ICE STORMS AS A DISTURBANCE FACTOR IN APPALACHIAN OAK FORESTS

by

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thesis submitted to the Graduate Faculty of the

Virginia Polytechnic Institute and State University

in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

in

Botany

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May, 1982
Blacksburg, Virginia

MB 8-13-82

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(ABSTRACT)

Ice (glaze) storms are frequent natural disturbances in eastern deciduous forests. Two opposing hypotheses exist in the literature regarding the effect of glaze on forest succession. In the first view, succession is said to be accelerated as pioneer species sustain greater damage than equilibrium species. The resistant equilibrium species would then fill canopy gaps, shifting the stand to a more advanced stage. Alternatively, extensive canopy damage allows more light to reach the forest floor, perhaps favoring the germination and establishment of pioneer seedlings. Survival of these individuals would return the community to an earlier successional stage, or maintain pioneer communities. This study examined the response of the reproduction and susceptibility of tree species (by damage and mortality) two growing seasons after an ice storm, across a moisture and successional gradient. Four stands were studied: *Liriodendron*, mesic and xeric *Pinus*, and *Quercus*.

Damage for most species was consistent across stands, with larger trees generally sustaining greater damage than smaller trees or saplings. Mortality increased with increasing stem size and severity of damage for most species. However, while damage to Liriodendron tulipifera was very high, actual mortality was low due to its ability to sprout. Also, because seedling reproduction of pioneer species was stimulated in this stand, succession appeared to be retarded. Succession was accelerated in the mesic Pinus stand where mortality of canopy trees was high and where removal of the canopy stimulated growth and sprouting of understory equilibrium species. Succession of the stands on drier sites (e.g. Quercus and xeric Pinus) appeared unaffected as the composition of tree seedlings remained essentially unchanged after disturbance. Thus, the response of a community to ice damage depends on the interrelated variables of vegetation composition, successional status, and topographic position.

ACKNOWLEDGEMENTS

I would like to express my sincere appreciation to Dr. W. Carter Johnson for his guidance and assistance during the course of this thesis project. He made it an invaluable and enjoyable learning experience. Thanks are also extended to Dr Terry Sharik and Dr. Ned Fetcher for their suggestions and constructive criticisms of this thesis.

I would also like to thank the many people who have helped me through: Jean Everett, for her field assistance; Tom Finn, Bill Plymale, and Scott Andrews, for their technical assistance. Special thanks go to all the friends for their cheerful encouragement, especially Toni and Lenoor Holthuyzen, Peggy Reily, Susan Darley-Hill, Kevin Morrison, Chris Aas, Steven Miller and Tom Wieboldt.

My parents, Warren A. and Claire A. Whitney, deserve special recognition for encouraging me to pursue my interests in plant ecology. It is to them that I dedicate this work.

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INTRODUCTION

Natural disturbances influence the structure, development and composition of forest communities. Perturbations characterized by frequency, predictability, and intensity vary within the landscape as a function of topography, other environmental variables and attributes of the community itself (White 1979). Natural disturbances recur in many plant communities and when coupled with the vegetation response they initiate, are an integral part of landscape pattern (Loucks 1970, Bormann and Likens 1979, White 1979).

Ice storms are perturbations which influence the dynamics of forest ecosystems (Abell 1934, Lemon 1961, Siccama et al. 1976, White 1979). Glaze or ice storms, are a recurring phenomenon in most deciduous forests of North America (Abell 1934, Bennett 1959, Lemon 1961). In the United States, a gradient of increasing frequency and intensity extends from the southwest to the northeast, with most of the Eastern Deciduous Forest Biome in a zone of heavy to moderate glaze (Lemon 1961).

Severe glaze storms, while infrequent and unpredictable events, cause extensive mechanical damage to vegetation. The severity of damage varies greatly over short distances, depending on microclimate, amount of precipitation, duration of ice on trees, stand density, tree species and size (Bennett 1959, Brender and Romancier 1965, Shepard 1975). Damage to forest communities is intensified when glaze deposition is followed by strong winds (Carvell et al. 1957, Bennett 1959, Lemon 1961). The poor form of trees in many Appalachian oak forests is thought to result primarily from repeated damage by ice storms, with site quality and growth form secondary factors (Abell 1934, Carvell et al. 1957).

Glaze is deposited when supercooled rain freezes on surfaces with temperatures below 0°C (Bennett 1959). In general glaze develops when a winter warm front follows ground temperatures that are below freezing. The type of ice formed (hoar, rime, glaze) depends on the rate of freezing, drop size, rate of fall, and degree of supercooling (Bennett 1959). A slow rate of freezing, large drop size, rapid fall rate and a slight supercooling favor glaze formation.

Ice loads commonly range from 13-15 times twig or branch weight (Bennett 1959). However, Rogers (1923) reported ice loads of thirty times the original weight of twigs in a Wisconsin storm. Glaze accumulation of 0.5 to

1.0 cm results in the breakage of small branches on trees or shrubs (Bennett 1959). Dead branches are particularly susceptible, resulting in natural pruning (Lemon 1961). Accumulations of up to 2.5 cm cause breakage of large branches which generally break before the main bole. Trees may overturn, break off, or bend to the ground under heavy ice loads.

Although the relative susceptibility to breakage among tree species has been studied (Rogers 1923, Downs 1938, Croxton 1939, Carvell et al. 1957, Lemon 1961, Siccama et al. 1976), there is considerable disagreement among investigators because damage sustained is related to a complex of factors. The branching pattern, crown pattern, stand exposure, tree height, tree vigor, wood strength, density, and taxonomic group are often cited as important factors (Bennett 1959, Shepard 1975). Generally, species with few stout twigs (*Quercus* spp., *Carya* spp.,) or short limbs are more resistant than those with many fine twigs (*Ulmus* spp., *Betula* spp.). The excurrent growth form of *Picea* spp. and other conifers permits heavier ice loads without damage, as the bending load changes to a pulling load (Rogers 1923). *Pinus* spp. and *Tsuga* spp., however, have a larger foliar surface not supported by strong branches which often results in extensive damage (Lemon 1961). Carvell et al. (1957) reported that conifers suffer less damage because their smaller crowns support ice loads, while deciduous species, with slender boles, brittle branches, and large crowns with deliquescent branching patterns, are more easily broken. The high resistance of oaks is attributed to wood strength and not to branching pattern or flexibility (Lemon 1961).

Two opposing hypotheses exist in the literature concerning the effects of ice storms on forest succession. The first, based on immediate post-storm sampling of successional stands, is that dominant pioneer species sustain greater canopy and bole damage than do other overstory and understory equilibrium species. The more resistant equilibrium species then gain a competitive advantage and fill canopy gaps, shifting the stand rather rapidly to a more advanced successional stage. This view, that ice storms accelerate forest succession, is supported by Abell (1934), Carvell et al. (1957), and Lemon (1961).

The alternate view is that extensive canopy damage allows more light to reach the forest understory, thereby favoring reproduction of pioneer species. Rapid growth of pioneer species would increase the abundance of the pioneer component and effectively return the community to an earlier successional phase. In this view (Downs 1938), ice storms rejuvenate pioneer ecosystems. Siccama et al. (1976) reported that damage to overstory species retarded succession in stands with dense liana (*Vitis* spp.) growth.

In an attempt to resolve the two opposing hypotheses, a study was conducted in the forests of southwestern Virginia which experienced a severe ice storm in January 1979. Previous studies have been limited to observations immediately following storms, with out quantitative sampling of seedling response or mortality of damaged trees in subsequent growing seasons. The major objective of this study was to examine the response of tree reproduction to canopy disruption across a range of site conditions by the second year following the ice storm. A secondary purpose was to identify the relative susceptibility of tree species to damage and mortality by glaze.

SITE DESCRIPTION

The study area was located in the Ridge and Valley Physiographic Province in southwestern Virginia (Figure 1a). Heavy glaze was deposited in a narrow band at mid to upper slope positions, mostly on southeasterly exposures. The storm damaged approximately 20,000 ha of forest (10% of the total) in the Blacksburg District of the Jefferson National Forest (USDA Forest Service, personal communication), but also caused extensive damage to Virginia Piedmont forests. Four ice damaged sites, each 5 - 10 ha in size, were sampled during the second growing season (June to September 1980) following the ice storm (Figure 1b). Canopy vegetation of the stands was dominated (species >100 importance value (IV); maximum value 300) by *Liriodendron tulipifera* L. (*Liriodendron* stand), *Quercus* spp. (*Quercus* stand), and *Pinus virginiana* Mill. (xeric (*Pinus* and mesic *Pinus* stands) (Table 1). The *Liriodendron* and mesic *Pinus* stands were on mesic sites with successional vegetation. The other two stands occupied more xeric sites with vegetation thought not to be strongly successional (Ross et al. 1982).

The sites form a gradient of available moisture, from *Liriodendron* with a Forest Productivity Index Value (Smith and Burkhart 1976, Wathen 1977, Meiners 1982) of 11, to the xeric *Pinus* site with an index value of 7. The mesic *Pinus* and *Quercus* sites had intermediate index values of 10 and 8,

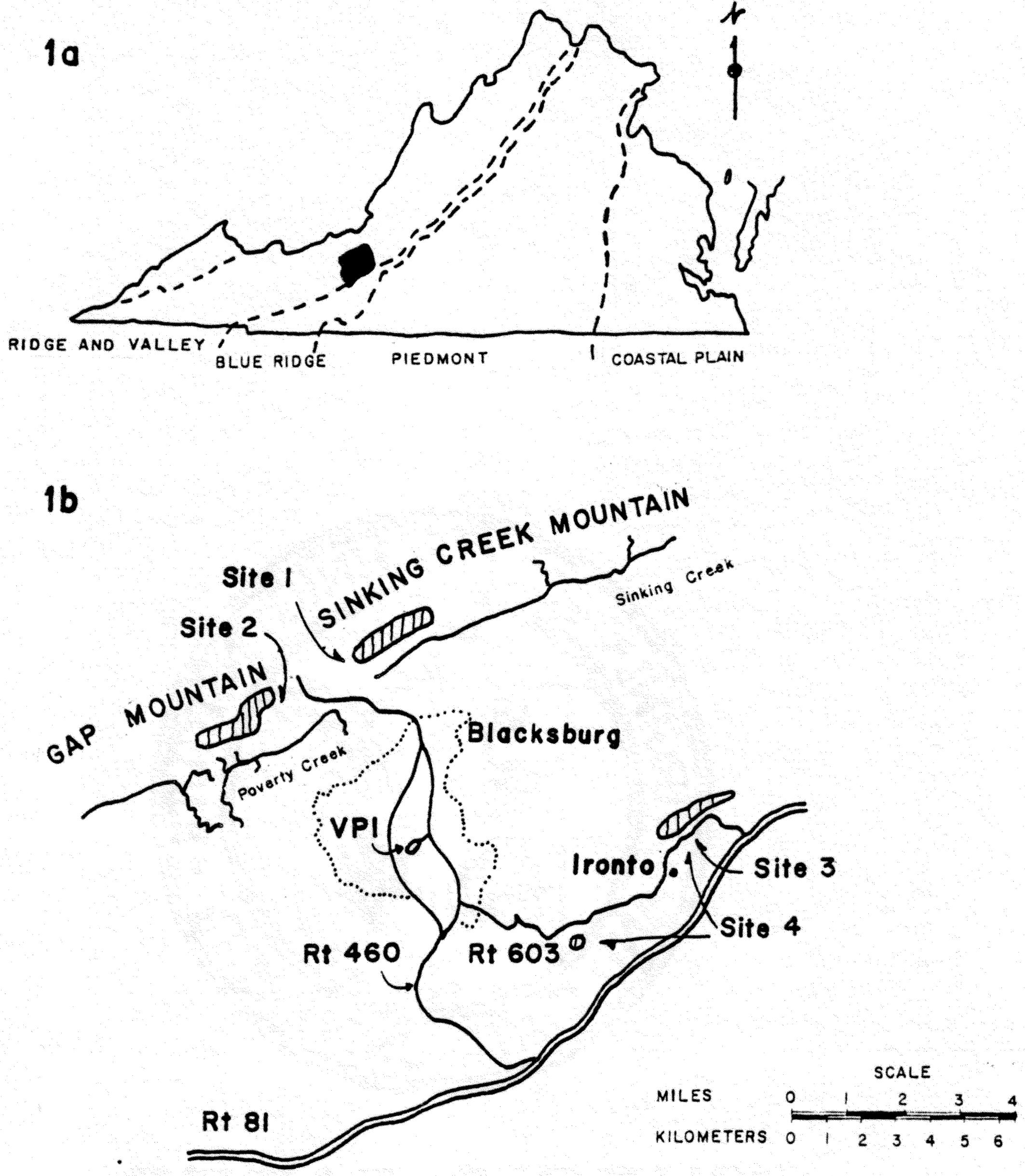

Figure 1. Location of the study sites in Montgomery County in the Ridge and Valley geologic province in southwestern Virginia. Site 1 includes the Liriodendron ice damaged and reference stands, on Sinking Creek Mountain. Site 2 includes the Quercus ice damaged and reference stands, on Gap Mountain. Site 3 includes the Mesic Pinus ice damaged and reference stands in Ironto. Site 4 includes the Xeric Pinus ice damaged and reference stands in Ironto with 4 additional plots located in the Falls Ridge Nature Conservancy.

Table 1. Study areas arranged along a moisture gradient from mesic to xeric, indicating the vegetation type, dominant tree species and topographic features.

Site No.	Vegetation Type	Condition	Dominant Species	Aspect	Slope Inclination (%)	Slope Position	Elevation	Bedrock	FPI
1	*Liriodendron*	Damaged	*L. tulipifera*	SE	24	Backslope	700-900 m	sandstone	11
1	*Liriodendron*	Reference	*L. tulipifera*	SE	23	Backslope	650-700 m	sandstone	11
3	Mesic *Pinus*	Damaged	*Pinus virginiana*	SE	34	Backslope	430-500 m	shale	10
3	Mesic *Pinus*	Reference	*Pinus virginiana*	SE	30	Backslope	400-450 m	shale	10
2	*Quercus*	Damaged	*Quercus prinus* *Q. velutina*	SE	39	Backslope	700-900 m	sandstone	8
2	*Quercus*	Reference	*Q. alba* *Q. prinus*	SE	25	Backslope	650-700 m	sandstone	8
4	Xeric *Pinus*	Damaged	*Pinus virginiana*	SE	30	Shoulder	490-550 m	shale	7
4	Xeric *Pinus*	Reference	*Pinus virginiana*	SE	30	Shoulder	490-550 m	shale	7

respectively. The FPI index is based on topographic variables which influence tree growth such as slope position, degree of inclination and aspect. Meiners (1982) demonstrated a strong positive relationship between FPI values and gravimetrically determined soil moisture on a range of sites underlain by sandstone in southwestern Virginia.

