FOREST MONITORING AT THE MARSH-BILLINGS-ROCKEFELLER NATIONAL HISTORICAL PARK

2005 RESEARCH REPORT

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TABLE OF CONTENTS

Page

ACKNOWLEDGMENTS 1

INTRODUCTION 2

Relevance of monitoring 2
Focus on succession..... 3
Conceptual basis for monitoring..... 4
Stressors, stress responses, and indicators..... 4
Ecosystem drivers and complex interactions..... 5
Benchmarks..... 5
Monitoring objectives..... 8

METHODS 8

Data collection 8
Data analysis 11

RESULTS 15

Stand inventory metrics 15
Productivity, growth, and yield..... 18
Stand dynamics 21
Size class distributions and dominance 21
Mortality processes and self-thinning..... 27
Compositional dynamics and regeneration demography 33
Deer browse impacts 36

Forest health 39
Crown condition 39
Beech bark disease 45
Regeneration trends 46

Biodiversity and habitat structure 49
Vertical structure 49
Downed coarse woody debris..... 52
Dead tree structure..... 54
Understory plant assemblages 57
Legacy trees 60

DISCUSSION AND CONCLUSIONS 63

SUMMARY OF MANAGEMENT AND MONITORING RECOMMENDATIONS 65

LITERATURE CITED 67

APPENDIX – Vascular Plant Species in Monitoring Plots 70

LIST OF FIGURES

Page

Figure 1. Map of the Marsh-Billings-Rockefeller National Historical Park …… …….. 3

Figure 2. Historic Range of Variability (HRV) conceptual diagram…… 6

Figure 3. Reference stands selected for forest ecosystem monitoring…… 9

Figure 4. Location of permanent monitoring plots…… 10

Figure 5. Design and parameters sampled in permanent plots……. 11

Figure 6. Permanent plot locations by natural community type…… 13

Figure 7. Basal area growth increment and volume production trends…… 20

Figure 8. Timber size class distributions in plantations…… 23

Figure 9. Simpson's dominance index for plantation size class distributions…… 24

Figure 10. Timber size class distributions in semi-natural stands …… 25

Figure 11. Simpson's dominance index for semi-natural stand size class distributions …… 26

Figure 12. Size class distributions and regression curves for selected reference stands…… 27

Figure 13. Live and dead tree diameter distributions (#1)…… 29

Figure 14. Live and dead tree diameter distributions (#2)…… 30

Figure 15. Comparison of dead to live tree quadratic mean diameters……. 32

Figure 16. Relationship between quadratic mean diameter ratios and reference stand age…… 32

Figure 17. Tree regeneration ratios for semi-natural stands……. … 35

Figure 18. Tree regeneration ratios for plantations…… 36

Figure 19. Deer browse on saplings by species…… 37

Figure 20. Deer browse effects by species as densities and proportions…… 38

Figure 21. Crown condition ratings by tree species across all reference stands…… 40

Figure 22. Crown density by reference stand for selected species…… 42

Figure 23. Foliage transparency by reference stand for selected species…… 43

Figure 24. Crown dieback by reference stand for selected species……. 44

Figure 25. Percent of beech trees infested with beech scale insect and *Nectria* fungus…… 45

Figure 26. Beech bark disease as a function of tree diameter…… 46

Figure 27. Percent decline for tree seedlings from 2001 to 2003……. 47

Figure 28. Conifer and hardwood regeneration trends from 2001 to 2003…… 47

Figure 29. Regeneration trends for sugar maples and pine species…… 48

Figure 30. Foliage height distributions for three reference stands…… 50

Figure 31. Foliage height diversity index values for all reference stands…… 51

Figure 32. Foliage height diversity index comparison by silvicultural regime …… 52

Figure 33. Reference stands ranked by downed coarse woody debris volume…….. 53

Figure 34. Downed coarse woody debris volumes compared to benchmark values…….. … 54

