Effects of Anthropogenic Disturbances on Endangered and Threatened Plants at the Indiana Dunes National Lakeshore

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ABSTRACT: Populations of 81 Indiana endangered and threatened plants were investigated and quantified in the Indiana Dunes National Lakeshore during 1984–1988. To assess the status and management needs of these species, we interpreted the effects of settlement and current land use on their populations and natural communities. Species populations were classified by their occurrences 1) in natural communities and 2) under various natural or anthropogenic disturbance regime categories. Over half of the populations of these plants were found to occur in habitats that either were under frequent disturbance regimes or supported successional communities. About 25 percent were in human-impacted communities, while anthropogenically-derived habitats accounted for over half of these occurrences. Thirty-five species were found to have strong negative or positive reactions to human disturbance; their status was affected by anthropogenic and natural disturbance processes, stochastic environmental events, national lakeshore management, and interactions between these factors. Lakeshore, lake bluff, and dune populations were found to be under stress from visitor impact and anthropogenic effects on shoreline processes. Fire protection has led to the decline of fire-tolerant species of savanna, prairie, fen, and white pine communities. Some species are essentially restricted to anthropogenically derived habitats such as utility rights-of-way. Under the current park management regime of low fire frequency and protection from disturbance, further decline of prairie and savanna species and other fire-adapted taxa is anticipated. Some species may become restricted to artificially disturbed habitats. Unless the accelerated lakeshore erosion cycle is changed, lakeshore vegetation and species loss will continue. Management is needed to increase the frequency of burning, protect beach and dune habitat from human use and erosion, and maintain rare species in anthropogenically disturbed habitats.

INTRODUCTION

Maintenance of rare plants is often considered a by-product of management for natural conditions, especially in large, species-rich preserves. Although this is a desirable management objective, few remaining natural areas are large enough to contain the natural disturbance regimes and community mosaics (Noss 1987) necessary for maintaining high species diversity. Indeed, under disturbed or isolated community conditions, specific or high-intensity management may be necessary to maintain species richness and rare species populations. Occurrences of rare species in habitats under anthropogenic disturbance regimes offer an extreme example of this concept. Here, where natural communities may be significantly altered, species management requires careful assessment; strategies will vary in relation to the intensity and history of human impacts and, paradoxically, may focus on the maintenance of unnatural conditions (White 1984).

Understanding the different dynamics of natural and anthropogenic disturbance processes is fundamental in selection of management options for rare plants and their associated plant communities. Natural disturbances are critical in the establishment and maintenance of plants and in shaping natural plant communities (Grubb 1977, Sousa 1985), and often occur in gradients of disturbance frequency and intensity within and across communities (White 1979). Anthropogenic disturbances can simulate these natural processes, represent disturbance extremes, or occur out-of-phase with natural processes under which plant associations have evolved. Results may include disruption of ecosystem resilience through selection for weedy or non-native taxa, and the establishment of new plant communities at the expense of native species assembleges (Denslow 1985).

We examined the status and distribution of 81 State of Indiana endangered or threatened plant species (Aldrich et al. 1986) at the Indiana Dunes National Lakeshore. Our objectives were to (1) assess the status of these plants in relation to natural and anthropogenic disturbance regimes, and (2) project the stability and management needs

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of these species. Critical questions are: To what extent do rare plants respond positively or negatively to anthropogenic disturbances? Can causal factors be identified or suggested for these responses? To what extent do anthropogenic disturbance regimes simulate or affect natural disturbance processes? Will affected plant species persist under the current national lakeshore protection and management program? If not, what management actions should be taken to ensure species survival?

STUDY AREA

The Indiana Dunes National Lakeshore (Figure 1) comprises 5250 ha (13,000 acres) owned and managed by the U.S. National Park Service (4367 ha) and the Indiana Department of Natural Resources (883 ha). These properties provide a wide array of habitats and plant communities containing more than 1000 native plant species and over 100 Indiana endangered and threatened plant taxa (Bowles et al. 1985, 1986a, 1986b, Wilhelm 1980). These rare species exhibit affinities for boreal, Atlantic Coastal Plain, prairie, and eastern deciduous forest floras, as well as endemism to the Great Lakes region (Peattie 1922, Welch 1935, Swink and Wilhelm 1979). This high species diversity is a result of the site's geographic location and the diverse, dynamic nature of the southern Lake Michigan environment. Bordering almost 40 linear km (25 mi) of the southern tip of Lake Michigan in Indiana, the national lakeshore includes both nearshore and inland dune systems (Reshkin 1981). The nearshore complex consists of geologically recent beach and foredunes, and older Calumet Dunes supporting extensive sand forest with savanna and prairie remnants (Figure 2). Located behind and parallel to the Calumet Dunes is a broad, linear, interdunal depression characterized by graminoid fen and marsh, and forested fen communities. Immediately to the south is the Northern Indiana Public Service Company (NIPSCO) utility corridor. This right-of-way contains electrical transmission lines and towers, a railway line, and a bicycle trail; it is mowed less than annually and is dominated by graminoid vegetation. Located further inland are the older Tolleston dunes, which were deposited during higher levels of glacial Lake Michigan and now support sand savanna vegetation. Located essentially within the national lakeshore are a steel mill and four villages, which fragment the Indiana DunesNational Lakeshore ecosystem, add to traffic flow and recreational use, and create a need for extreme care in prescribed burning and wildfire management. Also included in the national lakeshore are the satellite areas Pinhook Bog (sphagnum bog), Hoosier Prairie (state-owned and managed sand savanna, prairie, and marsh), and the Heron Rookery (floodplain forest).

Numerous studies have examined the roles of dune and soil formation processes, soil chemistry, fire regimes, and microclimate in developing plant community successional stages in the Indiana Dunes National Lakeshore (e.g., Cowles 1899, Fuller 1911, 1912, Kurz 1923, Olson 1958, Henderson