The successional status of each site was based on compositional differences between the overstory and understory. In the *Liriodendron* and mesic *Pinus* sites, the canopy dominants, yellow poplar (*Liriodendron tulipifera*) and Virginia pine (*Pinus virginiana*) were only reproducing poorly in their respective communities. Equilibrium (self-maintaining) species, primarily oaks, comprised the understory in both stands which suggested that they would eventually replace the current overstory, although yellow poplar may remain as a minor component of the equilibrium community because of its colonization potential and longevity (Skeen et al. 1980). In the *Quercus* and xeric *Pinus* sites, significant temporal shifts in composition are unlikely; species composition was similar for both the overstory and understory. The canopy dominants, Virginia pine and table mountain pine (*Pinus pungens* Lambert) maintain themselves on xeric sites (Zobel 1969, Ross et al. 1982).

METHODS

In each stand, five sampling transects were placed in a stratified random design, generally parallel to each other and to topographic contours (Figure 2). Six 1/20 ha macroplots were randomly selected within 50 m strata along A nested design was used to sample the vegetation. Trees > 10 cm diameter at breast height (dbh) were tallied by species, damage class, and mortality class in each macroplot. Importance values (IV) were determined for each species by summing the relative basal area, density and frequency of occurrence (maximum = 300). Stems < 10 cm dbh or >1 m in height were recorded by species, damage class, and mortality class in each of three randomly located 1/500 ha understory plots.

All trees and saplings sampled in the damaged stand were assigned to damage and mortality classes. Stems with no apparent damage or < 50% crown loss were placed in class 1; permanently bent or strongly leaning, but not broken, in class 2; >50% crown loss through the removal of major branches or bole breakage, class 3; and fallen stems, class 4. Trees that appeared to have died from ice damage were coded as mortality class 1; live, heavily damaged trees with little sprouting, class 2; and undamaged or damaged but vigorously sprouting trees, class 3. A spherical densiometer (Lemmon 1956) was used to estimate canopy cover

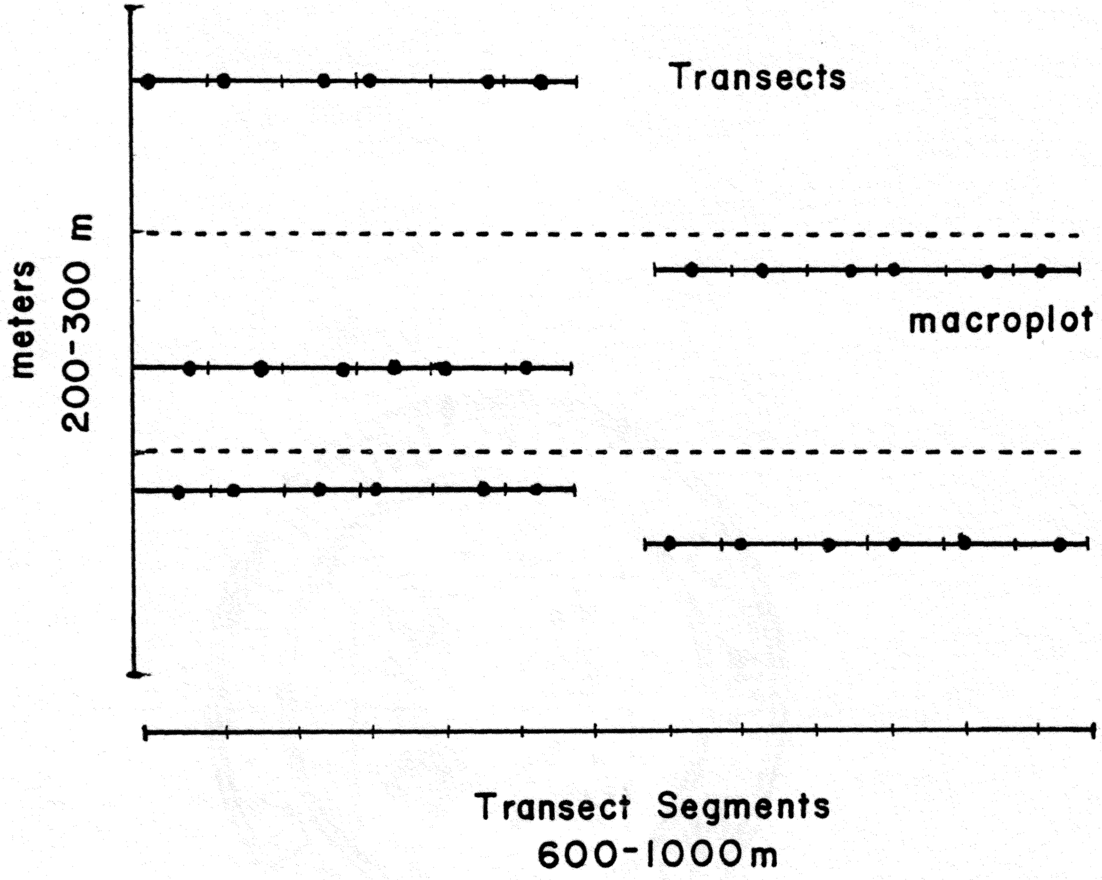

Figure 2. Diagrammatic stand showing an example of the stratified random sampling design.

in each macroplot.

Tree reproduction (stems < 1 m in height) was sampled along four transects radiating from the macroplot center. A transect was randomly located within each 90° quadrant, and five 1 m^2 circular plots were randomly placed along each transect resulting in a total of 20 plots per macroplot. Seedlings were counted and identified to species. Total ground cover by herbaceous plants was also recorded. Age of each stem was estimated from terminal bud scars to distinguish pre-storm from post-storm reproduction. Age of stems with indistinct terminal bud scars was determined from growth rings. Sprout or seedling origin was determined, as well as current year's height growth, height growth of the previous growing season (1979) and total height. A seedling was defined as an individual which had never died back. A seedling-sprout was considered to be an individual that had sprouted from an older stem.

Reference sites were selected for comparison with damaged sites. As the damage was predominantly in a narrow band on mountainsides, adjacent undamaged reference sites could usually be found at slightly lower elevations where differences in species composition, past disturbance, topography and other site factors were minimized. When adjacent sites were unsuitable, nearby nonadjacent plots were selected. The term reference was used rather than control because there were small differences in vegetation between sites (see Table 2, Results and Discussion). Sampling techniques in the reference stands were the same as those used in the damaged stands. Damage stands were reconstructed to approximate pre-storm conditions to evaluate the comparability of reference stands and damaged stands. Reconstruction was performed by including all trees damaged or killed in stand estimates of frequency, density, and basal area.

The effect of disturbance on forest structure was illustrated by constructing forest profiles corresponding to the method described by Halle et al. (1978) and Oldeman (1979) and applied to Appalachian oak forests by Oosterhuis et al. (1982). A representative area was selected within each stand. Within the profile sample area, a 10 x 30 m transect was laid out perpendicular to the topographic contours. If the height of canopy trees was less than 20 m as in the mesic *Pinus* and xeric *Pinus* stands, the dimensions of the transect were reduced to 5 x 15 m to obtain the same degree of biological complexity (Oldeman 1979). Slope was measured at each 10 m interval along the transect in order to develop a topographic profile. Dead or swept trees, branches, large boulders, and depressions were marked on a ground plan of the transect. Each tree over 5 m tall was identified, located in position, and its crown projected onto the ground plan. Field sketches were made of individual trees as viewed from the baseline. Total height, height to the first fork and/or lowest living branch, other structural reference points and dbh of each tree were measured. Field work was carried out in non-growing season months (fall 1980, early spring 1981). Profile diagrams were constructed from field measurements.

RESULTS AND DISCUSSION

Stand characteristics

A comparison of structural characteristics between reconstructed (pre-storm) damaged and reference sites showed few statistically significant differences (Table 2). Basal area was significantly different ($P < 0.05$) only between the *Quercus* damaged and reference stands. The only significant difference between stem density of damaged and reference stands occurred in the mesic *Pinus* site. This may have been due to the selection of the mesic *Pinus* reference stand from a nearby community as adjacent undamaged areas were unavailable.

Approximately one-third of the canopy of each stand was removed by the ice storm; the residual canopy of all damaged stands ranged from 54-67%, indicating the uniformity of damage sustained by each of the stands selected for study. The highest pre-storm canopies were in the *Quercus* and *Liriodendron* reference stands, with 94% and 93% canopy cover respectively, followed by the xeric and mesic *Pinus* stands with 90% and 85%. Damage reduced the canopy cover to 67% in the *Quercus* stand, 61% in the *Liriodendron* stand, 56% in the mesic *Pinus* and 53% in the xeric *Pinus* stands. Some differences in damage among stands were expected due to the local nature of the storm and varying resistance of canopy

Table 2. Structural characteristics (means and standard errors) of ice damaged and reference stands arranged from mesic to xeric sites. Trees include stems ≥ 10 cm dbh. Basal area and density were reconstructed for damaged stands to approximate pre-storm conditions. Significance was determined using the Student's t-test in SAS (Helwig et al. 1979). The sample size, n, represents the number of macroplots within each vegetation type.

Vegetation type	Basal area (m^2/ha)	Level of Sign.	Stem density (no./ha)	Level of sign.	Sample size (n)
Liriodendron					
Damaged	32.2 ± 1.0	NS	698.2 ± 32	NS	30
Reference	27.8 ± 0.9		622.0 ± 13		10
Mesic *Pinus*					
Damaged	21.2 ± 1.3	NS	1306.0 ± 68	$P < .05$	15
Reference	20.1 ± 1.6		976.0 ± 42		10
Quercus					
Damaged	29.1 ± 0.9	$P < .05$	666.0 ± 32	NS	30
Reference	24.1 ± 1.2		660.3 ± 26		10
Xeric *Pinus*					
Damaged	28.2 ± 0.9	NS	1346.8 ± 52	NS	15
Reference	24.0 ± 2.1		1045.0 ± 54		10

species. The percent canopy cover for damaged stands, however, included two years (post-storm) regrowth; canopy cover measured immediately after the storm would have been somewhat less.

To further evaluate the comparability of reconstructed damaged stands with reference stands, canopy species were ranked by importance value (IV), and the rankings compared statistically (Tables 3-6). Dominance relationships between reconstructed damaged and reference stands were most similar for the *Liriodendron* site (r = 0.90) followed by xeric *Pinus* (r = 0.85), *Quercus* (r = 0.71) and mesic *Pinus* (r = 0.54). In the *Liriodendron* site (Table 3), the damaged and reference stands shared the same four leading dominants. Positions of red maple (*Acer rubrum* L.) and white oak (*Quercus alba* L.) were reversed. Sourwood (*Oxydendrum arboreum* (L.) D.C.) was more important in the damaged stand (IV = 8.5 vs 1.2). Overall, the differences in ranking occurred mostly among species with very low importance values (e.g., IV = 1-5).

In the xeric *Pinus* site, Virginia pine was the leading dominant in both the reconstructed damaged and reference stands (Table 4). Oaks characteristic of dry sites and other pine species were important in both stands; pitch pine (*Pinus rigida* Mill.) was more important in the reference stand and table mountain pine was more important in the pre-storm damaged stands. Other differences in ranking occurred

Table 3. Importance values for overstory species (dbh ≥ 10 cm) occurring in the *Liriodendron* stand. Differences in species ranking between reference and reconstructed damaged stands were tested using Spearman rank correlation (r) in SAS (Helwig et al. 1979). An Index of Similarity (IS) was calculated between damaged and reference stands (Sorensen 1948). Initials following the species name identify species in Figure 6.

Species	Damaged stand	Reference stand
L. tulipifera (L.t.)	121.6	118.5
Quercus velutina (Q.v.)	49.1	49.3
Q. prinus (Q.p.)	27.6	34.7
Carya spp. (C.s.)	24.0	28.4
Acer rubrum (A.r.)	21.8	17.9
Quercus alba (Q.a.)	19.0	18.9
Q. coccinea (Q.c.)	9.5	12.2
Oxydendrum arboreum (O.a.)	8.5	1.2
Robinia pseudoacacia (R.p.)	8.1	7.2
Sassafras albidum (S.a.)	3.2	6.1
Betula lenta (B.l.)	2.6	-
Nyssa sylvatica (N.s.)	1.8	1.7
Quercus rubra (Q.r.)	1.6	-
Acer saccharum (A.s.)	0.5	-
Magnolia accuminata (M.a.)	0.5	2.2
Cornus florida (C.f.)	0.5	1.7

r = 0.90

IS = 0.93

note: *Carya cordiformis*, *C. glabra*, *C. ovata*, and *C. tomentosa* were grouped together as *Carya* spp.

Table 4. Importance values for overstory species (dbh $\geq$ 10 cm) occurring in the xeric *Pinus* stand. Differences in species ranking between reference and reconstructed damaged stands were tested using Spearman rank correlation (r) in SAS (Helwig et al. 1979). An Index of Similarity (IS) was calculated between damaged and reference stands.

Species	Damaged stand	Reference stand
Pinus virginiana (P.v.)	155.8	188.2
P. pungens (P.p.)	55.4	17.1
Quercus prinus (Q.p.)	18.9	19.2
Q. coccinea (Q.c.)	18.7	15.2
Q. velutina (Q.v.)	10.2	7.8
Q. alba (Q.a.)	8.2	10.3
Pinus rigida (P.r.)	7.0	29.7
Nyssa sylvatica (N.s.)	3.9	2.1
Oxydendrum arboreum (O.a.)	3.3	1.9
Prunus serotina (P.s.)	3.2	-
Robinia pseudoacacia (R.p.)	2.4	1.8
Acer rubrum (A.r.)	2.1	1.8
Pinus echinata (P.e.)	2.1	-
L. tulipifera (L.t.)	2.1	-
Pinus strobus (P.s.)	1.3	1.0
Cornus florida (C.f.)	1.1	1.0
Quercus falcata (Q.f.)	1.1	1.0
Sassafras albidum (S.a.)	1.1	1.0
Carya spp. (C.s.)	1.1	0.9
Quercus stellata (Q.s.)	1.1	-

r = 0.85

IS = 0.81

Table 5. Importance values for overstory species (dbh $\geq$ 10 cm) occurring in the *Quercus* stand. Differences in species ranking between reference and reconstructed damaged stands were tested using Spearman rank correlation (r) in SAS (Helwig et al. 1979). An Index of Similarity (IS) was calculated between damaged and reference stands.

Species	Damaged stand	Reference stand
Quercus prinus	91.7	81.9
Q. velutina	88.2	60.4
Carya spp.	31.4	11.6
Quercus alba	25.7	87.9
Q. coccinea	18.3	28.5
Acer rubrum	9.5	4.5
Oxydendrum arboreum	8.2	2.4
Pinus virginiana	5.8	-
Robinia pseudoacacia	4.5	5.1
Sassafras albidum	3.4	-
Quercus rubra	2.7	-
Nyssa sylvatica	2.6	4.8
Pinus echinata	2.5	-
Cornus florida	1.4	2.4
Acer saccharum	1.3	-
L. tulipifera	0.9	-
Acer pennsylvanicum	0.7	-
Pinus rigida	0.6	8.0
Prunus serotina	0.6	-
Fraxinus americana	-	2.4

r = 0.71

IS = 0.71

Table 6. Importance values for overstory species (dbh ≥ 10 cm) occurring in the mesic *Pinus* stand. Differences in species ranking between reference and reconstructed damaged stands were tested using Spearman rank correlation (r) in SAS (Helwig et al. 1979). An Index of Similarity (IS) was calculated between damaged and reference stands.

