

WINDSTORMS AND THE DYNAMICS OF TWO NORTHERN FORESTS

A THESIS

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ABSTRACT

Thunderstorm winds (estimated at 25-35 m/sec) often damage scattered trees in two northwestern Minnesota forest stands (Itasca State Park, Clearwater County). Windstorms have different consequences for populations of shade-intolerant trees in the two stands. In the pine-maple stand, sandy loam soils support a well-developed understory of Acer saccharum, Ostrya virginiana, and tall shrubs, which usually survive wind damage and continue to shade the forest floor. Damage and mortality rates are highest for Populus tremuloides, Pinus resinosa, and Pinus strobus, populations of which are infected with wood-rotting fungi. Windstorm-related microsites (mounds, pits, stumps, logs) have only 6% areal coverage and are dominated by seedlings of Acer saccharum and Acer rubrum, the same species that dominate control plots. Hence colonization opportunities for shade-intolerant trees rarely form when trees blow down.

In contrast, the pine-fir stand is on sandy soils and Acer saccharum and Ostrya virginiana are absent. The most shade-tolerant taxon, Abies balsamea, has weak wood and is prone to wind damage. Light gaps thus form more commonly than in the pine-maple stand. Microsites also have greater (18%) areal coverage. Rotting logs and stumps are major establishment substrates for Betula papyrifera, Abies balsamea, Populus tremuloides, Picea spp., and Pinus strobus in this stand. The resulting patchy distribution of understory trees makes for higher light levels and provides colonization opportunities

for shade-intolerant species, which are well-represented in smaller size classes in this stand.

The two stands differ in relative frequency of tree breakage and uprooting. However, mounds and stumps do not differ in colonizing flora, hence damage mode has little influence on forest composition.

This work illustrates two problems with the concept of ecological disturbance. First, many definitions of "disturbance" are based upon biotic responses and would include windstorms in the pine-fir stand but would exclude windstorms in the pine-maple stand where species diversity is not enriched. Second, fires and windstorms, both generally considered disturbances, have very different consequences and are not sufficiently analogous to be grouped together.

OVERVIEW OF THESIS

This dissertation explores the ecological effects of thunderstorm winds on two Minnesota forest stands. The research described here relates two bodies of ecological literature. One concerns disturbance, a term applied broadly to fires, windstorms, and many other forces. The disturbance literature reconstructs the frequency and consequences of historical events with special emphasis on how they can enrich species diversity by creating opportunities for inferior competitors (Paine and Levin 1971; Levin and Paine 1974; Armstrong 1976; Connell 1978). Past fire regimes have been inferred (Heinselman 1973, 1983; Frissell 1973; Foster 1983; Christiansen 1985), as have past windstorms with high-speed winds (>35 m/sec), such as hurricanes (Henry and Swan 1974; Oliver and Stephens 1977) and thunderstorm downbursts (Canham and Loucks 1984). Less is known about the importance of thunderstorm winds of lesser speed (25-35 m/sec) that blow down scattered trees and that occur with greater frequency than do more extreme windspeeds.

The second body of literature concerns gap dynamics in forests. Gap studies locate physical openings in the forest canopy, usually without knowledge of the cause of gap formation (Watt 1946; Bray 1956). Forest turnover rate is sometimes estimated from gap formation rate; and consequences for forest species composition and diversity are usually investigated (Williamson 1975; Barden 1979, 1981; Runkle 1981, 1984; Brokaw 1985a,b; Canham and Marks 1985).

The present study explores a mechanism for gap formation: moderate-velocity thunderstorm winds. I describe mortality and damage patterns caused by recent thunderstorms, and I discuss regeneration patterns resulting from such storms. In two forest stands just 8 km apart, the same windstorms have very different consequences for populations of shade-intolerant trees.

I argue that discussions of disturbance should uncouple physical forces (i.e., gusty winds of 40 m/sec) from biotic effects of those forces (i.e., increased species diversity). Otherwise windstorms qualify as diversity-enriching disturbances in one stand but would not be considered disturbances in the other stand, an odd and artificial distinction. I also conclude that fires and windstorms favor different sets of tree species and hence should not be grouped together under the umbrella of disturbance.

Chapter 1, "Windstorm Consequences in Two Minnesota Forests", describes mortality, gap formation, and tree regeneration resulting from recent windstorms in two forest stands within Itasca State Park in northwestern Minnesota. I asked if thunderstorm winds will benefit populations of shade-intolerant trees, hence maintaining or enriching species diversity. I found the answer to be yes in one stand and no in the other. The difference is traced to: (a) interspecific differences in mortality and damage rates, related in part to tree size distributions, species wood strength, and wood-rotting fungal pathogens; (b) different probabilities of canopy gap formation, as a result of forest structure and of characteristics of

understory tree species; and (c) differences in the importance of windstorm-caused microsites for tree regeneration.

Chapter 2, "Forest Microsites: Formation During Windstorms and Colonization By Trees," presents detailed information for the same two stands on how tree seedlings and sprouts are distributed among wind-related microsites: mounds, pits, stumps, and logs. These data provide insights into questions posed in Chapter 1, and they allow me to compare consequences of tree uprooting, which creates mounds and pits, with consequences of tree breakage, which creates stumps. Modes of tree damage and their correlates were surveyed for recent windstorms, and species patterns of damage mode and regeneration sites were compared.

The Appendix, "Description of a Vegetation Contact within the Pine-Maple Study Area," briefly examines two contrasting forest communities that meet at a sharp boundary. I present supplemental data on the vegetation, past vegetation, and soils across the contact, and I pose several hypotheses that might explain the observed differences, emphasizing the different consequences of windstorms and fires in this region.

Chapter 1. WINDSTORM CONSEQUENCES IN TWO FORESTS, ITASCA PARK,
MINNESOTA

INTRODUCTION

The frequency and ecological importance of severe windstorms has been demonstrated for several parts of the world (Sauer 1962; Lorimer 1977; Savill 1983; Canham and Loucks 1984). With windspeeds in excess of 35 m/sec (75 mi/hr), tornadoes, hurricanes, cyclones, and thunderstorm downbursts can produce large (>1 ha) blowdown areas in forests, causing forest turnover every 50 to 1200 years (Savill 1983; Lorimer 1977; Canham and Loucks 1984).

Windstorms of lower intensity occur more frequently but with different consequences for forests. Gusty winds of up to 35 m/sec (75 mi/hr) often precede thunderstorms (Battan 1961; Trewartha 1968) and are a major cause in some forests of mortality to scattered trees and of canopy gaps. Comparable windspeeds have a variety of other consequences: vine dominance in parts of North Queensland (Webb 1958), and fir waves, bands of tree mortality associated with rime ice buildup promoted by strong winds in subalpine forests of the northeastern U.S. (Sprugel 1976; Sprugel and Bormann 1981).

Here I describe consequences of thunderstorm winds that felled trees in two Minnesota forest stands. These two stands, though located just 8 km apart, were affected quite differently by the same windstorms because of floristic and structural differences. By examining effects of specific storm events, I differ in approach from

researchers who instead study physical gaps in forest canopies regardless of the time or cause of gap formation. Such canopy gaps have been the focus of much recent work because of their apparent importance to forest dynamics (Hartshorn 1978; Whitmore 1978; Runkle 1981, 1982, 1984; Brokaw 1985a,b; Pickett and White 1985). Gaps are the principal sites of establishment for certain light-demanding trees of neotropical forests (Van Steenis 1958; Brokaw 1985; Richards and Williamson 1975) and of deciduous forests in northeastern North America (Botkin et al. 1972; Williamson 1975; Bormann and Likens 1978; Barden 1979, 1981; Runkle 1982).

In some forests, however, light gaps are not the only sites of forest turnover (Lieberman et al. 1985). Not all dead trees form canopy gaps, as my work and that of Lieberman et al. (1985) show. Gaps that do form are often filled not by new colonists but by side growth of canopy trees (Gysel 1951; Oliver and Stephens 1977; Hartshorn 1978; Brokaw 1985a,b), or by extension growth of shade-tolerant saplings (Ehrenfeld 1980; Canham 1984; Oliver and Stephens 1977, Barden 1981; Hibbs 1982). Even the earliest studies of gap dynamics emphasized that existing plants are the usual beneficiaries of gap formation (Watt 1946; Bray 1956).

I examined tree mortality and regeneration resulting from thunderstorm winds that recur every 5-10 years at a given point in northwestern Minnesota (Simiu et al. 1979, 1980; Baker 1983). I asked if such storms will, over time, enrich species diversity in these forests by causing uneven mortality patterns and creating

regeneration opportunities that, taken together, favor shade-intolerant tree species. Alternatively, such storms could decrease or have no effect on species diversity, depending upon patterns of damage and tree reproduction.

STUDY AREAS

The two study areas are located in Clearwater County, Minnesota, within Itasca State Park. Itasca Park is a 13,000 ha forest preserve within a terminal moraine complex at about 47 degrees N latitude. The climate is continental, with a mean annual temperature of 3.7^o C and with mean annual precipitation of 640 mm, 2/3 during the growing season, which averages 90-100 days in length (Keuhnast 1972). Located near the current confluence of prairie, deciduous forest, and mixed coniferous-deciduous forest biomes (Figure 1), the park is a mosaic of forest types (Lee 1924; Kell 1938; Buell and Gordon 1945; Westman 1968; Hansen et al. 1974; Peet 1984) that is related to edaphic heterogeneity (Kell 1938; Buell and Gordon 1945; Hansen et al. 1974), to logging history (Aaseng 1976; Patterson 1978), and to past fires (Spurr 1954, Frissell 1973).

The two study areas (Figure 2) are similar in the presence (but not in the size distributions) of red pine, eastern white pine, paper birch, quaking aspen, and bigtooth aspen (Table 1 gives scientific names of plants mentioned in text, following Gleason and Cronquist 1963). The two stands have many structural and floristic differences that influence windstorm consequences.

Windstorms: The frequent occurrence of tree-damaging winds within Itasca Park is evident from abundant mounds, pits, stumps, and logs, most of which apparently resulted from wind damage (Chapter 2). Because of their frequency and larger areal extent, thunderstorm winds cause more property damage in Minnesota than tornadoes do, especially in northern areas like Itasca Park where tornado frequency is relatively low (Kuehnast 1972). Between July 1983 and July 1986 there were at least four windstorms that caused heavy tree mortality in the park (3 July 1983; 7 August 1984; 5 September 1985; 11 January 1986).

Absolute windspeed alone does not predict the amount of tree damage a storm will cause. Heavier damage may result from gusty winds, from wet storms (Brokaw 1985a), or from winds of unusual direction, to which tree reaction wood does not provide protection (Mergen 1954). Previous storms can injure trees and predispose them to breakage or uprooting in subsequent storms with only moderate windspeeds (Mergen 1954). On the other hand, a windstorm may have little effect on a forest if it follows other severe storms that have cleared out vulnerable trees.

For these reasons it is difficult to predict wind damage, and it is also difficult to infer windspeeds of past storms from the amount of damage. The most promising approach to understanding windstorm frequencies and consequences is long-term study of permanently marked forest plots where windstorm characteristics are also monitored.

This study provides only a tentative temporal framework for windstorm effects.

Prior to my work, windstorms were unstudied in northern Minnesota forests except for a damage survey in one stand (Hansen et al. 1974) and an unpublished investigation of a tornado strike (Lundgren 1954). The two study areas both sustained relatively heavy damage during a thunderstorm on 3 July 1983. Scattered trees were snapped or uprooted, but no large ($>2000\text{m}^2$) clearings were generated.

Windspeeds during this storm were not measured directly but probably reached a maximum between 27 and 34 m/sec (60-75 mi/hr), windspeeds that were recorded elsewhere in Minnesota and Wisconsin as part of the same storm system (NOAA 1983). The same storm system also spawned tornados and downburst winds (>45 m/sec) elsewhere. Heavy precipitation (125-150 mm in 24 hr) accompanied the storm in the Itasca State Park area (Minnesota State Climatologist's Office, unpublished), possibly increasing tree crown weight and contributing to tree damage rates.

Thunderstorms occur frequently in Minnesota (Kuehnast 1972), although not always accompanied by such high windspeeds. Windspeeds of 27 m/sec occur at a given place in Minnesota every 5-10 years on average (Simiu et al. 1979, 1980; Baker 1983), although this return interval probably has high variance in space and in time. Windspeeds are recorded at few weather stations. The return time range of 5-10 years comes from 4 weather stations: Minneapolis MN, Duluth MN, Sioux

City SD, and Fargo ND.

The pine-maple stand (N 1/2 NE 1/4 Sec.36 and S 1/2 SE 1/4 Sec.25, T.143 N, R.36 W) is a 40 ha study area surrounding a small lake (Budd Lake) and several marshes. It is located on glacial till within the Itasca moraine complex, with rolling topography (maximum relief of 35 m). The area's sandy loam soils are typic eutroboralfs (University of Minnesota 1980) whose physical and chemical characteristics were described by Kurmis (1969).

Vegetation is spatially heterogeneous within the 40-ha study area. Heterogeneity is most obvious in the well-developed understory. In some places the understory comprises several layers of sugar maple and ironwood saplings and seedlings. In other places it comprises dense growth of tall (2 m) shrubs, mostly beaked hazel and mountain maple, interspersed with red maple saplings. This heterogeneity is apparently related to edaphic factors and to fire and windstorm history (see Appendix). Parts of the stand are similar to that described by Peet (1984) but with less basswood and more red pine.

The top stratum of this forest is a broken supercanopy of large trees (50-70 cm DBH [diameter at breast height]) of red pine and eastern white pine. Few pines occur in smaller size classes (Figure 2a). Pines account for 55% of stand basal area but only 8% of stand density (for stems ≥ 2.5 cm DBH; Table 2). These scattered pines originated after a fire in 1727 A.D. (258 years old in 1985),

according to Frissell's (1973) analysis of fire scars. The maximum tree ring count from among 7 pines that I cored was 250 years, but precise ages are unavailable because of rotten tree centers. Red pine is rarely established without fire in this region (Frissell 1973). Most pines in the area have fire scars, attesting to at least one subsequent fire. Portions of the stand were affected by 8 major fires since 1700 A.D., according to Frissell (1973).

Beneath the supercanopy pines is an irregular canopy layer of paper birch, red oak, quaking aspen, and bigtooth aspen, which together account for 34% of stand basal area and 29% of stand density (Table 2). The concentration of these trees in one broad size class (20-25 cm DBH; Figure 2a) and their intolerance of heavy shade suggest a post-fire origin. Logging does not explain the establishment of these trees, because the only timber harvesting operation was a partial logging in 1918 A.D. of just the northern third of the study area (Aaseng 1976). The occurrence of a fire or several fires between 1880 and 1890 A.D. is inferred from my tree ring counts for 5 red oak trees (95-100 years old in 1983) and from tree age data from Ness (1971). Ness described the age structure of three stands (his plots #14, #62, #68) near my pine-maple study area. Some 80% of all birches (>28 trees cored), aspens (>40 trees), and red oaks (>19 trees) were 77 years of age in 1965, suggesting a fire date of 1888 for the origin of these tree populations. Frissell (1973) inferred fire dates of 1885 and 1891 for this area, based upon

fire scars on pines.

Subcanopy trees are scattered throughout the stand, including smaller paper birch and red oak trees and many sugar maple trees (31% of stand density, 4.1% dominance) and red maple trees (15.8% density, 5.4% dominance; Table 2). Most also date from the 1888 fire, with the exception of perhaps half of the sugar maple trees, which are younger but of varying ages (Ness 1971).

The pine-fir stand (W 1/2 NE 1/4 NW 1/4 Sec.2, T.143 N, R.36 W) is a 8-ha study area on a flat sandy outwash deposit along the shore of Lake Itasca (Figure 2). Soils are well-drained sands of undetermined series (University of Minnesota 1980).

The pine-fir stand is more homogeneous than the larger pine-maple stand. The canopy layer is more uniform, without supercanopy pines. Smaller white pine and red pine trees (ca. 30 cm DBH) make up 63% of stand basal area and share the canopy with balsam fir (15% of basal area), paper birch (4.6%), aspen (5.3%), white spruce, and, in wetter places, black spruce trees (10.8% of basal area, spruces combined; Table 3).

The pines and larger aspens and birches date from 1876, judging from tree core data obtained within this stand by Ness (1971; his plot #73). This was likely a fire date: the stand has never been logged (Aaseng 1976). Shade-tolerant firs and spruces became established less synchronously after that fire (Ness 1971).

The understory comprises a mosaic of dense patches of balsam fir

and spruce trees, open areas lacking tree growth, and scattered birch, aspen, and ash saplings. The latter three taxa are shade-intolerant, and their good representation in small size classes contrasts with the scarcity of small shade-intolerant trees in the pine-maple stand (Figure 2b).

The pine-fir and pine-maple stands differ in several other ways. Mesophytic deciduous trees and shrubs of the pine-maple stand, such as sugar maple, mountain maple, ironwood, and red oak, are absent from this pine-fir stand, perhaps because its sandier soil has low moisture retention, low cation exchange capacity, little available nitrogen, low pH, or all four (Buell and Gordon 1945; Kell 1938). Trees are smaller in the pine-fir stand, on average, and are more numerous (Table 3). Stand density is nearly twice that of the pine-maple stand (2166 stems per ha, vs. 1125 stems per ha), but tree basal area totals are similar (33.41 m^2 per ha vs. 30.43 m^2 per ha in the pine-maple stand). Birch and aspen trees are more minor components of this forest, while balsam fir and spruces, conifers scarce in the pine-maple stand, are the most numerous trees.

METHODS

Wind Damage and Correlates: In the 40-ha pine-maple study area I located all trees (stems ≥ 2.5 cm DBH) damaged during a windstorm on 3 July 1983. For each of 340 damaged trees, data were collected on species, cause of damage (wind or falling tree), survival of damage,

mode of damage (uprooted, snapped, bowed, branch broken), tree size (DBH and, where measurable, height), evidence of infection by heart-rotting and root-rotting fungi, and the number of other trees damaged by this tree's fall. For 80 of the trees damaged directly by wind, the existence and size of structural canopy gaps were noted, using Brokaw's (1982) suggested definition of a gap as an opening extending through the canopy down to a height of 2 m above ground. Both "base gaps," openings over the former base of a damaged tree, and "crown gaps," openings over the area where a tree's crown fell, were measured, and gap area was totalled for each tree.

Systematic strip sampling of the pine-maple stand was carried out to permit estimation of mortality rates within tree populations and to permit comparison of damaged and undamaged trees. I sampled 1.2 ha (0.03% of the study area) in linear plots measuring 1.65 by 50 m. All trees with DBH of at least 2.5 cm were identified and measured. Each stem of a multiple stemmed tree was tabulated separately because each represented a separate target for wind damage.

In the 8-ha pine-fir study area, effects of several recent windstorms were combined because distinguishing damage from the July 1983 storm was not possible in 1985 when field work began. Therefore mortality rates are not strictly analogous to those from the pine-maple study area, but relative damage rates within stands are generally comparable. Wind-damaged trees were identified within systematically spaced strip plots that covered 20,000 m², roughly 25%

of the stand. For each of 323 trees, data were collected, as in the pine-maple stand, on species, tree size, other trees damaged by this tree, and cause, survival, and mode of damage. No data were collected on fungal infections because of time elapsed since wind damage. For all 39 trees damaged directly by wind, structural canopy gaps were measured.

Background sampling for data on forest composition, density, and dominance was done in smaller strip plots covering 0.34 ha (0.04% of the pine-fir study area). All trees >1.5 m in height were identified and measured, but most analyses presented here include only those trees at least 2.5 cm in DBH, to make the data consistent with those from the pine-maple stand.

Windstorm-Related Regeneration: I combined two approaches to the difficult matter of documenting tree regeneration patterns. First, background sampling of saplings and seedlings was assumed to include some areas previously affected by windstorms, judging from the prevalence of wind-related microsites on the landscape (Chapter 2) and judging from frequency of comparable windspeed records from weather stations in the region (Simiu et al. 1979, 1980; Baker 1983). This approach assumes that absence of seedlings and saplings of a species indicates failure to regenerate in response to past thunderstorm winds. Tree data from systematic strip sampling were supplemented by data on tree stems smaller than 2.5 cm DBH, which were sampled in nested, systematically arranged seedling plots that

covered 272 m² in the pine-maple forest and 39 m² in the pine-fir forest.

In a more direct assessment of windstorm-related regeneration, I also censused vegetation on windthrow mounds, pits, stumps, and logs, most of which formed during windstorms. Methods for and results of this work are detailed in Chapter 2.

Data Analysis: Data were analysed using nonparametric and categorical tests (Sokal and Rolf 1981; Fienberg 1981) with formulae of the BMDP statistical software package (Dixon 1983).

RESULTS AND DISCUSSION

A. Mortality and Damage, Pine-Maple Stand: In the pine-maple study area, the July 1983 thunderstorm damaged an average of 8.5 trees per ha (340 trees in a 40 ha area), half of them killed and half surviving (Table 4a). Wind caused direct damage to 29%, while falling trees damaged 71% (Table 4a). The fall of the average wind-damaged tree thus damaged another 2.5 trees. In this stand, trees indirectly damaged by falling neighbors were more likely to survive (64% survival) than trees damaged directly by wind (23% survival; χ^2 test, $P < 0.01$, Table 4a).

Mortality rates (Table 5a) ranged from 0.1% to 3.0% of stems lost for various tree populations, with higher mortality rates for quaking aspen, bigtooth aspen, white pine, and red pine; and with

lower mortality rates for ironwood, sugar maple, red maple, paper birch, and red oak. Once damaged, stems of quaking aspen, red pine, and white pine were usually killed, while stems of ironwood, sugar maple, and red maple usually survived. For quaking aspen, a clonal species, ramet death represents loss of that site, although nearby ramets of the same genet may persist.

Uneven mortality rates among species are often seen within forest communities (Lemon 1961; Bruederle and Stearns 1985; Veblen 1986). Several factors contribute to these interspecific differences in mortality rates.

In the Minnesota pine-maple stand, tree size was one factor. Figure 4 compares average tree size (as DBH) among four groups of trees within each species: (1) background trees undamaged in the storm; (2) windstruck trees hit directly by wind (but not necessarily killed); (3) trees (ramets) killed, including trees killed by wind and by falling neighbors; and (4) all trees damaged, including those surviving. Asterisks (*) indicate a size distribution significantly different ($P > 0.05$) from that of background trees (first bar on the graph), based on Kruskal-Wallis tests.

