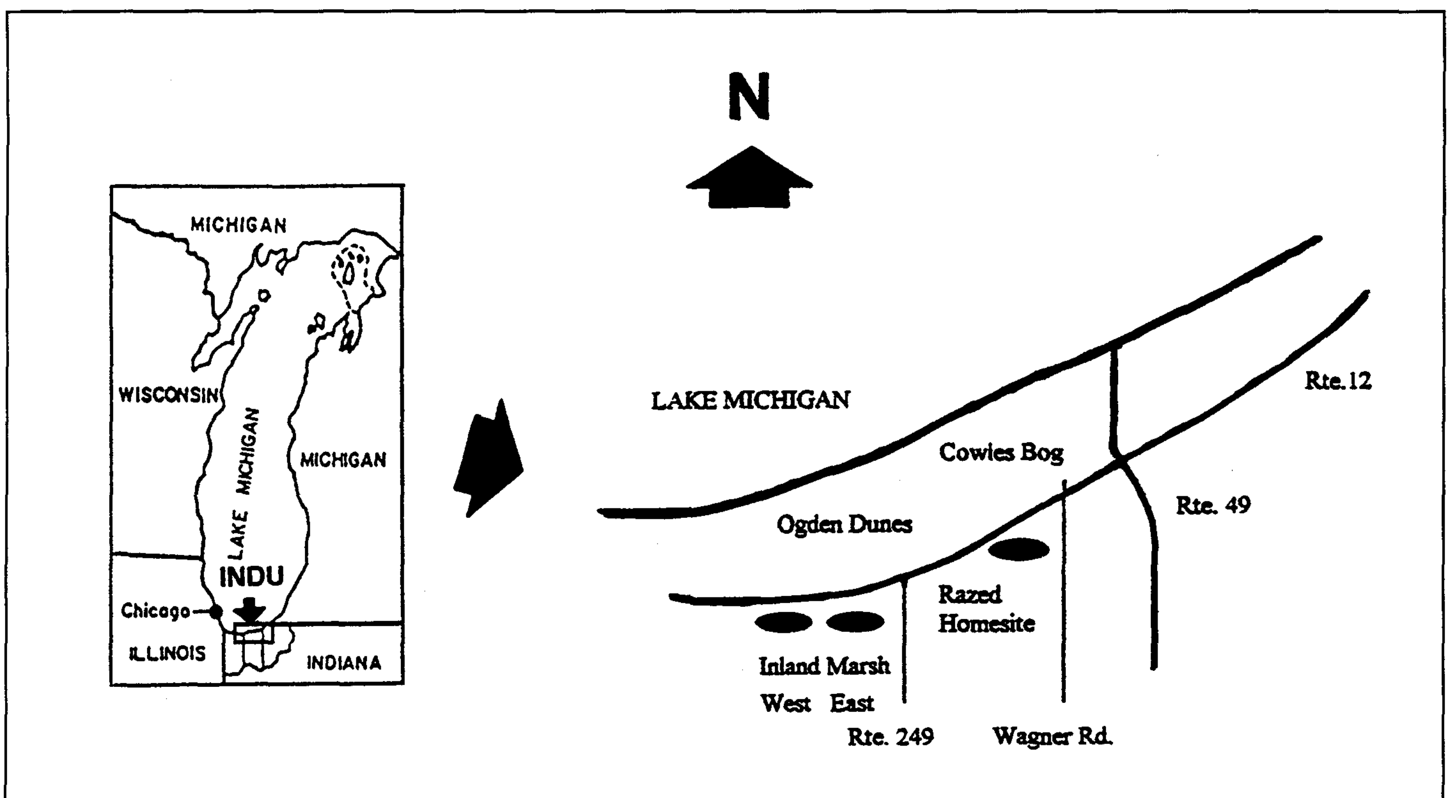

Figure 1. Geographical location of three study sites in the Indiana Dunes National Lakeshore (INDU), a part of the Indiana Dunes.

The federal government razed the house at the Razed Homesite along US Highway 12 (Tract 31,119-121) in 1971. The largest black locust individuals developed from trees that were apparently planted in the yard by former occupants in an irregular pattern. The largest black locust trees tend to be toward the center of the site, with increasingly smaller trees of this species found toward the perimeter.

Stratified random sample plots were established in each site in 1985 to determine (1) the sizes ("ages") of black locust trees in the population: source (largest trees), intermediate (smaller trees), and perimeter (smallest trees); (2) the black locust tree density and basal area of each size category; (3) the density of associated tree and shrub species; and (4) the percent cover of associated herbaceous species in 1985. The number and positioning of transects at each site, as well as the number and location of plots established along each transect, was varied according to the site-specific size distribution pattern and the scale (extensiveness) of each size category of black locust trees. At Inland Marsh East, plots were established at two intermediate distances in order to identify the effects on the associated vegetation of the extensive, increasingly smaller black locust trees (N. Pavlovic, Lake Michigan Ecological Research Station, U.S. Geological Survey, pers. com.). These plot positions are designated as "intermediate 1" (int. 1) and "intermediate 2" (int. 2), respectively, at increasing distances from the source plots.

The number of transects and sample plots (of each position) established at each study site were: Inland Marsh East—four transects (radiating outwards from the largest trees at the center), 4 plots of each size; Inland Marsh West—three transects, 10 plots of each size; and Razed Homesite—five transects, 4 source plots, 5 intermediate plots, and 6 perimeter plots.

One tree, one shrub and sapling, and two herbaceous subplots were established in each sample plot in 1985 using a center-marking stake. Circular tree and shrub subplots were 0.0025 ha and 0.000177 ha, respectively. Two herbaceous subplots, 0.5 m^2 each, were located 2 m north and south of each center stake.