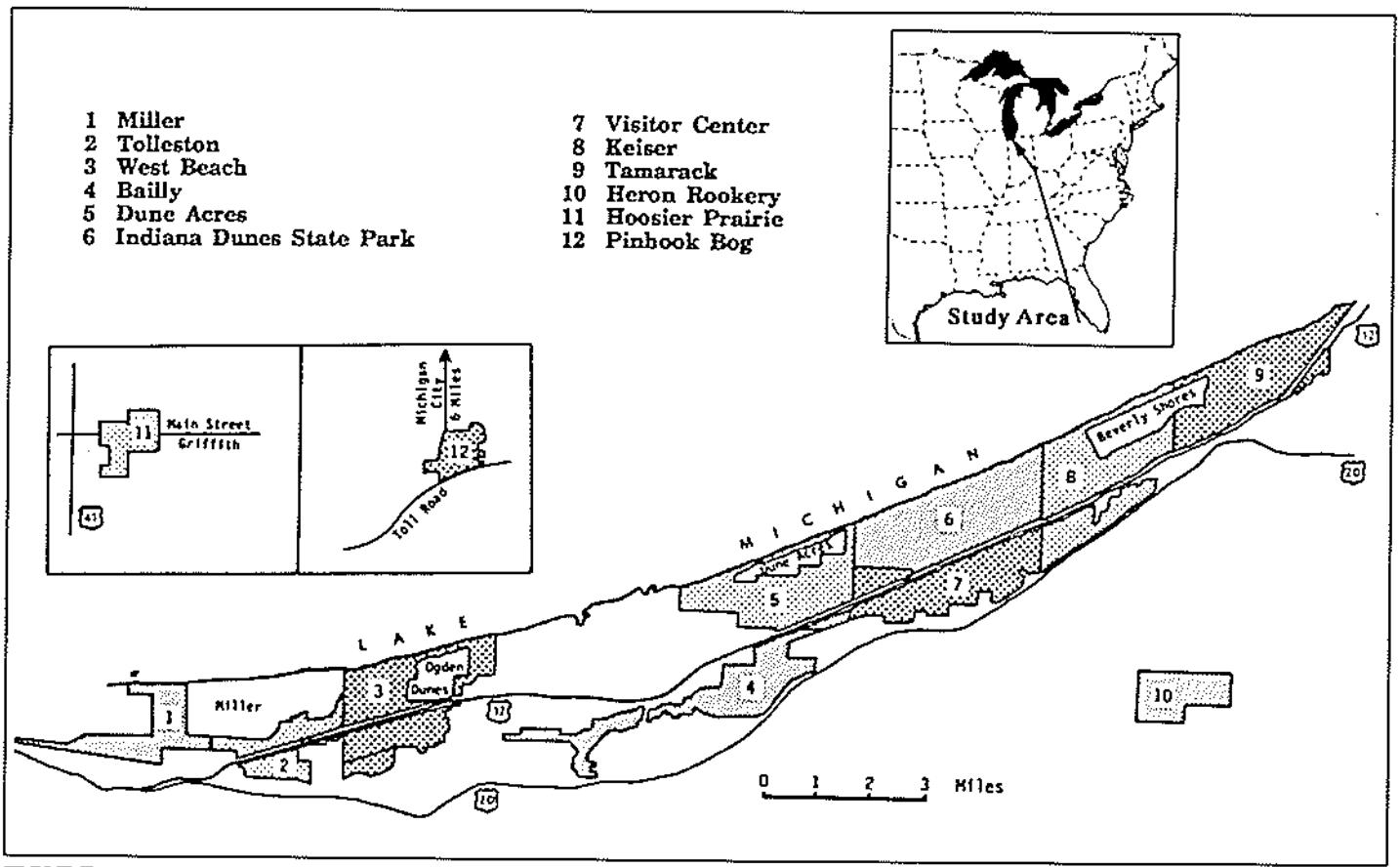

FIGURE 1. Vegetation survey units of the Indiana Dunes National Lakeshore.

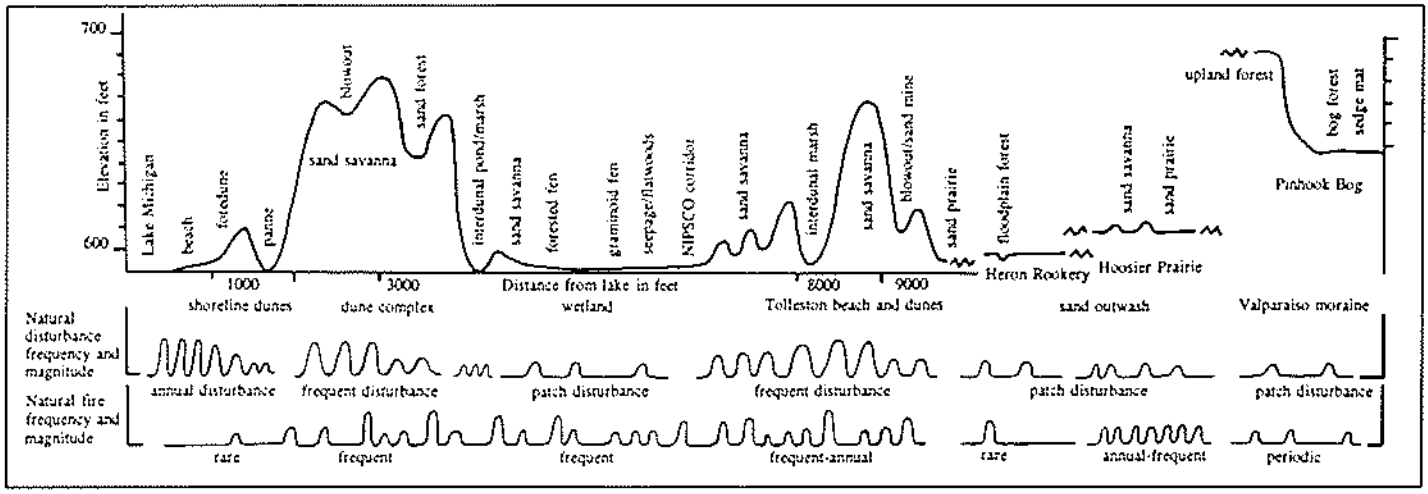

FIGURE 2. Natural community model for the Indiana Dunes National Lakeshore in relation to elevation, distance from Lake Michigan, and conceptual fire and disturbance regimes. See Table 2 for community and disturbance characterizations. Waveform patterns indicate relative disturbance frequencies between communities, height indicates disturbance severity, and width indicates disturbance intensity (sensu White and Pickett 1985).

and Long 1984). Fire, soil characteristics, and water table levels also are important factors affecting the character and distribution of prairie (Cole and Pavlovic n.d.), wetland (Wilcox et al. 1986, Wilcox and Simonin 1987, 1988), and dune panne (Hiebert et al. 1986) communities at the national lakeshore.

Imposed on the Indiana Dunes National Lakeshore ecosystem have been the historic impacts of European settlement (Lyon 1927, Peattie 1930, Pepoon 1927, Moore 1959, Apfelbaum 1984, Hiebert and Pavlovic 1987, Cole 1987, Wilhelm 1980). These include agricultural grazing and cropping, logging, sand mining, drainage, dune erosion and blowout formation, out-of-season burning, and invasion of natural areas by a Eurasian flora. Protection from natural fires has allowed burning under high fuel loads, while lowered water tables have allowed burning of normally hydric habitats. Major effects have included deterioration of most of the formerly widespread pine forest, wetland, and savanna communities, and elimination of virtually all upper level vertebrate carnivores (probably with a concomitant increase in vertebrate herbivores). Although examples of most plant communities were protected with establishment of the 900-ha Indiana Dunes State Park in 1927, and the surrounding national lakeshore in 1966, recreational beach use still exposes nearshore vegetation to high levels of impact. During recent years of high lake levels, natural beach and foredune erosion and replenishment processes have been destabilized by human impact in the eastern portion of the national lakeshore (Wood and Davis 1987). Here, sand movement by the westward-moving longshore currents is blocked by the Michigan City harbor structure and areas of private shoreline riprapping. In the inland dunes, the current lakeshore management regime has resulted in reduced fire frequencies (Henderson and Long 1984) and erosion rates in areas formerly burned or kept open by disturbance from off-road vehicles (ORVs) prior to National Park Service acquisition.

