WINDSTORMS IN ITASCA STATE PARK, MINNESOTA: CONSEQUENCES FOR THE PINES, FOR FOREST DYNAMICS, AND FOR BIODIVERSITY

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ABSTRACT

This project investigated the consequences of windstorms on the forests of Itasca State Park, Minnesota. Itasca Park has unique value as a preserve where old-growth stands of pines, now 200-350+ years old, escaped the logging that cleared nearly all other forests in the state. Following the infamous storm of July 1995, I undertook surveys of wind damage to trees and of windstorm-related regeneration, building on my past research on windstorms at Itasca, ongoing since 1983. The objectives were (1) to understand the consequences of windstorms for tree populations, succession, and species diversity in this unique natural area; (2) to continue to monitor changes in Itasca's vegetation, as it responds to windstorms and to global warming; (3) to evaluate the consequences of windstorm events for old growth pine populations. The focus is on moderate windstorms that damage scattered trees every year.

On the basis of three damage surveys (1983, 1987, 1995), it is clear that Itasca Park's older red and white pines sustain heavy mortality in windstorms. In a typical old pine/hardwoods forest, approximately 10% of each pine population was damaged, half the white pines surviving their damage but most red pines killed outright. This figure includes pines damaged in two major storm years (1983 and 1995) plus pines damaged over another three years (1984-1987) as surveyed in 1987; thus it represents five years of windstorm effects. In a younger pine/spruce/fir stand, red pines sustained less damage but white pines were heavily damaged as in the older forest.

The loss of ancient pines is not compensated for by pine regeneration. Windstorm events are not triggering pulses of pine reproduction in the way that fires do, judging from regeneration surveys repeated over time. Widely scattered white pine seedlings grow only on rotting logs, while red pine seedlings are exceedingly rare. Where storms admit sufficient light for pine reproduction, we see instead very rapid growth of aspen and other hardwood sprouts. Elsewhere, smaller treefall areas are apparently too shady for these pines. Efforts by park managers to obtain pine regeneration show a devastating role for deer.

More generally, the windstorm disturbance regime has very different consequences in different forest types, depending primarily on the wood strength of the understory trees. Although disturbances are theoretically expected to enrich diversity by setting back succession in open patches, this dynamic does not occur in the pine/hardwood forest type where a windfirm understory of maples, ironwood, and shrubs survive windstorms to grow upward toward the

canopy, shading the ground and precluding colonization of light-demanding species. Here windstorms accelerate succession by removing early-successional aspen, birch, and pine from the canopy. The overall effect is a depletion of diversity. In contrast, the pine/spruce/fir forest type has a weak-wooded understory and thus more frequent formation of discrete canopy light gaps. The highest damage rates within the park are seen for aspen (in overmature, fungus-infested stands) and for white spruce. Patterns of mortality differ between sites and between storms.

Moderate windstorms change the forest by imposing uneven mortality amongst the canopy trees, but have surprisingly little effect on tree regeneration, beyond the rotting log substrates they leave behind. Twelve years of observing regeneration plots (1984-1996, in the pine/hardwoods forest type) showed dramatic changes over time, but those changes did not differ between treefall and control areas.

Instead, alterations in the lower layers of the forest might result from a severe drought event in 1988 or might represent a general successional shift in composition as the aspen and pine canopies deteriorate. Major changes include thinning of small seedlings of sugar maple, red maple, and lowbush blueberry; decline in diversity of shrubs; a pulse of red oak seedling germination (long after the key windstorm, between 1992 and 1996), and increased numbers of tall (height>2 m, diameter<2.5 cm) seedlings of shade-tolerant species: sugar maple, red maple, and ironwood. The loss of shrub diversity across the drought period could be a harbinger of global warming consequences.

These findings have management implications. First, to preserve and replicate the old growth pine forests of Minnesota, there is a compelling need -for more and larger preserves. The rarity and fragmentation of ancient forest remnants puts the biodiversity of these forests at grave risk of destruction by catastrophic windstorms. Second, salvage logging should be avoided since the rotting logs represent major germination sites for the pines and other trees of Itasca, particularly the conifers and paper birch; these logs also support remarkable diversity of fungi and bryophytes. Third, continuing study is needed to elucidate the interactions between fire, windstorms, climate change, and deer as they together structure the forests of Itasca. Many species reach the limits of their natural ranges at this ecotone between conifer forest, deciduous forest, and prairie. Thus Itasca State Park is an invaluable laboratory for monitoring ecological sensitivity and forest dynamics in the future.

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INTRODUCTION

In July of 1995, a severe windstorm crossed northern Minnesota. With peak windspeeds of 100 mph, this storm caused extensive destruction (Hazard Mitigation Survey Team 1995) including damage to the forests of Itasca State Park.

Itasca Park was established originally to protect the headwaters of the Mississippi River, but it also has unique ecological value as a preserve where old-growth stands (to 350 years old) of red and white pine escaped the logging that cleared nearly all other forests in the state (Rusterholz 1996; Frelich and Reich 1995). The park is an island of old forests in a matrix of highly disturbed land including frequently logged, young forests. Even parts of the park that were once logged (Aaseng 1976) now support unusually mature forests (80 yr +) for the region. Thus the future of Itasca's forests is of great concern.

Other ancient forests have been struck by windstorms in recent years, from Wisconsin's Flambeau Tract (Dunn et al. 1983; Canham and Loucks 1984) to the Tionesta Forest of Pennsylvania (Peterson and Pickett 1995) to the Five Ponds Wilderness Area of New York's Adirondacks (Jenkins 1996), the latter site damaged days after Minnesota's July 1995 storm. Clearly these windstorm disturbances are natural. However, their consequences are devastating when so little old growth forest remains (Frelich 1995; Davis 1996) and thus a single storm takes out a large fraction of sparse remaining ancient forest.

In Itasca Park, the loss of majestic pines that date back as far as 1650 is especially troubling because the pines are not reproducing widely in Itasca Park today. Research and management work has shown that the pines are vulnerable to herbivory by deer (Ross et al. 1970) and require light and other conditions created by natural wildfire (Spurr 1954; Frissell 1973; Heinselman 1973; Frelich 1992). Whether or not windstorms might substitute for fires in this regard is a question addressed in this study.

Windstorms influence forest diversity and succession in two interacting ways: through the pattern and extent of damage, and through the pattern of regeneration following windstorms. Thus this project juxtaposes these two components of the windstorm response in order to understand how the windstorms change the forest and its diversity. Although disturbances like wind are theoretically expected to enrich diversity, there are circumstances under which diversity is depleted by wind disturbance (Webb 1989, 1998).

This report summarizes my research on windstorms in Itasca State Park in 1996-1997, with new studies of the 1995 windstorm and follow-up studies of 13 years of response to an earlier windstorm in 1983. The temporal framework includes, since 1983, three damage and mortality surveys and three sampling efforts for fixed plots where regeneration is being monitored, in treefall areas and in nearby control areas. The project had three major objectives:

OBJECTIVE #1. *To understand the consequences of windstorms* for *individual tree populations and thence* for *succession and species diversity.*

OBJECTIVE #2. *To continue and expand long-term studies (since 1983) of windstorm responses at Itasca Park in comparison with background changes in vegetation in an ecotonal location.*

OBJECTIVE #3. *To evaluate the consequences of windstorm events* for old *growth pine populations.*

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OBJECTIVES IN DETAIL

(1) Windstorm Consequences for Tree (and Shrub) Populations and Communities: This work was motivated in part by the complexity of windstorm responses by forest communities. There is an urgent need to examine the details of disturbance responses in order to understand the influence of disturbance on succession and diversity, and to gain new insight into the limits of the patch dynamics paradigm as a model for maximizing diversity. The static view of forests has given way long since to a dynamic view, first with the concept of succession and then (by various names) with the, patch dynamics perspective that recognizes how disturbances can produce within a community a mosaic of patches in various stages of succession (Watt 1947; Bray 1956; Connell and Slatyer 1977; Bormann and Likens 1979; Sousa 1984; Mooney and Godron 1983; Pickett and White 1985). Windstorms can create light gaps, potential nodes of diversity enrichment by providing sites that shade-intolerant plants can colonize (Williamson

1975; Denslow 1980, 1987; Hibbs 1982, 1983; Barden 1979, 1981; Runkle 1981, 1985, 1990; Brokaw 1982; Brokaw and Scheiner 1989; Orians 1982; Foster & Reiners 1986; Hubbell and Foster 1986; Uhl et al. 1988; Poulson and Platt 1989; Connell 1989; Worrall and Harrington 1988; Lertzman and Krebs 1991; Lertzman 1992; McClure and Lee 1993). Windstorm disturbance might also enrich diversity by generating substrate heterogeneity: rotting logs, mounds and pits when trees uproot, and stumps when trees snap in the wind (Falinski 1978; Putz 1983; Beatty 1984, 1991; Putz et al. 1983; Webb 1988; Schaetzl et al. 1989; Peterson et al. 1990).

However, not all disturbance events enrich species diversity or provide opportunities for new colonists (Webb 1989, 1998). Existing plants are the usual beneficiaries of gap formation, especially when gaps are small (Watt 1947; Bray 1956; Brewer and Merritt 1978; Canham 1985; Runkle 1984, 1990; Spies et al. 1990; Cho and Boemer 1991). Environmental heterogeneity is not always detectable or significant when openings are small (Collins and Pickett 1987, 1988). If windstorms neither create regeneration opportunities for light-demanding plants nor damage shade-tolerant trees most heavily (King 1986; Webb 1989), then disturbance can accelerate succession rather than setting it back in disturbed patches (Lertzman 1992; Webb 1989), and can deplete overall diversity rather than enriching it.

In a striking illustration of these two trajectories of disturbance-mediated change, two Itasca forest communities respond very differently to windstorms, despite their close proximity and similarities in climate and windstorm disturbance regime, as this report and my previous work (Webb 1989) show. The windfirmness of the understory species is the major controlling difference. Where the understory comprises strong-wooded trees (sugar maple, ironwood), little new light reaches the forest floor, and thus light-demanding species cannot establish. Where the understory is open or susceptible to windthrow (due to weak wood such as that of balsam fir), we see the formation of sizable light gaps where richness could be enriched. In the latter case, windstorms set back succession in open patches, allowing both shade-tolerant and shade-intolerant species to coexist at the landscape scale. However, in the other case with a windfirm understory, windstorms accelerate succession as that windfirm understory moves up into the canopy. Clearly, generalizations about major influences and about diversity/disturbance relationships must be made with caution and with full knowledge of the biology of each member of the forest community.

(2) Continuing longitudinal studies of the windstorm disturbance regime and forest responses: Beyond short-term elucidation of forest responses to windstorm events, this longitudinal work uses repeated sampling to shed light on the temporal dimensions of the windstorm disturbance regime as well as the response over time to individual windstorm events. Ecologists are increasingly recognizing the importance of historical events that disrupt equilibrial conditions and shape communities. However, in the effort to reconstruct the disturbance regime and to predict succession, we find that studies of single disturbance events or even short time periods can give us misleading and indeed contradictory estimates of forest turnover and disturbance return time. Some of our best knowledge about windstorm frequencies and consequences come from historical (Stearns 1949; Canham and Loucks 1984; Lorimer 1977; Seischab and Orwig 1991; Whitney 1986) and retrospective landscape reconstructions (Henry and Swan 1974; Oliver and Stephens 1977; Foster 1988; Foster and Boose 1995; Foster et al. 1996). These methods are better at detecting catastrophic windstorms than the moderate windstorms that occur more often. Other valuable studies of disturbance regimes that include windstorms determine disturbance dates by the establishment of shade-intolerant trees and by pulses of radial growth by shade-tolerant trees (Lorimer 1985; White et al. 1985; Glitzenstein et al. 1986; Frelich and Martin 1988; Lorimer et al. 1988; Canham 1989; Lorimer and Frelich 1989; Shiyatov 1990; Payette et al. 1990; Stewart et al. 1991; Frelich and Lorimer 1991; Foster et al. 1992). This approach identifies gaps of the past but can't always make a causal link to windstorms and cannot detect windstorm-driven turnover that did not create gaps (Webb 1998).

Clearly these generally coarse-grained studies of past disturbance events need to be supplemented by longitudinal field studies of wind damage if we are to understand rates of forest change and turnover at the level of individual plant populations. Another contribution of long term studies derives from the close relationship between vegetation change and climate change. Most global warming scenarios predict increases in storm frequency and severity. The Itasca, Minnesota, region is ideal for elucidating longitudinal change because of its ecotonal location, near the prairie-forest border which has shifted during past episodes of climate change (McAndrews 1966; Grimm 1983). Thus this location should continue to exhibit climatic sensitivity in its vegetation, lending unusual value to long term studies of change in forest structure and composition.

This project is unusual in evaluating multiple disturbance events over time at the same place. By assessing effects of specific known disturbance events, this project helped to uncover the temporal dimensions of the forcing disturbance events, unlike the widely used gap survey approach, which while elucidating forest structure does not always attribute known ages or causes to gaps and which omits forest turnover that does not occur through the gap mechanism (Liebermann et al. 1989). This study went beyond light gaps to understand even nongap transitions that derive from the disturbance regime, and to understand the importance and influence of windstorm disturbance over time. With documentation by long term research, we understand ecological changes much better than when we must instead make predictions from single surveys.

(3) Dynamics of pine populations in Itasca State Park: As already noted, few stands of old growth forest remain in the eastern and midwestem United States, and Itasca State Park is unusual for harboring extensive stands of unlogged old-growth red pine and (in mixtures with hardwoods) white pine. Although these stands do not meet the usual old-growth criterion of being uneven-aged, tree ages at >300 years and origins after natural (fire) rather than anthropogenic disturbance lead to their designation as old growth forest (Rusterholz 1996). Surrounding the park preserve are heavily logged county and state forest lands supporting virtually no pine (except jack pine in pure post-fire stands to the east) and extensive very young post-logging aspen stands. Within Itasca Park, as already noted, the park's resource managers and foresters have been working to achieve pine regeneration for decades, in light of the pines' dependence on fire (Spun 1954; Frissell 1973) and vulnerability to herbivory by deer, as demonstrated by several deer exclosures constructed in the park, the oldest constructed in 1937 (Ross et al. 1970). White pine does reproduce farther east in its range, in Michigan, in clumps within intact aspen forests (Roberts and Richardson 1985; Peterson and Squiers 1995). More generally it depends upon catastrophic fire at intervals of 150-300 years with surface fires every 20-40 years (Heinselman 1973; Frelich 1992). Red pine predominates with a fire cycle of 150-300 years (Heinselman 1973; Frelich 1992).

This project tracked the population dynamics of these pines over a period of 12 years, particularly as influenced by windstorms. At what rate are pines being blown down by windstorms? Are they sustaining more damage than .other trees in the forest? The pines were also examined in context of the two contrasting forest types which exhibited different windstorm responses in the past (Webb 1989) and where the pines' age structures differ. A further comparison scrutinized the two different windstorms and examines the possibility that more intense windstorms like that of 1995 could substitute for fires as regeneration triggers. If blowdowns are large enough, will pine regeneration take hold despite abundant deer and prolific aspen root sprouting? A program of controlled bums has begun, under the direction of Becky Marty, Resource Manager of Itasca State Park, prior to which windstorms had replaced wildfire as the dominant cause of disturbance. In the future, the interactions between windstorm and fire events also deserve close study.

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STUDY AREAS

This research focused on the two forest stands from my previous windstorm studies, both in Itasca State Park (Figure 1; Webb 1988, 1989). These represent typical upland forest types in the region, thus results should apply elsewhere in the park and beyond. The Budd Lake study area (Photo 1; n 1/2 ne 1/4 sec. 36 T.143N, R.36W) is ca. 40 ha in size with heterogeneous vegetation including elements of Northern Hardwoods, White Pine, Red Pine, and Aspen - Sugar Maple cover types (Eyre 1980). Clusters of red pine and scattered white pines date back 250+ years, based upon my tree ring counts. This site is located west of Deming Lake and generally bisected by the Red Pine Trail. The 16-ha subset of this Budd Lake study area used for 1987, 1992, and 1995 studies is roughly bounded by the Ozawindib, Red Pine, and Okerson Heights trails.

The Headwaters study area (Photo 2; w 1/2 ne 1/4 NW 1/4 sec. 2, T.143 N, R. 36 W) is a more homogeneous 8 ha stand with an overstory of white pine, red pine, balsam fir, white spruce, with scattered quaking aspen and paper birch. The pines are up to 110+ years of age while the spruces and first date back 80 years at most. The Headwaters site is located along the northern part of the Schoolcraft Trail near the Mississippi Headwaters. Density data are reported in Table 1 (including all stems with dbh > 2.5 cm. Additional work took place in an area of more extensive wind damage along the Bohall Trail just west of Bohall Lake (sw 1/4 sw 1/4 sec.9, T. 143 N, R. 36 W.).

The two major study areas represent the two successional pathways, toward sugar maple dominance and toward balsam fir dominance, identified for pine stands in the region after fire is suppressed (Buell and Gordon 1945; Buell 1956; Buell and Martin 1961; Westman 1968). A long history of vegetation work provides an unusual context for longitudinal studies (Lee 1924; Kell 1938; Buell and Gordon 1945; Buell and Wilbur 1948; Buell and Niering 1967;

Janssen 1967; Westman 1968; Ness 1971; Hansen et al. 1972, 1974; Peet 1984; Kurmis 1969, 1985; Kurmis and Sucoff 1989). Others have examined factors that structure Itasca's fine-grained mosaic of vegetation types, including edaphic heterogeneity (Kell 1938; Kurmis 1969, 1985; Ness 1971; Hansen et al. 1974), logging history (Aaseng 1976; Patterson 1978), and past fires (Spun 1954; Frissell 1973; Clark 1988, 1989, 1992). My previous research in Itasca Park studied the damage imposed by the 1983 windstorm in two stands (Webb 1989), the role of wind-generated microsites (Webb 1988), seed predation in treefall areas and at other edges (Webb and Willson, 1985) and the effects of edges and fragmentation for plant and lichen communities (Glenn and Webb 1997; Glenn et al. 1998).

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WINDSTORMS AT ITASCA

This project focuses not on rare blowdown phenomena but on the ongoing, frequent thunderstorm events that topple scattered trees in Itasca Park every year. The famous 1995 storm was best known for massive blowdowns where windspeeds were highest, but it also struck a large surrounding area with more moderate (but still tree-damaging) winds. In the future, the effects of larger blowdown events can be tracked thanks to new permanent plots I established in a site (Bohall Trail) more severely damaged in 1995.

Since 1983 I have censused mortality and damage caused by windstorms three times in the Budd Lake forest and twice in the Headwaters forest. The first windstorm event, on July 3, 1983, was a thunderstorm with peak windspeeds of ca. 60-75 mph as recorded elsewhere as part of the same storm system (NOAA 1983); downbursts and tornadoes with yet higher windspeeds occurred but not in the Itasca area. This was considered the storm of the decade at the time it occurred.

The intermediate survey at Budd Lake (1987) was not associated with a specific storm; thus it documents background wind damage from more modest storms over a 4-year period. Despite the absence during this time of any newsworthy windstorms, a good rate of windthrow was in evidence. At least four windstorm events of various magnitude occurred during this period.

The July 1995 windstorm was more severe with, as already mentioned, winds of up to 100 mph (Hazard Mitigation Team 1995) in some localities. However, the two major study areas sustained less extreme windspeeds judging from the scattered pattern of treefalls. Other distinct but less severe storm events were also in evidence at the time of this survey, including a storm from the northwest in May 1994 and another spring storm from the south in May 1996 (the 1995 storm, like that of 1983 and most others, came from the west). Thus an ongoing role is evident for moderate windstorms that damage scattered trees in these forests.

It seems possible that many of the historical fires in which pine stands originated in the park followed windstorms, which create flammable piles of fuel in the form of fallen trees. This possible interaction between windstorms and fires (Frelich 1992) would be more likely after catastrophic blowdowns, whose frequency is still poorly known, than after the moderate windstorms that often damage scattered trees.

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METHODS

TREE DAMAGE SURVEYS: In the Budd Lake area, damage from the July 1983 storm was documented for a 40-hectare area, within 4 months of the event. A 16-hectare subset was subsequently censused in 1987 for cumulative wind damage incurred in storms between 1983 and 1987. This same 16-ha area had a third census in 1996 for wind damage from the 1995 storm. The Headwaters forest was surveyed twice for wind damage: once in 1985 with focus on the 1983 storm (2 ha sampled within the 8 ha area) and secondly in 1996, with focus on the 1995 storm (full 8 ha censused). The complete area-wide census is the best method because it eliminates sampling problems. Other methods tend to oversample gap-forming, multiple-tree events while missing the more modest treefalls that do not form lightgaps.

For each damaged tree, data were collected on species, size (dbh=diameter at breast height), cause (direct by wind or indirect by falling tree), type of damage (uprooted, snapped, bent), and whether the tree survived its damage or was killed. This report combines the two major aspen species, quaking and bigtooth, because field crews were not consistent in distinguishing them.

The treefall surveys reveal the effects *of* tree size and tree species on mortality risk and permit comparison *of* the two storms and the two forest types. The damage data were analyzed in two ways. First, Kolmogorov-Smimov tests compared the size distributions of the trees damaged with the size distribution of the undamaged background population (Norussis 1994; Sokal and Rohlf 1981). These tests, coupled with histograms that show the size distribution graphically, explore the effect of tree size on damage risk within a tree species. Secondly, logistic regression analysis (Feinberg 1981; Webb 1988, 1989) was used to model the probability of mortality, or of windstrike, or of damage including nonfatal damage, on two independent variables: tree size and tree species (Table 4). The mixture of categorical and continuous variables necessitates the use of the logistic regression approach.

BACKGROUND SAMPLING: To place wind damage in context of the overall undamaged forest, both study areas were sampled not only for damage but also for intact trees. Such background sampling is essential (but often omitted!) for any wind-damage assessment; otherwise it is impossible to determine if mortality is simply proportional to abundance for a given species or size class of tree. I sampled both study areas twice, in 1985 and again in 1996, in case the earlier sampling was no longer accurate following a decade of change. The Budd Lake sampling results are not directly comparable because the 1984 work characterized the larger 40 ha study area (1.2 ha sampled), while the 1996 sampling focused on the smaller 16 ha study area (0.37 ha sampled). In the Headwaters forest, we sampled 0.34 ha in 1985 and, reducing the width of transects in this dense forest, 0.17 ha in 1996. Density data are presented in Table 1.

REGENERATION PLOTS: Following the 1983 windstorm, I established (in 1984) a set of small plots to follow over time to compare regeneration patterns in treefall areas and in control areas. I sampled these plots again in 1987 and then again in 1996.

The design of this regeneration study incorporates four plots for each treefall as shown in Figure 2: one plot each near the base ("treefall base, " ½ meter north of the stump's north edge) and in the fallen crown area ("treefall crown," north of the bole just beyond the first branch of the fallen crown); and two as paired control plots in parallel configuration at undamaged conspecific trees ("control base" and "control crown"). The control crown plots were placed at the same distance from their base plots as the treefall crown plots were placed from their base plots. Some locations were shifted to avoid stumps and windthrow mounds, in which case a record was kept to ensure the same shift in future surveys. For some treefalls, base or crown plots were omitted due to interference from trails or marshes. Note that the plot locations were not marked in the original survey; thus although the treefall plots are likely to coincide in location, the control plots were less likely to be placed in exactly the same location in subsequent surveys, especially the control crown plots.

In each 4x4 m regeneration plot, all woody plants were identified and counted within three height classes (small < 50 cm in height; medium = 50-200 cm; tall > 2 m in height).

Plot recovery was complicated by the absence of permanent plot markers and by the extent to which the forest had closed in around fallen trees. I utilized field notes, remnants of field flags, a few remaining aluminum tree tags, and most often the tags' galvanized nails! Of 30 treefall areas sampled originally in 1984 (each with 2 or 4 plots), 17 were still distinguishable in 1992, and 11 were distinguishable in 1996. Two of the 1996 relocations had not been found in 1992. In many other cases I am certain that I found the location of the old treefall but the primary windthrown tree had been obliterated by subsequent treefalls or (in the case of paper birch) entirely decomposed. Treefalls involving the old pines were still visible on the landscape and were all relocated; in contrast, aspen and other hardwoods were less persistent. The 11 old treefall areas found in 1996 were given permanent markers at that time to aid future relocation. Despite what seems a small remaining sample, the data set contained a total of 58 individual plot surveys in 1984 and 1992, and 40 plot surveys in 1996, and the design retained sufficient power to reveal significant differences in the statistical analysis.

The data from regeneration plots were analyzed with repeated-measures ANOVA to identify those changes that might be related to windstorm disturbance (Table 5). The independent variables, run one at a time, were overall species richness, density of stems within a growth form (shrubs, trees) and by size class, and individual species within a size class. The analysis modeled each of these diversity and density variables on three independent variables: treefall vs. control plot; base vs. crown plot; and year (1984, 1992, 1996). For those species for which "year" was significant, we checked for cant'-over effects using a test for sphericity. In cases where this assumption of the univariate model was violated we test again using a less powerful multivariate test (Von Ende 1993; Norusis 1993). This was appropriate for the factor "year" because it had three levels but was unnecessary for the other two factors with only two levels apiece.

BRYOPHYTE STUDIES: Fallen trees from 1983 provide an unusual opportunity to characterize the bryophytes on logs of known age. In a separate project without DNR funding, the logs relocated at the regeneration plot sites were surveyed for bryophytes by Dr. Mariette Cole of Concordia College. Results of that work are not reported here but are still being analyzed in the laboratory. Newly marked treefalls from the 1995 storm will also be monitored for bryophyte colonization in the future. The microflora of Itasca State Park, alongside the fungi, include an unusual amount of diversity, perhaps because of the old growth conditions in a relatively pristine airshed (Glenn and Webb 1997; Glenn et al. 1998).

GAP ANALYSIS: As a baseline work for future comparison, the permanent-plot treefall areas were characterized. While the old 1983 treefall areas have their permanent regeneration plots, the new treefall areas were studied in a different way, called "gap analysis", developed here to capture wider dynamics of the treefall area beyond small seedling-scale plots. This approach describes the vegetation in and around treefall gaps within layers of the forest. In Budd Lake treefalls, there are three or four layers with their own separate gap (or nongap) response: the pine layer [sometimes absent], aspen layer, understory (tree saplings), and shrub layer. The Headwaters forest has fewer layers, often only two: canopy (spruce/pine/mixed) and fir thicket. For each layer, I estimated the size of the gap opening that reaches down through that layer; I noted species present in the gap and their coverage; and I recorded tree species present at the gap edges, again all within each layer of the forest. I further noted adjacent contributing factors for the gap (nearby dead trees, other older treefalls, wet meadows) and the apparent gap beneficiaries.

Gap analysis was completed for permanently marked treefall areas from the 1995 storm (3 in the Headwaters area and 9 in the Budd Lake area), and for another 5 unmarked new treefalls at Budd Lake. After trial use in two older (1983) treefall areas, I concluded the method is not very effective there because older treefalls no longer seem to be responding to the windstorm event. Table 2 identifies permanent plots with gap analysis. As baseline data of interest primarily with future resurveys, these gap analyses are not attached to this report.

RELEVES: Another approach to characterizing the treefall areas, and adjacent "control areas" is the releve, or plant list with cover/abundance estimates for each species. Releves, in combination with physiognomic descriptions (Ed Cushing's system as used by the Natural

Heritage Program and others), provide a baseline description that when redone in the future will identify major structural changes and floristic changes in treefall gaps and in control areas sampled in the same way. In the Budd Lake area I did six treefall-plot releves, three each for red pine and aspen treefalls, and five "control" releves matched with the treefall localities. In the Headwaters forest I did three treefall-plot releves and two "control" releves. In both sites two treefalls shared a control releve because the terrain did not provide another comparable treefallfree plot. Each releve was 400 m2 in area. Table 2 lists the treefall areas with had releves.

PINES AND THE BOHALL TRAIL BLOWDOWN: I initiated a new study area because the original forests were only marginally influenced by the massive 1995 storm. In this red pine forest just west of Bohall Lake, more than 40 large pines were felled in an area approximately 50 m x 50 m, a dramatic opening much larger than any in the other study areas. Unlike most of the hard-hit Itasca forests, which were mostly aspen stands, this area is surrounded by old growth pines. It is also ideal for long-term study because it is protected from salvage logging, lying within the Bohall Wilderness Area Scientific and Natural Area. In this area I established two permanent plots (Table 2), one in the blowdown and one back in the undisturbed forest, and I did releves in each. This area should be especially interesting from the standpoint of pine population dynamics.

PERMANENT PLOTS: For the mixed purposes described above, and detailed in Table 2, I established 28 permanent plots by using two kinds of permanent markers: a magnetic "deep-1" marker in bright blue and black, buried at the base of the treefall, and a blue-painted rebar stake with a rebar cap (courtesy of Becky Marty, Itasca State Park Resource Manager) labeled with plot numbers. These plots are also marked with pink field flags. The permanent plots number 23 in the Budd Lake area: 13 old treefall areas from the 1983 storm (11 of which have regeneration plots being monitored) and 10 new treefall areas from the 1995 storm. The Headwaters area has 3 permanent plots, all at 1995 treefall areas. The final two permanent plots are in the Bohall Trail area, one in and one outside of the larger 1995 blowdown there.

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RESULTS

TREE DAMAGE FROM WIND IN AREAS OF EXTENSIVE DAMAGE

The windstorm of 1995 opened large tracts of forest in the northwestern part of Itasca State Park and in adjacent private and county lands to the north and west. Large blowdowns like this are uncommon in the region and differ from scattered treefalls that result from more moderate windspeeds. Most of this report focuses on scattered treefalls because moderate windstorms are a frequent structuring force in the Itasca forests, striking with more or less severity every year or two over the 14 years of my research. The two major study areas (Budd Lake, Headwaters) escaped the highest windspeeds of the 1995 storm track but experienced fringe-zone winds that blew down scattered individual trees.

