

Successional Relationships of Pine Stands at Indiana Dunes

ERIC S. MENGES AND THOMAS V. ARMENTANO

Holcomb Research Institute

Butler University

Indianapolis, Indiana 46208

Originally presented as

Demographic and Community Aspects of White Pine and Jack Pine
in Lake Michigan Dune Ecosystems

Introduction

Controversy about plant succession, its pathways, characteristics, rates, and mechanisms, continues to be a significant part of plant ecology today (e.g., 5, 10, 22, 25, 26). The first major formulation of succession as a theory (7) was based largely on research at Indiana Dunes. Cowles (6) recognized that the parallel sand ridges, each marking the southern border of the Lake Michigan shoreline for a definable period following regional deglaciation, provided a unique opportunity to interpret the temporal dynamics of vegetation development. Later, Olson (23, 24) more quantitatively analyzed vegetation and soil patterns at the dunes and advanced successional theory.

Cowles hypothesized that long-term changes in the vegetation composition of a site could be related to amelioration of harsh physical conditions, and that improvement in soil properties mediated changes by successive plant communities. Olson (23, 24) emphasized that at Indiana Dunes, several plant communities thought by Cowles to be seral might be more or less permanent, largely because of nutrient limitations. Recently, the role of periodic fire in maintaining the integrity of a variety of dune communities has been emphasized (3, 13, 32).

Within the Indiana Dunes area, individual species that are rare or at range limits have been considerable interest (32). These include two pine species, white pine (*Pinus strobus*) and jack pine (*Pinus banksiana*). Both species, particularly jack pine, are found at Indiana Dunes near their range limits (11) and are considered to be boreal relicts (32).

Both Cowles and Olson considered pine stands to be successional at the dunes, in keeping with their apparent role at other sites. Cowles concluded that upland pine communities were usually replaced by oak-dominated communities. He did not comment specifically on the fate of lowland pine stands. While Olson (24) convincingly demonstrated that conversions of oak to sugar maple as hypothesized by Cowles were unlikely, he also concluded that oak would usually "quickly replace" pine in upland sites. The present paper summarizes community and population characteristics of pine stands at Indiana Dunes, and interprets the data in relation to the successional status of the two species.

Our study was conducted in 1984, about 35 and 85 years after observations by Olson and Cowles, respectively. Although successional theory has evolved since these studies, interpretation of successional dynamics in forests still depends largely on inferences from stand structure and compositions at a single point in time. Long-term, replicable data sets are rare. Although we were unable to relocate plots established by Olson, our sampling stations were established at nearby locations closely similar in vegetation and site properties. In several cases we analyzed the same stands sampled by Olson (pers. comm.).

Methods

To evaluate white and jack pine populations, the present distribution of both species at Indiana Dunes National Lakeshore (IDNL) and Indiana Dunes State Park

(IDSP) was determined. Outside these properties, few undisturbed populations of either species exist on dunes habitat within Indiana. Low altitude aerial photographs (1:400) and previous reports by Wilhelm (32) and Krekeler (18) were used to locate stands. All sites likely to contain populations of either pine species were visited by the authors. For purposes of this investigation, a population was defined as a grouping of ≥ 15 individuals of a species within 0.4 ha.

Field work was done during the 1984 growing season. Pine stands were sampled using 100 m² (5.64 m) circular quadrats. Quadrats were stratified randomly along transects to efficiently cover intrastand variability. For stands limited in extent, contiguous square quadrats or complete sampling were used. All quadrat centers were marked with metal pins.

All trees (woody stems 2.5 cm dbh or larger) in the quadrat were measured for diameter at breast height (dbh). We also recorded the presence of herbaceous species in each quadrat. Community attributes were sampled in June and July, and follow-up surveys were conducted in late August and September. Vouchers were collected. Nomenclature follows Wilhelm (32).

We sampled pine trees more intensively, adding trees outside quadrats to increase sample size to 80 or more when possible. Heights of pine seedlings and samplings (< 2.5 cm dbh) in quadrats were measured. Increment cores were obtained from IDNL pines in late summer 1984. However, complete age-structures were taken for only two of the smaller populations of each species. Additional populations were partially cored nonrandomly to assure coverage of a range of sizes.

Community analysis considered species presence in quadrats, and weighted all species (trees, shrubs, herbs) equally. We included species with two or more occurrences in our samples. A polythetic divisive clustering technique called TWINSPLAN (two-way indicator species analysis) was used to group floristically similar quadrats and co-occurring species. This technique, described elsewhere (12, 16), is considered to give particularly lucid placement of samples within a dendrogram, and also forms divisions that may reflect secondary gradients (12). Community relationships also were interpreted, using detrended correspondence analysis (DCA). This iterative procedure ordines species and samples simultaneously, and is effective in removing the arch distortion characteristic of many other multivariate techniques (12).

Results

Distribution of Pine Stands

The largest populations of white pine remaining in the lakeshore area are located within state park boundaries. A total of seven white pine populations are located in the dunes area (Table 1). Population SP-7, located at the eastern end of the state park near the Keiser Survey Unit (KE-1), is the largest, consisting of 84 individuals (Figure 1, Table 1). This population is among the most diverse in terms of tree sizes. The second largest population is located in the Keiser Survey unit of the IDNL, less than 0.5 km east of the SP-7 and consists of 81 individuals located in a mesic pocket behind primary dunes. The remaining populations studied are far smaller in size (Table 1). These sites currently support mixed hardwood pine forests in mesic pockets or on dune slopes.

Nine populations of jack pine were selected for sampling (Figure 1, Table 1); these ranged in number of trees from less than 50 to over 300. Several populations were in interdunal depressions (pannes) that hold temporary standing water in the spring, or were located adjacent to permanent ponds. Others were found on open slopes, in woodlands on dune-complexes (*sensu* 32) or in mixed-hardwood stands on slopes or

TABLE 1. Location and Status of Studied Jack Pine (JP) and White Pine (WP) Populations in Indiana Dunes

Site	Population Size	Comments
<i>Ogden Dunes</i> —West Beach Unit, east of town of Ogden Dunes		
OD-5	34 WP, many JP	Old-growth woods on east facing dune slope, most JP on north and east edges; WP scattered in interior
OD-1	>300 JP	Open pine stand, edge of panne just behind lakefront dune
<i>West Beach</i> —West Beach Unit, west of Ogden Dunes, east of parking lot, just behind primary dunes		
WB-1	>300 JP (most tree-sized)	Open pine stand on well-drained dunes
WB-2	>300 JP (most seedlings)	Open pine stand adjacent to panne and ponds
<i>Dune Acres</i> —west of town of Dune acres, along shore (DA-1); in mesic pocket, south of DA-1 (DA-2); and east of Mineral Springs Road, ca 1 km north of Cowles Bog (DA-3)		
DA-1	5 WP, >300 JP (most sapling and tree-sized)	Open pine stand on lakefront dune
DA-2	22 WP (Nearly all old growth)	Old-growth forest in mesic pocket between dunes
DA-3	52 JP (all old growth)	Closed swamp forest adjacent to marsh
<i>Miller Dunes</i> —east of steel mills, near slag ponds		
MD-1	47 JP	Dunes, upslope from pond
MD-2	~300 JP	Dune flat adjacent to panne and pond
<i>Keiser</i> —east of state park road parking lot		
KE-1	81 WP	Mesic pocket and adjacent dune ridge
<i>State Park</i>		
SP-1	17 WP, >300 JP	Open lakefront dunes and mixed woods
SP-7	84 WP	Mixed secondary woods, west of State Park road, ca 1 km south of lake front.

in dune flats. Only one of the sampled populations was located in IDSP. Several other populations in IDSP were not sampled.

Our inventory of IDNL populations reveals that outside of Pinhook Bog (over 15 km to the southwest), no natural stands of jack or white pine are located east of the white pine population KE-1 or south of U.S. Route 12. Several additional stations of planted white pine were not considered in this study. These additional sites contain too few individuals of either species to meet our definition of a population.

All pine populations occurred on areas mapped in soil surveys (30, 31) either as dune land or Oakville fine sand. Soils are composed of fine sand with some medium sand and fine gravel, and have little or no horizon development. They are extremely low in moisture-holding capacity, with neutral to acid pH.

Community Analysis of Pine Stands

Classification of Pine Stands. Pine stands at Indiana Dunes were divided by TWINSPLAN into four groups (Figure 2). In labeling such stands, we relied both on field observations, known autecologies of major species, and previous work at Indiana Dunes (6, 18, 24, 32).