METHODS

The status and distribution of 81 Indiana endangered or threatened plant taxa in the national lakeshore were determined in 1984–88 by surveying, mapping, and quantifying population distributions (Bowles et al. 1985, 1986a, 1986b, Bowles 1987, 1988, 1989). Associated natural plant communities (cf. White 1978, Indiana Division of Nature Preserves 1979, Wilhelm 1980) were determined for each species as well. In addition, each species occurrence was assigned to one of five disturbance regime categories (Table 1) reflecting a gradient of successional stages and site disturbance histories. When discernible, anthropogenic vs. natural disturbances were differentiated for each category. For this study, species population occurrences were analyzed in a community by disturbance regime matrix. In this matrix, related plant communities were combined into ten community types for initial analysis (Table 2), and then further condensed for statistical analysis into six broad community groups:

- beach and dune complex
- sand prairie and savanna
- upland forest
- wetland forest
- graminoid wetland
- anthropogenic communities

Chi-square analysis was used to test for heterogeneity of species occurrences among each of the six community groups, and for independence of species occurrences from natural vs. anthropogenic disturbance regimes in the five natural community groups. Similarly, chi-square analysis was used to test for heterogeneity of species occurrences among all disturbance regime categories, and for independence of natural vs. anthropogenic disturbances in these categories. The distributions of species found to be strongly affected either positively or negatively by anthropogenic disturbances were further analyzed in table form.

Plant nomenclature follows Swink and Wilhelm (1979).

TABLE 1. Disturbance categories developed for assignment of species occurrences. Each successive category occurs along a conceptual gradient of decreasing frequency of disturbance. When discernible, anthropogenic vs. natural disturbances were differentiated for each occurrence.

1. *Annual/high-frequency disturbance* — Very frequent, widespread habitat disturbances often supporting annual, biennial strongly rhizomatous, or short-lived species. E.g., wave action or drawdowns along lakeshores or pannes, active blowouts, or managed trails and rights-of-way.
2. *Patch Disturbance* — Localized, frequent disturbance events allowing colonization or release of species within a larger, more stable community structure. E.g., tree-fall gaps or tip-ups, small natural blowouts, abandoned vehicle trails, or trail construction.
3. *Early-Successional* — Relatively widespread, often severe disturbances resulting in colonization by vegetation that does not represent original natural community richness or structure. E.g., old, large blowouts (usually of anthropogenic origin), abandoned sandmines, abandoned fields, or recently cleared and disturbed forests.
4. *Mid-Successional* — Relatively widespread, moderate disturbances resulting in species richness and community structure intermediate between early- and late-successional stages. E.g., second-growth forests following severe fire or logging, and grazed prairies.
5. *Late-Successional* — A disturbance history ranging from infrequent large-scale disturbances to a more predictable pattern of patch disturbances, resulting in more stable stand structure. In this successional stage, disturbance from fire is often a maintenance phenomenon, and species richness is high, with conservative perennial species. E.g., old growth or essentially undisturbed forest, prairie, savanna, or wetland communities.

RESULTS AND DISCUSSION

Statistical Summary

One hundred thirty-one population occurrences of 81 state-listed species were studied within the national lakeshore. These populations were distributed evenly among all six plant community groups (including human-derived habitats), and their distribution pattern was independent of natural vs. anthropogenic disturbances among the five natural communities (Figure 3). More than 25 percent of the populations were in anthropogenically disturbed habitats; of these, about half were in disturbed natural communities and half in habitats disturbed beyond recognition and classification as natural communities (Figure 3). When species were compared by types of disturbance regimes that they occupied, proportionately more occurrences were in the late-successional category (Figure 4). However, more occurrences were in other categories, and their overall distribution was not independent of natural vs. anthropogenic disturbances. As might be expected, population occurrences associated with human impact were concentrated in the most frequent disturbance regime categories, where anthropogenic disturbance is an important factor (Figure 4).

Thirty-five species (over 40 percent) exhibited either strong negative or positive responses to anthropogenic disturbances (Table 3). Species with negative responses represented almost 25 percent of this group, and occurred most often in the most heavily used recreational areas in the national lakeshore. More than half of the species responses to human impact were positive; the majority of these were in anthropogenically derived or artificial habitats. Here, human disturbances apparently simulate natural processes occurring elsewhere in the lakeshore, as is suggested by the additional presence of most of these species in natural communities (Table 3). However seven species were restricted entirely to artificial habitats, with no natural community analogs.

Factors affecting species status and distribution

When anthropogenic disturbances simulate natural processes, they may paradoxically support rare species. Or, when human disturbances are out of scale or phase with natural disturbance processes, they may destabilize or exacerbate natural disturbance regimes and threaten species with extirpation. These processes and resulting management problems have been documented at the Great Smoky Mountains National Park (White 1984) and national seashores on the east coast (Godfrey and Godfrey 1974), and they occur in the Indiana Dunes National Lakeshore. Within the national lakeshore, the occurrence, distribution, and relative stability of rare plant populations in habitats affected by human use can be accounted for by essentially five factors: (1) frequency and intensity of anthropogenic disturbances, (2) presence or absence of natural disturbance processes, (3) intensity of stochastic environmental events, (4) existing management regimes, and (5) interactions between these factors.

Negative anthropogenic impacts, and interactions with stochastic environmental events

The nearshore beach and dune environment receives the most intense anthropogenic impact of any natural system in the national lakeshore. Recreational use and shoreline erosion have caused the decline or loss of at least four plant species adapted to these habitats. The beach species *Cakile edentula* is known to be negatively affected by beach recreation (Payne and Maun 1984), and it declines along increasing gradients of beach use at the lakeshore (Bowles 1989). Although this species is rare on heavily used beaches, it apparently has high potential to recolonize this habitat during years of low disturbance. *Euphorbia polygonifolia* is more sensitive to beach

TABLE 2. Classification, characteristics, and anthropogenic effects for natural communities at the Indiana Dunes National Lakeshore. References: Apfelbaum 1984, Bacone et al. 1980, Cole and Pavlovic n.d., Haney 1986, Hiebert and Pavlovic 1987, Hiebert et al. 1986, Henderson 1987, Henderson and Long 1984, Indiana Division of Nature Preserves 1979, Olson 1958, White 1978, Wilhelm 1980, Wilcox and Simonin 1987, 1988, Wilcox et al. 1984, 1986, Wood and Davis 1987.