Here I briefly discuss two other areas within Itasca Park that sustained more extensive blowdown damage because of stronger and/or more turbulent winds. The first was the aspen--dominated forest in the western part of the park, near Lake Ozawindib. This area was mostly logged in the early 1900's and then colonized by quaking aspen and some bigtooth aspen. During the 1995 storm, these now-overmature aspens with their characteristically weak wood (Markquart and Wilson 1935) were damaged so heavily that the land resembled open fields and brushland, not forest (Photo 3). Itasca Park's Wilderness Drive was busy for days with logging trucks removing the downed timber.

The consequences of the storm for this area are quite different from consequences discussed elsewhere in this report, for two reasons: (1) The clonal aspens with their widespread root systems have resprouted to form a dense thicket; thus self-replacement of aspens seems highly likely. Unlike the aspens that were windthrown in the Budd Lake study area, these can resprout because abundant light penetrates to ground level. (2) Also in this Lake Ozawindib area, small "islands" of pine within the aspen matrix showed more resistance to wind damage than their neighboring aspens (Photo 4), reflecting stronger wood of both white and red pines. Thus some patches of pre-storm pines have survived and are likely to persist into the future. However, there is no sign of massive pine regeneration in the wake of the 1995 windstorm in this ,area. Pine seedlings have been planted in one locality in a project by Becky Marty, Itasca Park's Natural Resources Coordinator, and their fate is of great interest.

A second area with extensive wind damage is found just south of the Bohall Trail and west of Bohall Lake. Here a blast of heavy wind struck an old-growth stand of red pines and toppled at least 43 large pines (all but 2 white pines were red pines), creating an opening approximately 2500 m^2 in size (Photos 5 and 6). This blowdown is of interest because without a history of logging this locality, within the Bohall Wilderness Scientific and Natural Area, is not surrounded by aspen root suckers and thus a different trajectory of change seems likely. If windstorms can ever promote pine reproduction in Itasca Park, this blowdown size and location make it the most promising of scenarios. As already noted, I have established a permanent plot in this blowdown and another plot nearby, where I did releves in 1996, and where I will monitor future changes.

TREE DAMAGE FROM WIND: Scattered Wind Damage in Long-Term Study Areas

OVERALL DAMAGE

More moderate windstorms with their higher frequencies represent an important disturbance regime for the forests of Itasca Park. This section of the report describes the patterns of wind damage in the two forest stands at Itasca I have studied since a 1983 windstorm. I found that neither area was subjected to massive blowdowns in the 1995 storm, whose center with higher windspeeds passed to the north and west. However, small but conspicuous treefall areas were scattered throughout both forests. The type and magnitude of damage were similar to that I observed after the moderate storm in 1983 in these same forests.

Overall damage was higher in the Headwaters forest than in the Budd Lake forest, in both storms. This is true whether we measure absolute density (treefalls per hectare; Figure 3), which is higher at Headwaters in part because the forest is more dense, or percentage of trees damaged (Figure 4). The Headwaters forest lost 6% of its trees in the 1983 storm and nearly 4% in the 1995 storm, with another 1% or so damaged but surviving each storm. The Budd Lake forest sustained less than 1% mortality in each of three storm surveys; here nearly half of all damaged trees survived their wounds. This difference could be due in part to different windspeed conditions at the two sites, with the Headwaters adjacent to the fetch of Lake Itasca and closer to the center of the 1995 storm. However, autogenic features of the forests probably also play a role. The numerically dominant trees of the Budd Lake forest are strong-wooded sugar maples, ironwoods, and red maples which tend to bend rather than break when subjected to external forces. In contrast, the most abundant tree at the Headwaters forest is balsam fir, the weakest-wooded species in the region. Another difference lies in the structure of canopy trees of the two sites. When the narrow-crowned aspens and red pines fall in the Budd Lake area, they take down fewer neighbors than do the canopy spruces of the Headwaters area. Thus it appears that the different magnitude of damage between the two sites results from some combination of differences in storm conditions, windfirmness of common trees, and crown structure of windthrown species.

Tree size and species were analyzed as risk factors at each site and for the two major storms. Table 4 lists results of logistic regressions that test how strongly tree size (as DBH) and tree species help predict whether a tree is damaged or not. Results noted here are for the 1995 storm and, where tested, for the 1983 storm also.

At both sites, and not surprisingly, windstruck trees were significantly larger than trees in the background sample. This result from logistic regression is reinforced by Kolmogorov--Smirnov tests which show that the size distributions of the damaged trees and the sampled trees differ significantly from one another (Headwaters $Z=1.96$, $P=0.001$; Budd Lake $Z=2.91$, $P<0.0005$, for the 1995 storm). Size was not only related to direct wind damage. Within the group of all damaged trees, larger trees were more likely to be damaged directly by wind than by falling neighbors, and were more likely to be killed than to survive their damage. More surprising is the finding that size did not help predict which trees from the background population would be killed or damaged in the Headwaters site, because here much damage was caused indirectly by falling neighbors. In contrast, at the Budd Lake site the larger trees were most likely to be damaged and killed. This is troubling since the ancient red and white pines are by far the largest trees in this forest.

Differences amongst species are of yet greater interest. In the Headwaters forest where size did not correlate with mortality risk, the tree species differed significantly in risk of mortality, of direct windstrike, and of overall damage. At this site, the superabundant firs of all sizes were vulnerable to damage (Figure 37). Conversely, the pines that were so heavily damaged at Budd Lake were younger at the Headwaters site and did not protrude from the canopy as at Budd Lake; thus they sustained less damage. Meanwhile at Budd Lake where size explained so much there remained little additional difference among species in risks of windstrike or mortality in 1995. Here most species had narrow size distributions, and the species most heavily hit were those with the largest sizes. Thus size and species were not truly independent of one another in this forest. While different tree species sustained different rates of damage, these are explained by tree size. However, in the earlier 1983 storm, species did have significant additional effects beyond size, for both windstrike and mortality risk.

DAMAGE BY SPECIES FIGURES EXPLAINED

For each major tree species this report presents several graphs. One pair of graphs (Figures 6-24) shows for each storm survey and for both sites the density and proportion of trees killed and otherwise damaged, as in Figures 3 and 4 for all species combined. These graphs are based upon more detailed data from Table 3. Also for each species, another set of graphs, for the 1995 storm only, shows tree-size histograms within each major tree species, with separate graphs showing the background population ("sampled"), the treefalls including indirectly damaged trees, the windstruck trees (direct damage only), the stems killed, and the trees damaged but surviving (Figures 25-39). Similar information for the 1983 storm is in Webb (1989).

DAMAGE TO THE PINES

The most ancient of the park's red pines are being killed during windstorms at a worrisome rate. The park's white pines also sustain heavy losses to wind, across a wider spectrum of sizes. These losses are not compensated by new regeneration, as detailed later in this report. Pine seedlings sprout only on rotting logs, indicating that windthrown timber should not be salvaged but left to decompose in place in the forest. Controlled bums might also enhance pine reproduction, provided that aspen and hazel sprouts don't resprout excessively. For any of these pine seedlings to survive to maturity will necessitate measures to reduce herbivory by deer.

For the oldest (to 250 yr) red pines, like those at Budd Lake, damage is heavier than for the younger (120 yr) red pine population at the Headwaters stand. The amount of wind damage is reported on a density (per hectare) basis in Figure 5 and on a proportional basis (%) in Figure 6. Although treefall densities were low for red pine at both sites (Figure 5), the loss rate was high given the small population density at Budd Lake in particular. The three surveys at Budd Lake document 0.6%, 4.7%, and 5.1 % mortality, respectively, totaling a loss of over 10% of the red pine population in five years (1983-1987 and 1995). The higher damage in the second and third survey could reflect their inclusion of winter storm damage, to which the evergreen pines are more susceptible, while the 1983 survey was most focused on a single summer storm event. My field observations suggest that these loss rates are generally typical for the park's oldest red pines, although they cannot be extrapolated directly to other ancient red pine populations; some stands are more protected (for example east of Mary Lake) while others are more vulnerable and sustain higher mortality rates (for example, Preachers Grove, at the edge of Lake Itasca).

Meanwhile the younger red pines at the Headwaters sustained <1% mortality in each of the two major storms (Figure 6). Fallen red pines were just as abundant as at Budd Lake but this simply reflected a higher population density (Figure 5); red pine accounted for about 7% of the trees at the Headwaters site (Table 1). Red pines have relatively strong wood and should resist wind damage, as they do at this site. There are three key differences between the two populations. First is a size difference; at Budd Lake most red pines had diameters of 45-90 cm, while at Headwaters typical diameters are 15-55 cm (Figures 5, 6). Trees with larger diameters are typically taller and hence, as already noted, more susceptible to windthrow in this region. Also within each site, larger red pines appear to be most vulnerable, judging from histograms (Figures 25, 26) but with such small samples the statistics (Kolmogorov-Smimov tests) do not document this. Secondly, the older pines at Budd Lake and throughout the park have a high incidence of fire scars and wood-rotting fungal infestations (Webb 1989). Third is a structural difference; at Budd Lake the pines emerged above the main canopy, presenting easy targets for severe wind, while at Headwaters the pine crowns were level .with the rest of the forest canopy.

White pines are also majestic and ancient components of the Itasca Park forests, although less endemic than red pine and less commonly found in pure stands in this region. In the Budd Lake area, white pines were very sparse (1-2% relative density, Table 1) and, like red pines, were only present in large size classes (Figure 27). Thus white pine treefalls were also uncommon (Figure 7). However a moderately high rate of damage was sustained by this small population, with nearly 5% killed during the five year period surveyed (Figure 8). The surviving damaged white pines (Figures 7 and 8) have mostly lost the tops of their crowns, hence the future prognosis is not good for their long term survival. In contrast, white pine had relatively high survival over 26 years in a similar stand first sampled in 1955 and resampled in 1983 by

Peet (1984). That comparison, not focused on wind disturbance, showed much higher loss for aspen and birch, as in this study, but also more loss of maples over time than of pines.

At the Headwaters site, white pine is a more major component of the forest (5.5-7.5% of stems, Table 1), across a wider range of size classes (10-60 cm dbh). Despite these differences, white pine sustained similar rates of damage in the two stands (Figure 8). At Headwaters the 1983 storm was most damaging, killing 2.6°/a of the white pines, compared with 0.8% in 1996 (Table 3). Without a 1987 survey at this site, our records give only two years of damage, with a total of 3.4% lost over two years. Note however that these were unusual big-storm years so this rate should not be broadly extrapolated.

As for red pine, the future for white pine is quite bleak. Alongside steady wind damage, there are only scattered white pine seedlings found on rotting logs at a nearly undetectable density (Webb 1988), and no saplings or small trees. Interestingly, at the Headwaters site the largest white pines were not most vulnerable (Figure 28) but instead the wind damage was concentrated in lower and middle size classes.

DAMAGE TO ASPEN AND BIRCH

The aspen (quaking and bigtooth combined; see methods) succumbed to more wind damage than any other trees, in both study areas (Figure 9) as well as more widely throughout the park. In the Budd Lake area, 15% of all aspen tree stems were felled over the five years of record, with another 3.5% surviving their damage (Figure 10; Table 3). Aspen was abundant at this site, particularly the southern half, which had many large overmature stems (Figure 29) heavily infested with root-rotting and wood-rotting pathogens (Webb 1989). Furthermore aspen has weak wood by all measures (Markquart and Wilson 1934). Since aspen is clonal, these "mortality" rates refer to ramets, not genets. The paucity of successful resprouting in both sites suggests that these stem losses do represent a population decline. Clearly we are observing typical secondary succession at Budd Lake, with shade-intolerant aspens and pines that came in after fire now declining and shade-tolerant hardwoods taking over. It seems that windstorms are accelerating this process of successional replacement rather than setting it back by creating open patches in which early successional species, such as aspens and pines, can persist.

In the Headwaters forest, the two storms diverged with respect to aspen: nearly 7% of stems were killed in 1983 but only 1.3% in 1996 (Figure 9, 10). This reflects a difference in the intensity of the storms at this site (Figures 4 and 5). The undamaged aspens at Headwaters included small size classes (Figure 30), in contrast with the overmature Budd Lake population. Mortality was concentrated in the higher size classes but a few smaller stems were damaged indirectly by falling spruces (Figure 30). Windstorm consequences for the aspens might differ for the two sites; it is possible that aspen might increase in the Headwaters area in the larger wind-created gaps where sugar maple and hazel do not form dense windfirm layers as they do at Budd Lake.

Paper birch (the only birch present at these sites), like aspen, has weak wood and many wood-rotting pathogens. Periodic droughts decimate the Itasca birch population, which is at the west edge of its range. In the Budd Lake forest, a large pocket of paper birch occupied a low area north of Budd Lake itself; these relatively small (Figure 31) protected trees had little wind damage, hence low mortality in 1983 for paper birch (Figure 11, 12). An apparent drop of birch abundance, from 13% to 4% (Table 1) actually results from the exclusion of this birch zone from the smaller study area of subsequent surveys (1987 and 1996). These latter two surveys show that wind killed about 1 % of per year of birches in the upland areas (Figure 12). In the 1995 windstorm, none were struck directly by wind (Figure 31).

In the Headwaters forest, birches sustained much higher damage rates in the 1983 windstorm, with some 8% killed and another 4% surviving damage. Most were unusually large birches struck by wind (Webb 1989). The Headwaters mortality rate for birch went down to 1% in the 1995 survey, when half were struck by wind and half by falling trees (Figure 32). Again it appears that 1983 storm struck the Headwaters site with unusual severity. As with aspens, birches at the Headwaters site included some small trees and saplings (Figure 32) and thus some prospect of future persistence, while birches at Budd Lake did not (Figure 31).

PINE-HARDWOODS FOREST (BUDD LAKE SITE): DAMAGE PATTERNS

Beyond the damage to canopy pines, aspens, and birches, there was little destruction by moderate windstorms to the Budd Lake forest and others like it. A matrix of windfirm hardwoods such as sugar maple, red maple, ironwood, and red oak surrounded the windprone pines and aspens.

Sugar maple, the species with the highest density in this stand (Table 1) sustained minuscule damage (Figure 13., 14). Most sugar maple stems were small (dbh < 5 cm); note the change in scale on the "undamaged" histogram in Figure 33 to accommodate the large population. This shade-tolerant tree is also the strongest-wooded canopy tree in these forests (Markwardt and Wilson 1935; excluding the understory tree, ironwood). The typical mode of wind damage was bending under the weight of a fallen neighboring aspen or pine; only one sugar maple was damaged directly by wind in 1995 (Figure 33). Sugar maples usually survived this bowing mode of damage. Progression into the canopy might be less likely following this bending, but the abundant foliage of a bent maple casts deep shade in treefall areas that might otherwise represent gap opportunities for light-demanding trees. The superabundance of undamaged sugar maples means that windstorms hasten succession in this stand. The complete absence of sugar maple from the Headwaters site, apparently for edaphic reasons, gave that forest a very different windstorm response.

Red maple had a damage profile similar to that of sugar maple (Figures 15 and 16), with barely 1% mortality in the 5 years for which damage was surveyed, but with slightly more trees bent by falling pines and aspens (Figure 15 and 34). Red maple was not as abundant as sugar maple and is somewhat less tolerant of shade, but it predominated in the understory (Figure 34) within areas where sugar maple is sparse. Red maple often forms and understory layer beneath red oak canopies in eastern deciduous forests, where it is tolerant of shade and drought (Lorimer 1984). The Budd Lake area has an unusually patchy understory with various zones dominated by hazel, sugar maple, and mountain maple (shrubs); this zonation seems related to diverse soil deposits in within the Itasca moraine but could instead result from patterns of fire history or, in some hazel zones near the lakes, beaver activity.

A third understory tree that is increasingly abundant in the park is ironwood. Ironwood is not a canopy tree, and few stems reach diameters > 10 cm (Figure 35). However, ironwood has extremely slow growth and strong wood in its subcanopy position. Its population profile (Figure 35), like that of sugar maple, has been rescaled relative to other population histograms because of its high densities. Thanks to its wood strength, ironwood sustained virtually no mortality but some bending by fallen trees, especially in the 1995 windstorm (Figures 17, 18, and 35).

For red oak, the final major tree species in the Budd Lake area, mortality and damage rates were generally low (Figures 19 and 20) due to its relatively strong wood, in contrast with other light-demanding hardwoods in this forest (aspen, paper birch). Many damaged oaks survived their damage because they were multiple-stemmed with only one trunk toppled.

However, like aspens and birch, the red oak was uncommon in smaller size classes (Figure 36) and thus will not increase in abundance under current shaded conditions that prevail even in treefall areas.

Bur oak and basswood were also found while sampling the Budd Lake area but at low densities and without any treefalls (Table 1). The white spruce so abundant at the Headwaters site was present but at densities too low to appear in the background sample of undamaged trees; however, white spruce did appear among the treefalls in 1995 at this site.

PINE-SPRUCE FIR FOREST (,HEADWATERS AREA): DAMAGE PATTERNS

For the conifer-dominated forests of Itasca uplands, the role of shade-tolerant understory tree is played not by sugar maple but by balsam fir. Several graphs here for balsam fir are adjusted in scale to accommodate its very high densities (Figures 21 and 37). The extremely high density of wind-damaged firs resulted in large measure from the overall abundance of this tree. Actual mortality rates of 6% in 1983 and 4% in 1995 were high but still exceeded by aspen and (in 1983) by spruce. Balsam fir has the weakest wood of any in the region (Markwardt and Wilson 1935). Despite heavy damage to the small size classes (< 20 cm dbh, Figure 37), damage was significantly more likely as tree size increased for balsam fir (Kolmogorov-Smirnov test, Z=1.27, P=0.005). Most damaged firs were broken at the base and few survived their damage (Figure 37).

The other major player at this site is the white spruce, second in abundance to balsam fir (Table 1) and present in the understory but also in the canopy (Figure 38). No other tree sustained as much damage, in proportion to abundance, in the 1983 storm, when nearly the Headwaters forest lost 10% of its spruce with another 3% damaged but surviving (Figures 23 and 24). Lower mortality (3.4%) in the 1995 storm was more similar to that for balsam fir, and could result in part from previous windthrow of the most vulnerable trees. The overall density of white spruce decreased substantially in the 11 years between my two sampling efforts. Damaged spruces were significantly larger than undamaged spruces (Figure 38; Kolmogorov-Smirnov test, Z= 2.2, P<0.0005), were hit by both wind and falling trees, and rarely survived (Figure 38).

Several less common trees grow in the Headwaters forest. Among the sampled background but without wind-damage were red maples and green ash (Table 1). Trees found only in the more intensive wind-damage surveys were jack pine, basswood, and hickory, as well as unusually large stems of chokecherry, a shrub. Ironwood did not appear in sampled areas or treefalls in 1983 but was present in 1995 both in the background and amongst the indirectly damaged understory trees (Figure 39). This seems might be a sampling artifact rather than a new colonization.

The Headwaters area is a mosaic of large open glade-like patches and thickets of understory fir and spruce (Figure 2). These open areas might well have originated in windstorms, but they could instead result from human activity; this stand is very near the Mississippi Headwaters and likely has a history of scattered campsites or even buildings. The fate of these glades and their possible windthrow origin is of interest in the absence of tree reproduction except for small conifer seedlings on rotting logs, and requires long-term study.

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REGENERATION AFTER WINDSTORMS: 12 Years of Record in Treefall Plots

This section of the report describes how the woody undergrowth of shrubs and tree seedlings has changed in the Budd Lake area over a 12 year period (1984-1996), with comparison of plots in treefall areas and paired non-treefall "control" areas. Recall that plots arranged as in Figure 2 were sampled three times: 1984, 1992 (58 plots relocated), and 1996 (40 plots relocated). The patterns of change observed here are, in my experience, typical of the pine/aspen/maple forests throughout the park. All statements about differences and changes are based upon results of repeated-measures ANOVA in Table 5 where significant effects of treefalls, time, or base vs. crown location at $P<0.05$ are indicated with an asterisk (*). The multivariate test P value must be used instead when the sphericity test for carryover effects has $P<0.05$.

TREEFALL VERSUS CONTROL PLOTS

Twelve years after my initial post-windstorm surveys I found surprisingly little difference between treefall areas and adjacent control areas. The treefall and control plots did not differ significantly in their diversity of woody plants (Figure 40) nor in densities of any species or total stems present (Table 5). These results are surprising because disturbances such as windstorms are expected to enrich diversity by admitting shade-intolerant species into light gaps, and are expected to produce a thicket of new stems where the dead tree no longer usurps below-ground and above-ground resources.

This lack of an understory response to windstorms combines with heavy mortality to lightdemanding species (pines, aspen) to cause a shift toward late-successional forest. The same light-demanding trees that sustained heavy canopy losses due to their height were not present as seedlings or saplings in this shady forest even in treefall areas, where dense layers of maple, ironwood, and hazel continues to shade the forest floor.

Some modest differences between treefall and control areas are suggested by two significant interactions of treefall/control with year, in the repeated-measures ANOVA (Table 5). Small white pine seedlings were very scarce at all times but increased (from zero) in treefall plots while decreasing (from slightly higher abundances) in control plots; this result must be interpreted with caution given the small numbers and lack of significance for the single factors. Small blueberries showed a significant time/treefall interaction because their dramatic decrease over time everywhere in this forest was weakest in treefall/crown plots where initial densities were low. The notorious patchiness of plant distributions complicates efforts to understand their controls. However, this project design and size has sufficient power to detect differences, as shown by significance of changes observed over time. A major drought in 1988 contributed to these changes, alongside an apparent progression upward of shade-tolerant seedlings.

CHANGES OVER TIME

The understory structure and density did change dramatically and significantly over time; however these changes were equally manifest in both treefall and non-treefall areas (Table 5). Factors that might contribute to these shifts include the drought of 1988, the shadier conditions as tall seedlings increased in number, and combinations of those weather and seed predation factors that create good and bad years for seed germination.

The first eight year period (1984-1992) saw significant thinning in the small size class (height < 0.5 m) in both treefall and control areas (Table 5). The species that account for this decline in small seedlings were sugar maple (Figure 41) and red maple (Figure 42); low-bush blueberry also exhibited a trend toward a decline (P=0.07; Figure 43). While small seedlings were thinning out, the "medium" size class (height of 50 cm - 2 m) saw little net change, but there were significant increases in numbers of tall seedlings (height>2 m, dbh<2.5 cm) of sugar maple .(Figure 41), red maple (Figure 42), and ironwood (trend only; Figure 44), in both control and treefall areas. The sheer magnitude of the drop in maple seedling counts may result in part from height growth and related thinning, but the severe drought in 1988 is probably involved also. Meanwhile the average species richness of shrubs also declined during this period (Figure 40), although shrub densities did not change. Besides the tall ironwoods and maples, the only taxon that increased in abundance was chokecherry, a seed-banking light-demanding shrub; it subsequently dropped in abundance by the time of my next survey, four years later.

The years from 1992-1996 showed a continued significant (but more modest) thinning of small sugar maple seedlings (Figure 41), a continued thinning of blueberry shrubs (Figure 43), and the virtual disappearance of the small shrub called bush honeysuckle (Table 5). Mountain maple, a northern shrub, decreased in both small and medium size classes although the significance of this is lost when adjustments are made for the repeated-measures assumptions. A trend toward decreased densities of medium-sized shrubs (excluding hazel; Figure 45) was chiefly due to mountain maple. Also during this time period, the previous pulse of chokecherry seedlings, tall ironwoods, and tall red maples was reversed.

Hazel is by far the most abundant shrub throughout Itasca State Park, proliferating after fire and thriving amidst a large deer population. On mesic/wet sites with abundant sugar maple, like the Budd Lake area, Kurmis and Sucoff (1989) found a decrease in hazel shrub densities from 1965-1984, apparently due to shade from the maples. My findings for 1983-1996 show no such change at this site in either treefall areas or controls, nor any positive response by hazel to treefall events (Table 5).

One notable increase of significance during the later time period was a new prevalence of small seedlings of red oak, whose average density per 4 m^2 changed from 0.65 in 1984 to 0.40 in 1992 to 2.73 in 1996. In recent decades, scattered oak seedlings failed to move into taller height classes in this forest, perhaps because of insufficient light; it remains to be seen if the larger cohort now in evidence will be more persistent. This oak increase accounts for most of a significant gain by tree seedlings when the decreasing maples are excluded (Figure 46). Again, these changes were not more or less pronounced in treefall areas than in adjacent control areas; and in the case of oak seedlings the increase came 9 years after the windstorm; thus none can be attributed to windstorm disturbance.

BASE VERSUS CROWN PLOTS

Some modest differences in vegetation dynamics were also apparent when I compared plots at the bases of trees (either fallen or standing) with plots in the crown plots where the tree crown feel (Table 5). The complexity of this effect is illustrated in Figure 47 for red maples. Overall, base plots supported significantly fewer red maple seedlings than crown plots; this was also true for small ironwoods, bush honeysuckle, and small *Viburnum rainesquienum.*

Proximity to the base of a tree also influenced the pattern of change over time for several species in certain size classes, as indicated by significant interactions between year and the base/crown factor (Table 5). Medium-height chokecherry shrubs increased and then decreased in crown plots but decreased monotonically near the bases of trees, fallen or not. In contrast, small juneberry shrubs decreased more in crown zones than at tree bases. Meanwhile tall hazel shrubs increased in crown plots but decreased in base plots. These effects must be structural rather than competitive since they do not differ between fallen and intact tree bases; perhaps large tree roots, dead or alive, restrict vegetative spread by shrubs into the vicinity of the tree base.

PINE REGENERATION

As for regeneration of the pines, I found no red pine seedlings in any regeneration plots. For white pine, small seedlings did occur, mostly on rotting log microsites in the Headwaters study area and at very low densities in the Budd Lake community, despite the mid-level shade-tolerance of this species (Lorimer 1983), with no detectable change over the 12-year period in treefall or control areas (Table 5).

In 1996 I observed scattered white pine seedlings up to 1 m in height scattered throughout the park; this contrasts with conditions in the 1980's where the only pine reproduction was white pine seedlings < 10 cm in height. However, even this pulse of pine seedlings occurred at low densities not detectable at the scale of my studies. The distribution seems unconnected to treefalls except to the extent that the pines are more abundant on rotting logs and stumps in the park (Webb 1988).

EXPLANATIONS OF PHOTOGRAPHS OF TREEFALL AREAS

The photographs at the end of this report (note general localities shown in Figure 2) illustrate several key points, first about windstorm consequences in the pine--aspen-hardwood forest type. The cover page photo shows a typical red pine treefall in the Budd Lake area. The well-developed layers of shrubs and small tree stems at this site can be seen in Photo #1. The windfirmness of this understory helps .explain the failure of windstorms to produce deep light gaps and to produce regeneration opportunities for light-demanding species in this sort of forest. Two series of photos document changes in general appearance of two treefall areas monitored since 1983. Photos # 7, 8, and 9 show a windthrown aspen in the Budd Lake as photographed 2, 5, and 13 years after it blew down (in 1983). A well-developed layer of sugar maple seedlings was already present at the time of the storm; these thinned out and in some cases grew taller in this treefall area over time. The lack of a discrete gap over the base of the fallen tree is shown in photos #10 (2 years after windthrow) and #11 (13 years after windthrow). Tall understory maple trees were undamaged in the storm and formed continuous coverage even after the aspen blew down, precluding establishment of new light-demanding species, as regeneration plot data document for this site (treefall #36) and others. By 13 years post-storm, the rotting log was colonized by yet more sugar maple seedlings, as photo # 9 shows, not by conifer seedlings common on dead wood in many other forest types.

A second 1983 treefall area is illustrated by photos #12, 13, and 14. Here two large pines, one red and one white, blew down in parallel. Yet again no light gap formed over the base of the trees. The first photo (Photo #12), taken 2 years after the storm, shows the preexisting shrub layer including both undamaged and bent seedlings, mostly of red maple, mountain maple, and hazel in this locality. After another two years, pre-existing hazel and mountain maple shrubs continue to cover the area (Photo #13). By 13 years post-storm (Photo #14), the shrub layer has thinned and added height growth but without floristic changes. Regeneration plots at this site (treefall #1), as elsewhere, show no new colonization by light-demanding seedlings such as pines or birches because of deep shade cast by surviving understory vegetation.

The contrasting structure of the pine-spruce-fir forest type at the Headwaters forest is illustrated by photo #2. The understory here is dense with small balsam firs and (less abundantly) white spruce, although these small conifers are patchy in distribution. Because of their weak wood and the broad crowns of windthrown spruces in this forest, these understory trees sustain heavy damage in windstorms. Photo # 15 shows the most extensive blowdown documented at this site in 1995, and photo #16 provides an upward view of the large, discrete light gap that resulted. Photo #17 depicts another 1995 treefail in the Headwaters area and its large windthrow mound. All of the photographed treefall sites are now marked as permanent plots, along with a suite of other treefalls from 1983 and 1995 (Table 2).

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CONCLUSIONS

(1) Windstorms of moderate intensity represent a major organizing force for the forests of Itasca State Park. Tree-damaging winds strike almost every year, with more severe storms at irregular and unpredictable intervals. Most damaging in recent decades was the catastrophic windstorm of July 1995, although the July 1983 storm damaged more trees in some parts of the park.