We measured the diameter at breast height (dbh) of each tree $\geq$ 2.5 cm, and took core samples at breast height from all corable trees in 1985. Only black locust stems located 25 cm or closer to the central stem were considered part of the same tree when multiple stems occurred (field observations after a 10-year period confirmed that self-thinning or coalescence of clustered stems eliminated formation of multiple individuals at closer distances). Any black locust or black oak individual with dbh < 2.5 cm was considered a sapling. Similar-sized woody individuals of other species were considered shrubs. Together, these individuals formed the woody understory. In many cases, small black locust trees were clustered and probably existed as ramets, but they were treated as individual saplings.

Herbaceous Species Diversity

The average herbaceous species diversity of each plot position was calculated using the Shannon-Wiener index and the plot cover of each species. The mean total cover of each plot position at a site was used to determine whether a scarcity of individuals contributed to the low mean species diversity of any plot position. The average richness of each plot position was calculated from herbaceous species presence-absence data to clarify the role of richness in determining the herbaceous species diversity of plot positions.

Photosynthetically Active Radiation

Twenty random measurements of photosynthetically active radiation (PAR) were taken in 1996 with a GE Model 214 light meter at each of the following locations: (1) the full black locust canopy of Inland Marsh East and Razed Homesite source plots, (2) the intermittent black locust canopy of the ridge (source) transect at Inland Marsh West, and (3) the intermittent, mixed-species canopies of outlying plots of all sites. All of the 60 readings were taken at 0.15 m, the distance above ground of the hand-held meter's photosensitive plate. These readings were converted to PAR using the conversion factor, 1 klux = 18 μmoles sec^{-1} m^{-2}.

Soil and Litter Sampling and Analysis

Nine random soil and litter sampling locations were established along the ridge (source) transect at Inland Marsh West in 1992. Similarly, nine sampling locations were established in the same soil type along a 100-m control transect, which lacked black locust individuals, and which was located 20 m northwest of the ridge transect. Two random distances were identified 0.5–5.0 m from each stake at random azimuths. One soil sample was collected from the upper 10 cm of soil at each distance. One litter sample was collected at the closer distance only using a can with a 20-cm-diameter imprint. The total of 36 soil and 18 litter samples were refrigerated temporarily prior to analysis.

Five soil parameters that have been widely reported to be influenced by the presence of nitrogen-fixing black locust trees were the subject of this study (Auten 1945, Kerestezi 1988, Peloquin 1989, Montagnini et al. 1991). Analyses were completed by the Purdue Soil Testing Laboratory, Department of Agronomy, Purdue University, West Lafayette, Indiana. Major procedures for each parameter were as follows: (1) percent organic matter: 0.05–0.09 g of soil was treated with potassium dichromate and sulfuric acid (the Whatley-Black procedure); (2) percent ash organic matter: 1 g of soil was analyzed by the Whatley-Black procedure (this variation was used to confirmed the results of the standard Whatley-Black procedure, which had yielded low percentages of organic matter); (3) total percent nitrogen: 150 mg soil was tested by the TKN method, which consisted of Kjeldahl digestion, and the steam distillation of extract with sulfuric acid to produce NH_3; and (4) NH_4 and NO_3 : 10g of soil was extracted with 2N KCL; the NH_4 concentration was determined by the single steam distillation of extract with MgO_2, and by titration with H_3SO_4; the NO_3 concentration was determined by adding Devarde alloy (heavy metal reducing agent) to the extract, steam distilling, and titrating with H_3SO_4 (Page et al. 1982; J. Hertl, Soil Testing Lab, Purdue University, West Lafayette, Indiana, pers. com.).

The following procedures were used in the analysis of the three litter parameters: (1) dry matter: the total weight of the litter sample was taken after drying for four days at 60° C; (2) percent organic matter: 1 g of litter was ashed at 500° C for eight hours, followed by the same procedure as above for soil; and (3) total percent nitrogen: the same extraction procedure described above for soils was used for litter.

Statistical Analyses

Parametric and nonparametric tests were conducted to detect differences among plot positions in the basal area, density, and dbh of tree species; shrub and sapling species density; the cover, diversity, and richness of herbaceous species; and PAR. The level of significance was $P < 0.05$ in all tests. The equality of variances was checked by the F ratio test. When sample variances were approximately equal, and when the data were normally distributed, the one-way F-test (ANOVA) was used with three or more groups (treatments). The means of significant ANOVA were compared using the Tukey test and the Tukey-Kramer procedure. When one or both assumptions did not apply, the Kruskal-Wallis H test was completed. The value of H was corrected when multiple ties occurred. The means of significant H test results were compared using a procedure described by Devore (1982). For equal variances and normally distributed data the Student's *t*-test was used to analyze soil and litter parameters. The Mann-Whitney U test was used with soil and litter data when one of the *t*-test assumptions was not true.

RESULTS

Vegetation

One hundred sixty-six species were located in all of the plots, of which 19 were trees, 13 were shrubs, and 134 were herbs.

Black locust

The mean density of black locust trees declined from the source to the perimeter plots at each study site, but not linearly with respect to the intermediate plots (Figure 2). At Inland Marsh East and the Razed Homesite, source plot tree densities were lower than those of adjacent, intermediate plots due to the larger diameter black locust trees in the source plots. At Inland Marsh East the mean tree density did not differ significantly among the plot positions ($H_3 = 7.517$, $P > 0.05$). The density of source black locust trees at Inland Marsh West was significantly greater than those of the outlying plots ($H_2 = 13.374$, $P < 0.01$). At the Razed Homesite, the black locust density of the intermediate plots was significantly greater than in the perimeter plots; other plot means were similar ($F_{2,14} = 9.533$, $P < 0.01$).

The mean percentage of black locust tree stems was greater than the percentage of other species in each plot position at Inland Marsh East (source—98%, int. 1—100%, int. 2—90%, perim.—55%). In the open perimeter plots, the percentage of cottonwood *(Populus deltoides* Marsh.) tree stems reached 26%. At Inland Marsh West, the percentage of black locust stems consistently declined away from the source plots (source—77%, int.—15%, perim.—7%). In the mixed species woodland at the Razed Homesite, the percentage of stems that were black locust was comparatively low in each plot position (source—49%, int.—55%, perim.—17%).