COMMUNITY	CHARACTERISTICS	ANTHROPOGENIC IMPACTS
Beach/Foredune	Continuous wave action and sand movement. Dominated by annuals and rhizomatous perennial vegetation.	Negative impacts on beach and foredune vegetation by summer beach use. Natural shoreline processes are modified by shoreline development.
Dune Complex	Steep topography subjected to cycles of sand erosion and deposition in patches or blowouts. Recreational disturbances create smaller blowouts.	Creation of large (>50 ha) blowouts since settlement. Predominant features are large (up to 50 ha)
Sand Savanna	Probably the dominant presettlement vegetation of the national lakeshore. Usually on irregular dune topography. Open dune conditions maintained by frequent fires. Presettlement conditions were comparatively open.	Extent of community and species diversity reduced through fire suppression. Disturbance through ORV trails and utility rights-of-way.
Sand Prairie	Probably occurred throughout the lakeshore on usually level, frequently burned sites. Also occurs where lake level fluctuations maintain prairie as a successional stage.	Extent of community and species diversity reduced through fire suppression.
Upland Forest	Occurs on sites protected from frequent intense fires, such as dune hollows or ravine slopes. Ground fires may have been important in affecting species diversity and community structure.	Lake Michigan bluff erosion exacerbated by shoreline development. Disturbance through trail maintenance and development.
Forested Fen	Occurs on calcareous peat soils, supports relict boreal plant community. Structure affected by fire and water table.	Severely reduced and altered by drainage, logging, and fire protection.
Graminoid Fen	Occurs on calcareous peat soils, supports species with boreal and prairie affinities. Open conditions maintained by frequent fires and water table.	Severely reduced and altered by fire protection and drainage.
Forested Bog	Occurs on acid peat soils, supports relict boreal plant community. High species diversity in bog openings or pools. Blueberries dominate most portions.	Former management for blueberries (fire?). Impact from boardwalk construction and trail use.
Flatwoods	Occurs on seasonally wet mineral soils or seepages. Microtopography supports high species diversity.	Fire protection, drainage, and logging may have reduced species diversity.
Graminoid Wetlands	Formerly a widespread complex of fen and marsh in interdunal areas of high water tables and frequent fire.	Almost eliminated by extensive drainage and fire protection.
Anthropogenically derived communities:		
Utility and railroad rights-of- way	Graminoid communities maintained primarily by mowing along the NIPSCO right-of-way.	Apparently maintained by human intervention.
Abandoned sand pits	Wetland communities in areas excavated to the water table. Successionally unstable.	Occur as a result of human activity.
Abandoned home sites	Successional communities occurring on razed homesites. Highly compacted or altered soils limit succession.	Occur as a result of human activity.
Fly-ash drainage ponds	Interdunal ponds polluted by drainage of fly-ash ponds.	Heavily polluted by human activity.

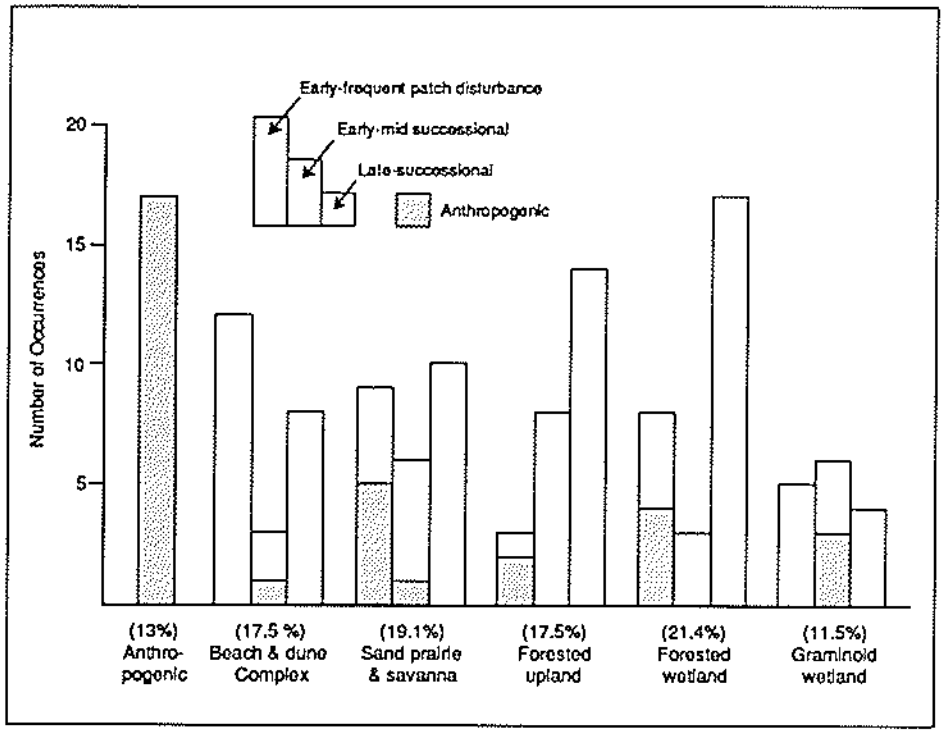

FIGURE 3. Distribution of 131 occurrences of 81 endangered or threatened plant species by natural community groups and disturbance regimes at Indiana Dunes National Lakeshore. Species occurrences are independent of communities ($X^2 = 5.4$, $P>.25$), and are independent of natural vs. anthropogenic disturbances within communities ($X^2 = 4.81$, $P>.25$).

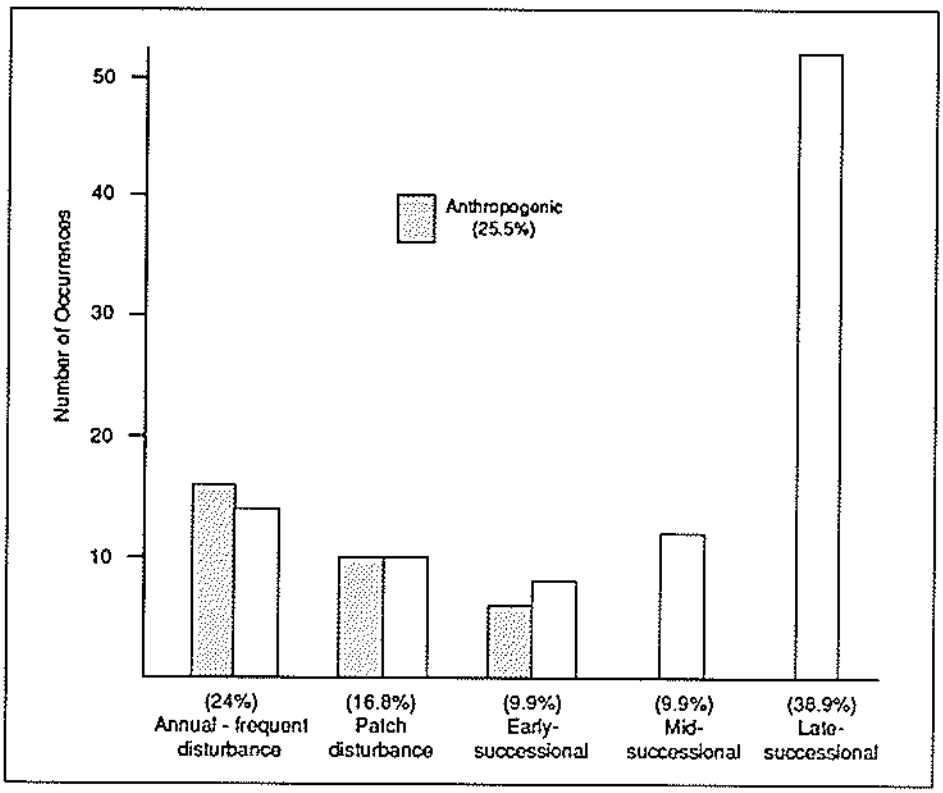

FIGURE 4. Distribution of 131 occurrences of 81 endangered or threatened plant species along a gradient of disturbance regimes at Indiana Dunes National Lakeshore. Species occurrences are not independent of communities ($X^2 = 38.73$, $P<.001$), and are not independent of natural vs. anthropogenic disturbances within disturbance regimes ($X^2 = 43.11$, $P<.001$).