- (1) Jack-pine-dominated, open panne communities with an incomplete canopy, located near temporary or permanent bodies of water (WB-2, MD-2, OD-1). These stands had moderately high similarity to each other.
- (2) Jack-pine-dominated woodlands and dunes in upland areas (WB-1, MD-1, SP-1, DA-1). These dune-complex areas were generally extensive, structurally heterogeneous areas. Canopies were mostly open. The four stands were very similar to each other compositionally.

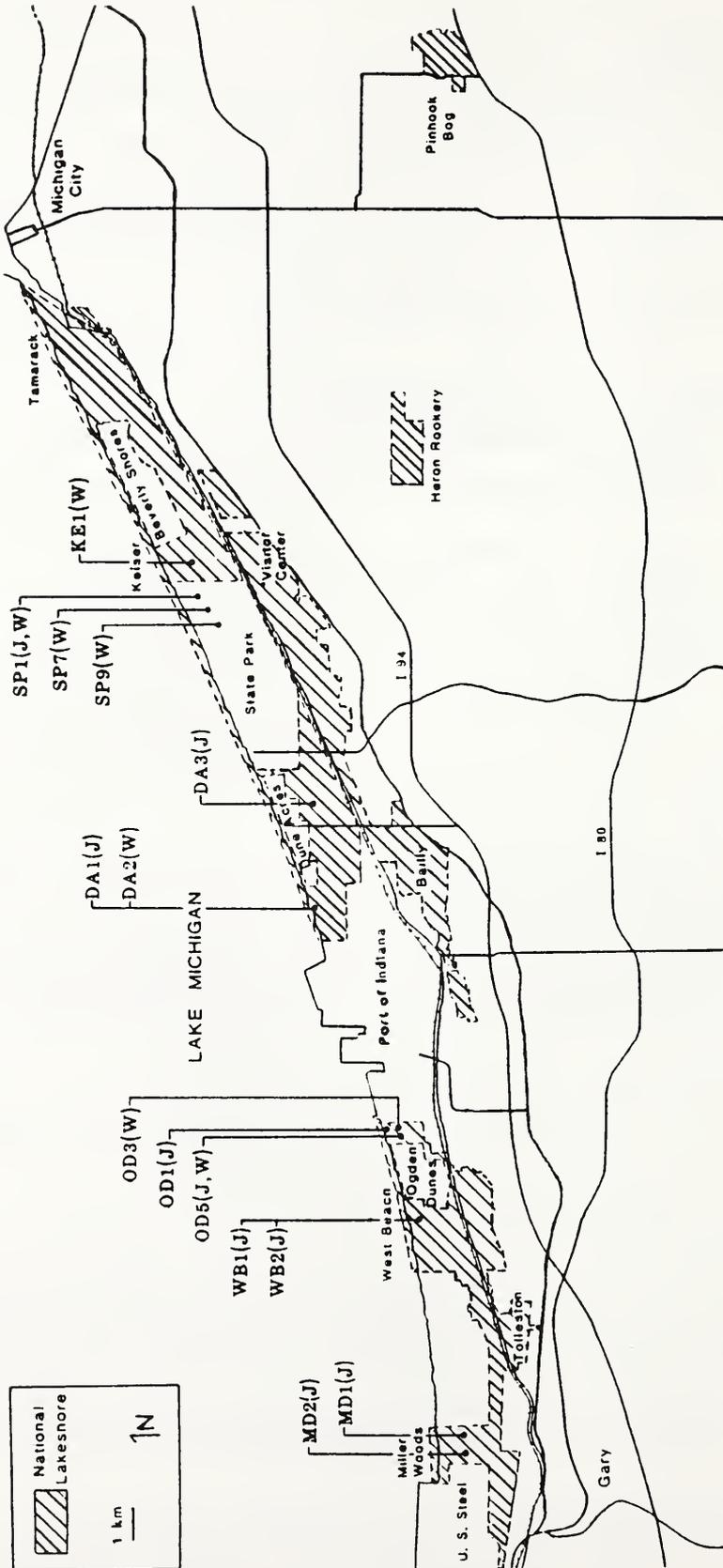


FIGURE 1. Location of white and jack pine populations analyzed in this study.

% Similarity (2W/A+B) Within Groups

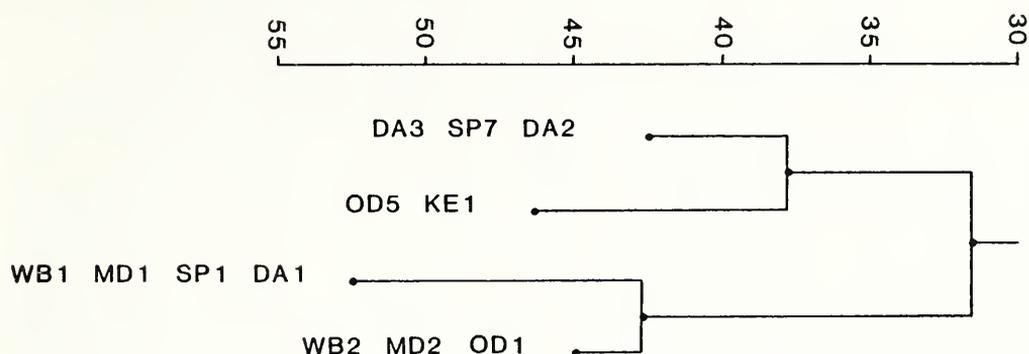


FIGURE 2. Cluster diagram of Indiana Dunes sites, based on TWINSpan classification analysis, with similarities within and between groups calculated by city-block distance ($2W/A + B$ where A are species in one quadrat, B those in the second, and W those in common; distance was averaged over all quadrats).

- (3) Mixed hardwood-pine forests, less protected or drier than the following group. The two sites included were OD-5, a slope forest with both pine species, and KE-1, a pocket behind large curving dunes with white pine and hardwood trees. We followed previous convention in describing these areas as “mesic pockets.”
- (4) Mesic or wet-mesic forests on dune flats. Two are mixed hardwood-pine stands: DA-3, a swamp forest with jack pine, and SP-7, a mixed hardwood forest with white pine. They contain species interpreted as indicating mesophytism or association with wet soils including *Fraxinus americana*, *Acer rubrum* and *Nyssa sylvatica*.

A TWINSpan classification at the quadrat level provided additional detail on what species are significant indicators of various groups of floristically similar quadrats.

Within pine stands at Indiana Dunes, the major division was between closed forest/woodland areas and more open woodlands and dune formations (Figure 3). Many other species, particularly shade-intolerant trees (e.g., *Populus deltoides*), wetland plants (e.g., *Hypericum kalmianum*), and dunes forbs (e.g., *Artemisia caudata*), were found only rarely in closed forests. Many other species, however, are characteristically restricted to forests, including *Acer rubrum*, *Prunus serotina*, and *Sassafras albidum*.

The major TWINSpan division within closed forests distinguishes wet-mesic forests on dune flats (DA-3, SP-7) from upland mesic forests and woodlands (Figure 3). In open areas, the major division also results from apparent moisture (Figure 3). Areas adjacent to standing water, often pannes (OD-1, WB-1), support shade-intolerant moisture-loving species such as *Hypericum kalmianum* and *Sabatia angularis*. The opposing species are characteristic of dry, open dunes and woodlands.

Further divisions in the cluster analysis often can be attributed to more local factors. For example, the driest open areas are subdivided (at level 3) into open formations dominated by dune grasses and annuals versus more shrubby thicket areas. A division of quadrats within the mesic pocket DA-2 reflects canopy gaps that favor

