

Forest Changes Due to Prescribed Burns and Windstorms in Itasca State Park, Minnesota: A Preliminary Report

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ABSTRACT

This report explores how the forests of Itasca State Park, Minnesota, have changed over a 35-year period, with particular emphasis on responses to management burns that were begun in 1995 with the goal of restoring the natural disturbance regime of the region over the next 50 years. The consequences of windstorms, a second natural element of the disturbance regime, were also examined, in the aftermath of a catastrophic storm in 1995. A network of permanently marked plots have been sampled periodically since 1965 by now-emeritus Professor Vilis Kurmis of the University of Minnesota's Department of Forest Resources. Now with post-fire and post-windstorm resampling conducted in 2000 and 2001, the changes over time at these sites can be interpreted in context of large disturbance events.

Of great concern is the conservation of old growth pine ecosystems within the park. The dependence of the region's three species of pine upon fire was a major motivation for the new controlled burn program. We found that red pine, white pine, and jack pine populations have been declining throughout the 35 year period of study but that fire caused no further damage; burned plots had no more pine mortality than unburned plots. Moreover, in both burned and undisturbed plots, those pines that continued to survive were adding girth and biomass even as their populations thinned. However, windstorms are plucking out the tallest and oldest red and white pines where they extend above the main canopy. Fires have not yet triggered new pine regeneration, and repeated burns as well as herbivore controls may be necessary to achieve this goal.

Fires thinned out some understory shrubs and trees, including the ubiquitous hazel and the scattered thickets of shade-tolerant balsam fir found in the spruce-fir forest type. In the maple-basswood forest type, fire correlated with a dip in sugar maple seedlings from superabundant to abundant, but also with a pulse of sprouting by ironwood, an understory tree.

Prescribed burns did not damage the richness of the vascular flora. Those forests treated with controlled, spring-season fires did not differ significantly from unburned forests in their trajectories of plant species richness. This resistance to fire was seen in the diversity data for trees, tree seedlings, shrubs, and forbs (wildflowers and ferns). Unlike fire, windstorms did influence diversity in at least one cover type, the maple-basswood forest, where forb richness dropped after wind damage. Richness has varied greatly over time and amongst different forest types, with a general downward trend for shrub richness and an upward trend for forbs.

Thus the current regime of management burns appears to be meeting objectives related to ecosystem restoration: favoring canopy pines, whose preservation and perpetuation is of primary concern, while thinning understory shrubs and shade-tolerant saplings without damaging the diversity of vascular plant species, although not yet generating new pine reproduction.

INTRODUCTION

Lightning strikes the earth 100 times each second, on average (Barbour et al. 1999); and wild fire is thus a major force in all but the wettest and coldest of ecosystems (Ahlgren and Ahlgren 1960). In Minnesota, the prairies of the west depend upon frequent fires, while many forest types also are linked with fire, at less frequent time intervals. The mosaic of deciduous forests and savannahs in southern Minnesota was shaped by fire (Grimm 1983). The flat sand plains of north-central Minnesota support jack pine stands that originated in fire, and in the Boundary Waters Canoe Area Wilderness of northeastern Minnesota, "the virgin forestswere literally born in fire," in the words of Heinselman (1996).

The same is true of Itasca State Park, in northwestern Minnesota (Spurr 1954; Frissell 1973; Clark 1988, 1989), the state's largest preserve of old growth forests, where red pine and white pine escaped the wholesale logging that converted pine forests to aspen stands elsewhere throughout the Lake States. However, in this region both pines depend upon fire for seed germination and removal of competition (Ahlgren 1976). Neither red nor white pine has been reproducing successfully since aggressive fire suppression began around 1910. Pine reproduction is curtailed by deer as well (Ross et al. 1970), whose population surged when the area was settled by European-Americans. Meanwhile the old pines are extremely vulnerable to windstorm damage (Webb 1989), but windstorms do not initiate pine reproduction (Webb 1998; Webb and Scanga 2001). Thus the fixture of these, old growth pine ecosystems is in serious doubt.

Fire was reintroduced at Itasca State Park beginning in 1995 to reduce dangerous fuel loads and begin the process of restoring the natural disturbance regime. One of us (Marty) has coordinated management burns that covered 7200 acres, 22.5% of the park, as of spring 2001. Over half this acreage (4000 acres) has been burned twice while another fifth of the burned acreage (1500 acres) has been burned three times. Such management burns are increasingly used as management tools for restoring natural ecosystems, from tall grass prairies to western lodgepole pine forests to southeastern longleaf pine forests. Natural wild fires are now allowed to burn in wilderness areas and some national parks, as in the case of the famous 1988 fires at Yellowstone National Park.

In Itasca State Park, the major goal is restoration of the pine ecosystems whose protection was the primary reason for park establishment. One objective is the reduction of shrub proliferation, particularly hazel (*Corylus cornuta*) whose dense growth is an unnatural consequence of fire suppression and poses an impediment to tree reproduction (Buckman 1964; Tappeiner 1971; Kurmis and Sucoff 1989). A related objective is protection of the park's remarkably intact and distinctive plant communities, which have evolved with, fire and which may be at risk from the suppression of fire. Another objective is the achievement of pine regeneration, so that as windstorms and old age remove mature canopy pines there will be a new generation to replace them. More generally, bringing fire back to these ecosystems represents restoration in and of itself, because fire is part of the ecosystems. However, the consequences of fire can be altered by fuel buildup during intervening years of fire suppression, and by differences between wildfires and prescribed fires in their timing and intensity.

It can be difficult to determine how management practices affect a natural area. Well-designed research is necessary, including control areas that are not treated (with fire or other actions). Ideally there will also be a temporal context documenting "before" and "after" conditions, because spatial comparisons are compounded by pre-treatment differences between localities. We have found this to be crucial in our project. However, land managers rarely have the resources or monitoring history for such an investigation of consequences. Moreover, a desirable prescription such as burns or removal of invasive plants is typically applied as widely as possible, rather than "wasting" time and space on control areas not treated.

We are very fortunate to have at Itasca State Park a history of vegetation studies in permanent plots established and sampled periodically since 1965 by now-emeritus Professor Vilis Kurmis of the University of Minnesota's Department of Forest Resources. This invaluable record of past changes over 35 years also permits assessment of fire consequences by comparing plots from burned and unburned areas, controlling for forest type. The consequences of windstorms, another natural element of the disturbance regime, were also examined, in the aftermath of a catastrophic storm in 1995. We resampled 15 of Dr. Kurmis' 29 remaining sites in summer 2000. This post-fire and post-windstorm resampling permits us to interpret changes over time in context of disturbance events.

However, it is imperative to regard this report as preliminary. An additional 13 sites were sampled in June 2001, just days before this report's completion. Those data must be entered, analyzed, and incorporated with data from 2004 to provide a more comprehensive picture that includes important replicate sites.

Given that caveat, the data set already analyzed, in concert with past records, provides initial answers to several questions about to change and disturbance in the forests of Itasca State Park.

1. Have management burns affected the vegetation and its trajectory of change? More specifically, how has fire influenced the old growth pines, the dense thickets of tall shrubs, the development of shade-tolerant understory firs and maples, and species richness amongst trees, shrubs, and wildflowers?
2. Have windstorms, like that of 1995, changed the forest? To what extent are wind-driven changes different from background changes in undisturbed forests?
3. Do windstorms and fires differ in their consequences for forest composition and dynamics? As the field of disturbance ecology expands, we need more empirical insights into the equivalence of different types of disturbance, and into the interactions between them.
4. How have the forests of Itasca State Park changed over the past 35 years, with and without disturbance events? What trends are seen in forest composition and structure? What is the future of the old growth pine stands and other intact forest ecosystems?

STUDY AREA

Itasca State Park is located in northwestern Minnesota where it encompasses the headwaters of the Mississippi River and 13,000 hectares of old forests, including Minnesota's largest expanse of old growth red pine forests (Rusterholz 1996; Frelich and Reich 1996). Other parts of the park were logged in the 1800s and now support unmanaged, mature forest ecosystems unusual in a region that is otherwise heavily managed for timber production. Situated on a terminal glacial moraine, the park has diverse soils and topography and a complex mosaic of diverse plant communities that has been related to soil conditions (Kell 1938; Kurmis 1969; Ness 1971; Hansen et al. 1974) and to fire history (Spun 1954; Frissell 1973; Clark 1988, 1989). Changes overtime have been examined in context of succession (Westman 1968; Peet 1984; Kurmis 1985), windstorm disturbance (Webb 1988, 1989; Webb and Scanga 2001), and development of the hazel shrub layer (Kurmis and Sucoff 1989).

During the summer of 2000, we resampled 15 of the original 36 stands (Figure 1, Table 1) established by Dr. Kurmis (Kurmis 1969) and Dr. Darwin Ness (Ness 1971). Several original stands had been dropped over the years because of destruction by logging or park development; by 1983 only 29 stands were resampled (Kurmis 1985; Kurmis and Sucoff 1989). We originally proposed to resample 6 of these stands in 2000, hence our tally of 15 stands went beyond original expectations (Table 1, Figure 1). As already noted, another 13 stands were sampled in 2001, and findings from those stands will provide additional insights into the picture of how different forest types have changed over time and into the ubiquity of fire- and windstorm effects we have documented.

Five major cover types were delineated by Dr. Kurmis in 1965 on the basis of ordinations that used a system called synecological coordinates (Bakuzis 1959; Kurmis 1965; Kurmis 1985). This system groups together those sites whose floras have similar affinities for moisture, nutrient, heat and light. We continued to use these cover types to categorize study sites, although much change and some blurring of categories has occurred in some cases since this framework was established.

Among the 15 stands analyzed in this report, all five of Kurmis' major upland forest types are represented, although unevenly, with three red pine stands, three spruce-fir stands, and four maple-basswood stands (Table 2). Only one aspen-birch stand was sampled during our first year because

we had no burned examples for this cover type; only two jack pine stands were sampled, and these differed strongly from one another even before one was struck by heavy wind damage.

The five cover types designated by Dr. Kurmis and general soils information (from Kurmis 1985 and Kurmis & Sucoff 1989) are as follows.

Jack pine - red pine type: Typically even-aged stands of fire origin, with excessively to well-drained loamy coarse sands to gravelly foams. Jack pine forests that are not disturbed by fire suppression tend to support a rich flora that includes prairie elements, but fire suppression promotes thick growth of tall shrubs.

Red pine type: In absence of fire, stands of old (to 350 yr) red pines are embedded in heavy undergrowth of hazel, other shrubs, and hardwood trees. Soils are well-drained loamy sands to foams.

Fir-spruce type: Shade-tolerant balsam fir and white spruce trees form a continuous canopy somewhat overtopped by older supercanopy red and white pines. The understory includes patchy thickets of young fir trees and glade-like areas high in forb diversity. Soils range from well-drained or moderately well-drained loamy sands to foams.

Aspen-birch type: The canopy is dominated by quaking aspen, bigtooth aspen, and paper birch, with associated oaks and maples. This cover type often develops after logging on a wide variety of sites, hence the understory vegetation and soils vary widely. Soils range from moderately well-drained or well-drained sandy foams to sandy clay foams. In 2000 only one aspen-birch stand was resampled.

Maple-basswood type: This distinctive forest type is traditionally considered the "climax" community for the region, but its capacity for spreading into other communities is limited, perhaps by edaphic factors. Sugar maple predominates with abundant understory ironwood to cast deep shade, alongside other hardwood associates: red oak, red maple, bur oak, and basswood. Widely scattered white pines are often present. A dense layer of wildflowers grows amidst patches of Pennsylvania sedges (*Carex pensylvanica*). Seedlings and saplings of the shade-tolerant sugar maple abound. Typical soils are well-drained sandy foams to silt foams.

FIRES AND WINDSTORMS

The disturbance events of interest include management burns and a major windstorm. In the stands we analyze here, management burns occurred during the spring season in 1998, 1999, and 2000. Of four burned stands, two were burned twice (in 1998 and 2000) while two had one burn each (see Tables 1 and 2). The burns varied in intensity between stands and were particularly light in the maple-basswood stand we examined, reflecting the lack of flammable coniferous litter and the moist forest conditions there. Fires burned most intensely in spruce-fir stands where patches of understory fir and spruce provided ladder fuels; and in blowdown areas where intense heat or flames reached the crown zone. Even where most intense these burns did not penetrate deep into the soil. The major effects of burns was scorch damage to woody plants. Burns were spatially patchy within stands.

The windstorm of 1995 also caused uneven degrees of damage. Over 3000 of the Park's 13,000 acres experienced extensive blowdowns with significant forest damage, suggesting winds of up to 100 miles per hour as clocked elsewhere within the same storm system (Hazard Mitigation Team 1995). Many other areas within the park experienced less severe winds that snapped a smaller proportion of trees (Webb 1998), a pattern of damage seen often over the years in this region (Webb 1989, Webb 1998).

It is important to note that even those stands classified as "undisturbed" have been subject to frequent moderate windstorm disturbance over the years, as have the recently burned stands. The term "undisturbed" is thus somewhat misleading, and while we focus on the most destructive of recent windstorms, the ongoing influence of strong winds produces some of the earlier dynamics in all of these forests.