Species	Damaged stand	Reference stand
Pinus virginiana	218.7	208.3
Quercus coccinea	17.3	28.7
Pinus rigida	13.7	21.8
Pinus strobus	9.3	4.0
Carya spp.	9.3	4.0
Quercus stellata	8.9	4.0
Q. prinus	6.7	4.0
Pinus pungens	6.6	16.4
Quercus alba	4.7	4.6
Q. velutina	2.4	-
Q. falcata	-	4.0

r = 0.54

IS = 0.89

primarily among species with low importance values.

At the *Quercus* site, the same five species of oak and hickory dominated the reconstructed damaged and reference stands, but the rankings differed among species (Table 5). For example, white oak was the leading dominant in the reference stand but was ranked fourth in the damaged stand, while hickory was ranked third in the damaged stand and fifth in the reference stand. Species richness was greater in the damaged stand, also affecting the rankings and statistical correlation.

The lowest statistical correlation ($r = 0.54$) occurred between the importance value rankings of mesic *Pinus* reconstructed damaged and reference stands (Table 6). However, the stands were more similar in vegetation than reflected by the ranking tests. For example, the three leading dominants were the same in each stand, comprising 83-86% of the IV. The disparity in rankings occurred among species with small importance values which lowered the correlation.

Therefore, an Index of Similarity ($IS = 2c/a+b$, Sorensen 1948) was used to compare species composition between reconstructed damaged and reference stands of each vegetation type. The similarity score for the mesic *Pinus* site of 0.89 indicated a strong similarity in IV between the damaged and reference stands based on species dominance.

Similarity scores for all other sites paralleled results obtained with the ranking procedure. For example, a similarity score of 0.93 for the *Liriodendron* damaged and reference stands compared well with the Spearman rank correlation (r = 0.90 Table 3).

In general, the reference stands appeared to be structurally and compositionally similar to the reconstructed damaged stands. Thus differences in post-storm reproduction between damaged and reference stands can be assumed to be a response to disturbance by ice, rather than to differences in site conditions.

Damage to Canopy Trees

All stands sustained extensive canopy damage through the removal of major branches and bole breakage as pictorially illustrated by the profile diagrams (Figures 3-6). Susceptibility of trees to ice damage was determined for dominant tree species (Table 7). Species were grouped into three standard susceptibility categories (Bennett 1959): 1. resistant, with less than fifty percent damage: hickory, 2. moderately susceptible, with fifty to seventy-five percent damage: white oak, scarlet oak (*Quercus coccinea* Muenchh.), chestnut oak (*Q. prinus* L.), black oak (*Q. velutina* Lam.), and red maple, and 3. susceptible, with greater than seventy-five percent damage: Virginia pine, yellow poplar,

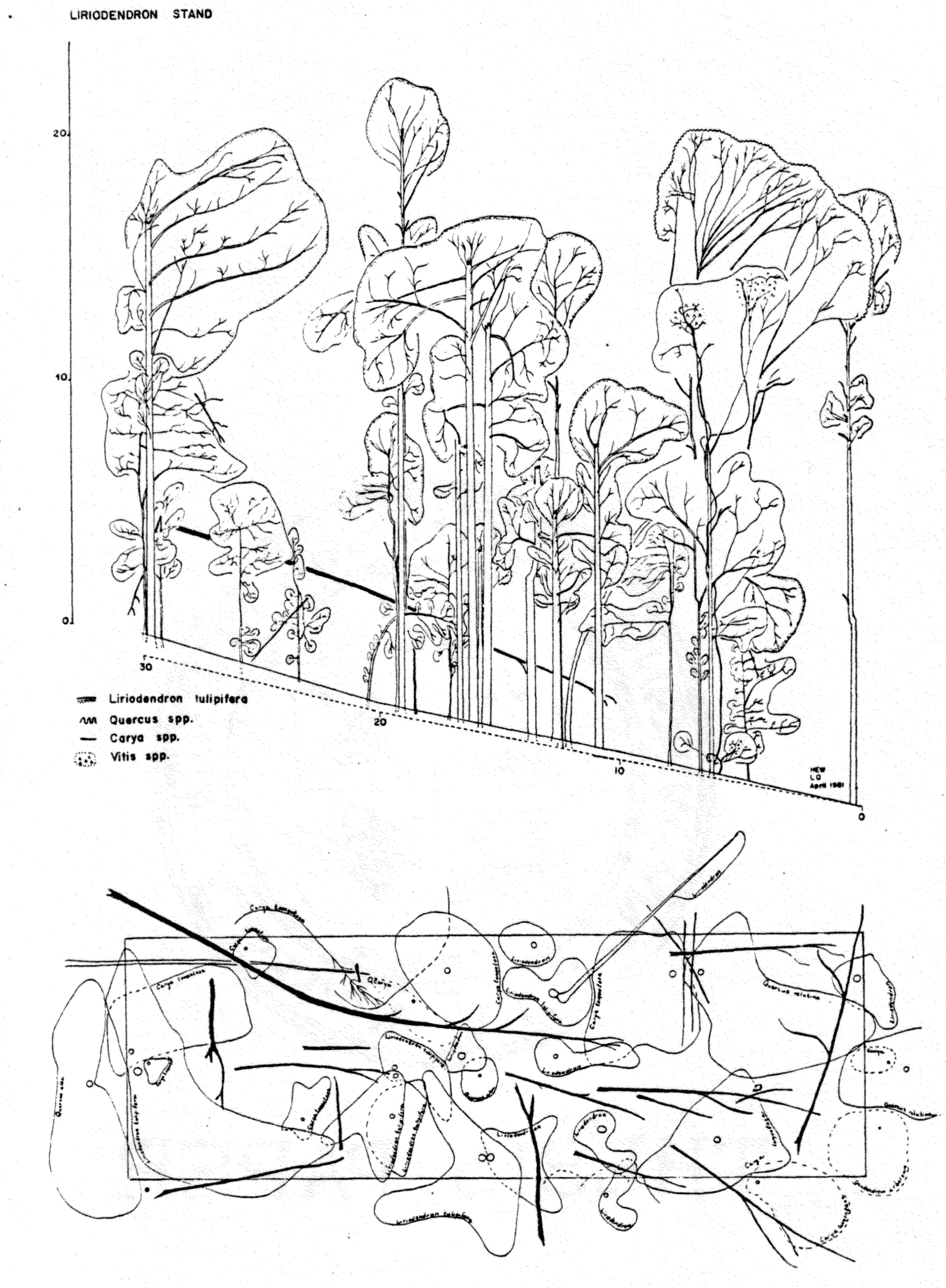

Figure 3. Liriodendron stand located within the ice damaged study area on Sinking Creek Mountain, Montgomery County, Virginia (elevation 750 m).

a) profile diagram
b) ground plan
(height and distance are in meters)

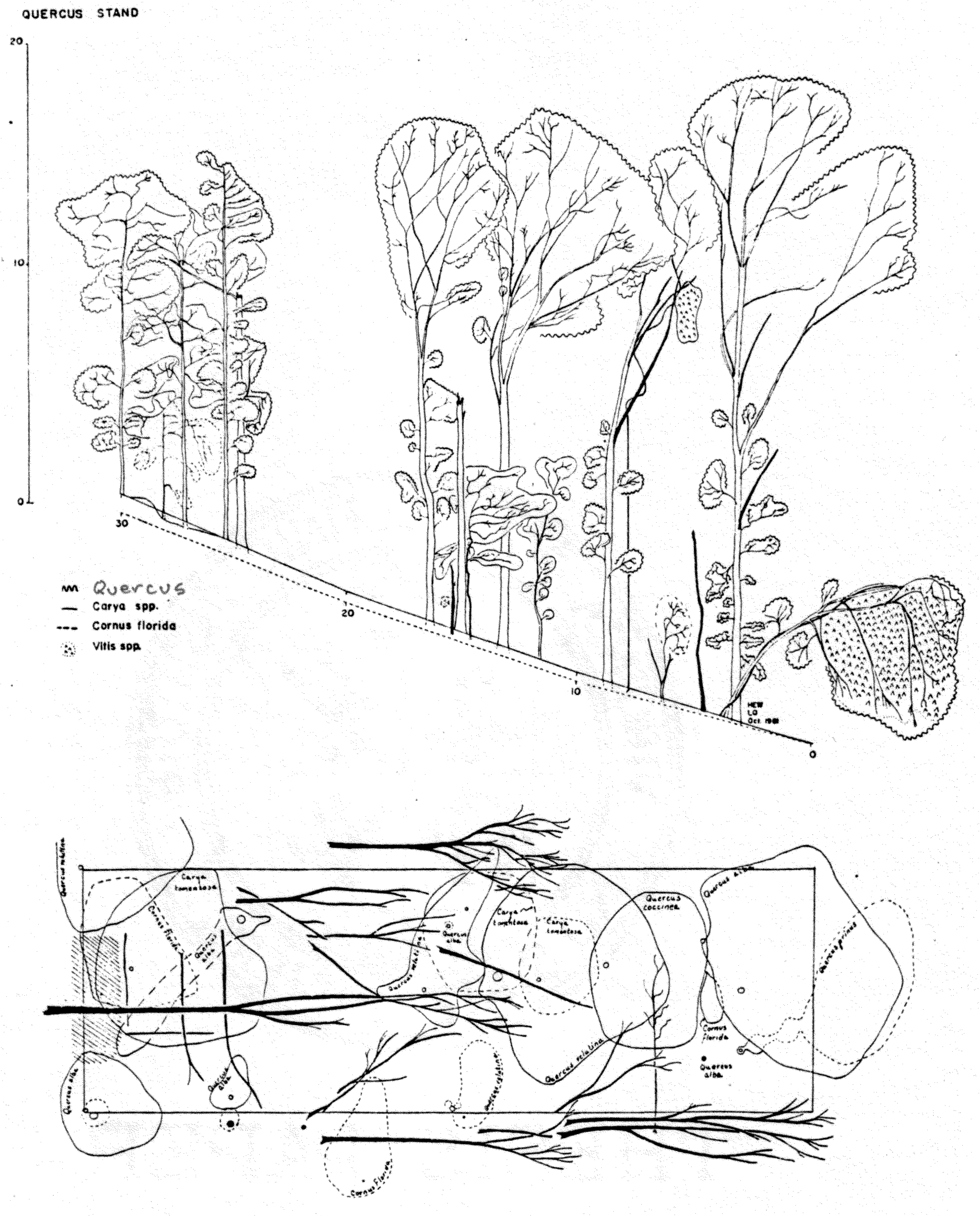

Figure 4. Quercus stand located within the ice damaged study area on Gap Mountain, Montgomery County, Virginia (elevation 750 m).

a) profile diagram

b) ground plan

(height and distance are in meters)

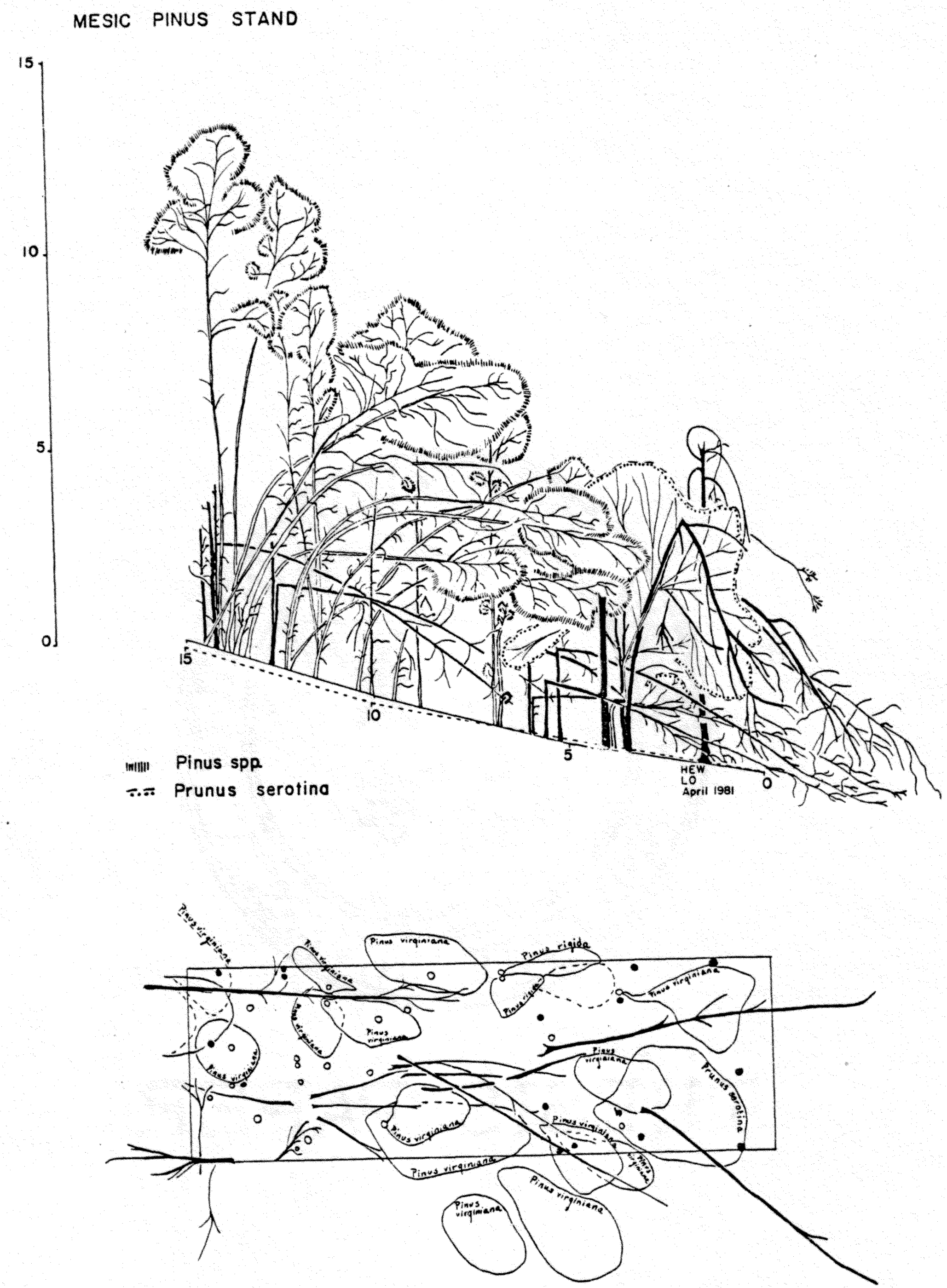

Figure 5. Mesic Pinus stand located within the ice damaged study area in Ironto, Montgomery County, Virginia (elevation 450 m).
a) profile diagram
b) ground plan
(height and distance are in meters)