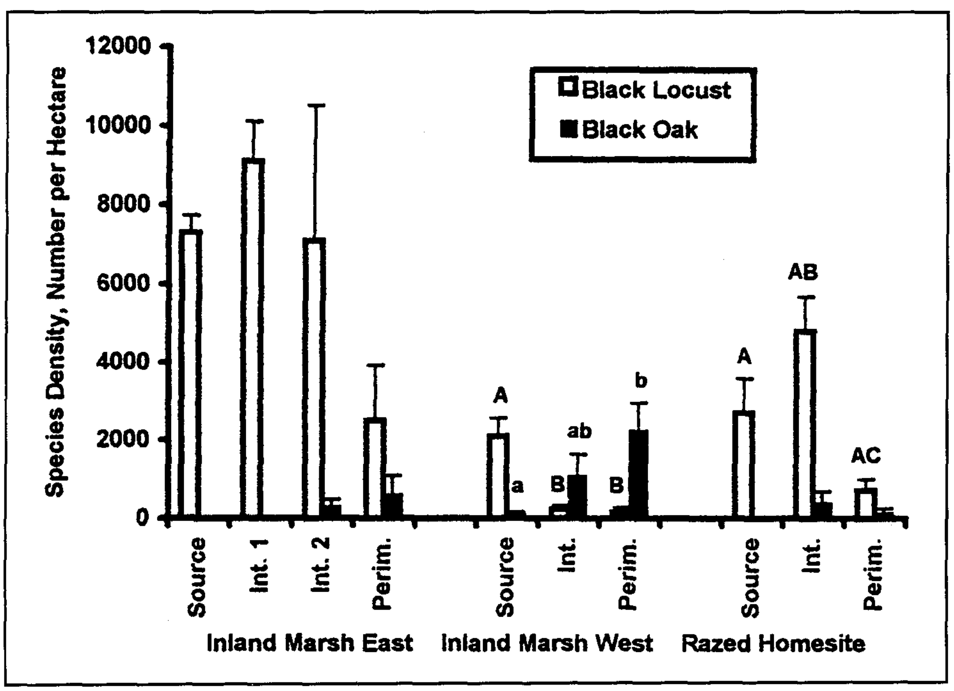

Figure 2. The mean densities (± SE) of black locust and black oak trees. Different letters of each case at a site show significantly different means for black locust based on the Kruskal-Wallis test or ANOVA (Razed Homesite only).

The mean basal areas of black locust trees generally declined from the source to the perimeter plots at all study sites (Table 1). The basal areas of source black locust trees were always significantly greater than those of the perimeter plots; patterns of significant differences for the other plot positions were inconsistent (Inland Marsh East: $H_3 = 12.217$, $P < 0.01$; Inland Marsh West: $H_2 = 16.907$, $P < 0.001$; Razed Homesite: $H_2 = 8.636$, $P < 0.01$).

Ages of corable black locust trees ranged from 1 to 18 years at Inland Marsh East, 2 to 20 years at Inland Marsh West, and 4 to 50 years at the Razed Homesite. Age was highly correlated with dbh ($r^2 = 0.85$, Figure 3). The pattern of decreasing stand basal area from the source plots toward the perimeter plots was due to both the general decline in black locust tree densities (Figure 2) and in stem diameters (Figure 4). The mean dbh of the source trees was significantly greater than those of the two

Table 1. Mean basal areas of principal trees in study plots at Indiana Dunes National Lakeshore. The levels of significance using the Kruskal-Wallis test are indicated by: * = $P < 0.05$, ** = $P < 0.01$. Means with different superscript letters are significant ly different at the 0.05 level using the Devore test. The numbers of sample plots are: Inland Marsh East—4 (all plot positions); Inland Marsh West—8 (Source), 10 (remaining plot positions); and Razed Homesite—4 (Source), 5 (Intermediate), 6 (Perimeter).

Species Study Area	Significance	Plot Position Species Basal Area ± SE (m²/ha) Source	Int. 1	Int. 2	Perimeter
Robinia pseudoacacia					
Inland Marsh East	**	77 ± 12^{A}	36 ± 5^{AB}	7 ± 3^{B}	9 ± 7^{B}
Inland Marsh West	*	17 ± 6^{A}	$< 1^{B}$	—	$< 1^{B}$
Razed Homesite	*	171 ± 47^{A}	48 ± 20^{AC}	—	10 ± 7^{BC}
Quercus velutina					
Inland Marsh East	ns	0	0	7 ± 5	2 ± 2
Inland Marsh West	**	$< 1^{A}$	17 ± 7^{B}	—	22 ± 10^{B}
Razed Homesite	ns	0	5 ± 5	—	< 1
Populus deltoides					
Inland Marsh East	ns	0	0	2 ± 3	21 ± 12
Inland Marsh West	—	0	0	—	0
Razed Homesite	—	0	0	—	0

outermost plot positions at each study site (Inland Marsh East: $H_3 = 10.010$, $P < 0.01$; Inland Marsh West: $H_2 = 16.848$, $P < 0.001$; Razed Homesite: $F_{2,14} = 10.384$, $P < 0.01$). At Inland Marsh East, the mean stem diameters of trees in the intermediate 1 position were not significantly different from those of the other plot positions, but the intermediate 1 trees were 44% smaller than those of the source plots (Figure 4).

The mean densities of sapling black locust generally increased from the source trees to the perimeter, but did not differ significantly among plot positions at any study area (Inland Marsh East: $H_3 = 7.001$, $P > 0.05$; Inland Marsh West: $H_2 = 4.247$, $P > 0.05$; Razed Homesite: $H_2 = 1.827$, $P > 0.05$) (Table 2). At Inland Marsh East, the sapling density increased away from the population center, then declined at the periphery under the shade of large-sized cottonwood trees ($H_3 = 7.580$, $P < 0.05$) (Table 2). Many of the peripheral black locust saplings at each site formed clusters through root suckering. A few isolated individuals occurred that were produced from seed.