(2) Itasca Park's older red and white pines sustained heavy mortality in windstorms (Figures 6 and 8). In the Budd Lake study area with its ancient pines, approximately 10% of each pine population was damaged, half the white pines surviving initially but most red pines killed outright. This figure includes pines damaged in two major storm years (1983 and 1995) plus pines damaged over another three years (1984-1987) as surveyed in 1987; thus it represents five years of windstorm damage surveys. The park's 200-350-year old trees are especially vulnerable due to their stature and increasingly scattered distribution, which leaves them emerging above the main canopy. Mortality was lower for red pine, but not for white pine, in the younger forests, like the Headwaters study area, where the canopy is more continuous and where younger trees have fewer fungus-admitting fire scars.

(3) None of the damage to pines is compensated for by pine regeneration. Windstorms triggered no new pine reproduction, either in forests with scattered treefalls, nor in more extensive aspen blowdown areas where aspen sprouts are proliferating. Regeneration surveys repeated over time did not reveal any new pulses of pine reproduction in response to windstorms. Widely scattered white pine seedlings were observed only on rotting logs, while red pine seedlings were exceedingly rare throughout the park over the 13 years of this project.

I expected more pine reproduction where windstorm severity was greatest, but instead the large blowdown areas were captured by aggressive hardwood sprouts of aspen and hazel. Small treefall events release too little light for pine establishment, and deer browsing has a devastating effect on pine regeneration in all cases. Future studies (Bohall Trail site) will investigate pine regeneration in a blowdown area unusual in lacking an aspen presence but large enough to admit sufficient light for pine establishment.

(4) Although fallen pines are most conspicuous due to their size, windstorms cause yet more damage to aspen and to white spruce (Figures 10 and 24); both trees have weak wood and aspen is also a victim of wood-rotting fungi in overmature stands (Webb 1989). In general, trees differ widely in their susceptibility to wind damage, with variance among tree species, among tree size classes, and also between sites.

(5) The consequences of windstorms for diversity and succession are not readily predictable but vary between forest types even with the same windstorm event. The trajectory of wind-induced changes depends largely on the forest understory, particularly the windfirmness of its species.

The two forest types studied here illustrate this. With a windfirm understory of sugar maple, red maple, ironwood, and hazel, the Budd Lake forest sustained little damage below the canopy layer, aside from the bending of strong saplings which typically survived this damage. Light gaps rarely formed, and shade-tolerant seedlings and saplings captured any newly available resources, excluding those less competitive species such as birch, aspen, and oak which might be expected to benefit from disturbance. In this situation, disturbance by wind depletes diversity, removing those wind-prone light-demanding taxa that are not reproducing, the net effect is acceleration of the classical case of secondary succession.

In contrast, the Headwaters forest had an understory of balsam fir and white spruce, both weak-wooded species that were easily killed by falling canopy trees. Light gaps formed with more regularity, and light-demanding species have seedlings, saplings, and a possible role in the future of the forest. Succession is set back in treefall areas, and the dynamics seem to fit the patch dynamics model whereby disturbance enriches overall diversity.

(6) Regeneration studies over 12 years showed no significant differences between treefall areas and control areas in either diversity or composition, in the pine/hardwoods forest type (Budd

Lake site) for which plots were monitored. Here a windstorm doesn't matter to understory dynamics; the well-developed pre-storm understory does not behave distinctively where trees blow down. This finding combines with past findings about low distinctiveness on windthrow mounds, pits, and stumps in this forest (Webb 1988) to reveal that windstorms only influence this vegetation type through the pattern of mortality and damage.

(7) In contrast, these 12 years of observing regeneration plots showed dramatic and significant changes over time, although these changes did not differ between treefall and control plots and thus cannot be attributed to windstorms. Instead a severe drought in 1988 might be the key influence although other factors are undoubtedly at work. The strongest change was a thinning of small seedlings of sugar maple, red maple, and lowbush blueberry. Diversity also declined, specifically shrub diversity, mostly with the loss of blueberry and bush honeysuckle stems. Increases over time, equally manifest in treefall and control areas, were seen for red oak seedlings, with a recent pulse of uncertain future, and for tall (height > 2 m) seedlings of sugar maple, red maple, and ironwood. These shade-tolerant understory taxa are advancing toward the canopy over time, even where the overstory aspens and pines have not blown down.

(8) Salvage logging should be avoided to the extent possible, since the rotting logs represent favorable germination substrates for pines and other trees in the coniferous forest types (Webb 1988). Unsalvaged areas also exhibit remarkable diversity of fungi and bryophytes, living on wind-generated substrates, to a degree unusual in forests of the eastern United States.

(9) The rarity and small size of old-growth forest remnants puts the biodiversity of these forests at grave risk. Windstorms are natural disturbance events that would create a mosaic of blowdowns and forests on a more intact landscape. However, in our highly fragmented landscapes, one windstorm can wipe out all that remains of unlogged forest in a region. Thus there is a compelling need for more and larger preserves that are protected from forest harvesting.

(10) These repeated surveys of wind damage and regeneration overtime provide an invaluable context for ongoing observations. This research will be continued to monitor future changes at this ecotonal location in response to windstorm events and to other events, with attention to the pines but also to overall diversity patterns. The permanent plots established as part of this project, for old and new treefall localities (and control sites), will be surveyed at regular intervals

for their structure and composition including the bryoflora of decomposing logs. This work will further our understanding of pine population dynamics, windstorm responses, global warming consequences at this ecotonal location. In addition, if controlled bums are conducted as anticipated, the baseline windstorm studies will help us understand the interaction of windstorms and fires as the major natural disturbance regimes shaping the original forests of Itasca State Park and indeed of the entire state of Minnesota.

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LITERATURE CITED

Aaseng, N.E. 1976. The history, nature, and extent of the major logging operations in Itasca State Park (1901-1919). M.S. Thesis, University of Minnesota, St.Paul MN.

Barden, L.S. 1979. Tree replacement in small canopy gaps of a Tsuga *canadensis* forest in the southern Appalachians, Tennessee. *Oecologia* 44:141-142.

Barden, L.S. 1981. Forest development in canopy gaps of a diverse hardwood forest of the southern Appalachian Mountains. Oikos 37:205-209.

Beatty, S.W. 1984. Influence of microtopography and canopy species on spatial patterns of forest understory plants. *Ecology* 65:1406-1419.

Beatty, S.W. 1991. Colonization dynamics in a mosaic landscape: the buried seed pool. *Journal of Biogeography* 18:553-563.

Bormann, F.H, and G.E. Likens. 1979. Catastrophic disturbance and the steady-state in northern hardwood forests. *American Scientist* 67:660-669.

Bray, J.R. 1956. Gap phase replacement in a maple-basswood forest. *Ecology* 37: 598-600.

Brewer, R., and P.G. Merritt. 1978. Wind throw and tree replacement in a climax beech-maple forest. Oikos 149-152.

Brokaw, N.V.L. 1982. The definition of treefall gap and its effect on measures of forest dynamics. *Biotropica* 14:158-160.

Brokaw, N.V.L. and Scheiner, S.M., 1989. Species composition in gaps and structure of a tropical forest. *Ecology,* 70: 538-541.

Buell, M.F. 1956. Spruce-fir, maple-basswood competition in Itasca Park, Minnesota. *Ecology* 37:606.

Buell, M.F., and W.E. Gordon. 1945. Hardwood-conifer contact zone in Itasca Park, Minnesota. *American Midland Naturalist* 433-439.

Buell, M.F., and W.E. Martin. 1961. Competition between maple-basswood and fir-spruce communities in Itasca Park, Minnesota. *Ecology* 42:428-429.

Buell, M.F., and W.A. Niering.1957. Fir-spruce-birch forest in northern Minnesota. *Ecology* 38:602-610.

Canham, C.D.1985. Suppression and release during canopy recruitment in *Acer saccharum. Bulletin of the Torrey Botanical Club* 112:134-145.

Canham, C.D. and Loucks, O.L., 1984. Catastrophic windthrow in the presettlement forests of Wisconsin. *Ecology, 65:* 803-809.

Canham, C.D., 1989. Different responses to gaps among shade-tolerant tree species. *Ecology,* 70: 548-550.

Clark, J.S. 1988. Effect of climate change on fire regimes in northwestern Minnesota. *Nature* 334:233-235.

Clark, J.S. 1989. Effects of long-term water balances on fire regime, north-western Minnesota. *Journal of Ecology* 77:989-1004.

Clark, J.S., 1992. Disturbance and tree life history on the shifting mosaic landscape. *Ecology* 72: 1102-1118.

Cho, D.-S., and R.E.J. Boemer. 1991. Canopy disturbance patterns and regeneration *of Quercus* species in two Ohio old-growth forests. *Vegetatio* 93:9-18.

Collins, B.S., and S.T.A. Pickett. 1987. Influence *of* canopy opening on the environment and herb layer in a northern hardwoods forest. *Vegetatio* 70:3-10.

Collins, B.S., and S.T.A. Pickett. 1988. Response *of* herb layer cover to experimental canopy gaps. *American Midland Naturalist* 119:282-290.

Connell, J.H. 1989. Some processes affecting the species composition in forest gaps. *Ecology* 70:560-561.

Connell, J.H., and R.O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* 111:1119-1144.

Connell, J.H., J.G. Tracey, and L.J. Webb. 1984. Compensatory recruitment, growth, and mortality as factors maintaining rain forest tree diversity. *Ecological Monographs* 54:141-164.

Davis, M.B. 1996. Eastern old-growth forests: prospects for rediscovery and recovery. Island Press, Washington, D.C.

Denslow, J.S. 1980. Patterns of plant species diversity during succession under different disturbance regimes. *Oecologia* (Berl.) 46:18-21.

Denslow, J.S. 1987. Tropical rain forest gaps and tree species diversity. *Annual Review of Ecology and Systematics* 18:431-451.

Dunn, C.P., Guntenspergen, G.R. and Dorney, J.R.,1983. Catastrophic wind disturbance in an old-growth hemlock-hardwood forest. *Canadian Journal of Botany,* 61: 211-217.

Eyre, F.H.1980. Forest cover types of the United States and Canada. Society of American Foresters, Washington, D.C.

Falinski, J.B. 1978. Uprooted trees, their distribution and influence in the primeval forest biotype. Vegetatio 38:175-183.

Feinberg, S.E. 1981. The analysis of cross-classified categorical data. MIT Press, Cambridge MA.

Foster, D.R.,1988. Species and stand response to catastrophic wind in central New England USA. Journal *of Ecology,* 76:135-151.

Foster, D.R. and Boose, E.R., 1995. Hurricane disturbance regimes in temperate and tropical forest ecosystems. In: M.P Coutts and J. Grace (Editors), *Wind and Trees.* Cambridge University Press, Cambridge, England, pp. 305-339.

Foster, D.R., Orwig, D.A., and J.S. McLachlan, 1996. Ecological and conservation insights from reconstructive studies of temperate old-growth forests. *Trends in Ecology and Evolution,* 11: 419-424.

Foster, J.F., and W.A. Reiners. 1986. Size distribution and expansion of canopy gaps in a northern Appalachian spruce-fir forest. *Vegetatio* 68:109-114.

Frelich, L.E. and Martin, G.L., 1988. Effects of crown expansion into gaps on evaluation of disturbance intensity in northern hardwood forests. *Forest Science,* 34: 530-536.

Frelich, L.E. and Lorimer, C.G., 1991. Natural disturbance regimes in hemlock-hardwood forest of the Upper Great Lakes region. *Ecological Monographs,* 61: 145-164.

Frelich, L.E. 1992. The relationship of natural disturbances to white pine stand development. Pp. 27-37 in: R.A. Stine and M.J. Baughman, editors. The White Pine Symposium: History, Policy, and Management.

University of Minnesota, Department of Forest Resources, College of Natural Resources and Minnesota Extension Service, St. Paul MN.

Frelich, L.E., 1995. Old forest in the lake states today and before European settlement. *Natural Areas Journal,* 15:157-167.

Frelich, L.E., and Reich, P.B.1995. Neighborhood effects, disturbance, and succession in forests of the western Great Lakes region. *Ecoscience* 2:148-158.

Frissell, S.S.,Jr. 1973. The importance of fire as a natural ecological factor in Itasca State Park, Minnesota. *Quaternary Research* 3:397-407.

Glenn, M.G. and S.L. Webb. 1997. Lichens as indicators of forest integrity. *Bibliotecha lichenologia.*

Glenn, M.G., Webb, S.L., and Cole, M.S.1998. Forest integrity at anthropogenic edges: air pollution disrupts bioindicators. *Environmental Monitoring and Assessment* (in press).

Glitzenstein, J.S., Harcombe, P.A. and Streng, D.R., 1986. Disturbance, succession, and maintenance of species diversity in an east Texas forest. *Ecological Monographs* 56: 243-258.

Grimm, E.C. 1983. Chronology and dynamics of vegetation change in the prairie woodland region of southern Minnesota, USA. *New Phytologist* 93:311-350.

Hansen, H.L., and V. Kurmis.1972. Natural succession in north-central Minnesota. Pp. 59-66 in: Aspen Symposium Proceedings. USDA Forest Service, Technical Report NC-1, North Central Forest Experiment Station, St. Paul MN.

Hansen, H.L., V. Kurmis, and D.D. Ness. 1974. The ecology of upland forest communities and implications for management in Itasca State Park, MN. University of Minnesota Agricultural Experiment Station, Technical Bulletin 298, Forestry Series 16. St. Paul MN.

Hazard Mitigation Survey Team (HMST).1995. HMST Report. FEMA-1064-DR-MN. Federal Emergency Management Agency, Region V. Chicago IL.

Heinselman, M.L., 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. *Quaternary Research,* 3: 329-382.

Henry, J.D. and Swan, J.M.A.,1974. Reconstructing forest history from live and dead material - an approach to the study of forest succession in southwest New Hampshire. *Ecology,* 55: 772-783.

Hibbs, D.E. 1982. Gap dynamics in a hemlock-hardwood forest. *Canadian Joumal of Forest Research* 12:522-527.

Hibbs, D.E. 1983. Forty years of forest succession in central New England. *Ecology* 64:1394-1401.

Hubbell, S. and R. Foster. 1986. Canopy gaps and the dynamics of a neotropical forest. Pp. 77-96 IN: M.J. Crawley, editor. Plant Ecology. Blackwell.

Jenkins, J. 1996. Notes on the Adirondack blowdown of July 15,1995: scientific background, observations, responses, and policy issues. Report to the Wildlife Conservation Society. White Creek Field School, White Creek, New York.

Kell, L.L. 1938. The effect of moisture-retaining capacity of soils on forest succession in Itasca Park, Minnesota. *American Midland Naturalist* 20:682-695.

King, D.A. 1986. Tree form, height growth, and susceptibility to wind damage in Acer saccharum. Ecology 67:980-990.

Kurmis, V. 1969. Dynamics of advance reproduction in upland forest communities of Itasca State Park, Minnesota. Ph.D. Thesis, University of Minnesota, St. Paul MN.

Kurmis, V. 1985. Changes in upland forest communities in Itasca State Park over a 19-year period. Staff Paper Series #52, Department of Forest Resources, University of Minnesota, College of Forestry. St. Paul MN.

Kurmis, V., and E. Sucoff. 1989. Population density and height distribution of Corylus *comuta* in undisturbed forests of Minnesota: 1965-1984. *Canadian Journal of Botany* 67:2409-2413.

Lertzman, K.P.1992. Patterns of gap-phase replacement in a subalpine, old-growth forest. Ecology 73:657669.

Lertzman, K.P., and C.J. Krebs. 1991. Gap-phase structure of a subalpine old-growth forest. *Canadian Journal of Forest Research* 21:1730-1741.

Lieberman, M., D. Lieberman, and R. Peralta.1989. Forests are not just Swiss cheese: canopy sterogeometry of non-gaps in tropical forests. Ecology 70:550-552.

Lorimer, C.G., 1977. The presettlement forest and natural disturbance cycle of northeastern Maine. *Ecology,* 58:139-148.

Lorimer, C.G.1984. Development of the red maple understory in northeastern oak forests. Forest Science 30:3-22.

Lorimer, C.G., 1985. Methodological considerations in the analysis of forest disturbance history. *Canadian Journal of Forest Research* 15: 200-213.

Lorimer, C.G., Frelich, L.E., and Nordheim, E.V. 1988. Estimating gap origin probabilities for canopy trees. *Ecology* 73:1124-1128.

Lorimer, C.G. and Frelich, L.E.,1989. A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. Canadian Journal *of Forest Research* 19: 651-663.

Markwardt, L.J., and T.R.C. Wilson. 1934. Strength and related properties of woods growth in the United States. US. Department of Agriculture, Technical Bulletin 479.

McAndrews, J.H.1966. Postglacial history of prairie, savannah, and forest in northwestern Minnesota. *Memoirs of the Torrey Botanical Club* 22:1-72.

McClure, J.W.and T.D. Lee. 1993. Small-scale disturbance in a northern hardwoods forest: effects on tree species abundance and distribution. Canadian Journal of Forest Research 23:1347-1360.

Mooney, H.A., and M. Godron.1983. Disturbance and Ecosystems: Components of Response. Springer-Verlag, New York NY.

National Oceanic and Atmospheric Administration. 1983. Storm data 25(7). National Climatic Center, Asheville, North Carolina, USA.

Ness, D.D.1971. Comparative dynamics of upland forest communities in Itasca State Park, MN. Ph.D. Thesis, University of Minnesota, St. Paul MN.

Norusis, M.J. 1993. SPSS for Windows (software), Version 6.0. SPSS INc., Chicago IL.

Oliver, C.D. and Stephens, E.P., 1977. Reconstruction of a mixed-species forest in central New England. *Ecology,* 58: 562-572.

Orians, G.H. 1982. The influence of treefalls in tropical forests on tree species richness. *Tropical Ecology* 23:255-279.

Patterson, W.A. III. 1978. The effects of past and current land disturbances on Squaw Lake, Minnesota, and its watershed. Ph.D. Thesis, University of Minnesota, St. Paul MN.

Peet, R.K. 1984. Twenty-six years of change in a Pinus strobus - Acer saccharum forest, Lake Itasca MN. *Bulletin of* the Torrey Botanical Club 111:61-68.

Peterson, C.J., W.P. Carson, B.C. McCarthy, and S.T.A. Pickett. 1990. Microsite variation and soil dynamics within newly created treefall pits and mounds. Oikos 58:39-46.

Peterson, C.J., and S.T.A. Pickett. 1995. Forest reorganization: a case study in an old-Broth forest catastrophic blowdown. *Ecology* 76:763-774.

Peterson, C.J., and E.R. Squiers. 1995. An unexpected change in spatial pattern across 10 years in an aspen-white pine forest. Joumal *of Ecology* 83:847-855.

Pickett, S.T.A., and P.S. White, editors. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, Orlando.

Poulson, T.L. and Platt, W.J.,1989. Gap light regimes influence canopy tree diversity. *Ecology,* 70: 553-555.

Putz, F.E. 1983. Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island, Panama. *Ecology* 64:1069-1074.

Putz, F.E., P.D. Coley, K. Lu, A. Montalvo, and A. Aiello. 1983. Uprooting and snapping of trees: structural determinants and ecological consequences. Canadian Journal *of* Forest *Research* 13:1011-1020.

Roberts, M.R., and C.J. Richardson. 1985. Forty-one years of population change and community succession in aspen forests on four soil types, northern lower Michigan, USA. Canadian Joumal *of Botany* 63:1641-1651.

Ross, B.A., J.R. Bray, and W.H. Marshall. 1970. Effects of long-term deer exclusion on a Pinus resinosa forest in north-central Minnesota. *Ecology* 51:1088-1093.

Runkle, J.R. 1981. Gap regeneration in some old-growth forests of the eastern United States. *Ecology* 62:1041-1051.

Runkle, J.R. 1984. Development of woody vegetation in treefall gaps in a beech-sugar maple woods. Holarctic *Ecology* 7:157-164.

Runkle, J.R. 1985. Disturbance regimes in temperate forests. Pages 17-33 IN: S.T.A. Pickett and P.S White, editors. Natural Disturbance and Patch Dynamics. Academic Press, Orlando FL.

Runkle, J.R.1990. Gap dynamics in an Ohio USA Acer-Fagus forest and speculations on the geography of disturbance. *Canadian Journal* of Forest Research 20:632-641.

Rusterholtz, K.A. 1996. Identification and protection of old growth on state owned land in Minnesota. In: M.B. Davis, editor: Eastern Old Growth Forests: Prospects for Rediscovery and Recovery. Island Press, Washington, D.C.

Schaetzl, R.J., S.F. Burns, D.L. Johnson, and T.W. Small. 1989. Tree uprooting: review of impacts on forest ecology. *Vegetatio* 79:165-176.

Seischab, F.K. and Orwig, D., 1991. Catastrophic disturbances in the presettlement forest of western New n
York, USA. Bulletin of the Torrey *Botanical Club* 118: 117-122.

Shiyatov, S.G., 1990. The use of dendrochronological methods in determining tree windthrow time. *Lesovedenie 2*: 72-81.

Sokal, R.R., and F.J. Rohlf. 1981. Biometry, 2nd edition. Freeman and Co., New York.

Sousa, W.P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* 15:353-391.

Spies, T.A., J.F. Franklin, and M. Klopsch. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. *Canadian Journal of Forest Research* 20:649-658.

Spurr, S.H. 1954. The forests of Itasca in the 19th century as related to fire. *Ecology* 35:21-25.

Stearns, F.W., 1949. Ninety years change in a northern hardwood forest in Wisconsin. Ecology 30: 350358.

Stewart, G.H., Rose, A.B. and Veblen, T.T.,1991. Forest development in canopy gaps in old-growth beech *(Nothofagus)* forests, New Zealand. *Journal of Vegetation Science* 2: 679-690.

Uhl, C., K. Clark, N. Dezzeo, and P. Mazuirino. 1988. Vegetation dynamics in Amazonian treefall gaps. *Ecology* 69:751-763.

von Ende, C.N.1993. Repeated-measures analysis: growth and other time-dependent measures. Pp.113137 IN: S.M. Scheiner and J. Gurevitch, editors: Design and analysis of ecological experiments. Chapman and Hall, New York.

Watt, A.S. 1947. Pattern and process in the plant community. *Journal of Ecology* 35:1-265.

Webb, S.L. and Willson, M.F.,1985. Spatial heterogeneity in post-dispersal predation on Prunus and *Uvularia* seeds. *Oecologia (Berlin)* 67:150-153.

Webb, S.L.1988. Windstorm damage and microsite colonization in two Minnesota forests. *Canadian Journal of Forest Research* 18:1186-1195.

Webb, S.L.1989. Contrasting windstorm consequences in two forests, Itasca State Park, Minnesota. *Ecology* 70:1167-1180.

Webb, S.L. 1998. Disturbance by wind in temperate-zone forests. Chapter 7 IN: L.Walker, editor: Ecosystems of disturbed ground. Elsevier Press (in press)

Westman, W.C. 1968. Invasion of fir forest by sugar maple in Itasca Park, MN. *Bulletin of the Torrey Botanical Club* 95:172-186.

White, P.S., MacKenzie, M.D. and Busing, R.T.,1985. Natural disturbance and gap phase dynamics in southern Appalachian spruce-fir forests. *Canadian Journal of Forest Research* 15: 233-240.

Whitney, G.G., 1986. Relation of Michigan's presettlement pine forests to substrate and disturbance history. *Ecology* 67:1548-1559.

Williamson, G.B. 1975. Pattern and seral composition in an old-growth beech-maple forest. *Ecology* 56:727-731.

Worrall, J.J. and Harrington, T.C., 1988. Etiology of canopy gaps in spruce-fir forests, Crawford Notch,. New Hampshire USA. *Canadian Journal of Forest Research* 18:1463-1469.

Table 1.
Tree densities and scientific names for plants mentioned in the report, including all stems with dbh 2.5 cm +.
Nomenclature follows Gleason and Cronquist, 1991.
Relative density is the per centage of tree stems with dbh=2.5 cm+ represented by each species.

			RELATIVE DENSITY			
SCIENTIFIC NAME	COMMON NAME	CODE	Budd Lake Area		Headwaters Area	
			1984	1996	1984	1996
TREES:						
Abies balsamea	Balsam fir	BF			58.9	65.1
Acer rubrum	Red maple	RM	15.8	7.5	0.3	0.3
Acer saccharum	Sugar maple	SM	30.6	48.2		
Betula papyrifera	Paper birch	PB	13.8	4.1	3.1	3.4
Carya spp.	Hickory	HI				
Fraxinus pennsylvanica	Green ash	GA			4.9	0.7
Ostrya virginiana	Ironwood	IW	14.3	28.9	0	2.4
Picea glauca	White spruce	WS	5.1	0	14.8	8.2
Pinus banksiana	Jack pine	JP				
Pinus resinosa	Red pine	RP	6	1.3	6.4	7.2
Pinus strobus	White pine	WP	2	0.9	5.5	7.5
Populus tremuloides & grandidentata	Aspen (quaking & bigtooth)	QA, BT	6.5	3.4	6.5	5.1
Quercus macrocarpa	Bur oak	BO	0.2	0.2		
Quercus rubra	Red oak	RO	8.5	4.3		
Tilia americana	Basswood	BW	1.2	1.3		
SHRUBS						
Acer spicatum	Mountain maple	MM				
Amelanchier cf. laevis	Juneberry	JB				
Cornus racemosa	Grey dogwood	DG				
Cornus rugosa	Round-leaf dogwood	DW				
Corylus cornuta	Hazel	HA				
Diervilla lonicera	Bush honeysuckle	HB				
Lonicera canadensis	Canada honeysuckle	HT				
Prunus virginiana	Chokecherry	CC				
Rubus alleghaniensis	Blackberry	BK				
Rubus flagellaris	Dewberry	DB				
Rubus idaeus	Raspberry	RB				
Toxicodendron radicans	Poison ivy	PI				
Vaccinium angustifolium	Lowbush blueberry	BB				
Total Tree Density /ha			1125	1198	2165	1671

Table 2

Permanent plot and releve localities, Itasca windstorm project

Treefall Number	Site	Date of Treefall	Tree Species	Photos	Regen. Plots (m to crown plots)	Releve (& control)	Gap analysis*
1	Budd Lake	1983	White pine	12-14	x (35 m)		
2	Budd Lake	1983	Aspen		x (13.5 m)		
5	Budd Lake	1983	Red pine		x (20 m; crown only)		
34	Budd Lake	1983	Red pine		x (21.5 m)		
35	Budd Lake	1983	Aspen		x (11 m)		
36	Budd Lake	1983	Aspen	7-11	x (19 m)		
38	Budd Lake	1983	Aspen		x (18 m)		x
39	Budd Lake	1983	Red pine		x (10 m)		x
46	Budd Lake	1983	Aspen		x (3 m)		
47	Budd Lake	1983	Aspen		x (10.5 m)		
67	Budd Lake	1983	Red pine				
74	Budd Lake	1983	Aspen		x (base only)		
212	Budd Lake	1995	Aspen			x (x)	x
214	Budd Lake	1995	Aspen			x	x
216	Budd Lake	1995	Aspen				x
217	Budd Lake	1995	Aspen				x
232	Budd Lake	1995	Red pine				x
238	Budd Lake	1995	Red pine			x (x)	x
250	Budd Lake	1995	Red oak			x (x)	x
120	Budd Lake	1983	Red pine				
201	Budd Lake	1996	Red pine			x (x)	x
240-1	Budd Lake	1995	Red pine			x (x)	x
240-2	Budd Lake	1995	Red pine				
330	Headwaters	1995	W. spruce	15, 16		x	x
378	Headwaters	1995	W. spruce			x (x)	x
390	Headwaters	1995	W. spuce	17		x (x)	x
B1	Bohall Trail	1995	Red pine (many	5, 6		x	
B2	Bohall Trail	1995	"Control"			(x)	

*Added gap analyses were done for five 1995 treefalls not permanently marked (213, 215, 218, 231,242)

Table 3.

Mortality and damage rates, and density of damage, by tree species for all damage surveys at the two Itasca study sites.

	Per Centage of Trees in Population Damaged										Density of Trees in Population Damaged									
	Trees Killed as % of Population					Trees Surviving Damage, %					Trees Per Hectare Killed					Trees Per Hectare Surviving Damage				
Tree Species	Budd Lake			Headwaters		Budd Lake			Headwaters		Budd Lake			Headwaters		Budd Lake			Headwaters	
	1983	1987	1995	1983	1995	1983	1987	1995	1983	1995	1983	1987	1995	1983	1995	1983	1987	1995	1983	1995
Sugar maple	0.13	0.097	0.12	0	0	0.47	0.403	0.504	0	0	0.45	0.562	0.68	0	0	1.625	2.3	2.92	0	0
Red maple	0.18	0.62	0.42	0	0	0.22	1.46	1.02	0	0	0.325	0.56	0.375	0	0	0.425	1.31	0.925	0	0
Paper birch	0.13	3.45	0.89	8.1	1.75	0.17	1.14	0.95	3.8	1.32	0.2	1.69	0.438	5.5	1	0.3	0.56	0.462	2.5	0.75
Ironwood	0.06	0.07	0.018	0	0	0.24	0.29	0.792	0	1.6	0.1	0.25	0.063	0	0	0.4	1	2.737	0	0.625
White spruce	0	0	0	9.9	3.38	0	0	0	1	0.34	0	0	0.125	31.5	4.625	0	0	0	3	0.475
White pine	0.9	2.27	1.71	2.6	0.79	0.6	1.73	1.93	0.5	0.3	0.2	0.25	0.188	3	1	0.15	0.19	0.212	0.5	0.375
Red pine	0.6	4.7	5.1	0.7	1.14	0	0	0.4	0	0.03	0.375	0.75	0.813	1	1.375	0.025	0	0.063	0	0.025
Aspen	3.6	6.17	5.23	6.8	1.31	1.7	0.62	1.17	0.6	1.01	1.675	2.5	2.12	5.5	1.175	0.5	0.25	0.48	0.5	0.825
Balsam fir	0	0	0	5.9	4.24	0	0	0	0.9	1.46	0	0	0	75.5	46.125	0	0	0	11	15.775
Basswood	0	0	0	0	0	0	7.35	0	0	0	0	0	0	0	0	0	1	0	0	0.125
Red oak	0.4	0.73	0.48	0	0	0.3	0.48	1.45	0	0	0.35	0.375	0.25	0	0.25	0.325	0.26	0.75	0	0
Jack pine	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chokecherry	0	0	0	0	0	0	0	0	0	0	0	0	0.06	0	0	0	0	0	0	0.125
Cornus rugosa	0	0	0	0	0	0	0	0	0	0	0	0	0.06	0	0	0	0	0	0	0
Mtn maple	0	0	0	0	0	0	0	0	0	0	0	0	0.06	0	0	0	0	0	0	0
Green ash	0	0	0	0	0	0	0	0	0	0.9	0	0	0	0	0	0	0	0	0	0.1
Hickory	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1
Bur oak	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total for Site	0.33	0.62	0.44	5.6	3.4	0.33	0.69	0.73	0.8	1.1	3.675	6.937	5.232	122	55.55	3.75	6.87	8.55	17.5	18.425

Table 4. Patterns of wind damage with respect to tree size and tree species. "Windstruck" = trees damaged directly by wind. "Killed" = tree stems killed, whether by wind or falling trees. "Survived" = trees damaged but surviving. "All damaged" includes both trees killed and trees surviving their damage. "Sampled" are undamaged background trees.
Results are from logistic regression analysis, modelling the comparison on tree size and tree species.
Results of the 1983 windstorm are from Webb 1988 and Webb 1989.
For 1983, species wood strength fully explained the species effect in Headwaters in the wind vs. sampled comparison. Differences are considered signficant if P>0.05, as indicated by asterisk (*).