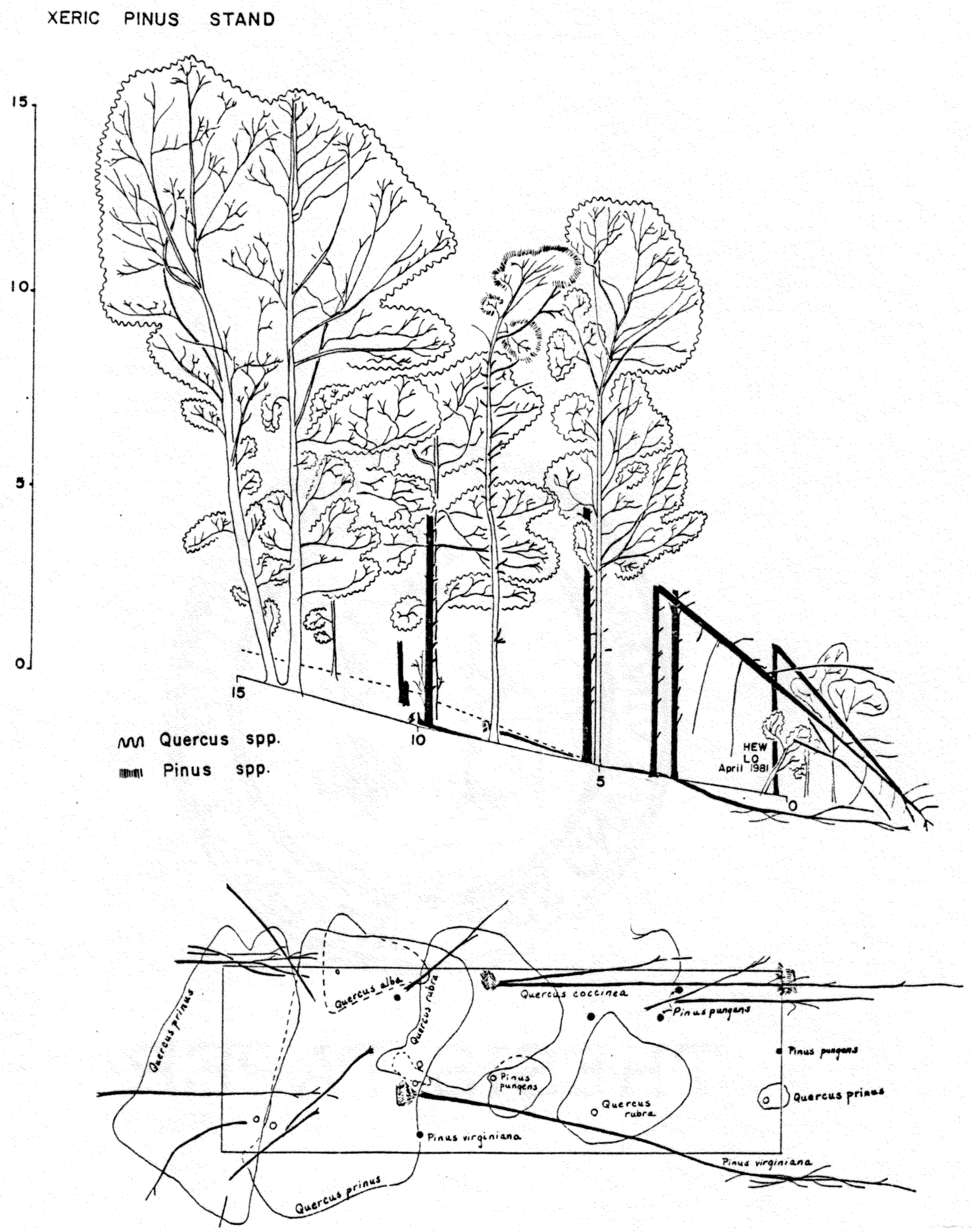

Figure 6. Xeric Pinus stand located within the ice damaged study area in Ironto, Montgomery County, Virginia (elevation 500 m).
a) profile diagram
b) ground plan
(height and distance are in meters)

Table 7. Percent of stems of dominant tree species damaged by ice for all stands by size class. Size class 1 stem dbh between 10.0-19.9 cm; size class 2: 20.0-29.9; and size class 3: ≥ 30 cm. Damage (%) includes damage classes 2, permanently bent or swept, damage class 3, greater than 50% crown loss, and damage class 4, fallen. Only species with importance value > 10 for any stand are shown.

	Size class			Overall
Species	1 (small)	2 (medium)	3 (large)	Damage (%)
Pinus rigida	90	100*	50*	90
P. pungens	86	47	33*	82
L. tulipifera	78	84	83	82
Pinus virginiana	79	67	67*	78
Quercus velutina	75	71	75	76
Acer rubrum	67	47*	100*	65
Quercus alba	61	55	60	59
Q. coccinea	48	65	84*	57
Q. prinus	56	51	57	54
Carya spp.	38	40*	80*	38
Average	73	66	74	71

* denotes sample size less than 25 trees

table mountain pine, and pitch pine.

Differences exist among authors in the categorization of species susceptibility (Bennett 1959) due to variation in sample size, location (urban vs natural stands), vegetation type, storm intensity, and damage classification systems. For example in this study, white oak was moderately damaged by glaze (53%, Table 7) although others found that it was only lightly damaged (Rogers 1923, Croxton 1939). Yellow poplar was heavily damaged in the present study (Table 7) although Lemon (1961) classified it as only moderately susceptible. Pine was heavily damaged in this study; pines have been observed to sustain heavy damage in plantations (Shepard 1975).

Damage patterns in relation to stem size varied considerably among species (Table 7). For example, hickory, scarlet oak, and red maple exhibited greater damage with increasing size class. (The small sample size, n = 3, for size class 3 of hickory was inadequate to assess its actual resistance to damage). The height and crown size of canopy trees allowed for greater exposure and therefore greater ice accumulation, which in conjunction with decreased flexibility of branches and boles, probably contributed to greater damage of large trees (Downs 1938, Bennett 1959). Also, greater apparent damage may have occurred because of decay in older canopy trees (Buttrick 1922, Downs 1938).

In contrast, an inverse relationship between degree of damage and tree size was observed for pines (Virginia pine and table mountain pine) although only a few large trees were sampled. Other field observations (W.C. Johnson, unpublished data), supported the inverse relationship between size and damage for pines, which may be due to previous removal of major branches by former ice storms or increased strength from greater bole volume.

All size classes of yellow poplar and black oak were heavily damaged (Table 7). With respect to yellow poplar, comparable damage among size classes resulted from the presence of most individuals in the canopy, despite a wide range in stem diameter, i.e., individuals were the same relative height and received similar ice accumulations despite occurring in different diameter classes. In contrast, black oak varied considerably in canopy height and thus comparable damage among size classes may have been due to moderate wood strength coupled with deliquescent branching patterns (Lemon 1961).

Damage for most species was consistent across stands (Table 8). For example, Virginia pine had an overall damage of 78%, with a narrow range from 77% in the xeric *Pinus* stand to 82% in the *Quercus* stand. Chestnut oak showed a similar pattern, while hickory, white oak, and black oak had a somewhat wider range of damage among stands. In contrast,

Table 8. Percent damage of dominant tree species for each damaged stand. Damage (%) includes damage class 2, permanently bent or swept, damage class 3, greater than 50% crown loss, and damage class 4, fallen. Only species with importance value > 10 for any stand are shown.

	Vegetation type				Overall
Species	Liriodendron	Mesic Pinus	Quercus	Xeric Pinus	Damage (%)
Pinus rigida	-	90	-	89	90
P. pungens		25*	-	83	82
L. tulipifera	82	-	100*	-	82
Pinus virginiana	-	79	82*	77	78
Quercus velutina	81	-	71	55*	75
Acer rubrum	70	100*	46	-	65
Quercus alba	71	67	53	42*	59
Q. coccinea	67	27	71	47	57
Q. prinus	60	67	54	47	54
Carya spp.	53	43*	27	-	38

* denotes sample size less than 25 trees

scarlet oak exhibited a wide range in damage among stands; from 27% in the mesic *Pinus* stand to 71% in the *Quercus* stand. The wide range was probably due to the high proportion of scarlet oak stems in small size classes in the mesic *Pinus* and xeric *Pinus* stands, and small stems were shown to experience less damage than larger stems (Table 7). Also, the highest damage for many species was in the *Liriodendron* stand, which may have been caused by falling branches and boles of heavily damaged yellow poplar and black oak canopy trees.

In the *Liriodendron* stand, the dominant canopy species, yellow poplar and black oak, were heavily damaged (82% and 81% respectively), followed by white oak, red maple, scarlet oak and chestnut oak (Table 8, Figure 3). Hickory was the least damaged. This may in part be due to the greater number of individuals in smaller size classes, which exhibited less overall damage (Table 7) from less accumulation of ice. The high wood strength (Lemon 1961) and flexibility of branches (Rogers 1923) probably also contributed to its resistance. Damage sustained by yellow poplar and black oak was primarily from bole breakage in damage class 3 (Figure 7). Many red maple trees were also included in damage class 3, but approximately fifty percent of the stems were lightly damaged (damage class 1). A high proportion of individuals of chestnut oak, white oak, and hickory were lightly damaged.

Damage in the mesic *Pinus* stand was primarily to dominant overstory species, Virginia pine and pitch pine (Table 8, Figure 5). Extensive canopy and bole breakage (damage class 3) was the predominant type of damage sustained by pines (Figure 7). Pines showed little resistance to glaze damage since a greater proportion of stems occurred in classes of severe damage (3 and 4), in contrast to most deciduous species. Chestnut oak was moderately damaged, followed by hickory and scarlet oak, which were lightly damaged.

Black oak and scarlet oak sustained the greatest damage in the *Quercus* stand (Table 8, Figure 4). Moderate damage was sustained by the other canopy species chestnut oak and white oak. Again, hickory was only lightly damaged. The greatest damage to dominant species occurred through branch and bole breakage in damage class 3 (Figure 7). Hickory, red maple, white oak, and chestnut oak had a large proportion of individuals lightly damaged.

In the xeric *Pinus* stand, pines sustained the greatest damage, while oaks the least damage, narrowly ranging from 42-55% (Table 8, Figure 6). Again, black oak sustained the greatest damage among the oaks. Damage to all species occurred primarily through crown removal or bole breakage (damage class 3) (Figure 7). Fallen trees (damage class 4)

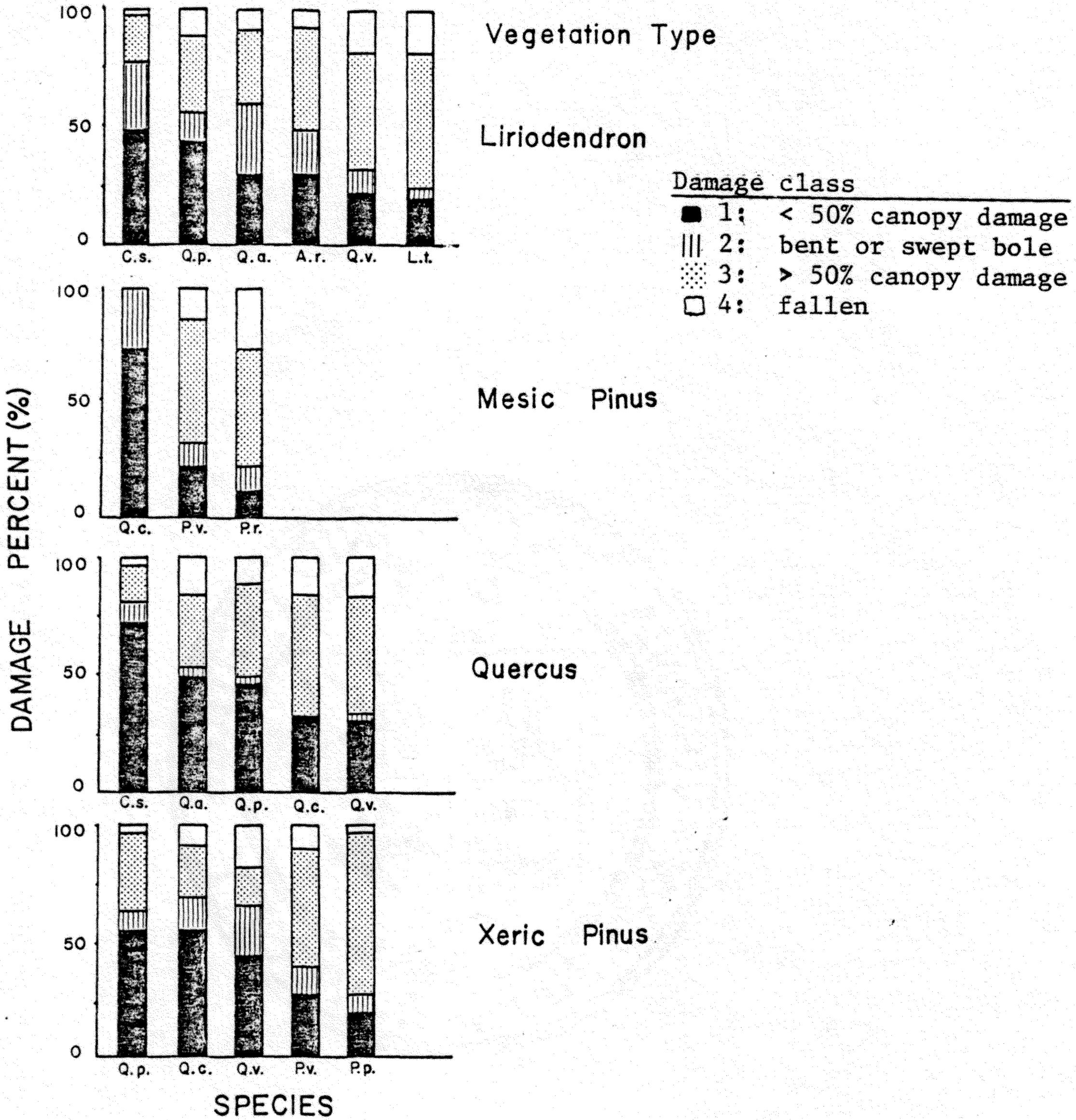

Figure 7. Proportion of damaged species (importance value > 10) within each damage class for individual stands. Species are arranged in order from least to most severely damaged. Damage classes were arranged by increasing severity. See Tables 2,3 for key to species abbreviations.

and permanently bent or swept trees (damage class 2) contributed to the high degree of destruction of pines (Figure 6).

Thus, yellow poplar and pine, were most susceptible to ice damage. McCarthy (1933) and Carvell et al. (1957) also reported extensive damage to yellow poplar, which has a low wood strength (Lemon 1961). Others have considered yellow poplar relatively resistant based on its cylindrical crown, straight central bole and short side branches (Rogers 1923, Windirsch 1936, Lemon 1961). For conifers, the greater winter surface area contributed by needles increased ice accumulation. This can result in extensive damage particularly when coupled with low flexibility or strength of wood characteristic of Virginia pine (Rogers 1923, Lemon 1961).