As expected, larger trees were in general most prone to direct damage by wind. Windstruck trees were significantly larger than background trees of quaking aspen, red pine, and red maple. Mortality risk, like windstrike risk, was higher for large trees within these three species. For these same species and for ironwood, damaged trees including those surviving were also larger than

undamaged trees. For other species, tree size did not differ, on average, between background trees and trees either windstruck, killed, or damaged, although small sample sizes might explain this lack of pattern in some cases. These species included paper birch, bigtooth aspen, sugar maple, red oak, and white pine (Figure 4a)

Interspecific differences in mortality risk are not fully explained by the tree size effect. An additional species effect contributes to damage patterns. When background trees and damaged trees are pooled, stepwise logistic regression analysis (Fienberg 1981, Dixon 1983) shows that both tree diameter ($P < 0.01$) and tree species ($P < 0.01$) improve predictions of which trees were killed. The species effect on damage risk results from several confounded factors: infection by wood-rotting fungal pathogens, species wood strength, topographic position of trees, and tree geometry.

Heavy damage to the quaking aspen population is likely related to wood rotting fungal pathogens. By breaking down cellulose or lignin in wood and root tissues, fungi render trees more susceptible to wind damage (Hubert 1918; Romme and Martin 1982; Putz et al. 1983). In the pine-maple stand, pathogens infected many quaking aspen trees, as evidenced by fungal fruiting bodies, mostly of Phellinus igniarius, and numerous standing dead trees. I did not measure the background incidence of infections in undamaged trees, but 59 of 62 broken quaking aspen trees had clear evidence of heart rot, and all uprooted quaking aspen trees had rhizomorphs of the

root-rotting Armillaria mellea (Table 6).

Although I cannot relate fungal infections to damage patterns within species, it is likely that pathogens contribute to interspecific differences in damage rates. Besides quaking aspen, species whose damaged trees usually showed signs of fungal infection were red pine, white pine, and bigtooth aspen (Table 6), the same species with mortality rates higher than expected on the basis of tree abundance alone. Most pines in this forest had fire scars that admit heart-rotting fungal pathogens (Frissell 1973), which probably weaken resistance to wind damage. In contrast, damaged maples and ironwoods rarely evidenced heart rot. Damaged red oak and paper birch trees had intermediate frequencies of obvious fungal infections (Table 6).

The strength of healthy wood is another factor in wind damage patterns. Maximum tensile strength perpendicular to wood grain is perhaps the most relevant wood characteristic because tension wood breaks before compression wood in wind-damaged trees (Mergen 1954). Tensile wood strength corresponds well with species wind damage rates in this stand (Figure 5a; data from Markwardt and Wilson 1935). Species wood strength covaries with the incidence of fungal infection incidence, however.

Sugar maple has the strongest wood, by a variety of wood strength measures, of all tree species in the region (Markwardt and Wilson 1935), and its growth form also contributes resistance to wind damage, particularly in contrast with aspen (King 1986). These

characteristics permit sugar maple to benefit from windstorms. Although wood strength may be a simple consequence of slow growth rate, its adaptive value is clear. A search for different maple ecotypes among regions that vary in storm frequency could elucidate the possibility that windstorms have been selective forces favoring genotypes with strong wood or with wind-resistant growth forms.

Other factors, such as tree geometry and the topographic correlates of species distributions, may contribute to interspecific differences in damage rates. For example, the abundance of paper birch in low protected areas might help explain its low overall damage rate.

Given these large interspecific differences in damage rates, did mortality patterns favor shade-intolerant species normally expected to benefit, at least through regeneration opportunities, from disturbance? On the contrary, mortality rates were highest for several shade-intolerant species (aspen, white pine, red pine). When shade tolerance, as approximated on a relative scale by Fowells (1965) is plotted against mortality rate, there is no obvious relationship (Figure 6a), but it is clear that shade-intolerant species do not benefit from windstorm-related mortality patterns alone. Heavier mortality to several shade-intolerant species is not surprising, because shade-intolerant trees are in this stand taller and more exposed and are in general fast growing and weak wooded (Fowells 1965).

B. Mortality and Damage: Pine-Fir Stand: In the second stand, recent windstorms damaged approximately 143 trees per ha (285 trees in 2 ha), 86% of them killed and only 14% surviving (Table 4b). The higher density of damaged trees results from a higher density of living trees (2164 stems/ha, compared with 1123 stems/ha in the pine-maple stand), from the longer period of storm damage surveyed, and from susceptibility of understory trees to damage in this stand. Wind caused direct damage to only 14% of these trees, while 86% were damaged by other trees (Table 4b). There were thus 18 direct windthrows per ha, compared with 2.5 per ha in the pine-maple stand. The fall of the average wind-damaged tree in this pine-fir stand damaged another 6 trees (versus 2.5 in the pine-maple forest). Rates of survival were not significantly different and were low both for trees damaged by wind and for trees damaged by falling neighbors (X^2 test, $p=0.2552$; Table 4b).

Species mortality rates, which range from less than 1% to nearly 10% (Table 5b), were highest for spruce (combining white and black spruce) and for paper birch; and were lowest for white pine and red pine. The abundant balsam fir, though a conspicuous understory victim of falling canopy trees, had a mortality rate that was average for this stand. Damaged trees of all species were unlikely to survive, but paper birch had a slightly higher (31.3%) probability of surviving damage than did other species, most of which were conifers in this stand.

The correlates of wind damage in the pine-fir stand were complex. Direct damage by wind was a function of both tree diameter (Logistic regression, $P < 0.01$) and tree species (LR, $P < 0.01$), with paper birch and spruce hit more often than tree size alone would predict.

Within several species, direct damage by wind was more likely for large than small trees (Figure 4b). This pattern held for quaking aspen, balsam fir, spruce, and paper birch (Figure 3b), all of whose populations included a range of tree sizes. Mortality (black bars on Figure 4b) and damage were also more likely for large than for small trees within these populations except for birch. Damaged and undamaged birch trees did not differ in average size.

Heavy damage to understory trees complicates this size-damage relationship when direct and indirect causes of damage are combined. Within some species, small trees were the most damage prone overall and most likely to be killed. This was true for spruce and possibly for red pine and white pine, for which sample sizes were small (Figure 4b). The smaller, susceptible pines were probably old, suppressed trees.

Large interspecific differences in mortality rates followed patterns quite opposite those in the other stand, for species held in common. Paper birch had the highest mortality rate in the pine-fir stand but one of the lowest in the pine-maple stand. The converse is true for red pine and white pine, which had the lowest of mortality

rates in the pine-fir stand but among the highest in the pine-maple stand. Quaking aspen had an average mortality here in contrast to its very high mortality rate in the pine-maple stand.

These intraspecific differences between populations illustrate the difficulty of generalizing about windstorm consequences. Within a species, one population may be susceptible to wind damage while another is resistant. Different damage and mortality rates for red pine, white pine, and aspen are related to tree stature, tree age, and wood-rotting fungal infections. The pattern for paper birch, which had more mortality where trees were smaller on average (pine-fir stand), remains unexplained.

In the pine-fir stand, tensile wood strength does not help explain interspecific differences in mortality rate (Figure 5b). The strong-wooded species that sustained low damage rates in the pine-maple stand (Figure 5a) were absent from the pine-fir stand (Figure 5b). No data are available on pre-storm fungal infections of downed trees because of the time elapsed between damage and survey.

Windstorms did not preferentially remove trees of shade-tolerant species from the pine-fir stand. As in the pine-maple stand, there was no relationship between a species' shade-tolerance and its mortality rate (Figure 6b). Damage rates were the same (5.9%) for the most shade-tolerant taxon, balsam fir, and the least shade-tolerant taxon, quaking aspen. Damage rates for species intermediate in shade tolerance ranged from less than 1% for red pine to 10% for spruce. These results indicate that while windstorms do impose

species-selective damage, the pattern of damage does not directly favor shade-intolerant species.

C. Canopy Gap Formation: Pine-Maple Stand: Windstorms can influence forest composition not only through uneven mortality rates but also through creation of regeneration opportunities. Canopy openings may benefit established, shade-tolerant understory trees, or they may be colonized by new seedlings or sprouts of shade-intolerant trees. Which type of tree benefits will depend in part upon forest structure and the resulting shapes and sizes of canopy gaps.

In the pine-maple stand, few large treefall gaps formed during the 1983 windstorm (Figure 7a). Among 80 canopy trees felled by wind, 60% formed no canopy gap while 8% fell at edges of natural forest openings (marshes, lakes) not resulting from windstorms. Another 20% formed gaps smaller than 20 m^2 in size, while only 12% formed larger gaps ($20\text{-}94 \text{ m}^2$). Mean gap size, when gaps did form, was 27 m^2 . Gaps, defined as openings extending down through the canopy to a height of 2 m above ground (Brokaw 1982), would be larger using Runkle's (1981) extended gap criterion (area within trunks of surrounding trees), but the density of measurable gaps and their average size would remain small. Although the death of a canopy tree undoubtedly increases resource availability to other plants, it rarely does so in this stand by opening a discrete light gap.

In this stand, gaps were formed by only 32% of the canopy trees killed. If damaged understory trees were included, the proportion of

trees forming gaps would be still lower. This result is a consequence of an irregular, multilayered forest structure. Treefalls in monolayered forests are more likely to create light gaps than are treefalls in an uneven forest with a well-developed understory (Figure 8). The Itasca Park pine-maple stand is not the only virgin forest with a multilayered structure. Other examples include certain tropical rain forests of the far east (Whitmore 1984, pp.15-36) and of Costa Rica (Lieberman et al. 1985). In such forests, tree death will only occasionally result in canopy gaps of sufficient depth to benefit shade-intolerant colonists.

In general, the chief beneficiaries of small canopy openings are existing canopy trees and shade-tolerant understory trees (Gysel 1951; Bray 1956; Minckler and Woerheide 1965; Hibbs 1982; Canham 1984; Veblen 1985). Both red oak (Hibbs 1982) and sugar maple (Canham 1984) respond with rapid extension growth to adjacent canopy openings. As gap size increases, shade-intolerant plants may appear. The gap size threshold for shade-intolerant trees, placed at 25 m² by Gysel (1951), at 50 m² by Runkle (1985), and at 78 m² by Hibbs (1982), will vary with latitude (Canham 1985) and with extension growth capacity of canopy species. In the Minnesota pine-maple stand, small gap size and relatively high latitude combine with developmental plasticity of canopy trees to produce few colonization opportunities for shade-intolerant species.

D. Gap Formation: Pine-Fir Stand: In the pine-fir stand, the majority of windthrown trees did form canopy gaps (Figure 7b). Of 34 canopy trees felled by wind, 21% created no measurable canopy gap, while 38% formed small ($<20 \text{ m}^2$) gaps and 41% formed larger ($20 - 269 \text{ m}^2$) gaps. Mean gap size was 35 m^2 , only slightly larger than the pine-maple stand average. However, the greater probability of gap formation, with over 70% of windthrown canopy trees forming gaps, results in more colonization opportunities for shade-intolerant trees.

Frequency of gap formation is related to forest structure and to windfirmness of understory trees. Like the pine-maple stand, the pine-fir stand has an irregular physical structure but with important differences: there is no broken supercanopy of pines, and there is no multiple-layered understory of deciduous trees and shrubs. Pines and other canopy trees of spruce, fir, and birch approximate a canopy monolayer. The understory is a patchy thicket of small fir and spruce trees that have weak wood (Markquardt and Wilson 1935) and a tendency to fall when canopy trees come down. The average windthrown tree kills 6 understory fir trees, while in the pine-maple stand the typical windthrown tree bends two or three small sugar maples or ironwoods, the region's strongest-wooded trees, which survive their damage and continue to shade the forest floor. In contrast, a fallen tree in the pine-fir forest clears out the understory and exposes the forest floor, where shade-intolerant plants might get established through sprouting or seed germination.

Another factor promoting shade-intolerant species, in addition to the greater frequency of gap formation and the greater susceptibility of the understory to damage, is the lack of extension growth capacity of the coniferous species that dominate this stand. Spruce, fir, and pine grow only vertically in response to release. Their growth form permits little side growth into adjacent openings, in contrast to angiosperm trees prevalent in the pine-maple stand. A canopy gap in this stand will thus persist longer than a gap in the pine-maple stand.

E. Tree Regeneration after Windstorms: Pine-Maple Stand: Background sampling of saplings and seedlings, assumed to include areas affected by past windstorms, shows relatively few small individuals of shade-intolerant aspen, paper birch, white pine, and red pine in the pine-maple forest. Aspen produces many small root suckers ($21.7/100 \text{ m}^2$), but few reach sapling size (defined here as stems 2.5-10 cm DBH) in this forest ($0.13 \text{ saplings}/100 \text{ m}^2$; Table 7a). Paper birch seedlings and sprouts are scarce ($3.4/100 \text{ m}^2$), as are saplings ($0.18/100 \text{ m}^2$). White pine seedlings are quite rare ($0.4/100 \text{ m}^2$) and saplings are nonexistent. Red pine is not present in the seedling stage and has only $0.02 \text{ saplings per } 100 \text{ m}^2$ (Table 7a). For all of these shade-intolerant species, size-frequency diagrams show them to be declining populations with individuals concentrated in larger size classes (Figure 3a).

In contrast, size distributions for shade-tolerant sugar maple and ironwood suggest increasing or stable populations (Figure 3b). For sugar maple, seedlings (1220/100 m²) and saplings (2.8/100 m²) are numerous; and for ironwood, seedlings (6.9/100 m²) and sapling-size trees (1.6/100 m²) account for most of the population (Table 7a). Red maple and red oak, species intermediate in shade-tolerance, are also intermediate in representation within small size classes (Figure 3b; Table 7a).

Where small gaps form, shade-tolerant species fill openings through side growth from adjacent canopy or subcanopy positions. Where large gaps form, beneficiaries are tall shrubs (hazel, mountain maple) in some places and previously-established seedlings of red and sugar maple in other places. Even in closed forest where no trees blow down, the ground is carpeted with maple seedlings or covered by a continuous shrub layer. New colonization opportunities for shade-intolerant trees are infrequent in time and space.

Forest microsites that formed during past windstorms were also covered with seedlings of sugar and red maple, which outnumber other tree species in control plots, on mounds, in pits, on stumps, and on logs (Figure 9). Compared with control areas, windthrow mounds support slightly higher densities of aspen and ironwood stems. Stumps support higher than background densities of white pine seedlings, but white pine seedlings do not survive intensive herbivory by deer in this region except in deer exclosures (Ross et

al. 1970). Rotting logs favor red maple over sugar maple, at least in density of seedlings. An occasional aspen, red oak, or red maple tree might therefore become established as a result of thunderstorms, but most shade-intolerant sprouts and seedlings will be shaded out by ubiquitous maples and tall shrubs.

F. Tree Regeneration after Windstorms: Pine-Fir Stand: In contrast, the pine-fir stand has abundant seedlings and saplings of several shade-intolerant tree species. Size frequency diagrams show that paper birch and aspen trees are abundant in small size classes (Figure 3a), as are more shade-tolerant spruce and fir trees (Figure 3b).

Aspen saplings are present at six times their pine-maple stand density (0.82 vs. $0.13/100 \text{ m}^2$), while birch saplings are present at 1.4 times their pine-maple stand density (0.26 vs. $0.18/100 \text{ m}^2$; Table 7b). White pine seedlings reach 24 times their pine-maple stand density (14.3 vs. $0.6/100 \text{ m}^2$), but saplings are absent from both stands, presumably because of deer. Saplings ($0.76/100 \text{ m}^2$) and seedlings ($19/100 \text{ m}^2$) of shade-intolerant ash are also abundant in the pine-fir stand (Figure 3b; Table 7b). Despite heavy herbivory by deer, which stunts but does not eliminate ash seedlings and saplings, ash might increase in importance in the future, given the size and density of light gaps in this stand. Spruce saplings ($1.9/100 \text{ m}^2$) and seedlings ($0.9/100 \text{ m}^2$) are numerous. Very shade-tolerant balsam fir has a much higher density of saplings ($21.9/100 \text{ m}^2$) and seedlings

(11.2/100 m²), but not to the exclusion of other species (Table 7b).

Balsam fir is found in or around 69% of recent treefall gaps and represented roughly 60% of potential treefall beneficiaries (i.e., trees already established in or at edges of gaps). However, less shade-tolerant taxa are also present in treefall gaps: quaking aspen in 22% of gaps (comprising 5% of beneficiaries); paper birch in 14% (4% of beneficiaries); white spruce in 11% (6% of beneficiaries); and ash in 28% of gaps (12% of beneficiaries).

In most measurable gaps, potential beneficiaries are found at gap edges. Open, uncolonized ground is exposed in the gap center where the falling tree cleared out the understory. Such openings apparently can persist for years without reforestation, filling with Pteridium aquilinum, Rubus sp., and Fragaria sp. Tree establishment depends upon the presence of partially decomposed wood and rarely occurs on litter or mineral soil in this forest.

Windstorm-related microsites are thus very important (Figure 9; Chapter 2). Rotted stumps support very high densities of white pine seedlings and paper birch seedlings and sprouts, and moderately high densities of aspen and spruce stems. Decomposing logs are major sites of balsam fir germination and also support higher than background densities of paper birch, white pine, and spruce (Figure 9).

G. Mortality and Regeneration Patterns Juxtaposed: Repeated windstorms will, in the pine-maple stand, remove large aspen, red

pine, and white pine trees, trees of species that are not regenerating in this stand. The resulting shift in forest composition will be toward increased dominance by shade-tolerant, wind-firm sugar maple. Sugar maple indirectly benefits from windstorms that remove neighboring aspens and pines, and its seedlings get established throughout the stand on sandy loam soils enriched by sugar maple litter. Low damage rates for paper birch, red oak, and red maple populations suggest persistence of these less shade-tolerant taxa, although a dearth of birch and oak regeneration suggests eventual decline for both species. Over a large area, discrete light gaps will form at low densities from time to time, and aspen and oak trees will occasionally become established. On any spatial scale, however, density of and dominance by shade-intolerant trees will decrease in this forest over time, in the absence of fire or storms with higher windspeeds.

Other forest communities show similar patterns of response to low-intensity windstorms. Windstorms that removed up to 24-35% of stand biomass did not generate new age classes but benefitted existing trees in one New England forest (Oliver and Stephens 1977), and scattered windthrown trees were replaced by shade-tolerant sugar maples in a Minnesota maple-basswood forest (Bray 1956). Both large and small gaps formed not by windstorms but by gypsy moth damage were filled by existing shade-tolerant plants in a New Jersey deciduous forest (Ehrenfeld 1980).

In contrast, low-intensity windstorms in the pine-fir stand do

benefit shade-intolerant species. Shade-tolerant balsam fir is not directly disadvantaged by windstorm-related mortality patterns, nor is it unable to replace windthrown trees. However, weak wood renders small fir trees vulnerable to damage from falling canopy trees and thus promotes both the creation of light gaps and the creation of dead wood microsites on the forest floor. Rotting wood is important for seedling establishment within this stand, whose acid sandy soil is made less fertile by conifer litter. Where light gaps and dead wood occur together, several shade-intolerant tree species can become established. Although balsam fir tolerates shade (Fowells 1965), it is dependent on the same germination microsites where paper birch, white pine, aspen, and spruces grow.

Hence balsam fir is patchy in distribution, and trees of less shade-tolerant species, particularly paper birch whose seedlings outnumber all others, will often get established where trees blow down. Heavy mortality suggests further decline of spruce populations, which generally form a small component of fir-spruce-birch forests of Minnesota. Herbivory will likely prevent establishment of white pine trees, but this study shows that efforts to reestablish white pines must not only exclude herbivores but must also provide favorable germination sites, preferably stumps. Shade-intolerant paper birch and quaking aspen will persist at relatively high densities in this forest as a result of windstorms.

The same set of windstorms thus has different consequences in

these two forests. These different consequences can be traced to the autecology of each stand's shade-tolerant trees and to edaphic differences between the stands.

The Concept of Disturbance: Some problems with the concept of disturbance are pointed up by the different roles of windstorms in these two communities. Equilibrium or climax communities rarely exist in nature, because a wide variety of biotic and abiotic processes prevent their formation. These processes often prevent competitive exclusion and maintain or enrich species diversity (Raup 1957, 1964; Paine 1966; Levin and Paine 1974; Armstrong 1976; Davis 1976, 1981, 1983; Connell 1978; Lubchenco 1978; White 1979; Levins 1979; Pickett 1980; Paine and Levin 1981; Tilman 1982; Connell et al. 1984).

The term "disturbance" has been applied to those processes that explain nonequilibrium systems. The concept is too broad, however, for the processes included to be analogous. Diverse abiotic and biotic factors have been labelled disturbances: windstorms, fires, drought, herbivory, wave action on intertidal substrates, soil exposure by fossorial rodents, and even tree death, as well as most activities of humans. These events have little in common except the capacity to influence biotic populations and communities.

Other processes, moreover, have the same potential influence: competition, resource depletion, litter fall, pollination, germination, growth, and cessation of growth all can affect

populations and communities in similar ways. Whether disturbance is defined in terms of its effects on resources (Sousa 1985, Canham and Marks 1985), population structure (Bazzazz 1983; Pickett and White 1985), or community composition (Loucks et al. 1985), there are few abiotic or biotic processes that do not qualify as disturbances.

Although the study of such processes is important, the value of the disturbance concept for grouping an arbitrary subset of these processes is questionable. Fires and windstorms, for example, have very different consequences in northwestern Minnesota and in other ecosystems (Stearns 1949, 1951; Vitousek 1985). Combining fire and wind under one heading, "disturbance," is more misleading than useful.

A second problem with the concept of disturbance arises from its connotation of community response. Disturbance is rarely defined as a physical stress alone but also requires, by most definitions, a specific strain, or biological response: the disruption of equilibrium and the enrichment of species diversity. This criterion has led some to rule out as disturbances certain physical processes, such as prairie fires (Loucks et al. 1985), when they do not enrich species diversity. By the same criterion, windstorms would qualify as disturbances in the Minnesota pine-fir stand but not in the pine-maple stand, an odd and artificial distinction.

Our inability to settle on a universal, precise definition of disturbance (see for example papers in Mooney and Godron, 1983, and in Pickett and White, 1985) calls into question the value of the

concept, which often serves more to confuse than to enlighten. I propose that we avoid the term "disturbance," with all its ambiguity and circularity, as I have done in this thesis. The problem is not merely semantic. Instead, semantic problems result from problems with the concept, which is unavoidably vague because it combines nonanalogous processes while arbitrarily excluding other homologous processes.

CONCLUSIONS

(1) Strong interspecific differences in windstorm-related damage rates were observed in two Minnesota forest stands. These differences were not predictable on the basis of tree size alone, and remaining interspecific differences in damage rates were not fully explained by strength of undiseased wood. Heart-rotting and root-rotting fungal pathogens might explain the vulnerability of several tree populations, and might also help explain within-species differences in relative mortality rate from one stand to the next, differences which were large for paper birch, quaking aspen, red pine, and white pine.