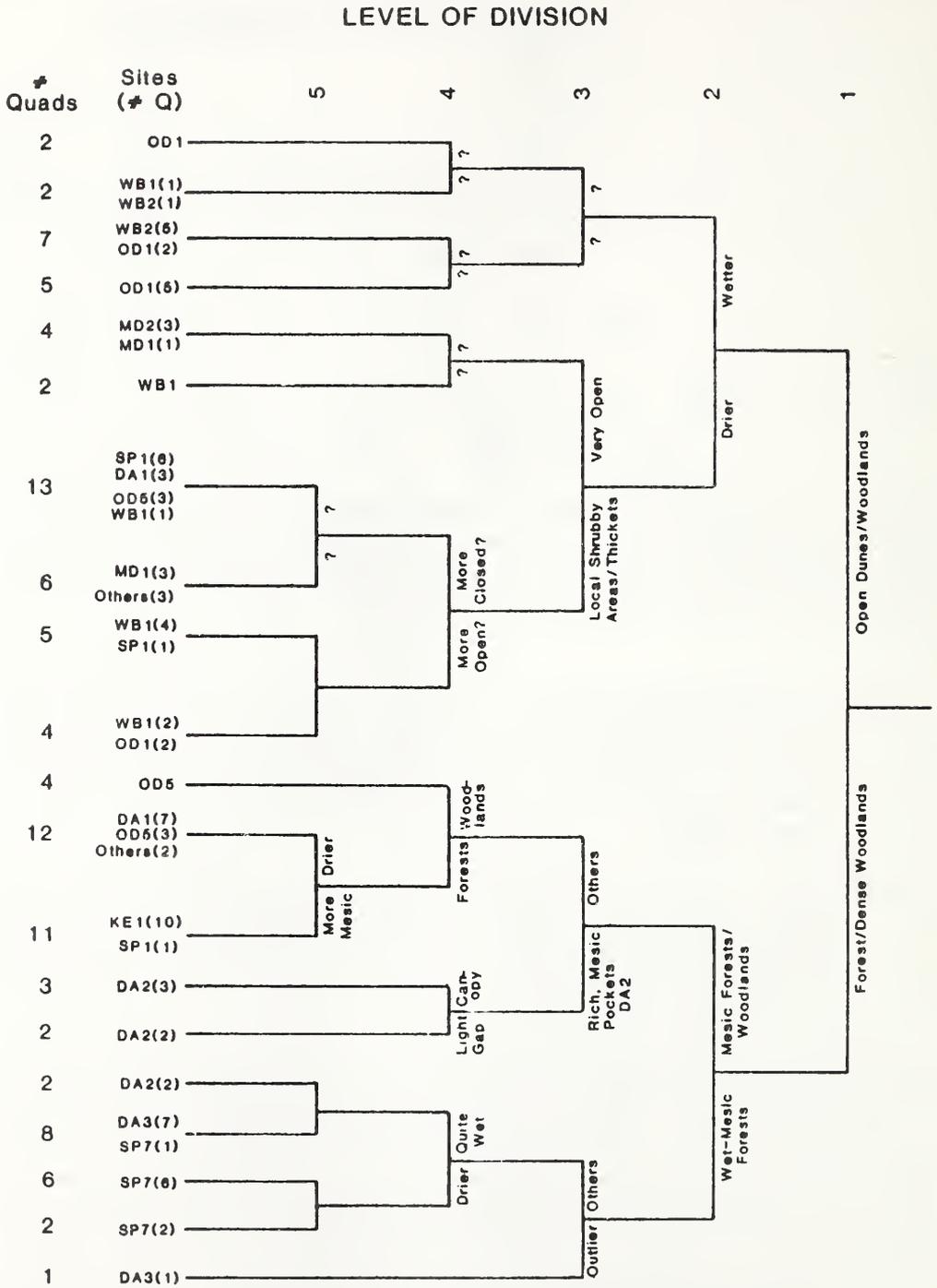


FIGURE 3. Cluster diagram of IDNL quadrats, based on TWINSpan classification analysis. Indicated within dendrogram are environmental differences between branches. Along the left are shown the sites to which the quadrats belong and the number of quadrats found in each cluster.

gap-phase trees over shade-tolerant shrubs and herbs. Although some subsequent divisions reflect finer distinctions in moisture, cover, and species diversity, other clusters are not associated with recognizable environmental factors.

Ordination of Pine Stands. The major axis of variation in the DCA ordination reflects crown cover: it extends from open sites (dry and wet) to closed forests. Quadrats from OD-1 to SP-7 define the endpoints of this axis, which passes respectively through wet open areas, dry open areas, drier forests and woodlands, and mesic forests (Figure 4). The second major axis separates forests stands only, from the swamp forests at DA-3 to the mesic pocket at DA-2. SP-7 and KE-1 occupy intermediate positions.

This ordination emphasizes the distinctness of several sites: the mesic pocket DA-2, the swamp forest DA-3, and the panne site MD-2. Other sites feature a compositional range. For example, OD-1 contains quadrats in temporary pannes with unique floristic elements, and also quadrats on sandy ridges similar to the upland dunes sites (Figure 4). A compositional continuum is also evident in the upland dune areas, from quite open areas all the way to fairly mesic forests. Some sites (KE-1, MD-1) have rather narrow ranges within the continuum, but WB-1, SP-1, DA-1, and OD-5 all span a broad compositional range. SP-1 is the most heterogeneous, with some forest area similar to the mesic pocket KE-1, and other open areas similar to OD-1.

DCA uses both sample (quadrat) and species distributions in its iterative analysis; thus, a map of species centroids is directly comparable to the sample map. In Figure 5, some species centroids are indicated. Their distribution is generally similar to sample distribution, with first-axis variation showing a gradient from open (*Typha latifolia*, *Opuntia humifusa*) to closed (*Osmunda claytoniana*), and second-axis reflecting mesic (*Viburnum acerifolium*) to wet-mesic (*Quercus palustris*) species. The species distribu-

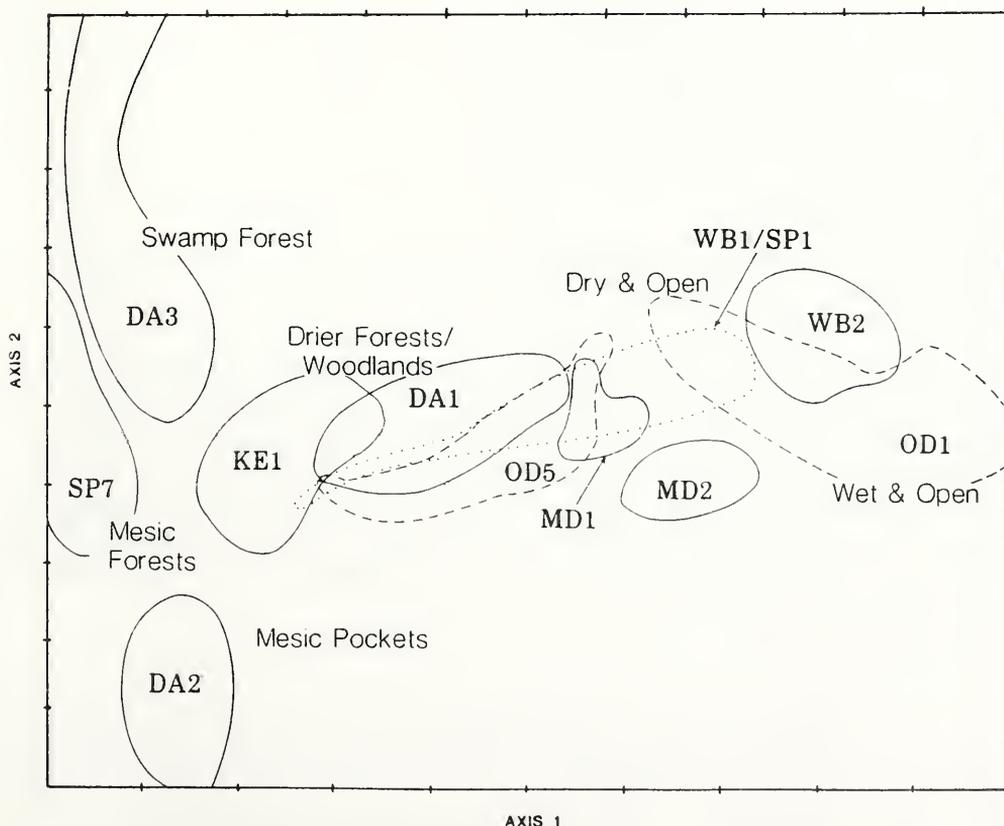


FIGURE 4. Location of sample quadrats on first two axes of DCA ordination. Lines encompass all quadrats belonging to sites indicated in bold letters; major environmental factors are also indicated.

tion shows more intermediate centroid placement for species occupying a range of habitat conditions. For example, *Rhus radicans* and *Pinus banksiana*, both located near the center of the ordination, range from wet-mesic to dry forests and woodlands to more open dune areas, although *Pinus banksiana* is notably absent from most closed forests (Figure 5).