Mortality Patterns of Canopy Trees

Damage sustained from glaze has been used to infer mortality rates for tree species (Rogers 1923, Abell 1934, Lemon 1961). A positive correlation would be expected between damage and mortality, i.e., higher mortality would result from greater damage. Virginia pine and table mountain pine, which were heavily damaged had a correspondingly high mortality. For example, in the mesic and xeric *Pinus* stands about sixty percent of the pines in the stands died by the end of the second growing season following the ice storm (Table 9, Figures 5, 6). Overall mortality was much greater in these two stands than in the *Liriodendron* or *Quercus* stands (Figures 3,4), as shown by the higher proportion of darkened stems (Figures 5,6). Species moderately damaged such as black oak, white oak, scarlet oak and chestnut oak were intermediate in mortality, ranging from 10-30%. Of the oaks, black oak sustained the greatest mortality.

There were important exceptions to the correlation between species damage and mortality. For example, damage to yellow poplar and red maple, although high (82 and 70% respectively in the *Liriodendron* stand) resulted in very low mortality, only 3-5% (Figure 3). Pitch pine in the mesic *Pinus* stand also had low mortality associated with heavy damage.

Mortality of species also varied by stand. Mortality of white oak and chestnut oak was least in the *Liriodendron* stand, despite higher damage than in the *Quercus* stand (Table 9). Hickory generally exhibited low mortality in all stands. Many deciduous species have the ability to sprout from dormant buds (Kramer and Kozlowski 1979, Ross 1982) which reduces their mortality. Individual species mortality was highest for pines, which generally do not sprout. Virginia pine sustained similar damage in both the mesic

Table 9. Damage (%) and mortality (%) of species within each damaged stand. Damage (%) includes damage classes 2, permanently bent or swept, 3, greater than 50% crown loss, and 4, fallen, compared with the total number for each species. Mortality reflects those individuals that died of the total number of individuals of each species.

	Vegetation type							
	Liriodendron		Mesic Pinus		Quercus		Xeric Pinus	
Species	Damage (%)	Mortality (%)	Damage (%)	Mortality (%)	Damage (%)	Mortality (%)	Damage (%)	Mortality (%)
Acer rubrum	70	3	–	–	–	–	–	–
Carya spp.	53	6	–	–	27	11	–	–
L. tulipifera	82	–	–	–	–	–	–	–
Pinus pungens	–	–	–	–	–	–	83	77
Pinus rigida	–	–	90	20	–	–	–	–
Pinus virginiana	–	–	79	53	–	–	77	65
Quercus alba	71	11	–	–	52	25	–	–
Quercus coccinea	–	–	27	0	71	26	47	10
Quercus prinus	60	10	–	–	54	18	47	11
Quercus velutina	81	5	–	–	71	28	55	25

Pinus and xeric *Pinus* stands but mortality was greater in the xeric *Pinus* stand. Sprouting occurs in pitch pine (Kramer and Kozlowski 1979) and sprouts on damaged individuals were observed in the mesic *Pinus* stand, decreasing its overall mortality (Table 9).

Mortality increased with increasing damage class for all trees and saplings (Figure 8). That is, mortality was greatest for fallen trees, damage class 4, where seventy-five percent of the damaged individuals died. Damage classes 1 and 2, generally considered light damage, sustained less than 20% mortality.

Tree mortality within each size class also increased with increasing damage class (Figure 9). Fallen trees (damage class 4) had the greatest mortality in all size classes. The high mortality of the four damage classes in size class 1 relative to size class 2 and 3 was due to the large proportion of pine stems in size class 1. Mortality was also greater in damage class 2 (swept) for small trees due again to the high proportion of pine. Although their flexible stems tolerate a higher degree of bending without breakage, damage is more severe than for deciduous species, with low recovery (Bennett 1959).

A marked contrast existed in the mortality patterns of pioneer species yellow poplar and Virginia pine. Both species sustained heavy damage. However, while yellow

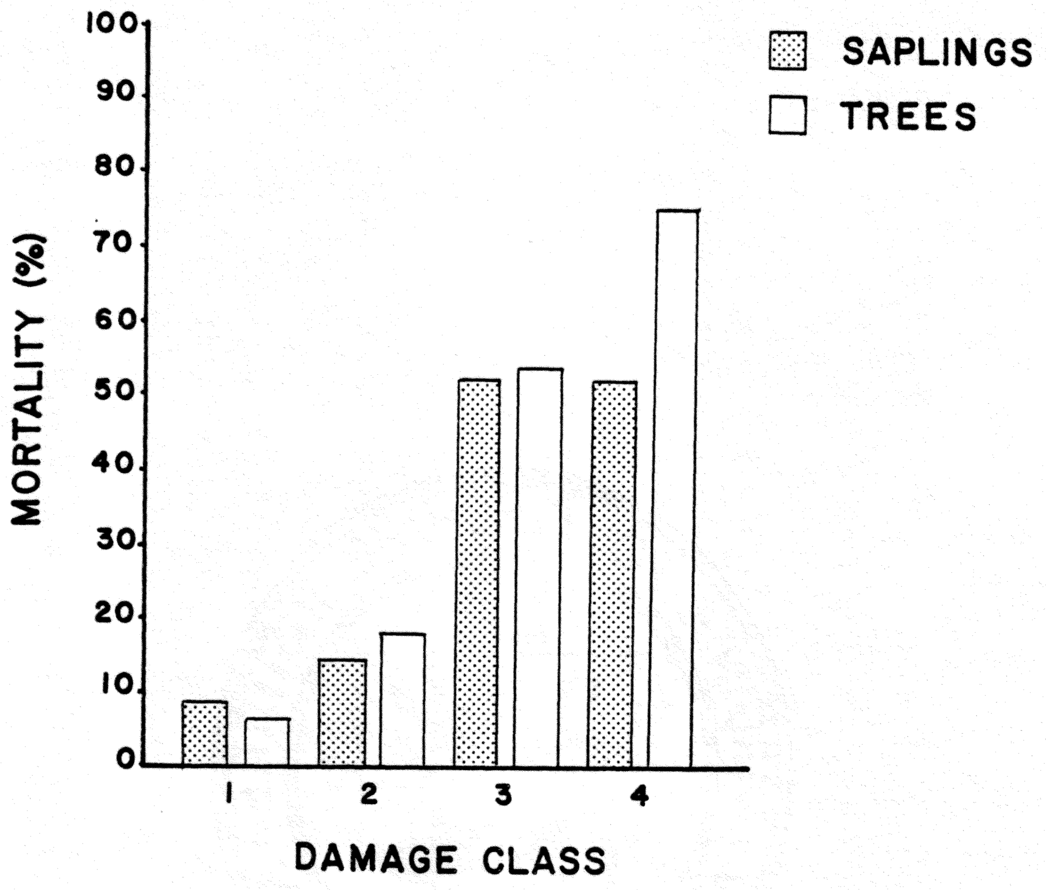

Figure 8. Percent mortality by damage class for all damaged stands. Trees included stems ≥ 10 cm dbh; saplings were individuals that were < 10 cm dbh or > 1 m tall. Damage class 2 includes stems permanently bent or swept, damage class 3, greater than 50% crown loss, and damage class 4, fallen.

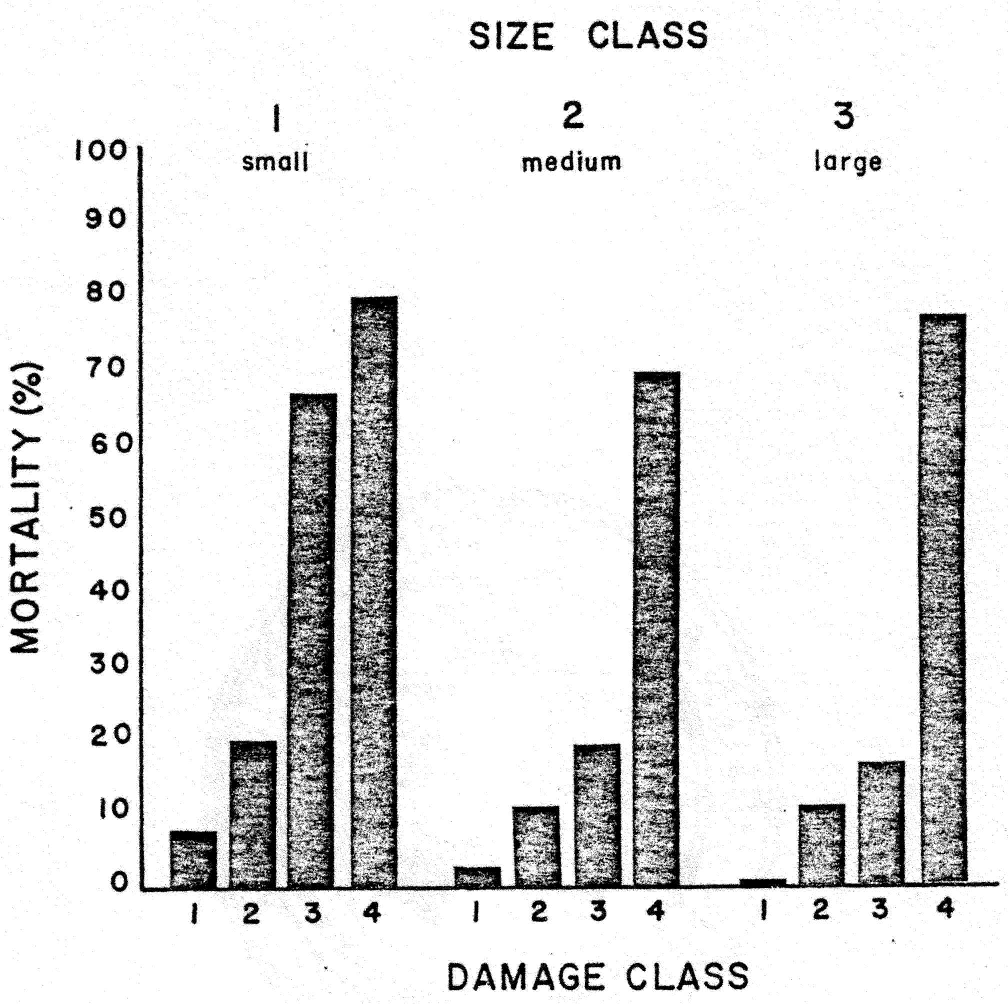

Figure 9. Percent mortality by size and damage classes for trees ≥ 10 cm dbh for all damaged stands. Size class 1 includes stem dbh between 10.0-19.9 cm; size class 2: 20.0-29.9; and size class 3: ≥ 30 cm. Damage class 2 includes those stems permanently bent or swept, damage class 3, greater than 50% crown loss, and damage class 4, fallen.

poplar exhibited little mortality, over 53% of the Virginia pine trees died. The low mortality of yellow poplar was a result of its ability to sprout prolifically after damage. Red maple followed a similar pattern. Regrowth of damaged boles from dormant and adventitious buds (reiteration, Oldeman 1979) has been observed for these species (Carvell et al. 1957). Regrowth of the canopy by sprouting of damaged boles was important in the *Liriodendron* stand (Figure 3). Past sprouting from disturbance was evident from crooked boles of many trees in this stand. The actual mortality of yellow poplar may increase upon canopy closure if fallen trees die that are presently sprouting. The high mortality associated with Virginia pine resulted from low recovery by damaged individuals (Figures 4, 5).

Sapling Damage and Mortality

Understory trees (dogwood *Cornus florida* L., black gum *Nyssa sylvatica* Marsh., sassafras *Sassafras albidum* (Nutt.)Nees) and saplings of overstory trees, generally sustained less damage and mortality than canopy trees (Table 10, Figure 8). Damage to saplings was predominantly from fallen branches or boles of canopy trees. Damage appeared to be rather uniformly distributed among species. Oaks sustained moderate damage (20-51%) followed by hickory and yellow

Table 10. Damage (%) and mortality of sapling species combined for all damaged stands. Damage (%) includes the number of individuals in damage classes 2, permanently bent or swept, 3, greater than 50% crown loss, and 4, fallen compared with the total number of stems of each species. Mortality (%) includes individuals which died of the total number for each species. Only species with n > 25 are shown.

	Vegetation type									
	Liriodendron		Mesic Pinus		Quercus		Xeric Pinus		Combined	
Species	Damage (%)	Mortality (%)	Damage (%)	Mortality (%)	Damage (%)	Mortality (%)	Damage (%)	Mortality (%)	Damage (%)	Mortality (%)
Pinus virginiana	–	–	95	61	–	–	100	76	91	65
Oxydendrum arboreum	–	–	–	–	57	2	–	–	53	4
Quercus alba	–	–	–	–	51	23	–	–	51	20
L. tulipifera	40	12	–	–	–	–	–	–	40	13
Carya spp.	40	0	81	0	46	10	–	–	40	4
Quercus velutina	32	10	–	–	–	–	52	11	36	19
Cornus florida	39	3	42	5	41	7	34	0	35	5
Acer rubrum	32	2	–	–	20	2	26	0	27	2
Nyssa sylvatica	23	9	–	–	–	–	–	–	24	9
Quercus prinus	–	–	–	–	27	6	–	–	23	6
Q. coccinea	–	–	41	10	–	–	–	–	20	8
Prunus serotina	–	–	16	0	–	–	18	0	17	0
Sassafras albidum	10	0	18	4	24	10	25	7	16	10

correlation coefficient between combined damage and mortality: 0.828

poplar (40%), red maple (27%), and black cherry (*Prunus serotina* Ehrh. 17%). The range of mortality was narrow, from 0-20%; a result of the ability of most saplings to sprout from dormant buds (Kramer and Kozlowski 1979, Ross 1982) coupled with the greater flexibility of young stems (Bennett 1959). Mortality was the greatest (13-20%) for yellow poplar, black oak, and white oak. Sourwood, hickory, chestnut oak and red maple which also sustained moderate damage, had lower mortality (2-8%). Damage to understory species, dogwood, black gum, and sassafras ranged from 16-35%, with 5-10% mortality.

Only saplings of Virginia pine were heavily damaged, with 91% of the stems in damage classes 2,3,4 (Table 10). Mortality was also high (65%), again due to the inability to sprout upon damage, regardless or age or size. Damage was greater than for other saplings as a result of their occurrence in the heavily damaged pine stands.

Saplings generally maintained their pre-storm density as a result of light damage and very low mortality. Fifty to eighty percent of the saplings were undamaged. The disproportionate mortality between overstory and understory indicates that succession would be significantly advanced for stands with a susceptible pioneer overstory and equilibrium species in the understory.

Reprodution

Damaged Stands

Differences in pre-storm reproduction densities (stems > 2 years old) between damaged and reference stands at each site were not statistically significant, suggesting that ecological and historical conditions of the sites were similar and that reference stands paired with damaged stands represented good controls (Table 11). Although reproduction densities were similar between the damaged and reference stands at the time of measurement, this may be the result of different survivorship. For example, establishment may be greater in one stand, but increased mortality could result in the reproduction of the two stands being comparable.

The response to canopy disturbance was through both seedling establishment and sprouting (Table 11). Post-storm reproduction densities (stems < 2 years old) were significantly greater in disturbed stands by at least an order of magnitude than in the corresponding reference stands. The greatest difference between damaged and reference stands occurred at the *Liriodendron* stand (0.6/10 m^2 compared to 41.0 /10 m^2). The highest reproduction density in the damaged stands occurred in the *Liriodendron* stand (51.1/10 m^2) followed by *Quercus* (27.2), mesic *Pinus* (14.9),

Table 11. Total reproduction (seedling and seedling-sprout) densities (no./10 m^2) in damaged and reference stands. One and two year-old stems are of post-storm origin, while three to nine year-old stems originated prior to the 1979 ice storm.