Comparison	**1995 Windstorm** Size (dbh)	Species	**1983 Windstorm** Size (dbh)	Species
HEADWATERS AREA				
Windstruck vs sampled	0.039* [larger: wind]	0.002*	<0.001* [larger: wind]	<0.005*
All damaged vs sampled	0.137	0.001*		
Killed vs sampled	0.708	0.0007*	>0.05	<0.001*
Killed vs survived	0.004* [larger killed]	0.62		
Cause: wind vs. falling tree	0.000* [larger: wind]	0.163		
Mode: uprooted vs. snapped	0.29	0.73	0.01* [larger: snapped]	0.16
BUDD LAKE STUDY AREA				
Windstruck vs sampled	0.000* [larger: wind]	0.26	<0.001* [larger: wind]	<0.001*
All damaged vs sampled	0.000* [larger: damaged]	0.002*		
Killed vs sampled	0.000* [larger: killed]	0.5	<0.001*	<0.001*
Killed vs survived	0.000* [larger: killed]	0.49		
Cause: wind vs. falling tree	0.000* [larger: wind]	0.26		
Mode: uprooted vs. snapped	0.309	0.19	>0.10	0.07

Table 5

Changes in species richness and stem densities over time in regeneration plots, Budd Lake forest study area.
Crown-base" is the comparison of base plots with plots in the fallen crown zone.
"Treefall/control" is the comparison of treefall plots with control plots.
"Year" compares the three sampling dates, broken down into T2 (1983 vs. 1992) and T3 (1992 versus 1996).
Significant differences are indicated by *, based upon repeated measures ANOVA at P=0.05.
Increase = ^; decrease = v; ^v=increase followed by decrease.
Sphericity results with P<0.05 call for use of the multivariate ANOVA instead, as reported.
Size classes are small (height<50 cm), medium (50cm<height<2 m), and tall (height > 2 m).

Species	Size Class	Treefall vs Control	Base vs. Crown	Year	'83 vs. '92	'92 vs. '96	Sphericity W	Sphericity P	Multivariate Test (year)	Significant interactions
SPECIES RICHNESS										
Shrubs only		0.623	0.688	0.037*v	0.046*v	0.148	0.82	0.074	0.111	
Tree species only		0.954	0.862	0.356	0.858	0.222	0.87	0.152	0.482	
Trees and shrubs		0.617	0.549	0.074	0.154	0.075	0.93	0.35	0.136	
DENSITY OF ALL WOODY STEMS COMBINED										
All trees & shrubs	all sizes	0.982	0.315	0.001*v	0.001*v	0.023*v	0.82	0.075	0.898	
All trees & shrubs	small	0.988	0.338	<0.0005*v	<0.0005*v	0.029*v	0.71	0.01	0.794	
	medium	0.51	0.786	0.728	0.359	0.862	0.76	0.027	0.143	base/year
	tall	0.629	0.362	<0.0005*^	0.001*	0.093	0.94	0.44	0.003*	
DENSITY OF TREE STEMS										
Tree stems	all sizes	0.995	0.216	<0.0005*v	0.001*v	0.071	0.78	0.033	0.937	
	small	0.889	0.245	<0.0005*v	0.000*v	0.043*v	0.69	0.007	0.001*	
	medium	0.291	0.204	0.146	0.198	0.162				
	tall	0.257	1	<0.0005*^	0.000*^	0.464	0.45	0.000	0.000*	
Trees w/out maples	small	0.761	0.283	0.009*^	0.131	0.028*^	0.31	0.000	0.031*	
	medium	0.399	0.061	0.781	0.363	0.521				
	tall	0.645	0.926	<0.0005*^	0.001*^	0.191	0.69	0.006	0.005*	
TREES BY SPECIES										
Sugar maple	small	0.928	0.373	<0.0005*v	0.001*v	0.029 *v	0.44	0.000	0.006*	
	medium	0.396	0.365	0.107	0.154	0.134				
	tall	0.233	0.913	0.007*^	0.010*^	0.538	0.65	0.003	0.006*	
Red maple	small	0.571	0.052*	0.005*v	0.005*v	0.177	0.99	0.871	0.013*	
	medium	0.36	0.36	0.766	0.767	0.362				
	tall	0.63	1	0.054*^v	0.049*^	0.401	0.27	0.000	0.058	
Aspen	small	0.958	0.958	0.271	0.478	0.285				
Ironwood	small	0.84	0.033*	0.677	0.853	0.313	0.83	0.078	0.662	
	medium	0.646	0.255	0.071	0.07	0.142	0.74	0.016	0.161	
	tall	0.926	0.782	0.009*^	0.015*^	0.61	0.69	0.007	0.833	
Paper birch	small	0.66	0.66	0.737	0.833	0.326				
Red oak	small	0.61	0.367	0.005*^	0.069	0.021*^	0.09	0.000	0.022*	
White pine	small	0.771	0.771	0.729	0.461	1	0.97	0.666	0.763	control/year
DENSITY OF SHRUB STEMS										
All shrub species	all sizes	0.716	0.154	0.176	0.337	0.088				
	small	0.477	0.153	0.601	0.686	0.313				
	medium	0.961	0.223	0.058	0.073	0.128				
	tall	0.935	0.434	0.268	0.435	0.151				
Shrubs w/out hazel	small	0.694	0.475	0.258	0.373	0.149				
	medium	0.832	0.658	0.065v	0.173	0.030*v	0.58	0.001	0.076	
	tall	0.779	0.403	0.196	0.15	0.42				
SHRUBS BY SPECIES										
Hazel	all	0.84	0.161	0.818	0.606	0.724				
(*Corylus*	small	0.467	0.13	0.36	0.276	0.382				
cornuta)	medium	0.882	0.193	0.43	0.28	0.514				
	tall	0.804	0.547	0.329	0.428	0.192	0.43	0.000	0.417	base/year
Blueberry	small	0.112	0.657	0.005*v	0.020*v	0.029*v	0.08	0.000	0.071	control/year
Chokecherry	small	0.775	0.634	0.399	0.045*^	0.745	0.59	0.001	0.111	
	medium	0.299	0.299	0.183	0.181	0.239	0.38	0.000	0.402	base/year
Dewberry	small	0.542	0.454	0.583	1	0.454	0.1	0.000	0.584	
Bush honeysuckle	small	0.507	0.053*	0.377	0.756	0.053*v	0.7	0.007	0.16	
Honeysuckle	small	0.274	0.195	0.441	0.491	0.195	0.7	0.003	0.434	
Juneberry	small	1	0.244	0.175	0.087	1	0.51	0.001	0.071	base/year
	medium	1	0.375	0.092	0.079	0.342	0.2	0.000	0.104	
Mountain maple	small	0.486	0.125	0.189	0.739	0.050*v	0.95	0.485	0.136	
	medium	0.919	0.267	0.203	0.406	0.025*v	0.58	0.001	0.081	
	tall	0.542	0.227	0.128	0.195	0.082	0.09	0.000	0.141	
Arrowood	small	0.893	0.052*	0.938	0.75	0.901	0.72	0.013	0.95	
	medium	0.458	0.096	0.224	0.175	0.411	0.64	0.003	0.403	

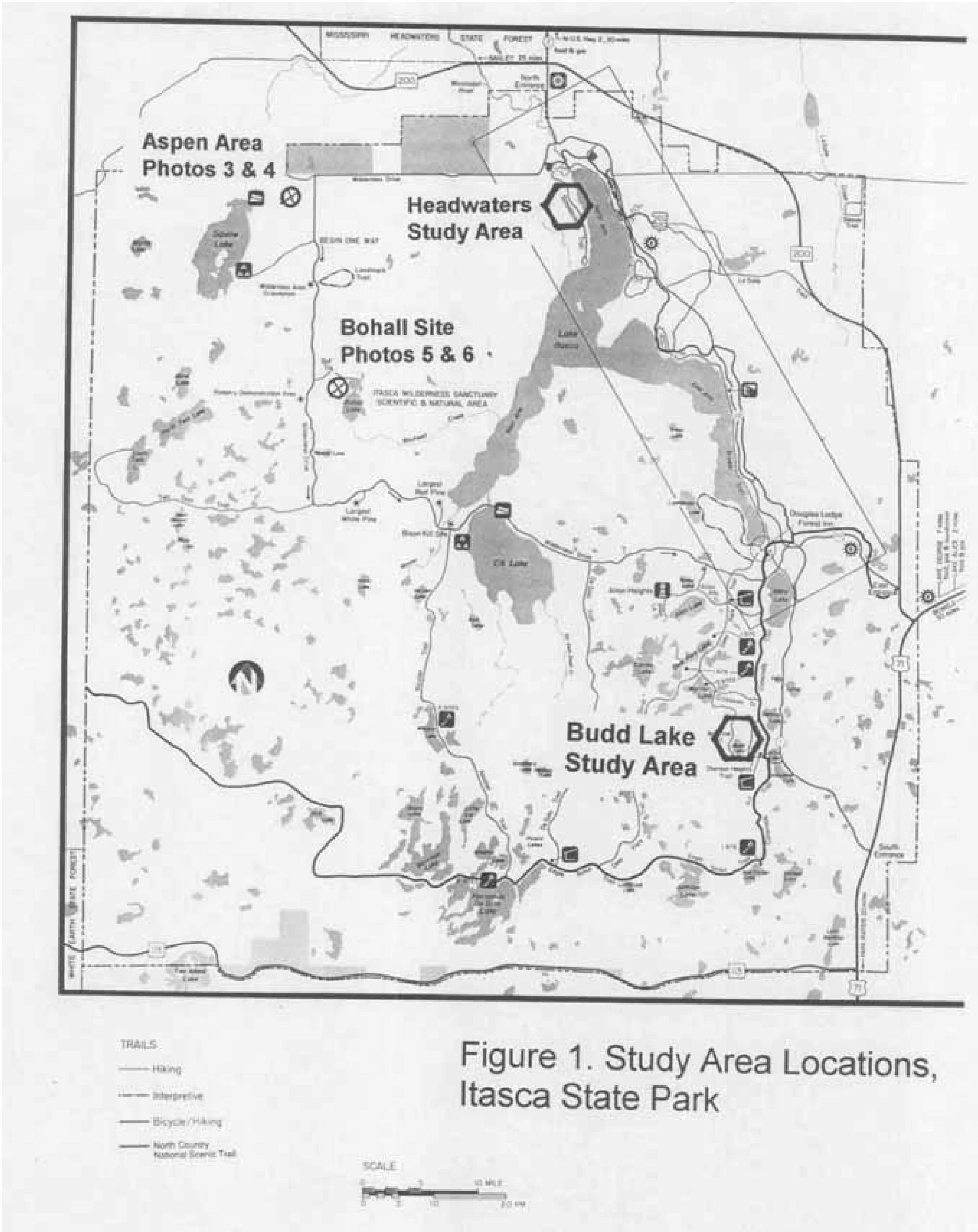


Figure 1. Study Area Locations, Itasca State Park

Figure 2.
Sampling scheme for regeneration plots at 1983 treefalls, Budd Lake study area. In 1984, each treefall had a set of four 4x4 meter plots: one located 0.5 m north of the base of the fallen tree (treefall-base); the second located where the tree crown fell, just beyond the first canopy branches (treefall-crown); the third located at the base of the nearest undamaged conspecific tree located sufficiently far to be uninfluenced by the treefall (base-control); and the fourth located at the same distance and direction from the base control plot as the crown-treefall plot was from the crown-base plot (crown-control).

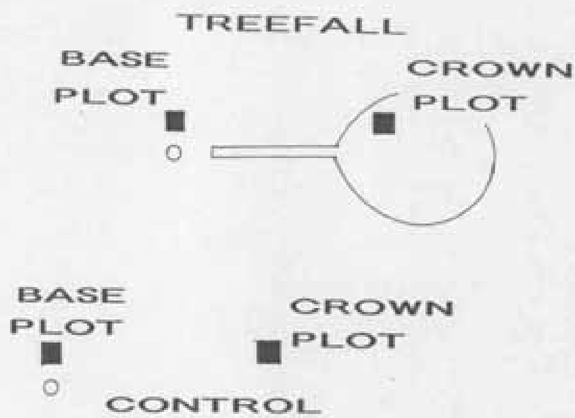


Figure 3.
Overall density of treefalls due to windstorms in the two Itasca forests, for all three windstorm surveys, for all species combined.

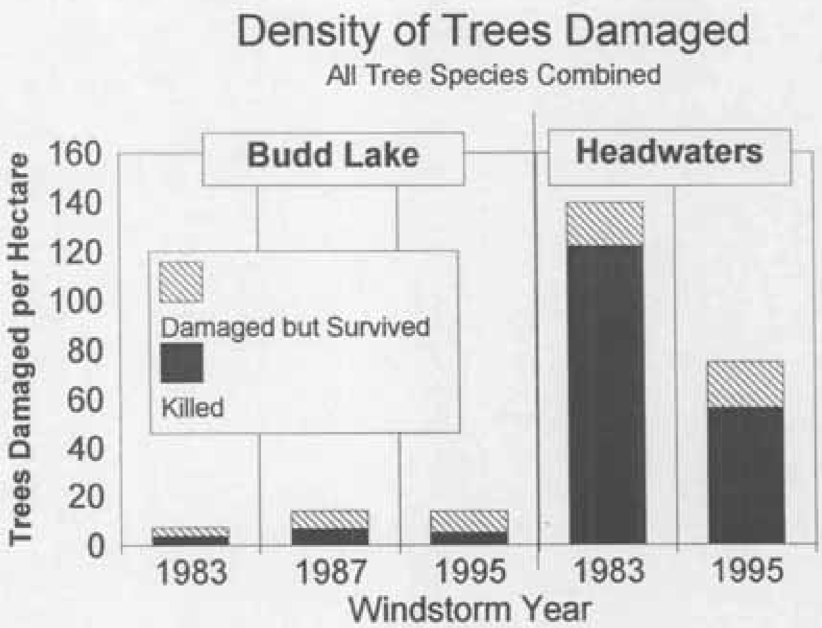


Figure 4.
Overall % of trees damaged by windstorms in the two Itasca forests, for all three windstorm surveys, for all species combined.

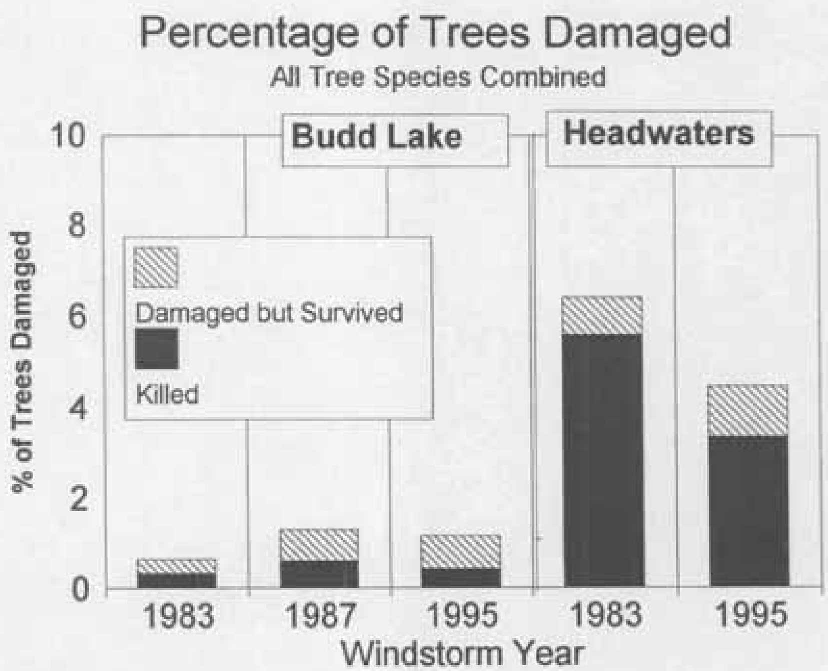


Figure 5.
Red pine, damaged tree density (per hectare), for both sites and all windstorm surveys.

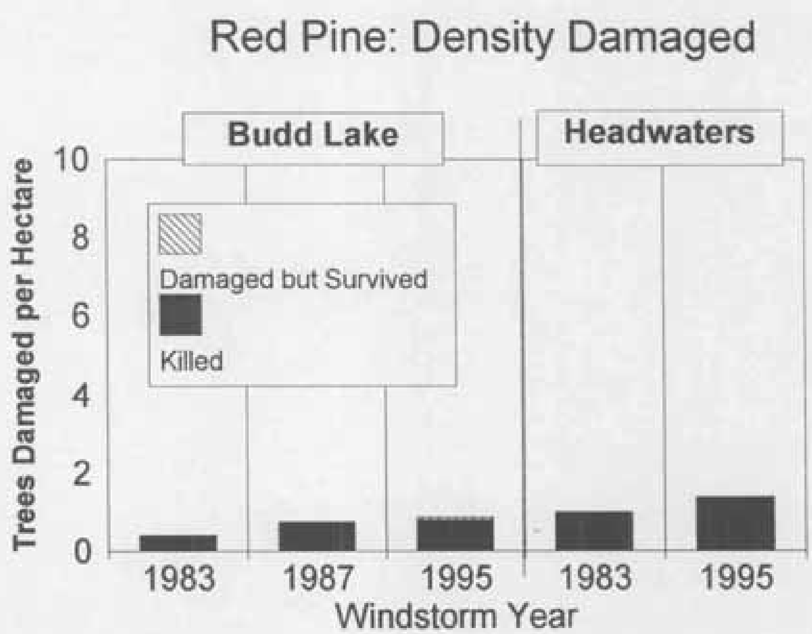


Figure 6.
Red pine, % of trees damaged , for both sites and all windstorm surveys.

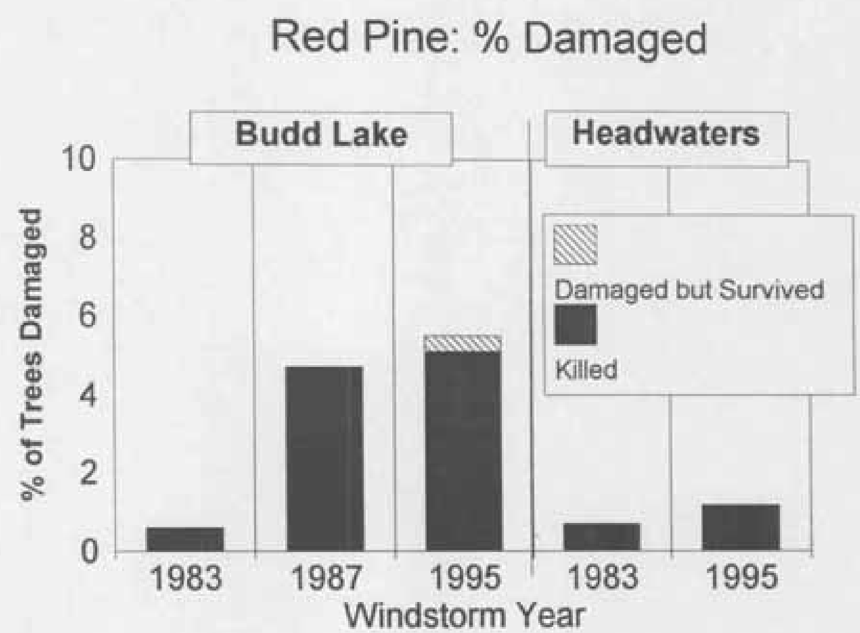


Figure 7. White pine, damaged tree density (per hectare), for both sites and all windstorm surveys.

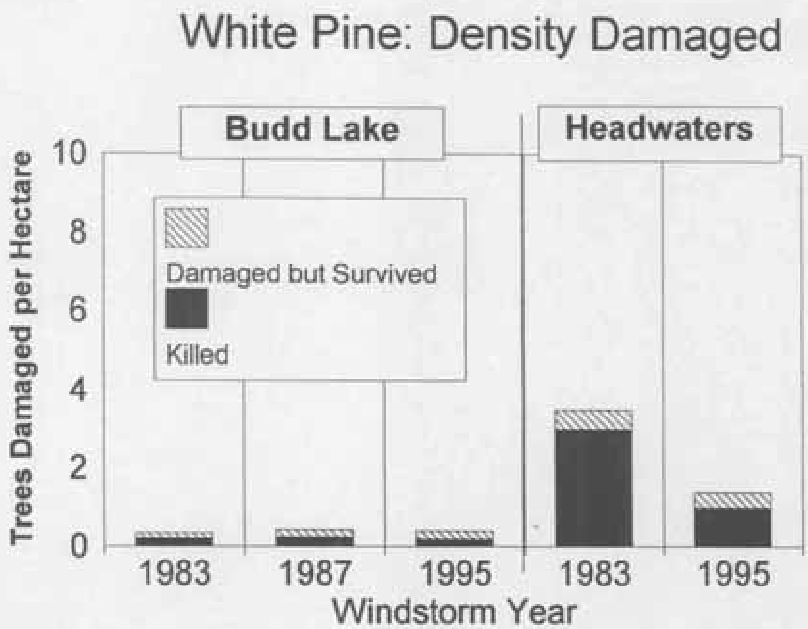


Figure 8. White pine, % of trees damaged, for both sites and all windstorm surveys.

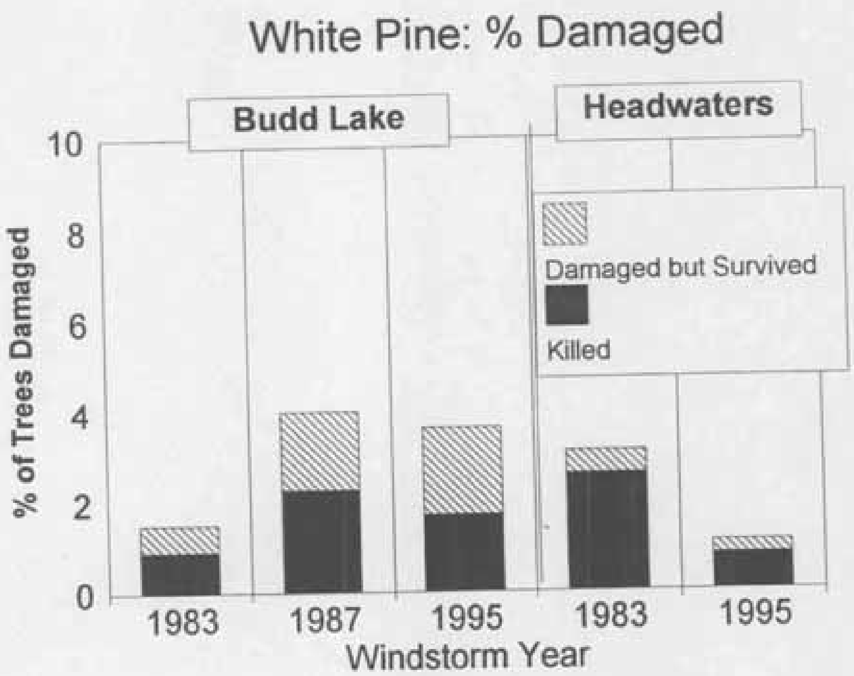


Figure 9. Aspen, damaged tree density (per hectare), for both sites and all windstorm surveys.

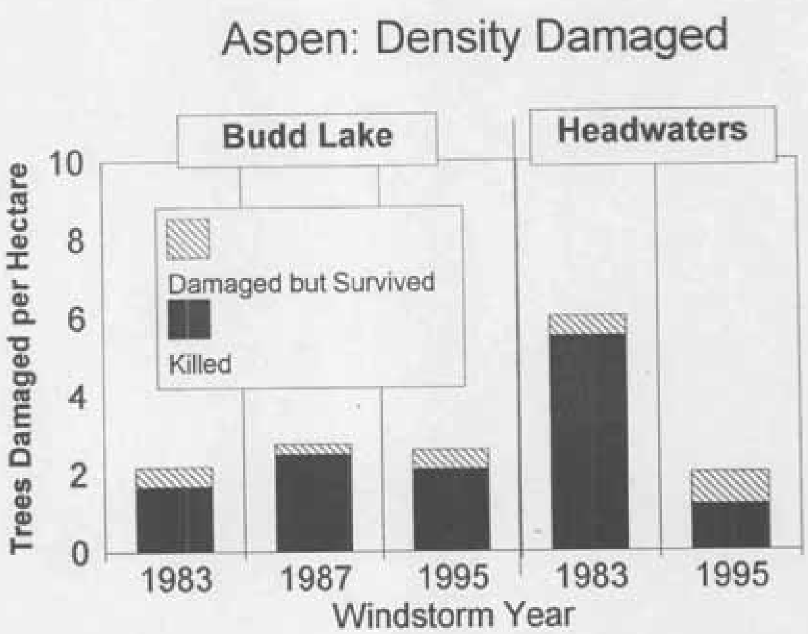


Figure 10. Aspen, % of trees damaged , for both sites and all windstorm surveys.

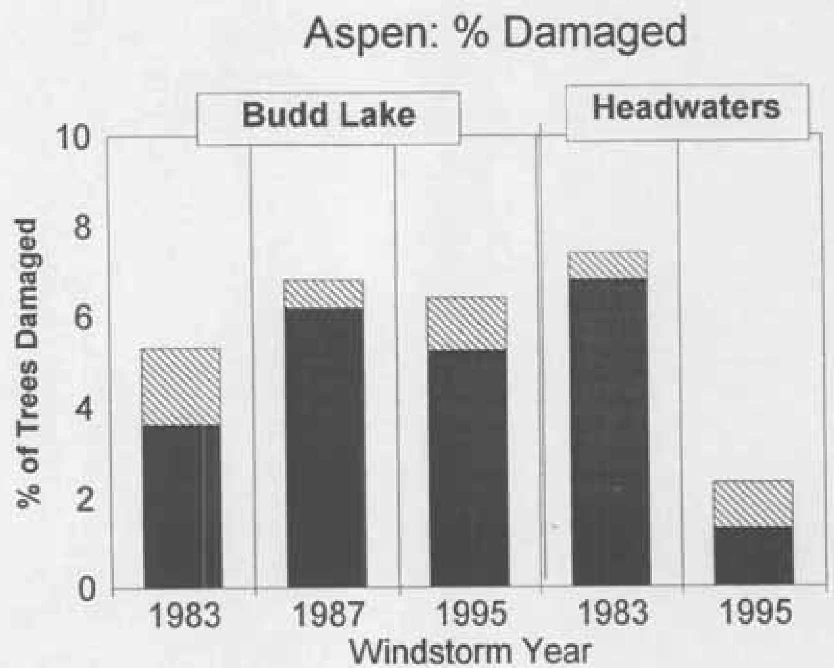


Figure 11. Paper birch, damaged tree density (per hectare), for both sites and all windstorm surveys.

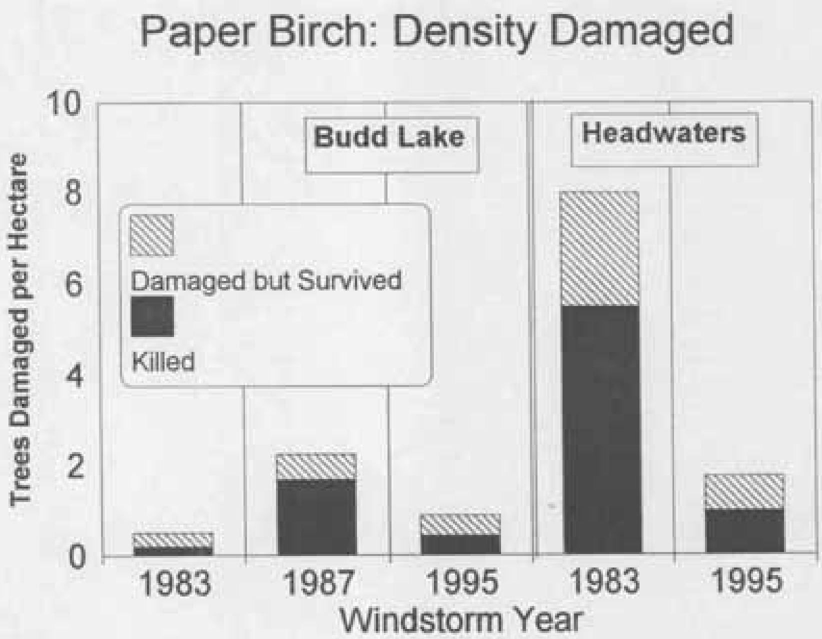


Figure 12. Paper birch, % of trees damaged, for both sites and all windstorm surveys.