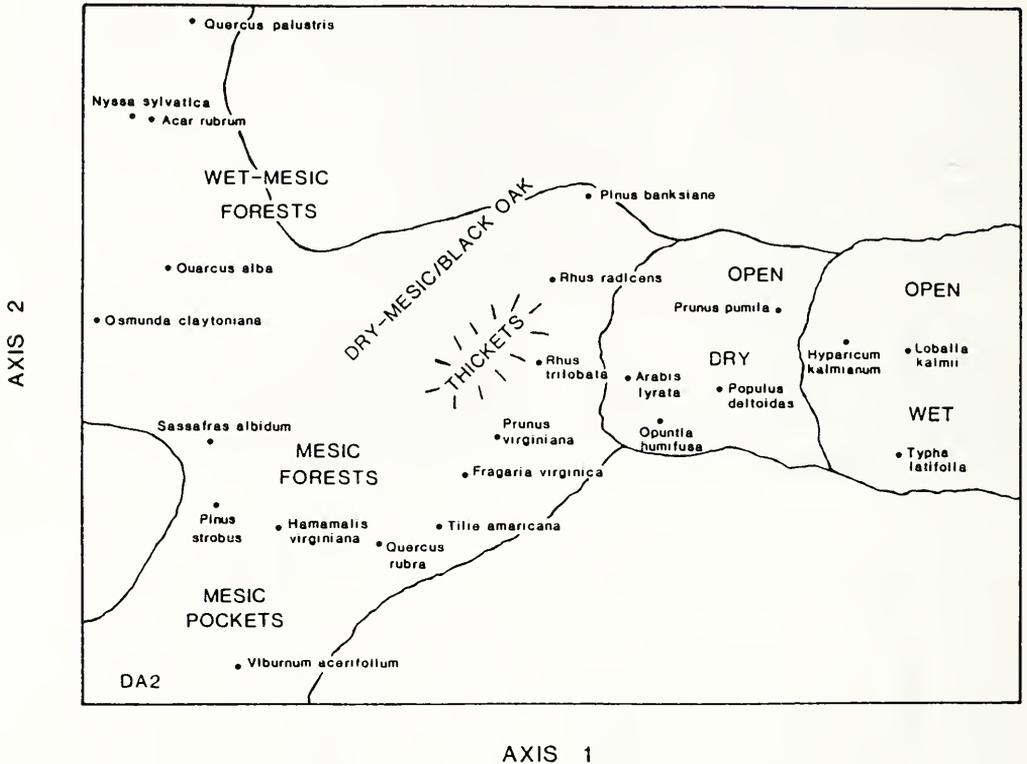


FIGURE 5. Location of major species centroids on first two axes of DCA ordination. Lines encompass all species locations.

The preceding discussion was based on sample and species locations or graphs of the first two axes of DCA, i.e., those explaining the greatest amount of variation. The major effect of the third axis is to better separate some quadrants in WB-1 from the majority of those in SP-1 and DA-1. Species with strong correlations in the direction of this separation include open-sand specialists such as *Opuntia humifusa* and *Populus deltoides*, as well as some weedy elements (e.g., *Saponaria officinalis*). We believe this compositional gradient reflects erosional damage from heavy recreational use of the West Beach Unit.

Structure of Pine Stands

Five jack pine populations occurred in areas with little other tree cover. WB-2 has no other tree-size vegetation, while at MD-1, MD-2, and OD-2, only a few individuals of other tree species occurred. These four sites all have less than 650 dm² basal area/ha. Reproduction of jack pine is especially dense in the panne areas, but few seedlings of other species were sampled.

At WB-1, jack pine accounted for 81% of sampled stems greater than 2.5 cm in diameter. Nearly all other species were understory trees or shrubs (*Prunus virginiana*, *Amelanchier* sp., *Ptelea trifoliata*) but seedlings were relatively sparse. At DA-1,

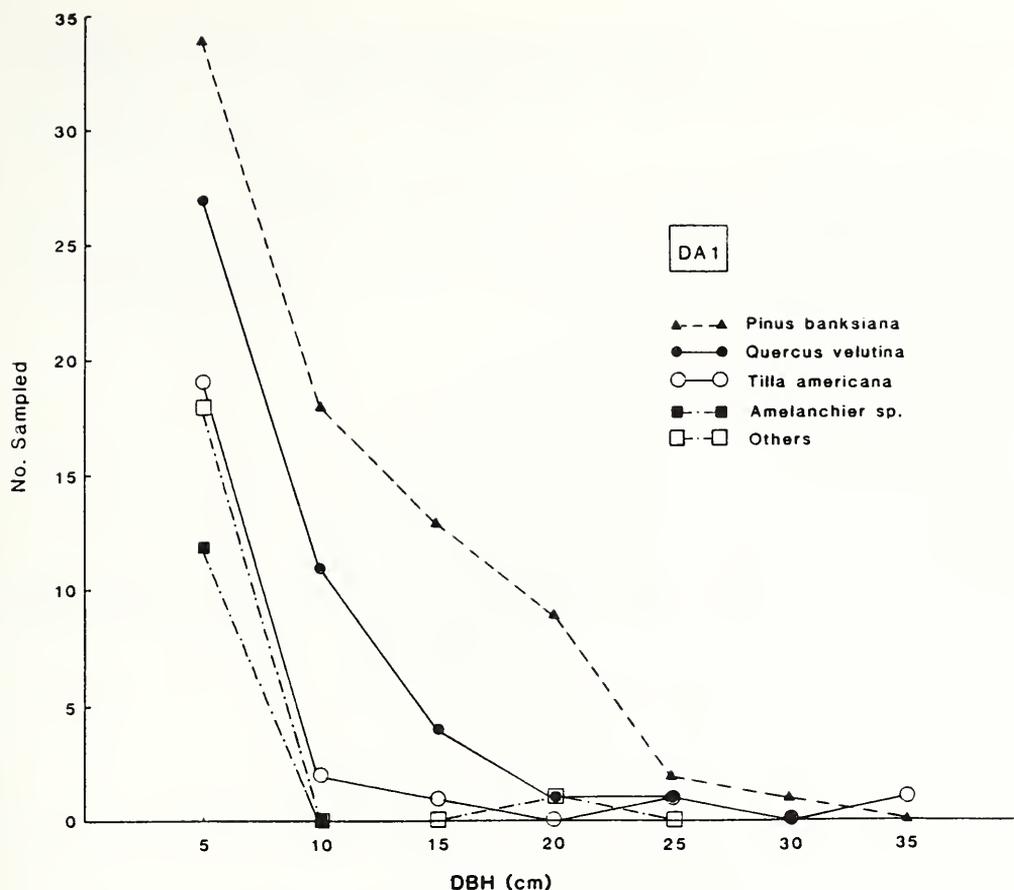


FIGURE 6. Forest structure at DA-1.

44% of the tree-sized stems present were jack pine, as were many smaller trees and seedlings (Figure 6). Reproduction of black oak, witch hazel (*Hamamelis virginiana*), and basswood is restricted to the highest parts of the dune slope.

Mixed jack and white pine populations are present in the pine woodlands and mixed forests at SP-1 and OD-5. At both sites, white pine, along with black oak at SP-1, comprise the largest trees. However, white pine seedlings and midsized and smaller trees are scarce compared to jack pine and other species (Figure 7). Jack pine reproduction is found largely in more open areas with cottonwood, red cedar (*Juniperus virginiana*), and sand cherry (*Prunus pumila*).

In forests at the closed end of the first DCA axis, the forest structure is different. White pine dominates the mesic pockets KE-1 and DA-2, as well as the mixed secondary woods SP-7. In KE-1, it is the most common tree in every tree size class except the two smallest. The smallest tree-size classes are dominated by understory tree species (witch hazel, sassafras, and *Amelanchier* sp.), with few canopy species represented. Seedlings are quite dense at KE-1, consisting mainly of hardwoods. In the mesic pocket DA-2, white pine are mainly large, with no seedlings and only one sapling. In contrast, the next largest tree species, red oak, has been reproducing well (Figure 8). This stand has a high basal area (4,260 dm²/ha), half again as great as KE-1. Small stems of white ash (*Fraxinus americana*), red maple, and basswood are present, although seedling density is low for all species.

SP-7 has a substantial number of smaller white pine, although seedlings are sparse.