(2) Shade intolerant species were not directly favored by mortality patterns but instead sustained high damage rates in most cases.

(3) The risk of indirect mortality by falling trees during storms was greater in the higher density stand whose understory trees had

weak wood. Fewer understory trees were killed in the lower density stand whose understory trees had strong wood and usually survived any damage.

(4) Probabilities of gap formation are influenced by forest structure and by flexibility of understory trees. Canopy gaps formed infrequently in one stand (32% of damaged canopy trees) but more frequently in the other (60% of damaged canopy trees). Average size of gaps formed was small (27-35 m²), below size limits suggested in the literature for shade-intolerant tree establishment.

(5) Shade-tolerant seedlings, saplings, and shrubs had continuous coverage in the pine-maple stand, even on windthrow mounds, stumps, pits, and logs. These will be chief beneficiaries of wind damage to canopy trees, although a very low density of less shade-tolerant trees (aspen, red oak, red maple) may become established on forest microsites within occasional large canopy gaps.

(6) In the pine-fir stand, mineral soil and litter support few seedlings of any species. Windstorm-produced microsites are principal sites of tree establishment, and shade-intolerant seedlings are more numerous than shade-tolerant seedlings on these microsites. This pattern of germination, coupled with more frequent gap formation and with limited lateral growth capacity of canopy conifers, favors establishment of shade-intolerant trees in many treefall areas.

(7) The same windstorms have different consequences for shade-intolerant tree populations in these two stands. This finding illustrates a problem with how physical forces such as fire and wind are commonly viewed in ecology. Confusion results from labelling as disturbances only those processes that prevent competitive exclusion or otherwise enrich species diversity. Windstorms would qualify as disturbances in one of these Minnesota forests but not in the other. Such a definition for disturbance is at the same time too broad and too narrow to be useful: too broad for all included processes to be truly analogous, and too narrow for inclusion of processes that do not have the expected effect of enriching species diversity.

Chapter 2. FOREST MICROSITES: FORMATION DURING WINDSTORMS AND COLONIZATION BY TREES

INTRODUCTION

When trees are damaged in windstorms, new microsites often form on the forest floor: windthrow mounds and pits from uprooting of trees, tree stumps from the snapping of trees, and dead logs in either case. The importance of such forest microsites for tree regeneration has been suggested for various forests. Differences among such microhabitats might also increase plant species diversity in forest communities.

Windthrow mound formation causes soil horizons to be inverted (Lutz and Griswold 1939; Lutz 1940; Goodlett 1954; Denny and Goodlett 1956; Stephens 1956; Lyford and Maclean 1966; Putz et al. 1983) and exposes mineral soil that permits germination of plant species unsuccessful in deep litter (Hutnick 1952; Raup 1957; Beatty 1980, 1984). Soil pits created where root balls are removed may be more favorable sites for seedling establishment, perhaps because of higher concentrations of organic matter and mineral nutrients (Beatty 1980, 1984) or because of protection from desiccation (Dixon and Place 1952; Falinski 1978) or from temperature extremes (Beatty 1984).

Rotting wood of stumps and of logs is important for tree regeneration in some forests, notably in coniferous forests of the Pacific northwest (Berntsen 1960; Minore 1972; Graham 1982; Franklin et al. 1981; McKee et al. 1982; Maser and Trappe 1984). Rotting logs

accumulate and retain moisture and, through bacterial nitrogen fixation, accumulate nitrogen as well (Sharp and Milbank 1973; Larsen et al. 1978; Franklin et al. 1981; Maser and Trappe 1984), although nutrient content may instead decrease over time (Lambert et al. 1980). Mycorrhizal activity can be higher in dead wood than in mineral soil (Harvey et al. 1976, 1979). Dead wood may also provide seedling establishment sites that are free of rhizomes of vegetatively-reproducing plants (Berntsen 1960). Characteristics of coarse woody debris in forest ecosystems are reviewed by Harmon et al. (1985). Although stumps and logs are recognized as tree regeneration sites in some forests, the influence of these microsites on species diversity has not been explored fully, despite evidence that some tree species are more dependent than others on organic seed beds (Minore 1972; Veblen 1985).

No previous studies that I know of compare the colonization of stumps resulting from tree breakage with the colonization of mounds and pits resulting from uprooting. Putz et al. (1983) examined correlates of these two damage modes and suggested (as did Denslow 1985) that whether a tree uproots or snaps off may have consequences for forest composition and diversity.

This chapter of the thesis investigates differences between stumps, mounds, pits, and logs as sites of tree regeneration. The work was done in the two forest stands within Itasca State Park, northwestern Minnesota, described in detail in Chapter 1 (Figures 1 and 2).

I asked two major questions: (1) What patterns of tree damage and microsite formation result from windstorms? Can we predict whether a tree will uproot or snap on the basis of tree size, species, or cause of damage?

(2) Does uprooting differ from tree breakage in consequences for future forest composition? Mound/pit complexes may differ from tree stumps in several ways: in time before colonization, in types of substrate available for seed germination, in probability of resprouting by damaged trees. If different microsites favor establishment of different tree species, then tree damage mode will influence the future of a stand.

My approach to these questions was first to examine modes of tree damage (uprooting, breakage) and their correlates (tree size, tree species, wood strength) during recent windstorms in the two Minnesota forest stands. I then examined old microsites on the forest floor, which provide a record of past windstorm damage and a record of which plants benefited from which type of microsite. These data permit comparison of uprooting and tree breakage consequences for regeneration patterns.

METHODS

Microsite Formation: In addition to work described in Chapter 1 (Methods section), I collected data to further elucidate the formation of windthrow mounds, pits, and stumps during windstorms.

For trees damaged by recent windstorms I recorded mode of damage (uprooted, snapped, bowed, branch broken), and height of breakage for trees that snapped.

I assessed the value of tree size and tree species as predictors of windstorm damage mode (uprooting, vs. snapping) by using χ^2 tests. To consider size and species effects together in one model, I used logistic regression analysis, an iterative test of model fit for binomial response variables modeled on a mixture of categorical and interval factors (Fienberg 1981).

Microsite formation in the past was elucidated by sampling both study areas for mounds, pits, stumps, and boles. Systematic strip sampling covered 1591 m² in the pine-maple stand (0.004% of an 40-ha area) and 1474 m² in the pine-fir stand (0.02% of an 8-ha area). For each microsite, I recorded total size, size within the strip plot, and species (if identifiable). These data allowed me to estimate areal coverage by microsities and to identify interspecific differences in damage mode (uprooting versus snapping) in the past.

I also estimated microsite age (time since microsite formation). Relative age estimates were based upon decomposition of logs and stumps and, for recent microsities, from release dates for sugar maple seedlings, as indicated by bud scars. Age categories were different from the decomposition stages of Franklin et al. (1981) for Douglas fir logs, but similar criteria were used to define relative age classes appropriate to tree species present in Itasca Park. Age

categories were as follows:

RECENT (Bark intact, small twigs present, wood firm)

MODERATELY OLD (Bark only partially intact, small twigs absent, wood firm, logs still off ground)

OLD (Bark mostly separated from sapwood and sloughed off [except in paper birch], large branches present, wood soft, logs mostly on ground)

VERY OLD (Bark absent [except in birch: only bark remains], wood very soft and usually covered with vegetation, logs on ground)

EXTREMELY OLD (No wood remains; applies to mounds and pits that no longer have associated wood)

Wood decomposition rates vary with tree species and tree size. Despite my efforts to subjectively correct for such variance, microsites in adjacent age classes may not differ in true age. Some microsites were assigned intermediate ages (e.g., "old to very old").

Absolute dates cannot be assigned to microsites older than 5-10 years until decomposition rates within these or similar stands are monitored. Log decomposition rates vary widely, from 10 years for large trees in one tropical forest (Lang and Knight 1979) to nearly a century for small fir trees in subalpine New Hampshire stands (Lambert et al. 1980) and up to perhaps 180 years in Douglas fir stands in Oregon (Franklin et al. 1981).

In my Minnesota study areas, mounds and pits classified as "extremely old" may be centuries old (Beatty 1980), while microsites characterized by rotting wood (up to "very old") are probably less

than 100 years in age. Smaller logs and stumps decompose more quickly and rarely occur in the older age classes.

Microsite Colonization: I censused vegetation on old microsites in the strip plots described above and (in the pine-fir study area) on additional old microsites outside plots in order to increase sample size. The total surface area of stumps, mounds, and logs that was censused ranged from 6.4 m² for pine-maple stand stumps to 366 m² for pine-fir stand logs. The actual numbers of microsites sampled also varied, from 14 pine-maple stand pits to 320 pine-fir stand logs (Table 12). The picture of tree regeneration patterns is therefore more reliable for logs and mounds than for stumps and pits, and it is more reliable for the pine-fir stand than for the pine-maple stand, where microsite density and areal coverage was lower.

Vegetation on each microsite was categorized as (1) no vegetation, (2) mosses only, (3) herbs and shrubs, or (4) tree seedlings or saplings (or both) present. Tree seedlings and saplings were tabulated by species and size class (<0.5 m, 0.5-2.0 m, >2.0 m tall).

For comparison, background vegetation away from microsites was sampled in systematically arranged 1-m² plots, 4 of which were nested within each strip plot sampled for trees (see Chapter 1). Plot locations were shifted 1 m along the transect if necessary to exclude windstorm-related microsites. These control plots covered 272 m² in the pine-maple stand and 39 m² in the pine-fir stand.

I tested the effects of microsite type, size, relative age, and species on the vegetation of the microsite and on its colonization by trees of various species, using nonparametric statistics, analysis of variance, and logistic regression (Dixon 1983; Fienberg 1981; Sokal and Rohlf 1985).

RESULTS

A. MICROSITE FORMATION IN RECENT WINDSTORMS

In the pine-maple stand, 4 trees were snapped off for every tree uprooted during the July 1983 windstorm. This single storm snapped 163 trees (55% of damaged trees), uprooted 44 trees (13%), bowed 98 trees (29%), and removed large branches of 11 trees (3%) (Table 8). These damage patterns translate into the formation of 4 stumps per ha and 1 windthrow mound per ha (in 40 ha sampled), assuming that all uprooted trees created mounds.

In the pine-fir stand, 3 trees were snapped off for every 5 trees uprooted during recent windstorms. These storms snapped 92 trees (33%), uprooted 157 trees (57%), bowed 24 trees (9%), and broke branches of 3 trees (1%) (Table 8). Theoretically these patterns represent 23 stumps and 39 mounds per ha, but fewer mounds actually formed; uprooting often fails to produce windthrow mounds in this forest, because of root breakage at ground level (Figure 10). This damage mode, also described by Beatty (1980), is common among smaller

fir and spruce trees in the pine-fir stand.

B. CORRELATES OF DAMAGE MODE

Pine-Maple Stand: In the pine-maple stand, bowed trees were significantly smaller than uprooted and broken trees. Bowing was usually caused by falling trees rather than wind, and it was most likely for sugar maple and ironwood (Table 8; Figure 11), trees of which are concentrated in small size classes and have stronger wood than trees of other taxa of the region (Chapter 1; Markwardt and Wilson 1935). These bowed trees usually survive, at least for several years, hence their damage does not create post-storm microsites on the forest floor.

When uprooted and broken trees are compared in this pine-maple stand, few differences emerge. Uprooting was more common among trees hit by other trees while snapping was more likely for trees damaged by wind (X^2 test, $P=0.04$; Table 9). Uprooted and snapped trees did not differ in size (Logistic Regression (LR), $P>0.10$; Figure 12) or in survival of damage (X^2 test, $P=0.37$; Table 10). This latter result indicates that, in this stand, dead logs are equally likely to result from uprooting and from snapping of trees.

There were only slight differences among species in tendencies to uproot or snap (X^2 test, $P=0.068$). Damage patterns for 8 major species (Figure 11) show strong interspecific differences only when bowed trees are included in the analysis along with broken and

uprooted trees (X^2 test, $P < 0.01$).

For snapped trees, height of breakage varied with species (ANOVA, $P < 0.01$) (Figure 13). Seedlings on stumps are more likely to survive to maturity where trees break off near ground level, as pines and maples do in this forest, than where tall tree stubs remain upright, as with aspen. Boles that are upright support less vegetation than boles on the ground and may decompose more slowly, although this is not always the case (Franklin et al. 1981).

Pine-Fir Stand: Bowing damage was uncommon in the pine-fir stand, where strong-wooded maples, ironwoods, and oaks were absent. Most damaged trees were either uprooted or broken, and most were killed (86%, versus 48% killed in the pine-maple stand), forming rotting logs in either case. Survival was equally unlikely for uprooted and snapped trees (X^2 test, $P = 0.16$; Table 10), just as in the pine-maple stand.

Also as in the pine-maple stand, trees damaged by wind tended to break along the bole while trees damaged by other trees tended to uproot (X^2 test, $P < 0.01$; Table 9). In the pine-fir stand, however, snapped and uprooted trees differed in size, on average (Figure 12). Large trees hit by wind usually were broken, while small trees hit by other trees usually were uprooted.

These size differences in damage mode account almost entirely for an apparent but spurious species difference: fir and spruce trees usually uprooted, while aspen and paper birch followed the pattern

seen in the pine-maple stand, snapping more often than uprooting (Figure 11). The uprooting of fir and spruce trees is, however, contingent on their size and prevalent only among small understory individuals. There is no strong species effect on damage mode beyond this size effect (LR, $P < 0.01$ for size, $P = 0.158$ for species).

For snapped trees, height of breakage differed between species, with birch and aspen snapping off higher, on average, than fir, spruce, or pine (Figure 13; ANOVA, $P < 0.01$).

C. OLD MICROSITES: DENSITY AND AREAL COVERAGE

Pine-Maple stand: Windthrow mounds, pits, stumps, and boles of various ages are sparse, covering just 6% of the pine-maple stand floor (Figure 14). Dead wood covers 4.12%, nearly all in logs (3.98%) rather than stumps (0.14%). Windthrow mounds (1.45% cover) and pits (0.47% cover) have low areal coverage (Table 11).

Taken together, mounds (180/ha) and stumps (80/ha) provide a record of relatively few dead trees. Stumps (representing trees wind-snapped or killed upright) outnumber windthrow mounds (representing uprooted trees) by more than 2:1 (Table 11). Of 260 extrapolated trees per ha, 69% formed stumps and 31% formed mounds. Apparently more trees were snapped than uprooted in past storms, just as was true in this forest during the recent (1983) storm. The shifting ratio of stumps to mounds, from 5:1 in that recent storm to 2:1 for the longer time period, may result in part from the longer

persistence of mounds on the landscape.

The average mound (3.7 m^2) is 1.7 times the size of the average stump (0.2 m^2) in this stand, a significant difference (Kruskal-Wallis test, $P < 0.01$). Because tree size does not differ, on average, for broken and uprooted trees in this stand, it appears that tree breakage alters a smaller area than uprooting of a comparable tree.

The species distribution of identifiable mounds does not differ from that of stumps (χ^2 test, $P = 0.2269$). This result parallels the finding that species did not differ in uprooting or breakage tendencies in this stand during the 1983 storm (Figure 11).

Pine-Fir Stand: In the pine-fir stand, microsites cover more of the landscape, accounting for 17.6% of the forest floor (Figure 14).

Dead wood as stumps (0.46% cover) and logs (9.7% cover) is conspicuous, as are numerous but small mounds (6.7% cover) and less numerous pits (0.8% cover; Table 11).

Mounds (580/ha) and stumps (420/ha) together represent an extrapolated 1000 dead trees per ha, nearly 4 times the density of dead trees evident in the pine-maple stand. Also in contrast to the pine-maple stand, mounds outnumber stumps in this pine-fir stand by a ratio of 6:4 (Table 11), a trend similar to the 5:3 ratio of trees uprooted and snapped in recent windstorms.

Average mound size (1.1 m^2) is ten times the average stump size (0.1 m^2), despite the tendency here for smaller trees to uproot. As in the pine-maple stand, this significant difference (Kruskal-Wallis

test, $P < 0.01$) indicates that uprooting changes a much larger portion of the forest floor than does tree breakage.

Among mounds and stumps identifiable to species, species distributions differ in this stand (χ^2 test, $P < 0.01$), with more mounds of fir and spruce and more stumps of birch and aspen. This pattern among old microsites matches damage patterns in recent storms (Figure 11).

D. COLONIZATION OF MICROSITES

Colonization Sequence: In both forests, logs and stumps are colonized by bryophytes and then by herbs and shrubs, whose spread is accompanied by a decline in moss cover (Table 12). Tree seedlings appear later, although stump sprouts of red oak, paper birch, and aspen may be present from the start. For windthrow mounds, a similar sequence occurs but bryophytes may not be involved. For pits in these forests, bryophytes are rarely present.

The absolute length of time involved in these vegetation changes on microsites is not known and is likely quite variable from one microsite to the next (Maser 1972). Not surprisingly, microsite size plays a major role in colonization patterns. Small microsites may not acquire vegetation before they decompose completely, while large microsites are bigger targets for seeds and are more likely to persist long enough to support tree seedlings (ANOVA, $P < 0.01$).

Frequency of Tree Seedlings and Sprouts: Vegetation varies, in both stands, with microsite type, size, relative age, and species (of the dead tree) (Table 12), but these effects often are confounded. Mounds are larger than stumps, for example (Kruskal-Wallis test, $P < 0.01$ for both stands), and greater abundance of mounds than stumps in older age classes suggests that mounds persist longer than stumps (X^2 test, $P < 0.01$ for both stands). I used stepwise logistic regression to model presence versus absence of tree seedlings and sprouts as a function of microsite size, age, and species. The results (Table 13) indicate strong differences among microsite types in which factors control colonization by trees.

On dead logs, presence of tree seedlings or sprouts depends upon both microsite size ($P < 0.01$) and microsite age ($P < 0.01$) (Table 13). Tree regeneration is most likely on large, very old logs.

The species of dead wood is important in the pine-maple stand ($P < 0.01$) because of abundant paper birch logs (26% of all logs sampled in the stand), whose persistent papery bark resists colonization. Wood species is unimportant to tree generation in the pine-fir stand ($P = 0.5446$), where paper birch accounts for few logs (<5%).

For stumps alone, species is the major predictor of tree regeneration, while size is only marginally important ($P = 0.0723$) and age effects are not significant ($P = 0.8690$; Table 13). This pattern suggests that stump sprouts account for much tree regeneration on

stumps, because trees of seedling origin would increase in frequency with stump age, as they do with log age. For windthrow mounds, tree regeneration is influenced by mound age ($P=0.0457$) but not by size ($P=0.3048$) nor by species of mound-forming tree ($P=0.5533$). The effect of size becomes significant ($P=0.0492$) when sample size is increased by excluding species from the model, which allows inclusion of many additional mounds of unknown species (Table 13).

For pits, microsite age helps predict seedling presence or absence ($P=0.0467$), with seedlings more likely in older pits. Size ($P=0.8388$) and species ($P=0.9989$) do not help explain seedling distributions among pits.

Density of Tree Seedlings and Sprouts: The density of tree seedlings and sprouts varies with substrate and varies with forest type (Figure 9; Tables 14 and 15). In the pine-maple stand, seedling densities are highest ($1646 \text{ stems}/100 \text{ m}^2$) in control plots that do not include mounds ($552 \text{ stems}/100 \text{ m}^2$), pits ($323 \text{ stems}/100 \text{ m}^2$), stumps ($328 \text{ stems}/100 \text{ m}^2$), or logs ($169 \text{ stems}/100 \text{ m}^2$). Most stems in control plots are sugar maple seedlings, which also occur on microsites but at lower densities (Figure 9; Table 14). Ironwood and aspen stems reach higher than background densities on mounds, while white pine seedlings reach highest densities on stumps. Basswood, an uncommon tree in this forest, and red oak are the only tree species regenerating well in pits, aside from red maple which is ubiquitous on all substrates.

In contrast, in the pine-fir stand, seedling densities are low in control areas (133 stems/100 m²) and highest on stumps (742 stems/100 m²) and logs (284 stems/100 m²) (Figure 9, Table 15). Mounds (149 stems/100 m²) are similar to control areas, while pits have very low seedling densities (24 stems/100 m²). Neither litter (in control areas and pits) nor mineral soil (on mounds) provides good germination sites for trees in this stand. Stumps support relatively high densities of birch and aspen, many of sprout origin, and high densities of white pine, spruce, and balsam fir seedlings. Logs support higher densities of balsam fir and somewhat lower densities of paper birch stems (Figure 9).

DISCUSSION

A. Old Microsites as Windstorm Records

The prevalence of uprooting during recent storms in the pine-fir stand is paralleled by an abundance of old windthrow mounds. Likewise, the greater likelihood of tree snapping during recent storms in the pine-maple stand is paralleled by higher densities of old stumps than of old mounds. Species patterns of damage during recent storms also parallel species damage patterns of the past as inferred from microsites.

Several problems complicate the use of old microsites to reconstruct past windstorm damage. (1) Stumps disappear more quickly

than pits, which disappear more quickly than mounds (Beatty 1980), hence the landscape provides a longer record of uprooted trees than of snapped trees. In addition, dead trees of different sizes and different species may disappear at different rates. A more accurate reconstruction might be possible using intensive methods destructive of the forest floor (Oliver and Stephens 1977; Henry and Swan 1974).

(2) While mounds and pits can nearly always be attributed to windstorms, stumps can result either from breakage during windstorms or from standing death of trees due to pathogens, drought, and other causes. The gradual breakup of snags (standing dead trees) produces a different configuration of dead wood on the forest floor, with the bole falling in several chunks near the stump instead of in one continuous log. Hence some former snags and wind-snapped trees can be distinguished in the field. Old stumps that persist after boles disappear cannot be easily categorized, however. Furthermore, not all species are equally likely to form snags (Cline et al. 1980). In these Minnesota forests, snags now present include quaking aspen, apparently killed by pathogens; a few paper birch, many now disintegrating and possibly killed during a 1976 drought; and white pine (in the pine-fir stand only), perhaps victims of suppression by neighboring trees or of white pine blister rust, a fungal pathogen. For these and possibly other taxa, old stumps overrepresent trees broken by wind in the past.

(3) Mounds and pits do not always form when trees are uprooted. As Beatty (1980) pointed out, pits do not form if a tree's root ball

rotates in place instead of pivoting as if hinged (Figure 10b). In addition, mounds may not form if tree roots are broken near the tree base (Figure 10c), a common mode of uprooting for small fir and spruce trees in the Minnesota pine-fir stand.