	Seedling		Seedling-Sprout		Total	
Vegetation type	Damaged	Reference	Damaged	Reference	Damaged	Reference
Liriodendron						
1 - 2 year	41.0	0.6^{ab}	10.1	0.6^{ab}	51.1	1.2^{ab}
3 - 9 year	2.7	4.5^{aa}	4.2	6.6^{aa}	6.9	11.1^{aa}
Mesic *Pinus*						
1 - 2 year	5.2	0.3^{ab}	9.7	1.0^{ab}	14.9	1.3^{ab}
3 - 9 year	5.0	3.4^{aa}	5.6	7.3^{aa}	10.6	10.7^{aa}
Quercus						
1 - 2 year	10.4	2.9^{ab}	16.8	7.5^{ab}	27.2	10.4^{ab}
3 - 9 year	4.0	4.1^{aa}	7.0	13.0^{aa}	11.0	17.3^{aa}
Xeric *Pinus*						
1 - 2 year	5.0	0.5^{ab}	8.1	1.2^{ab}	13.1	1.7^{ab}
3 - 9 year	4.3	4.4^{aa}	6.8	11.1^{aa}	11.1	15.5^{aa}

ab statistically significant at $P < 0.01$ (Students' t-test, SAS, Helwig et al. 1979)

aa nonsignificant at $P < 0.05$

and xeric *Pinus* (13.1) stands. Seedling establishment was stimulated after the ice storm in all stands, but in the mesic *Pinus*, *Quercus*, and xeric *Pinus* stands, sprouting continued to be the major component of stand regeneration (Table 11).

A seedling to seedling-sprout ratio (no. seedling/ no. seedling-sprouts) was used to identify shifts in the type of regeneration in each vegetation type (Figure 10). A ratio of less than 1 indicated that reproduction by seedling-sprouts was greater than seedlings, as seen in the mesic *Pinus*, *Quercus*, and xeric *Pinus* reference stands. Sprouting continued to be important in the damaged communities when compared to reference stands, but seedling establishment stimulated by the ice storm reduced the seedling to seedling-sprout ratio. Only in the *Liriodendron* damaged stand was pre-storm (and reference) seedling and seedling-sprout reproduction balanced.

Post-storm seedling-sprout densities for damaged stands were significantly ($P < 0.01$) greater than reference stands (Table 11). The greatest increase occurred in the *Liriodendron* stand, although seedling-sprouts were proportionally more important in the mesic *Pinus* and xeric *Pinus* damaged stands. The major species which sprouted in the reference stands sprouted more prolifically in the damaged stands (Tables 12-15). Additionally, hickory, black

Figure 10. Seedling to Seedling-sprout ratio (no./10 m^2) of one and two year old reproduction for each ice damaged and reference stand.

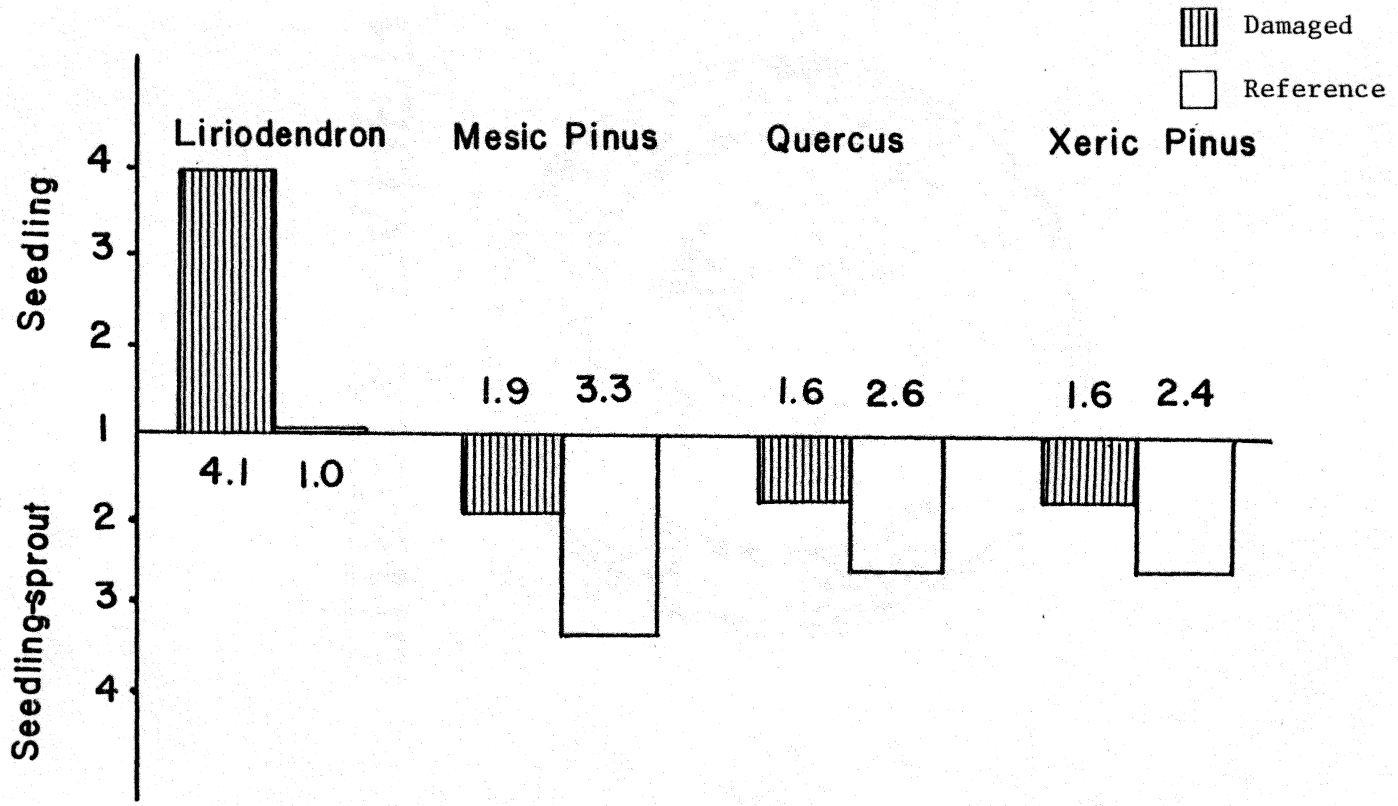

Table 12. Total reproduction (seedling and seedling-sprout) density by species for *Liriodendron* damaged and reference stands (no./10 m^2). Proportion of total reproduction comprised of seedlings is given in parentheses.

	Damaged		Reference	
Species	1-2 year	3-9 year	1-2 year	3-9 year
L. tulipifera	29.6 (98)	0.4 (96)	0.3 (100)	0.2 (100)
Sassafras albidum	11.8 (60)	1.8 (33)	0.4 (25)	2.4 (21)
Acer rubrum	4.1 (92)	1.1 (95)	0.2 (100)	1.6 (100)
Cornus florida	1.8 (0)	1.5 (0)	0.1 (0)	3.3 (0)
Quercus prinus	0.6 (0)	0.6 (0)	0.1 (0)	0.8 (12)
Q. alba	0.7 (8)	0.2 (33)	0.1 (0)	0.8 (93)
Q. velutina	0.4 (12)	0.4 (40)		0.4 (57)
Nyssa sylvatica	0.6 (0)	0.1 (29)		0.1 (0)
Carya spp.	0.4 (35)	0.2 (62)		0.7 (92)
Oxydendrum arboreum	0.2 (45)	0.1 (33)		0.1 (50)
Quercus coccinea	0.1 (25)	0.2 (67)		0.1 (100)
Prunus serotina	0.2 (0)	0.1 (33)		0.2 (50)
Castanea dentata	0.2 (0)	0.1 (0)		0.1 (0)
Betula lenta	0.1 (60)			0.1 (100)
Amelanchier arborea	0.1 (50)	0.1 (100)		0.1 (100)
Magnolia accuminata		0.1 (100)		0.1 (100)
Robinia pseudoacacia	0.1 (14)			
Pinus virginiana	0.1 (100)			
Acer saccharum				0.1 (100)

Table 13. Total reproduction (seedling and seedling-sprout) density by species for mesic _Pinus_ damaged and reference stands (no./10 m^2). Proportion of total reproduction comprised of seedlings is given in parentheses.

Species	Damaged 1-2 year		Damaged 3-9 year		Reference 1-2 year		Reference 3-9 year	
Quercus coccinea	3.5	(43)	4.0	(52)	0.5	(50)	2.1	(65)
Sassafras albidum	3.1	(45)	1.3	(35)	0.6	(30)	0.8	(25)
Pinus virginiana	2.5	(100)	0.3	(100)			0.1	(100)
Acer rubrum	1.6	(95)	0.5	(64)	0.2	(100)	0.3	(96)
Quercus velutina	0.6	(6)	1.4	(41)			1.1	(31)
Prunus serotina	0.7	(24)	0.9	(49)			1.4	(36)
Cornus florida	0.7	(0)	0.1	(0)			2.8	(2)
Betula lenta	0.3	(5)	0.3	(6)			0.1	(20)
Carpinus caroliniana	0.4	(35)	0.2	(16)			0.3	(15)
Amelanchier arborea	0.4	(2)	0.4	(21)			0.1	(28)
Quercus alba	0.3	(21)	0.2	(31)			0.6	(34)
Q. prinus	0.1	(12)	0.1	(9)			0.3	(21)
Q. stellata	0.2	(6)	0.1	(12)			0.4	(13)
Carya spp.	0.1	(34)	0.2	(71)			0.2	(62)
Pinus rigida			0.2	(100)			0.1	(100)
Oxydendrum arboreum	0.2	(0)	0.1	(10)				
Pinus pungens	0.1	(100)	0.1	(100)				
Quercus falcata	0.1	(45)						
Q. rubra	0.1	(60)	0.1	(72)				
Nyssa sylvatica			0.1	(35)				

Table 14. Total reproduction (seedling and seedling-sprout) density by species for *Quercus* damaged and reference stands (no./10 m^2). Proportion of total reproduction comprised of seedlings is given in parentheses.

	Damaged		Reference	
Species	1-2 year	3-9 year	1-2 year	3-9 year
Sassafras albidum	17.6 (38)	6.3 (36)	5.6 (11)	4.8 (7)
Cornus florida	2.9 (0)	1.6 (0)		4.8 (1)
Acer rubrum	3.0 (68)	0.8 (88)	2.5 (71)	2.3 (93)
L. tulipifera	1.0 (100)	0.2 (100)	0.2 (100)	
Quercus prinus	0.5 (7)	0.6 (5)	0.3 (20)	1.2 (4)
Q. velutina	0.6 (11)	0.3 (50)	0.2 (0)	0.8 (33)
Prunus serotina	0.4 (16)	0.4 (15)	0.2 (25)	
Castanea dentata	0.3 (0)	0.1 (0)		0.1 (0)
Quercus alba	0.2 (33)	0.1 (0)	0.5 (33)	1.5 (43)
Nyssa sylvatica	0.2 (38)	0.1 (33)	0.2 (0)	0.4 (14)
Oxydendrum arboreum	0.2 (22)	0.1 (67)		0.1 (54)
Carya spp.	0.1 (20)	0.1 (71)	0.1 (0)	0.2 (25)
Quercus coccinea	0.1 (0)	0.1 (63)	0.4 (0)	0.9 (41)
Fraxinus americana		0.1 (100)	0.1 (100)	0.2 (99)
Quercus rubra	0.1 (100)	0.1 (100)		
Acer saccharum				0.1 (100)
Pinus virginiana			0.1 (100)	0.1 (100)
Betula lenta				0.1 (100)

Table 15. Total reproduction (seedling and seedling-sprout) density by species for xeric *Pinus* damaged and reference stands (no./10 m^2). Proportion of total reproduction comprised of seedlings is given in parentheses.

	Damaged		Reference	
Species	1-2 year	3-9 year	1-2 year	3-9 year
Cornus florida	2.3 (0)	0.5 (0)	0.4 (0)	4.8 (10)
Sassafras albidum	3.6 (38)	2.4 (0)	0.9 (30)	2.1 (6)
Quercus coccinea	1.3 (7)	2.1 (47)	0.4 (0)	1.8 (18)
Acer rubrum	1.4 (62)	0.2 (75)	0.2 (61)	0.6 (57)
Quercus velutina	0.8 (17)	1.8 (64)		1.3 (35)
Pinus virginiana	0.9 (100)	0.3 (100)		0.2 (100)
Carpinus caroliniana	0.7 (24)	0.5		0.4 (20)
Amelanchier arborea	0.3 (90)	0.6		0.6 (35)
Quercus alba	0.3 (0)	0.8 (12)		1.5 (33)
Q. prinus	0.2 (0)	0.6 (27)		0.5 (48)
Prunus serotina	0.1 (0)	1.1 (87)		0.1 (100)
Oxydendrum arboreum	0.1 (0)			0.1 (15)
Pinus pungens	0.8 (100)			
L. tulipifera	0.1 (100)			
Pinus strobus	0.1 (100)			
Carya spp.	0.1 (0)			
Nyssa sylvatica	0.1 (0)			
Diospyros virginiana	0.1 (0)			

gum, and sourwood increased through sprouting. The increased sprout production following the ice storm may have been due to a number of causes, including dieback and sprouting of seedlings established the first year after the storm, sprouting of small stems damaged by ice, and root sprouting, especially by dogwood and sassafras.

Reproduction of understory species, dogwood, sassafras, and black gum, also increased following disturbance. Dogwood is a long lived understory species (May 1952) while sassafras rarely exceeds thirty years of age on steep slopes in Appalachian oak forests of southwest Virginia (Ross et al. 1982). Prolific sprouting probably resulted in response to increased light following canopy removal.

The post-storm increase in seedling densities for all damaged stands was primarily by pioneer species, including yellow poplar, red maple, sassafras and Virginia pine (Tables 12-15). They are classified as typically shade intolerant, requiring full sun for germination and development (Spurr and Barnes 1973). Seedlings of pioneer species are generally adapted to grow under a wide range of environmental conditions, from hydric to xeric. Establishment of pioneer species is clearly favored in canopy gaps created by ice storms, as these gaps are generally larger than those created by senescence. The rate of canopy closure appears to be slow (Trimble and Tryon

1966, Woods and Shanks 1959), particularly in stands dominated by yellow poplar, whose strong apical dominance inhibits lateral growth (Kramer and Kozlowski 1979).