Black oak

Black oak trees were scarce or absent in the source plots at all sites (Figure 2). The mean tree density increased toward the perimeter plots at Inland Marsh East ($H_3 = 3.075$, $P > 0.05$) and at Inland Marsh West where the differences were significant ($H_2 = 9.700$, $P < 0.05$). The high densities of the perimeter plots at Inland Marsh West occurred in a natural black oak savanna. In the Razed Homesite mixed species woodland, the tree densities of all positions were equal ($H_2 = 2.105$, $P > 0.05$).

The mean basal areas of black oak trees (Table 1) followed the same patterns as the tree densities (Figure 2), except for Inland Marsh East, where the tree basal area increased in the intermediate 2 plots, then declined toward the perimeter ($H_3 = 4.343$, $P > 0.05$) (Table 1). The basal areas significantly increased toward the black oak savanna (perimeter) at Inland Marsh West ($H_2 = 12.508$, $P < 0.01$). At the Razed Homesite, the basal areas of all the plot positions were equal ($H_2 = 2.504$, $P > 0.05$).

The mean black oak sapling density was significantly greater in the perimeter plots than in the source plots at Inland Marsh West ($H_2 = 8.449$, $P < 0.05$) (Table 2). There was no consistent pattern among plot positions in black oak sapling densities at Inland Marsh East ($H_3 = 2.628$, $P > 0.05$) or at the Razed Homesite ($H_2 = 1.307$, $P > 0.05$).

Pasture rose

Pasture rose (*Rosa carolina* L.) was the only native savanna shrub species found in any abundance under the dense black locust canopy. The pattern of mean densities of pasture rose was inconsistent among sites and the differences were not dramatic (Table 2). Pasture rose density at Inland Marsh West was significantly lower under the source black locust canopy, increased in the intermediate plots, then declined toward the perimeters ($H_2 = 26.559$, $P < 0.001$). At Inland Marsh East, the pattern of change was similar but not significant ($H_3 = 7.745$, $P > 0.05$). The perimeters of these two study sites were shaded by large-diameter black oak trees and large-diameter cottonwood trees (Table 1), respectively. Pasture rose shrubs were absent under the closed canopy of the Razed Homesite source plots ($H_2 = 1.801$, $P > 0.05$), and increased moderately toward the perimeter (Table 2).

Herbaceous species diversity and cover

The average herbaceous species diversity (Shannon-Wiener index) was significantly reduced under the oldest black locust trees at Inland Marsh East ($F_{3,31} = 9.100$, $P < 0.001$) and at Inland Marsh West ($F_{2,59} = 24.684$, $P < 0.001$) (Figure 5). The herbaceous species diversity at the Razed Homesite did not differ among plot positions (Figure 5), but there was a slight increase at the perimeter plots ($F_{2,29} = 0.113$, $P >= 0.05$).

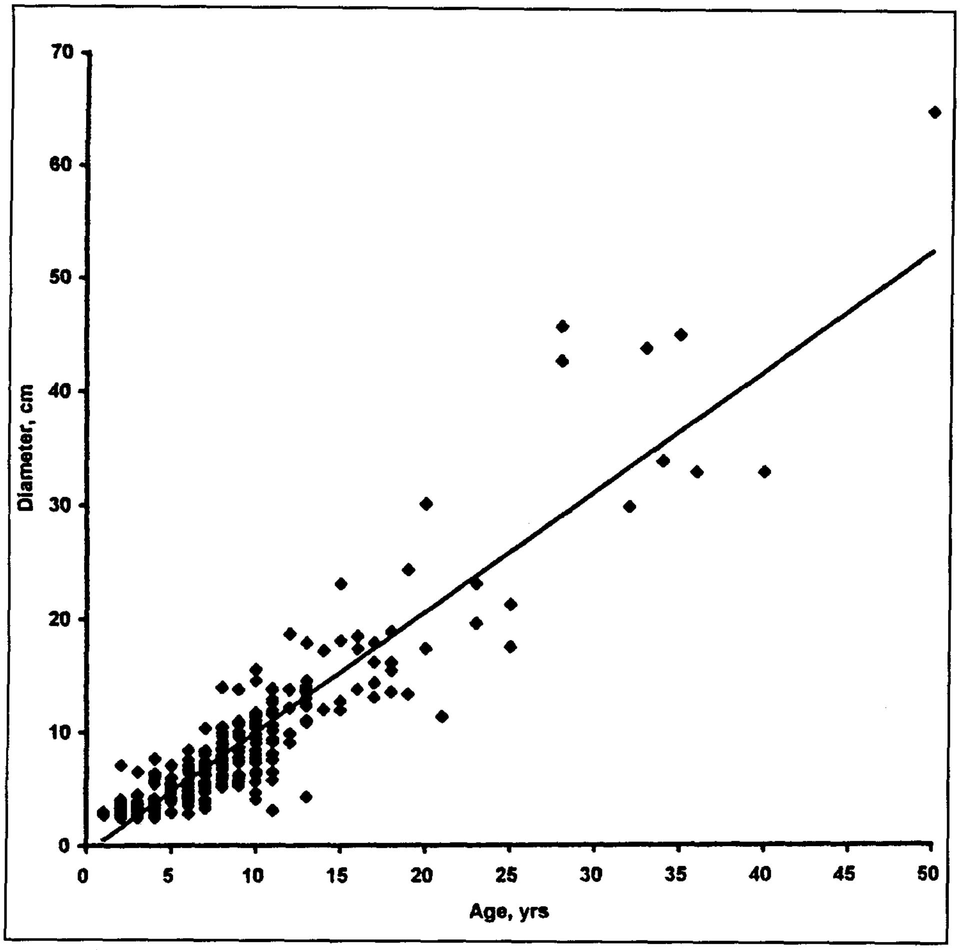

Figure 3. Black locust stem diameter versus age for all corable trees.