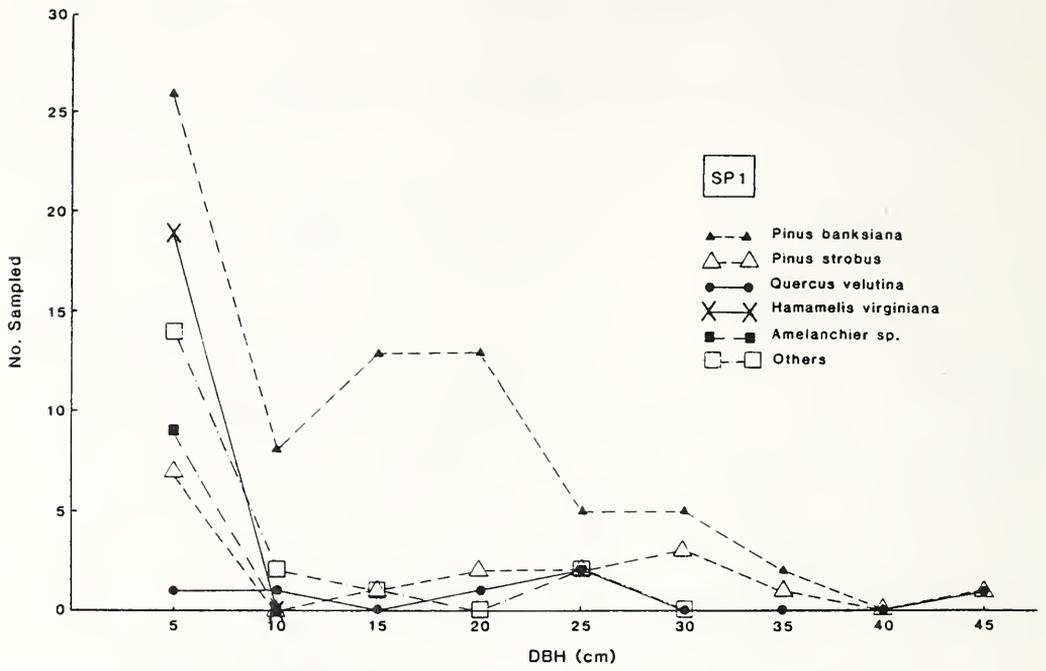


FIGURE 7. Forest structure at SP-1.

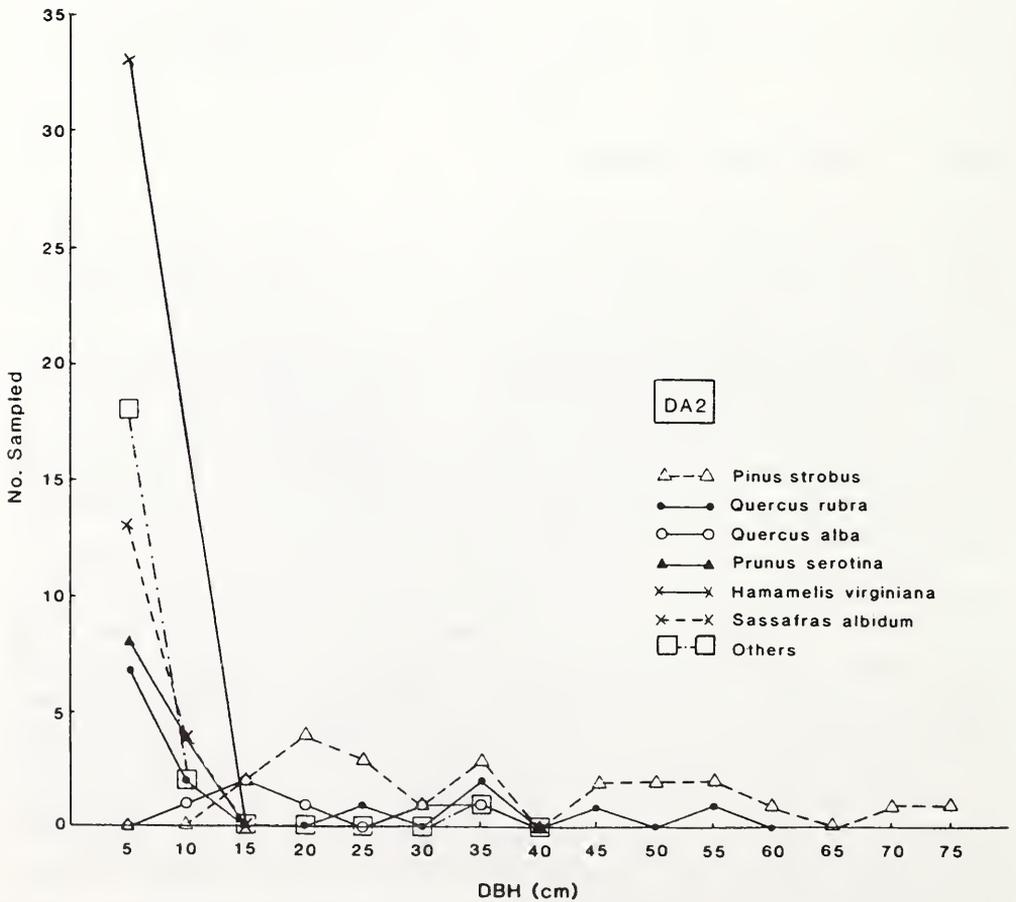


FIGURE 8. Forest structure at DA-2.

All sizes of white oak are widely distributed, whereas many young black gum and red maple are found mainly in the wetter areas of this stand. Shrub density at SP-7 is the highest of any of the sites sampled, with six species occurring in 20% or more of sampled segments.

At DA-3, a swamp forest, neither small jack pine nor reproduction were noted. The larger adult jack pine have very small crowns high on the bole and some appeared to be senescent. In contrast, small trees and seedlings of several hardwood species, especially red maple (*Acer rubrum*), are common. Basal area is quite high (3400 dm²/ha) in this stand.

Size Distributions of Pines

Among the natural populations of white pine in the IDNL region, diameter distributions ranged from 2.5 cm (the minimum by definition), to a 75.1 cm tree found at DA-2. Sapling and seedlings were less common, with only 50 individuals under 2.5 cm dbh encountered in the lakefront—less than a quarter of trees tallied.

Size distribution of white pine within individual populations varied (Figure 9). The population in one mesic pocket (DA-2) consisted mainly of trees ranging from 15 to 75 cm, and completely lacked small trees, saplings, or seedlings. In contrast, the third mesic pocket at Keiser (KE-1) lacked the largest size classes (> 65 cm) but contained some seedlings. Many of these, however, were diseased. We found few recruits into small tree classes at Keiser. Overall, recruitment of white pine in mesic pockets is poor.

The other three white pine populations sampled consisted primarily of medium-sized or small trees (Figure 9). All contained small numbers of saplings and/or seedlings, probably insufficient at present to maintain population levels in the future. Perhaps the most unusual stand was found at SP-7, where small white pine form a scattered but consistent understory beneath part of a mixed hardwood forest.

Jack pine exists as a small tree in the lakeshore areas, with increasing numbers from larger to smaller size classes. Over 40% of tree-sized individuals were 7.5 cm dbh or less. Reproduction, as interpreted by seedling and sapling occurrence, was common, and these size classes contained twice the number of trees. At all locations, small trees and juveniles were uncommon under closed canopies.

The distribution of jack pine sizes was much less variable than that of white pine (Figure 10). Seven of the nine sampled populations were dominated numerically by seedlings or sapplings, with small trees (2.5-7.5 cm dbh) making up the majority of > 2.5 cm dbh individuals. Populations MD-2, WB-2, and OD-1, all located near pannes or ponds, lacked larger trees and were numerically dominated by seedling size classes. Drier sites with abundant reproduction and medium-sized dominants were found at WB-1 and MD-1. The two populations with somewhat lower levels of reproduction and relatively large trees were at OD-5 and DA-1. Both sites contained trees in fairly open areas, dominated entirely by jack pine, but grading into nearly closed woodland with a mixture of hardwoods, some overtopping the pines.

An eighth population, SP-1, was similar to OD-1 and DA-1 in physiognomy and site, but reproduction was poor. The jack pine population, located in a swamp forest at DA-3, consists of medium-sized and larger trees, nearly all with meager crowns located far from the ground.