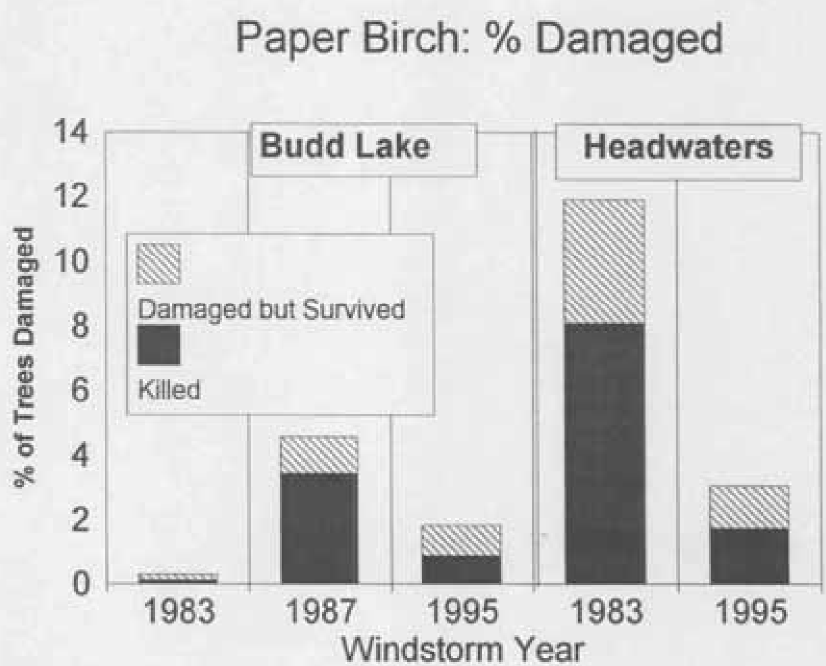


Figure 13. Sugar maple, damaged tree density (per hectare), Budd Lake, for all windstorm surveys.

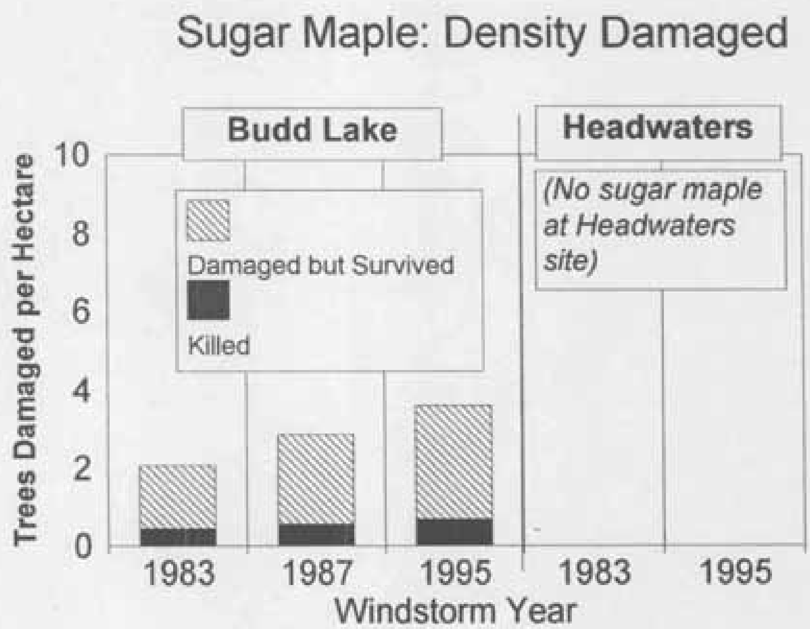


Figure 14. Sugar maple, % of trees damaged , Budd Lake, for all windstorm surveys.

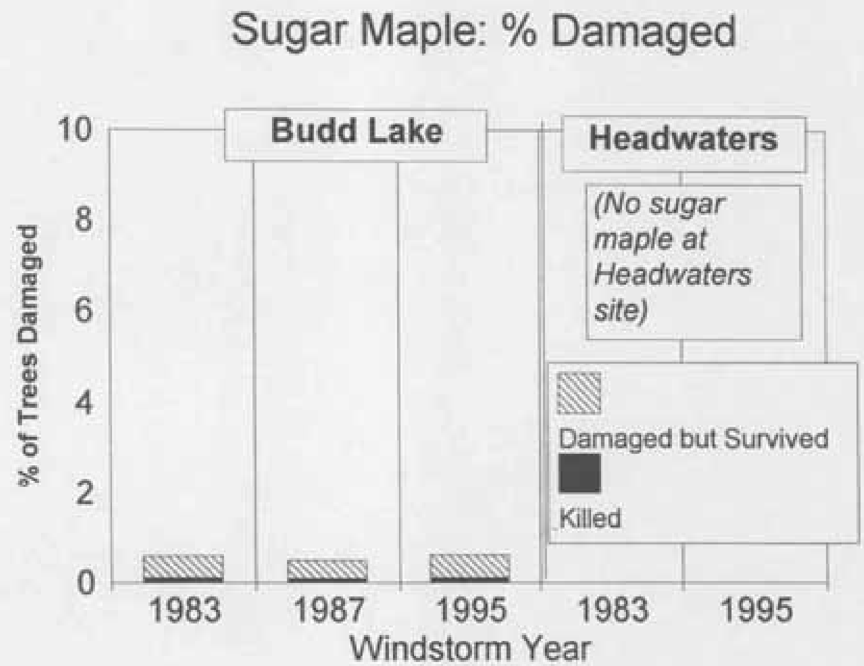


Figure 15. Red maple, damaged tree density (per hectare), for both sites and all windstorm surveys.

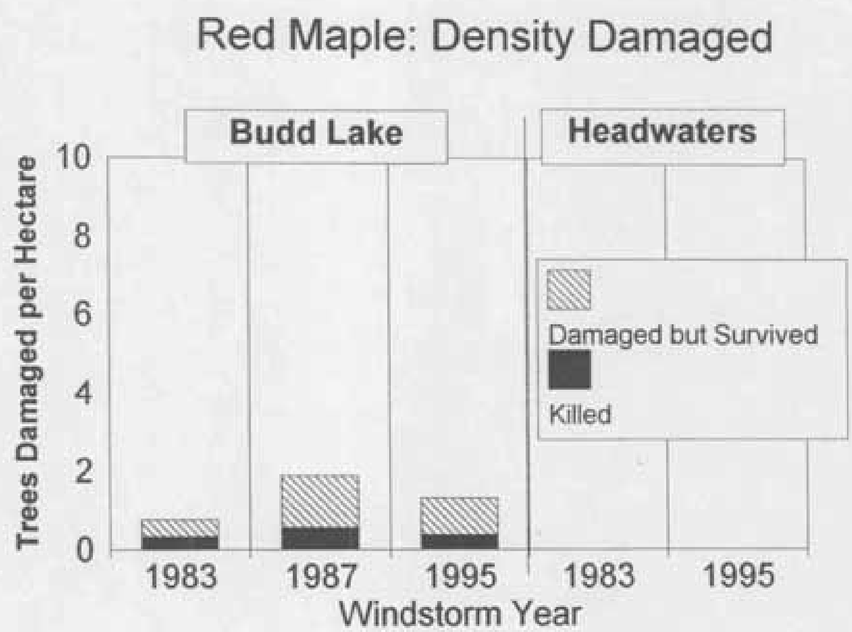


Figure 16. Red maple, % of trees damaged, for both sites and all windstorm surveys.

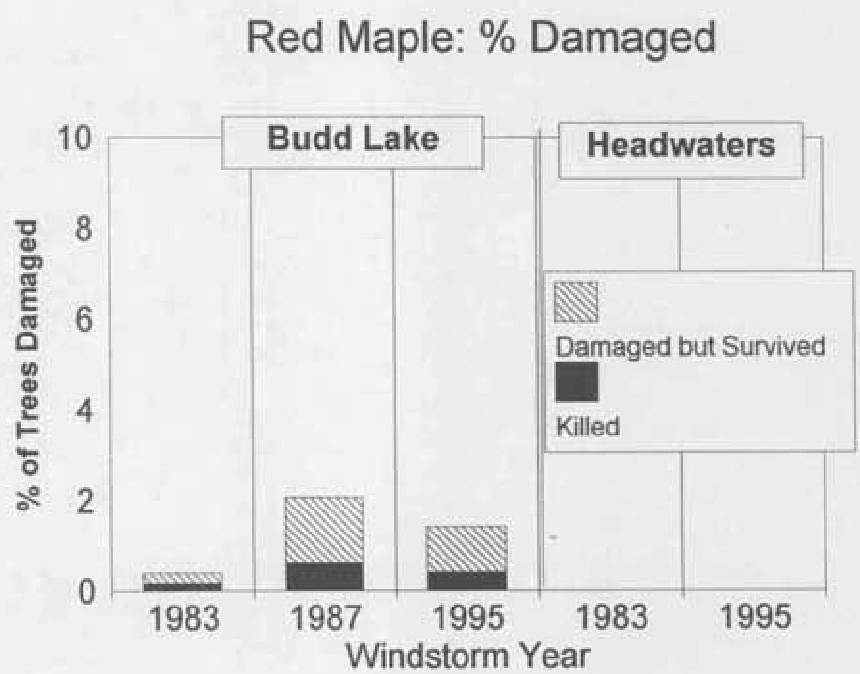


Figure 17. Ironwood, damaged tree density (per hectare), for both sites and all windstorm surveys.

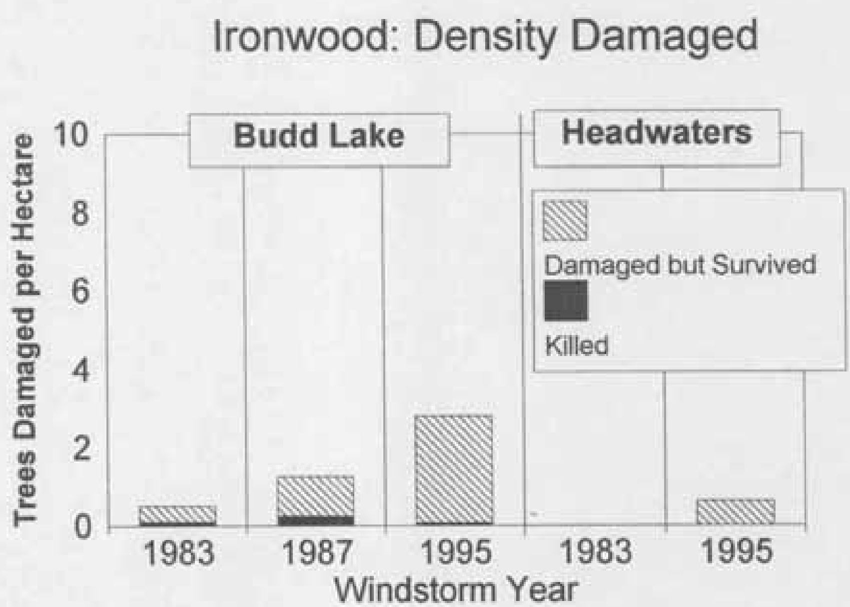


Figure 18. Ironwood, % of trees damaged, for both sites and all windstorm surveys.

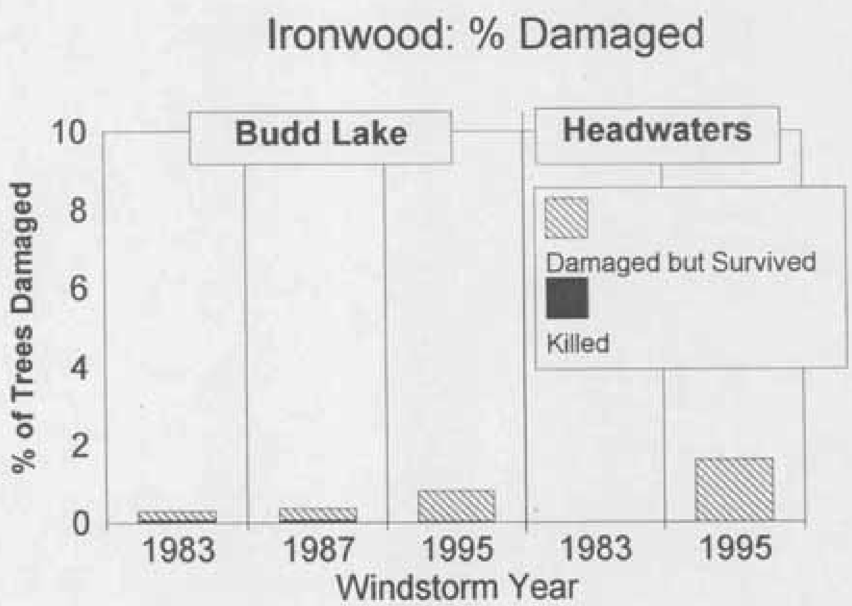


Figure 19. Red oak, damaged tree density (per hectare), Budd Lake, for all windstorm surveys.

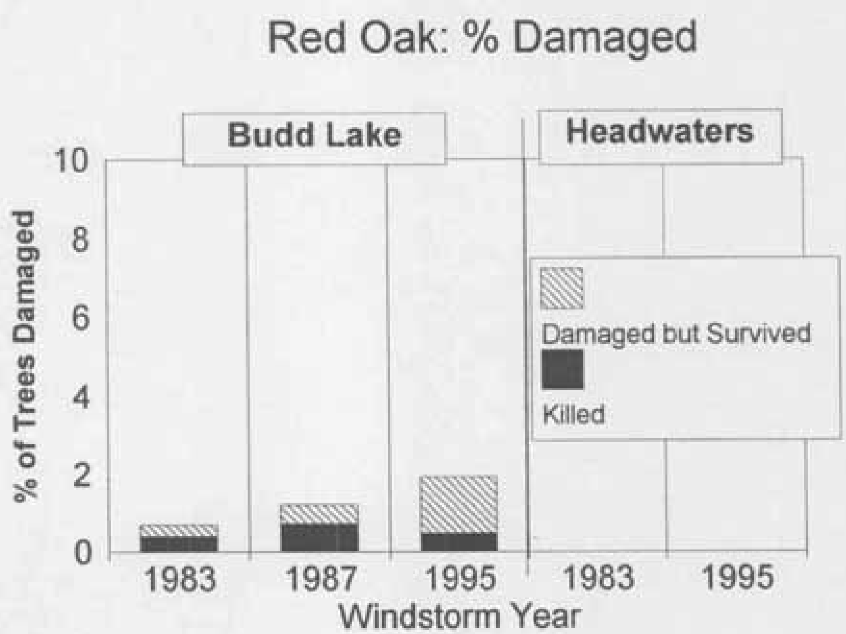


Figure 20. Red oak, % of trees damaged, Budd Lake, for all windstorm surveys.

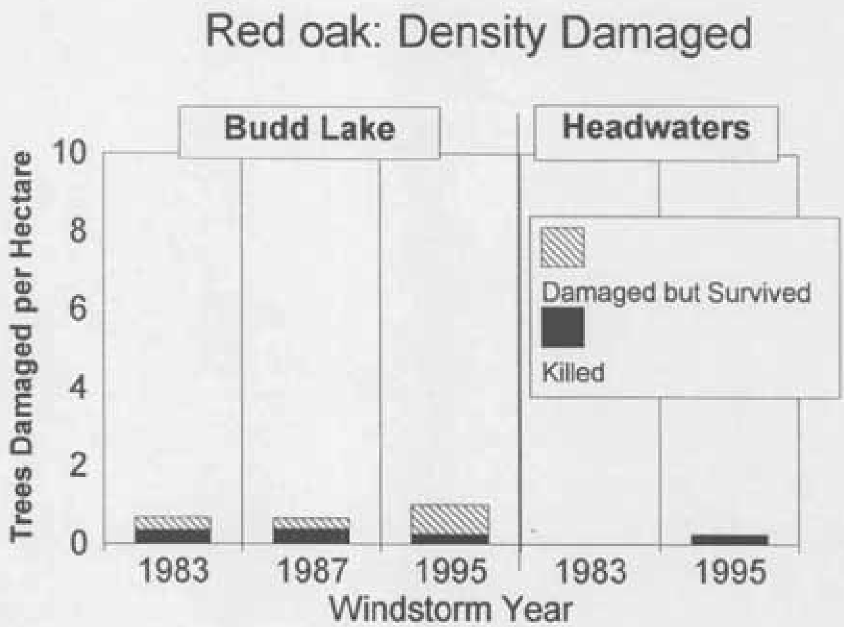


Figure 21. Balsam fir, damaged tree density (per hectare), Headwaters, for both windstorm surveys.

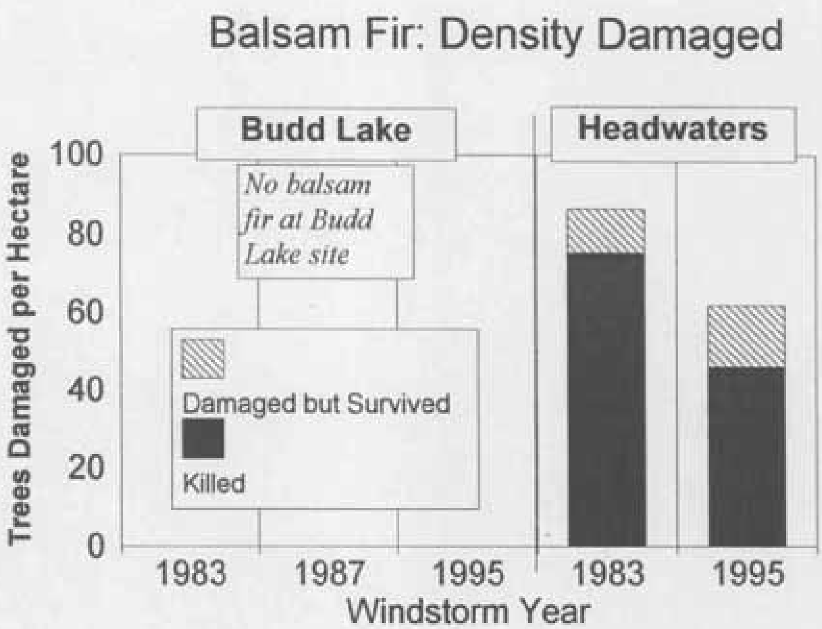


Figure 22. Balsam fir, % of trees damaged, Headwaters, for both windstorm surveys.

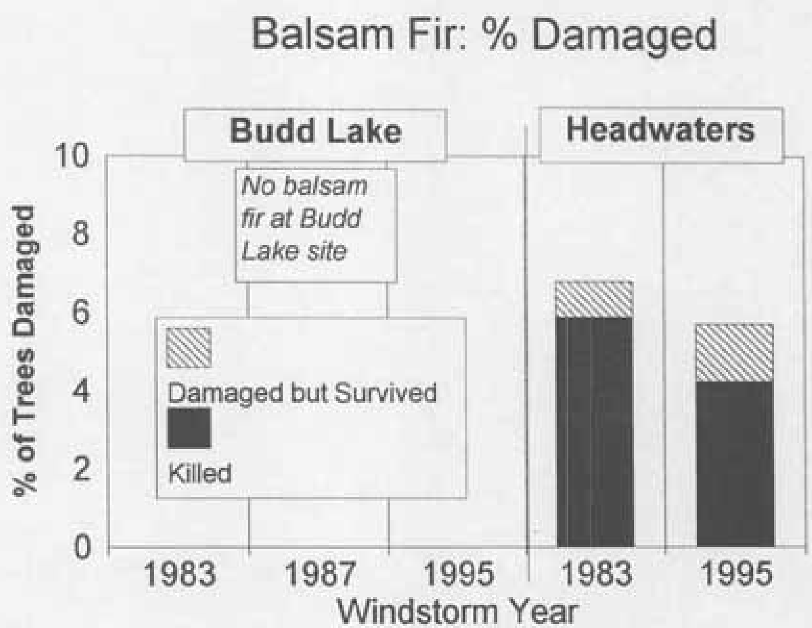


Figure 23. White spruce, damaged tree density (per hectare), Headwaters, for both windstorm surveys.

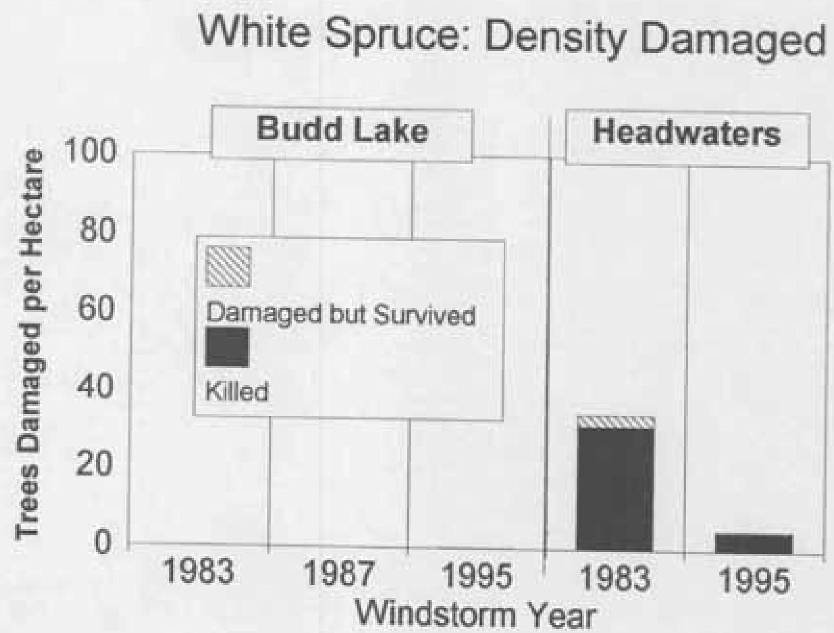


Figure 24. White spruce, % of trees damaged, Headwaters, for both windstorm surveys.

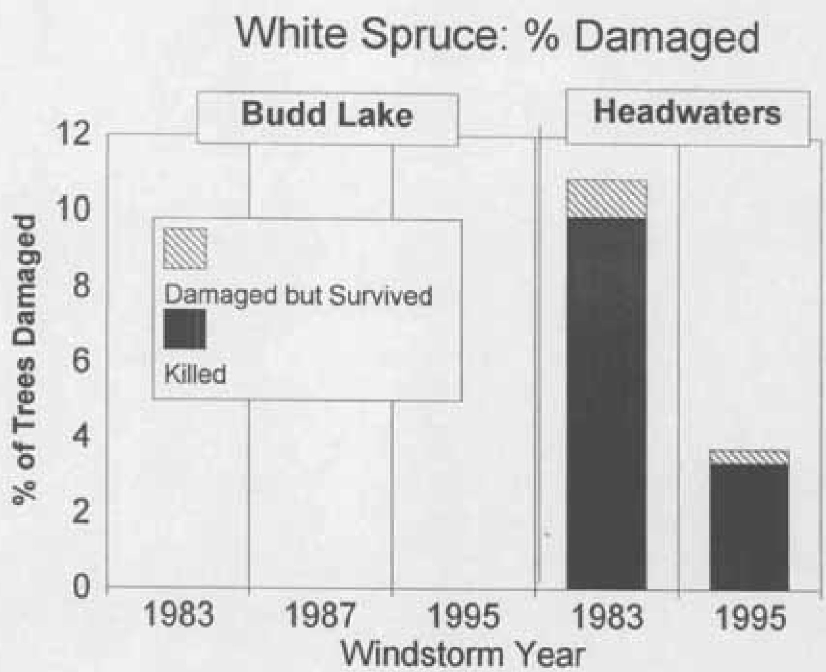


Figure 25

Red Pine, Budd Lake Forest, 1995 Storm

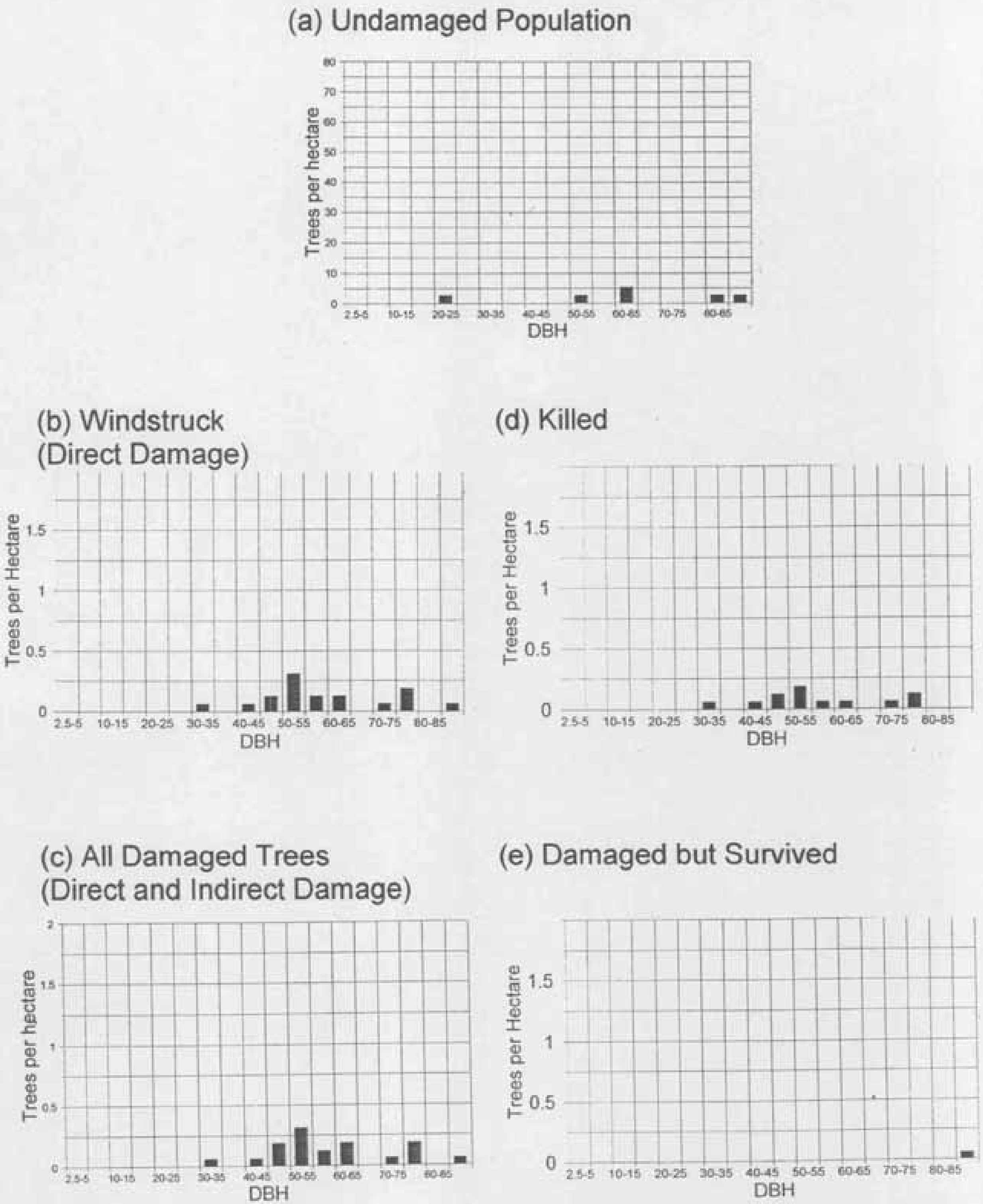
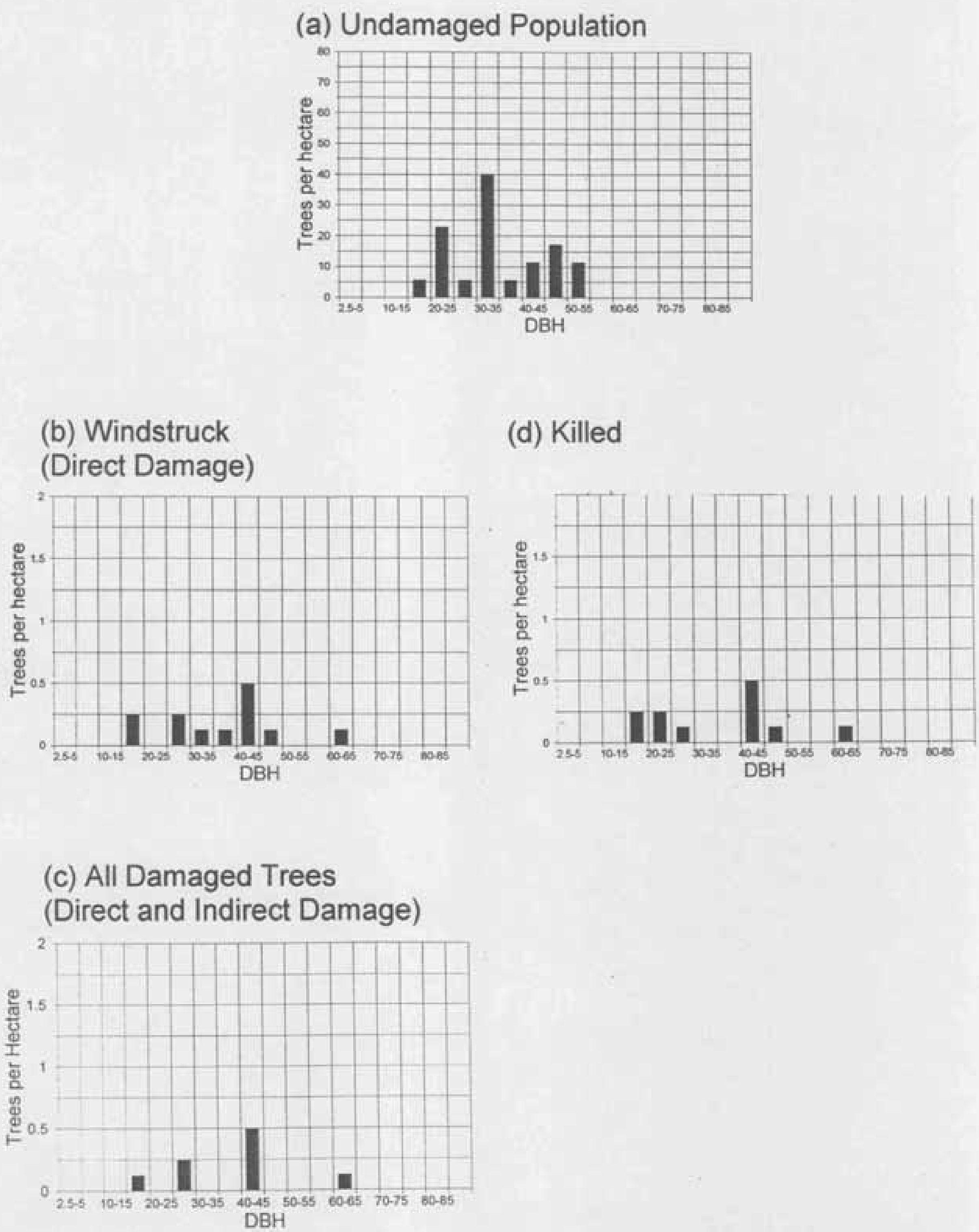