The most common species exhibiting increased seedling densities in the damaged successional stands (*Liriodendron* and mesic *Pinus*) included yellow poplar, sassafras, red maple and Virginia pine (Tables 12, 13). Seed-producing individuals of these species were present in the pre-storm stands, hence seeds were abundant. In contrast, young seedlings were uncommon in pre-storm forest conditions. The dramatic increase in yellow poplar reproduction density (Table 12) may have been facilitated by a rich seed bank; seed longevity of yellow poplar is estimated to be 2-5 years (Marquis 1975). A similar response was not observed for other species such as oaks where seedling densities remained at low pre-storm densities. The absence of additional pioneer species in the mesic *Pinus* damaged stand (e.g. yellow poplar) may be due to the lack of seed source, or more probably, failure to become established under more xeric site conditions.

Reproduction before the disturbance in the mesic *Pinus* stand was primarily by deciduous species typical of more advanced successional stages such as chestnut oak, white oak, black oak, scarlet oak, and dogwood. The absence of reproduction of pioneer species and dominance of the reproduction component by oak suggests that future successional shifts may occur in overstory composition in both reference stands.

Seedlings of pioneer species which increased in the *Quercus* and xeric *Pinus* damaged stands included red maple, yellow poplar, Virginia pine, and sassafras (Tables 14,15). Seedlings of pioneer species, however, were a minority of post-storm reproduction, comprising 39% in the *Quercus* stand and 30% in the xeric *Pinus* stand. The increase of table mountain pine seedlings in the xeric *Pinus* stand may replace damaged canopy individuals, thereby facilitating the maintenance of the pre-storm composition of the stand. Reproduction was similar between damaged and reference stands for each site.

Thus, reproduction of pioneer species by seedlings was stimulated by the ice storm. All sites had an increase in density of seedlings as canopy damage and mortality increased the amount of light reaching the forest floor, thus favoring germination and growth. Germination and establishment were greatest for yellow poplar in the mesic *Liriodendron* site, while pine colonized the drier sites (mesic *Pinus* and xeric *Pinus*). Most seedlings were pioneer species while sprouts were predominantly of equilibrium tree or understory species. Sprouting of deciduous understory equilibrium species was more important in the mesic *Pinus*, *Quercus*, and xeric *Pinus* stands.

Growth of Reproduction

Post-storm height growth of reproduction (seedling and seedling-sprout) established before the storm was significantly greater in damaged stands when compared to reference stands (Table 16). The magnitude of increase was similar in the *Liriodendron* and mesic *Pinus* sites, but less in the xeric *Pinus* site. Growth measurements were not made at the *Quercus* site.

In the *Liriodendron* damaged stand, post-storm height growth of reproduction was greatest for the oaks (Table 16), and least for pioneer species, yellow poplar and red maple. Small sample sizes of individual species prevented statistical analysis, but general trends can be illustrated with mean growth. In the mesic *Pinus* and xeric *Pinus* stands, red maple, dogwood, and sassafras had the greatest growth. Thus, growth response in the mesic *Liriodendron* stand was greatest for oak, while growth of understory trees and red maple was stimulated most in the mesic *Pinus* and xeric *Pinus* stands.

Post-storm height growth was greatest for reproduction of sprout origin (Table 17). For example, growth of sprouts of red maple and sassafras was greater than seedlings. Sprouts of dogwood, yellow poplar, and red maple had the greatest post-storm growth. Increased growth of sprouts may be a result of greater water and nutrient availability from

Table 16. Mean post-storm height growth (cm) for reproduction in the damaged and reference stands. Reproduction includes seedlings and seedling-sprouts greater than 2 years of age present in each stand. Mean height growth is presented for individual species to illustrate trends within stands and between species. Only species with n > 25 are shown.

	Vegetation Type					
	Liriodendron		mesic *Pinus*		xeric *Pinus*	
Species	Damaged	Reference	Damaged	Reference	Damaged	Reference
Acer rubrum	4.8	2.3	14.8	3.8	13.0	2.5
Cornus florida	5.0	4.3	15.0	5.8	27.0	3.8
L. tulipifera	4.3	4.0	-	-	-	-
Pinus pungens	-	-	-	-	10.0	5.4
Pinus virginiana	-	-	5.8	2.2	7.0	2.5
Prunus serotina	-	-	5.0	4.3	-	-
Quercus alba	10.5	1.3	-	-	-	-
Q. coccinea	-	-	7.3	4.0	-	-
Q. prinus	16.5	8.5	-	-	-	-
Q. velutina	9.0	1.3	8.8	2.3	6.5	2.5
Sassafras albidum	8.8	5.0	10.0	10.0	13.3	5.5
Overall mean height growth	17.3	7.6*	16.9	6.8*	13.3	6.3*

* statistically significant at $P < .05$ (Students' t-test in SAS, Helwig et al. 1979).

Table 17. Mean post-storm growth (cm) of all reproduction seedlings and seedling-sprouts in each damaged stand. Mean height growth is presented by species to illustrate trends within stands and between species. Only species with n > 25 are shown.

	Vegetation type					
	Liriodendron		Mesic Pinus		Xeric Pinus	
Species	Seedling	Seedling-Sprout	Seedling	Seedling-Sprout	Seedling	Seedling-Sprout
Acer rubrum	4.5	7.3	6.3	22.8	5.0	24.5
Cornus florida	-	5.2	-	15.0	5.8	17.8
L. tulipifera	4.0	25.3	-	-	-	-
Pinus pungens	-	-	-	-	7.5	-
P. virginiana	-	-	5.8	-	7.3	-
Prunus serotina	-	-	9.5	16.3	-	-
Quercus alba	-	10.5	-	-	-	-
Q. coccinea	-	-	5.0	8.0	4.8	8.5
Q. prinus	-	16.5	-	-	-	-
Q. velutina	2.5	10.3	4.8	10.0	5.3	7.3
Sassafras albidum	5.3	15.3	7.0	11.8	8.0	17.0

an established root system (Kramer and Kozlowski 1979).

In general, canopy damage from ice storms stimulated the growth of existing reproduction. Sprout growth of all species was greater than reproduction of seedling origin. Growth of species characteristic of advanced successional stages was greater than that of pioneer species.

SUCCESSIONAL TRENDS

Neither of the previously stated hypotheses (page 4) concerning the effects of ice storms on forest succession adequately characterized the response of vegetation to ice damage in the Ridge and Valley landscape of southwestern Virginia. Each hypothesis may be valid for specific forest conditions in a landscape, but would not apply generally. Several factors interact to complicate community response to canopy disturbance. For example, under certain conditions succession may be advanced slowly or rapidly, while under other conditions an early successional community may be maintained. Some conditions may have no affect on species composition.

Two of the four stands (*Quercus* and xeric *Pinus*) selected for study were not successional, i.e., shifts in composition were not expected; these occurred on relatively xeric sites. Based on composition of tree reproduction, overstory vegetation in these stands would appear not to change in the aftermath of an ice storm. Canopy disturbance by ice storms stimulated reproduction but the composition of tree reproduction was little different from pre-storm conditions (Figure 11, arrows 3,4). Most seedlings were pine in the xeric *Pinus* stand; table mountain pine may be restricted to this habitat in the absence of fire (Zobel 1969). Although not the focus of this study, an important

Successional transitions following disturbance by ice storms

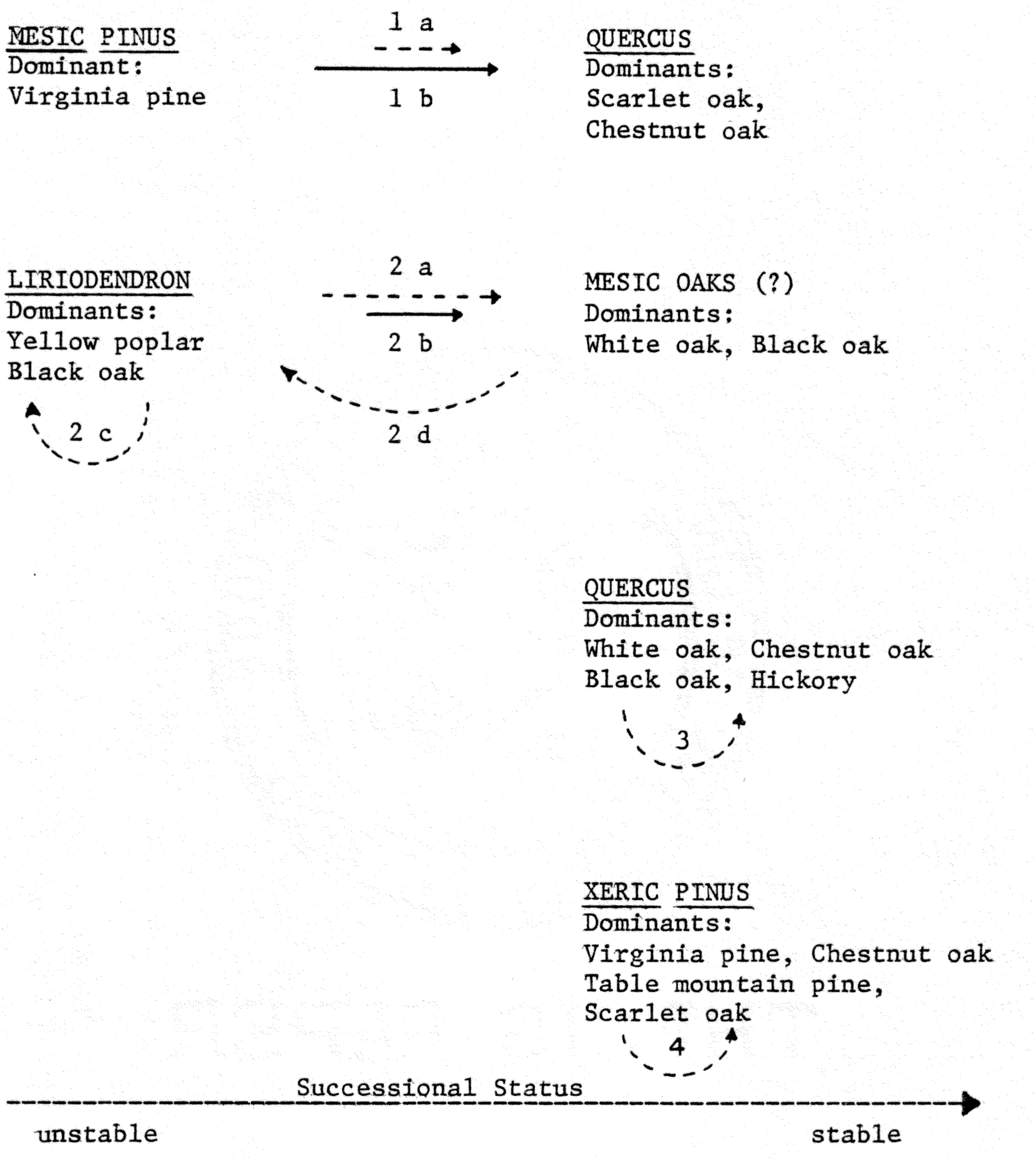

Figure 11. Species replacement sequences for different Appalachian forest communities as a response to natural succession and ice damage. Transitions in undisturbed communities due to natural succession are shown by solid line arrows; the broken line arrows show those caused by ice damage. Arrow length reflects the relative time required for the conversion, e.g. flux 1 a (ice storm) would be faster than 1 b (natural succession).

effect of ice storms on these communities may be the stimulation of flowering, fruiting, regeneration of wild grape, *Vitis* spp. and numerous understory species.

The remaining two stands, *Liriodendron* and mesic *Pinus*, were early successional communities on more mesic sites. Canopy dominants were not reproducing in the understories of these stands, and therefore a successional shift in composition would have been expected in the absence of ice damage. Succession would appear to be accelerated in the mesic *Pinus* stand, where canopy damage and mortality of Virginia pine permitted rapid growth of established oak reproduction (Figure 11, arrow 1a).

Two possible pathways characterize future shifts in composition of the ice damaged *Liriodendron* stand (Figure 11). While the importance of yellow poplar in the canopy was generally maintained due to low mortality, its importance in the understory was greatly increased by the stimulation of seedling reproduction. Thus periodic disturbances by ice could maintain the pioneer community, or alternatively, shift the stand more slowly to an equilibrium community than would normally occur during succession in the absence of disturbance (Figure 11, arrows 2 a,b,c).

To maintain the pioneer *Liriodendron* community, seedlings established after canopy damage must grow more rapidly than pre-storm reproduction and reach the canopy before closure. Because pioneer species such as yellow poplar are capable of rapid height growth (Williams 1964, Kramer and Kozlowski 1979) and slow canopy closure for yellow poplar has been reported (Trimble and Tryon 1966), this appears to be a distinct possibility. Alternatively, there is evidence that stems of sprout origin may maintain a competitive advantage over stems of seedling origin (Ross 1982), which may enable equilibrium species to increase at the expense of yellow poplar. Resolution of these two possibilities can only come from a longer term study based on repeated measurements of the permanently located sample plots.

Disturbance by ice storms does not appear to result in establishment of pioneer communities from communities of more advanced successional status (Figure 11). Canopy damage within a community and site alterations were not as severe as other disturbances, e.g. clearing and fire. Therefore, ice damage did not result in significant changes in composition of tree reproduction in the *Quercus* or xeric *Pinus* communities, i.e. converting the stand to pioneer successional status. Reproduction in the damaged stands included only a minor proportion of pioneer species, e.g. yellow poplar and table mountain pine. Virginia pine reproduction was not stimulated by ice storms as this species requires more intense soil or litter disturbances such as cultivation, logging, or fire. It is possible that in a successionally advanced stand of *Liriodendron* (e.g. mesic oak, Figure 11 arrow 2d) a pioneer stand could result in the aftermath of an ice storm, although this stand type is unusual in the landscape, and none was available for study.

CONCLUSIONS

The effects of ice storms on vegetation dynamics are complex and depend on site conditions, initial composition, species susceptibility to damage and mortality, and the response of reproduction.

1. Light or moderate damage was sustained by most equilibrium species, including white oak, chestnut oak, and hickory. The greatest damage was associated with pioneer species, yellow poplar and table mountain pine.

2. Mortality increased with increasing severity of damage. For example, trees that were uprooted from heavy ice loads had the greatest mortality. Larger trees also had a higher mortality, perhaps due to a decreased ability to sprout. Saplings sustained less damage and mortality than larger stems, due to smaller ice loads and greater ability to sprout.

3. There was often a poor correlation between degree of damage and mortality. For example, while table mountain pine and Virginia pine sustained severe damage with a corresponding high mortality, yellow poplar sustained severe

damage, but had very low mortality.

4. Damage to canopy trees through crown removal or uprooting created gaps suitable for colonization by pioneer species. The seedling proportion of reproduction increased, although sprouting continued to be an important component of reproduction in the *Pinus*, and *Quercus* stands. The greatest increase in seedling reproduction occurred in the mesic *Liriodendron* stand. Determination of competition effects between pioneer seedlings, existing regeneration, and canopy closure will require measurement of the permanently located plots in the future.

5. Neither of the two hypotheses concerning the effects of ice storms on vegetation suggested in the literature is adequate to characterize the variety of community responses in the landscape. Compositional changes in communities occupying xeric sites (*Quercus* and xeric *Pinus*) would be minimal after an ice storm because composition of tree reproduction after canopy disturbance remained relatively unchanged. Alternatively, succession would appear to be accelerated in the mesic *Pinus* stand, where canopy damage and mortality permitted rapid growth of established oak species. Although disturbances stimulated yellow poplar reproduction, the long term consequences of disturbance are less clear. For example, stimulation of the pioneer

seedling reproduction from repeated storms may maintain this community, or if seedling survival is low as competition increases during regrowth, the stand may shift to an equilibrium community.