use and is essentially absent from heavily used beaches. Although this species occurs in adjacent foredunes, its recovery potential is limited by recreational impacts on these habitats. In contrast, the perennial *Lathyrus japonicus* var. *glaber* and the monocarpic *Cirsium pitcheri* no longer occur on their former (Lyon 1927, Pepoon 1927, Peattie 1930, Deam 1940) beach and foredune habitats. These plants now are extremely rare and are restricted to blowout areas in the nearshore dune complex (Bowles et al. 1985). Here populations are isolated from gene flow because shoreline disturbances prevent establishment and migration of plants along the shoreline corridors that they once occupied. Larger blowouts that are apparently of anthropogenic origin (Bacone et al. 1980) now contribute to the maintenance of these species in the lakeshore. However, herbivory on seedlings by rabbits limits some *C. pitcheri* population sizes in blowouts (S. Weller pers. comm.), while trampling by humans also may contribute to local extinctions (Gibson 1988).

Erosion and trampling from overuse of beach access and hiking trails have been extreme in traditional recreation areas of the Indiana Dunes. Locally, loss of sand from the peaks and slopes of formerly stable dunes has exposed more than one vertical meter of tree roots. Two of the most potentially threatened species are *Melampyrum lineare* and *Polygala paucifolia*. One *M. lineare* population is now under impact from slope erosion, while one of two known *P. paucifolia* populations is threatened by an eroding dune trail.

In the eastern survey units, severe erosion of beach and lake bluff occurred during a series of high lake-level years. This process was activated by storm events and exacerbated by human altering of the shoreline that blocked normal sand replenishment by long shore currents. Since 1984, the lake bluff has eroded more than 50 m inland (Wood and Davis 1987) through mature upland forest, resulting in loss of habitat for one of two known Indiana populations of *Oryzopsis asperifolia*. The last two remaining individuals of this colony were removed and transplanted into inland habitat for use in restoration (Bowles 1988).

TABLE 3. Community occurrences by disturbance, and responses of 35 endangered (E) and threatened (T) plant species to anthropogenic disturbances at the Indiana Dunes National Lakeshore. F = annual or frequent disturbance, E-M = early- to mid-successional, L = late-successional disturbance regime. Positive (+) response = apparent survival or increase under anthropogenic disturbance, negative (-) response = apparent decline or absence from once occupied habitat, neutral (o) response = occurrence is under natural conditions, asterisk (*) indicates that the anthropogenic disturbance regime provides the primary habitat for this species in the national lakeshore. Note: species responses to fire suppression are not included; see text for discussion.

SPECIES (Status)	Anthro-pogenic	Beach/Dune Complex			Sand Savanna and Prairie			Upland Forest			Forested Bog/ Fen & Flatwoods			Graminoid Fen/wetlands		
		F	E-M	L	F	E-M	L	F	E-M	L	F	E-M	L	F	E-M	L
Actaea rubra (T)					(-)											
Aristida tuberculosa (T)					(+o-)											
Cakile edentula (T)		(-)														
Carex flava (E)	*(+)[1]															
Carex chordorrhiza (E)											(+)	(o)				
Carex conoidea (E)	(+)[1]				(o)											
Carex folliculata (E)	(+)[1]												(o)			
Carex limosa (E)											(+)	(o)				
Cirsium pitcheri (T)		(-)	(+o)													
Eleocharis melanocarpa (E)	(+)[2]						(o)									
Eleocharis wolfii (E)	(+)[1]				(o)											
Euphorbia polygonifolia (T)		(o-)														
Hudsonia tomentosa (T)	(+)[3]				(+o-)											
Juncus scirpoides (E)	*(+)[1,4,5]															
Lathyrus japonicus (E)		(-)	(+o)													
Ludwigia sphaerocarpa (T)	(+)[2]															(o)
Lycopodium inundatum (E)	*(+)[1]															
Melampyrum lineare (T)							(o)	(-)		(o)			(o)			
Milium effusum (T)								(+-)		(o)						
Myosotis laxa (E)	(+)[1]	(-)									(+o)					
Oryzopsis asperifolia (E)								(-)		(o)						
Poa alsodes (T)								(+-)		(o)						
Polygala paucifolia (E)								(-)		(o)						
Psilocarya scirpoides (T)	(+)[2]															(o)
Polygonella articulata (T)					(+o-)											
Rhynchospora globularis (E)	*(+)[1]						(o)									
Rhynchospora macrostachya (T)	(+)[2]															(o)
Scirpus hallii (E)	*(+)[5]															
Selaginella rupestris (T)					(+o-)	(+o)										
Sisyrinchium angustifolium (E)	*(+)[1,6]															
Spiranthes lucida (T)	*(+)[6]															
Talinum rugospermum (E)					(+o-)											
Utricularia geminiscapa (E)											(+o)		(o)			
Utricularia subulata (E)	(+)[1]	(o)														
Xyris caroliniana (T)											(+)					
TOTALS	(* = 7) (+) = 20	(-) = 5 (o) = 4 (+) = 2			(-) = 6 (o) = 10 (+) = 6			(-) = 5 (o) = 5 (+) = 2			(-) = 0 (o) = 8 (+) = 6			(-) = 0 (o) = 3 (+) = 0		

[1] Mowed railroad/utility right-of-way (wet-mesic).
[2] Polluted fly-ash drainage pond (wet-mesic).
[3] Abandoned ORV trails and utility right-of-way (dry-mesic).
[4] Abandoned roadbed (mesic).
[5] Abandoned sand mine (wet-mesic).
[6] Abandoned homesite (mesic).