METHODS

Field Methods: Stands where Dr. Kurmis established permanent plots were relocated before leaf emergence in May 2000. In a few cases where plot markers were missing; plot centers were established using vegetation data. In 15 stands, 117 of 120 individual plot centers (there were 8 plots per site) were located with confidence. Two of the three missing plot centers were subsequently found, using a metal detector, and resampled in 2001.

In July, after vegetation had fully emerged, each of these 15 stands was resampled following procedures established by Dr. Kurmis in 1965 and utilized in subsequent surveys. Within each stand, 8 plot centers were established randomly. Large circular plots measuring 400 m² were used for tree sampling. Each tree with dbh (diameter at breast height) > 2.5 cm was measured (for dbh), identified, and assigned to one of 5 concentric rings. Dead trees were also measured and tallied. Such tree surveys were done previously in 1965 and 1983.

Smaller nested circular plots measuring 8 m² (radius 1.6 m) were sampled in three ways. Small woody plants with dbh < 2.5 cm were identified and tallied by height class: 01 foot, 1-3', 3-5', 5-T, 7-9; 9-11', and 11'+, (In 2001 the height classes > T were merged). Also in the small plots, forbs (herbaceous wildflowers, ferns, and fern allies) and certain half-shrubs (*Rubus* spp.) were listed and assigned % cover values established previously by Dr. Kurmis (0.5%, 1%, 2%, 3%, 4%, 5%, 6%, 8%, 10%, and thence by 5% increments).

A third set of records characterized overall cover types within the small plot. We assigned percentage cover estimates (using the same increments above for forbs) for 11 categories: tree canopy, tree reproduction, shrubs, forbs, graminoids, mosses & lichens, live tree trunks, slash (dead fallen wood), rock, soil, and litter. These categories normally sum to more than 100% because of overlap.

Small plots had been sampled in 1965, 1970, 1975, 1983, and 1991. However, not all measurements were made at each point in time.

Plant species are listed in the appendix, which includes all taxa from our surveys and those of Dr. Kurmis. Nomenclature follows Gleason and Cronquist (1991), with updates on ferns and fern allies from the Flora of North America (FNAEC 1993).

In 2000, we sampled 4 burned stands, 3 windstorm-disturbed stands, 6 undisturbed stands, and one stands disturbed by logging, and one stand exhibiting heavy spruce mortality not related to fire or wind (Table 2). Data from these disturbed and undisturbed stands provide only preliminary results. Many cover/disturbance categories, such as burned red pine, are represented by only one stand at this point in time, and the addition of replicate stands is essential for separating effects of fire from effects of other differences between stands. Other cover/disturbance categories have no representative stands, in some cases because certain combinations do not exist where plots were established.

Just prior to the submission date for this report, we relocated and sampled another 13 stands. Table 2 indicates that these stands will provide important replication. However, some gaps cannot be filled given the spatial juxtaposition of disturbance events and the long-standing permanent plots. Despite these limitations, the 15 study areas taken together provide key insights into fire and windstorm consequences for the pines, for shrub growth, and for diversity.

Methods of Analysis: An enormously rich data set has been produced by this research. We focus here on our original questions about changes due to fire, with additional emphasis on windstorm consequences. A more detailed analysis of how different forest types have changed over time will be made after we incorporate data from the 2001 sampling of 13 more stands. Note that new insights into fire and windstorms are also likely to emerge from analysis that includes the replicate stands. More data entry is also needed to bring all past surveys into usable form; fewer past data were in computer files than we thought at the start of our study. All tree data are now computerized as are small woody plant data from 1991 and 2000 but not from previous years. Forb data have been compiled for analysis of species richness across all 6 surveys but are not yet entered in a format that permits analysis of individual species or ordination of communities.

Toward the more immediate objectives, three data sets were analyzed separately.

(1) Tree data from the large plots, which were collected thrice (1965, 1983, 2000) were converted to density (stems per hectare) and basal area (m² per hectare), by tree species. Basal area is an estimate of

cover and biomass, obtained by summing the cross-sectional areas of tree trunks at a standard height above the ground. These attributes of stands and species, as well as richness of canopy tree species, were then modeled with repeated measures ANOVA on three factors: time, disturbance (fire > wind control), and cover type. For some general analyses, a fourth disturbance category - logging - and its single stand - #13 - were included; this stand is also partially covered by a deer exclosure. A spruce-fir stand (stand #2) with heavy, unexplained tree mortality was excluded from those tests that probed fire and windstorm responses because it did not represent a meaningful control situation.

All repeated-measures results were tested for sphericity; where this assumption was not satisfied, adjusted significance values (using the Greenhouse-Geiser epsilon) were used for the factor "time" and its interactions. For factors and interactions that were significant, LSD and Tukey's post-hoc tests at the $P=0.05$ significance level were used to determine which disturbances and time periods differed from one another. This and all other analyses used SPSS version 10.0 software.

(2) Smaller plots provided quantitative count data for smaller ($\text{dbh} < 2.5 \text{ cm}$) woody plants, which were analyzed together and in three *life-form categories*: tree seedlings, small shrubs and vines, and tall shrubs. Note that "small" and "tall" refer to the species life form rather than individual stems. Thus all hazel stems are counted together in the "tall" category while all bush honeysuckle and gooseberry stems are "small." Separate analysis was also made for some individual woody species that were sufficiently abundant to exhibit patterns.

The analysis of small woody plants focused on the most recent time period during which fires and the key windstorm occurred, comparing the 1991 and 2000 surveys only. For the small woody plant analysis, we excluded three unusual stands: the aforementioned logged stand (#13), the atypical spruce-fir stand with unexplained spruce mortality (#2), and an aspen-birch stand that was the sole representative of this cover type (#37). Just as for trees, the small woody plots were analyzed using repeated measures ANOVA, modeling densities on time, disturbance, and stand cover type. When the disturbance/time interaction was significant, LSD post-hoc tests determined which disturbance categories (fire, wind, no disturbance) differed from one another.

(3) Species richness was evaluated using species lists from the small plots, which provided not only counts for small woody plants (above) but also presence/absence records for herbaceous plants. Richness, a simple count of species per plot, was used rather than various diversity indices, which incorporate evenness as well as richness and thence underemphasize rare taxa. Richness was examined as a total

(number of species per 8 m² plot) and also within life form categories: forbs (ferns, fern allies, wildflowers), shrubs, and tree seedlings. Graminoids were not recorded in the original surveys so are not included in richness counts. Species richness across six different surveys (1965, 1970, 1975, 1983, 1991, 2000) was analyzed with repeated measures ANOVA for 14 stands, excluding the logged stand (#13). Analyses with and without the spruce-fir stand with unexplained mortality (#2) did not differ substantially.

RESULTS AND DISCUSSION

Recent windstorms and fires have had very different consequences, and these consequences vary amongst different forest types. Moreover, consequences vary between stands of a given cover type. Within the complex vegetation mosaic of Itasca State Park, each locality has an individualistic physical setting and history. Thus it can be difficult to distinguish effects of fire from basic differences among stands; it can be misleading to directly juxtapose a burned and an unburned stand and presume they had similar predisturbance characteristics. This challenge is met in part by the long-term records and in part by the addition of replicate stands through the research team's current expansion of the data set.

Our access to longitudinal data has turned out to be crucial. Any discussion of fire in these forests must be placed in a rather complex context of background changes that are taking place in the absence of fire, due for example to forest fragmentation and to natural and anthropogenic climate changes. This is a key finding: comparisons of burned to unburned or windstruck stands will be misleading unless pre-disturbance conditions are known, because each individual locality has its own history and its own distinctive trajectory of change even before the fire or windstorm event occurs.

The results to date show striking patterns of change over time alongside stasis in some major forest elements across the 35 Years of study. Moreover, the results show that management burns have reduced densities of hazel and fir while having little effect on the pines or on diversity of the plant community. Windstorm disturbance has had a stronger impact than fire on tree biomass in general, on the pines in particular, and on plant diversity.

Here we present results that show how changes over time have varied with disturbance events and amongst cover types. The figures (2-8) illustrate these changes. Table 3 presents results of repeated-measures ANOVA that tested how stand attributes, species richness, and individual tree populations varied with three factors: time, cover type, and disturbance. Post-hoc tests determined which time periods and disturbances differed from one another, as also reported in Table 3. Table 4 gives a detailed account of the key interaction between time and disturbance, providing post-hoc breakdowns of which years differed significantly within a disturbance category (fire, wind, no disturbance), and also of which disturbance categories differed at each point in time. Only those attributes and species with a significant interaction of time with disturbance can be tested in this way. This analysis of the interaction is crucial because it takes into account the temporal context within which windstorms and fires operate.

Total Tree Density

The total density of trees, across all cover types and disturbances, did not vary significantly over time (Figure 2; Table 3). However, many individual tree species did change in abundance, as the figures show.

Disturbance by fire and wind influenced some tree populations, as discussed below, and had subtle effects on overall tree abundance. Wind-disturbed stands had significantly lower tree densities than burned or undisturbed stands (Table 3). Insights into the influence of fire come from a closer look at the significant interaction between time and disturbance (Table 4), as the different lines on the graph (Figure 2) imply. For undisturbed stands, tree densities decreased significantly from 1965 to 1983 and then recovered upward to 1965 levels by 2000. For burned stands, the opposite pattern was seen: a significant increase from 1965 to 1983 followed by a decrease during the interval with fire. The earlier increase was mostly from development of understory fir thickets which were subsequently thinned by fire.

Clearly, different trajectories of change characterized the different sets of stands before the disturbance events. Again the importance of long-term records cannot be overstated. Were we to examine only one point in time, post-fire, we would not realize that the undisturbed stands happened to have higher tree densities than stands later burned or windthrown, even 30 years before the disturbance events (Figure 2). Thus rather than simply comparing burned and unburned stands we must examine the

interaction of time and disturbance to understand what changes are linked with the fire and windstorm events. On the basis of the time/disturbance interaction, it appears that management burns contributed to reduced density of tree-sized stems between 1983 and 2000.

Total Basal Area

The basal area of trees, a measure of biomass, did change over time, generally and significantly (Table 3) increasing and then decreasing slightly or, in wind-disturbed stands, decreasing substantially (Figure 3). Burned stands did not diverge in basal area from undisturbed stands (Figure 3; Table 3), because the massive pines were rarely damaged by fire. Meanwhile windstruck stands did experience significant loss of basal area (Figure 3; Table 3), because large trees in these forests are vulnerable targets of severe winds (Webb 1989, Webb 1998).

Tree Density and Basal Area: Differences Among Cover Types

Different types of forest showed different patterns of change in tree abundance over time and in response to disturbance (Figures 2 and 3). Trees were thinned most by fire in spruce-fir forests, with their fire-vulnerable understory fir trees and saplings (Figure 2d). Meanwhile basal area increased in burned spruce-fir forests as surviving pines thrived (Figure 3d). Red pine forests also lost tree stems (Figure 2c) and lost some basal area, but not pine basal area, to fire (Figure 3c). These losses in red pine stands included fir, red maple, and paper birch. However, the maple-basswood forest gained stems (Figure 2e) while losing basal area (Figure 3e) to fire, suggesting that losses of large trees will be replenished by new smaller stems moving toward the canopy. Windstorms depleted basal area in all forest types (Figures 2 and 3), typically targeting larger trees, and depleted tree density in all forest types except maple-basswood where windfirm maples and ironwoods typically survive wind damage. These divergent changes amongst cover types boil down to distinctive responses to specific disturbances by individual tree species.

The Pines Across All Cover Types

For Itasca's ancient red pines, burned and undisturbed stands differed very little across the years (Figure 4a and 4b). Red pine density did decline significantly over time under all disturbance regimes (Table 3 and 4; Figure 4a), while red pine basal area increased (1965-1983) and then decreased (1983-2000) but no more so in burned than undisturbed plots (Figure 4b; Table 4). Clearly and not surprisingly, the fire-adapted red pine normally survives controlled burns, and current fire management procedures have succeeded in ensuring its survival despite a long period of fire suppression and fuel buildup.

The background decline of the park's red pine population includes some natural die-off but also losses to wind which is a major, ongoing force in these forests before and since the 1995 storm. This wind damage to red pine, shown by Webb (1989,1998), is not as obvious from our present study because wind-struck plots in this study happened to have low red pine abundance both before and after the windstorm (Figure 4).

White pine, also typically large but more widely scattered than red pine, decreased in density but increased in basal area over time, across all stands and disturbance categories (Table 3; Figures 4c and 4d). Thus while some trees were lost, the survivors gained significantly in girth. Windstorm disturbed plots, with relatively low white pine abundance throughout the study, did not exhibit these changes over time, but burned and undisturbed stands were quite parallel with one another (Table 4). Disturbance was not a significant influence on either density or basal area of white pine (Table 3). Thus like red pine, white pine resisted damage during fires and lost no more ground over time in burned than in unburned areas.