Age Structures and Long-term Growth of Pine Populations

Jack pine populations at IDNL differ in age. Although the small population at Miller Dunes (MD-1) consists of trees ranging up to 73 years of age (Figure 11), most trees originated between 15 to 30 years ago. A conspicuous gap in the age distribution indicates that no trees presently found were recruited between 1928 and 1949. This

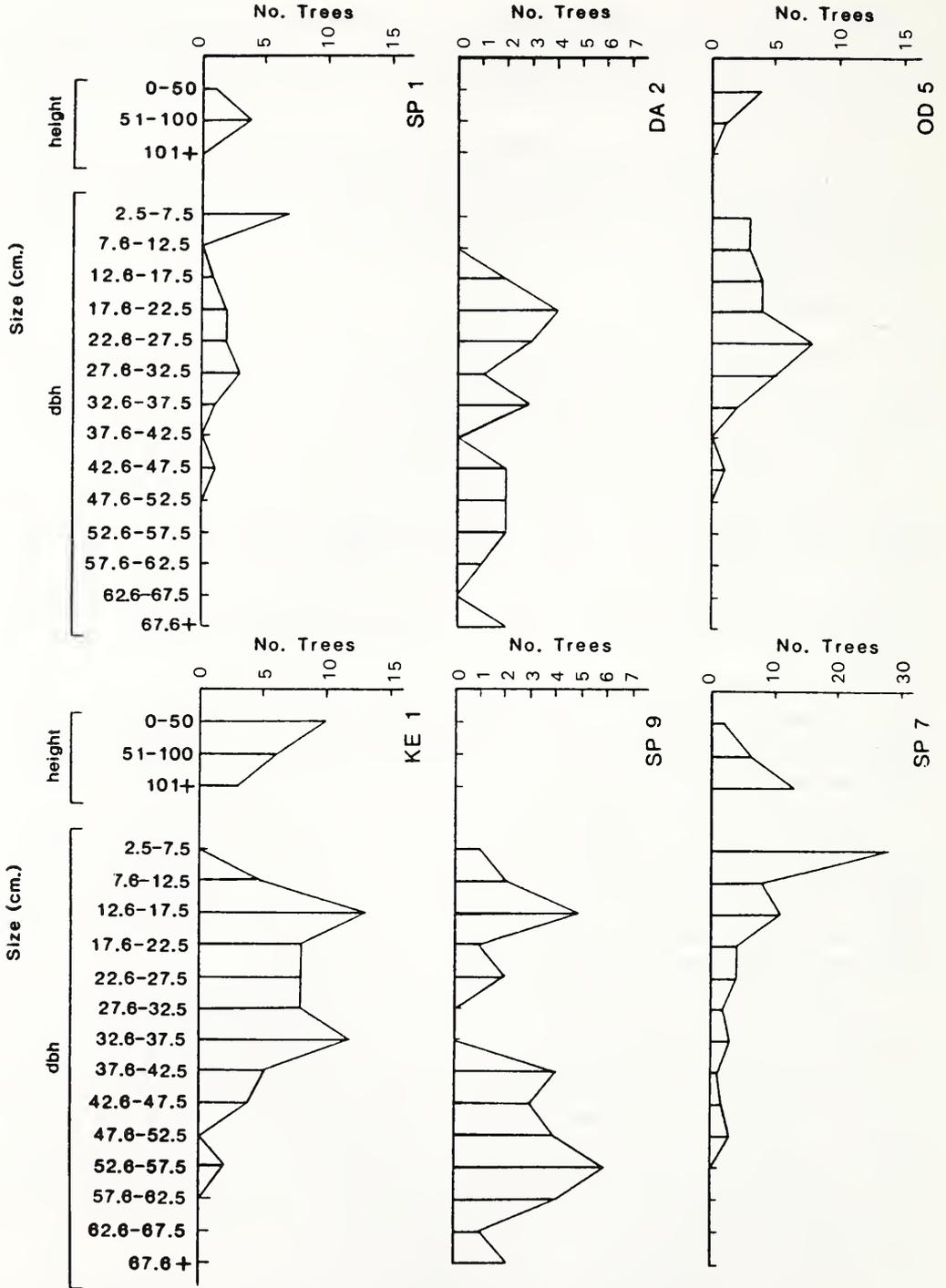


FIGURE 9. Size distribution of white pine populations sampled in the Indiana Dunes region.

age gap, however, is not reflected in a similar gap in size structure.

Jack pine populations in the wetter areas are both smaller and younger than at MD-1. The age of the 20 trees cored at MD-2 ranged only up to 24 years. The largest tree at OD-1 was 64 years old, but most were probably much younger. At MD-2, trees have been continuously recruited since the recent origin of the population.

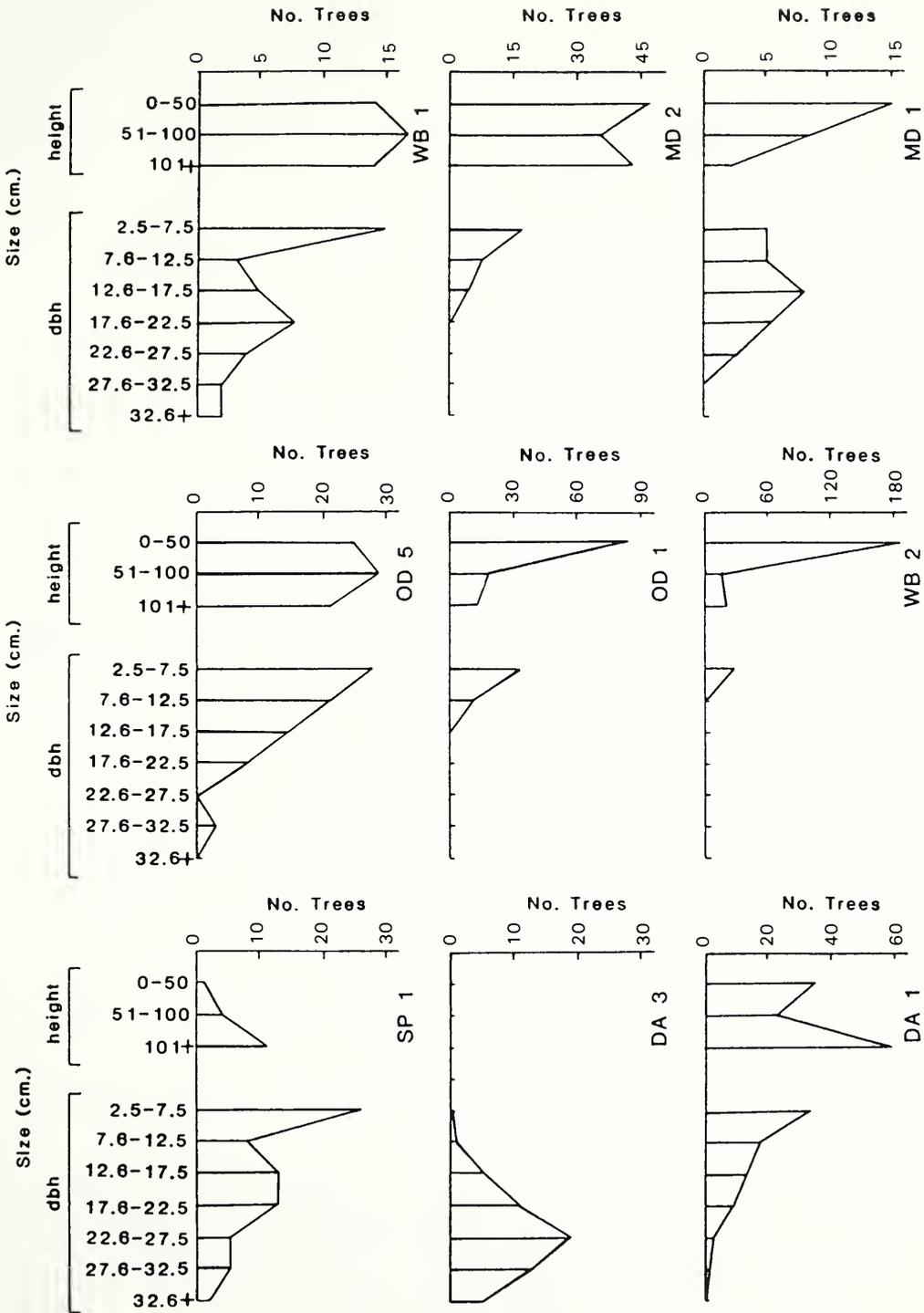


FIGURE 10. Size distribution of jack pine populations sampled in the Indiana Dunes region.