B. Modes of Damage and Microsite Formation

The two Minnesota stands I studied differ in density of trees damaged during recent and past windstorms. A higher density of damaged trees and of forest microsites occurred in the pine-fir stand, owing in part to a tendency for numerous small firs and spruces to uproot when a single canopy tree is blown down. Heavy damage rates to these understory trees are related to low tensile wood strength, coarse-grained soils, and a higher density of living trees.

The two stands differ in the relative densities of uprooted and broken trees and in the relative densities of mounds and stumps. Uprooting is prevalent in the pine-fir stand, while breakage is more common in the pine-maple stand. In other forests, windstorms generally cause more breakage than uprooting (Brokaw 1985b), but variance among stands and among storm types is not surprising.

Whether a tree is uprooted or broken during a windstorm depends, in these Minnesota forests, on the cause of damage and on the size of the tree. Breakage is most likely for large trees damaged directly

by wind. Uprooting is more likely for small trees damaged by falling neighbors, although bowing is possible for small trees with strong wood (Figure 11). Where understory trees have weak wood, as in the pine-fir stand, many mounds will form but average mound size will be small, representing limited colonization opportunities. Where understory trees have strong wood, as in the pine-maple stand, few mounds of any size will form.

For a given tree species, damage mode is not always predictable on the basis of species wood strength alone. Variance in damage mode is high within species, with, for example, breakage more likely for older, taller birches and firs and uprooting more likely for smaller birches and firs. Another complication is posed by wood-rotting fungi, which promote breakage of aspen trees and which are widespread among pines in one stand (pine-maple), where breakage in storms is likely, but which apparently are less prevalent among pines of the other stand (pine-fir), where few pines are damaged (Chapter 1). Root-rotting fungi are also present in these forests. Further study is needed to elucidate the influence of pathogens on the formation of forest microsites.

Differences in damage mode also reflect soil depth and soil texture. Loose sands, like those of the pine-fir stand (Ness 1971), provide minimal resistance to uprooting, especially when not water-saturated (Mergen 1954). Soils of finer texture, like those of the pine-maple stand, add cohesive forces to friction and reduce uprooting probabilities. However, lateral root development may be

more extensive in looser soils, complicating this relationship (Mergen 1954).

C. Regeneration on Microsites

Microsites are colonized differently in the two forests. In the pine-maple stand, microsites support lower than background seedling densities of the dominant sugar maple. On microsites, lower densities of this superior competitor for light might benefit those shade-intolerant trees, such as white pine, quaking aspen, and red maple, that are less tolerant than sugar maple of deep shade but more tolerant than sugar maple of microsite substrates (Figure 9). Red maple in particular is almost as abundant as sugar maple in pits (as also reported by Henry and Swan, 1974) and more abundant on dead logs. However, windstorms provide few establishment opportunities for other tree species in this stand for several reasons: (1) sugar maple still outnumbers other trees in control areas, on mounds, and on stumps, although its density on microsites is low relative to that on background substrates. (2) Low areal coverage by microsites (6%) in this stand lends extra importance to sugar maple dominance away from microsites. (3) Well developed understory layers of shade-tolerant maples and shrubs cast deep shade on the forest floor, even where canopy trees blow down (see Chapter 1). (4) Herbivory by deer prevents establishment of white pine and possibly other trees in the region (Ross et al. 1970).

In the pine-fir stand, microsites are more important regeneration sites because of their greater areal coverage and because of infertile soils that apparently exclude maples and several other tree species. The few tree seedlings found in control areas grow on chunks of wood, not on litter. Stumps and boles are clearly the major regeneration sites in this stand, as in some forests of the Pacific Northwest (Minore 1972; Graham 1982; Franklin et al. 1981; McKee et al. 1982). The paucity of fir, spruce, and birch seedlings on mineral soil of mounds is surprising, given their usual success on such substrates (Place 1955; Marquis 1965).

Paper birch is likely to persist here through stump sprouts and through seedling establishment on stumps and on logs of species other than birch. The persistent bark of birch logs excludes seedlings of all species, including birch itself, except where cracks in the bark expose heartwood. Paper birch germination is, in greenhouse experiments, better on moisture-constant substrates like mineral soil, and presumably dead wood, than on litter and humus (Marquis et al. 1964; Marquis 1965). Again surprising is the dearth of birch regeneration on mounds, perhaps because these coarse-textured soils are too droughty to maintain moisture levels adequate for seedling germination.

White pine, whose regeneration in the Itasca Park region is of special concern to park managers, germinates almost exclusively on stumps and logs. Establishment of white pine populations from seed

without fire will require provision of organic seed beds as well as protection from herbivory. No seedlings of red pine, another tree of concern to managers, are found in either stand, suggesting that either (1) windstorms cannot substitute for fires to produce germination sites or (2) pre-germination mortality to seeds, perhaps by seed predators or pathogens, is restricting establishment of red pine.

Balsam fir, the most abundant tree of this stand, is also dependent on dead wood. Its greater abundance on logs than on stumps results from its inability to form stump sprouts. Balsam fir seedlings are thought to establish fairly well on litter but are susceptible to drought on sandy soils within openings (Place 1955). The patchy distribution of shade-tolerant firs in this stand might be explained by its dependence on rotting wood or related moss substrates. If so, this constraint could permit sprouting species (aspen, paper birch) to glean immediate benefit from windstorms and from fires, with balsam fir establishment delayed until dead wood is partially decomposed.

Black spruce and white spruce seedlings are less numerous. Spruce seeds are smaller than balsam fir seeds, and spruce seedling establishment requires moist, well-lighted seed beds (Place 1955). Sparse seedling establishment combines with heavy spruce mortality in windstorms to suggest a decrease in the future importance of spruce in this stand.

Seed source and seed dispersal constraints might account for

some of the differences between regeneration patterns in the two stands. Higher densities of quaking and bigtooth aspen trees might explain greater abundance of aspen suckers in the pine-maple stand. The scarcity in the pine-fir stand of red oak and red maple regeneration, and possibly also of sugar maple and ironwood seedlings, could be related to distance from seed sources, as might the scarcity of fir and spruce seedlings in the pine-maple stand. Mature trees of paper birch, white pine, and red pine are abundant and presumably provide a good seed source in both stands.

I did not examine the pool of buried viable seeds. Red maple and possibly paper birch have seeds that are stored 2-5 years or more in the soil (Marquis 1975), while seeds of sugar maple (Marquis 1975), spruce, and balsam fir (Place 1955) normally germinate within one year. Seeds of pin cherry, shrubs of which are found in both study areas, are likely present within the soil seed banks of these stands as they are in other eastern forests (Marks 1974; Marquis 1975). The congeneric chokecherry is more common than pin cherry, but long-term viability of its seeds has not been studied. Seed predation risks are for cherry seeds lower in treefall gaps than in closed forest (Webb and Willson 1985). Such spatial heterogeneity in seed predation patterns could influence the distribution of cherry and other plants in these stands.

Trees that do not produce abundant seed every year do not seem to be disadvantaged in microsite colonization in these forests.

Year-to-year variation has been described for seed production or seedling establishment by sugar maple (Curtis 1959), red oak, balsam fir, the pines, and the spruces (Fowells 1965).

D. Comparison of Uprooting and Tree Breakage Consequences

Uprooting and tree breakage have only subtly different consequences for tree regeneration patterns in both stands, although the importance of these differences depends upon the spatial scale of interest.

The average uprooted tree modifies a larger area than does the average broken tree in both forests, despite the tendency of small trees to uproot. Mound and pit areal coverage is 5-17 times stump areal coverage. If stumps and mound-pit complexes were equivalent colonization sites, uprooting would provide more benefit to microsite colonists.

The total areal coverage of windstorm-related microsites (6% and 18%) is low in both Minnesota stands relative to other northern forests (Table 16; Stephens 1956; Falinski 1978; Beatty 1980; Thompson 1980; Franklin et al. 1981; Graham 1982; Putz et al. 1983; Maser and Trappe 1984). Mounds, pits, and stumps are especially scarce in the pine-maple stand, where understory maples and ironwoods have strong wood and survive the fall of neighboring trees without forming microsites. The occasional mound may be colonized by aspen, while the occasional pit may be colonized by red maple or red oak. Most such colonists will be shaded out by understory trees and

shrubs. More numerous but smaller stumps cover a still smaller area than mounds and pits in this stand, and these stumps support few tree stems.

In the pine-fir stand, mounds and stumps are present at nearly 30 times their pine-maple stand density, but because of smaller average size they cover just 4 times the area. This greater areal coverage suggests that such microsites represent more colonization opportunities. Tree breakage and resulting stumps favor establishment of paper birch, white pine, balsam fir, spruce, and quaking aspen. Uprooting and resulting mounds are less favorable for all of these species, while pits support few seedlings of any species. Uprooting and tree breakage do not differ in the tree species they benefit (Figure 9), but they do differ in the density of colonists in this stand.

Dead logs have substantially higher areal coverage than do mounds, pits, or stumps (Table 11). Logs therefore may be the most important result of wind damage. In these stands, whether a tree is uprooted or snapped does not affect the probability of tree (ramet) death or, therefore, of dead log microsite formation. Whether a tree uproots or breaks thus may not matter to overall community composition and structure. Salvage logging of windthrown tree boles could, on the other hand, have major consequences for the regeneration of several tree species.

D. Sprouting and Self Replacement

The tree regeneration pattern in these forests results in part from resprouting after stem loss, which is common for aspen, birch, red oak, and red maple. The prediction of Putz et al. (1983) that snapped trees resprout more readily than uprooted trees is not supported for any species in the pine-maple stand, where birch, aspen, and oak sprouts were absent from stumps (Figure 13) but were present on some mounds of uprooted trees, possibly conspecifics. Intraspecific differences are seen between stands: more sprouting from stumps than from mounds does seem to occur for birch and aspen in the pine-fir stand.

The capacity for resprouting after stem loss has been proposed as an adaptive compensation for weak wood (Putz et al. 1983), but in these Minnesota stands the weaker wooded trees are conifers incapable of resprouting, while 3 of the 4 strongest-wooded trees (red oak, red maple, ironwood, but not sugar maple) often do resprout. Sprouting capacity could be for these species an adaptation to fire (Christiansen 1985; Keeley and Zedler 1978) or a result of fire and windstorm regimes together. For a tree that does not resprout, replacement by conspecifics is most likely if the tree damage mode provides microsites favorable to seedlings of that species. This pattern is seen for white pine, which usually breaks instead of uprooting and whose seedlings are most common on stumps, and for ironwood, which usually uproots and whose sprouts are most common on

mounds.

In other cases there is poor fit between characteristic damage mode and characteristic regeneration sites. Paper birch, which usually breaks along the bole, does sprout and establish seedlings on stumps, but as already noted its principal establishment sites are the logs of other species. Balsam fir and spruce usually uproot in these stands but their seeds germinate much more commonly on stumps than on mounds. Red oak usually snaps, but its seedlings are most common in pits. Quaking aspen commonly snaps in both stands but grows more abundantly on mounds in one stand and on stumps in the other.

This complex juxtaposition of damage modes and regeneration sites may help perpetuate floristic heterogeneity. In the pine-maple stand, the trend toward sugar maple dominance will not be reversed by the dynamics of windstorm-generated microsites. Over a broad region, however, a very low density of trees of red maple (on logs and in pits), aspen (on mounds), and red oak (in pits) may persist on microsites, where competition from sugar maple seedlings is less intense (Figure 9).

In the pine-fir stand, different tree species do not specialize on different germination sites: all are most numerous on dead logs and stumps. No reciprocal replacement scenario seems likely on the basis of regeneration sites, but self-replacement (within a species) is also unlikely under most circumstances.

CONCLUSIONS

(1) Windstorms leave a record of damage patterns in the form of forest microsites, but the record is difficult to interpret. Stumps disappear more quickly than mounds; stumps can result from causes other than wind damage; some uprooted trees form no visible mound or pit; and variable decomposition rates frustrate efforts to reconstruct storm chronologies without long-term studies.

(2) Windstorm-related microsites are more numerous and have greater areal coverage where understory trees have weak wood, as is true for balsam fir and spruce trees. Strong understory maple and ironwood trees are more likely to survive wind damage and are less likely to form forest microsites.

(3) In these Minnesota forests, breakage was most likely for large trees damaged directly by wind, while uprooting was more likely for small trees damaged by falling neighbors. Species wood strength is not a reliable predictor of damage mode because mode varies within species, perhaps because of effects of fungal pathogens, tree size, soil texture, or all three.

(4) In one stand (pine-maple), microsites are relatively unimportant to tree regeneration patterns because of microsite scarcity, because of ubiquitous and numerous sugar maple seedlings on all substrates, and because of deep shade cast by understory trees and shrubs even

where canopy trees blow down. Establishment by shade-intolerant species is therefore unlikely. A very low density of red maple, red oak, and aspen trees may persist on microsites in rare light gaps.

(5) In the other stand (pine-fir), microsites are more important tree regeneration sites. Control areas (and pits) have very low tree seedling densities, possibly because of soil droughtiness or infertility. Rotting wood of logs and stumps supports the majority of tree seedlings and sprouts in this stand: paper birch sprouts on stumps and seedlings on logs; balsam fir seedlings on logs; white pine and spruce seedlings on stumps. Mounds support lower densities of seedlings but do not differ from stumps floristically.

(6) Despite the smaller size of uprooted trees, mound/pit complexes are larger than stumps. If mound/pit complexes and stumps were equivalent colonization sites, uprooting would provide more benefit to microsite colonists.

(7) Dead logs have greater areal coverage and therefore make a greater contribution to tree regeneration than other microsites. Whether a tree uproots or breaks does not affect tree survival probability or, therefore, dead log formation in these stands. Given this and given the qualitative similarity of mound and stump colonists, damage done in windstorms has only minor consequences for composition and structure of these two forest stands.

(8) Salvage logging of wind-damaged tree boles will reduce natural regeneration by conifers and by paper birch. The pines of concern to park managers are not reproducing at present, red pine because of pre-germination constraints and white pine because of its dependence, in absence of fire, on rotting wood microsites and because of herbivory by deer.

(9) These two stands differ strongly in patterns of formation and colonization of windstorm-related microsites. The predominantly coniferous pine-fir stand resembles hemlock forests of the Pacific Northwest in the importance of dead wood. The pine-maple stand is unlike other forests where microsite dynamics have been studied in its low areal coverage and sparse colonization of mounds, pits, stumps, and logs.

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Table 1. Scientific and common names of plant species mentioned in text.
Nomenclature follows Gleason and Cronquist (1963).

COMMON NAME	SCIENTIFIC NAME	COMMON NAME	SCIENTIFIC NAME
Ash, green	<i>Fraxinus pennsylvanica</i>	Elm, American	<i>Ulmus americana</i>
Ash, black	<i>Fraxinus nigra</i>	Elm, red	<i>Ulmus rubra</i>
Aspen, bigtooth	<i>Populus grandidentata</i>	Hazel	<i>Corylus cornuta</i>
Aspen, quaking	<i>Populus tremuloides</i>	Ironwood	<i>Ostrya virginiana</i>
Balsam fir	<i>Abies balsamea</i>	Maple, mountain	<i>Acer spicatum</i>
Balsam poplar	<i>Populus balsamifera</i>	Maple, red	<i>Acer rubrum</i>
Basswood	<i>Tilia americana</i>	Maple, sugar	<i>Acer saccharum</i>
Birch, paper	<i>Betula papyrifera</i>	Oak, bur	<i>Quercus macrocarpa</i>
Birch, yellow	<i>Betula lutea</i>	Oak, northern red	<i>Quercus borealis</i>
Cherry, black	<i>Prunus serotina</i>	Pine, red	<i>Pinus resinosa</i>
Cherry, pin	<i>Prunus pensylvanica</i>	Pine, eastern white	<i>Pinus strobus</i>
Chokecherry	<i>Prunus virginiana</i>	Spruce, white	<i>Picea glauca</i>
		Spruce, black	<i>Picea mariana</i>

Table 2. Tree density and basal area by species, pine maple stand.
Included are stems ≥ 2.5 cm DBH within plots covering 1.1861 ha.

Taxon	DENSITY		cm ² /tree	BASAL AREA		Mean DBH (cm)	Sample Size
	Trees/ha	Relative		m ² /ha	Relative BA		
White pine	22.8	2.0%	2333.	5.32	15.9%	54.5	27
Red pine	67.5	6.0%	1948.	13.15	39.4%	49.8	80
Red oak	95.3	8.5%	311.	2.96	8.9%	19.9	113
Quaking aspen	53.9	4.8%	594.	3.20	9.6%	27.5	64
Bigtooth aspen	18.6	1.7%	423.	0.79	2.4%	23.2	22
Paper birch	155.1	13.8%	274.	4.26	12.8%	18.7	184
Red maple	177.9	15.8%	102.	1.82	5.4%	11.4	211
Sugar maple	345.8	30.6%	40.	1.38	4.1%	7.1	409
Ironwood	160.2	14.3%	17.	0.28	0.8%	4.7	190
Basswood	13.5	1.2%	49.	0.07	0.2%	7.9	16
White spruce	5.1	0.4%	200.	0.10	0.3%	15.9	6
Black & green ash	3.4	0.3%	61.	0.02	0.06%	8.8	4
Bur oak	2.5	0.2%	55.	0.01	0.04%	8.4	3
American elm	1.7	0.1%	37.	0.006	0.02%	6.9	2
Balsam poplar	0.8	0.7%	642.	0.05	0.02%	28.6	1
Yellow birch	0.8	0.7%	14.	0.001	0.003%	4.2	1
Black cherry	0.8	0.7%	20.	0.002	0.006%	5.1	1
Total	1124.7	100.0%		33.4	100%		1334

Table 3. Tree density and basal area by species, pine-fir stand.
Included are stems ≥ 2.5 cm DBH within plots covering 0.341 ha.

Taxon	DENSITY		cm ² /tree	BASAL AREA		Mean DBH (cm)	Sample Size
	Trees/ha	Density		m ² /ha	Relative BA		
White pine	114.4	5.5%	693.	7.9	27.1%	29.7	39
Red pine	137.9	6.4%	799.	11.0	36.1%	31.9	47
Quaking aspen	85.1	3.9%	111.	0.9	3.0%	11.9	29
Bigtooth aspen	55.7	2.6%	123.	0.7	2.3%	12.5	19
Paper birch	67.5	3.1%	206.	1.4	4.6%	15.2	23
Spruce	319.8	14.8%	103.	3.3	10.8%	11.5	109
Balsam fir	1273.4	58.9%	36.	4.6	15.1%	6.8	434
Ash	105.6	4.9%	53.	0.6	2.0%	8.2	36
Red maple	5.9	0.3%	43.	0.03	0.1%	7.4	2
Total	2165.5	100.0%		30.4	100.0%		738

Table 4. Trees damaged by cause and by survival of damage. (a) Pine-maple stand: trees damaged directly by wind were less likely to survive than were trees damaged by falling trees ($X^2=44.612$, $P<0.00005$). (b) Pine-fir stand: survival was equally unlikely for trees damaged directly by wind and trees damaged by falling trees ($X^2=1.51$, $P=0.2191$).

PINE-MAPLE STAND

Cause	Survived	Killed	Total
Wind	21	71	92
Falling tree	146	82	228
Total	167	153	320

PINE-FIR STAND

Cause	Survived	Killed	Total
Wind	3	26	39
Falling tree	36	203	239
Total	39	237	278

Table 5. Tree species mortality and damage rates, for stems ≥ 2.5 cm DBH.
 (a) Pine-maple stand; (b) pine-fir stand.

(a) PINE-MAPLE STAND

Taxon	# killed (/40 ha)	% of killed trees	mortality rate	# damaged (/40 ha)	% of damaged trees	damage rate	# sampled (/1.19 ha)	% of sampled trees
White pine	8	5.4%	0.9%	14	4.7%	1.5%	27	2.1%
Red pine	15	10.2%	0.6%	16	5.4%	0.6%	80	6.2%
Red oak	14	9.5%	0.4%	27	9.1%	0.7%	113	8.7%
Quaking aspen	62	49.2%	2.9%	73	24.6%	3.4%	64	4.9%
Bigtooth aspen	5	3.4%	0.7%	14	4.7%	1.9%	22	1.7%
Paper birch	8	5.4%	0.13%	20	6.7%	0.3%	184	14.2%
Red maple	13	8.8%	0.18%	30	10.1%	0.4%	211	16.2%
Sugar maple	18	12.2%	0.13%	83	27.9%	0.6%	409	31.5%
Ironwood	4	2.7%	0.06%	20	6.7%	0.3%	190	14.6%
Total	147	100.0%		297	100.0%		1300	100.0%

Table 5, continued: (b) Pine-Fir Stand (Tree species mortality and damage rates, for stems ≥ 2.5 cm DBH)

(b) PINE-FIR STAND

Taxon	# killed (/2 ha)	% of killed trees	mortality rate	# damaged (/2 ha)	% of damaged trees	damage rate	# sampled (/0.34 ha)	% of sampled trees
White pine	6	2.5%	2.6%	7	2.5%	3.1%	39	5.6%
Red pine	2	0.8%	0.7%	2	0.7%	0.7%	47	6.7%
Quaking aspen	10	4.1%	5.9%	11	3.9%	6.5%	29	4.1%
Bigtooth aspen	1	0.4%	0.9%	1	0.4%	0.9%	19	2.7%
Paper birch	11	4.5%	8.1%	16	5.7%	11.9%	23	3.3%
Spruce	63	25.8%	9.9%	69	24.7%	10.9%	108	15.5%
Balsam fir	151	61.9%	5.9%	173	62.0%	6.8%	434	62.1%
Total	244	100.0%		279	100.0%		699	100.0%

Table 6. Incidence of obvious fungal infections in trees prior to wind damage, by species, pine-maple stand.

Species	Numbers of trees:		
	Damaged	With Obvious Heart Rot	With Obvious Root Rot
Quaking aspen	73	59 (81%)	14 (19%)
Red pine	16	12 (75%)	4 (25%)
White pine	14	6 (43%)	1 (7%)
Bigtooth aspen	14	3 (21%)	2 (14%)
Paper birch	20	3 (15%)	0
Red oak	27	3 (11%)	0
Sugar maple	83	1 (1%)	1 (1%)
Red maple	30	0	0
Ironwood	20	0	0

Table 7. Seedling and sapling densities. "Seedlings" are tree stems, including possible sprouts, measuring less than 2.5 cm DBH, counted in seedling plots and, in column 2, estimated by including seedlings on microsites, weighted by areal coverage of microsite types. Saplings are tree stems measuring 2.5-10.0 cm DBH, estimated from plots covering 1.186 ha. (a) Pine-maple stand; (b) pine-fir stand.