Jack pine is the third pine of Itasca State Park, a short-lived fire-dependent species more abundant on flat sandy outwash plains east of the park. Within the park, only one of our 2000 stands (#12) had any jack pine trees, and in this windstruck stand the once dominant jack pines have declined precipitously but both before and after the 1995 windstorm (Figure 4e). Jack pine within the park is deteriorating in general, apparently due to overmaturity. The jack pine forest type in the Itasca State Park region is extremely rich in plant and lichen diversity (Glenn et al. 1998) and is presumably resilient to, and enhanced by, fire, but our results cannot address this response.

Spruce-Fir Forests: Spruce and Fir Trees

Balsam fir and white spruce are major trees in their namesake forest type (sprucefir), alongside red pine, white pine, and paper birch, but are nearly absent from other upland forests of Itasca State Park. In absence of a wind-disturbed stand of this forest type, the graphs show only low densities of these species from other stands, and conclusions about windstorm effects cannot be drawn. However, previous research showed both balsam fir and white spruce to be highly vulnerable to windthrow in Itasca Park spruce-fir forests (Webb 1989; Webb 1998).

Both balsam fir and white spruce lack resistance to fire as seen in the pines. Firedamaged understory firs are conspicuous by their red foliage after management burns. However, many of these trees survive their fire damage, at least initially. Patterns of change for fir and spruce suggest a role for fire, when we evaluate such changes through post-hoc tests of the interaction between disturbance and time (Table 4). In stands that were burned, balsam fir abundance peaked in 1983 and dropped significantly during the period with fire (Figure 5a). In contrast, in unburned areas balsam fir continued to increase in unburned areas during the fire period (Table 4; Figure 5a). White spruce abundance also dropped steeply in burned plots during the period with fire (Figure 5b), although it did not proliferate like balsam fir in unburned sites.

Maple-Basswood Forests

The distinctive maple-basswood forest type is not considered a fire-adapted forest and is generally predicted to develop on fire-protected sites. Such forests, dominated by sugar maple and ironwood in the Itasca State Park region, also resist fire because deep shade keeps the forest floor relatively moist and because maple litter is far less flammable than that of the needle-leaf conifers.

When trees (dbh > 2.5 cm) are considered, we find great constancy over time in abundance of sugar maple (Figure 5c; Table 3), basswood (Figure 5d), red oak (Figure 5e), and bur oak trees (Figure 5f), and an increase over time in ironwood (Figure 5g) and red maple (Figure 5h) densities. In this forest type and elsewhere, both paper birch (Figure 5i) and aspen (combining quaking and bigtooth aspen species, Figure 5j) have decreased significantly over time. Episodic birch mortality has been in evidence during droughts, and aspen are becoming overmature and blowing down at an extremely high rate even in low-intensity windstorms (Webb 1989; Webb 1998).

Fire had little impact on the trees of this forest type. Our one burned maple-basswood stand had less sugar maple than other stands before and after fire. Without long-term data, we might be misled and blame fire for the lower sugar maple densities in burned areas rather than recognizing this as a long-standing, pre-fire difference among the stands (Figure 5c). The management burn in question was light and patchy; a more severe burn, if possible in this mesic forest type, might cause more tree mortality.

Other Hardwood Trees in All Forest Types

Few hardwood tree species lost ground due to fire, in maple-basswood or other forest types. ANOVA results (Table 3) show that disturbance was not significant for ironwood or red oak; both resprout after stems are lost, but for this tabulation of tree-size stems the results indicate high survival of existing trees. For red maple trees, disturbance was not a significant factor on its own, but its interaction with time was significant, showing a tendency to cut back red maple abundance (Table 4; Figure 5h). Red maple increased throughout the study period in all stands and this increase continued in the undisturbed stands but leveled off where there was disturbance by fire or wind.

Besides red maple, only sugar maple and paper birch had lower densities in burned stands. Densities in burned stands were not significantly different from densities in undisturbed stands for aspen, bur oak, or basswood.

Reproduction by Pines

No pulse of pine reproduction was seen during the study, even after windstorms or fires. Fire-dependent jack pine is disappearing from Itasca State Park as trees become overmature and disappear from the canopy without new recruitment. Seedlings of red pine are equally sparse, while occasional but tiny white pine seedlings appear widely scattered in various forest types but at densities undetectable by our sampling network. Rotting logs support more pine seedlings than background litter in the spruce-fir forest type (Webb 1988). Today as in 1965 and 1983 (Kurmis 1985), these white pine seedlings rarely reach more than 30 cm in height except inside deer-excluding fences. The suppression of pine reproduction by white-tailed deer is clear from experimental deer exclosures (Ross et al. 1970). Fire is generally expected to facilitate pine seed germination by exposing mineral soil and removing competition from shrubs. To date, the Itasca State Park management burns have not met germination needs of the pines. Therefore repeated fires will be necessary following such a long period of fire suppression in these forests, but other measures may also be required to obtain pine reproduction.

Other Tree Seedlings and Sprouts

The paucity of pine seedlings notwithstanding, other tree seedlings have increased in the past decade (1991-2000) across all study sites (Figure 6a; Table 3), the vast majority representing sugar maple seedlings (Figure 6b) and these generally confined to maple-basswood forests.

Tree seedlings were significantly thinned by fire. Most of this thinning represented sugar maple, the most abundant seedling which did decrease when analyzed alone (Table 3). Meanwhile sugar maple seedlings increased in both wind-disturbed and undisturbed plots (Figure 6b). However, sugar maple seedlings are still abundant even in the burned maple-basswood forest and are not yet challenged by other new recruits for future dominance of this forest type.

Seedlings (and sprouts) of ironwood, an extremely shade-tolerant understory tree showed the opposite response, increasing in burned plots across the time period with fire while not changing in abundance in either unburned or wind-disturbed plots (Table 4).

Ironwood, like sugar maple, is by far most important in maple-basswood forests. Most and perhaps all of the new ironwood stems were sprouts from root systems where fire had damaged a pre-existing stem.

In addition to ironwood, many of the region's woody plants have a great capacity for resprouting from established root systems after fire, including the aspens, basswood, red maple, red and bur oak. However, deer browse pressure is heavy on such resprouting stems which thus may not routinely reach the canopy. Moreover, browsing appears to interact with repeated fires to eventually kill these trees.

Other tree reproduction, by red maple, aspen, and red oak, showed no significant response to fire or windstorms (Table 3). We might predict fire to reduce numbers of fir and birch seedlings which tend to germinate on moss-covered logs in Itasca's conifer forests (Webb 1988), because such moss layers are damaged by fire. However, such seedlings are too sparse to exhibit measureable patterns at the scale of our plot network. In our experience, these tiny seedlings rarely survive on logs for more than a few years, even in the absence of fire. Preliminary observations in 2001 at another burned maple-basswood stand suggest an unusual pulse of basswood seedling establishment following fire.

Shrub Abundance

One goal of the Itasca State Park management burns was to reduce the heavy growth of hazel and other tall shrubs, which obscure views while apparently choking out tree reproduction and other plants. These shrubs reach 90% cover in red pine stands, 80% in the park's jack pine stands, and 70% in aspen-birch stands; the shrubs have lower coverage and generally lower stature in spruce-fir (50%) and maple-basswood (40%) stands (Kurmish and Sucoff 1989). A previous report on hazel dynamics in these stands (Kurmish and Sucoff 1989) showed significant fluctuations over time and variation between cover types but no overall directional trend in density over a 19-year period (1965-1984) prior to the management burns examined in this report.

Although hazel resprouts after fire, its densities were curtailed by recent burns and subsequent browsing. Disturbance was significant, with a greater proportion of hazel stems lost in burned plots (Figure 6d) than in undisturbed or wind-disturbed plots (Table 3). Note however that differences existed in 1991, before the disturbance events, amongst the plots subsequently burned or windstruck. Inherent differences between plots obscure disturbance effects to some extent, a problem to be corrected with additional replicate stands in the future. Nevertheless, the current results and our observations support a role for fire in thinning hazel stems. Further analysis of hazel size distributions would help elucidate this role. The next important question is to what extent the root systems will resprout. Repeated fires clearly will be necessary to suppress hazel enough for pine regeneration (Buckman 1964).

When other tall shrubs are tabulated along with hazel, the same results are obtained (Figure 6c), with less shrub growth in burned plots than in undisturbed plots. Wind-disturbed plots had yet higher shrub densities, a response we might expect from the opening of the canopy. Both the shrub and pine data clearly show that windstorms and fires are not equivalent ecological forces.

One exception amongst tall shrubs was chokecherry which, although generally recognized as a disturbance-adapted shrub, was significantly less abundant in burned and wind-disturbed plots than in control plots (Table 3). This surprising result illustrates the complexity of disturbance responses, possibly reflecting heterogeneous forest conditions and disturbance intensities.

Vines and small shrubs, which we define as those species characteristically low in stature, did not change significantly in abundance over time during the most recent decade (1991-2000) nor when subjected to disturbance by fire or windstorm (Table 3, Figure 6e). This was also true for bush honeysuckle, the most abundant of this group, analyzed by itself. Figure 6e suggests that burned areas supported less proliferation of stems of these clonal plants, as we might expect, but this difference was not statistically significant. Small shrubs did vary in abundance with cover type, with the fewest in maple-basswood forests and the most in jack pine forests.

Wildflowers and Other Forbs

Despite concerns that fire might damage wildflowers and other small plants, we found that disturbance did not influence species richness of these so-called forbs (Table 3; Figure 7c). It is not surprising that the wildflowers and ferns of these forests recover rapidly from fire, a force with which they have coexisted for millenia prior to recent fire suppression efforts. Note that, as with the other figures, only the last segment of each graph, the time period during which the windstorm and fires occurred, can be attributed to these disturbance events. Fluctuations over time have been significant (Table 3; Figures 7c, 8b, 8e, 8h, 8j), with general upward trends in all red pine forests (Figure 8e) and in some maple-basswood forests: those undisturbed and burned but not those struck by windstorms (Figure 8k).

Species Richness

Species richness, commonly used as an indicator of ecological integrity, was measured in our study not only for forbs but also for shrubs, trees, and tree seedlings. However, changes in species richness and other diversity measures must be interpreted with careful consideration of other descriptors of forest status. Diversity often increases after anthropogenic disturbance introduces weedy species, and low-diversity natural ecosystems may be undervalued if only diversity currency is used.

The Itasca State Park management burns have had no impact on species richness of trees (Figure 7a), tree seedlings (Figure 7e), shrubs (Figure 7d), or forbs (Table 3; Figure 7c). Any negative effects would be in evidence already, but enrichments may emerge some years after repeated fires. Suppression of fire is perhaps more likely to damage diversity in these forests, by allowing heavy growth of hazel and of sugar maple and balsam fir, two shade-tolerant and shade-casting trees beneath which diversity is fairly low.

Overall richness in small plots (excluding canopy trees) has fluctuated significantly over the past 35 years (Figure 7b). While forb richness has generally increased (Figure 7c), shrub richness has generally decreased overall (Figure 7d).

The mix of species varies amongst cover types, as do patterns of change and responses to disturbance. Figure 8 depicts changes in species richness by cover type. In jack pine forests, richness has generally declined as the jack pine canopy broke down and shrubs proliferated in density though not in diversity (Figures 8a,b,c). In red pine forests, plots later burned had begun diverging from undisturbed plots in shrub diversity long before management burns. Moderate fluctuations characterize all plots in this cover type (Figures 8d,e,f). In spruce-fir forests, richness has been generally increasing; an apparent dip in burned plots during the fire time interval was not statistically significant but deserves further study (Figures 8g,h,i). In maple-basswood forests, richness plummeted in the first decade of this study, rebounded and continued to increase (Figure 8g) as forbs accumulated in burned and undisturbed plots but decreased in wind-disturbed plots (Figure 8h). Meanwhile shrub richness steadily declined in maple-basswood forests throughout the study (Figure 8i). Fire is not a controlling factor behind these changes.

CONCLUSIONS

(1) Pine Trees and Fire: Fire did not cause increased mortality to red pine or white pine trees. In burned as in unburned plots, pines gained biomass over time at an equal rate. However, both pines have been declining in abundance throughout the 35 years of study, in burned and unburned plots. Jack pine has also declined, but fire effects on this pine aren't clear from existing plot data; the literature shows vulnerability of jack pine stems to fire but the ability to rapidly reseed after fire.

(2) Pine Trees and Windstorms: Unlike fire, windstorms do impose heavy mortality to the ancient red and white pines, particularly where they protrude above the main canopy.

(3) Pine Regeneration: Neither fires nor windstorms triggered new pine regeneration. Windstorms instead promote prolific growth of pre-existing shrubs and maple seedlings. Fires must be repeated to reduce competition and to expose mineral soil, and herbivore :4 controls may be needed before a new generation of pines gets started.

(4) Shrubs and Fire: Fires thinned out tall shrubs in the forest understory to some extent, particularly the ubiquitous hazel which nevertheless resprouts after fire. The diversity of shrubs was not, however, impacted by fire.

(5) Balsam Fir in the Understory: Fire damaged and in some cases killed saplings of balsam fir, a shade-tolerant, late-successional tree found in the spruce-fir forest type. Removal of these fir thickets changes the character of the forest and may open the forest floor to more diverse vegetation. Canopy pines in these spruce-fir forests were charred at the base but undamaged by fire.