The other two jack pine populations that were partially sampled for age, WB-1 and DA-1, consist of trees with age distributions similar to MD-1. Maximum ages are 65 years in WB-1 and 58 years in DA-1. Both have a preponderance of individuals between 15 and 20 years of age. Another parallel is apparent in these three popula-

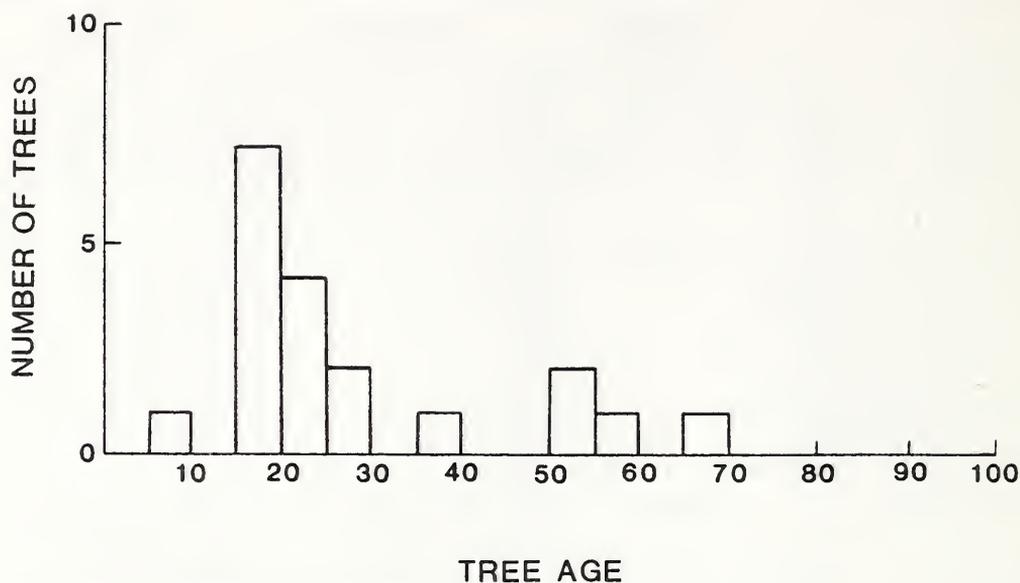


FIGURE 11. Age distribution of jack pine at MD-1.

tions: a striking gap in the number of individuals recruited in the 1930s and 1940s (Table 2).

TABLE 2. Apparent Absence of Jack Pine Recruitment over Two Decades as Determined by Increment Coring, Indiana Dunes National Lakeshore

Population	No. Trees Cored	Entire Population Sampled	Oldest Tree	Year of First Seedling	
				Youngest Pre-1935 Recruit	Oldest Post-1935 Recruit
MD-1	19	Yes	1911	1928	1949
MD-2	20	No	1960	—	1964
WB-1	27	No	1919	1930	1949
DA-1	25	No	1926	1932	1949
OD-5	2	No	1914*	—	—
OD-1	2	No	1920*	—	—

*Largest trees found at these sites were cored and aged.

Overall, jack pine size and age distributions are highly correlated, suggesting a lack of suppression. Jack pine size is a good predictor of age with correlation coefficients about 0.7 in 3 of 4 populations. Regression slopes indicate that diameter increases by 0.69 to 1.27 cm in an average year. This high growth rate, if maintained for 60 years, places lakeshore jack pines into a "good" site index (11).

White Pine. A complete age distribution for white pine is available from DA-2, a mesic pocket site on the lakefront (Figure 12). This population includes the largest (75.1 cm dbh) and oldest (162 years) white pines sampled. The latter individual has a fire scar dating from about 1879, the approximate date that the five next largest pines were established. All other white pines in DA-2, with one exception, are 68-111 years old; the number present slowly declines in younger age classes. Only one living tree originated within the last 64 years—a 19-year-old tree established on an encroaching dune.

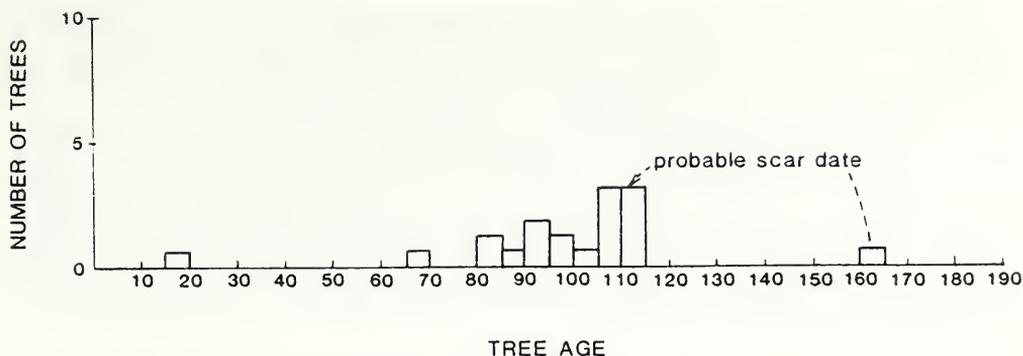


FIGURE 12. Age structure of white pine population at DA-2.

The history of population KE-1, the only other white pine population available for aging, was similar in history to DA-2. The oldest tree was 132 years old; peak recruitment occurred between 80 and 110 years ago; and only two trees sampled were younger than 60 years. While seedlings exist in this population, poor recruitment of canopy trees since 1900 suggests that high seedling mortality has prevailed.

The size of white pine at DA-2 is fairly closely related to age ($r = 0.69$, $p < 0.001$), and the average year resulted in an increment of 0.47 cm dbh. This growth is near the bottom of a range cited for dominant white pine (11). Growth at Keiser has been slower and more variable, and the age size correlation ($r = 0.30$) is not significant.

Discussion

Significant differences in the structure of the pine stands and the makeup of the pine populations reflect both the highly diverse dune environments and the distinct roles of the two species. Most evident is that white pine is less widely distributed and less vigorous than jack pine at Indiana Dunes. This distinction is curious, given that jack pine is at its southern range limit and is uncommon in most other southern Lake Michigan dunes (6; person. observ. of authors), whereas white pine is or was found widely in the region. However, industrial and urban development have destroyed areas that supported stands of both species (29, 32). White pine was highly valued as lumber, and merchantable trees may have been largely removed from the dunes area by the early twentieth century.

Based on site physiognomy, and confirmed by quantitative vegetation analyses, jack and white pine are components of many community types in the dunes. Based on ordinations, cluster analyses, and analysis of forest structure, five types of pine communities can be distinguished: lowland pannes, pine woodlands, dry-mesic mixed slope forests, mesic pockets, and swamp forests. Jack pine is lacking only in mesic pockets, while white pine is absent in lowland pannes, dune-complex woodlands, and some swamp forests. The pine woodlands [pine dune of Krekeler (18)] are most widespread. Such woodlands are one of several intergrading community types in the dune-complex (32). Lowland pannes [pine bottoms, (6)] and mesic pockets are the most floristically distinct [see (6) for a detailed discussion]. The swamp forests are a heterogeneous group; our stands resemble the hydromesophytic forest/conifer swamp and pin oak flat classifications of Wilhelm (6). Pines were heavily logged in these communities (6) and current stands may be recovering from that disturbance.

The ordering of community types from open to closed formations also suggests the successional sequences proposed by Cowles (6, 7) and Olson (24). Pines are generally

assumed to play a seral role at the dunes. What evidence does our data provide to suggest that those community types represent a successional series? We examined the evidence separately for jack pine and white pine communities.

Jack Pine. Size and age distribution and seedling recruitment of jack pine suggest that at several sites the species is a long-term feature of the dunes landscape. Jack pine should survive in the near future at all but one (DA-3) of the studied sites, although it may share dominance with basswood and black oak in some local areas. Reproduction and dominance are particularly impressive in the wet open areas lacking significant numbers of other tree species. Jack pine establishment is commonly highest in moist, open situations (4, 11, 27).

The role of fire in jack pine persistence at the dunes is unclear. Although over most of its range the species carries serotinous cones, this is not generally true of dunes populations. In most areas, however, jack pine success is related to periodic burning (3, 8, 28), although Cowles (6) thought that fire would promote a shift from pines to oaks in dune systems. The availability of unforested areas with a mineral soil seedbed at the dunes appears to allow continued recruitment and survival of jack pine without fire. Fire currently occurs at fairly high frequencies in oak stands characteristically lacking either pine species at Indiana Dunes (13), but little information has been summarized for other communities.

Among the several tree survivorship models suggested to have general interpretative value, the negative exponential or "reverse J" size distribution is thought to represent a population in which mortality is constant over a range of sizes, and reproduction is sufficient to maintain population levels (20, 21). White pine recruitment is quite low, causing important deviations from a negative exponential curve. In contrast, jack pine distribution at Indiana Dunes is very closely modeled by the negative exponential ($r^2 = .922$, $P < 0.001$), strong evidence that jack pine self-replacement is likely. Rapid and consistent jack pine growth at four dunes sites suggests its lack of shade tolerance (11) and the lack of success of competing species. We suspect that stands dominated by jack pine, those with abundant reproduction, have been characterized generally by open canopies.

Jack pine populations also contain all ages, a typical condition for self-reproducing stands (1, 19). Although jack pine has established periodically during this century, no survivors were found that established between 1928 and 1949. The recruitment gap may be related to the effect of drought on germination and subsequent establishment, but pollution stress also may have been involved.