(a) PINE-MAPLE STAND

	Seedlings per 100m ²		Saplings	Larger Trees per 100m ²
	Microsites excluded	Included		
White pine	0.4	0.6	0	0.22
Red pine	0	0	0.02	0.66
Red oak	11.0	10.6	0.21	0.95
Quaking & bigtooth aspen	23.2	21.7	0.13	0.60
Paper birch	3.3	3.4	0.18	1.42
Red maple	207.0	200.7	0.9	0.88
Sugar maple	1290.0	1220.4	2.8	0.64
Unidentified maple	102.0	97.0	0	0
Ironwood	7.4	6.9	1.6	0
Basswood	1.9	2.9	0.10	0.35

(b) PINE-FIR STAND

	Seedlings per 100m ²		Saplings	Larger Trees per 100m ²
	Microsites excluded	Included		
White pine	12.8	14.3	0	1.14
Red pine	0	0	0	1.38
Quaking & bigtooth aspen	0	1.0	0.82	0.59
Paper birch	79.5	93.8	0.26	0.40
Spruce	0	0.9	1.88	1.31
Balsam fir	12.8	21.9	11.16	11.47
Green & black ash	23.1	19.01	0.76	0.30

Table 8. Damage mode by species, (a) pine-maple stand; (b) pine-fir stand.

(a) PINE-MAPLE STAND

Species	Uprooted (%)		Broken (%)		Bowed (%)		Branch (%)		Total
Quaking aspen	12	(15%)	62	(79%)	2	(3%)	2	(3%)	78
Bigtooth aspen	4	(31%)	9	(69%)					13
Paper birch	4	(19%)	10	(48%)	7	(33%)			21
Ironwood	4	(17%)	1	(4%)	19	(79%)			24
Red maple	3	(9%)	24	(69%)	7	(20%)	1	(3%)	35
Sugar maple	8	(8%)	32	(32%)	58	(59%)	1	(1%)	99
Red oak	3	(10%)	19	(61%)	3	(10%)	6	(19%)	31
Red pine	3	(19%)	13	(81%)					16
White pine	2	(14%)	11	(79%)			1	(7%)	14
Other	1		2		2				5
Total	44	(13%)	183	(55%)	98	(29%)	11	(3%)	336

(b) PINE-FIR STAND

Species	Uprooted (%)		Broken (%)		Bowed (%)		Branch (%)		Total
Quaking aspen	3	(27%)	8	(73%)					11
Paper birch	5	(31%)	11	(69%)					16
Red pine	1	(50%)	1	(50%)					2
White pine	3	(43%)	3	(43%)			1	(14%)	7
Spruce	40	(52%)	25	(36%)	4	(6%)			69
Balsam fir	104	(63%)	42	(25%)	18	(11%)	1	(1%)	165
Other	1		2		2		1		6
Total	157	(57%)	92	(33%)	24	(9%)	3	(1%)	276

Table 9. Cause and mode of damage. (a) Pine-maple stand: cause of damage versus mode: all modes, $\chi^2=59.655$, $P<0.00005$; uprooted vs. broken only, $\chi^2=4.205$, $P=0.403$. (b) Pine-fir stand: cause of damage versus mode: all modes, $\chi^2=62.575$, $P<0.00005$; uprooted versus broken only, $\chi^2=58.540$, $P<0.00005$.

(a) PINE-MAPLE STAND

CAUSE OF DAMAGE	Uprooted	Broken	Bowed	Branch damaged	Total
Wind	12	82	1	3	98
Tree	31	100	97	8	236
Total	43	182	98	11	334

(b) PINE-FIR STAND

CAUSE OF DAMAGE	Uprooted	Broken	Bowed	Branch damaged	Total
Wind	5	34			39
Tree	147	57	24	3	231
Total	152	91	24	3	270

Table 10. Survival versus mode of damage. (a) Pine-maple stand: survival of damage versus mode: all modes, $\chi^2=96.421$, $P<0.01$; uprooted vs. broken only, $\chi^2=0.801$, $P=0.37$. (b) Pine-fir stand: survival of damage versus mode; all modes, $\chi^2=114.319$, $P<0.01$; uprooted versus broken only, $\chi^2=1.935$, $P=0.16$.

(a) PINE-MAPLE STAND

<u>SURVIVAL OF DAMAGE</u>	<u>Uprooted</u>	<u>Broken</u>	<u>Bowed</u>	<u>Branch damaged</u>	<u>: Total</u>
Survived	16	56	85	10	: 167
Killed	24	116	11	1	: 152
Total	40	172	96	11	: 319

(b) PINE-FIR STAND

<u>SURVIVAL OF DAMAGE</u>	<u>Uprooted</u>	<u>Broken</u>	<u>Bowed</u>	<u>Branch damaged</u>	<u>: Total</u>
Survived	8	9	19	3	: 39
Killed	149	84	5		: 238
Total	157	93	24	3	: 277

Table 11. Areal coverage and density of microsites. (a) Pine-maple forest; plots covered 1474 m², 0.004% of the 40 ha study area. (b) Pine-fir forest: plots covered 1591 m², 0.02% of the 8 ha study area.

(a) PINE-MAPLE STAND

	Stumps	Mounds	Pits	Boles
Area in plots(m ²)	2.12	21.35	7.01	58.62
% Cover	0.14%	1.45%	0.47%	3.98%
N in plots ⁽¹⁾	27	12	10	178
Density/100m ²	1.8	0.8	0.7	

(b) PINE-FIR STAND

	Stumps	Mounds	Pits	Boles
Area in plots(m ²)	7.2	107.3	13.3	154.28
% Cover	0.45%	6.7%	0.8%	9.70%
N in plots ⁽¹⁾	67	92	8	317
Density/100m ²	4.2	5.8	2.5	

(1): N = number of microsites partially or entirely in plots.

Table 12. Vegetation and other characteristics of microsites sampled.
 These data include all microsites sampled for vegetation, whether
 in or out of plots. (a) Pine-maple stand; (b) pine-fir stand.

(a) PINE-MAPLE STAND

	Stumps	Mounds	Pits	Boles	Control plots
Number sampled for seedlings	30	16	14	180	68
Area sampled for seedlings, m ²	6.42	59.94	23.47	215.9	272
Mean size, cm ²	2139.6	46,837.5	19,067.9	11,800.5	40,000.
# with no vegetation	15	0	0	80	0
# with moss only	10	0	0	44	0
# with herbs & shrubs	1	2	0	11	7
# with tree sdls/sprouts	4	14	14	45	59

(b) PINE-FIR STAND

	Stumps	Mounds	Pits	Boles	Control Plots
Number sampled for seedlings	110	122	64	320	39
Area sampled for seedlings, m ²	12.404	124.682	28.732	366.28	39
Mean size, cm ²	1127.6	10,137.	4489:4	11,229.9	10,000
# with no vegetation	32	8	21	95	4
# with moss only	43	17	1	105	
# with herbs & shrubs	10	50	37	37	19
# with tree sdls/sprouts	25	47	5	88	16

Table 13. Presence of tree seedlings and sprouts on microsites as a function of microsite size, age, and species (of dead tree). Only microsites of known species were used in the analysis, unless otherwise noted. Stepwise logistic regression analysis entered factors whose X^2 values for improving model fit had $P < 0.10$.

Microsite Type	N	Significance of Effects		
		Size	Age	Species
<u>(a) Logs</u>				
	357	* ($P < 0.00005$)	* ($P < 0.00005$)	($P = 0.621$)
<u>(b) Stumps</u>				
	106	($P = 0.0723$)	($P = 0.8690$)	* ($P < 0.00005$)
<u>(c) Logs and Stumps Combined</u>				
	463	* ($P < 0.00005$)	* ($P < 0.00005$)	($P = 0.0740$)
<u>(d) Mounds</u>				
	64	($P = 0.3048$)	* ($P = 0.0457$)	($P = 0.5533$)
Size & Age Model (includes mounds of unknown species):				
	137	* ($P = 0.0492$)	* ($P = 0.0006$)	--Excluded from model--
<u>(e) Pits</u>				
	31	($P = 0.8388$)	* ($P = 0.0467$)	($P = 0.9989$)

Table 14. Tree seedling/sprout frequency and density on microsites, pine-maple stand.

Species of regeneration	STUMPS (N=30)			MOUNDS (N=16)		
	Stumps with regeneration	Total # of stems	Stems per 100m ²	Mounds with regeneration	Total # of stems	Stems per 100m ²
Paper birch	0			3	5	8.34
White pine	1	1	15.6	2	2	3.3
Aspen	0			5	20	33.3
Balsam fir	0			1	1	1.7
Spruce	0			1	1	1.7
Red oak	0			2	3	5.0
Red maple	2	7	109.4	9	71	118.5
Sugar maple	2	6	93.8	7	197	328.
Unknown maple	1	7	109.4	2	18	30.03
Ironwood	0			3	13	21.7
Basswood	0			0		
TOTAL			328			552

Table 14, Continued (Tree seedling/sprout frequency and density on microsites, pine-maple stand)

Species of regeneration	PITS (N=14)			BOLES (N=180)			CONTROL PLOTS	
	Pits with regeneration	Total # of stems	Stems per 100m ²	Boles with regeneration	Total # of stems	Stems per 100m ²	Plots w/regen. (# stems)	Stems/100m ²
Paper birch	0			8	26	12.04	8 (9)	3.3
White pine	0			4	7	3.2	1 (1)	0.4
Aspen	0			1	1	0.5	25 (63)	23.2
Balsam fir	0			0			0	0
Spruce	0			0			0	0
Red oak	3	3	12.7	4	4	1.85	20 (30)	11.0
Red maple	10	27	114.9	34	202	93.6	53 (563)	207
Sugar maple	8	40	170.2	29	116	53.7	45 (2219)	1290
Unknown maple	0			2	8	3.7	34 (277)	101.8
Ironwood	1	1	4.3	0			7 (20)	7.4
Basswood	2	5	21.3	0			3 (5)	1.8
TOTAL			323.4			168.6		1645.9

Table 15. Tree seedling/sprout frequency and density on microsites, pine-fir stand.

Species of regeneration	STUMPS (N=110)			MOUNDS (N=124)		
	Stumps with regeneration	Total # of stems	Stems per 100m ²	Mounds with regeneration	Total # of stems	Stems per 100m ²
Paper birch	17	62	500	26	125	100
White pine	9	19	153	12	18	14.4
Aspen	2	2	16.1	7	8	6.4
Balsam fir	7	7	56.5	25	35	20.0
Spruce	2	2	16.1	5	4	4.0
Balsam poplar	0			3	2	2.4
Red oak	0			0		
Red maple	0			0		
Green ash	0			1	1	0.8
Cherry	0			1	1	0.8
TOTAL			742			149

Table 15, Continued. (Tree seedling/sprout frequency and density on microsites, pine-fir stand)

Species of regeneration	PITS (N=65)			BOLES (N=320)			CONTROL PLOTS	
	Pits with regeneration	Total # of stems	Stems per 100m ²	Boles with regeneration	Total # of stems	Stems per 100m ²	Pits with regen. (stems)	Stems/100m ²
Paper birch	1	1	3.5	74	832	227	6 (31)	79.5
White pine	0			33	74	20.2	5 (5)	12.8
Aspen	1	1	3.5	8	15	4.1	0	0
Balsam fir	1	1	3.4	36	97	26.5	4 (5)	12.8
Spruce	0			8	18	4.9	0	0
Balsam poplar	1	2	7.0				1 (1)	2.6
Red oak	1	1	3.5				1 (1)	2.6
Red maple	1	1	3.5	"OTHER": 3	4	1.1	0	0
Green ash	0						5 (9)	23.1
Cherry	0						+	
TOTAL			24.5			283.8		133.4

Table 16. Areal Coverage by microfossils in forests, as reported in the literature. ND=no data reported.

Forest Location and Type	Source	Areal Coverage by Mounds and Pits	Areal Coverage by Dead Wood
Pine-maple stand, northwestern Minnesota	This study	1.6%	4.4%
Pine-fir stand, northwestern Minnesota	This study	7.2%	10.5%
Harvard Forest	Stephens 1956	14%	ND
Huyck Preserve, New York	Beatty 1980	50%	ND
Eastern Illinois	Thompson 1980	ND	1.9%
<u>Tilio-carpinetum</u> and <u>Pinus-quercetum</u> stands, Poland	Falinski 1978	2.2% (pits only)	12.0-15.0%
<u>Pseudotsuga</u> stands, Washington & Oregon	Maser & Trappe 1984	ND	45%
<u>Pseudotsuga</u> stands, Pacific Northwest	Franklin et al. 1981	ND	27%
Hoh Rain Forest, Washington	Graham 1982	ND	6-11%
Barro Colorado Island, Panama	Putz et al. 1983	<1%	ND

Figure 1. Location of Itasca Park, Minnesota, U.S.A.

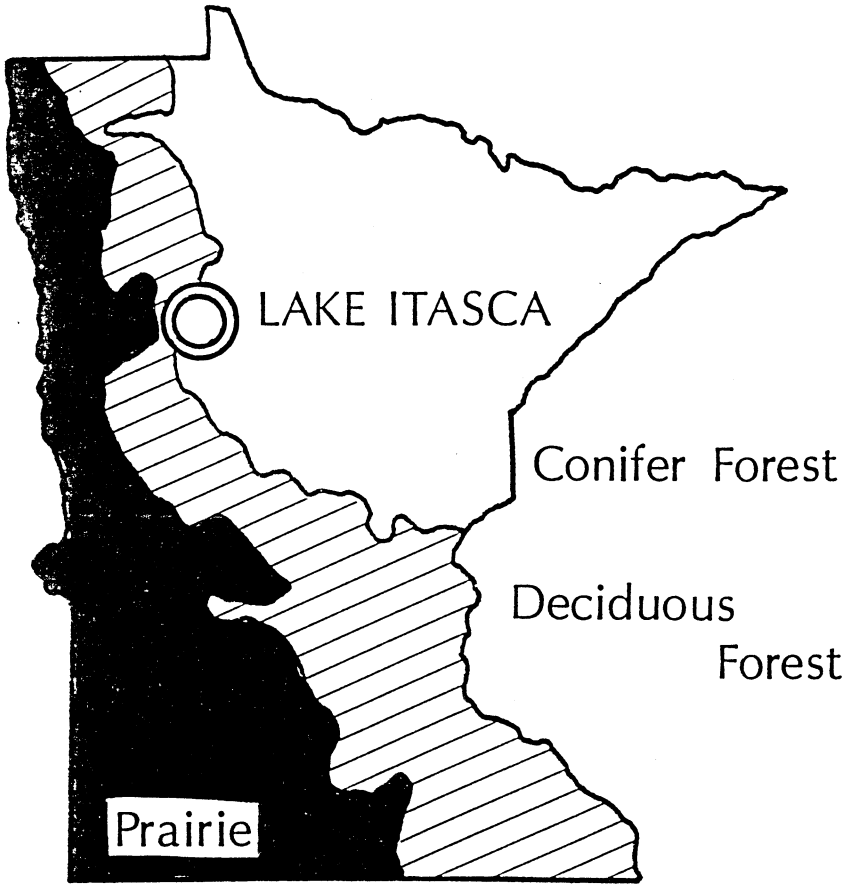


Figure 2. Location of the two study areas within Itasca Park.

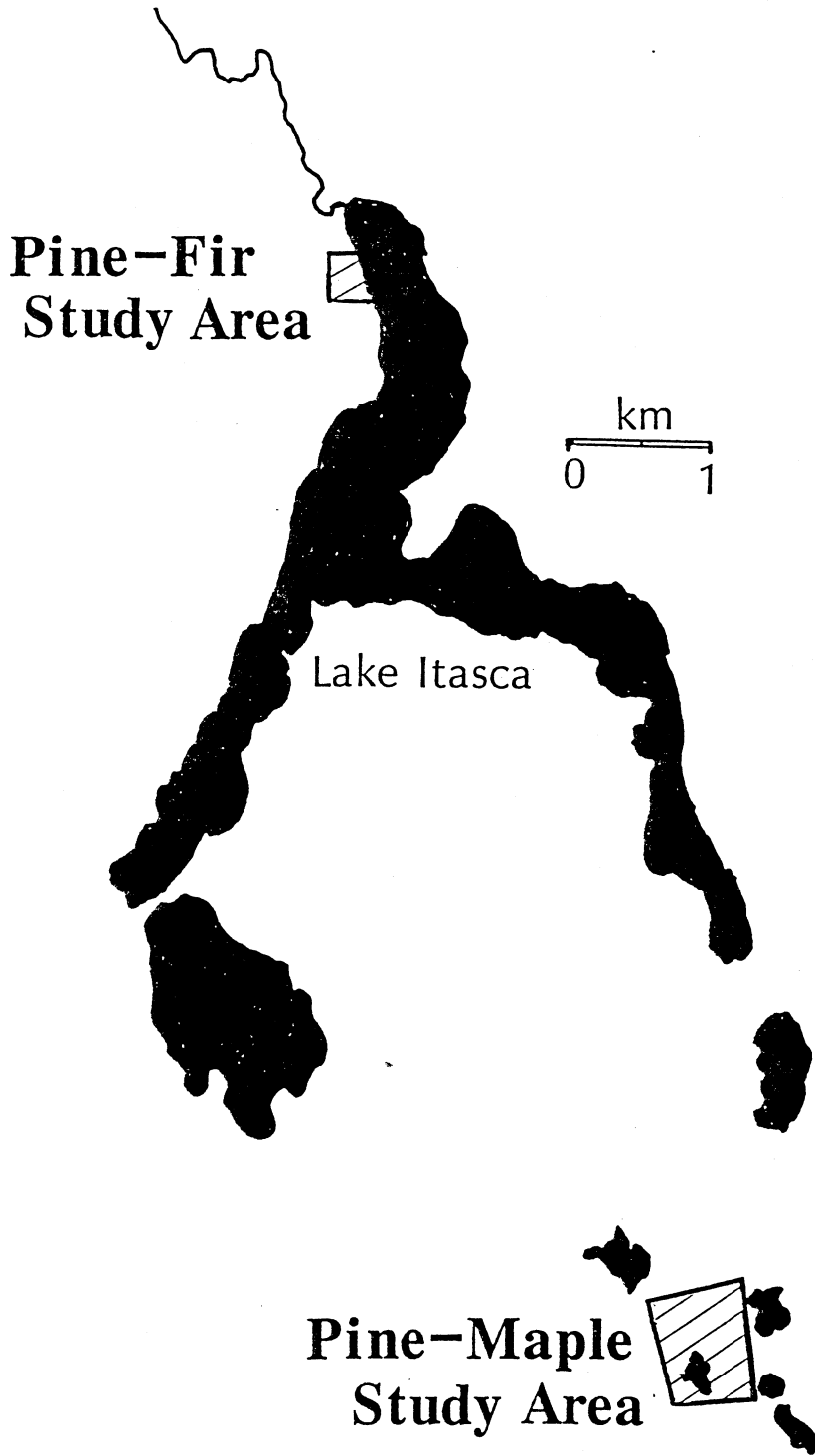
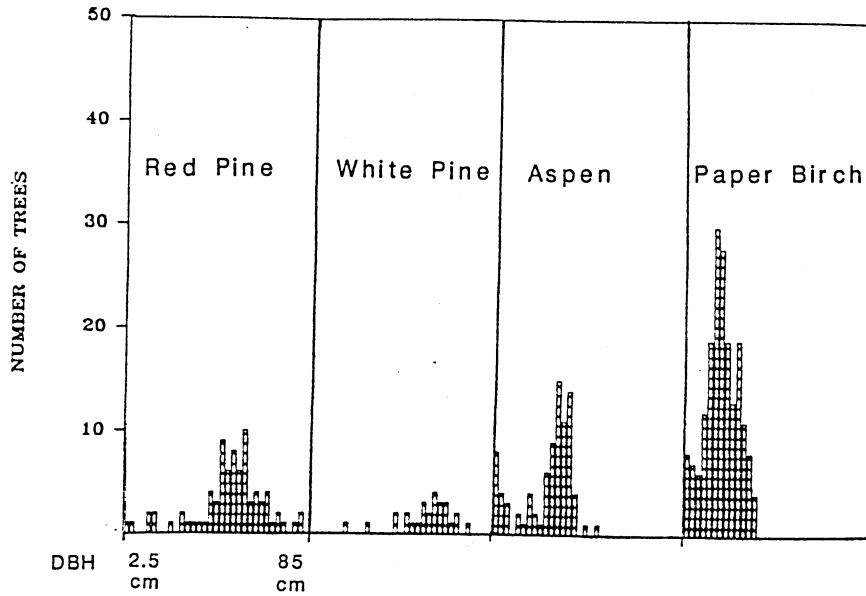


Figure 3a. Tree size distributions by species, shade-intolerant taxa. Note greater abundance of small trees and saplings in the pine-fir stand.

TREE SIZE DISTRIBUTIONS
 (A) Shade-Intolerant Taxa
 PINE-MAPLE STAND



PINE-FIR STAND

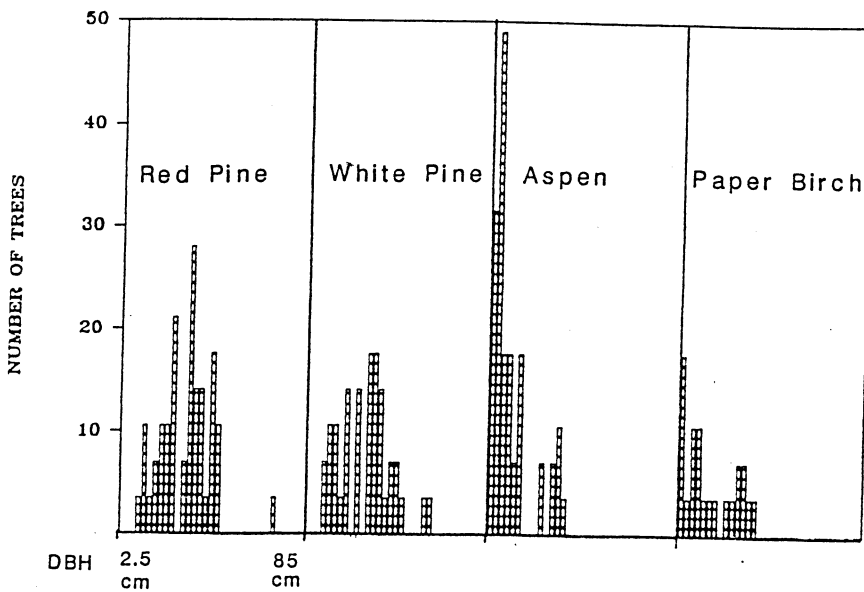
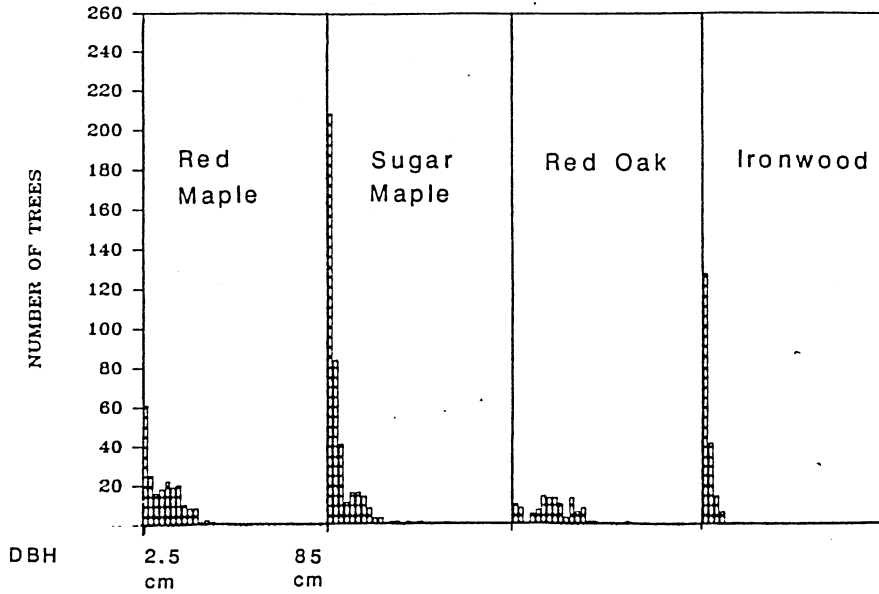


Figure 3b. Tree size distributions by species, shade-tolerant taxa.
 Note change from part (a) in scale of y-axis.