(6) Sugar Maple and Ironwood Seedlings: In the maple-basswood forest, dense seedlings of sugar maple seedlings were thinned slightly but significantly by fire, but continued to dominate the forest understory. Meanwhile ironwood, a shade-tolerant understory tree, increased in abundance after fire when stems died back and when surviving root systems resprouted vigorously. Maple-basswood forests are not highly flammable, and our one fire site was only lightly burned; more intense fires, if possible in this forest type, may have different consequences.

(7) Other Tree Species and Fire: For deciduous trees, distinctive patterns of change over time were altered by fire in only two cases. Red maple, on the increase everywhere for some time, leveled off in burned plots; paper birch, declining in abundance everywhere, declined most steeply in burned plots.

(8) Tree Populations: Changes Over Time: Aside from fire and windstorm effects, general changes in forest composition over time were apparent. Declining were the pines, aspen, and paper birch, trees that establish after fire or other disturbances but whose intolerance of shade precludes reproduction in the closed forest. On the increase were shade-tolerant ironwood and red maple. Different cover types followed different patterns of change, with remarkable constancy within the distinctive spruce-fir and maple-basswood forest types but with some signs of convergence amongst jack pine, red pine, and aspen-birch stands. More analysis utilizing additional stands is needed to synthesize overall patterns of change.

(9) Species Richness and Fire: The richness of wildflowers and ferns (forbs) did not diverge upward or downward after fire. Nor did fire influence species richness of other plant groups: shrubs, tree seedlings, or (in the large plots) tree species. This result is not surprising when we consider that these forest communities have evolved with fire over millennia and only recently grew under conditions of fire suppression. Moreover, the management burns under study here were light, patchy, short in duration, and

timed during the spring when most species are just beginning to break dormancy. Late summer fires of greater intensity could have different consequences.

(10) Species Richness and Wind: The only disturbance effect on diversity was caused by wind: lower richness of forbs after wind damage in the maple-basswood forest, perhaps because of increased shade as understory maples responded to release.

(11) Species Richness Over Time: Disturbance aside, species richness has varied greatly over time and amongst different forest types. In general the richness of shrubs has decreased while the richness of forbs has increased over the past 35 years. These changes deserve closer scrutiny for individual taxa of interest. A variety of forces might be at work including local successional shifts and concomitant changes in resource availability, weather events such as drought, broader trends of climate change, and dynamics of herbivore populations.

(12) Windstorms vs. Fires: Windstorms did not resemble fires in their consequences for forest composition or structure in these forests. For many taxa, wind-disturbed conditions were significantly different from those in burned and unburned treatments (which did not themselves differ). Windstorms, whether severe or moderate, tend to remove pines and favor shrub development and, where present, sugar maple.

(13) Windstorm - Fire Interactions: The two disturbance regimes interact with each other. Where fires follow windstorms, the fallen timber fuels the fire and can provide a ladder toward the canopy. Thus post-windstorm fires generate more heat and are more likely to cause canopy mortality through either heat damage or crown fire.

(14) Management Objectives: The current regime of management burns is thus meeting several ecological objectives: protecting and favoring old growth pines, removing shrub and sapling undergrowth, and maintaining plant diversity. Repeated fires and herbivore controls may help meet the additional restoration objective, not yet met, of pine regeneration.

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Table 1. Summary of stand information as of June 2001.

Site #	Site Nick Name	Cover Type 1965	Disturbance
Sites resampled in 2000			
2	Nicollet Trail North	Spruce-fir	budworm
5	Bohall Trail West	Red pine	fire 1998 and 2000
7	South Park Hazel	Red pine	no
12	Jack Pine Blowdown	Jack red-pine	wind
13	Centennial Pines	Jack-red pine	logged/exclosure
14	Aiton Heights Blowdown	Maple-basswood	wind
21	Elk Lake Maple Basswood	Maple-basswood	fire 1999
27	Nicollet Cabin	Spruce-fir	no
31	Sign Spruce Fir	Spruce-fir	fire 1998, 2000
36	Eagle Scout Trail	Red pine	wind
37	Gilfillan Lake	Aspen-birch	no
56	No Name Road	Maple-basswood	no
66	Ozawindib Trail South	Jack-red pine	no
68	Aiton Heights Maple-Basswood	Maple-basswood	no
73	Headwaters	Spruce-fir	fire 2000
Additional sites sampled June 2001 (results not yet analyzed)			
6	Southwest Trail Pines	Red pine	no
8	South Park No-see-ems	Aspen-birch	wind
20	Two Spot Trail	Red pine	spruce planted, light wind
22	Wilderness Maple-Basswood	Maple-basswood	fire 2000
28	South Nicollet Trail Pines	Jack-red pine	wind
34	Ozawindib Lake Aspen	Aspen-birch	blowdown, part logged
38	Wilderness Red Pine	Red pine	fire 1998 & 2000
47	Beaver Trail Aspen	Aspen-birch	no
50	Bohall Trail	Maple-basswood	fire 2000
60	Beaver Trail Pines	Spruce-fir	no
62	Ozawindib Trail Maple-Basswood	Maple-basswood	no
70	Mid DeSoto Blowdown	Aspen-birch	wind
75	South DeSoto Trail	Red pine	no

Table 2.									
Stands by disturbance and cover type.									
Numbers are stand numbers; see previous table for details.									
Stands resampled in 2000 are analyzed in this report.									
Cover Type 1965	Fire		Wind		No Disturbance		Other Disturbance		
Resampled -->	2000	2001	2000	2001	2000	2001	2000 13 (logged/exclosure)	2001	
Jack pine-red pine			12	28	66				
Red Pine	5	38	36		7	6, 75		20 (spruce planted)	
Pine-spruce-fir	31, 73				27	60	2 (unexplained mortality)		
Aspen-birch				8, 70	37	47		34 (wind & part logged)	
Maple- basswood	21	22, 50	14		56, 68	62			

Table 3. Results of repeated measures ANOVA tests; see text for explanations.								
P with GH Geiser adjustment where sphericity assumption not met.								
"x" indicates not significant at P=0.05 level. "nd"=not disturbed by key wind or fire events.								
See table 4 for post-hoc tests on interactions.								
	Time	Time	Disturbance	Cover	Disturb.	Time x	Disturb.	
		posthoc	Disturb. posthoc	x Cover	x Cover	Cover	x Time	
TREE DATA: Three surveys: 1965, 1983, 2000.								
Based upon 13 stands (excluding stands 2 and 13).								
Tree density	x	x	0.009	fire=nd>wind	<0.0005	<0.0005	0.002	<0.0005
Total basal area	0.005	65<83=00	<0.0005	fire=nd>wind	<0.0005	x	x	0.001
Tree richness	x	x	x	x	<0.0005	x	<0.0005	<0.0005
Red pine density	<0.0005	65>83>00	<0.0005	fire=nd>wind	<0.0005	<0.0005	<0.0005	<0.0005
Red pine basal area	0.038	65=00<83	<0.0005	fire=nd>wind	<0.0005	<0.0005	0.011	x
White pine density	<0.0005	65>83>00	x	x	<0.0005	<0.0005	<0.0005	0.017
White pine basal area	0.006	65<83<00	x	x	0.003	<0.0005	0.048	x
Balsam fir density	0.003	65<83=00	0.01	fire>nd>wind	<0.0005	<0.0005	<0.0005	<0.0005
White spruce density	0.021	65>83=00	0.04	x	<0.0005	<0.0005	<0.0005	<0.0005
Sugar maple density	x	x	0.003	fire<wind=nd	<0.0005	<0.0005	x	x
Red maple density	<0.0005	65<83<00	x	x	<0.0005	<0.0005	<0.0005	<0.0005
Ironwood density	<0.0005	65<83<00	x	x	<0.0005	0.46	<0.0005	x
Paper birch density	<0.0005	65>83>00	0.011	fire=wind<nd	x	x	0.019	0.008
Aspen: bt+quaking	<0.0005	65>83>00	0.002	fire=nd<wind	0.008	x	0.034	0.001
Ash, green + black	x	x	<0.0005	wind=nd<fire	x	0.0016	<0.0005	0.006
Red oak density	0.045	65=83>00	x	x	0.006	0.005	0.0005	x
Bur oak density	x	x	0.029	wind<nd(==fire	<0.0005	0.018	<0.0005	0.003
Basswood	x	x	0.008	wind=fire=nd	<0.0005	0.001	<0.0005	x
SMALL WOODY PLANTS								
Two surveys (91-00); based on 12 plots (excl. 2, 13, 37)								
Tree seedlings	0.032		0.001	fire<nd=wind	<0.0005	<0.0005	0.001	0.025
Tall shrubs	<0.0005		0.004	fire<nd<wind	<0.0005	<0.0005	0.002	x
Small shrub taxa	x		x	x	p=0.012	0.025	x	x
Total density	x		<0.0005	fire<nd<wind	<0.0005	0.011	<0.0005	x
Richness small woodies	x		x	x	x	x	x	x
Hazel	0.001		0.006	fire<nd<wind	<0.0005	x	0.001	x
Sugar maple sdls	0.039		<0.0005	fire<nd=wind	<0.0005	<0.0005	0.001	0.015
Red maple sdls	x		x	x	<0.0005	x	x	x
Red oak sdls	x		x	x	<0.0005	<0.0005	0.01	x
Ironwood	x		x	x	<0.0005	x	x	0.038
Chokecherry	(0.06)		0.004	fire=wind<nd	0.002	0.014	x	x
Diervilla lonicera	x		x	x	0.014	0.014	x	x
Aspen	x		x	x	0.006	<0.0005	x	x
SMALL PLOT RICHNESS								
Six surveys, 1965, 70, 75, 83, 91, 00								
Richness small plts	<0.0005		x		<0.0005	x	<0.0005	x
Tree sdlg richness	<0.0005		x		<0.0005	<0.0005	<0.0005	0.027
Forbs richness	<0.0005		x		0.014	<0.0005	<0.0005	0.014
Shrub richness	<0.0005		x		<0.0005	0.001	0.007	0.003

Table 4. Results of post-hoc tests on disturbance types and time of sampling, the interaction of the two factors.

For those taxa for which the disturbance/time interaction was significant, the post-hoc tests explore which sampling times differed						
within disturbance categories (fire, wind, no disturbance), and also explore which disturbance categories differed in a given						
sampling year. Note that disturbances of interest occurred during the later time period, between 1983 and 2000, so pre-disturbance differences are important to note and cannot be attributed to fire or wind events under study.						
Significance criterion is P=0.05. "nd"=no disturbance.						
Measurement	Undisturbed	Fire	Wind	1965	1983	2000
Total Tree Density	1965=2000>1983	1965=2000<1983	1965=1983=2000	fire=wind<nd	fire>nd=wind	fire=wind>nd
Total Basal Area	1965<1983=2000	1965<1983=2000	1965=1983>2000	fire=wind<nd	fire=nd<wind	nd<fire<wind
Tree Richness	1965=1983<2000	1965=1983>2000	1965<1983>2000	fire=nd=wind	fire=nd<wind	nd<fire<wind
Red Pine Tree Density	1965>1983>2000	1965>1983>2000	1965=1983=2000	wind<fire<nd	wind<fire=nd	wind<fire=nd
White Pine Tree Density	1965>1983>2000	1965>1983>2000	1965=1983=2000	fire=nd>wind	wind<nd	wind=fire=nd
Balsam Fir Tree Density	1965=1983<2000	1965<1983>2000	1965=1983=2000	fire=nd>wind	fire>nd>wind	fire>nd>wind
White Spruce Tree Density	1965<1983=2000	1965=1983<2000	1965=1983=2000	fire=wind<nd	fire=wind=nd	fire=wind=nd
Red Maple Tree Density	1965<1983<2000	1965<1983=2000	1965<1983=2000	fire=nd<wind	nd<fire<wind	fire=wind<nd
Paper Birch Tree Density	1965>1983=2000	1965<2000	1965>1983=2000	nd>fire>wind	nd>fire>wind	fire=wind=nd
Aspen Tree Density	1965=1983>2000	1965=1983=2000	1965>1983>2000	fire=nd<wind	fire<nd<wind	fire<nd<wind
Ash Tree Density	1965=1983<2000	1965<1983	1965=1983=2000	fire>nd>wind	fire>nd>wind	fire=nd>wind
Bur Oak Tree Density	1965=1983<2000	1965=2000<1983	1965=1983=2000	fire=wind=nd	fire=nd>wind	nd>wind
Small Plot Measures	Undisturbed	Fire	Wind	1991	2000	
Tree Seedlings	1991 <2000	1991=2000	1991 <2000	fire=nd<wind	fire=nd<wind	
Sugar Maple Seedlings	1991 <2000	1991=2000	1991 <2000	fire=nd<wind	fire=nd<wind	
Ironwood Seedlings	1991=2000	1991 <2000	1991=2000	fire=nd<wind	fire=nd=wind	