The mean percent total cover of herbaceous species differed significantly among plot positions only at Inland Marsh East ($F_{3,31}$ = 3.517, $P < 0.05$) (Table 3). The highest cover values occurred here under the oldest black locust trees, where the lowest species diversity was found (Figure 5). At Inland Marsh West, where the cover values were nearly equal ($F_{2,59}$ = 0.030, $P > 0.05$), the species diversity of the source plots was significantly reduced. At the Razed Homesite the cover values ($F_{2,29}$ = 0.039, $P > 0.05$) and the index values were each nearly equal. These results indicate that the herbaceous species richness was lowest beneath the oldest black locust but cover was not. The average herbaceous species plot richness increased significantly toward the perimeter at Inland Marsh East ($F_{2,31}$ = 6.549, $P < 0.01$) and Inland Marsh West ($F_{2,59}$ = 15.596, $P < 0.001$) (Table 3). There were no differences in plot richness at the Razed Homesite ($F_{2,29}$ = 1.220, $P > 0.05$) (Table 3). The reduction in species diversity in source plots was due, therefore, to fewer species in a plot and not to the same species being spread out thinner in the plot.

The mean percent total cover of downy brome grass (*Bromus tectorum* L.) was highest under the oldest black locust trees at all sites and declined sharply toward the perimeter plots where smaller-diameter black locust trees and saplings predominated (Table 4). At Inland Marsh East the cover of downy brome was significantly greater in the source and intermediate 1 plots than in the outlying plots (H_3 = 30.154, $P < 0.001$). Downy brome was present only in the source plots at Inland Marsh West (H_2 = 29.095, $P < 0.001$). The cover of downy brome at the Razed Homesite did not differ among plot positions ($F_{2,29}$ = 0.967, $P > 0.05$).

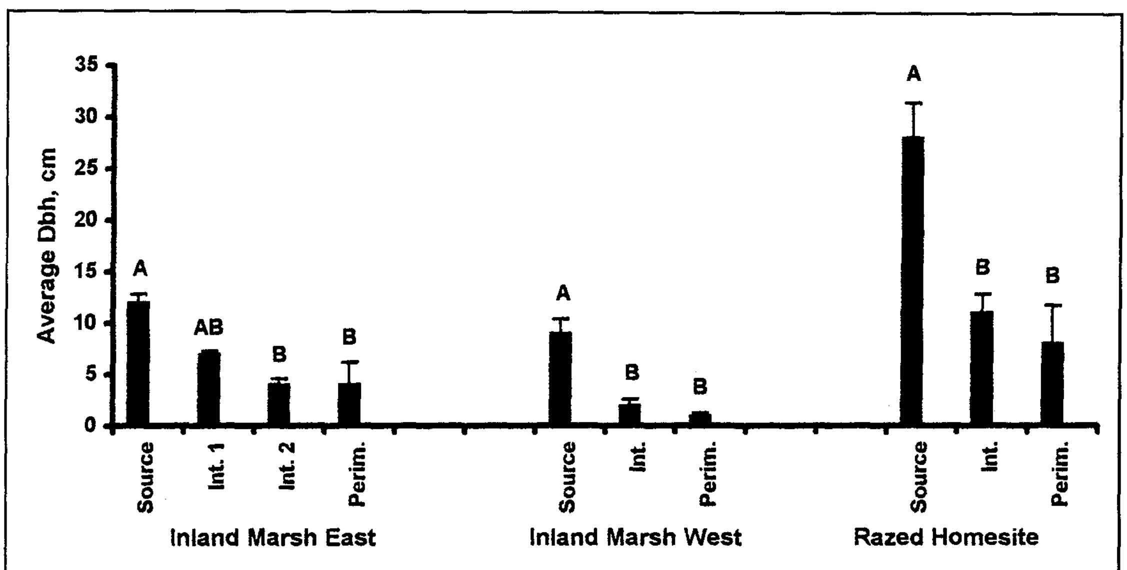

Figure 4. The average diameter breast height (± SE) of black locust trees. Different letters of each case at a site show significantly different means for black locust based on the Krukalis-Wallis test or ANOVA (Razed Homesite only).

Only at Inland Marsh West did additional herbaceous species have a cover total greater than 10% for all plots, a significant difference in cover among plot positions, and a total frequency > 1 at each occupied plot position. The highest mean percent total cover of two species occurred in the Inland Marsh West source plots: Pennsylvania sedge (*Carex pensylvanica* Lam.; $F_{2,59} = 3.831$, $P < 0.05$) and common spiderwort (*Tradescantia ohioensis* Raf.; $H_2 = 10.437$, $P < 0.01$) (Table 5). Three species were absent from the source plots, but had their highest cover values in the intermediate or perimeter plots: wild lupine (*Lupinus perennis* S. Wats.; $H_2 = 8.048$, $P < 0.05$), little bluestem (*Schizachyrium scoparium* [Michx.] Nash-Gould; $H_2 = 15.117$, $P < 0.001$), and goat's rue (*Tephrosia virginiana* [L.] Pers.; $H_2 = 9.504$, $P < 0.01$) (Table 5).

Table 2. Mean densities of common woody understory species in study plots at Indiana Dunes National Lakeshore. Only these species had significant test results for one or more life history stages. The levels of significance using the Kruskal-Wallis test are indicated by: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. Means with different superscript letters are significantly different at the 0.05 level using the Devore test. The numbers of sample plots are: Inland Marsh East—4 (all plot positions); Inland Marsh West—10 (all plot positions); and Razed Homesite—4 (Source), 5 (Intermediate), 6 (Perimeter).