The forest structure of jack pine stands, its continued recruitment in most stands, the present density of juvenile individuals, and a healthy growth rate all suggest that jack pine is self-replacing in many Indiana Dunes stands. Conditions appear too harsh for more shade-tolerant species to be important invaders.

Although Cowles (6, 7) emphasized the great resistance of the dune systems to change, he stated that "probably the oaks follow the pines, but the evidence on which this is based is not voluminous" (7, p. 174). He excluded exposed dune crests from this shift; there, pines might persist (6). Olson (24) suggested that first-generation pine stands would be "rapidly replaced" by black oak. He compared "invading" stands of young pine with decadent, adjacent stands at OD-5. However, 34 years later, hardwoods are still absent from jack-pine-dominated portions of these stands; the pine species being replaced are largely white pine. Thus, jack pine replacement by oaks, if it occurs, takes place only quite gradually. In contrast to assertions of both Cowles and Olson, jack pine upland communities are largely stable, compositionally.

Cowles suggested that oaks should be excluded by the hydric conditions of pine bottoms, but did not speculate on succession there. Downing (9) described pannes as temporary phases in dune formation and Olson (24) implied as much in his model

of community change. However, we agree with Wilhelm (32) that jack-pine-dominated pannes have a high degree of stability.

White Pine. Unlike jack pine forests, white pine forests appear to be a temporary stage of vegetation succession throughout Indiana dunes. White pine appears to be in demographic decline at all sites, because more shade-tolerant species dominate all but the upper vegetation stratum. Only at SP-7 is there evidence that white pine is competing successfully. Depending on site, replacement by oaks (black, red, white), basswood, or red maple is likely, although dense populations of understory trees (especially witch hazel) and shrubs in mesic and wet-mesic forests may slow the transition. The growth rates of adult white pine at two sites have been slow and variable, suggesting that competition may be inhibiting vigor.

The low levels of current white pine recruitment are long-standing, judging by age distribution in residual stands. At one mesic pocket, fire may have eliminated most white pine trees established before 1879, while providing suitable conditions for recruitment. This evidence is consistent with previous work showing that white pine establishment often responds well to fire (14, 17), although other disturbances such as clearing can initiate regeneration. Further recruitment is sometimes possible in the absence of major disturbance (15). Data on fire frequency at the Indiana Dunes area, with the exception of oak stands (13), is not available.

The poor recruitment of white pine in the last half-century, the low numbers of seedlings currently established, and the slow growth rate of adults suggest that white pine forests may indeed be shifting toward hardwood domination. These results agree with Cowles's (6) and Olson's (24) assessment of white pine stands at IDSP.

Acknowledgments

We wish to thank Jane Molofsky and Jeanette Daniel for their assistance in the field, and Jane Molofsky for her help in data analysis. Jerry Olson contributed useful ideas during several field trips. This research was supported by the Denver Office of the Air and Water Quality Division of the National Park Service, and by Holcomb Research Institute.

Literature Cited

1. Abrams, M.D. 1984. Uneven-aged jack pine in Michigan. *Journal of Forestry* 82(5):306-307.
2. Bacone, J.A., R.K. Campbell, and G.S. Wilhelm. 1980. Presettlement vegetation of the Indiana Dunes National Lakeshore. Proc. Second Conference on Scientific Research in the National Parks, San Francisco. Vol. 4. Resource Analysis and Mapping. National Park Service, Washington, D.C. 364 pp.
3. Carlton, T.J. 1982. The composition, diversity, and heterogeneity of some jack pine (*Pinus banksiana*) stands in northeastern Ontario. *Canadian Journal of Botany* 60(12):2629-2636.
4. Cayford, J.H., Z. Chrosiewicz, and H.P. Sims. 1967. A Review of Silvicultural Research in Jack Pine. Canada Department of Forestry and Rural Development, Forestry Branch, Departmental Publication No. 1173.
5. Connell, J.H. and R.O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *Am. Nat.* 111:1119-1144.
6. Cowles, H.C. 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. *Botanical Gazette* 27:95-117, 167-202, 281-308, 361-391.
7. Cowles, H.C. 1901. The physiographic ecology of Chicago and vicinity; a study

- of the origin, development, and classification of plant societies. *Botanical Gazette* 31:73-108, 145-182.
8. Cwynar, L.C. 1977. The recent fire history of Barron Township, Algonquin Park, *Canadian Journal of Botany* 55(11):1524-1538.
 9. Downing, E.R. 1922. A naturalist in the great lakes region. Univ. of Chicago Press, Chicago, IL (cited in Wilhelm 1980).
 10. Drury, W.T. and I.C.T. Nisbet. 1973. Succession. *J. Arnold Arbor.* (Harvard Univ.) 54:331-368.
 11. Fowells, H.A. 1965. Silvics of Forest Trees of the United States. U.S. Department of Agriculture, Forest Service. Agriculture Handbook 271.
 12. Gauch, H.G., Jr. 1982. Multivariate Analysis in Community Ecology. Cambridge University Press, Cambridge.
 13. Henderson, N.R. and J.N. Long. 1984. A comparison of stand structure and fire history in two black oak woodlands in northwestern Indiana. *Bot. Gaz.* 145:222-228.
 14. Henry, J.D. and J.M.A. Swan. 1974. Reconstructing forest history from live and dead plant material—An approach to the study of forest succession in southwest New Hampshire. *Ecology* 55(4):772-783.
 15. Hibbs, D.E. 1982. White pine in the transition hardwood forest. *Canadian Journal of Botany* 60(10):2046-2053.
 16. Hill, M.O. 1979. TWINSPAN—A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Ithaca, NY. Cornell University (Cited in Guach 1982).
 17. Horton, K.W. and G.H.D. Bedell. 1960. White and Red Pine: Ecology, Silviculture, and Management. Canada Department of Northern Affairs and National Resources, Forestry Branch. Bulletin 124. Ottawa, Ontario, Canada.
 18. Krekeler, C.H. 1981. The Biota of the Indiana Dunes National Lakeshore. Chapter 3. In M. Reshkin, W.E. Keifer, C.H. Krekeler, N.V. Weber, and L. Brunansky (eds.), *Ecosystem Study of the Indiana Dunes National Lakeshore, Volume Two*. Indiana Dunes National Lakeshore Research Program, Report 81-01. U.S. Department of the Interior, National Park Service, Midwest Region. pp. 3-1 to 3-346.
 19. Larsen, W.C. 1982. Structure, Biomass, and Net Primary Productivity for an Age-Sequence of Jack Pine Ecosystems. Ph.D. Dissertation, Michigan State University. (Cited in Abrams 1984.)
 20. Lorimer, C.G. and L.E. Frelich. 1984. A simulation of equilibrium diameter distributions of sugar maple (*Acer saccharum*). *Bulletin of the Torrey Botanical Club* 111(2):193-199.
 21. Meyer, H.A. and D.D. Stevenson. 1943. The structure and growth of virgin beech-birch-maple-hemlock forests in northern Pennsylvania. *Journal of Agricultural Research* 67:465-484. (Cited in Lorimer and Frelich 1984.)
 22. Odum, E.P. 1969. The strategy of ecosystem development. *Science* 164:262-270.
 23. Olson, J.S. 1951. Vegetation-substrate relations in Lake Michigan sand dune development. Ph.D. Dissertation, University of Chicago, Department of Botany, Chicago, IL.
 24. Olson, J.S. 1958. Rates of succession and soil changes on southern Lake Michigan and sand dunes. *Botanical Gazette* 119(3):125-170.
 25. Peet, R.K. and N.L. Christensen. 1980. Succession: a population process. *Vegetatio* 43:131-140.
 26. Pickett, S.T.A. 1982. Population patterns through twenty years of old field succession. *Vegetatio* 49:45-59.
 27. Shirley, H.L. 1945. Reproduction of upland conifers in the Lake States as affected by root competition and light. *American Midland Naturalist* 33(3):537-612.

28. Swain, A.M. 1973. A history of fire and vegetation in northeastern Minnesota as recorded in lake sediments. *Quaternary Research* 3(3):383-396.
29. Swink, F.A. and G. Wilhelm. 1979. Plants of the Chicago Region. 3rd edition. Morton Arboretum. Lisle, IL.
30. U.S. Department of Agriculture. 1981. Soil Survey of Porter County, Indiana.
31. U.S. Department of Agriculture. 1972. Soil Survey of Lake County, Indiana.
32. Wilhelm, G.S. 1980. Report on the Special Vegetation of the Indiana Dunes National Lakeshore. Indiana Dunes National Lakeshore Research Program, Report 80-01. U.S. Department of the Interior, National Park Service.