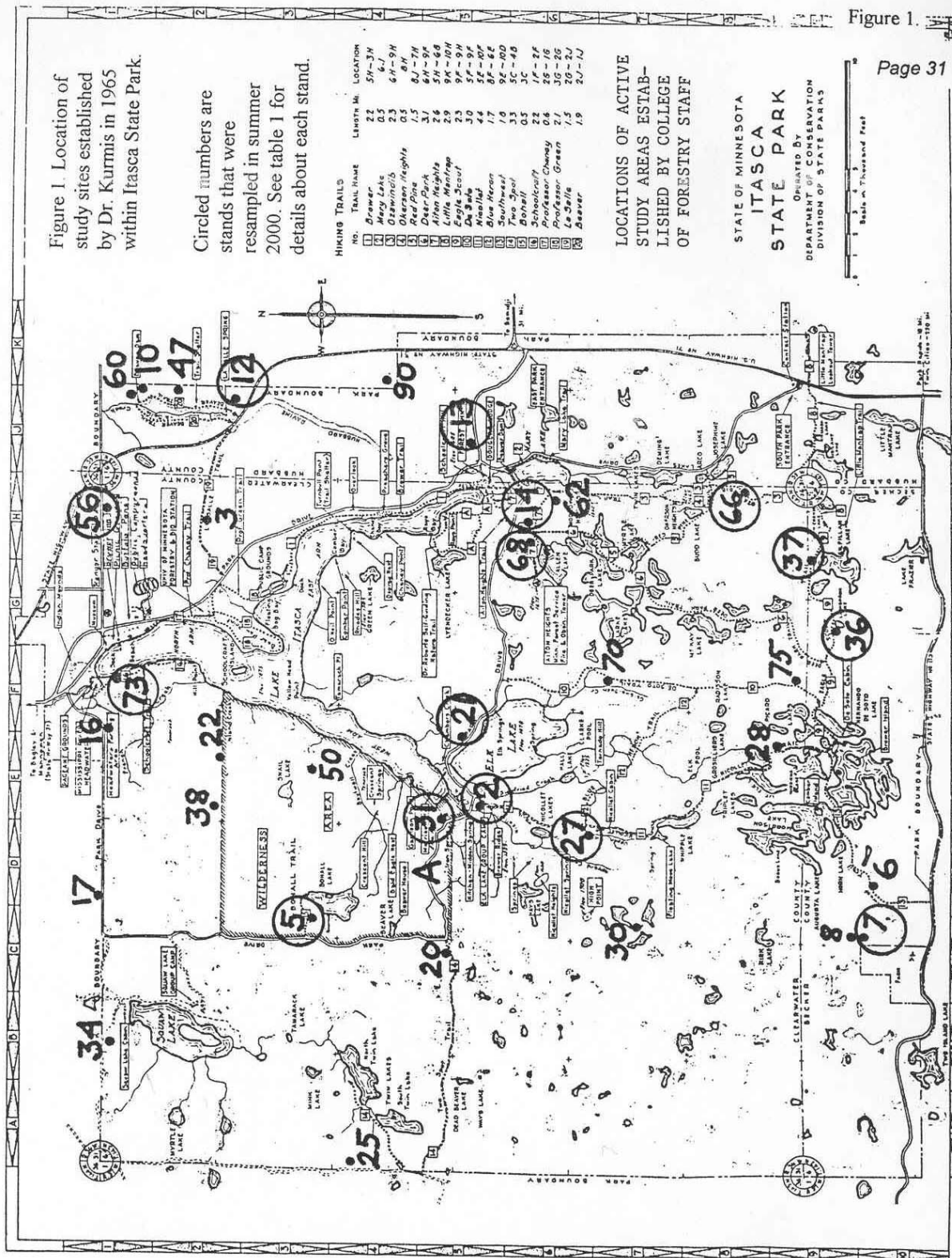


Figure 1.

Figure 2. Changes in total tree density over time by disturbance type, (a) overall for all plots and within four cover types: (b) Jack pine cover type, (c) Red pine cover type, (d) Spruce-fir cover type, (e) Maple-basswood cover type. Note that disturbance events took place in the last time interval.

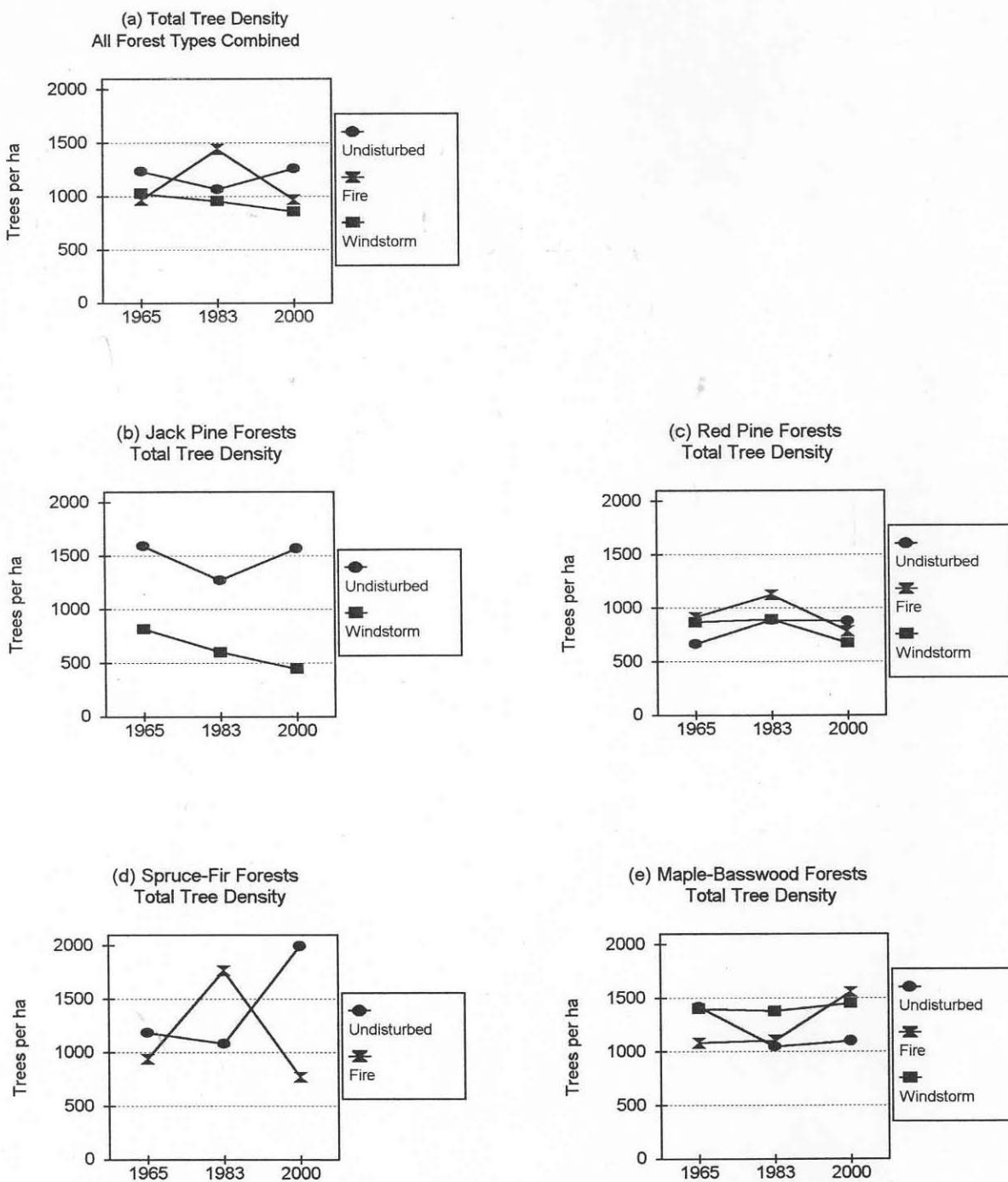


Figure 3. Changes in basal area, a measure of tree biomass, by disturbance type, (a) overall for all plots and within four cover types: (b) Jack pine cover type, (c) Red pine cover type, (d) Spruce-fir cover type, (e) Maple-basswood cover type. Note that disturbance events took place in the last time interval.

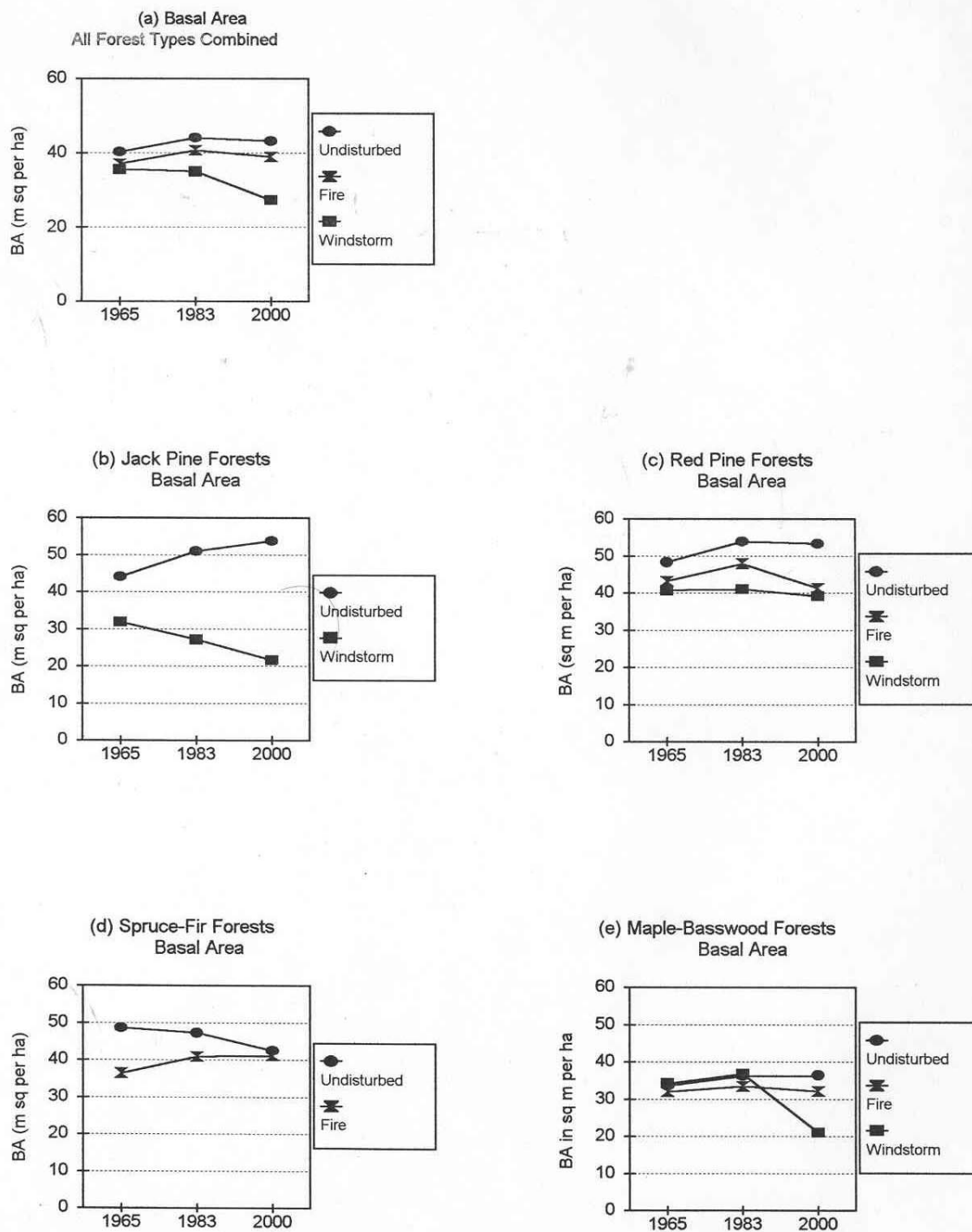


Figure 4. The pines, changes over time for red pine (a) density and (b) basal area; for white pine (c) density and (d) basal area; and for (e) jack pine density. Note different scales for the y-axes.