TREE SIZE DISTRIBUTIONS
 (B) Relatively Shade-Tolerant Taxa

PINE-MAPLE STAND



PINE-FIR STAND

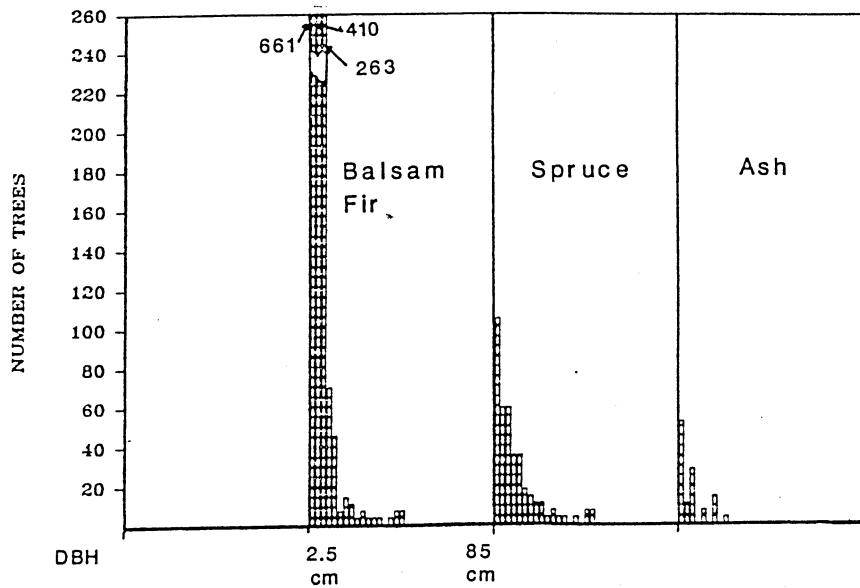


Figure 4. Tree size comparisons within species: sampled; directly hit by wind; killed; and damaged. * = mean diameter significantly different ($P < 0.05$) from mean diameter of sampled trees (first bar). (a) Pine-maple stand; (b) pine-fir stand.

TREE DIAMETER COMPARISONS

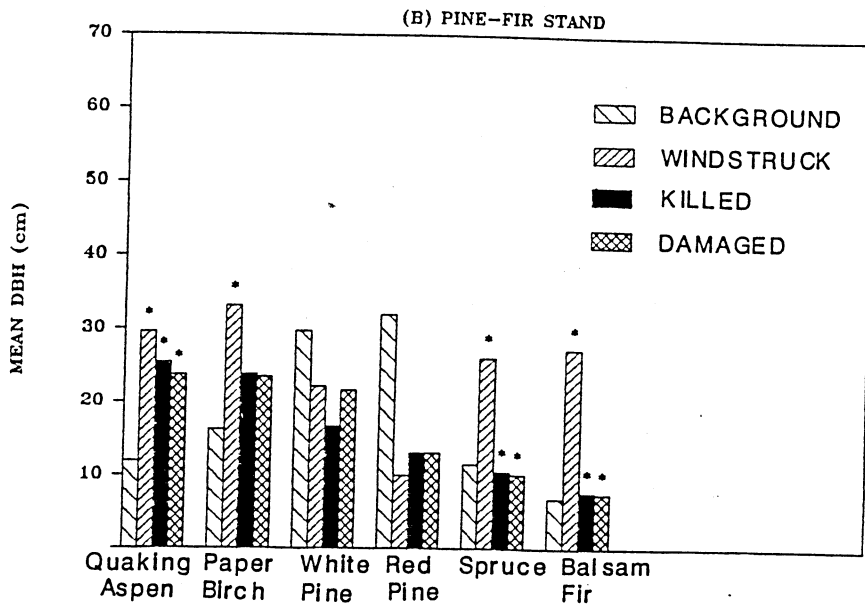
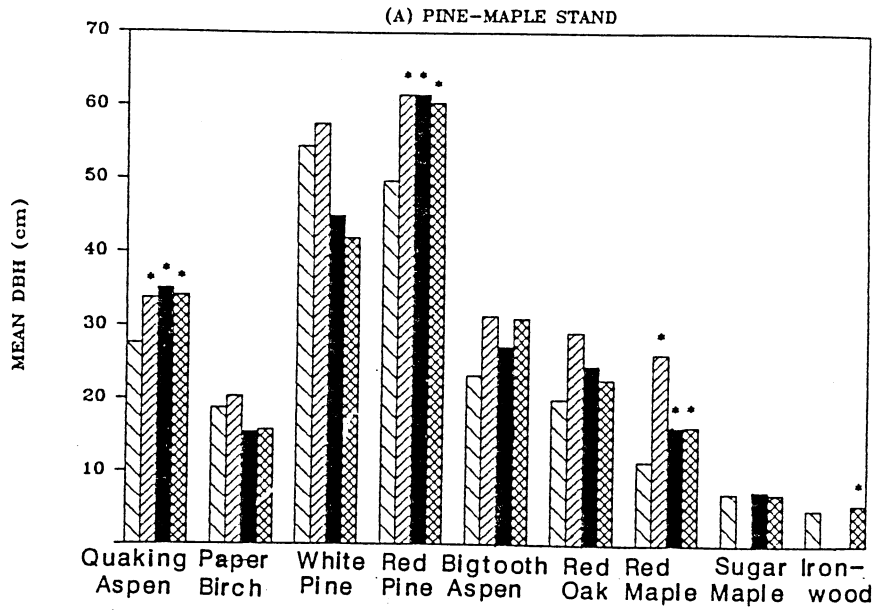


Figure 5. Tree species mortality rate as a function of wood strength. The wood strength parameter is maximum tensile strength perpendicular to the grain, from Markwardt and Wilson (1935). (a) Pine-maple stand; (b) pine-fir stand. Note the absence of relationship between tensile wood strength and mortality rate in both stands.

WOOD STRENGTH & MORTALITY RATE

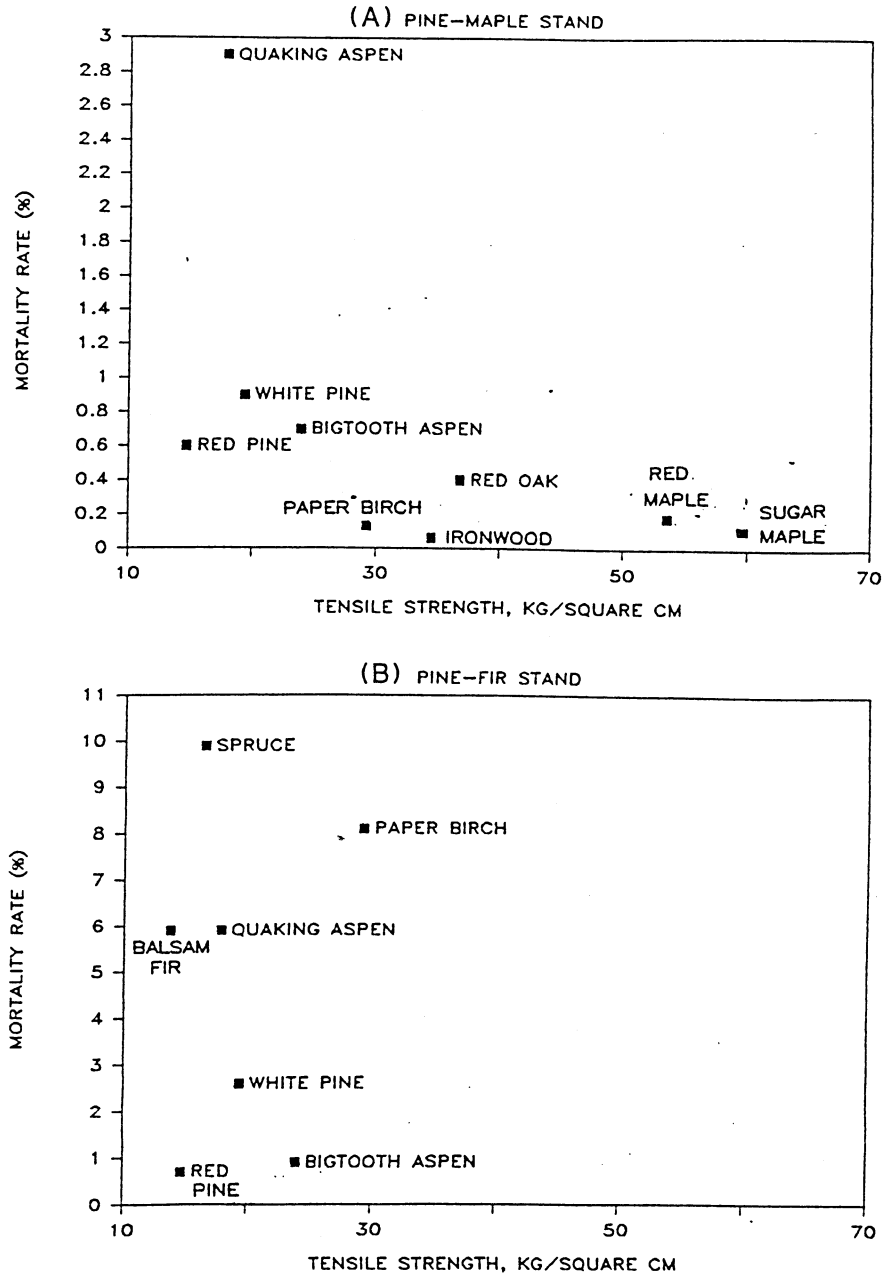


Figure 6. Tree species mortality rate as a function of shade tolerance. Shade tolerance approximations are from Fowells (1965), ranging from very intolerant to very tolerant. (a) Pine-maple stand; (b) pine-fir stand.

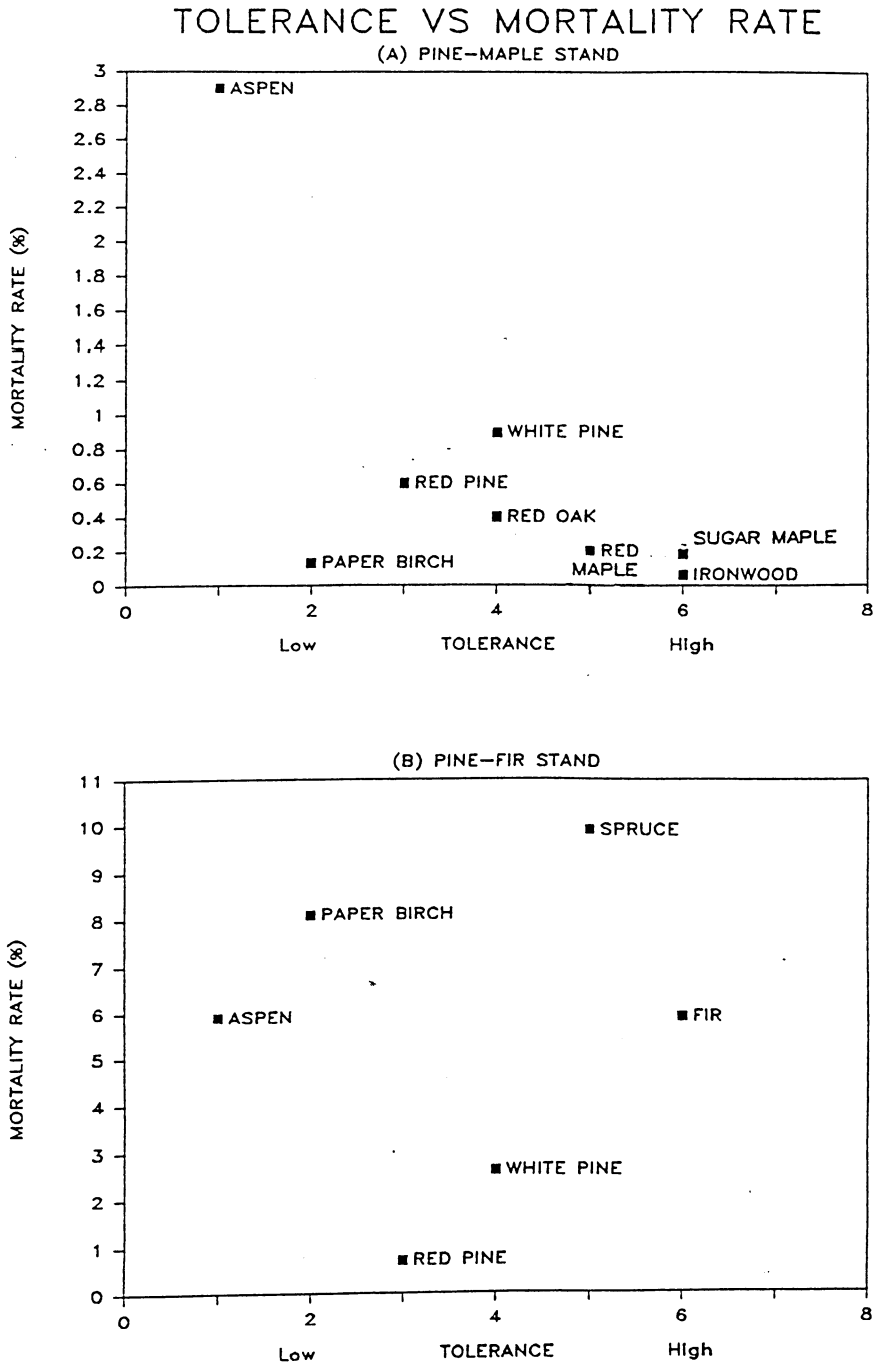


Figure 7. Gap formation and gap size histograms. Gaps were defined as openings extending from a height of 2 m up through the canopy. (a) Pine-maple stand; (b) pine-fir stand.

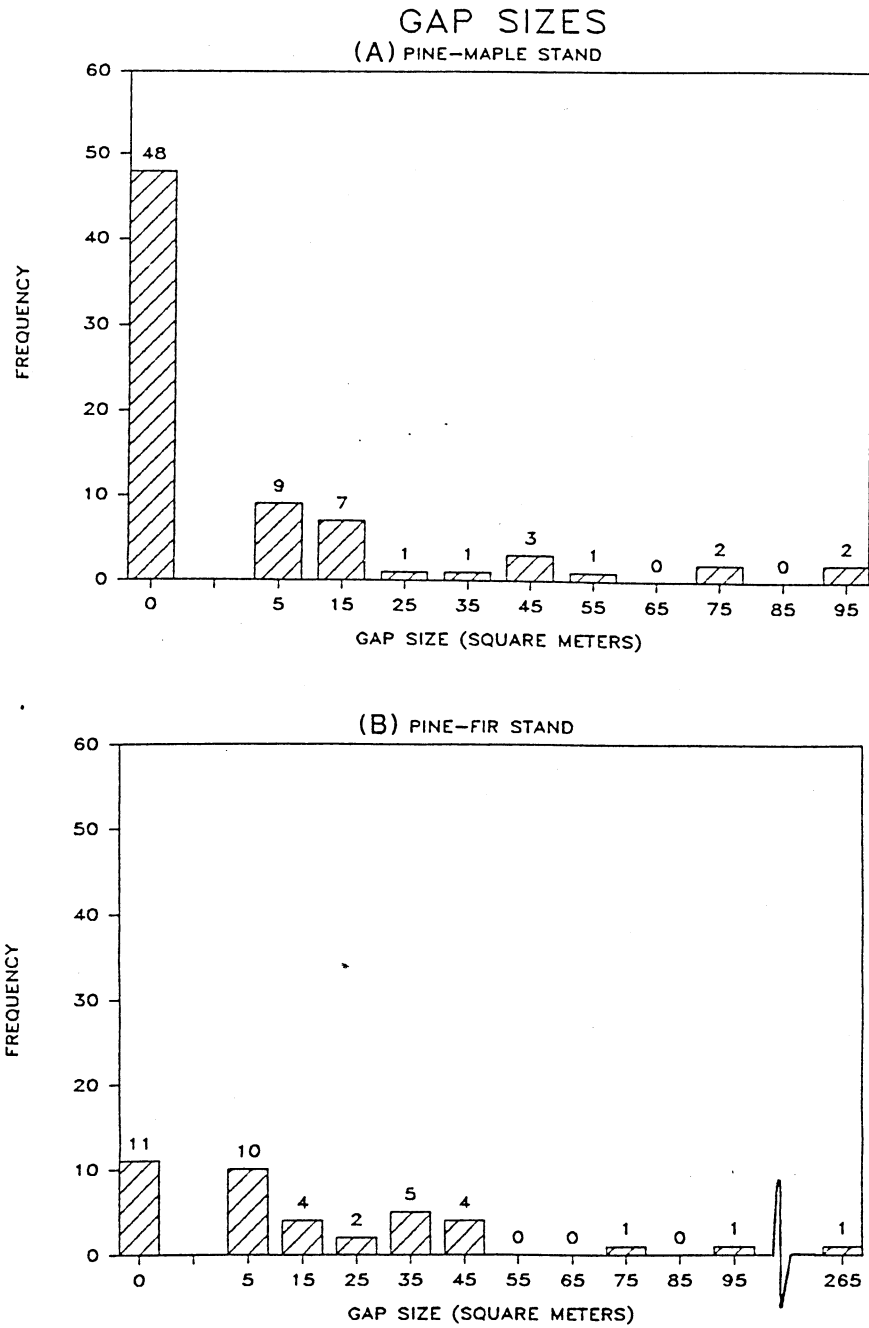


Figure 8. Gap formation in monolayered and multilayered stands: schematic diagram. Discrete canopy gaps are more likely to form in a monolayered forest (a and b) than in an irregular forest with a well developed understory (c and d).

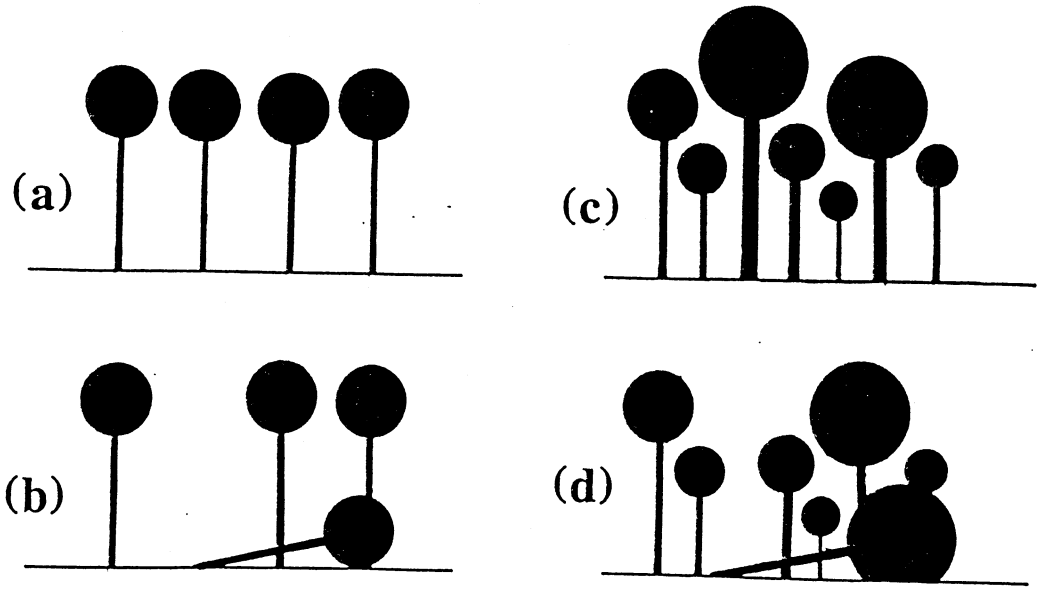


Figure 9. Tree seedlings and sprouts on microsites and control plots. Densities are given as stems per 100 m² of microsite or control plot surface.