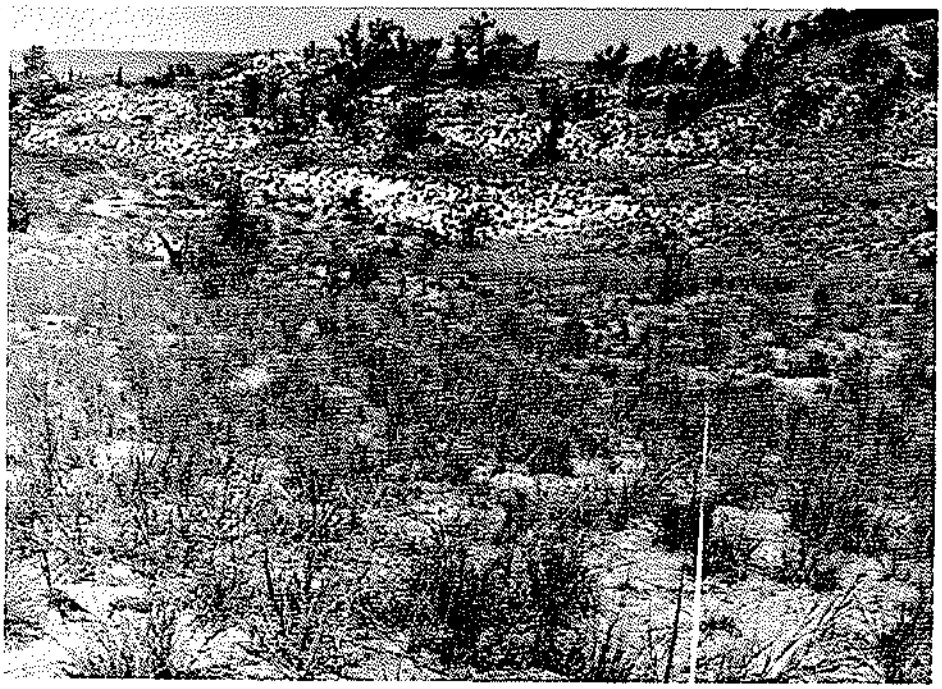

FIGURE 5. Large blowouts (>50 ha) in the dune complex near Lake Michigan are probably of anthropogenic origin, and provide habitat for *Cirsium pitcheri*.

FIGURE 6. *Hudsonia tomentosa* occupies open sand habitat maintained under power lines in the Tolleston Dunes.

Extreme shoreline erosion and degradation of seepage habitat near the eastern border of the national lakeshore also has apparently caused the local extirpation of the wetland species *Myosotis laxa*, which was reported from this area by Krekeler (1981).

Suppression of natural fire processes: negative impacts

Fire suppression is one of the most significant postsettlement causes of natural community deterioration and species decline at the Indiana Dunes National Lakeshore, primarily through woody canopy closure and succession to shade-tolerant species (Bacone et al. 1980, Wilhelm 1980). Most assessments of these effects have been made at the structural level—e.g., community-dominant species in sand savanna (Henderson and Long 1984, Henderson 1987), pine stands (Menges and Armentano 1985, Haney 1986), sand prairie (Cole and Pavlovic n.d.), and graminoid wetlands (Apfelbaum 1984). Information on the historic distribution of associated rare species is primarily anecdotal (e.g., Lyon 1927, Pepoon 1927, Peattie 1930, Deam 1940, Wilhelm 1980), and observations on fire effects are often obtained without experimental controls. However, information on species' historic distributions, their absence from fire-suppressed areas, and their appearance in areas now under fire management regimes, can suggest strong correlations with fire frequencies.

Examples of highly fire-dependent savanna species are the annual or biennial herbs *Corydalis sempervirens* and *Geranium bicknelii*. These plants characteristically appear (primarily from seed banks) following fire (Wilhelm 1980, Swink and Wilhelm 1979). They are essentially restricted in distribution to the fire-managed Hoosier Prairie, though *G. bicknellii* also appeared at Howes Prairie (a remnant within the dune complex) after initiation of prescribed burning (Bowles 1988). Similarly, the perennial species *Aralia hispida*, *Aster sericeus*, and *Stipa avenacea* are most frequent in high-quality savanna remnants with recent fire histories.

Although white pine has been reduced in extent at the Indiana Dunes National Lakeshore by many factors (Cole 1987), the structures of remnant stands indicate lack of pine reproduction and invasion by deciduous tree species — apparently correlating with lack of fire (Menges and Armentano 1985, Haney 1986). In addition, fire protection may have led to the loss of at least one species, *Habenaria hookeri*. This orchid was last observed to occur in a single pine stand in the national lakeshore (Swink and Wilhelm 1979), where it has not been relocated.

Fire protection also has led to severe decline or loss of graminoid fen and sand prairie, except in the fire-managed Hoosier Prairie. Here, population size of the fire-adapted (Bowles 1983) orchid *Cypripedium candidum* has increased more than 50 percent since 1983 in association with frequent prescribed burns (Bowles 1988). In contrast, at Cowles Fen this species occurs as a few individual plants in a graminoid community (Bowles 1987), which has been reduced in size and diversity by cattail invasion (Wilcox et al. 1984) and fire suppression (Apfelbaum 1984). At Howes Prairie, the historically known *Habenaria ciliaris* disappeared after years of fire suppression (Wilhelm 1980), and it has not reappeared after an initial burn at this site. Also at Howes Prairie, *Buchnera americana* populations have declined almost 50 percent (Bowles 1988) with or without burning. This decline could be related to population fluctuations occurring as a result of the parasitic biology of this species, and may be insignificant over a large time scale.

Simulation of natural processes by anthropogenic disturbances: benefits and threats

In the Tolleston Dunes savannas, artificial disturbance patches are occupied by the annuals *Aristida tuberculosa* and *Polygonella articulata*, and perennials *Hudsonia tomentosa*, *Selaginella rupestris*, and *Talinum rugospermum*. Under natural conditions, these species colonized blowouts and other small disturbances kept free of competing vegetation in part by frequent presettlement fires (e.g., Tolstead 1942, Henderson 1987). Now they occur at relatively high densities in patches opened by disturbance from off-road vehicles and power line maintenance (Figure 5, Bowles et al. 1985, Bowles 1989). Paradoxically, these species may decline from succession and competition under current National Park Service management, which excludes prescribed burning and protects against anthropogenic disturbances at Tolleston. Fire protection also promotes fuel buildup and potential for intense wild fires that could negatively affect the fire-sensitive perennial species. Recently, *T. rugospermum* has been negatively affected by illegal ORV use of trails colonized by this species. Although power line right-of-way habitat contributes to maintenance of these species, use of herbicides or grading for right-of-way maintenance could eliminate their populations.

In mesic sand forest, trail construction and moderate trail use has created linear patches colonized by *Poa alsodes* and *Milium effusum*, species of forest tree gaps and openings. Now, large and high-density populations of these species occur along trails (Bowles 1989) in the national lakeshore. Ongoing trail maintenance and widening also present a management dilemma, threatening these populations that occur as a result of past trail construction. An analogous situation occurs with the perennial herb *Myosotis laxa*, which occurs naturally along spring runs and colonizes natural tip-up disturbances in forested fen habitat. However, its highest density colonies occur in disturbances along trail corridors (Bowles et al. 1985). At Cowles Fen, construction of improved boardwalk facilities will lessen the anthropogenic disturbance habitat available for colonization by this species.

At Pinhook Bog, disturbances from foot traffic are frequent along the boardwalk trail. These patches add to habitat heterogeneity and species richness in a bog environment where many herbaceous species are restricted to natural openings around bog pools. Blueberries (*Vaccinium* spp.) are the dominant vegetation. For example, *Xyris caroliniana* primarily occurs along the boardwalk; it was unknown from the site until 1980 and may be a recent addition to the bog flora. The native species *Carex limosa* and *C. chordorrhiza* also occur naturally around bog pools; but their population levels are supplemented by high densities in disturbance openings along the boardwalk (Bowles et al. 1985). The native bladderwort *Utricularia geminiscapa* is most abundant in bog pools at Pinhook Bog, but also occurs in smaller openings associated with the boardwalk. In Ontario, Canada, at the Mer Bleue Bog, this species was most abundant in large bog pools caused by bombing practice during World War II (Haber 1979).