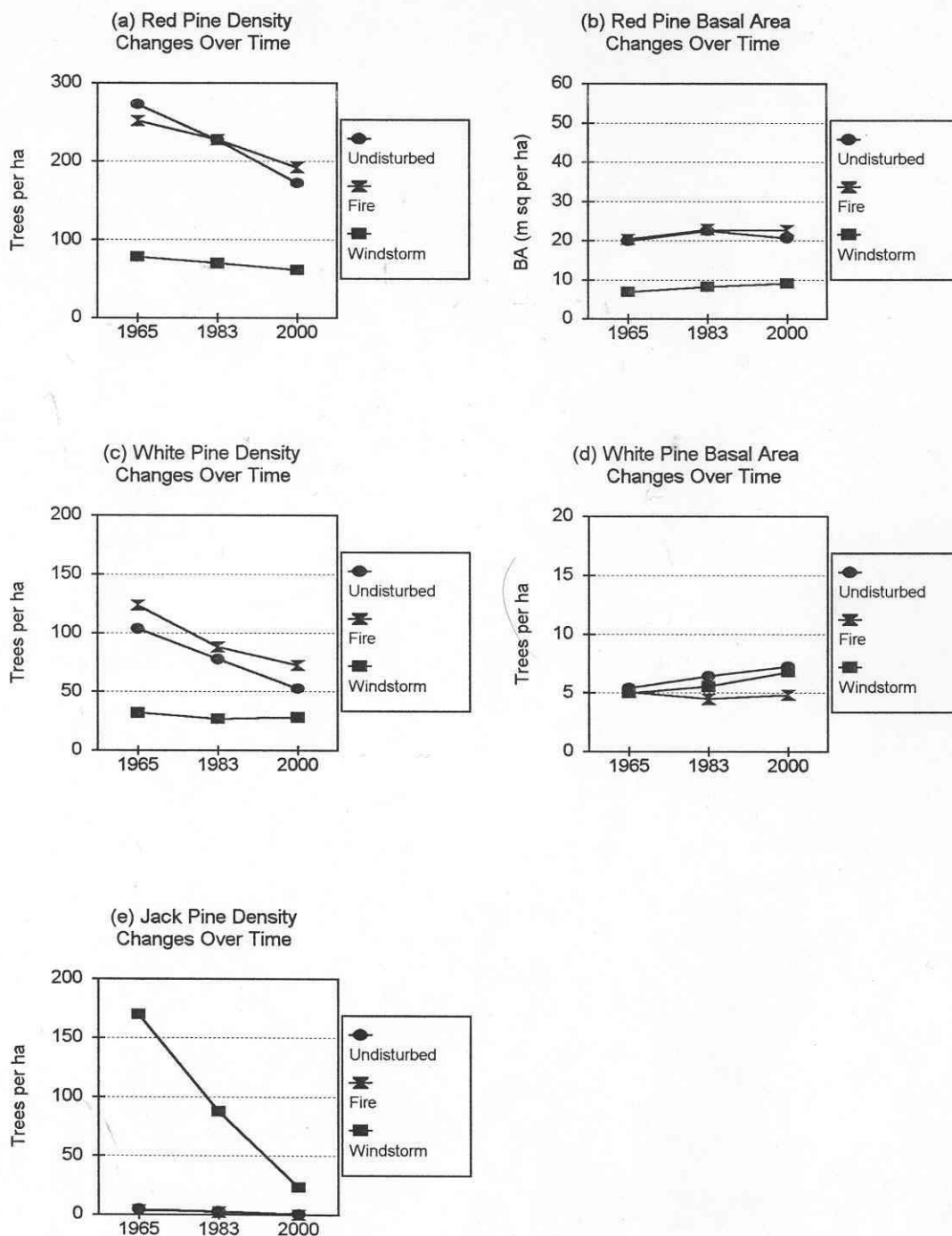
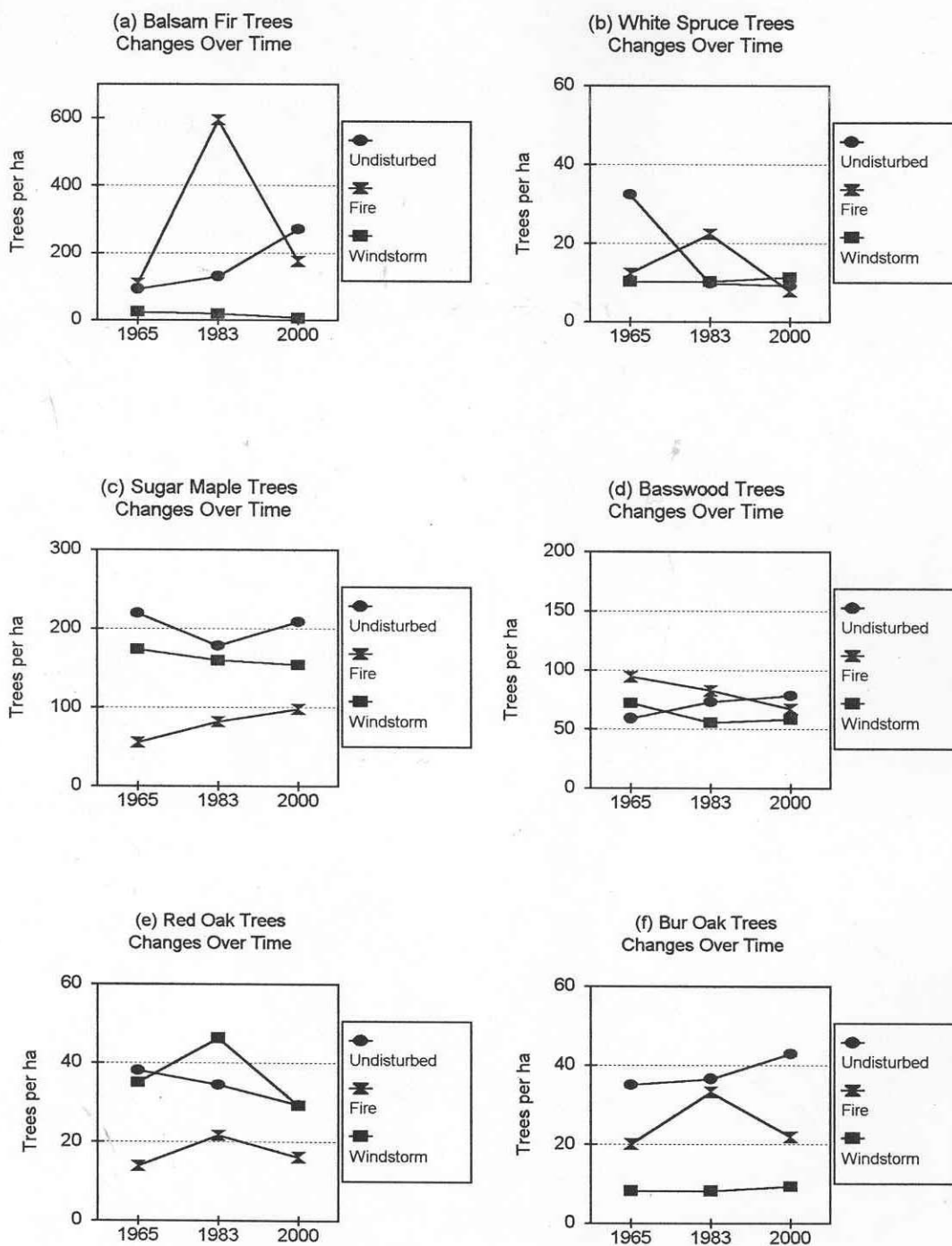


Figure 5. Changes over time for individual tree species by disturbance type. (a) Balsam fir, (b) white spruce, (c) sugar maple, (d) basswood, (e) red oak, (f) bur oak, (g) ironwood, (h) red maple, (i) paper birch, (j) aspen (quaking plus bigtooth aspen). Note shifts in scale of y-axis between graphs.



Continuation of Figure 5. Changes over time for individual tree species by disturbance type. (g) ironwood, (h) red maple, (i) paper birch, (j) aspen (quaking plus bigtooth aspen), (k) ash (green plus black ash combined).

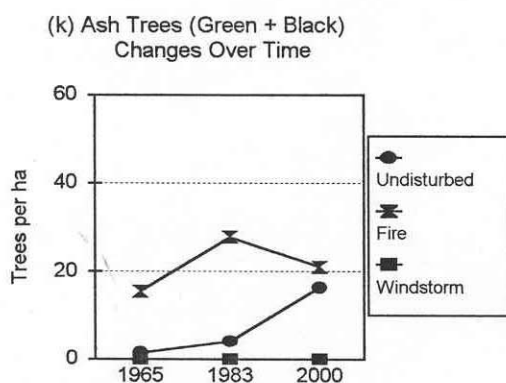
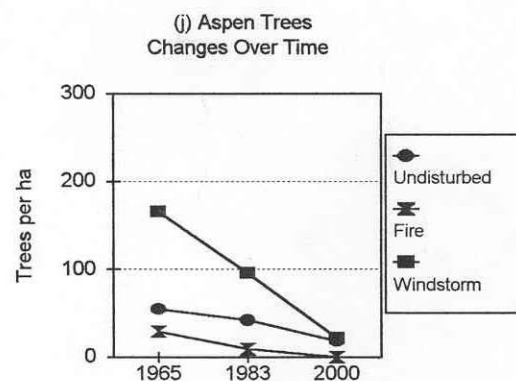
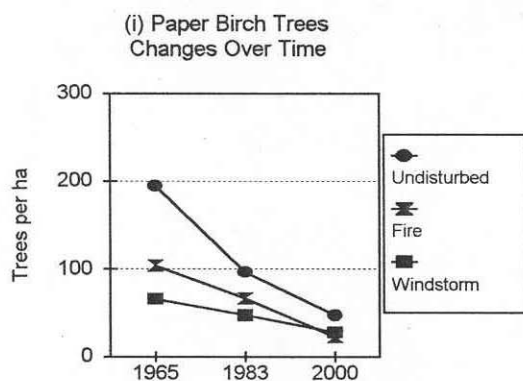
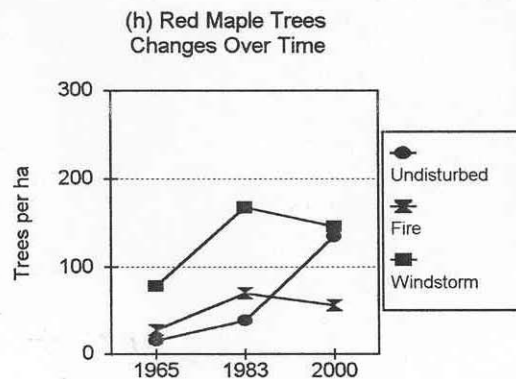
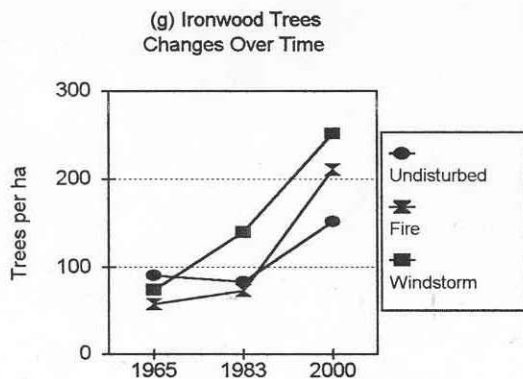


Figure 6. Small woody plants, changes in density over time by disturbance type. (a) Tree seedlings (dbh < 2.5 cm); (b) seedlings of sugar maple alone; (c) tall shrub stems; (d) hazel shrub stems alone; (e) stems of small shrub species and vines.

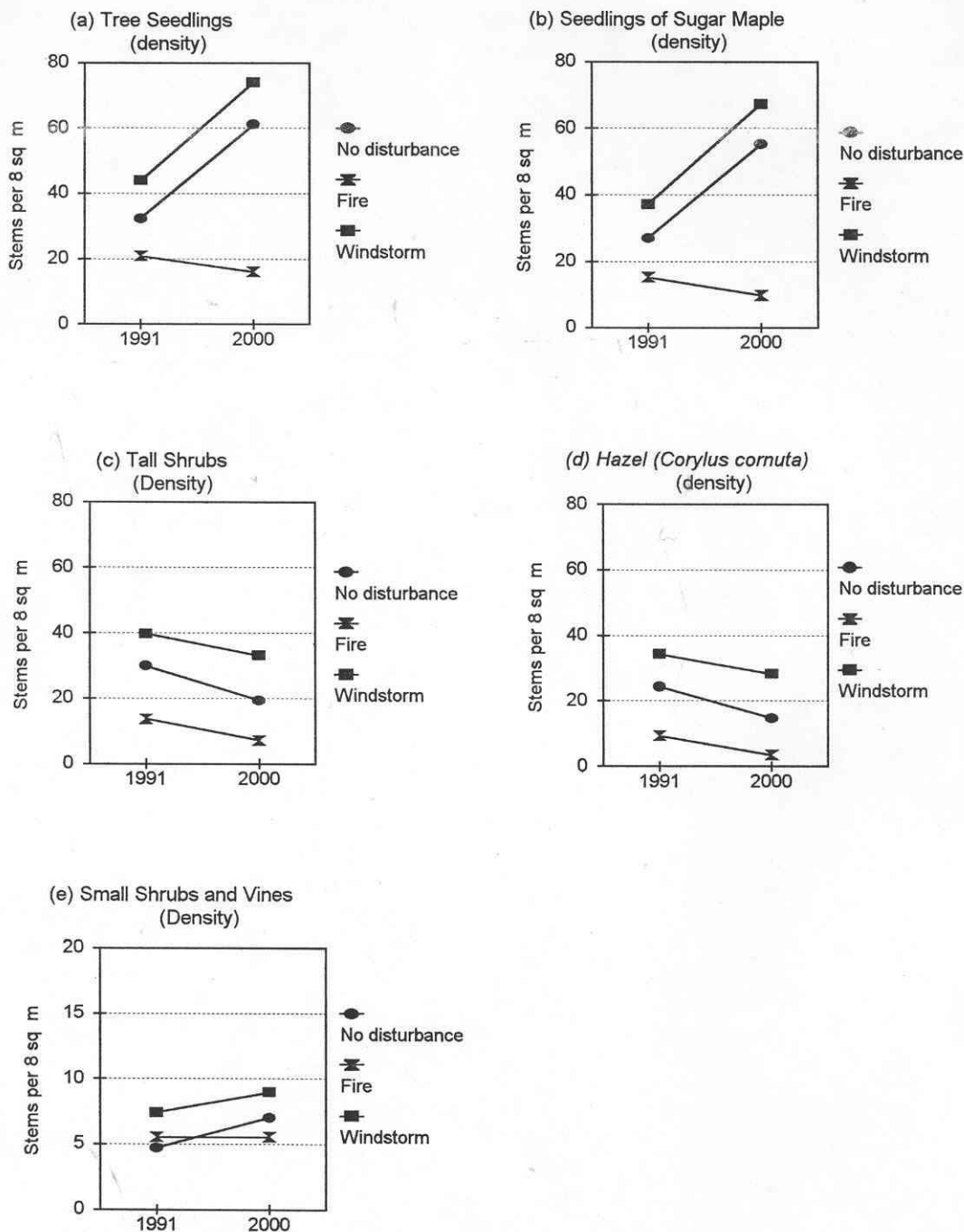
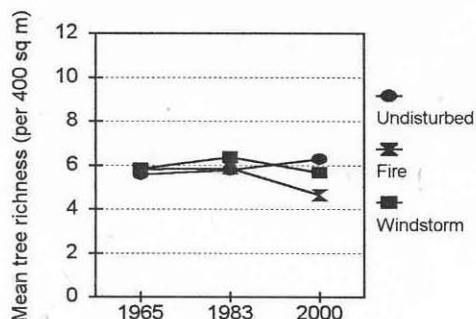
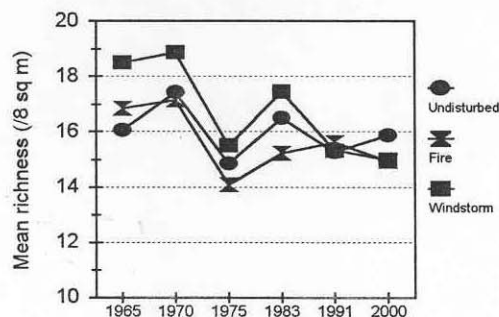