Figure 35. Snag densities as a percentage of total stems……. 55

Figure 36. Snag basal area as a percentage of total basal area…… 56

Figure 37. Snag basal area distributions by decay class ……. 57

Figure 38. Mean percent cover for understory vascular and non-vascular plants…….. . 59

Figure 39. Mean Shannon-Wiener Diversity Index for understory vascular plants……. 59

Figure 40. Map showing locations of remnant old-growth trees and open-grown wolf trees……. 60

Figure 41. Legacy tree total, park-wide abundance by species…… 61

Figure 42. Park-wide diameter distributions for live and dead legacy trees……. 62

Figure 43. Crown dieback, bole condition, and habitat attributes of legacy trees…… 62

Figure 44. Conceptual stand development model for MBR ……..… 64

LIST OF TABLES

Page

Table 1. Conceptual model for forest monitoring at MBR ……. 7

Table 2. General descriptive informative for reference stands…… 16

Table 3. Forest inventory metrics for reference stands…….…… 17

Table 4. Growth and yield by reference stand…… 19

Table 5. Change in basal area…… 19

Table 6. Simpson's dominance index by timber size class…… 22

Table 7. Statistical tests of mortality trends……...… 31

Table 8. Tree regeneration demography…… …… 33

Table 9. Downed coarse woody debris …...……..……. … 53

Table 10. Snag availability data: densities and basal area. …… …… 55

Table 11. Understory plant metrics…….……..…… …… 58

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2001 Field Crew (left)
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Introduction

In 2001 the Marsh-Billings-Rockefeller National Historical Park (the Park) initiated a cooperative program with the University of Vermont, establishing a long-term forest ecosystem monitoring system within the forested portion of the 555 acre (223 hectare) Park. The three-year initial phase of the program ended in 2003. The objectives during this time period were to establish a system of permanent plots distributed throughout the Park, collect intensive field data on a full compliment of ecological indicators, and determine baseline forest ecosystem conditions. Monitoring data were analyzed at the University of Vermont. The next phase of the program will consist of long-term monitoring with protocol and plot remeasurement schedules yet to be determined. This report presents the final results of analyses using data collected over the initial three year period. The findings presented are intended to inform on-going management planning efforts and, thus, focus on relevant indicators of ecosystem dynamics and integrity. Recommendations are provided related to both park management and the potential for continued monitoring in the future.

Relevance of monitoring

The Mt. Tom woodland near Woodstock, VT is one of the oldest surviving examples of scientifically informed reforestation and forest management in the United States. Early and evolving forest conservation efforts and silvicultural practices, beginning with Frederick Billings' first large scale tree plantings in 1874, left a legacy that is still very apparent throughout much of what is now the Marsh-Billings-Rockefeller National Historical Park (MBR) (Figure 1). The enabling legislation for the Park directed that the tradition of professional forestry practiced on Mt. Tom for almost 125 years be continued by the National Park Service as an educational demonstration of forest stewardship and to preserve this cultural landscape. Places of cultural and historic significance in the forest mosaic are to be managed as "readable landscapes," maintaining the character defining features that tell this story.

The rich history of land management at Mt. Tom created an unusual variety and juxtaposition of experiential characteristics. There are many large trees, unusual for eastern second growth woodlands; including a number of old-growth hemlocks, many close to 400 years old; tall, graceful Norway spruces, originally planted under the direction of Frederick Billings; and old maples dating back to George Perkins Marsh and the earliest settlements on Mt. Tom. The Park represents one of the oldest examples in New England of a continuously managed forest and active reforestation. For instance, a number of coniferous plantations of both native and non-native species were established beginning in the 1880s and continuing through the early 20th century. Today these comprise 26% (61 hectares) of the Park's area. But reforestation also occurred without planting in many areas of the forest, largely as a result of agricultural abandonment, resulting in naturally regenerated northern hardwood, hemlock, and mixed forests. In some areas this natural regeneration was augmented with scattered planting of native hardwood species, although often using non-local planting stock. Semi-natural forests represent 63% (142 hectares) of the Park. The Park's diverse forest mosaic reflects this history of alternate reforestation approaches and varied successional trajectories.