Species occurrences in anthropogenically derived communities

Habitats supporting anthropogenically derived communities occur throughout portions of the national lakeshore. They are represented by managed rights-of-way, sand mines, abandoned homesites, and fly-ash drainage ponds. These habitats present a management dilemma where their persistence maintains rare species and adds to floristic diversity of the national lakeshore. Under these conditions, species maintenance needs are not well defined and management prescriptions or treatments are essentially unknown. Furthermore, although management or restoration toward more natural community conditions might seem desirable, methods to achieve this goal while maintaining rare plant species will require knowledge of individual species' ecological requirements.

A 10 km (6 mi)-length of the NIPSCO right-of-way bisects one of the most ecologically diverse sections of the national lakeshore. This corridor contains unnatural assemblages of native and introduced graminoid vegetation. To keep the corridor free of woody vegetation, it is mowed and herbicided prior to 1983 by NIPSCO. The periodic mowing probably simulates fire by maintaining open conditions for shade-intolerant plants, while the past chemical treatments may account for the absence of many native species and presence of other weedy plants. Native species may be relicts of former open natural communities that occurred in the vicinity of the right-of-way,

while others appear to have colonized from adjacent natural areas. Alternative sources of species include seed banks and introductions. Seven state-listed species occur in the NIPSCO right-of-way, three of which are also in natural communities within the national lakeshore (Table 3). *Carex flava* var. *fertilis* occurs only in a single locality at NIPSCO, while *Juncus scirpoides*, *Lycopodium inundatum*, and *Sisyrinchium angustifolium* also are found in similar anthropogenic habitats elsewhere in the lakeshore. *L. inundatum* was reported from the general area of the right-of-way by Lyon (1927), which suggests that at least some of these species have been here for many decades. A smaller NIPSCO right-of-way maintained by mowing at Hoosier Prairie provides habitat for five species (*Carex conoidea*, *Eleocharis wolfii*, *Lycopodium inundatum*, *Rhynchospora globularis* var. *recognita*, and *Utricularia subulata*).

Sand mining occurred in the inland Tolleston Dunes area before 1938, leaving abandoned sand pit depressions at or near the water table. Such habitats are colonized by graminoid and herbaceous vegetation (often including rare species), which eventually succeeds to woody vegetation (Swink and Wilhelm 1979). The unique diversity and persistence of sand pit communities may be related to contributions from seed banks and disturbance from surface water table fluctuations similar to that of lake and pond borders (e.g., Keddy and Reznicek 1982, 1986). Two sand pits on lakeshore property contain *Juncus scirpoides*. One contains *Scirpus hallii*, which is known to occur in Indiana only at this and one other sand pit. In addition, the colonizing species *Aristida tuberculosa*, *Polygonella articulata*, and *Hudsonia tomentosa* occur in sand spoil adjacent to sand pits. In the Indiana Dunes National Lakeshore, species such as *Scirpus hallii* may be restricted to seed banks for long time periods and appear vegetatively only as an artifact of human or natural disturbances.

More than 800 abandoned homesites occur in the national lakeshore; they are characterized by altered soil profiles and soil chemistry, and successional vegetation stages (Hiebert and Pavlovic 1987). Two listed species are restricted to these or other anthropogenic habitats in the lakeshore. The only known lakeshore occurrence of *Spiranthes lucida* is from a single observation at one homesite. This orchid is often characteristic of successional communities in human-disturbed habitats, where its populations may not persist over time (Case 1987). Though most frequent in the NIPSCO right-of-way, *Sisyrinchium angustifolium* is also known from one abandoned homesite.

Fly-ash pond drainage sites are highly polluted wetland habitats that were formerly used as drainage sites for dewatering of fly-ash ponds. They are now undergoing primary succession after halting of drainage and pollution. Four state-listed species (*Eleocharis melanocarpa*, *Ludwigia sphaerocarpa* var. *deamii*, *Psilocarya scirpoides*, and *Rhynchospora macrostachya*) have appeared at these sites (Figure 7). These species occur in natural wetland habitat adjacent to the east (Figure 8) and probably arose in situ from seed banks left from former vegetation.

MANAGEMENT ASSESSMENT AND RECOMMENDATIONS

Negative human impacts on natural vegetation are often chronic and severe problems in areas associated with excessive or uncontrolled recreational use. Such impacts are often associated with trampling or ORV use of dune systems (Bowles and Maun 1982, Carlson and Godfrey 1989) and desert areas (e.g., Webb and Wilshire 1983). The positive responses of species to anthropogenic disturbance identified in this paper do not necessarily imply that human impact is beneficial to endangered species. Rather, they document interactions between species and disturbance that are in need of further investigation at both the species and community level. Researchers and preserve managers should focus on resolving these paradoxes by understanding their underlying mechanisms and then applying this information toward restoring the natural disturbance processes simulated by human disturbance.

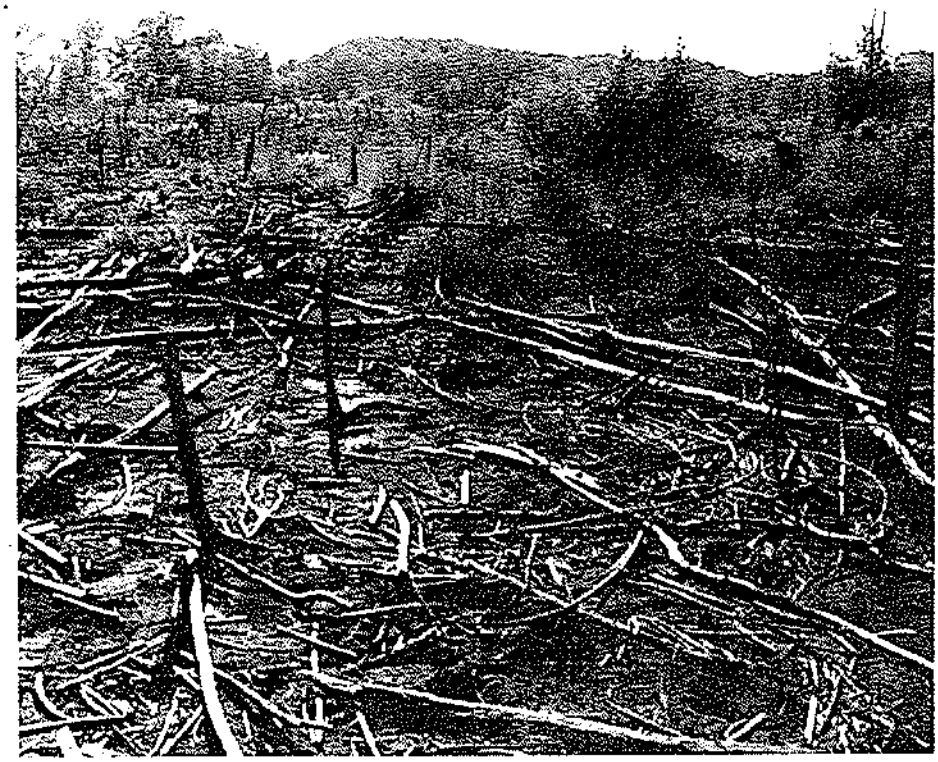

FIGURE 7. Polluted fly-ash drainage ponds provide habitat for the rare species *Eleocharis melanocarpa*, *Ludwigea sphaerocarpa*, *Psilocarya scirpoides*, and *Rhynchospora macrostachya*, which may have appeared from seed banks.