Figure 7. Species richness of various plant life forms, changes over time in relation to disturbance. (a) Tree richness as mean number of tree species present in tree size class ($\text{dbh} \geq 2.5 \text{ cm}$) per 400 m^2 plot, (b) overall species richness as number of plant species per small (8 m^2) plot, (c) richness of forbs (species per small plot), (d) richness of shrubs (species per small plot), (e) richness of tree seedlings (species per small plot). Notice shift in scale of the y-axis for the first two graphs.

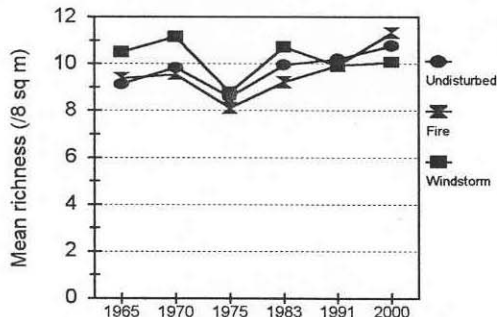
(a) Changes in Tree Species Richness



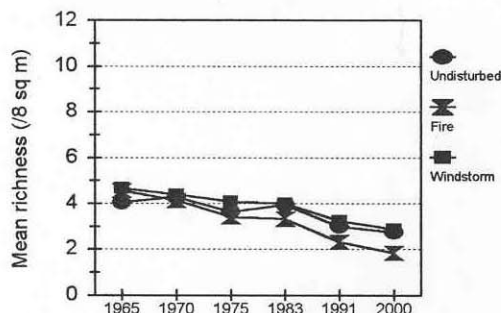
(b) Species Richness in Small Plots



(c) Changes in Forb Richness



(d) Changes in Shrub Richness



(e) Changes in Tree Seedling Richness

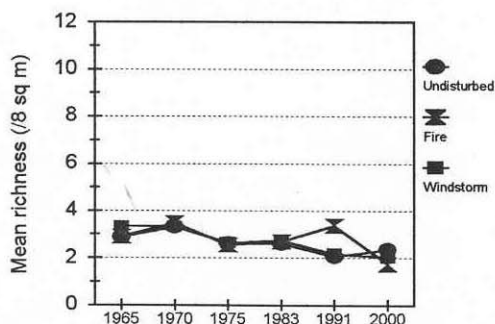
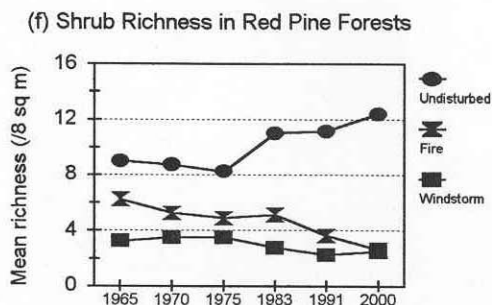
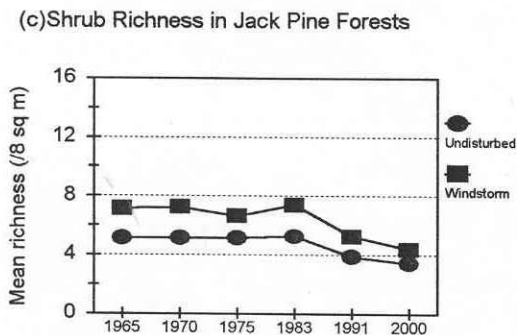
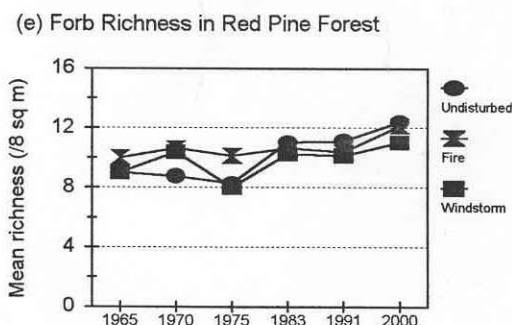
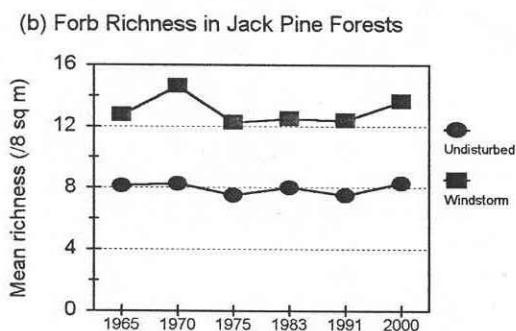
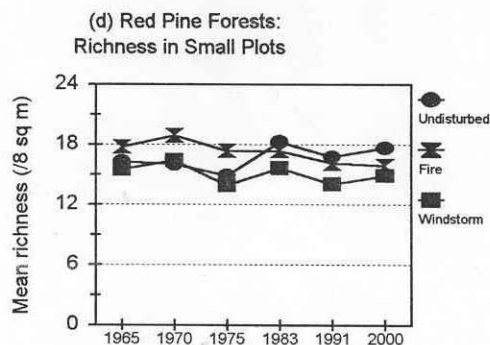
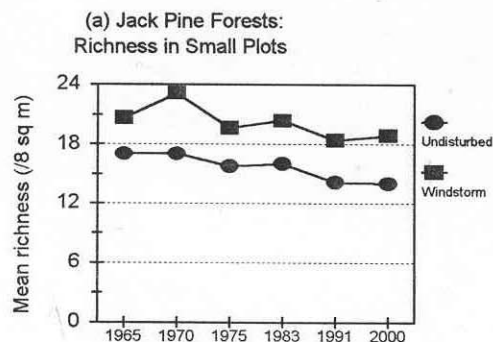
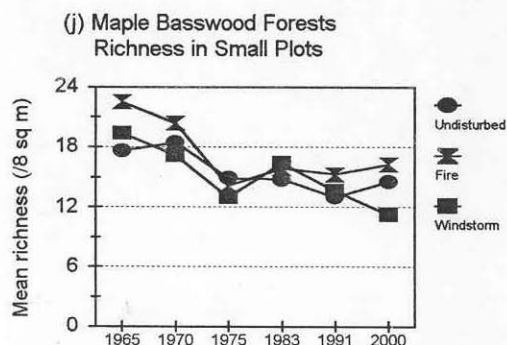
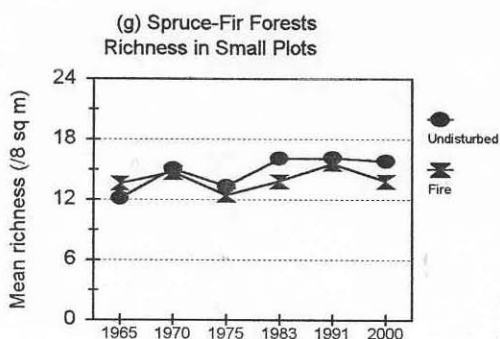


Figure 8. Species richness in small plots by cover type and life form, overall and with separate consideration of forbs and of shrubs. Note that fire and windstorm disturbance occurred in the last time interval only. Note changes in y-axis scale between graphs. For jack pine forest type, (a) overall richness, (b) forb richness, (c) shrub richness. For red pine forest type, (d) overall richness, (e) forb richness, (f) shrub richness. For spruce-fir cover type, (g) overall richness, (h) forb richness, (i) shrub richness. For maple-basswood cover type, (j) overall richness, (k) forb richness, (L) shrub richness.

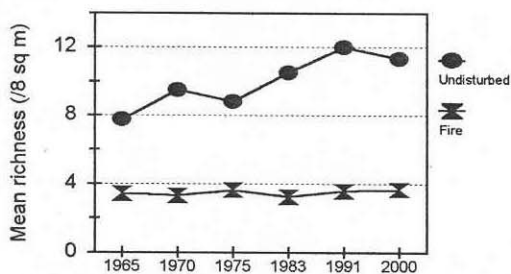


Continuation of Figure 8. Species richness in small plots by cover type and life form, overall and with separate consideration of forbs and of shrubs:

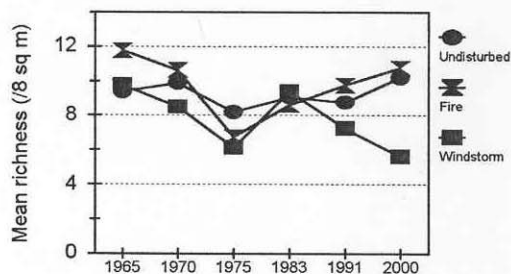
For spruce-fir cover type, (g) overall richness including forbs, shrubs, and tree seedlings; (h) forb richness; (i) shrub richness. For maple-basswood cover type, (j) overall richness, (k) forb richness, (L) shrub richness.



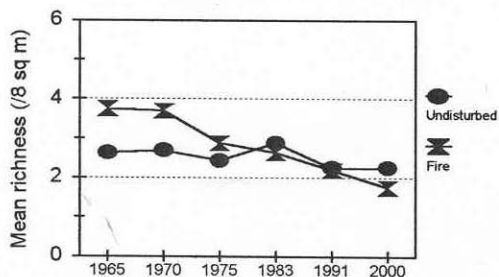
(h) Forb Richness, Spruce-Fir Forests



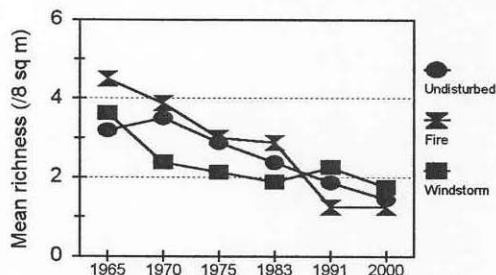
(k) Forb Richness: Maple-Basswood



(i) Shrub Richness: Spruce-Fir Forests



(L) Shrub Richness: Maple-Basswood



Appendix. List of plants in Kurmis Itasca forest project, including common names and growth forms. Old nomenclature revised since the study began is indicated in parentheses. Nomenclature follows Gleason and Cronquist and, for ferns and fern allies, Flora of North America.