Species Study Area	Significance	Plot Position — Species Basal Area ± SE (m^2/ha) Source	Int. 1	Int. 2	Perimeter
Robinia pseudoacacia					
Inland Marsh East	ns	0	0	16 ± 10	7 ± 5
Inland Marsh West	ns	< 1	8 ± 5	—	9 ± 4
Razed Homesite	ns	3 ± 2	12 ± 12	—	21 ± 13
Quercus velutina					
Inland Marsh East	ns	6 ± 4	1 ± 1	1 ± 1	6 ± 4
Inland Marsh West	*	$< 1^{A}$	7 ± 5^{AB}	—	23 ± 8^{B}
Razed Homesite	ns	3 ± 3	14 ± 8	—	5 ± 2
Rosa corolina					
Inland Marsh East	ns	35 ± 25	430 ± 98	173 ± 113	45 ± 41
Inland Marsh West	***	17 ± 6^{A}	220 ± 67^{B}	—	104 ± 22^{AB}
Razed Homesite	ns	0	15 ± 9	—	26 ± 20

Photosynthetically Active Radiation

The mean PAR measurements taken beneath the closed black locust source canopies at Inland Marsh East and the Razed Homesite ($87 \pm$ SE 20^{A} mmoles sec^{-1} m^{-2}) were significantly lower than those of the outlying plots ($319 \pm$ SE 68^{B} mmoles sec^{-1} m^{-2}, $H_2 = 15.990$, $P < 0.01$, n = 20). (Different superscript letters among plot locations indicate significantly different means based on ANOVA.) The PAR values under the intermittent canopy of the Inland Marsh West source plots were intermediate ($239 \pm$ SE 44^{B} mmoles sec^{-1} m^{-2}).

Soil and Litter Analysis

The Inland Marsh West control soil mean percent organic matter ($U_{18,18} = 30.5$, $P < 0.01$), percent ash organic matter ($U_{18,18} = 81$, $P < 0.01$), and percent total nitrogen ($t_{34} = 7.376$, $P < 0.01$) were significantly greater than the corresponding values in the source black locust soil samples (Table 6). The black locust soil nitrate level (t_{34} =

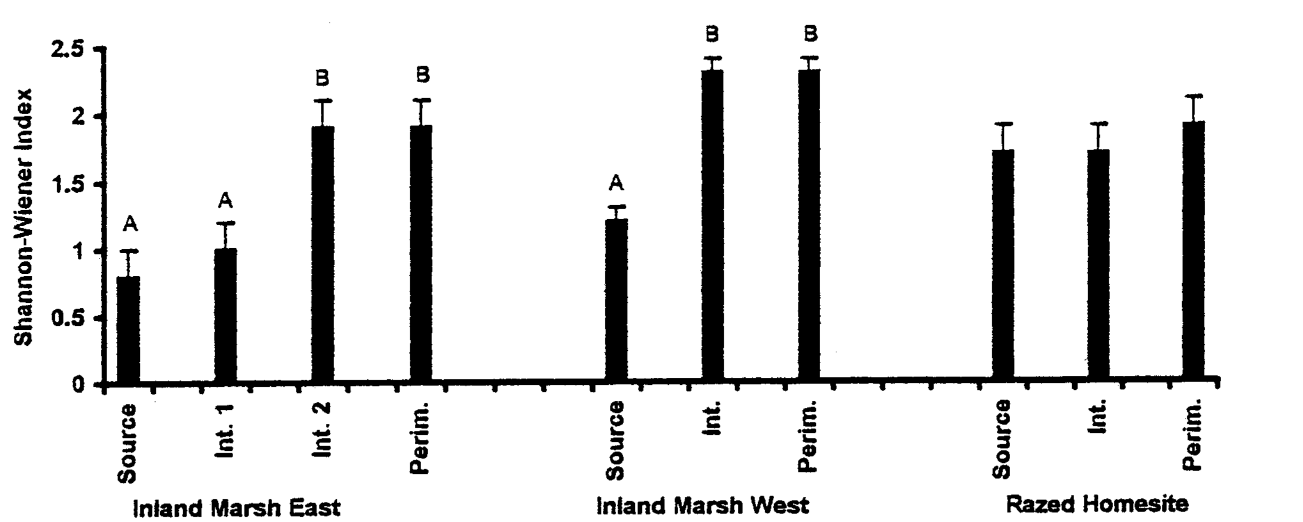

Figure 5. Shannon-Wiener diversity index values (± SE). Different letters within a site indicate significantly different means based on ANOVA.

Table 3. Mean percent total cover and richness of herbaceous species in study plots at Indiana Dunes National Lakeshore. The levels of significance using ANOVA are indicated by: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. Means with different superscript letters are significantly different at the 0.05 level using the Tukey test. The numbers of sample plots are: Inland Marsh East—8 (all plot positions); Inland Marsh West—20 (all plot positions); and Razed Homesite—8 (Source), 10 (Intermediate), 12 (Perimeter).

Study Area		Plot Position			
Parameter	Significance	Source	Int. 1	Int. 2	Perimeter
Inland Marsh East					
Total Cover ± SE (%)	*	70 ± 9^{A}	59 ± 7^{B}	38 ± 10^{B}	42 ± 6^{B}
Richness ± SE (# Spp.)	**	$3 \pm 4\ E^{-1A}$	4 ± 1^{AB}	5 ± 1^{B}	$6 \pm E^{-1B}$
Inland Marsh West					
Total Cover	ns	46 ± 7	47 ± 4	—	45 ± 3
Richness	***	4 ± 1^{A}	8 ± 1^{B}	—	8 ± 1^{B}
Razed Homesite					
Total Cover	ns	42 ± 3	45 ± 3	—	40 ± 8
Richness	ns	$5 \pm 4\ E^{-1}$	$5 \pm 4\ E^{-1}$	—	6 ± 1

Table 4. Mean percent total cover of *Bromus tectorum* in study plots at Indiana Dunes National Lakeshore. The levels of significance using ANOVA[F] or the Kruskal-Wallis test[H] are indicated by * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. Means with different superscript letters are significantly different at the 0.05 level using the Devore test. The numbers of sample plots are: Inland Marsh East—8 (all plot positions); Inland Marsh West—20 (all plot positions); and Razed Homesite—8 (Source), 10 (Intermediate), 12 (Perimeter).