The Park today includes a wide diversity of stand types as well as pronounced visual contrasts and view corridors created by open pastures and fields surrounded by forest plantations. Visitor experience of alternating openness and enclosure is further enhanced by the roughly 14-mile system of 19th century carriage roads winding through the forest and over Mt. Tom (Figure 1). As a unit of the National Park system, the forest will be managed to maintain these unique and distinctive cultural and visual qualities.

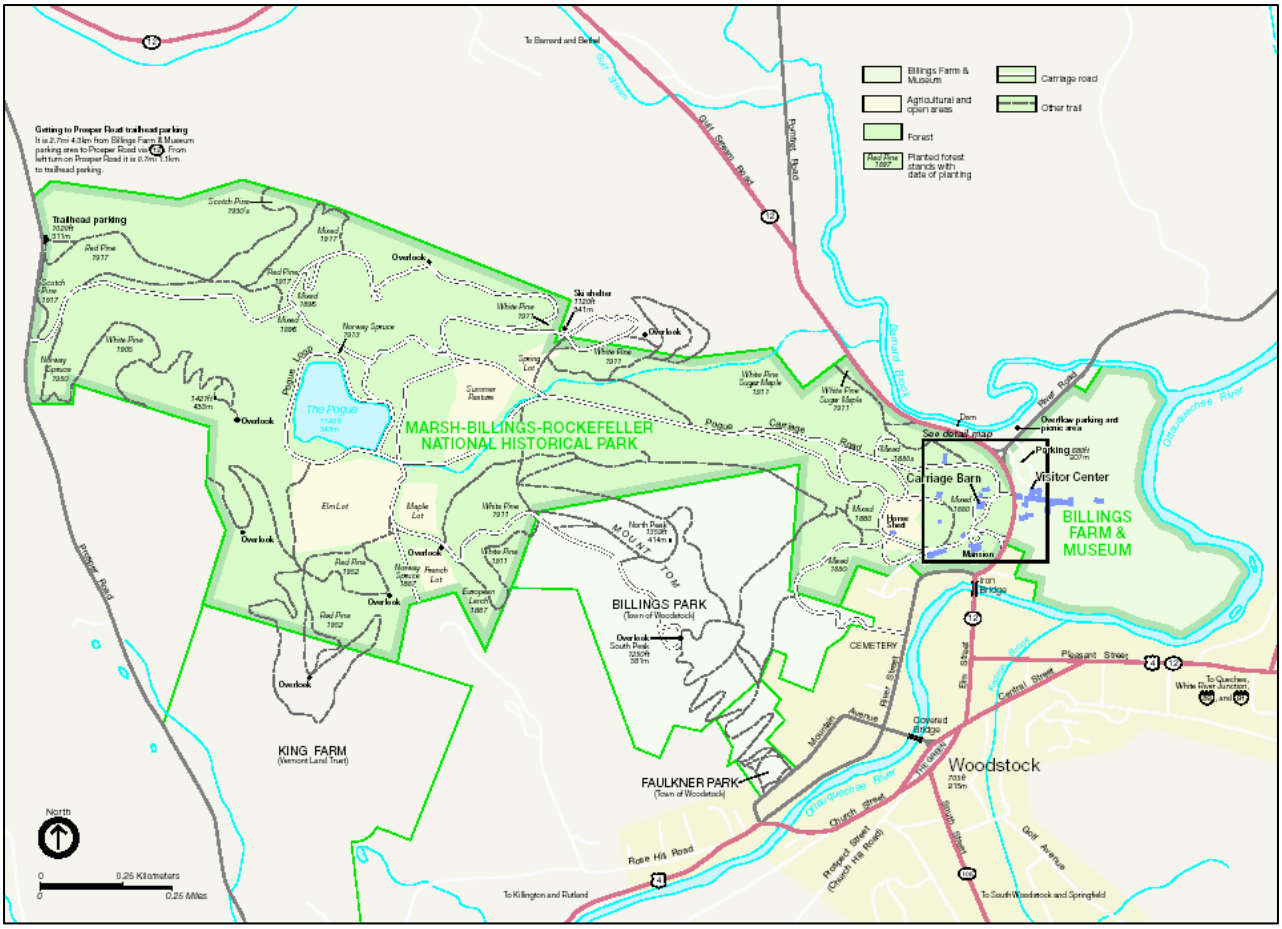


Figure 1. Map of the Marsh-Billings-Rockefeller National Historical Park, Woodstock, Vermont, U.S.A. (reprinted with permission of the USDI National Park Service).

The Park has a mission that is largely unique within the National Park System: demonstrating active forest stewardship while adhering to the mandate shared by all units of the National Park System, which is to "conserve park resources unimpaired for the enjoyment of future generations." Fulfilling this mission will necessitate an active science program to inform management activities, such as long-term planning. The forest monitoring program is designed to achieve this goal. Monitoring will help Park managers determine the health, productivity, development, and sustainability of both plantations and semi-natural forests. It informs planning to conserve plant and animal populations and manage recreational activities, visual qualities, and cultural interpretation accordingly. Long-term challenges, such as climate change, acid deposition, spread of exotic insects and pathogens, and ever-changing public expectations of natural areas, require an adaptive approach to park management. This report presents data relevant to each of these management concerns.

Focus on succession in plantations and semi-natural forests

The Park is an ideal place to monitor and interpret long-term reforestation and recovery processes. Restoration at the property, beginning as early as 1880, involved a range of direct planting and augmented natural regeneration

methods. The Park bears the profound legacy of 19th century clearing and land-use, as well as the subsequent influences of evolving cultural notions about reforestation and forestry. It is a microcosm, therefore, of the human-influenced successional dynamics and recovery processes now occurring across forested landscapes in the northeastern United States.