FIGURE 8. Natural occurrences for the rare species *Eleocharis melanocarpa, Ludwigia sphaerocarpa, Psilocarya scirpoides,* and *Rhynchospora macrostachya* are in relatively undisturbed interdunal ponds that undergo summer drawdowns.

Minimizing direct anthropogenic impacts

The shoreline and adjacent dunes of the national lakeshore have been severely affected by summer recreational use and anthropogenic destabilization of natural shoreline processes. Recommendations for protecting beach and nearshore dune vegetation include (1) removal and prevention of shoreline stabilization structures in and near the national lakeshore, (2) isolation of selected beach and foredune areas from recreational use, and (3) continued protection of fragile areas from visitor impact through trail and boardwalk construction. However, maintenance of natural assemblages of beach vegetation in the eastern lakeshore units may be precluded by exacerbated beach erosion, even with fenced beach exclosures (Post and Bowles 1989). Beach-adapted annual species are expected to persist within the national lakeshore, with lower population densities in areas of high beach use. However, the more conservative *Cirsium pitcheri* and *Lathyrus japonicus* need recovery actions to reestablish populations in beach areas kept free of recreational use. These areas could provide corridors to genetically link fragmented blowout populations. Such a beach corridor system should be developed in the more stable central portion of the lakeshore, linking nearshore dune systems along beaches that can be isolated from recreational use.

Trail-use damage to naturally occurring plant populations can be avoided through proper maintenance. Species threatened by erosion from overuse of steep dune trails can best be protected by trail closures or construction devices that will prevent erosion. Where rare species occur along trails, visitor use should be restricted to trail boundaries, and direct management such as mowing or cutting should be avoided. Monitoring should be continued for damage from trail use on species that have colonized patches originally created by these trails. More long-term research is needed to determine how maintenance of these populations will relate to overall survival of the species in the national lakeshore.

Fire protection and anthropogenic disturbance interactions

At the Indiana Dunes National Lakeshore, fire research, protection, education, and management policies regulate burning frequency. Prescribed burns are experimental in approach and thus are limited. Efforts should be made to accelerate the transition from this limited experimental approach to this program. Research findings on effects of various fire regimes should be applied to a parkwide fire management program, with objectives of simulating, to the extent possible, the known presettlement burning regime; reducing fuel loads; maintaining or restoring fire-dependent vegetation types; and maintaining high plant species diversity. Wildfires should be allowed to spread naturally through areas where cultural or other significant features are not threatened, thereby increasing burning frequency.

Communities most severely impacted by low fire frequency include extensive savanna areas, graminoid fen and prairie remnants, and white pine stands. For example, at the Tolleston Dunes savannas, rare species occupy anthropogenically derived habitats and smaller natural openings. An increased fire frequency is needed to help maintain natural openings and reduce fuel loads that threaten perennial species. The pattern of frequent prescribed burning used to manage Hoosier Prairie should be used as a model for management of other savanna complexes within the lakeshore, especially sites with high species diversity and recovery potential such as Howes Prairie. Similarly, burning should be initiated to recover graminoid fen portions of Cowles Fen supporting rare species such as *Cypripedium candidum.* Recovery of white pine stands (especially the site known to historically support *Habenaria hookeri*) should be initiated. Ground fires are needed to reduce invasion of deciduous tree species and stimulate establishment of white pine.

Anthropogenic habitat maintenance

Because of the restriction of some rare species to the NIPSCO right-of-way, and its maintenance of possibly remnant

graminoid vegetation, management of this area is critical. Experimentation and monitoring are needed to determine if successional changes are occurring, and to learn how to manage for species diversity and rare species in this habitat. NIPSCO currently maintains an advance notification agreement with the national lakeshore for mowing on the right-of-way. In addition, management burns by the lakeshore on the right-of-way are allowed by agreement but have not been initiated. Prescribed burning probably is the most useful and practical management alternative to mowing and should be used. However, there are hazards associated with burning under high-voltage power lines, especially with the high public use of this area.

Abandoned sand pits containing rare species present a unique management problem. Long-term succession may be toward woody vegetation at the expense of herbaceous annual or early-mid successional species such as *Scirpus hallii* and *Juncus scirpoides*. These sites also are being invaded by the exotic purple loosestrife (*Lythrum salicaria*), which should be eliminated. Prescribed burning could be used experimentally to maintain herbaceous vegetation, but may result in succession toward other graminoid vegetation at the expense of rare species. Management for natural sand pond conditions with water table fluctuations that prevent woody succession and select for seed-banking species appears most appropriate, but may not be easily achieved.

Management needs of fly-ash drainage ponds are encompassed by long-term monitoring to track successional changes and moderation of pollution. The national lakeshore maintains such a monitoring program for this area.

CONCLUSIONS

Although the Indiana Dunes National Lakeshore comprises a cluster of relatively large management units, it represents a fragmented and impacted ecosystem. Species respond both positively and negatively to frequency and intensity of human disturbances, management, and natural disturbance processes. As a result, active management will be required to conserve some endangered and threatened plant species and the national lakeshores' species richness. Clearly, natural disturbance processes must be maintained or simulated for these species and anthropogenic disturbances that have negative effects must be avoided. Monitoring and research should be continued on rare species and community requirements, and the knowledge obtained should be applied toward overall park management.

Negative impacts are most severe along the Lake Michigan shoreline. In addition to recreational impacts, destabilization of the natural shoreline erosion and replenishment processes have resulted from interactions between shoreline development and recent high lake levels. Such effects and their related negative impacts on sensitive species and ecosystems are often symptomatic in dynamic natural systems (e.g., Menges and Gawler 1986, Bowles 1989); their reversals require reduction of human disturbance, efforts that may be difficult or improbable in some areas.

The negative effects of fire suppression on communities and species richness have been widespread through savanna, pine forest, prairie, and fen. Although human disturbance has simulated fire disturbance processes to some extent in savanna areas, species occurrences in these habitats appear successionally unstable and, paradoxically, may decline under total protection from human disturbance. Similarly, in other communities, increased burning is needed to maintain communities and species diversity.

The presence of rare species in anthropogenically derived habitats presents a second management paradox. Species maintenance adds to overall lakeshore species richness, and is desirable; so when natural communities for these species do not exist, management must be identified that can simulate natural processes that maintain the species and communities.

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