6. Ice storms are a natural disturbance of an intermediate spatial scale. Gaps created are often larger than the single or few tree gaps usually produced by senescence, but not as extensive as those created by other disturbances such as fire, cultivation, and logging.

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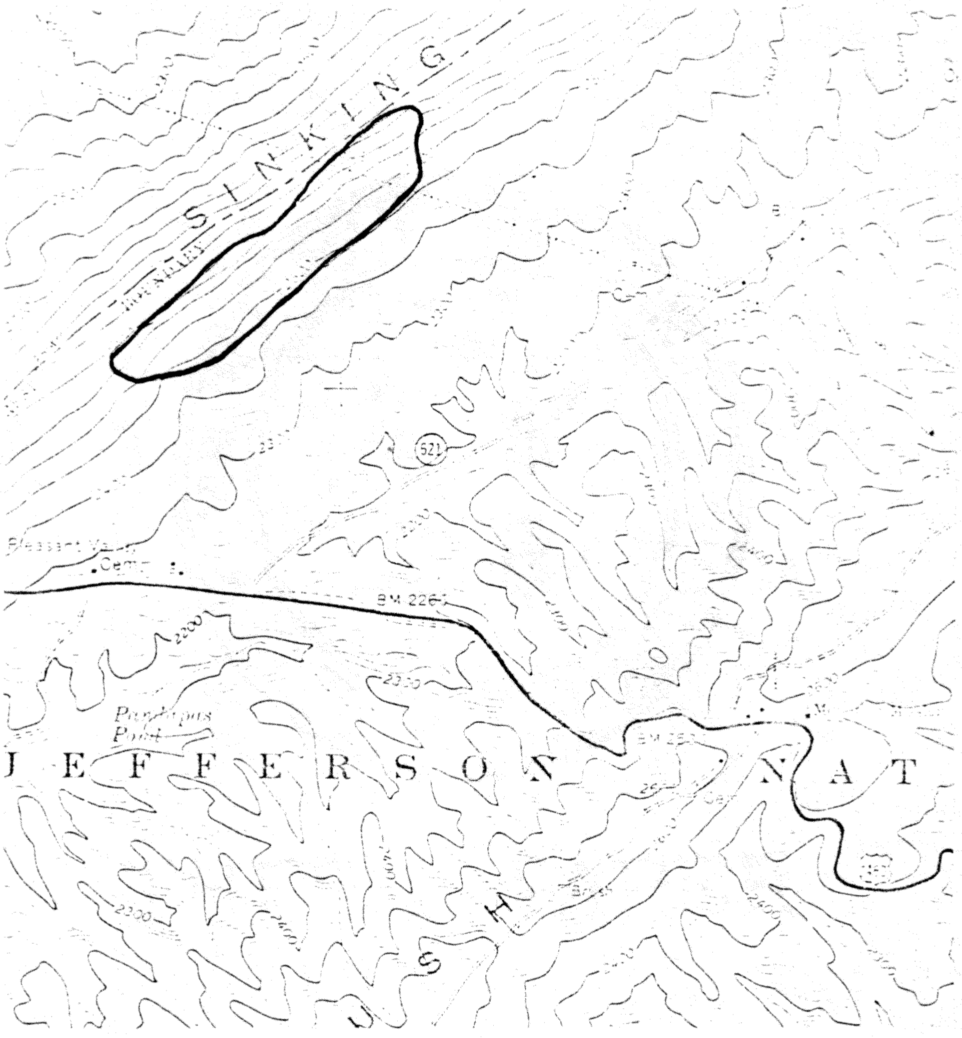
Appendix I

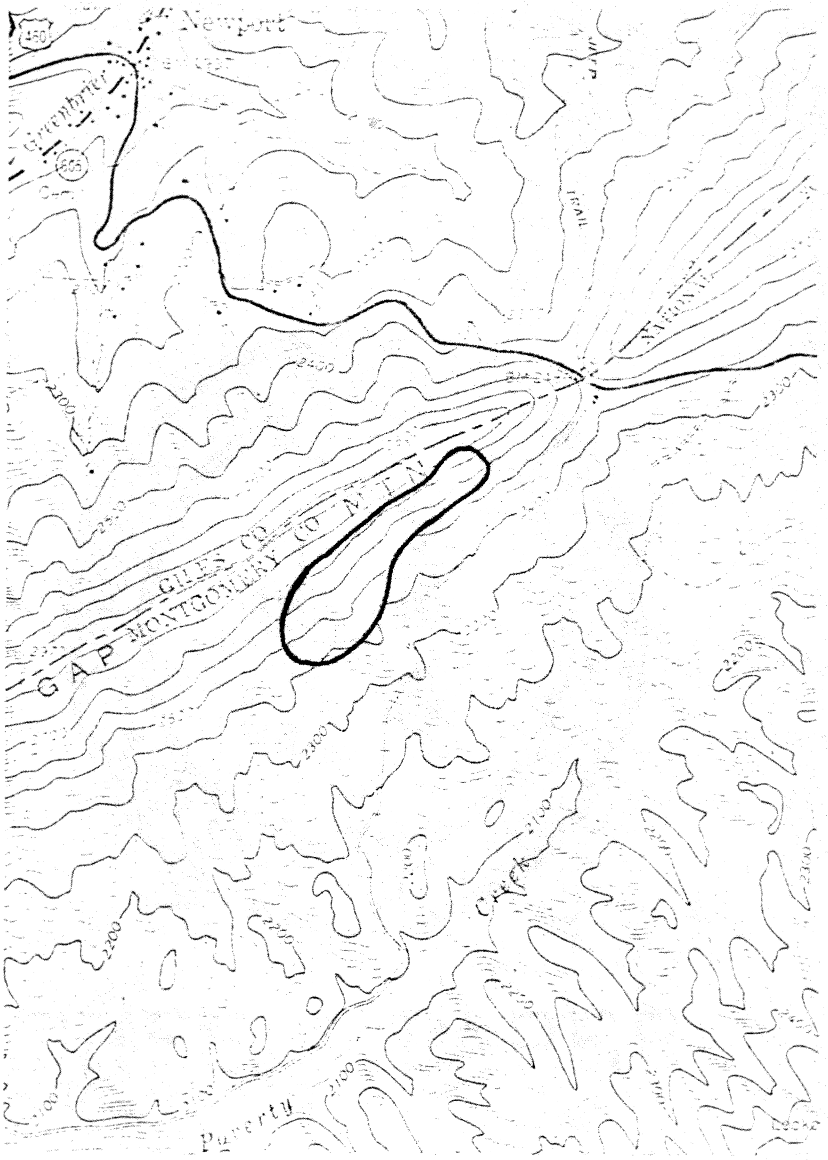
STAND LOCATION

Figure I.1



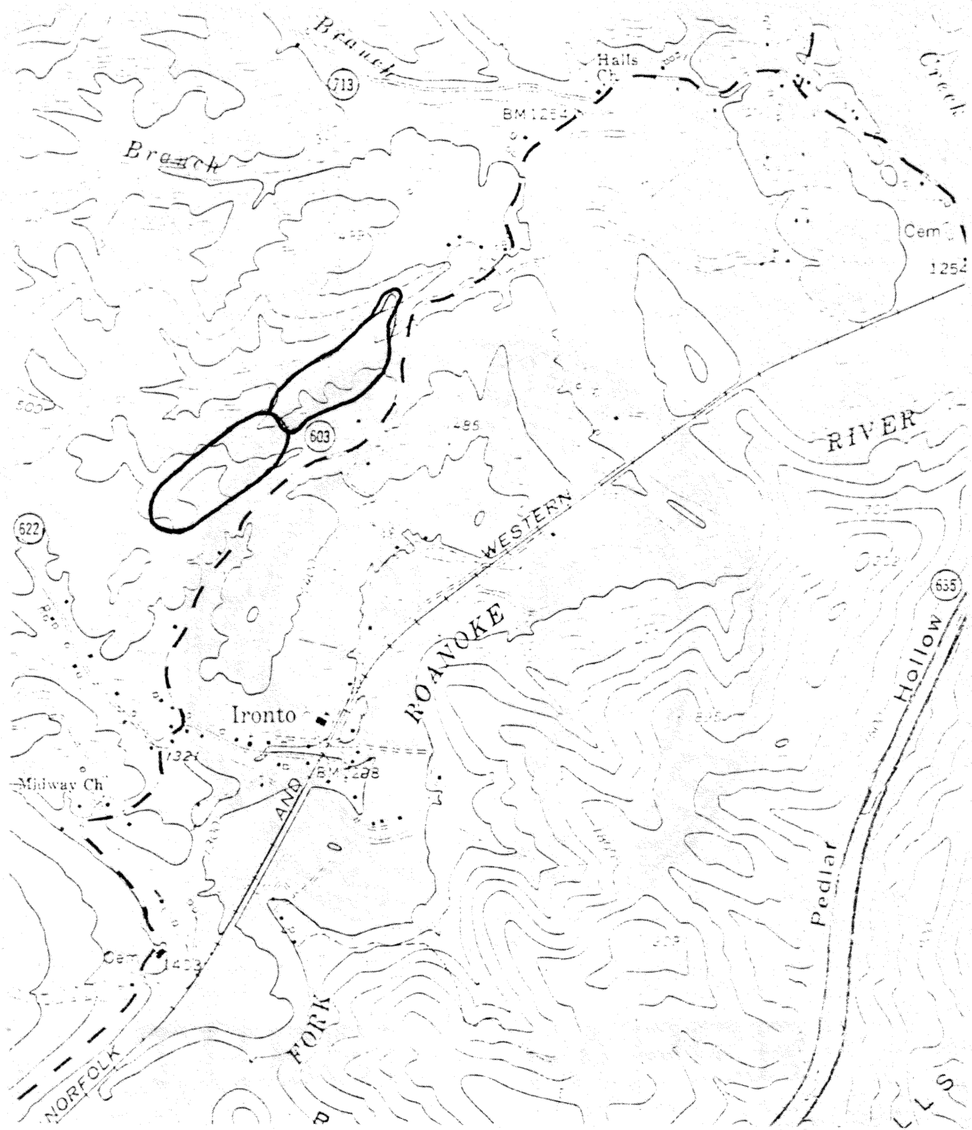
The Liriodendron stands were located on Sinking Creek Mountain in Montgomery County. (from USGS topographic map, Newport Quadrangle 1/24,000 1978.)

Figure I.2



The Quercus stands were located on Gap Mountain in Montgomery County. (from USGS topographic map, Newport Quadrangle 1/24,000 1978)

Figure I.3



The Mesic and Xeric *Pinus* stands were located north of Ironto in Montgomery County. (from USGS topographic map Ironto Quadrangle 1/24,000 1978)

Appendix II

Figure II.1

Sample plot layout for *Liriodendron* stands including transect and macroplot distances

Distance between macroplots

plot	Transect No. 1	2	3	4	5
1	28	5	23	23	35
2	38	54	65	36	42
3	47	41	30	47	43
4	60	38	40	51	95
5	41	75	37	46	18
6	36	40	42	41	43

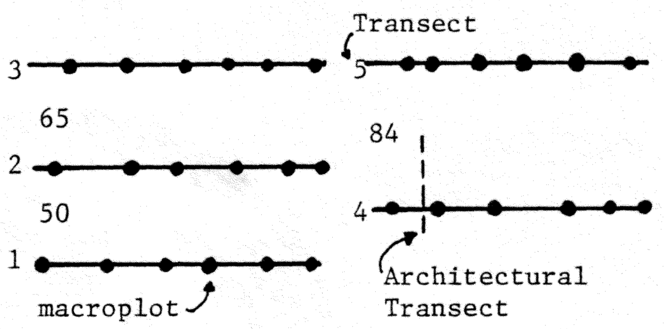


Figure II.2

Sample plot layout for *Quercus* stands including transect and macroplot distances

Distance between macroplots

plot	Transect No. 1	2	3	4	5
1	30	15	54	20	15
2	31	30	30	37	45
3	28	26	40	48	37
4	26	30	65	54	35
5	42	42	67	50	53
6	34	35	33	24	48

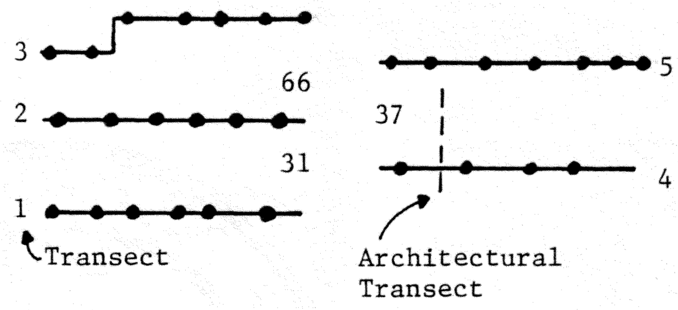
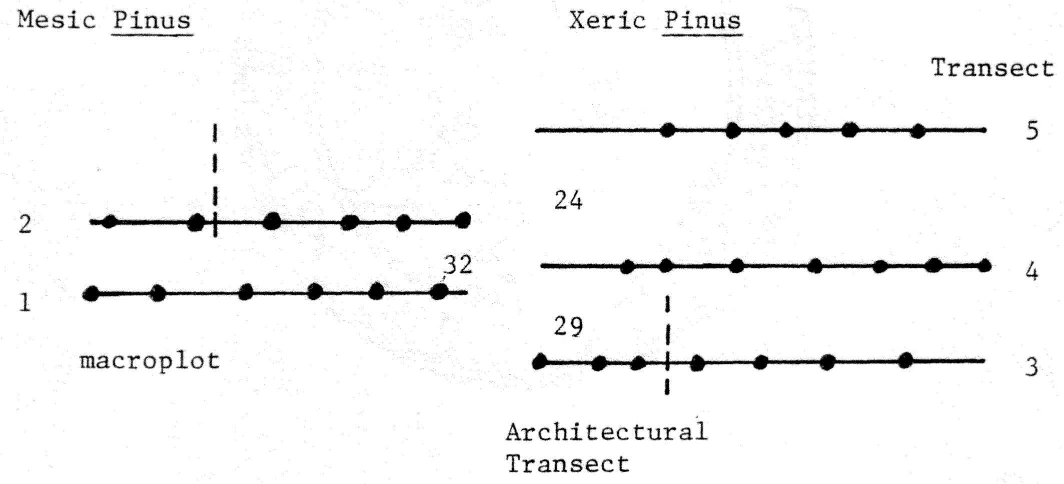


Figure II.3

Sample plot layout for Mesic and Xeric Pinus stands including transect and macroplot distances

Distance between macroplots

	Transect No.				
plot	1	2	3	4	5
1	50	23	12	25	62
2	32	25	90	34	37
3	33	54	12	27	21
4	36	35	34	45	45
5	45	29	35	52	35
6	33	15	42	34	34



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