		Plot Position Mean Cover Total ± SE (%)			
Study Area	Significance	Source	Int. 1	Int. 2	Perimeter
Inland Marsh East	***H	53 ± 7^{A}	35 ± 7^{A}	5 ± 4^{B}	2 ± 1^{B}
Inland Marsh West	***H	13 ± 5^{A}	0^{B}	—	0^{B}
Razed Homesite	nsF	16 ± 9	7 ± 4	—	6 ± 3

6.177, $P < 0.01$) was signficantly greater than that of the control. The ammonium concentration of black locust plots ($U_{18,18} = 119.5$, $P > 0.05$), while not significantly greater, averaged 50% higher than that of the control plots (Table 6).

In the litter, the average percent ash organic matter ($U_{9,9} = 12$, $P < 0.05$) and dry matter ($t_{16} = 4.412$, $P < 0.01$) of the control plots were significantly greater than those of the source black locust plots (Table 6). The percent litter nitrogen was significantly greater in the black locust samples than in the control samples ($t_{16} = 6.686$, $P < 0.01$).

DISCUSSION

Vegetation Changes

Trees and saplings

Black locust was found in closed stands only as a dominant tree; in open perimeter plots black locust saplings were abundant (Figure 2; Table 2). Three features of the black locust contribute to this distribution pattern. The species' naturally low germination of seeds results from high seed coat impermeability and shade; any seedlings produced are eventually eliminated due to the closed canopy shade (Fowells 1965, Burns and Honkala 1990, Mebrahtu and Hanover 1991). Established saplings are eliminated upon canopy closure due to self-thinning and self-pruning (Kerestezi 1988). The moderate to high densities of black locust saplings found in the perimeter plots of all study sites, as well as the presence of a few isolated seedlings, indicate the invasion of black locust into the adjacent communities.

Seedlings and saplings of the moderately shade-tolerant black oak die in response to the inadequate light levels beneath the full black locust canopy (Burns and Honkala 1990, Ashton and Larson 1996). Recent observations (R. Peloquin, pers. obs.) confirm that none of the infrequent, sapling black oak present at the beginning of this study have survived under the full canopy of the source black locust at the Inland Marsh East site (Table 2). The scarcity of black oak saplings and trees under the densest black locust canopies (where only two black oak trees were present in 16 sample plots) indicates that black oak is unable to compete against colonizing black locust on disturbed sites.

Herbaceous species diversity

Site disturbance, black locust shade, downy brome abundance, and a species' response to soluble nitrogen levels are primary factors that interact to determine the diversity and distribution patterns of herbaceous species in this study. The decline in herbaceous species diversity toward the source plots (Figure 5) corresponds to increasing black locust canopy shade at all sites. The lowest species diversity, which occurred in the Inland Marsh East source plots, reflected the greatest combined black locust tree densities and stand basal areas, few canopy gaps, a history of severe disturbance, and the highest downy brome mean cover values of any plot position. The Inland Marsh West intermediate and perim-

Table 5. Mean percent total cover of herbaceous species at Inland Marsh West, Indiana Dunes National Lakeshore. Only at this site was a species (other than *Bromus tectorum*) cover total > 10% for all plots, its cover significantly different among plot positions, and its total frequency > 1 at each occupied plot position. The levels of significance using ANOVA[F] or the Kruskal-Wallis[H] test are indicated by: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. Means with different superscript letters are significantly different at the 0.05 level using the Tukey test (with ANOVA) or the Devore test (with Kruskal-Wallis). The numbers of sample plots are Inland Marsh West— 20 (all plot positions).

		Plot Position Mean Total Cover ± SE (%)		
Species	Significance	Source	Intermediate	Perimeter
Carex pensylvanica	*F	3 ± 1^{A}	1 ± 1^{B}	1 ± 1^{B}
		9	2	2
Tradescantia ohioensis	**H	5 ± 2^{A}	$< 1^{B}$	1 ± 1^{AB}
		11	3	7
Lupinus perennis	*H	0^{A}	1 ± 2 E^{-1B}	1 ± 4 E^{-1B}
		0	7	6
Schizachyrium scoparium	***H	0^{A}	5 ± 1^{B}	3 ± 1^{B}
		0	9	6
Tephrosia virginiana	**H	0^{A}	6 ± 3^{B}	8 ± 3^{B}
		0	5	9

Table 6. Average soil and litter values along two Inland Marsh West transects: Source Transect, which contained mature black locust trees, and Control Transect, which lacked black locust trees. Significant results of the *t*-test[t] or the Mann-Whitney test[U] are indicated by: * = $P < 0.05$, ** = $P < 0.01$. N = 18 for soil samples, n = 9 for litter samples.

	SOIL PARAMETER Mean ± SE				
	OM (%)^{U}	Ash OM (%)^{U}	Tot. N (%)^{t}	NH_4 (ppm)^{U}	NO_3 (ppm)^{t}
Transect					
Control	**4.4 ± 0.7	**5.7 ± 0.7	**0.078^{s}	2.8 ± 0.2ns	1.4 ± 0.1
Source	1.7 ± 0.2	2.5 ± 0.2	0.032^{s}	4.2 ± 0.7	**3.3 ± 0.3

	LITTER PARAMETER Mean ± SE		
	Ash Om (%)^{U}	Dry Matter (g)^{t}	N (%)^{t}
Transect			
Control	*43 ± 17	**35 ± 14	1 ± 0.3
Source	24 ± 5.4	13 ± 6.0	**2 ± 0.4

[S] Control N, SE ± 4 x 10^{-3}; Source N, SE ± 5 x 10^{-3}.

eter plots, with the lowest combined black locust tree densities and stand basal areas, frequent canopy gaps, lack of disturbance, absence of downy brome, and intact savanna flora, had the highest herbaceous species diversity. In these plots, the continued growth of black locust individuals and the further invasion of black locust into the oak savanna probably will cause a decreased variety of less shade-tolerant species. For example, little bluestem grass and wild lupine, whose cover values at Inland Marsh West were significantly greater in the more open intermediate and perimeter plots than in the source plots, are known to be limited by shade (Tilman 1987, Wedin and Tilman 1993, Grigore and Tramer 1996).