TREE REGENERATION ON MICROSITES

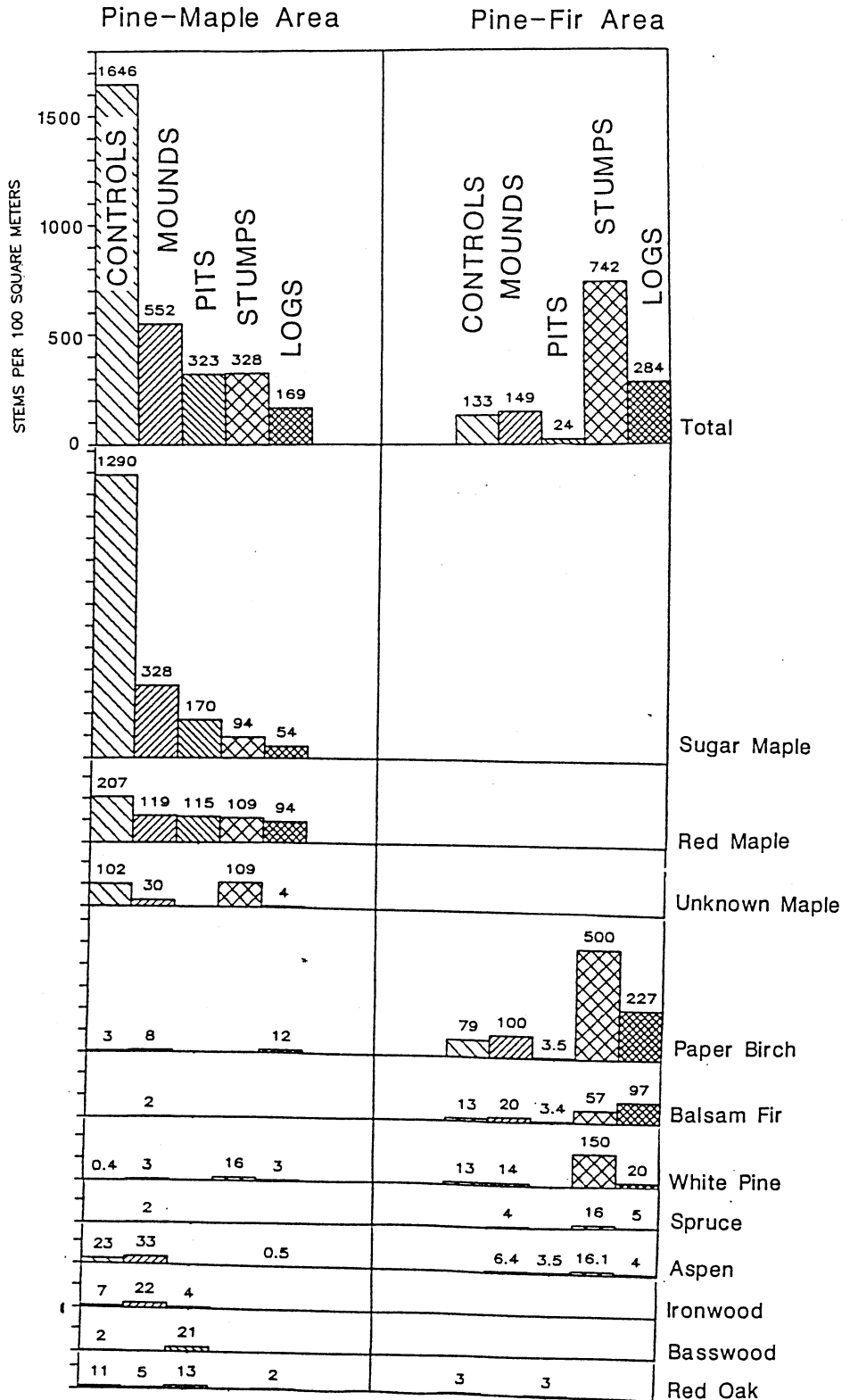


Figure 10. Microsite formation by wind damage. (a) Uprooted trees may form both mounds and pits but (b) do not always form pits. (c) Some wind-damaged trees break just below the ground, forming neither mound nor stump. (d) Tree breakage forms stumps.

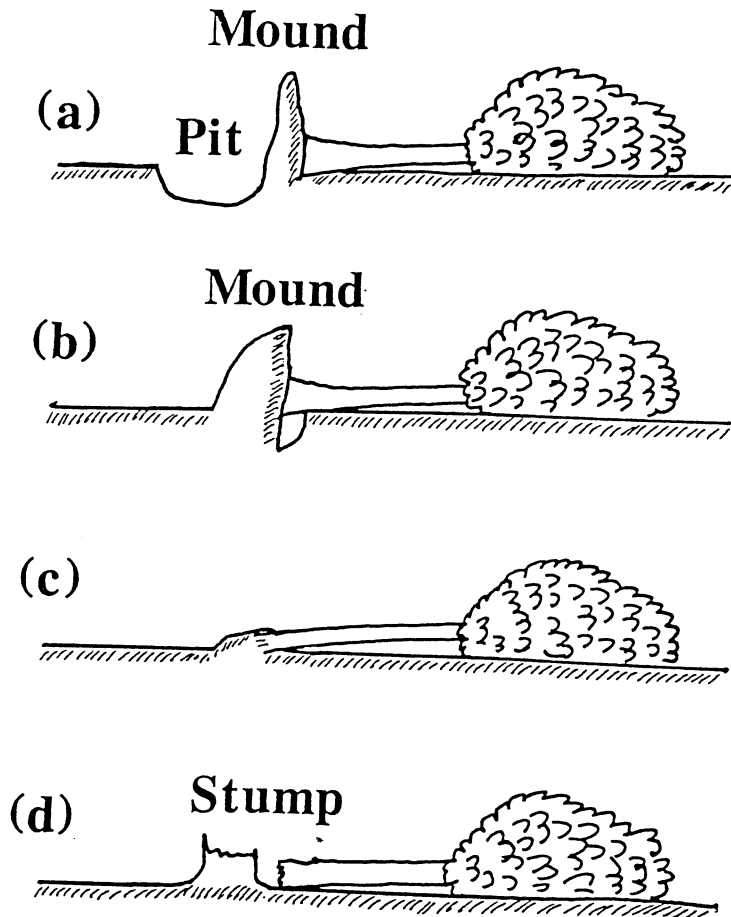


Figure 11. Damage mode by species. Bars show the proportion of damaged trees, within a species, that was uprooted, snapped, bowed, or had branches broken.
 (a) Pine-maple stand; (b) pine-fir stand.

DAMAGE MODE BY SPECIES

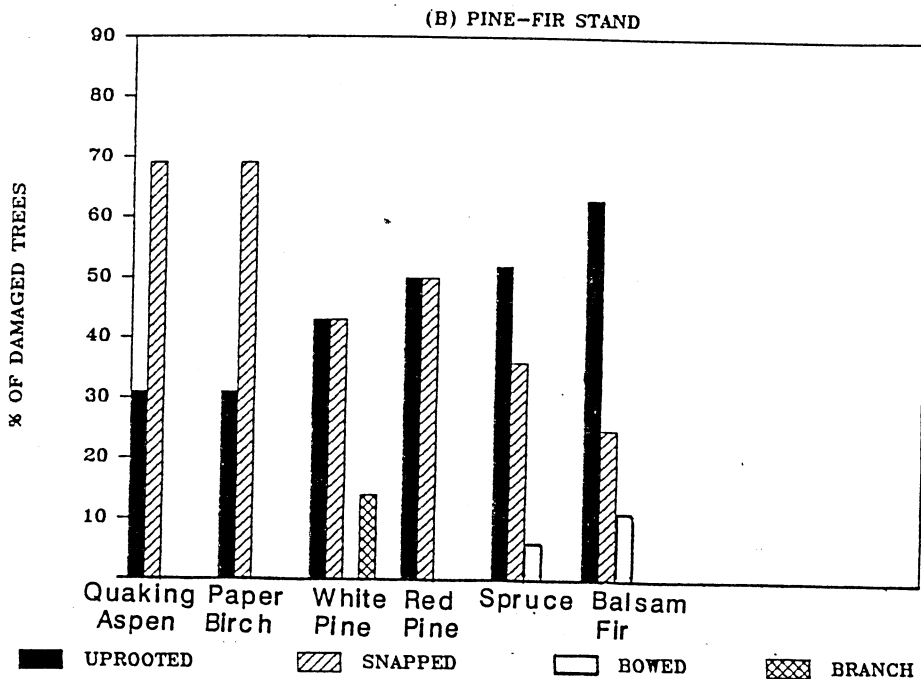
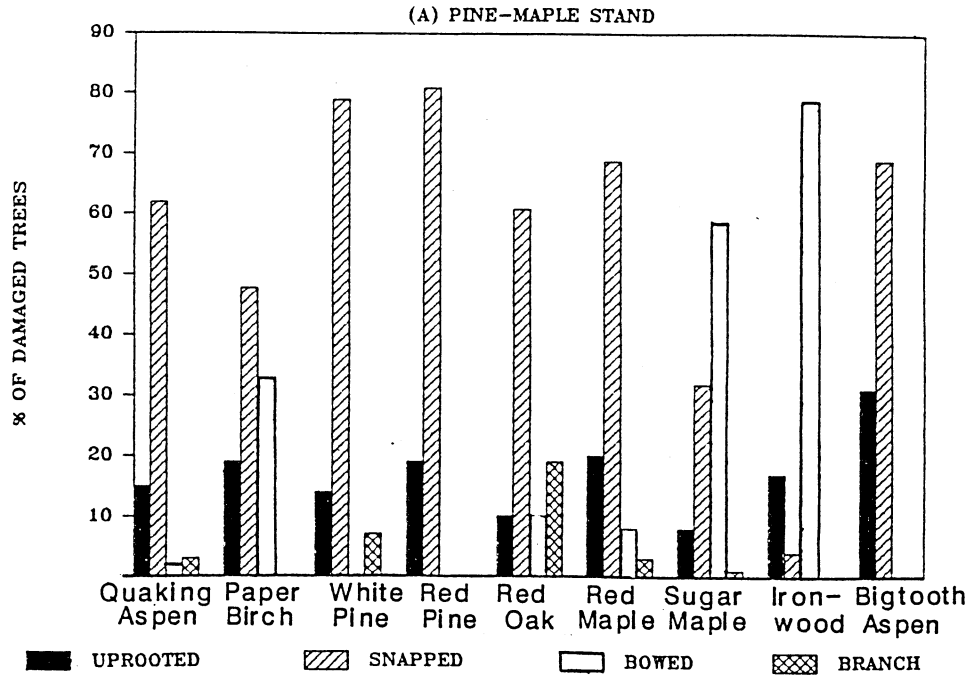


Figure 12. Damage mode as a function of tree size.
 (a) Pine-maple stand; (b) pine-fir stand.

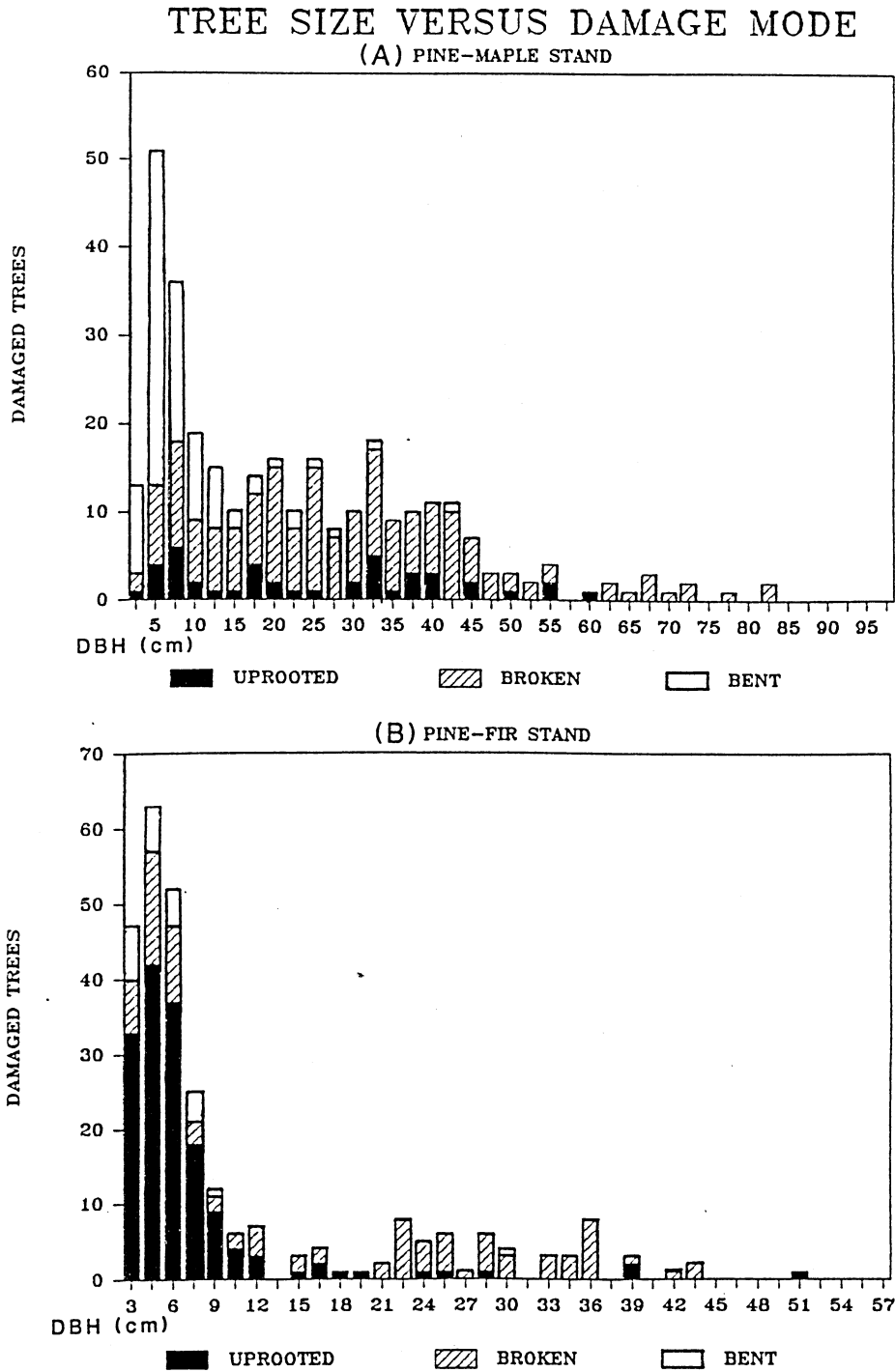
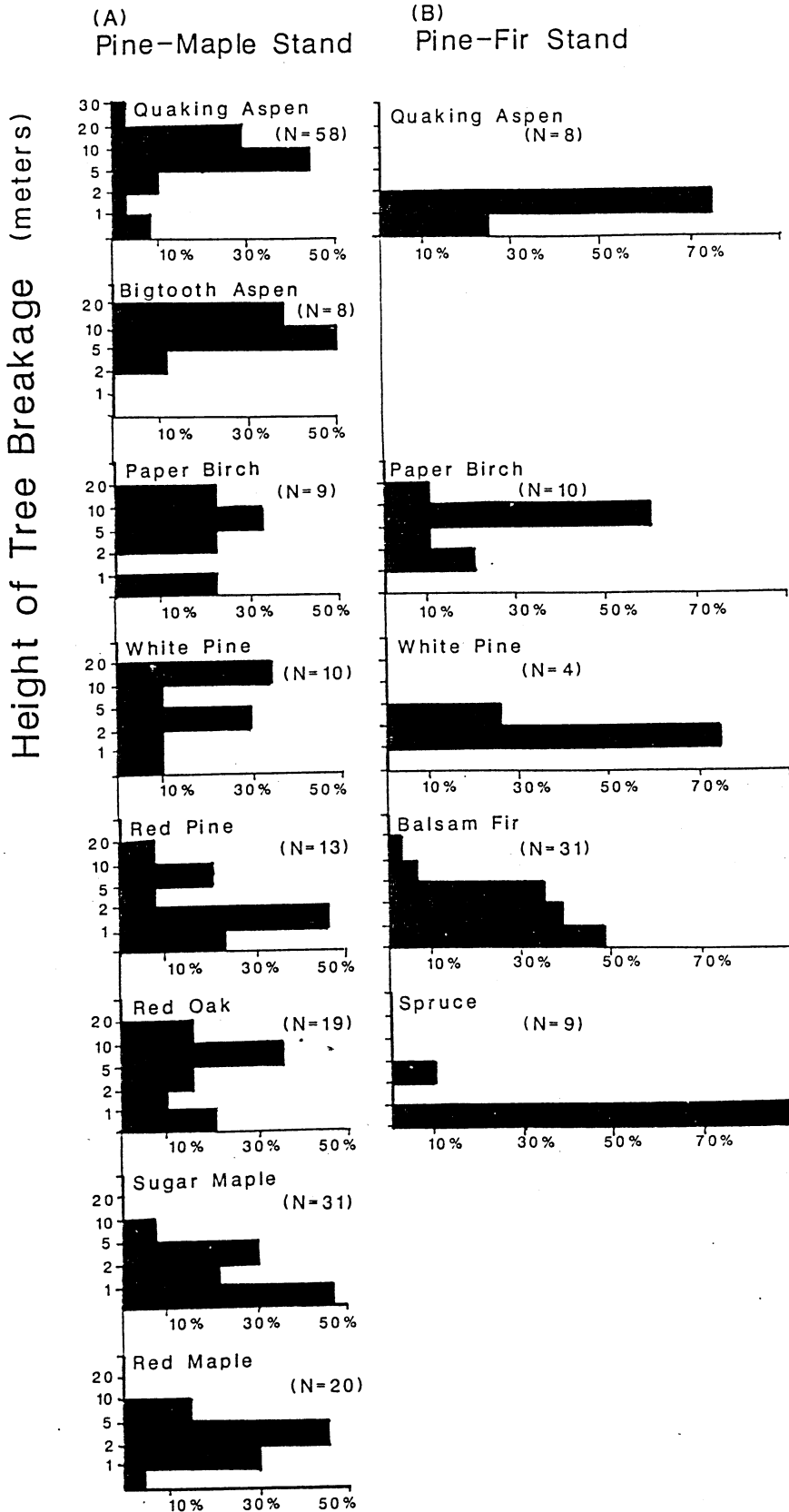
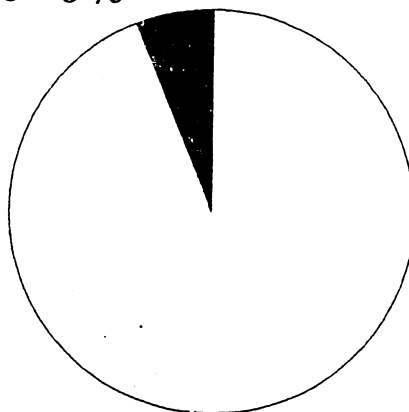


Figure 13. Breakage height by species. Bars show percentages of broken trees that snapped within a given height range. (a) Pine-maple stand; (b) pine-fir stand.



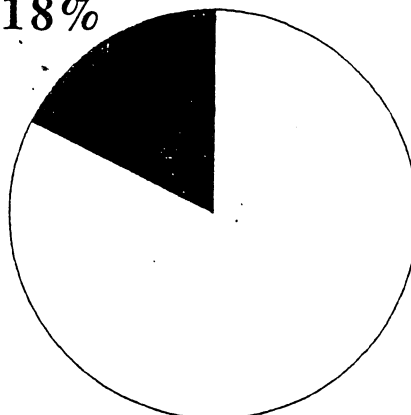
PINE-MAPLE STAND

Microsite Areal
Coverage 6%



PINE-FIR STAND

Microsite Areal
Coverage 18%



Appendix. DESCRIPTION OF A VEGETATION CONTACT WITHIN THE PINE-MAPLE STUDY AREA

INTRODUCTION

This Appendix explores a vegetation boundary located within the pine-maple stand where I studied windstorm consequences (Chapters 1 and 2). This boundary, called the hazel-maple contact, is the meeting of two forests of different canopy composition and dramatically different understory structures. One is a red pine forest with a dense understory of hazel ("hazel area"); the other is a sugar maple forest with an open understory ("maple area"). Vegetation contacts are found throughout Itasca Park; they are traditionally ascribed to edaphic transitions but might also be influenced by historical factors.

I began this study by asking whether or not past windstorms might explain vegetation differences across this contact zone. It quickly became clear that the origin of this vegetation line is complex, and that explanations other than windstorms must also be considered. The hazel-maple contact could instead result from differences in soil texture, soil fertility, fire history, herbivory by beaver, or interactions of these factors. Further research, using techniques described by Oliver and Stephens (1972), Henry and Swan (1974), and Lormier (1980) is needed to distinguish these possibilities.

In this Appendix, I describe the vegetation on either side of

the hazel-maple contact and within a transition zone. I also present information on the inferred vegetation, windstorms, and fires of the recent past, and I present information on soil texture and fertility from a small number of soil samples across the line.

STUDY AREA

The hazel-maple contact is located in Itasca State Park, Clearwater Co., Minnesota (Figure 14; W.1/2 NE 1/4 NE 14 Sec.36, T. 143 N., R. 36 W.). The line is located east of and roughly parallel to the Okerson Heights ski trail, 25 m away, and the west shore of Budd Lake, a small lake 50 m away. It runs NNW along a ridgetop of modest relief within the Itasca Moraine (Figure 15). The hazel area is on a west-facing slope above Budd Lake, while the maple area is on the upper east slope of the ridge. Soils are typical entroboraals of undetermined series.

The contact is distinct for a distance of approximately 150 m. It comprises a transition zone 25-40 m in width, where both hazel and sugar maple grow.

METHODS

Vegetation: Living and standing dead trees (DBH \geq 2.5 cm) were censused and measured within three 330 m² plots apiece in the maple and hazel areas. Seedlings and shrubs (DBH $<$ 2.5 cm) were censused within three 4-m² plots apiece in the maple and hazel areas. All vegetation plots were systematically arranged as part of a sampling

project covering a larger area (Chapter 1).

The age structure of tree populations was extrapolated from the data of Ness (1971) from nearby plots (see Chapter 1). Those data agree with tree ring counts I made for a small number of trees (8 red pines and 4 red oaks) that were actually located along the hazel-maple contact.

Past Vegetation: For clues to the vegetation, fires, and windstorms of the past, I established single 500 m² plots within the maple, transitional, and hazel areas. A census was made of windthrow mounds and pits, tree stubs and stumps, surface charcoal, and multiple stemmed trees. Multiple stemmed paper birch, red oak, and red maple trees were noted because they usually result from the loss of a previous stem during fires or windstorms. For each former tree in evidence, the time of tree death was approximated from the decomposition stage of associated wood (see Chapter 2, Methods Section) or from ages of resprouted stems. Tree species was also identified when possible.

Fire and Windstorm Chronology: I made the assumption that red pine became established only after fire in this forest (Ahlgren 1976; Frissell 1973) and that red pine ages therefore provide dates for major fires. I also assumed that most paper birch, red oak, and aspen stems became established after fires or windstorms, because all

three species are intolerant of shade (Fowells 1965) and because most trees of these species became established more or less synchronously, judging from uniformity of tree size (Chapter 1) and from age data of Ness (1971; discussed in Chapter 1). The area has not been logged (Aaseng 1976), although one cut stump is found within the hazel area, perhaps a result of salvaging a dead or damaged tree.

Soils: Shallow (50 cm) soil pits were dug within each of the three areas (hazel area, transition area, maple area) along three east-west transects that crossed all three zones (Figure 16). Transects were 15 m apart within the central 50 m of the 150-m contact zone. Each transect included two soil pits in the transitional area (8 m from the zone edges), two pits in the maple area (2 m and 10 m from the edge), and two pits in the hazel area (2 and 10 m from the edge).

Thickness was measured for upper soil horizons, and soil samples from the A1 horizon were analyzed for texture through hydrometer analysis performed by the University of Wisconsin Soil and Plant Analysis laboratory. Cation exchange capacity was estimated from exchangeable calcium, magnesium, and potassium as determined by the same laboratory, which also measured organic matter content, phosphorous content, and pH.