Figure 26

Red Pine, Headwaters Forest, 1995 Storm



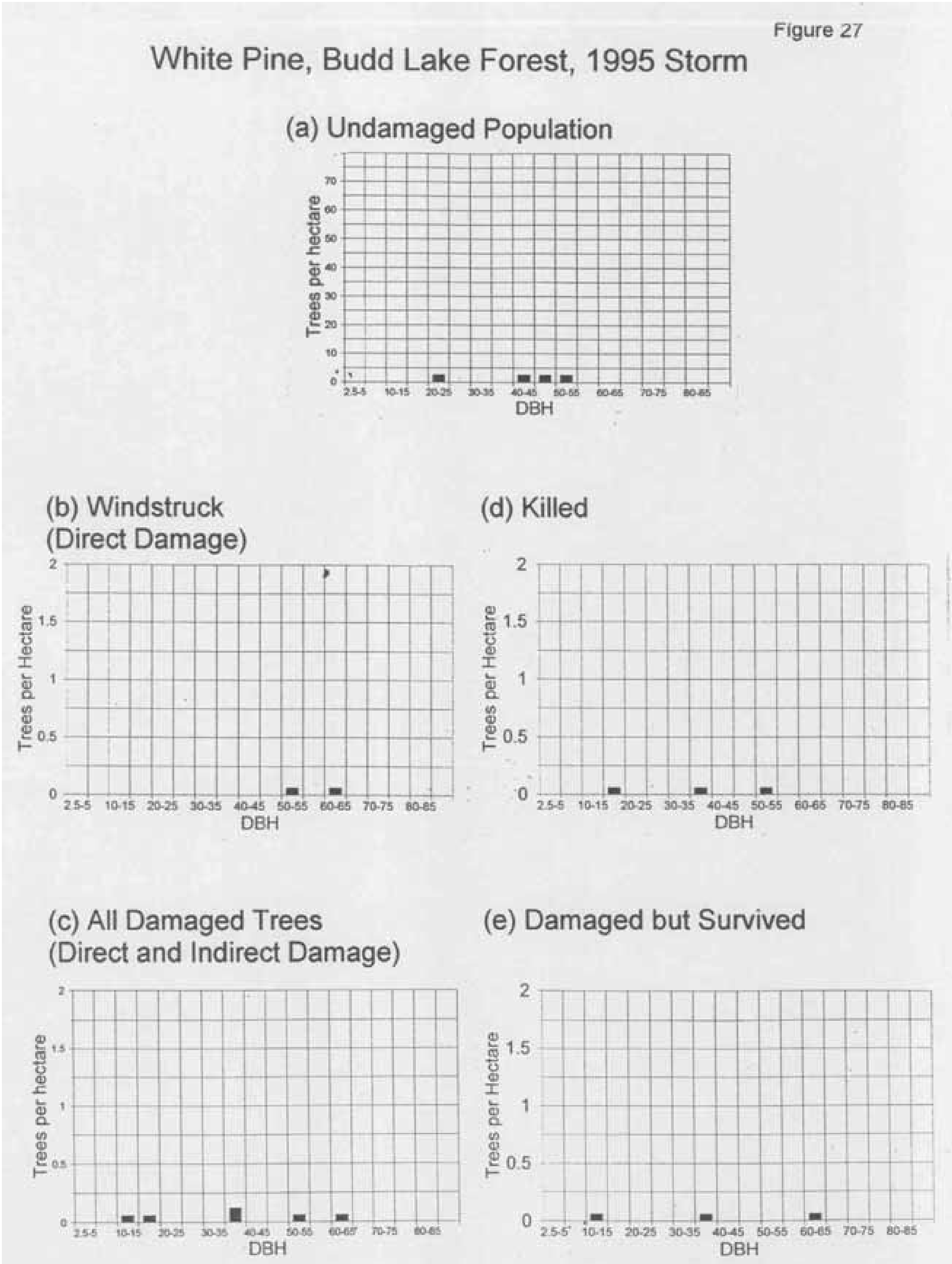


Figure 27
White Pine, Budd Lake Forest, 1995 Storm
(a) Undamaged Population
Trees per hectare
DBH
(b) Windstruck
(Direct Damage)
Trees per Hectare
DBH
(d) Killed
Trees per Hectare
DBH
(c) All Damaged Trees
(Direct and Indirect Damage)
Trees per hectare
DBH
(e) Damaged but Survived
Trees per Hectare
DBH

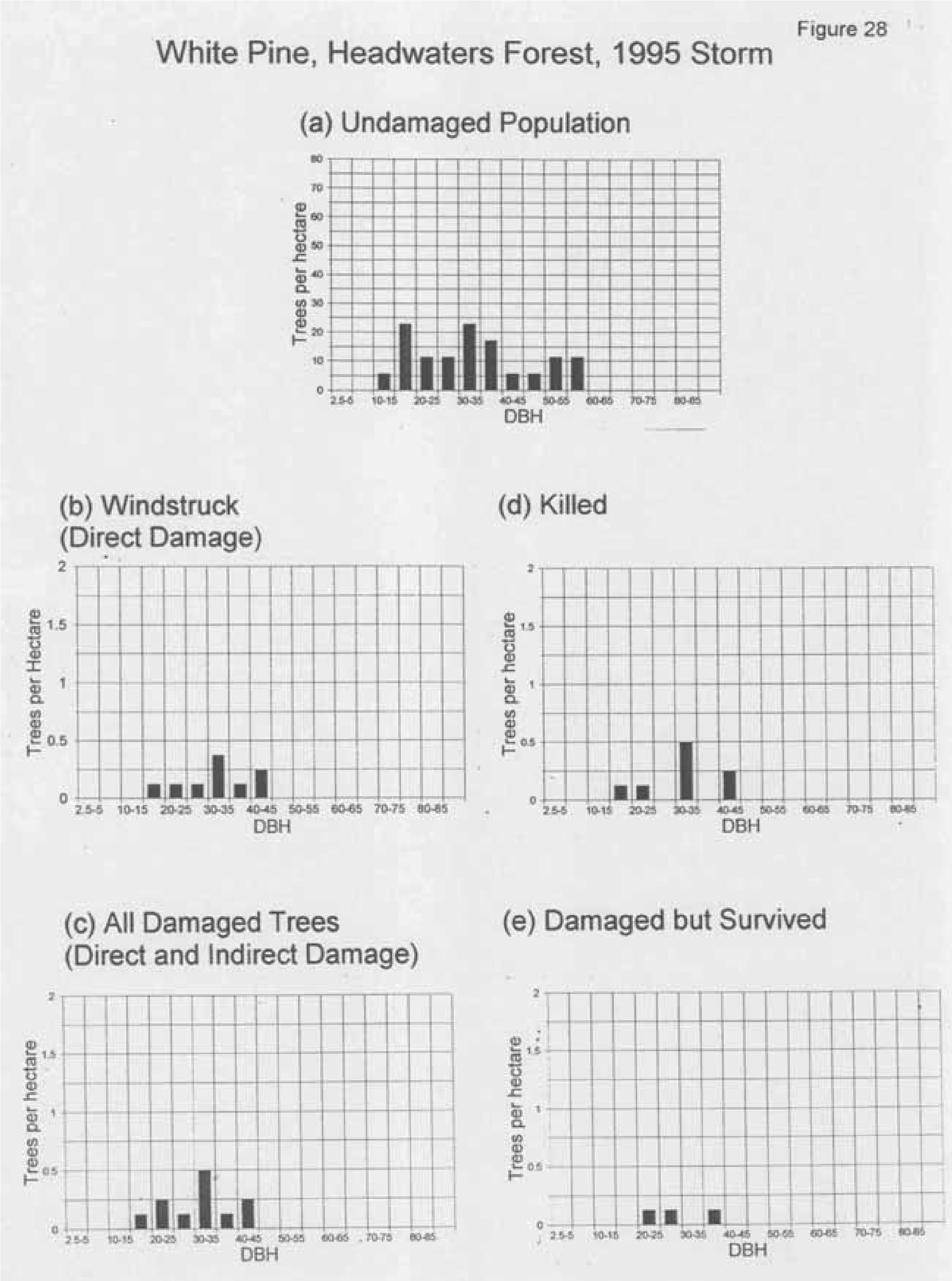


Figure 28
White Pine, Headwaters Forest, 1995 Storm
(a) Undamaged Population
Trees per hectare
DBH
2.5-5
10-15
20-25
30-35
40-45
50-55
60-65
70-75
80-85
(b) Windstruck
(Direct Damage)
Trees per Hectare
DBH
(d) Killed
Trees per hectare
DBH
(c) All Damaged Trees
(Direct and Indirect Damage)
Trees per hectare
DBH
(e) Damaged but Survived
Trees per hectare
DBH

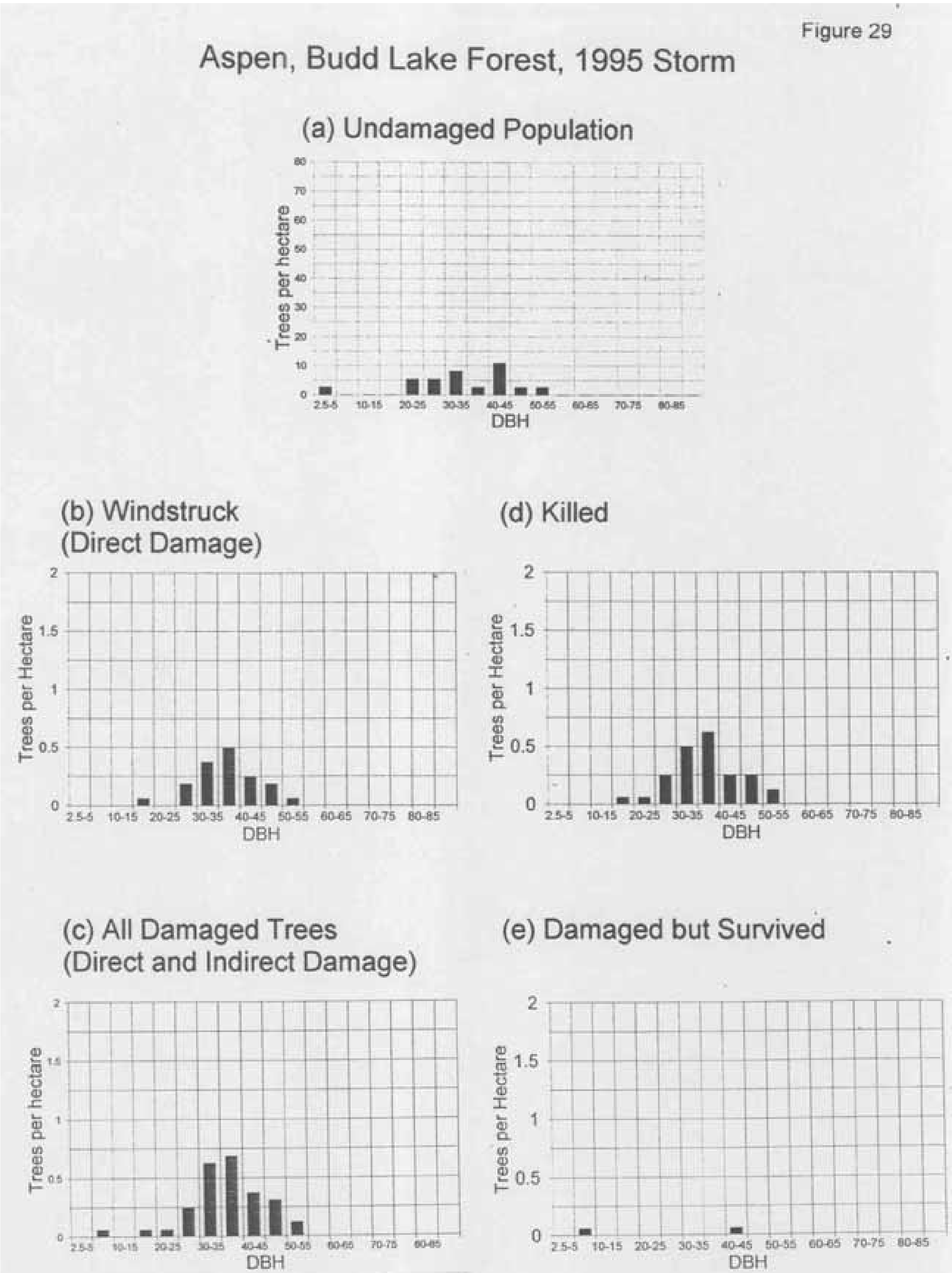


Figure 29
Aspen, Budd Lake Forest, 1995 Storm
(a) Undamaged Population
Trees per hectare
DBH
(b) Windstruck
(Direct Damage)
Trees per Hectare
DBH
(d) Killed
Trees per Hectare
DBH
(c) All Damaged Trees
(Direct and Indirect Damage)
Trees per hectare
DBH
(e) Damaged but Survived
Trees per Hectare
DBH

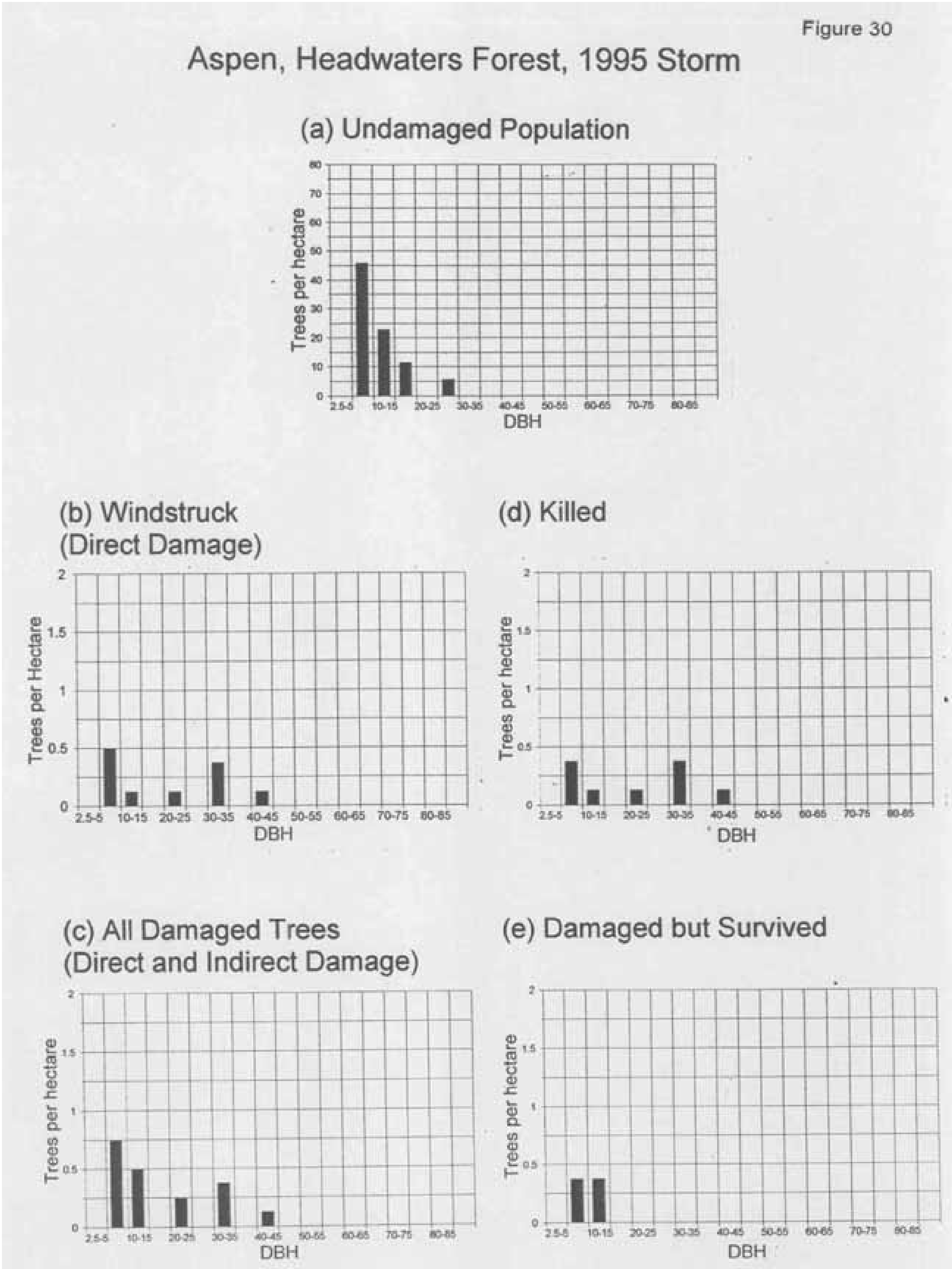


Figure 30
Aspen, Headwaters Forest, 1995 Storm
(a) Undamaged Population
Trees per hectare
DBH
2.5-5
10-15
20-25
30-35
40-45
50-55
60-65
70-75
80-85
(b) Windstruck
(Direct Damage)
Trees per Hectare
DBH
(d) Killed
Trees per hectare
DBH
(c) All Damaged Trees
(Direct and Indirect Damage)
Trees per hectare
DBH
(e) Damaged but Survived
Trees per hectare
DBH

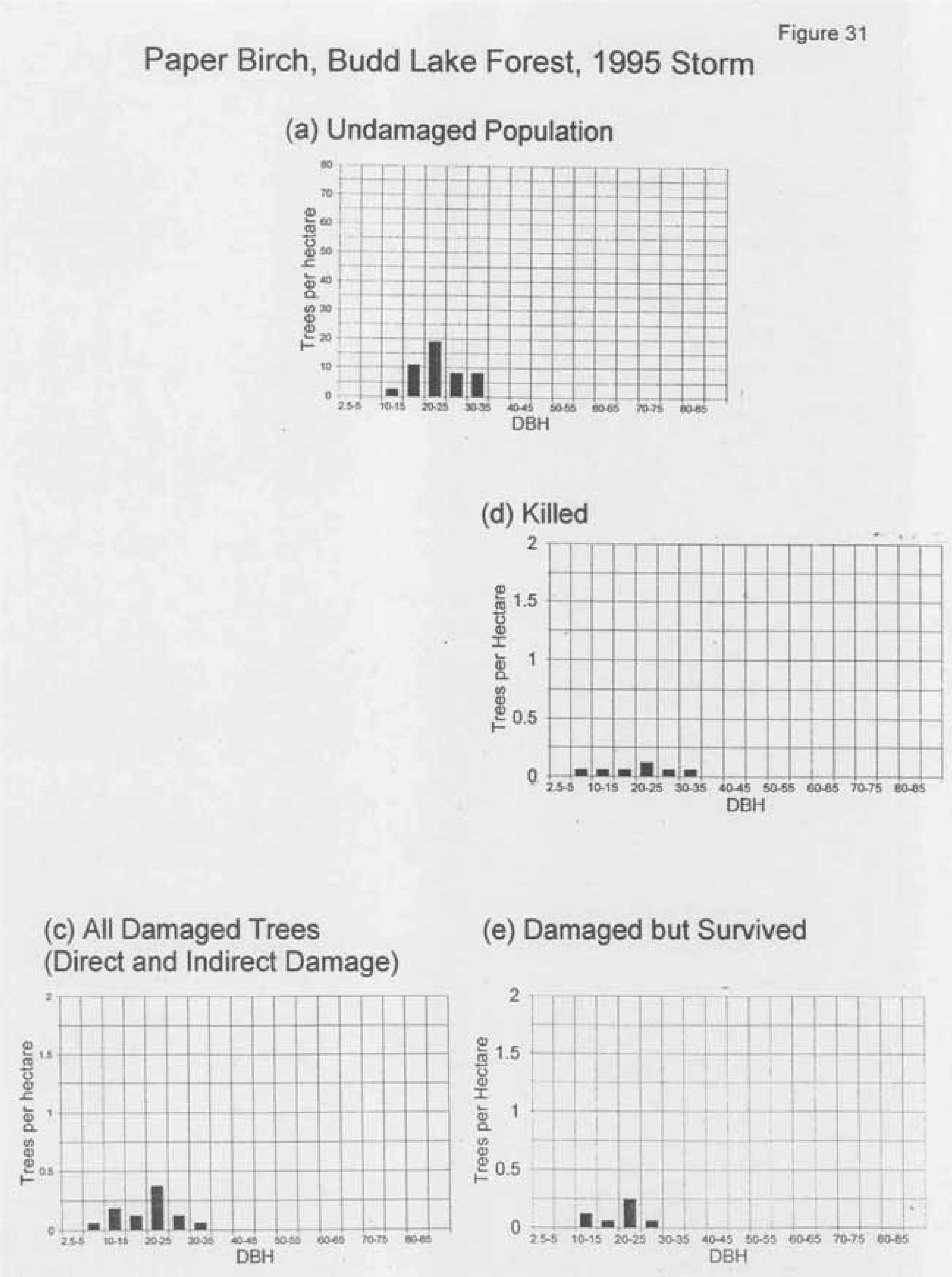


Figure 31
Paper Birch, Budd Lake Forest, 1995 Storm
(a) Undamaged Population
Trees per hectare
DBH
(d) Killed
Trees per Hectare
2.5-5
10-15
20-25
30-35
40-45
50-55
60-65
70-75
80-85
DBH
(c) All Damaged Trees
(Direct and Indirect Damage)
Trees per hectare
DBH
(e) Damaged but Survived
Trees per Hectare
2.5-5
10-15
20-25
30-35
40-45
50-55
60-65
70-75
80-85
DBH

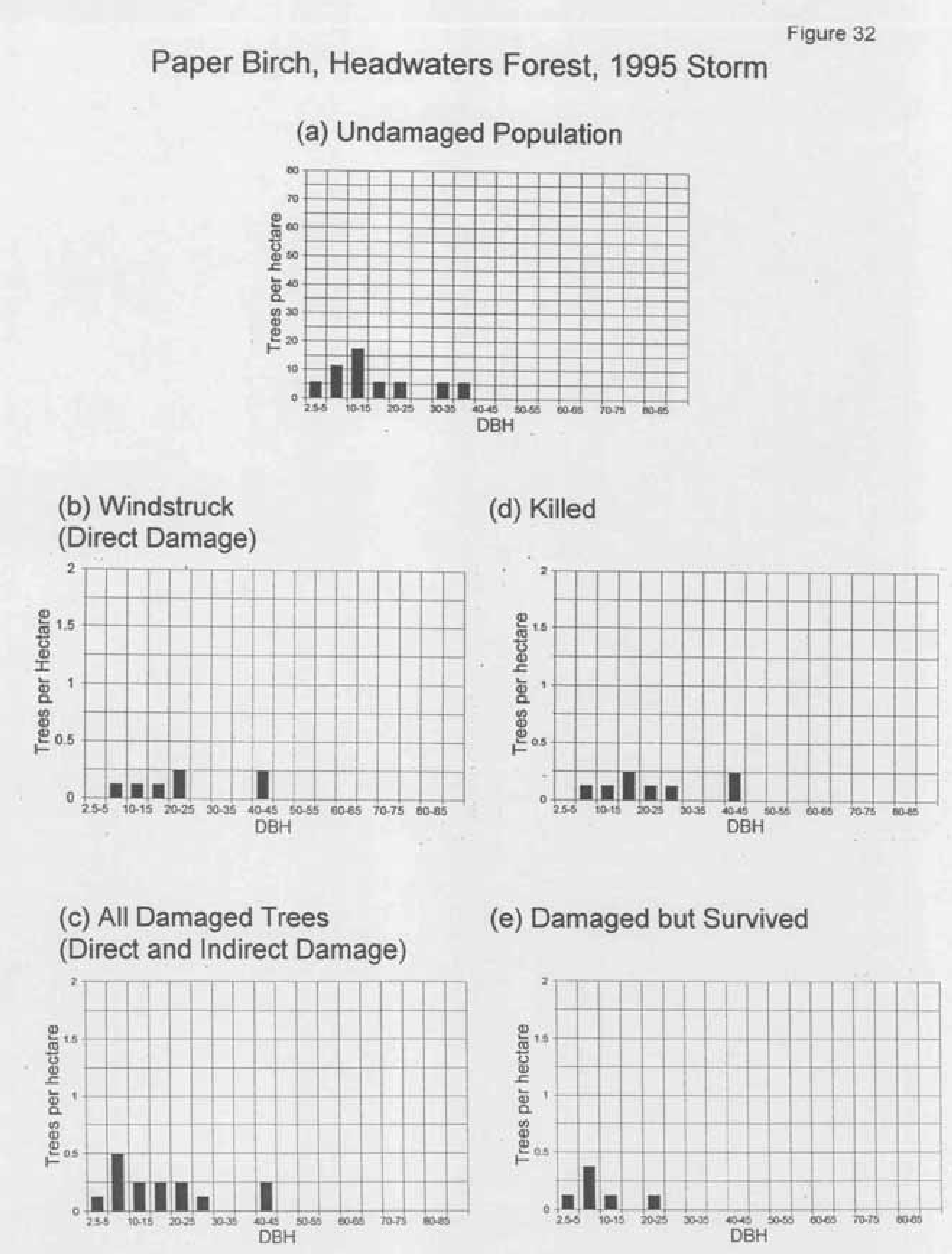
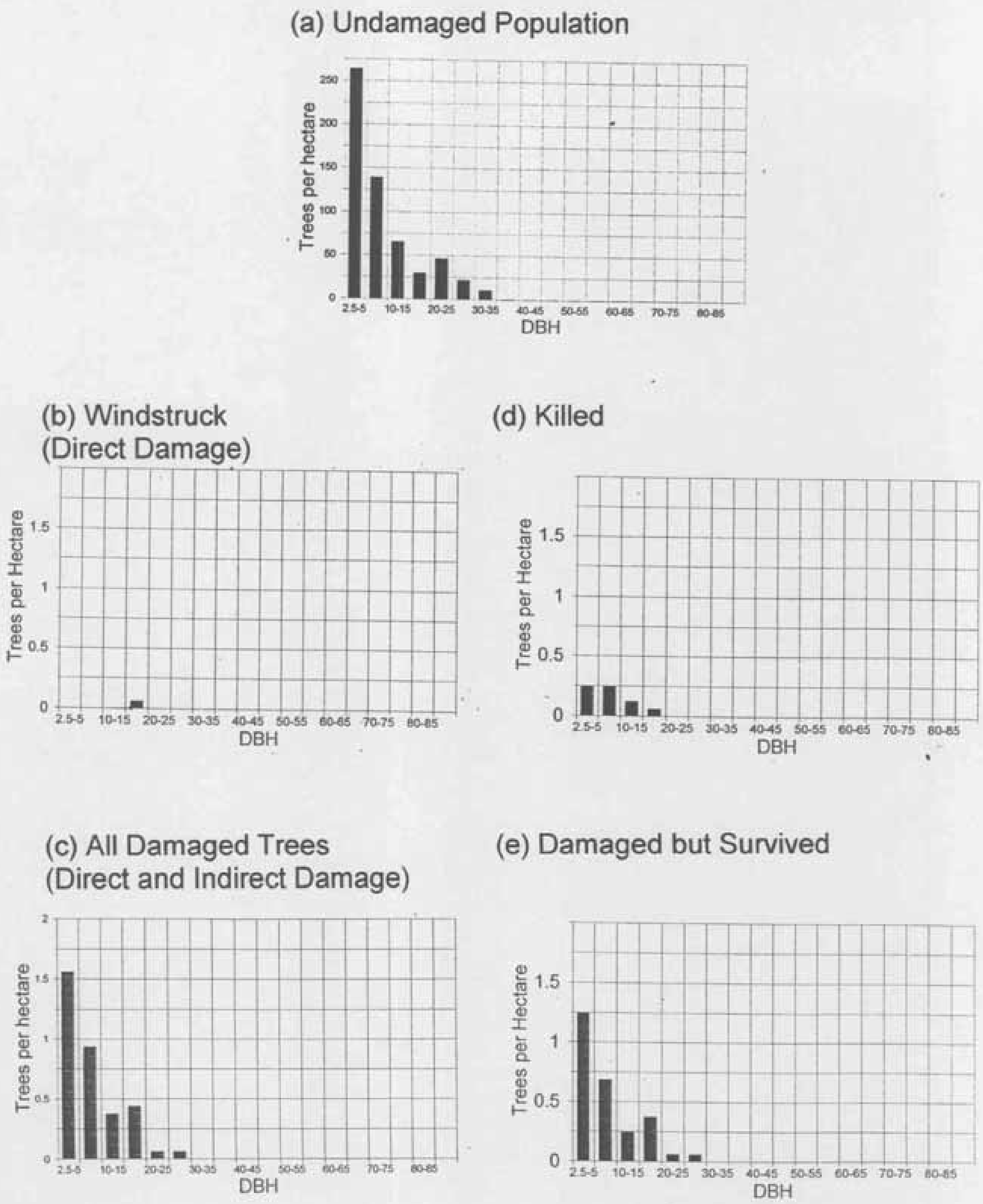