Consequently, an emphasis of monitoring at MBR is successional development within forest stands that are representative of the Park's diversity of reforestation strategies, stand ages, silviculural management, and plant assemblages. Successional development is a key measure of the long-term success or effects of the variable reforestation approaches. It is also an indicator of wildlife habitat representation (Keddy and Drummond 1996; Kruse and Porter 1994), as exhibited by the mix of successional stages (e.g. early, mid, or late-successional) and structural classes (e.g. single vs. multi-layered forest canopies). As such, it facilitates evaluation of the Park's contribution to local and regional biodiversity conservation. The monitoring program evaluates a number of specific parameters that reflect successional or stand development processes (Franklin et al. 2002; Oliver and Larson 1996). These include diameter distributions, canopy layering or vertical structure, tree species reproduction and demography, mortality rates and processes (e.g. density-dependent vs. density independent), coarse woody debris, and understory plant community composition and diversity. Tree health indicators and growth rates are also analyzed. This report evaluates data on these and other forest metrics, providing a basis for biodiversity conservation, sustainable forest management, and recreation management.

Stand development processes in plantations are a particular focus of management planning at MBR. The long-term maintenance of current species composition is in question, with respect to both plantations of exotic species and plantations of native conifers established on inappropriate sites, for instance where a given species is not locally endemic. Consequently, the monitoring program is designed to contrast stand development in plantations with development in semi-natural forests. Much of the analysis presented in this report is organized in this manner.

With a substantial portion of the Park in stand conditions (e.g. ages 80 to 110 years old) approaching transition to late-successional structure and composition, it is important to monitor factors, such as diseases and insects affecting shade-tolerant tree species, that may infleunce that potential. The monitoring program is designed to detect such a perturbation of stand development, thereby allowing managers to plan appropriate silvicultural interventions as needed.