RESULTS

Vegetation: Total density of trees (DBH >2.5 cm) is higher in the

maple area ($10/100 \text{ m}^2$) than in the hazel area ($7/100 \text{ m}^2$; Table 17). Species composition of the two areas also differs strongly (Table 17). The maple area has twice as many red oak stems, ten times as many sugar maples, and fourteen times as many ironwoods as the hazel area. The hazel area has over twice as many paper birch trees and five times as many red pines as the maple area.

Understory differences are also strong (Table 18). In the hazel area, there are high densities of hazel (21 stems/m^2) and other shrub stems ($13/\text{m}^2$), while in the maple area shrubs are sparse (hazel: $0.08/\text{m}^2$; other shrubs: $3.0/\text{m}^2$). In contrast, the maple area has a dense carpet of small sugar maple seedlings ($19/\text{m}^2$) and scattered small aspen sprouts ($1/\text{m}^2$), both of which are virtually absent from the hazel area (0.08 sugar maple seedlings/ m^2 and 0 aspen sprouts/ m^2).

Past Vegetation: Evidence from windthrow mounds, tree stubs, and multiple stemmed trees suggests that the two sides of the hazel-maple contact differed in the recent past much as they do today. Table 19 lists trees whose past presence was inferred. The maple area had a higher density of inferred trees than the hazel area (4.6 dead trees/ 100 m^2 , versus 2.2 dead trees/ 100 m^2), just as is true of extant tree densities (Table 17). The transitional area was intermediate in density of inferred past trees ($3.8/100 \text{ m}^2$).

The major floristic differences in the past involved red pine and aspen. There is no evidence that red pine ever grew in the maple

area, although several pine stumps were found in the hazel area where pines still grow today. No mounds or stumps in the maple area were identifiable as pines. Most of the identifiable mounds in the maple area were from aspen trees, indicating greater aspen abundance in the past (Table 19).

Fire Chronology: The earliest record of fire is inferred from tree cores from long-lived red pines. Large red pines in and near the hazel area were approximately 258 years old in 1985 A.D, suggesting a major fire around 1727 A.D. (Frissell 1973). The absence of present and inferred past red pine trees from the maple and transitional areas suggests a difference in fire regime. Either these areas did not burn during the 1727 fire, or fire intensity or some other factor did not favor red pine establishment. If pines did get established there in 1727, they were eliminated soon thereafter. This seems unlikely, because young (<100 yr) red and white pines are windfirm in this region (Chapter 1), and because drought or disease is unlikely to have preferentially removed only those pines in the moister, east-facing maple area.

Evidence for at least one subsequent fire is seen throughout the area, as discussed in Chapter 1. Evidence includes fire scars on 250-year old red pines and the synchronous establishment around 1883 A.D. of shade-intolerant aspen, red oak, and paper birch trees in surrounding areas (Ness 1971) and, according to my tree ring counts, within the hazel-maple contact area.

Windstorm Chronology: Windthrow mounds are much more abundant in the maple area (2.8 mounds/100 m²) than in the hazel area (0.2/100 m²). Mound density is intermediate in the transitional area (1.4 mounds/100 m²).

Windstorms often break trees rather than uprooting them in this forest today (Chapter 2), and tree stubs might also result from wind damage. However, some tree stubs apparently resulted from fire damage, from death of trees while standing, and--in one case--from logging. Combining uprooted and broken trees, the deaths of 3-8 trees in the hazel plot (0.6-1.6/100 m²) could be ascribed to windstorms, while the deaths of 14-23 trees in the maple plot (2.8-4.6/100 m²) could be ascribed to windstorms. During 1983 and 1984, thunderstorm winds felled four trees rooted in the maple area plot (0.8 trees/100 m²) and two trees in the hazel area plot (0.4 trees/100 m²).

Soils: Upper soil profiles differ among the three areas (maple, transitional, hazel) (Table 21). A thin A1 horizon (2-7 cm) of very dark brown sandy loam and a thick layer (>50 cm) of grayish brown to brown sandy loam (E horizon) were evident in every soil pit. Soil samples from the A1 horizon have 59-75% sand, 20-36% silt, and 4-6% clay, with significantly more silt in soils of the maple area (Wilcoxon 2-Sample Test, P<0.05; Figure 17). Organic matter content ranged from 4.2 to 8 per cent, with no significant difference between

the hazel and maple area samples (Wilcoxon 2-Sample Test, $P > 0.05$).

In the hazel zone, the litter layer is thicker and contains undecomposed pine needles. In the maple zone, litter is slightly thinner, on average (Table 21; 3.33 cm, versus 4.08 cm in the hazel area), but the difference is not statistically significant (Wilcoxon Sign-Rank Test). Maple zone litter lacks needles and contains more roots.

Soil fertility, as measured by cation exchange capacity, is variable among samples, ranging from 7 to 13.5 millequivalents per 100 g of soil, but it does not vary between zones for the small number of samples analyzed (Figure 18).

DISCUSSION AND CONCLUSIONS

Fires: The frequency of fire or the results of fire have apparently differed on the two sides of the hazel-maple contact. Both sides of the line burned around 1883 A.D., when oak, birch, and aspen trees became established. The two areas were affected differently by an earlier fire, however. Apparently the occurrence of red pine in the hazel area indicates that a fire occurred there around 1727 A.D., while the maple area did not burn or burned with intensity insufficient for red pine establishment (Frissell 1973). This difference might be related to local topography, which is known to influence fire frequency on a regional scale (Grimm 1984). The west-slope hazel zone might burn more often or more intensely because of

drier conditions or greater fuel accumulation rates. It is possible that topography established a vegetation boundary in this location long before the present generation of red pines became established.

Windstorms: In contrast to fires, windstorms have caused more damage, over the past century or two, in the maple area than in the hazel area. The east-facing slope of the maple area is on the upper lee side of a ridge with respect to prevailing summer winds, a topographic position very prone to high windspeeds and turbulent gusts (O'Conneide 1975; Lee 1978).

Might windstorms substitute for fire in the future to help reduce differences between the two areas? The answer is no. On the contrary, thunderstorm winds promote wind-firm, shade-tolerant trees in this area (Chapter 1). Even storms with higher windspeeds may favor trees already established rather than initiating an age class of shade-intolerant pines, oaks, and birches (Oliver and Stephens 1977).

Frequent windstorms might reduce fire frequency or fire intensity in this stand. The mesic deciduous forests that follow windstorms retard fire more than do pine stands, with their drier, slower-decomposing litter, that often originate after fire in this region. The different consequences of fires and windstorms illustrate the inadvisability of grouping together such disparate processes under the umbrella of disturbance.

Edaphic Factors: Spatial heterogeneity in vegetation is often correlated with heterogeneity in soil moisture or soil nutrients or both (Kell 1938; Tilman 1982; Kurmis 1969; Kurmis et al. 1986). Vegetation-soil relationships are complicated by feedback loops by which vegetation itself modifies soil characteristics, for example through litter effects on nutrient cycling (Trudgill 1977; Pastor et al. 1984). As a result, the history of vegetation may influence later vegetation.

The absence of sugar maple from the hazel area might result in part from the influence of past vegetation, the pines in particular, upon litter decomposition and soil fertility. Sugar maple may be a poor competitor for nitrogen (Pastor et al. 1984), although other nutrients might instead be limiting. The litter of some needle-leaf conifers is poor in nutrients and does not recycle nutrients but keeps them tied up in the litter layer (Nihlgard 1972; Fogel and Cromack 1977; McClaugherty et al. 1985; Pastor et al. 1984). Sugar maple litter, in contrast, is rich in available nitrogen and exchangeable cations (Pastor and Bockheim 1984; Pastor et al. 1984). Perhaps long-lived red pines now control the hazel-maple boundary through this mechanism, although chemical analysis of a small number of soil samples does not support or rule out this idea. Soils are notoriously heterogeneous spatially, and their chemical characterization requires more intensive sampling (Trudgill 1977; Armson 1977; Alban 1974).

Soil moisture is another edaphic characteristic that might explain sugar maple absence from the hazel area. Lower soil moisture availability could result from lower soil silt content or from greater insolation on the west slope or both. The tendency of soil moisture and nitrogen availability to covary (Stanford and Epstein 1974; Pastor et al. 1984) complicates efforts to assign a cause to the sugar maple boundary.

Light Intensity: The scarcity of hazel in the maple area is likely related to competition for light. Multiple layers of sugar maple saplings and trees cast deep shade where hazel does not grow in abundance. Hazel does grow commonly in association with red pines and other conifers throughout the Great Lakes region and hence tolerates the nutrient regimes in coniferous forests. Hazel is more abundant on nutrient-medium sites than on nutrient-rich sites in this region (Buckman 1964; Kurmis 1969; Tappeiner 1971), perhaps because of higher light levels on less rich sites (Kurmis and Sucoff 1985).

The transition zone between the hazel and maple areas contains scattered maple seedlings that presumably will shade out hazel as they grow taller. The influence of the old pines on soil conditions may be declining as windstorms reduce pine densities (Chapter 1). Such a change may be analogous to the spread of sugar maple into old fir forests along Buell's line (Westman 1968), a contact zone between maple and fir stands within Itasca Park where changes have been examined periodically (Buell and Gordon 1945; Buell 1956; Buell and

Martin 1961; Westman 1968). Buell's line might be an old fire line whose expression persists because of the influence of post-fire vegetation on soil characteristics.

Beaver: Another factor that might restrict abundance of maples and also of aspen (Table 17) is herbivory by beaver. The hazel zone is closer to (within 50-75 m of) Budd Lake, where beaver activity is in evidence. During a period of overpopulation in the 1930's, beaver depleted food plants within 150 m of open water (Hansen et al. 1974) and might well have removed aspen and maple stems from the hazel zone.

CONCLUSIONS

(1) The hazel-maple contact can be viewed as several coinciding local species limits that might result from various related constraints: the red pine limit from a fire line or fire-intensity line; the aspen limit from beaver foraging distances; the sugar maple limit from a soil moisture transition influenced by pines; the hazel limit from a light availability line influenced by sugar maple.

(2) Many of the differences between the two vegetation zones can be traced to fundamental differences in topography. The hazel area is near a beaver pond and situated on a west-facing slope, an exposed location more prone to drought, more favorable to xerophytic and

flammable vegetation, and more vulnerable to beaver damage, but less prone to windthrow. The maple area is on an east-facing slope where soils are less droughty, favoring mesophytic, less flammable vegetation. The maple area is also farther from the beaver pond but on the vulnerable lee side of a hill, with respect to both prevailing and summer storm winds. Further study would elucidate the importance of these factors to the position and persistence of the hazel-maple contact and to other vegetation contacts in the region.

Table 17. Densities of living trees (2.5+ cm DBH) within maple and hazel areas. Each plot is 110 m² in size. Numbers in parentheses indicate additional standing dead stems.

Species Mean/330m ²	MAPLE AREA				HAZEL AREA			
	Plot 1	Plot 2	Plot 3	Mean/330m ²	Plot 1	Plot 2	Plot 3	
Red pine	0	0	2	0.7	5	2	4	3.7
White pine	0	0	1	0.3	1	0	1 (1)	0.6
Paper birch	6	4	0 (3)	3.3	13	3 (1)	8 (1)	8.0
Red oak	7	5	6 (1)	6.0	3	2	3 (1)	2.7
Quaking aspen	1	2 (3)	1	1.3	0	4 (1)	1 (1)	1.7
Bigtooth aspen	0	0	0	0	0	1	3	1.3
Sugar maple	23	4	14	13.7	0	4	0	1.3
Red maple	1 (3)	5 (2)	1	2.3	0	6	1	2.3
Ironwood	5	8	0	4.3	0	1	0	0.3
American elm	0	0	0	0	0	0	1	0.3
Tall shrubs	0	0	0	0	0	3	0	1.0
TOTAL				32/330m ²				23/330m ²
				(10/100m ²)				(7/100m ²)

Table 18. Seedling and shrub densities in 4m^2 plots within the maple and hazel areas.

	MAPLE AREA				HAZEL AREA			
	Plot 1	Plot 2	Plot 3	Mean/ m^2	Plot 1	Plot 2	Plot 3	Mean/ m^2
Plot size:	4m^2	4m^2	4m^2	1m^2	4m^2	4m^2	4m^2	1m^2
Sugar maple	139	12	78	19	0	1	0	0.08
Red maple	3	0	32	3	1	1	11	1
Aspen	5	1	6	1	0	0	0	0
Paper birch	1	0	0	0.08	1	0	0	0.08
Red oak	2	0	0	0.02	0	0	1	0.08
Ironwood	0	2	0	0.2	0	0	0	0
Hazel	1	0	0	0.08	80	92	21	21
Other shrubs	6	29	4	3	1	58	61	13
TOTAL				26.6/m^2				35.2/m^2

Table 19. Trees of the past inferred from stumps, windthrow mounds, and multiple-stemmed trees, in 50m x 10 m plots within the maple, hazel, and transitional areas.

	Maple area	Transition	Hazel area
Pine	0	0	4
Paper birch	1	2	1
Red oak	3	3	0
Aspen	9	2	3
Sugar maple	1	0	0
Red maple	0	1	0
White spruce	0	1	0
Balsam poplar	0	1	0
Unknown	9	9	2
Total	23/500m ² (4.6/100m ²)	19/500m ² (3.8/m ²)	11/500m ² (2.2/100m ²)

Table 20. Stumps, windthrow mounds, and multiple-stemmed trees in 50 x 10 m plots.

	Maple Area	Transition	Hazel Area
Mounds	14	7	1
Stumps	5	5	9
Multiple trees	4	7	1

Table 21. Thickness of soil litter and soil A horizons for samples from maple, hazel, and transition areas.

LITTER THICKNESS (cm)

Sample #	Maple Plot	Transition Plot	Hazel Plot
1	3 cm	2.5 cm	5 cm
2	4	3	3
3	5	5	4
4	4	7	6
5	2	2	3
6	2	4	3.5
Mean	3.33	3.917	4.083
S.D.	(1.21)	(1.855)	(1.201)

THICKNESS OF THE A1 HORIZON

Sample #	Maple Plot	Transition Plot	Hazel Plot
1	4.5	9.5	5
2	3	6	3.5
3	2	5	2.5
4	4	3.5	4
5	4	2	3
6	1.5	3	4
Mean	3.167	4.833	3.667
S.D.	(1.211)	(2.696)	(0.876)

Figure 15. Location of the hazel-maple contact zone, Clearwater Co., MN, on an orthophoto map drawn from 1969 air photos. Notice presence of pines (dark green) on the west side of the contact, in the hazel area.

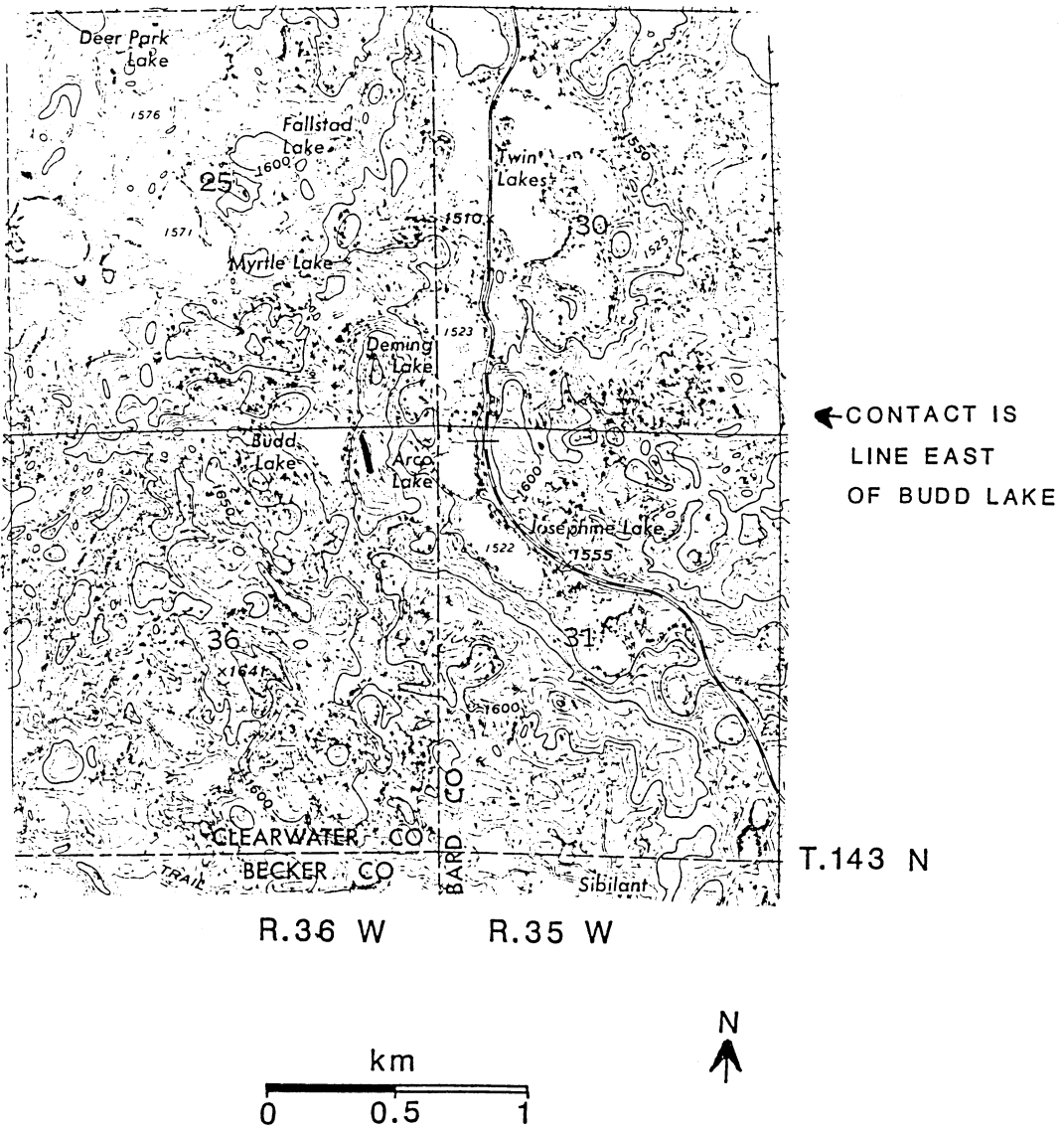


Figure 16. Arrangement of soil sampling sites along the hazel-maple contact.

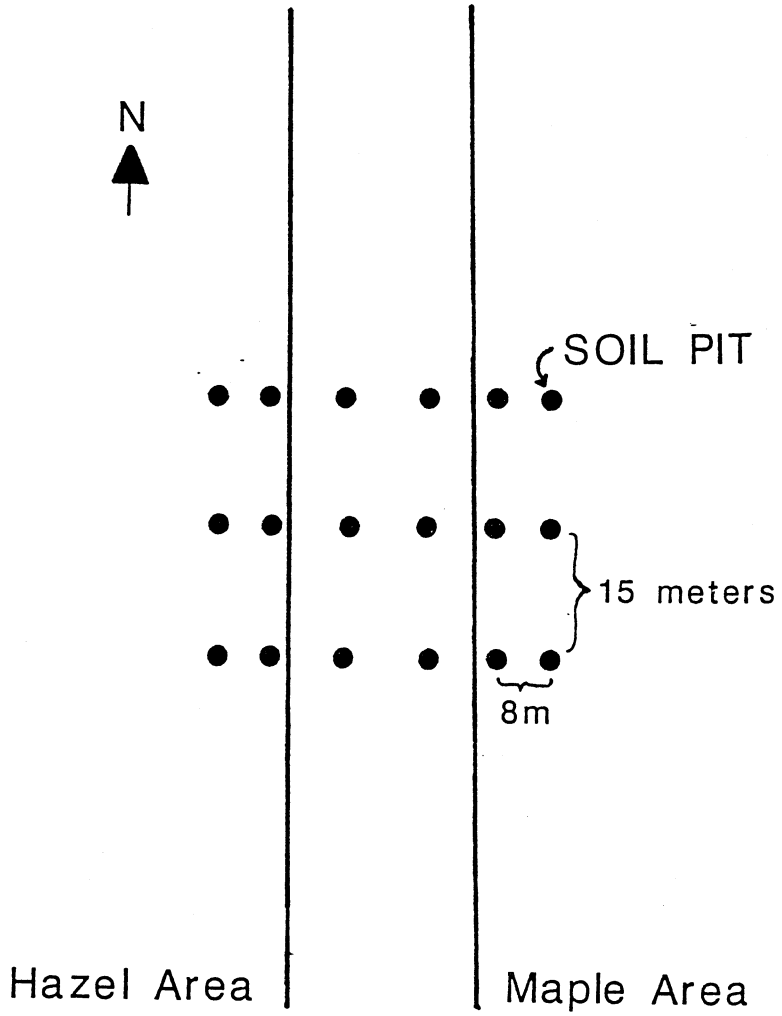


Figure 17. Soil textural analysis of A1 horizon samples from maple, hazel, and transition areas. Silt content is greater in maple-area samples than in hazel-area samples ($P < 0.05$; Wilcoxon Two-Sample Test).

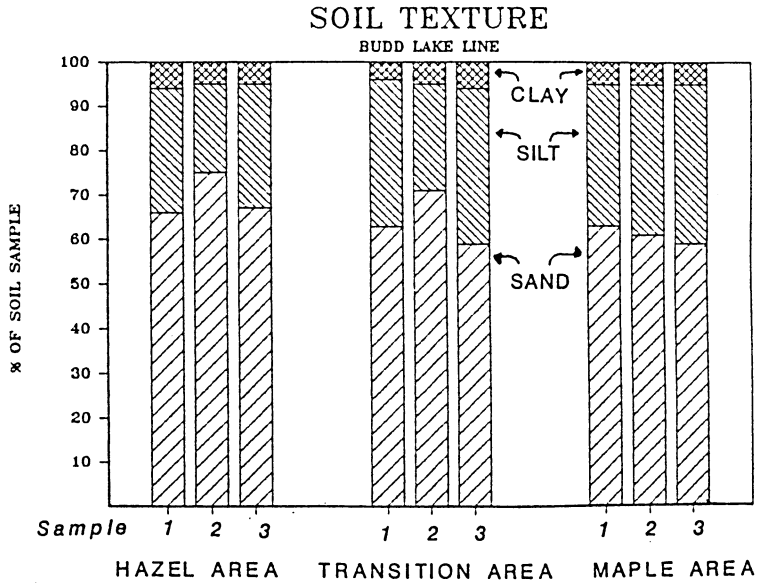


Figure 18. Cation exchange capacity of soil samples from maple, hazel, and transitional areas.