Figure 32
Paper Birch, Headwaters Forest, 1995 Storm
(a) Undamaged Population
Trees per hectare
DBH
(b) Windstruck
(Direct Damage)
Trees per Hectare
DBH
(d) Killed
Trees per hectare
DBH
(c) All Damaged Trees
(Direct and Indirect Damage)
Trees per hectare
DBH
(e) Damaged but Survived
Trees per hectare
DBH

Figure 33

Sugar Maple, Budd Lake Forest, 1995 Storm



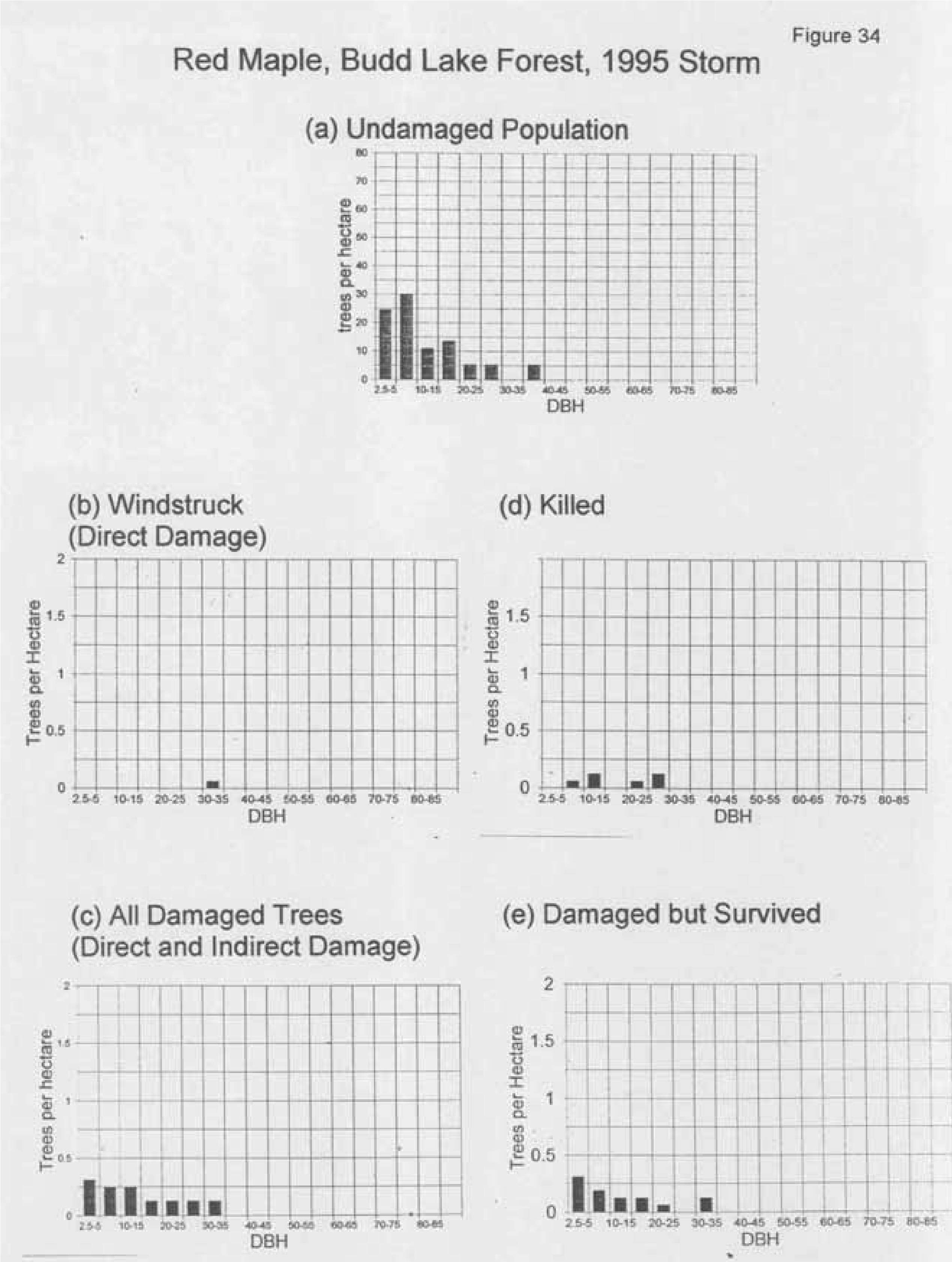
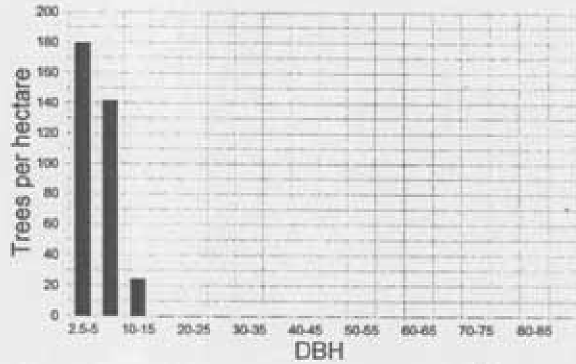


Figure 34
Red Maple, Budd Lake Forest, 1995 Storm
(a) Undamaged Population
trees per hectare
DBH
(b) Windstruck
(Direct Damage)
Trees per Hectare
DBH
(d) Killed
Trees per Hectare
DBH
(c) All Damaged Trees
(Direct and Indirect Damage)
Trees per hectare
DBH
(e) Damaged but Survived
Trees per Hectare
DBH

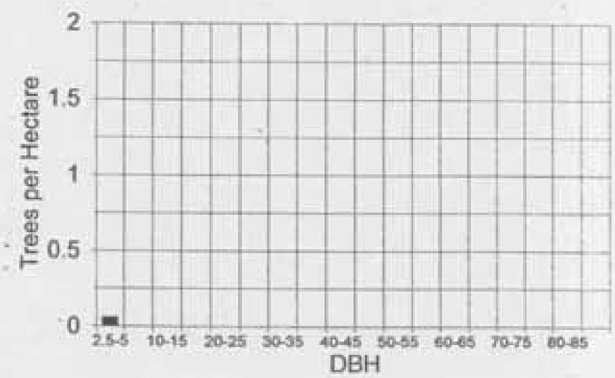
Figure 35

Ironwood, Budd Lake Forest, 1995 Storm

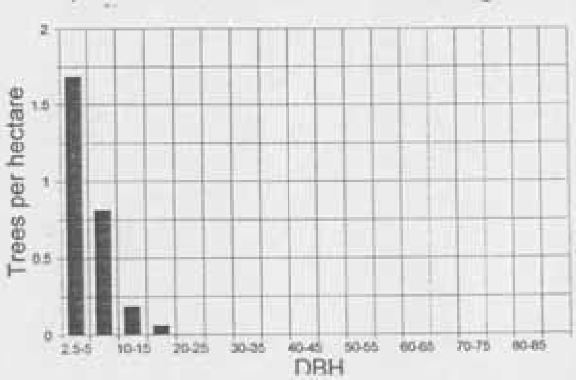
(a) Undamaged Population



(d) Killed



(c) All Damaged Trees (Direct and Indirect Damage)



(e) Damaged but Survived

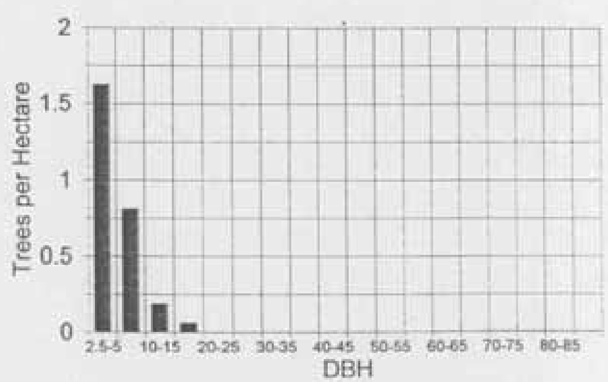


Figure 36

Red Oak, Budd Lake Forest, 1995 Storm

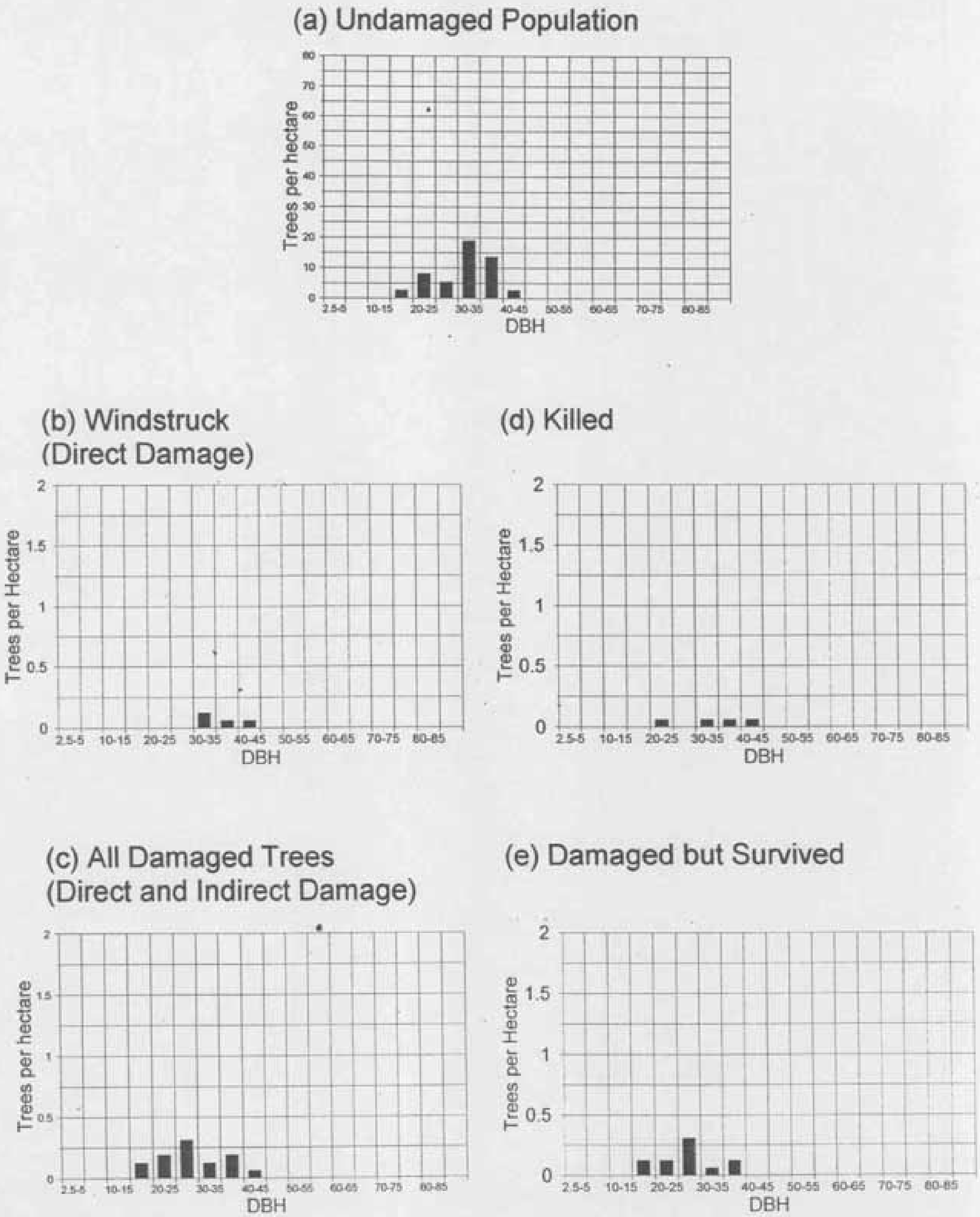
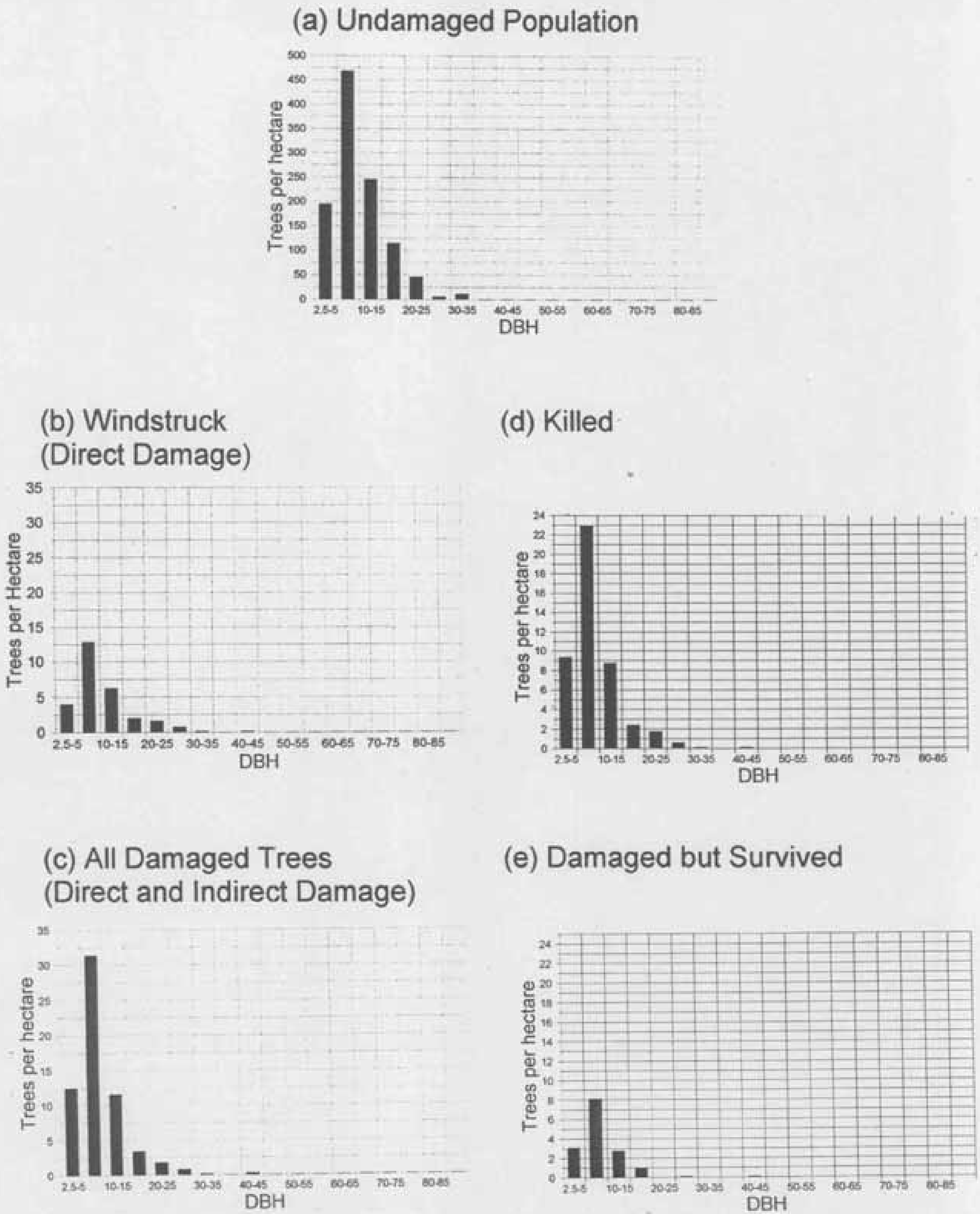


Figure 37

Balsam Fir, Headwaters Forest, 1995 Storm



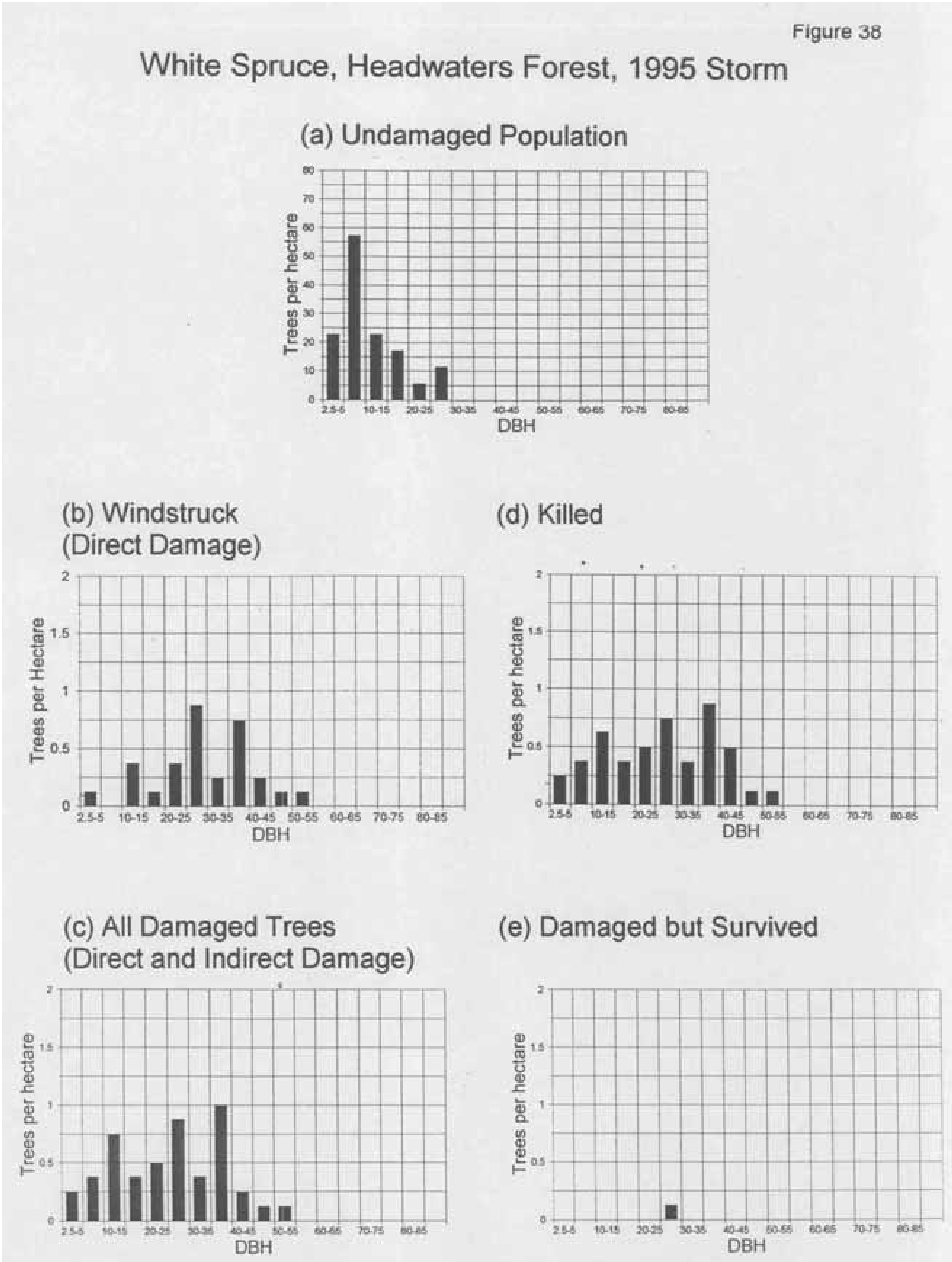
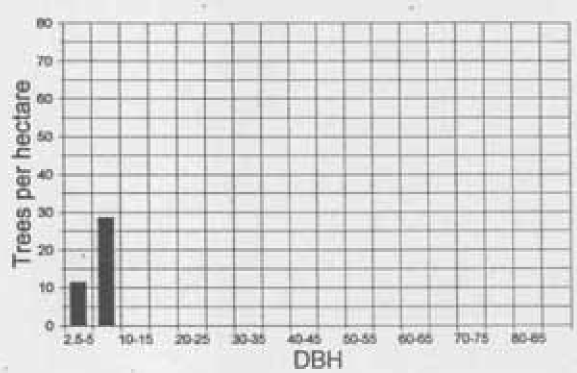


Figure 38
White Spruce, Headwaters Forest, 1995 Storm
(a) Undamaged Population
Trees per hectare
DBH
(b) Windstruck (Direct Damage)
Trees per Hectare
2.5-5 10-15 20-25 30-35 40-45 50-55 60-65 70-75 80-85
DBH
(d) Killed
Trees per hectare
DBH
(c) All Damaged Trees (Direct and Indirect Damage)
Trees per hectare
DBH
(e) Damaged but Survived
Trees per hectare
DBH

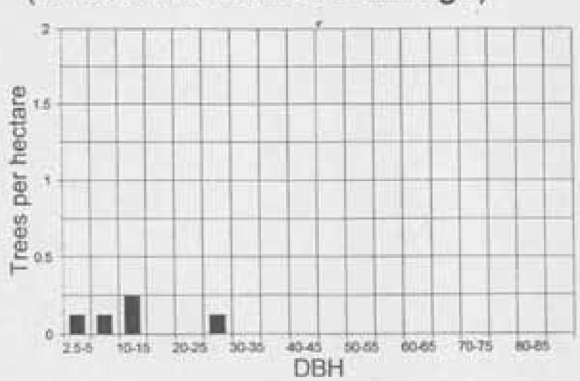
Figure 39

Ironwood, Headwaters Forest, 1995 Storm

(a) Undamaged Population



(c) All Damaged Trees (Direct and Indirect Damage)



(e) Damaged but Survived

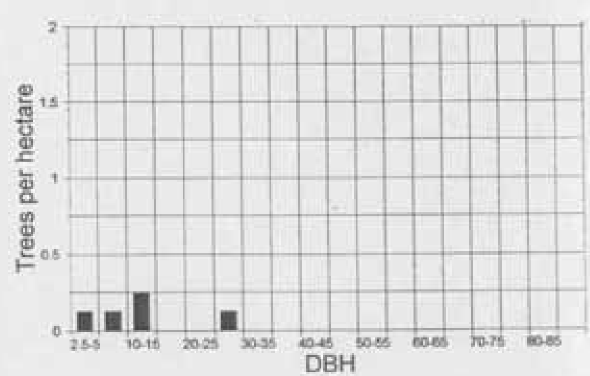


Figure 40. Richness in treefall and control plots over the 12 year period, for shrubs and trees. The richness of shrubs dropped significantly between 1984 and 1992; other changes were not significant, nor did treefall areas differ from control plots.

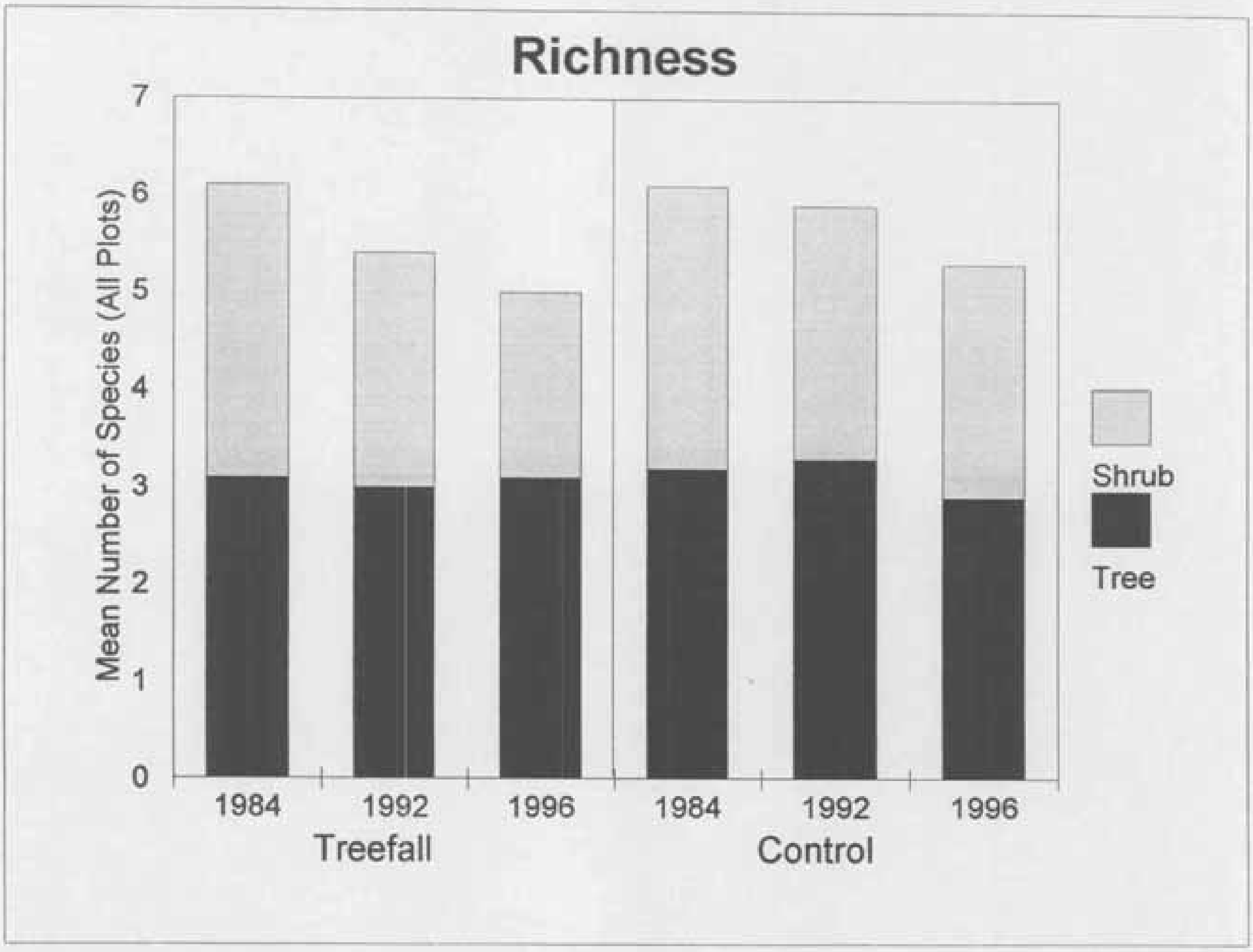


Figure 41. Sugar maple: changes in density in permanent plots over the 12 year period. Treefalls did not differ from control areas. However, small seedlings decreased significantly during both time periods, while tall seedlings increased significantly during the first 8 years.

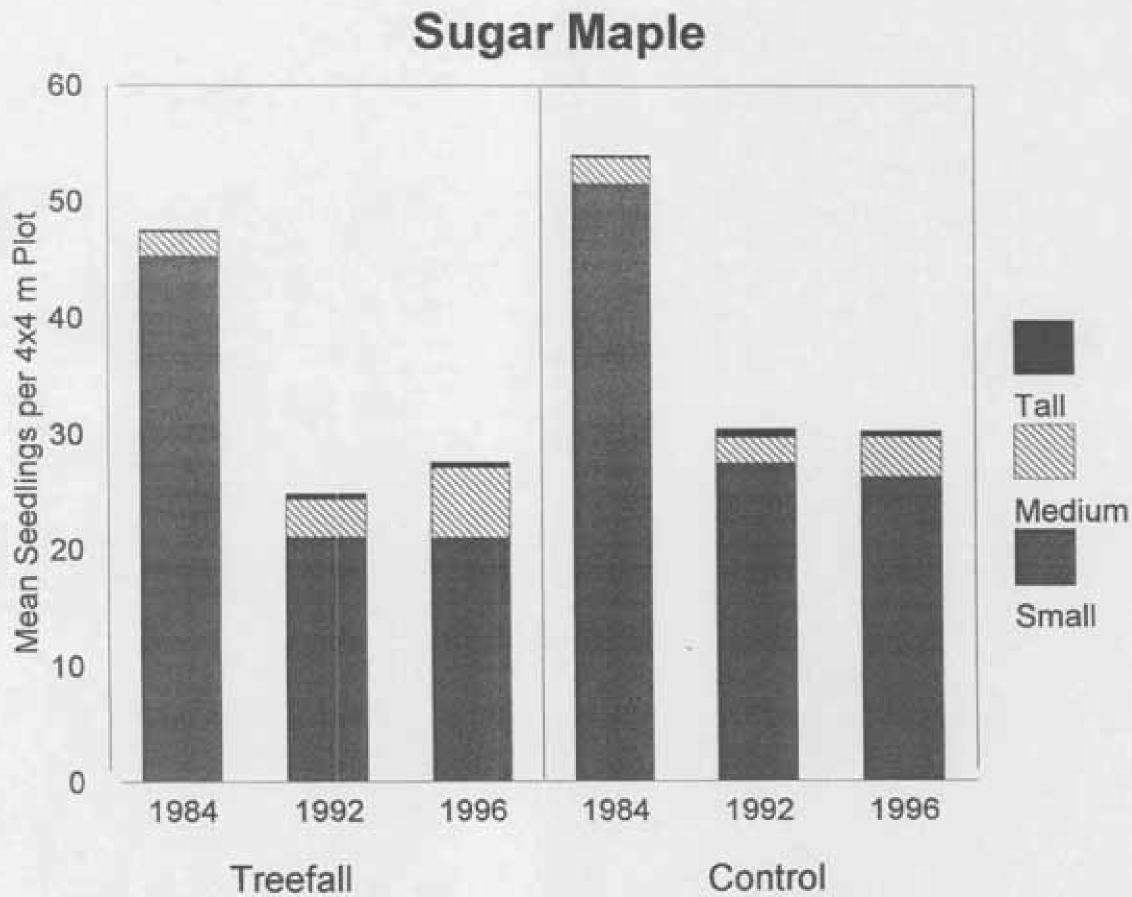


Figure 42. Red maple: changes in density in permanent plots over the 12 year period. Treefalls did not differ from control areas. However, during the first 8 years, small seedlings thinned out significantly while tall stems increased significantly in density. See also Figure 47 illustrating differences between base and crown plots.