Scientific Name	Common Name	Growth Form	VK #
WOODY PLANTS			
<i>Abies balsamea</i>	balsam fir	Tree	4
<i>Acer rubrum</i>	red maple	Tree	14
<i>Acer saccharum</i>	sugar maple	Tree	10
<i>Acer spicatum</i>	mountain maple	Shrub	24
<i>Alnus viridis</i> (=crispa)	green alder	Shrub	32
<i>Alnus incana</i> (=rugosa)	speckled alder	Shrub	25
<i>Amelanchier</i> sp.	juneberry	Shrub	21
<i>Betula papyrifera</i>	paper birch	Tree	8
<i>Carpinus carolinensis</i>	blue beech	Tree	34
<i>Celastrus scandens</i>	bittersweet	Vine	
<i>Corylus americana</i>	American hazel	Shrub	36
<i>Corylus cornuta</i>	beaked hazel	Shrub	30
<i>Cornus alternifolia</i>	pagoda dogwood	Shrub	
<i>Cornus racemosa</i>	no. swam dogwood	Shrub	
<i>Cornus rugosa</i>	round-leaved dogwood	Shrub	23
<i>Crataegus</i> sp.	hawthorn	Shrub	22
<i>Diervilla lonicera</i>	bush honeysuckle	Small shrub	
<i>Dirca palustris</i>	leatherwood	Shrub	
<i>Fraxinus nigra</i>	black ash	Tree	17
<i>Fraxinus pennsylvanica</i>	green ash	Tree	19
<i>Juniperus communis</i>	horizontal juniper	Shrub	
<i>Lonicera canadensis</i>	fly honeysuckle	Small shrub	
<i>Lonicera dioica</i>	wild honeysuckle	Small shrub	
<i>Lonicera hirsuta</i>	hairy honeysuckle	Vine	
<i>Malus baccata</i> (<i>Pyrus</i> sp.)	apple	Tree	
<i>Ostrya virginiana</i>	ironwood	Tree	15
<i>Parthenocissus uin uifolia</i>	Virginia creeper	Vine	
<i>Picea lauca</i>	white spruce	Tree	5
<i>Picea mariana</i>	black spruce	Tree	18
<i>Pinus banksiana</i>	jack pine	Tree	3
<i>Pinus resinosa</i>	red pine	Tree	1
<i>Pinus strobus</i>	white pine	Tree	2
<i>Populus balsamifera</i>	balsam poplar	Tree	9
<i>Populus deltoides</i>	cottonwood	Tree	35
<i>Populus randidentata</i>	bigtooth aspen	Tree	7
<i>Populus tremuloides</i>	quaking aspen	Tree	6
<i>Prunus americana</i>	wild plum	Shrub	26
<i>Prunus Pennsylvanica</i>	pin cherry	Shrub	28
<i>Prunus virginiana</i>	choke cherry	Shrub	20
<i>Prunus serotina</i>	black cherry	Tree	27
<i>Quercus macrocarpa</i>	bur oak	Tree	13
<i>Quercus rubra</i>	red oak	Tree	12
<i>Rhamnus cathartica</i>	buckthorn	Shrub	
<i>Ribes cynosbati</i>	dogberry	Small shrub	
<i>Ribes hirtellum</i>	northern gooseberry	Small shrub	

<i>Ribes triste</i>	swamp red currant	Small shrub	
<i>Ribes sp.</i>	gooseberry	Small shrub	
<i>Rosa acicularis</i>	wild rose	Shrub	
<i>Salix humilis</i>	prairie (upland) willow	Shrub	29
<i>Sambucus pubens</i>	elderberry	Shrub	38
<i>Sorbus cf. americana</i>	mountain ash	Shrub	33
<i>Symphoricarpos albus</i>	snowberry	Small shrub	
<i>Tilia americana</i>	basswood	Tree	11
<i>Toxicodendron radicans</i>	poison ivy	Vine	
<i>Ulmus americana</i>	American elm	Tree	16
<i>Vaccinium angustifolia</i>	dwarf blueberry	Small shrub	
<i>Vaccinium myrtilloides</i>	down dwarf blueberry	Shrub	
<i>Viburnum rafinesquienum</i>	down arrowwood	Shrub	
<i>Viburnum trilobum</i>	high-bush cranberry	Shrub	

FORBS, DWARF SHRUBS, OTHER PLANTS GIVEN % COVER

Scientific Name	Common Name	VK Code
<i>Achillea s p.</i>	yarrow	ACHILANU
<i>Actaea rubra</i>	baneberry	ACTERUBR
<i>Agastache foeniculum</i>	giant hyssop	AGASFOEN
<i>Agrimonia gryposepala</i>	common agrimony	AGRIGRYP
<i>Amphicarpa bracteata</i>	hog peanut	AMPHBRAC
<i>Anaphills margaritacea</i>	pearly everlasting	ANAPMARG
<i>Anemone quinquefolia</i>	wood anemone	ANEMQUIN
<i>Anemone virginiana</i>	tall anemone	ANEMVIRG
<i>Antennaria canadensis</i>	pussy toes	ANTECANA
<i>Apocynum androsaefolium</i>	dog bane	APOCANDR
<i>Aquilegia canadensis</i>	columbine	AQUICANA
<i>Aralia nudicaulis</i>	wild sarsaparilla	ARALNUDI
<i>Aralia racemosa</i>	wild spikenard	ARALRACE
<i>Arctostaphylos uva-ursi</i>	bearberry	ARCTUVA
<i>Arisaema triphyllum (=atrorubens)</i>	jack-in-the-pulpit	ARISATRO
<i>Asarum canadensis</i>	wild ginger	ASARCANA
<i>Aster ciliolatus</i>	northern heart-leaved aster	ASTECILI
<i>Aster laevis</i>	smooth aster	ASTELAEV
<i>Aster lateriflorus</i>	goblet aster	ASTELATE
<i>Aster macrophyllus</i>	large-leaved aster	ASTEMACR
<i>Aster umbellatus</i>	tall flat-topped white aster	ASTEUMBE
<i>Athrium felix-femina</i>	lady fern	ATHYFILI
<i>Botanidium virginianum</i>	rattlesnake fern	BOTRVIRG
<i>Campanula rotundifolia</i>	harebell	CAMPROTU
<i>Chenopodium hybridum</i>	goosefoot	CHENHYBR
<i>Chenopodium simplex (sp. changed?)</i>	goosefoot	
<i>Chimaphila umbellata</i>	pipsissewa	CHIMUMBE
<i>Circaea alpina</i>	alpine enchanters nightshade	CIRCALPI
<i>Circaea lutetiana var. canadensis</i>	common enchanters nightshade	
<i>Clintonia borealis</i>	northern bluebead lily	CLINBORE
<i>Comandra umbellata (=richardsiana)</i>	bastard toadflax	COMARICH
<i>Calystegia spithamea (=Convolvulus spith.)</i>	low bindweed	CONVSPIT
<i>Coptis groenlandica</i>	goldthread	COPTGROE

<i>Cornus canadensis</i>	bunchberry	CORNCANA	
<i>Cynoglossum virginianum</i> (=boreale)	wild comfrey	CYNOBORE	
<i>Cypripedium calceolus</i>	yellow lady slipper	CYPRCALC	
<i>Desmodium glutinosum</i>	tick trefoil	DESMGLUT	
<i>Dryopteris carthusiana</i> (=spinulosa)	toothed woodfern	DRYOSPIN	
<i>Dryopteris</i> sp.	woodfern		
<i>Dryopteris dijuncta</i> now <i>Gymnocarpium djsjuncta</i>	western oak fern	DRYODISJ	
<i>Epilobium angustifolium</i>	fireweed	EPILANGU	
<i>Equisetum arvense</i>	field horsetail		
<i>Equisetum sylvaticum</i>	woodland horsetail	EQUISYLV	
<i>Fragaria vesca</i>	wild strawberry		
<i>Fragaria virginiana</i>	wild strawberry	FRAGVIRG	
<i>Galium boreale</i>	northern bedstraw	GALIBORE	
<i>Galium triflorum</i>	sweet-scented bedstraw	GALITRI2	
<i>Gaultheria procumbens</i>	wintergreen	GAULPROC	
<i>Geranium bicknellii</i>	geranium		
<i>Geranium macrophyllum</i>	wild geranium		
<i>Geum macrophyllum</i>	big-leaved avens		
<i>Goodyera repens</i>	rattlesnake plantain	GOODREPE	
<i>Gymnocarpon dryopteris</i>	oak fern		
<i>Hepatica americana</i>	round-lobed hepatica	HEPAAMER	
<i>Heuchera richardonia</i>	alum root	HEUCRICH	
<i>Hieracium kalmii</i> (=canadense)	Canada hawkweed	HIERCANA	
<i>Hieracium scabrum</i>	sticky hawkweed	HIERSCAB	
<i>Impatiens capensis</i>	jewelweed	IMPACAPE	
<i>Kriga biflora</i>	orange dwarf dandelion	KRIGBIFL	
<i>Lactuca biennis</i>	tall blue lettuce	LACTBIEN	
<i>Lactuca</i> sp.	wild lettuce		
<i>Lathyrus ochroleucus</i>	pale pea	LATHOCHR	
<i>Lathyrus venosis</i>	veiny pea	LATHVENO	
<i>Liatris aspera</i>	blazing star	LIATASPE	
<i>Linnaea borealis</i>	twinflower	LINNBORE	
<i>Lithospermum canescens</i>	hoary puccoon	LITHCANE	
<i>Lycopodium annotinum</i>	stiff clubmoss	LYCOANNO	
<i>Lycopodium clavatum</i>	running pine clubmoss	LYCOCLAV	
<i>Lycopodium complanatum</i> (now <i>Diphasiastrum compl.</i>)	northern round cedar	LYCOCOMP	
<i>Lycopodium obscurum</i> *	princess pine clubmoss	LYCOOBSC	
<i>Lycopus uniflorus</i>	northern water-hound	LYCOUNIF	
<i>Maianthemum canadense</i>	false lily-of-the-valley	MAIACANA	
<i>Malampyron lineare</i>	cow-wheat	MELALINE	
<i>Menthe arvensis</i>	field mint	MENTARVE	
<i>Mitella nuda</i>	bishops cap	MITENUDA	
<i>Moneses uniflora</i>	one-flowered shinleaf	MONEUNIF	
<i>Monotropa uniflora</i>	Indian pipe	MONOUNIF	
<i>Osmorhiza claytoni</i>	bland sweet cicely	OSMOCLAY	
<i>Osmorhiza longistylus</i>	long-styled sweet cicely	OSMOLONG	
<i>Petasites frigidus</i> (=palmatus)	coltsfoot	PETAPALM	
<i>Phryma leptostachya</i>	lopseed	PHRYLEPT	
<i>Physalis virginiana</i>	round cherry		
<i>Pilea pumila</i>	clearweed		
<i>Polygala paucifolia</i>	milkwort		

<i>Polygonatum pubescens</i>	hairy solomons seal	POLYPUBE
<i>Polygonum cilinode</i>	fringed bindweed	
<i>Polygonum convouulus</i>	black bindweed	
<i>Prenanthes alba</i>	rattlesnake root	PRENALBA
<i>Pteridium aquilinum</i>	bracken fern	PTERAQUI
<i>Pyrola asarifolia</i>	pink shinleaf	PYROASAR
<i>Pyrola elliptica</i>	elliptic shinleaf	PYROELLI
<i>Pyrola rotundifolia</i>	rounded shinleaf	PYROROTU
<i>Pyrola secunda</i>	one-sided shinleaf	PYROSECU
<i>Pyrola chlorantha</i> (=virens)	shinleaf	PYROVIRE
<i>Pyrola sp.</i>	shinleaf	
<i>Rubus alleghaniensis</i>	blackberry	RUBUALLE
<i>Rubus pubesens</i>	dwarf red raspberry	RUBLIPUBE
<i>Rubus idaeus</i> (=strigosus)	raspberry	RUBUSTRI
<i>Sanguinaria canadensis</i>	bloodroot	SANGCANA
<i>Sanicula marilandica</i>	black snakeroot	SANIMARI
<i>Senecio pauperculus</i>	northern meadow groundsel	SENEPAUP
<i>Silene latifolia</i> (=Lychnis alba)	white campion	LYCHALBA
<i>Silene sp.</i>	catchfly	
<i>Smilax herbacea</i>	greenbrier	SMILHERB
<i>Smilacina racemosa</i>	false solomons seal	SMILRACE
<i>Smilacina stellata</i>	star-flowered false sol. seal	SMILSTEL
<i>Solidago canadensis</i>	Canada goldenrod	SOLICANA
<i>Solidago flexicaulis</i>	zig-zag goldenrod	SOLIFLEX
<i>Solidago giganteus</i>	smooth goldenrod	SOLIGIGA
<i>Solidago hispida</i>	hairy goldenrod	SOLIHISP
<i>Sonchus sp.</i>	sow-thistle	
<i>Streptopus roseus</i>	twisted stalk	STREROSE
<i>Taraxacum officinale</i>	dandelion	TARAOFFI
<i>Thalictrum dioicum</i>	early meadow rue	THALDIOI
<i>Trientalis borealis</i>	northern star flower	TRIEBORE
<i>Trifolium sp.</i>	clover	
<i>Trillium cernuum</i>	nodding trillium	TRILCERN
<i>Trillium grandiflorum</i>	large flowered white trillium	TRILGRAN
<i>Urtica dioica</i>	stinging nettle	URTIDIOI
<i>Uvularia grandiflora</i>	large-flowered bellwort	UVULGRAN
<i>Uvularia sessilifolia</i>	bellwort	UVULSESS
<i>Vicia americana</i>	American vetch	VICIAMER
<i>Viola adunca</i>	hook-spurred violet	VIOLADUN
<i>Viola canadensis</i>	Canada white violet	VIOLCANA
<i>Viola blanda</i> (=incognita)	sweet white violet	VIOLINCO
<i>Viola pubescens</i>	downy yellow violet	VIOLPUBE
<i>Viola renifolia</i>	kidney-leaved violet	VIOLRENI
<i>Viola sp.</i>	violet	