Maximum downy brome cover occurred under the closed canopies of black locust source plots at Inland Marsh East and the Razed Homesite, as well as in the high-density intermediate plots at Inland Marsh East (Table 4). Other shade-tolerant herbaceous species were infrequent or absent in these plots. Downy brome cover was marginally lower under the more open black locust canopy of Inland Marsh West source plots. Native common spiderwort and Pennsylvania sedge reached their greatest abundance in these plots. Under closed savanna and woodland canopies, some shade-tolerant savanna and mixed woodland species probably are unable to compete with downy brome, which is a successful competitor in a wide range of soil positions (Monsen 1994). Downy brome is a nitrogen-response species whose interference with, and dominance over the growth of associated species in nitrogen-enriched soils was noted by Anderson (1991), Dakheel et al. (1993) and Rasmussen (1995). Downy brome is also a spring ephemeral at the Indiana Dunes. And while it may exclude some shade-tolerant species under closed canopies, downy brome is unlikely, under intermittent canopies, to exclude all native perennial herbaceous species that propagate vegetatively throughout the growing season. Increased black locust shade would probably be needed for downy brome to successfully compete or dominate in a natural black oak savanna.

Effects of Black Locust on Soil and Litter

The high levels of organic matter in the control soil and litter samples are consistent with the high biomass return of black oak savanna herbaceous species, and the rapid decomposition of that biomass (Table 6). The significantly higher levels of total nitrogen and organic matter in control soils, and the low amounts of these values in the black locust soils of this study, agree with Tilman (1987), who found the two parameters to be highly correlated. The low amounts of organic matter and total nitrogen (the latter is tied up in organic matter and mineralizes slowly—less than 10% per annum; Keeney and Nelson 1982) in the black locust soils can be attributed, during the first year, to rapid litter decomposition (forming soluble nitrogen products) (Auten 1945, White et al. 1988) followed by slow, lignin-inhibited decay (in one of those studies, the highest initial nitrogen concentration in black locust leaf litter was 22.0 mg N/g; percent original nitrogen at 863 days was 81%; percent lignin at 863 days was 49.7 %; White et al. 1988). Lignin interferes with cellulose degradation by preventing the access of degradative enzymes to cellulose and hemicellulose. The total nitrogen and organic matter that accumulate below the relatively short-lived black locust may be utilized by succeeding species (White et al. 1988).

The higher levels of observed soluble soil nitrogen in the oldest black locust plots at Inland Marsh West result from a combination of several processes. Contributing nitrate or ammonium to a black locust soil are root exudation; the decomposition and mineralization of abundant, N-rich black locust leaf litter (litter dry weights in this study were 10–30 times greater than those of a black oak savanna control site) (Auten 1945, Kerestezi 1988, White et al. 1988); nitrogen fixation (which may reach 590 kg ha^{-1} $year^{-1}$ in the upper 50 cm of soil in 16- to 20-year-old black locust stands, Kerestezi 1988); and insect frass and fine particulates (Boring and Swank 1984, White et al. 1988). Precipitation increases leaching of soluble nitrogen in dune soils.

Consequences of Black Locust Invasion

Black locust populations appear to be altering the characteristics of ecosystems of the Lake Michigan shoreline. Other invasive species possessing attributes similar to the black locust have produced comparable ecological consequences in suitable habitats with low-fertility soils. *Acacia saligna* (Labill.) Wendl. (Leguminosae; invasive in South African coastal fynbos and naturalized in California), *Acacia cyclops* A. Cunn. ex G. Don (Leguminosae; invasive in the South African strandveld and in California), and *Myrica faya* Ait. (Myricaceae; invasive in Hawaii) are three of the worst woody invasive species (Cronk and Fuller 1995). Like the black locust, these species (1) fix nitrogen (important in low-fertility soils), (2) establish colonies through single individuals (*A. saligna*—seeds and sprouting after cutting or burning; *A. cyclops*—seeds, particularly rapid development after fire; *Myrica*—seeds), (3) undergo rapid population expansion, (4) tolerate a range of soil types, (5) grow rapidly, and (6) replace native species through a combination of shade and elevated nitrogen (Vitousek and Walker 1989, Witkowski 1991, Cronk and Fuller 1995). We found a positive association between the abundance of black locust and downy brome.

In conclusion, black locust is invading newly disturbed dune habitats and established ecosystems of the Indiana Dunes. Soluble nitrogen is significantly increased in the usually infertile sandy dune soils beneath the oldest black locust individuals. The shade of the dense black locust canopy is reducing the photosynthetically active radiation known to be required by black oak associates (Bray 1958). Understory dominance by another exotic plant species, downy brome, seems to have been facilitated by the presence of the black locust. A significantly reduced species diversity in the black locust herbaceous understory has occurred at the savanna sites under the modified environmental conditions.

Management Implications

Black locust appears to alter the vegetation composition of former residential sites, sand-mined areas, and other disturbed sites at Indiana Dunes, changing from native dune vegetation to a less diverse community that includes downy brome. Black locust may not only slow the rate of succession but may have long-term effects on the trajectory of succession due to the increased soil nitrogen in a naturally low-nutrient soil.

To restore residential sites and historic dune plant communities, site managers should remove black locust trees and the associated root sprouts. Chemical treatment of stumps to retard stump sprouting and root sprouting will be required over a 2- to 4-year period (Fleming et al. 1986). Associated downy brome stands should also be chemically treated in the plant's most active growth phase in spring. If downy brome persists, soil treatments to reduce soil nitrogen may be necessary.

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Robert Peloquin is Associate Professor of Biology at Purdue University Calumet. Additional studies that he has conducted at the Indiana Dunes National Lakeshore include the ecology of Miller Woods and the effects of fire on the spread of black locust.

Ronald Hiebert is currently serving as Associate Regional Director for Resource Stewardship and Science in the Midwest Region of the National Park Service. As Chief Scientist at Indiana Dunes National Lakeshore, he conducted research in plant ecology.

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