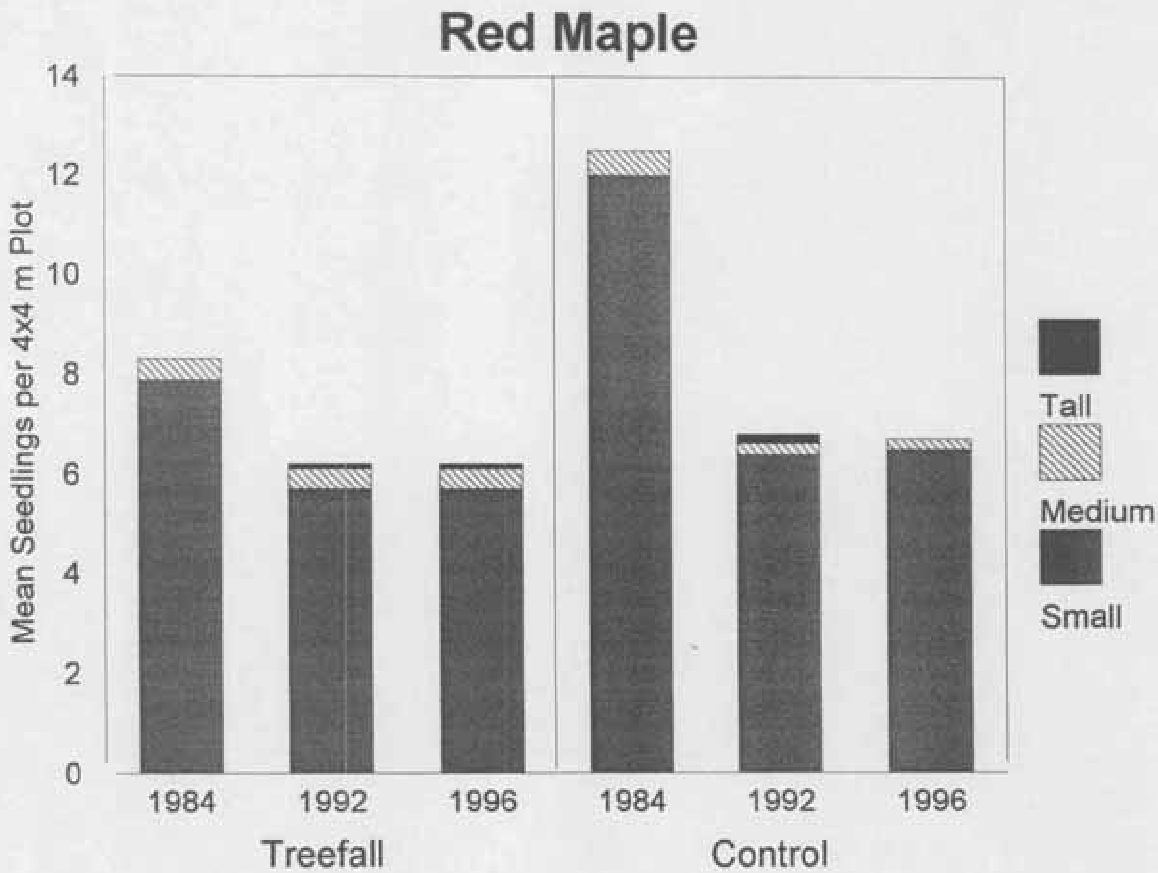


Figure 43. Blueberry densities in regeneration plots over the 12 year period. Densities of this dwarf shrub dropped during the first 8 years and again during the later 4 years of the study (statistical trend at P=0.07), but did not differ between treefall and control areas.

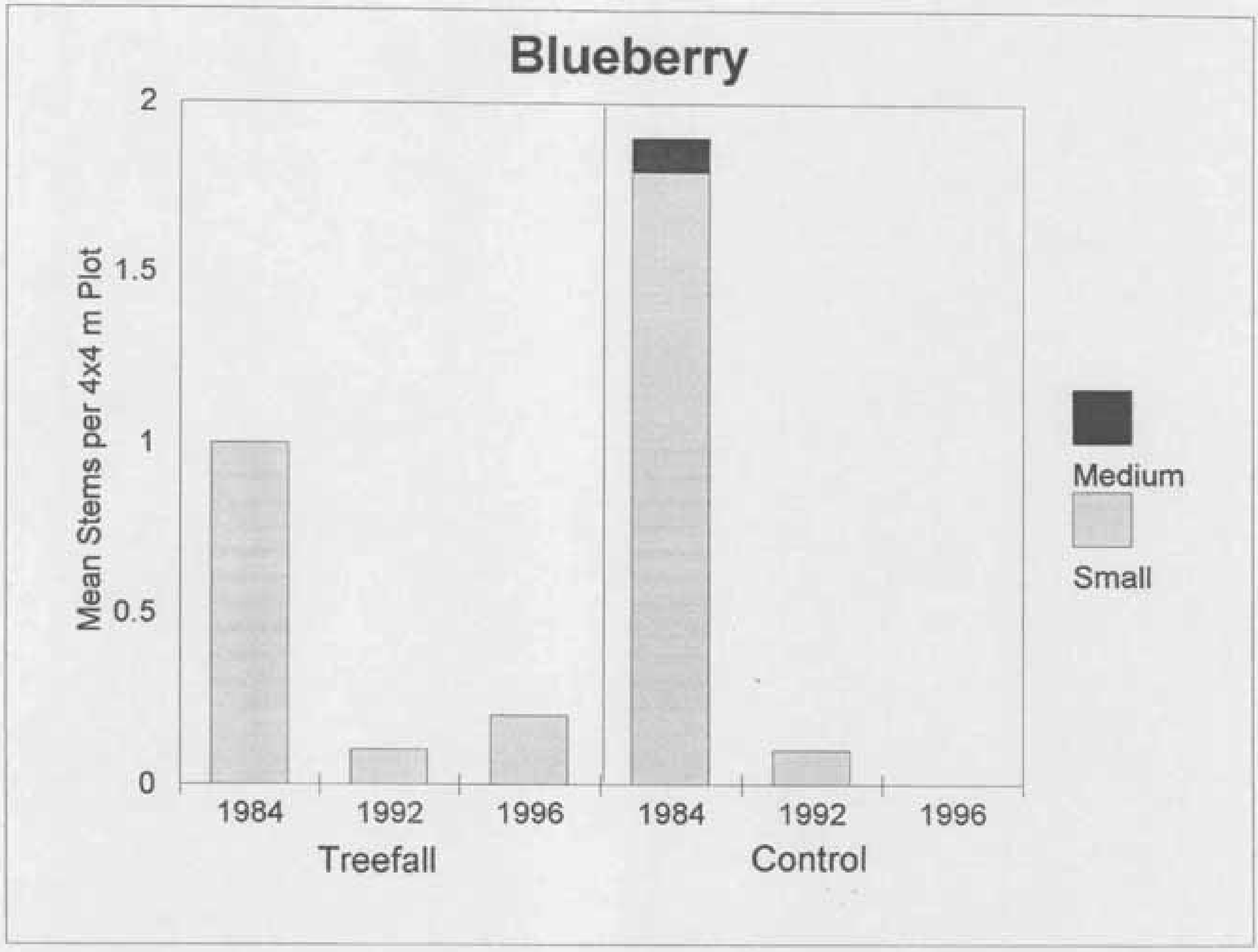


Figure 44. Ironwood densities in regeneration plots over the 12 year period. Tall stems increased significantly during the first 8 years of the 12 year study. Treefalls did not differ significantly from control areas.

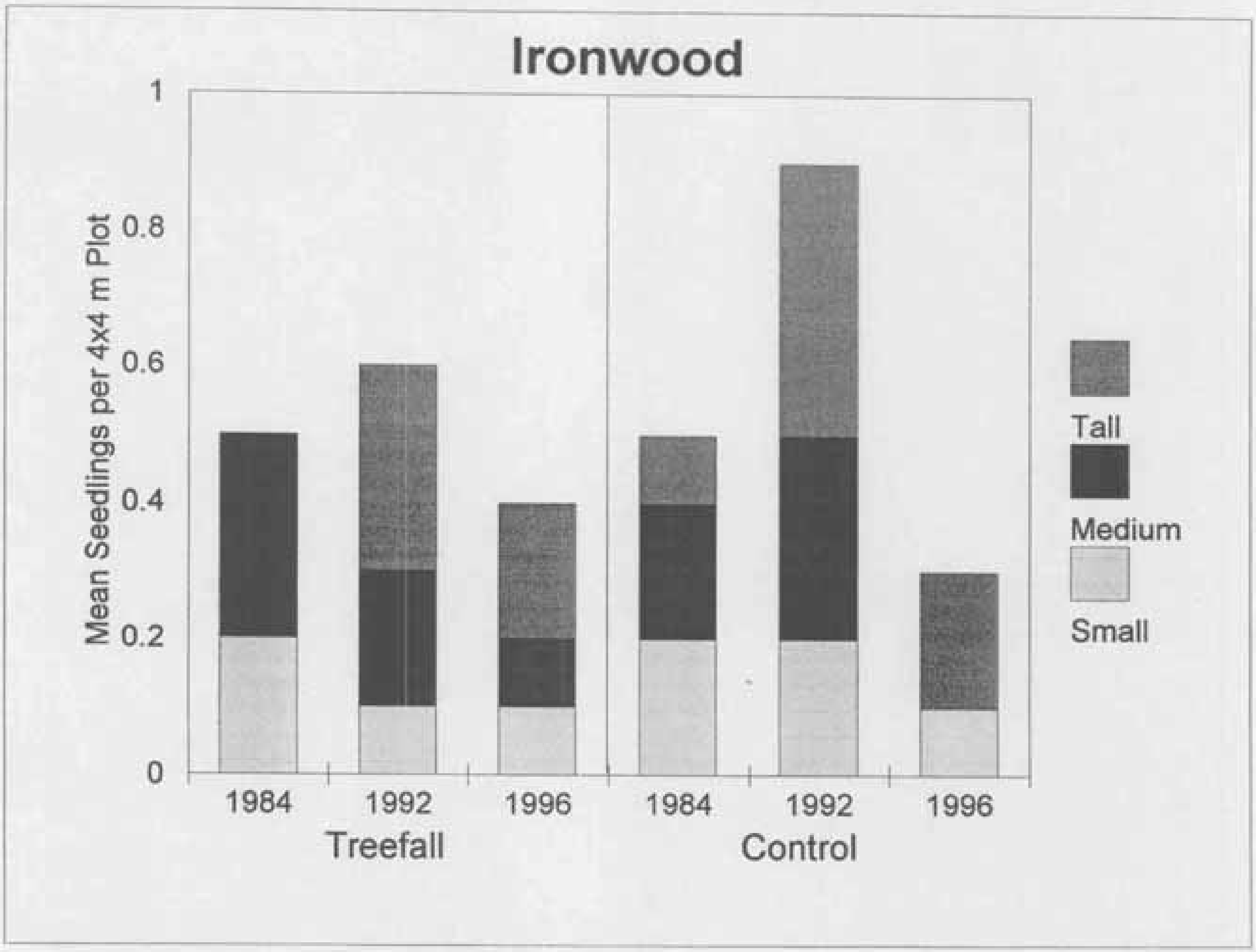


Figure 45. Shrub densities in regeneration plots over the 12 year period. Treefall and control areas did not differ. The graph suggests a decrease over time but this was not significant except for the medium size class when ubiquitous hazel is excluded from the analysis.

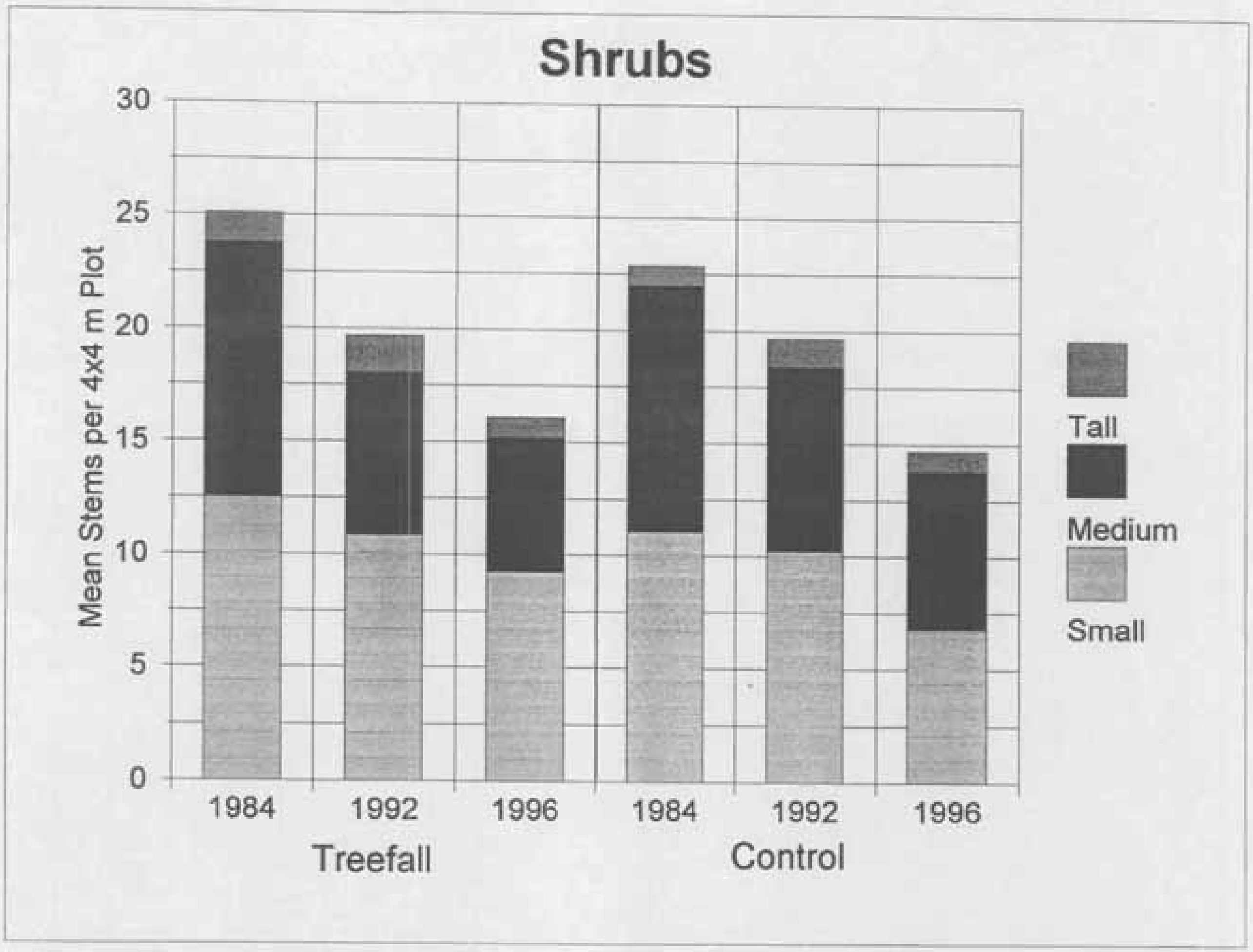


Figure 46. Trees excluding sugar maple and red maple, in regeneration plots over the 12 year period. Treefall and control areas did not differ. Unlike the maple seedlings which declined overall, small seedlings of other, shade-intolerant tree species increased during the last 4 years of the study. Species included in this sum were red oak, white pine, quaking aspen, paper birch, and (shade-tolerant) ironwood.

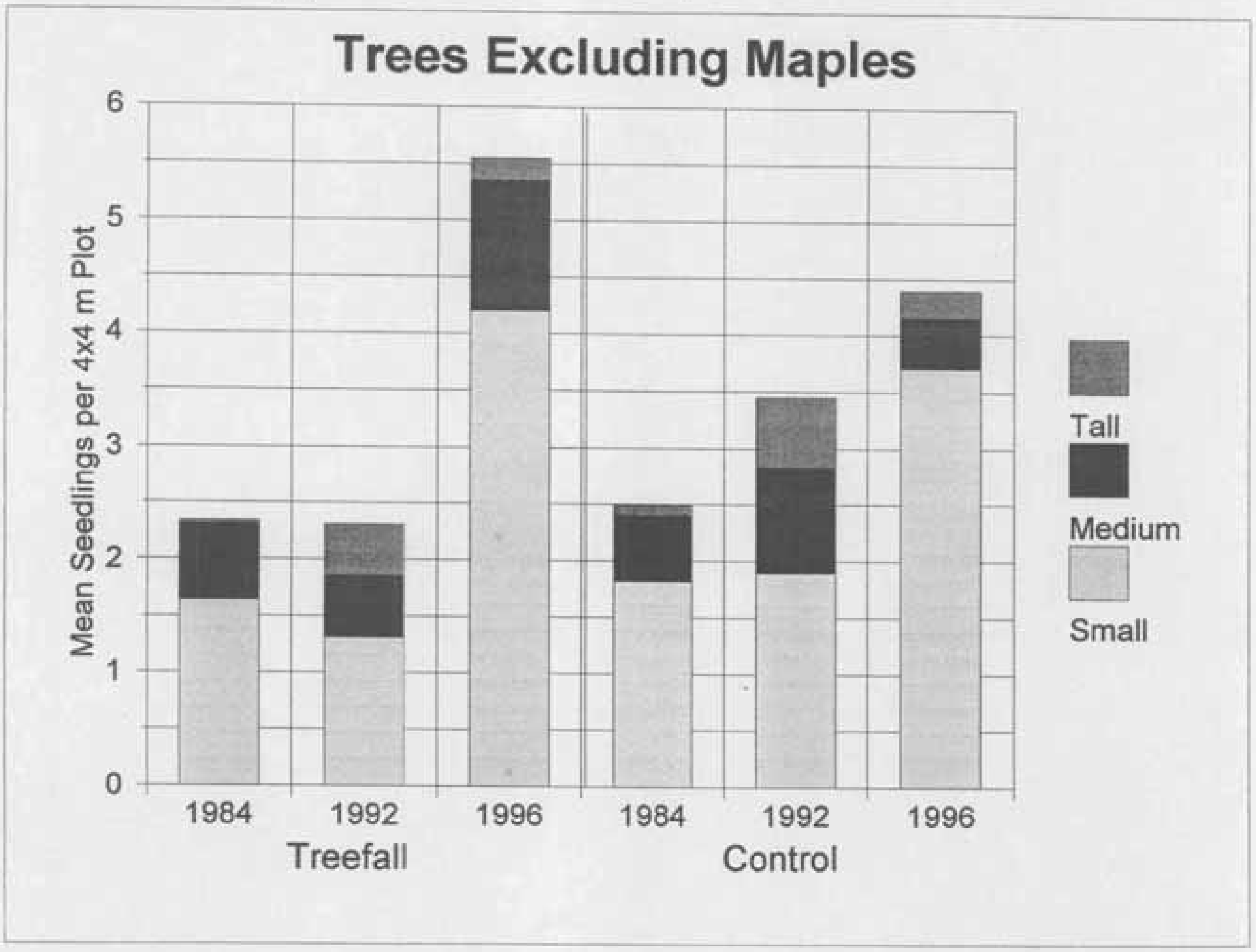


Figure 47. Red maple densities in regeneration plots, broken down by crown/base, treefall/control, and year of sampling. Red maple, in the small size class, was significantly less abundant in base than in crown areas. As in Figure 42, small seedlings decreased while tall seedlings increased in density over time.

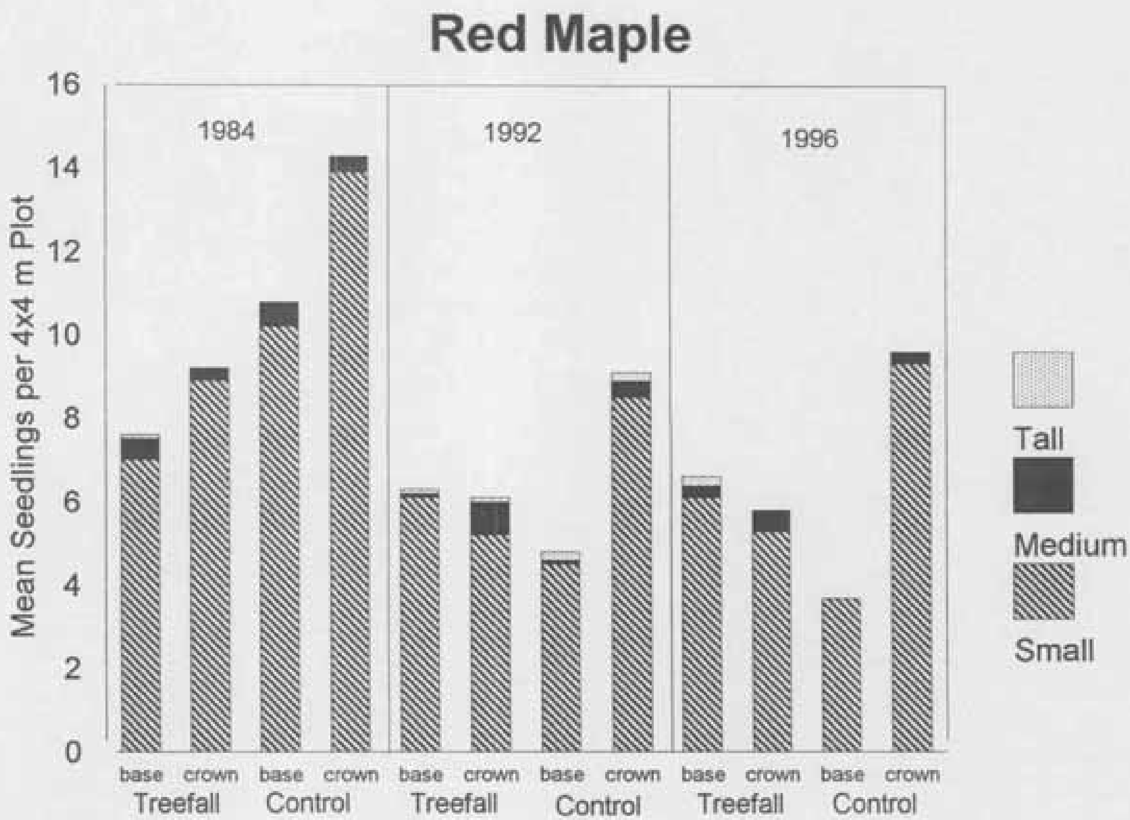


Photo 1.
Budd Lake Forest area of long-term windstorm studies, general appearance. Scattered pines and abundant hardwoods have extensive windfirm layer of maples and shrubs in the understory.

Photo 2. Headwaters Forest study area for long-term windstorm studies, general appearance. White spruce and pines dominate the canopy, while patchy thickets of balsam fir and spruce characterize the understory.

Photo 3. Heavy wind damage to aspen forests outside major study areas, in 1995. The north and west portions of Itasca Park sustained massive blowdown damage. By the time of this photo after one year, aspen sprouts formed a dense understory layer in response to high light levels in this very open area. Photo is from northern portion of Wilderness Drive.

Photo 4. Cluster of red pine in undamaged "island" within a matrix of windthrown aspen, Wilderness Drive/Ozawindib Lake area of Itasca Park. These younger red pine show considerable windfirmness compared with older pines and compared with the aspens. 1995 storm effects, photographed in 1996. (The figure is Dr. Marian Glenn)

Photo 5. Bohall Trail blowdown of 1995, photographed in 1996. High windspeeds caused this blowdown where 40+ pines were windthrown. Permanent plot and releve site.

Photo 6. Bohall Trail blowdown of 1995, photographed in 1996.

Photo 7. Aspen windthrown in 1983 in the Budd Lake study area, photographed in 1985. (see photos 8 and 9 for comparison). Permanent plot site, treefall #36.

Photo 8. 1987 photo of an aspen (treefall #36) windthrown in 1983, in the Budd Lake study area. (see photos 7 and 9 for 1985 and 1996 views).

Photo 9. 1996 photo of an aspen (treefall #36) 13 years after windthrow in 1983, in the Budd Lake study area. (see photos 7 and 8 for earlier photos). Note colonization of log by sugar maple seedlings, and denser mid-height layer of sugar maples.

Photo 10. Canopy over aspen treefall where no gap formed over the base, due to windfirm subcanopy trees. Budd Lake area; photo of 1983 treefall taken in 1985. Compare with canopy shot in 1996, photo 11. (same treefall #36 as in figures 7-9)

Photo 11. Canopy over base of aspen treefall 13 years after windthrow, photographed in 1996. This is the same shot shown 11 years earlier in photo 10; apparent differences in tree angles and brightness are artifacts of camera settings. (treefall #36 in Budd Lake area.)

Photo 12. First in series of three photos of red pine treefall (#1) in Budd Lake area from 1983 windstorm. This first shot from 1985 shows bent shrubs and saplings but well-established undamaged understory layer

Photo 13. Second in series of three photos of red pine treefall (Budd Lake area, 1983 treefall #1). Four years later (1987), tree bark is still intact and pre-existing hazel and mountain maple shrubs continue to cover the area.

Photo 14. Third in series of three photos of red pine treefall (Budd Lake area, 1983 treefall #1). Thirteen years after the storm, the shrub layer has thinned but without floristic changes. The log now supports bryophytes and has lost bark in patches.

Photo 15. Treefall area in Headwaters Forest study area from 1995 windstorm. This was the most massive blowdown I found in this area (#330). The weak-wooded balsam fir understory contributes to larger treefall openings. Photo 1996; permanent plot site.

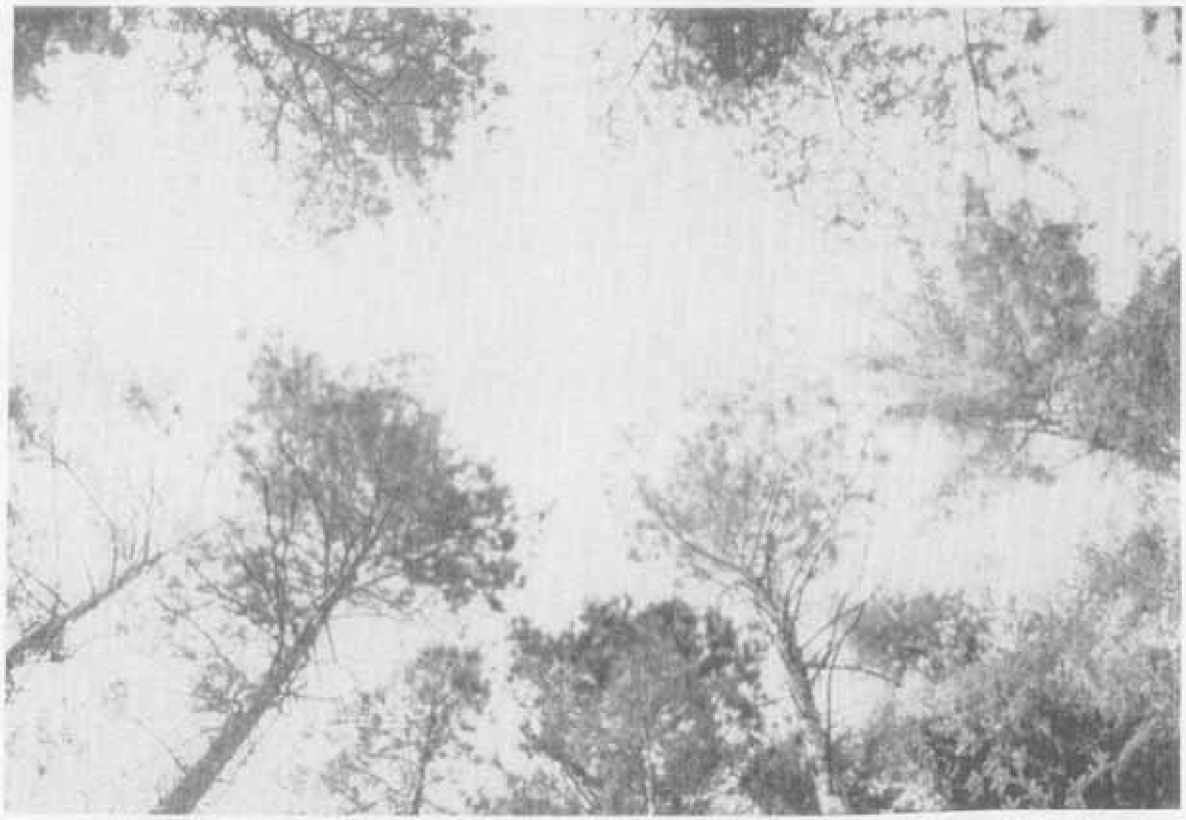


Photo 16. Canopy photograph over the base of 1995 treefall in the Headwaters Forest area. Discrete and sizable gaps form more commonly in this forest because of its structure. (Treefall #330; permanent plot site; photo in 1996).

Photo 17. Treefall mound, unusually large, in Headwaters Forest. Formed in 1995; permanent plot site #390. (Principal investigator Sara Webb is pictured).