Much of the continuing forest stewardship in the Park will involve demonstrations of sustainable forestry practices, such as logging methods that minimize disruption to wildlife and sensitive plant habitats. An adaptive management approach is critical for these purposes as well as overall resource management planning, allowing park managers to learn from past successes and failures and make adjustments as needed. Baseline monitoring is required for robust evaluation of forest management effects. Visitor-use in the National Park System has increased dramatically in recent decades. This places additional pressures on Park resources, requiring management of recreation impacts and competing uses. Monitoring will allow Park managers to evaluate the ecological impacts of recreational activities and plan management interventions accordingly. Thus, the forest dynamics monitoring system is an essential component of an adaptive management approach.

Conceptual basis for monitoring

Stressors, stress responses, and indicators

Forest dynamics monitoring at the Park is based on a conceptual model (Table 1) similar to those currently being developed by the National Park Service under the nation-wide "Vital Signs Monitoring" program. The model for MBR identifies ecosystem stressors (primarily human-caused) that are likely to be operative at the Park either at present or in the future. Stress responses are ecological effects resulting from stressors;

indicators are the direct measures signaling a change in a particular stress response. The challenge in any monitoring program is deriving a set of measurable indicators that are mechanistically related to specific stressors via stress responses. There are several obstacles in this regard. First, potential indicators are limited to those that can be generated from the available data. Second, indicators sometimes correspond to multiple stressors, making it hard to determine causal relationships. Ideally indicators would correlate discretely with only one stressor. In forest ecosystems, however, this is rarely the case: indicators of physiological vigor, productivity, community composition, and forest structure often exhibit similar responses to a suite of stressors (Vogt et al. 1997).

Thus, the conceptual model presented here identifies a number of useful indicators – these can readily be generated from monitoring data – but it is recognized that additional explorative analysis is required to make well supported inferences regarding causal relationships. Forest managers will need to analyze monitoring data carefully in order to understand a change in any given indicator over a given time period. First-hand field knowledge of the forest stands in question will prove invaluable in helping to tease apart possible explanatory relationships among variables. Thorough record keeping will be needed to track the long-term effects of forest management activities.

Ecosystem drivers and complex interactions

While not specifically presented in Table 1, the conceptual model for MBR recognizes that there are important ecosystem drivers (primarily due to intrinsic ecosystem processes) affecting ecosystem dynamics. Stressors are superimposed on these. Indicators often will be most directly influenced by ecosystem drivers, such as ecological succession, stand structural development, natural disturbances, herbivory, and natural climate variability (Franklin et al. 2002). Ecosystem drivers interact with human-related stressors, resulting in complex stress responses and measurable changes in multiple indicators. Interactions between drivers and stressors may create positive feedbacks, increasing rate and magnitude of change in a particular indicator, as in the case of shifts in community composition resulting from a combination of natural disturbance effects and climate change impacts (Keeton et al. 2005). In other cases, drivers may retard or buffer changes caused by stressors, for example when successional change leads to reduced susceptibility to invasive organisms, or when a favorable growing season (related to natural climate variability) increases physiological vigor in trees, thereby reducing susceptibility to human-caused insect or pathogen outbreaks. Indicators will alert forest managers to changing conditions, but further analysis usually will be required to fully understand these complex dynamics.

Benchmarks

The NPS Vital Signs Monitoring program stresses the need for quantifiable benchmarks. These are thresholds beyond which a change in ecosystem condition (as measured by an indicator) is deemed unacceptable or “abnormal.” However, ecosystem conditions are naturally variable over time (Aplet and Keeton 1999). Process rates, composition, and structure change dynamically in response to climate variability, natural disturbances, and succession (Figure 2). It is not possible, therefore, to identify one particular condition that is “acceptable” or “normal” in an ecological sense. For this reason the concept of Historic Range of Variability (HRV) has gained increasing credibility as a useful benchmark for monitoring (Aplet and Keeton 1999, Landres et al. 1999, Lindenmayer and Franklin 2002; Davis et al. 2001).

HRV provides a benchmark for understanding system dynamics and changes brought about by humans. It describes the bounded behavior of changes in ecosystem structure and process rates over a specified time period before significant alteration by industrialized societies. Ecosystem conditions outside this range signal changes in, and possible impairments of, ecosystem functions. Although challenging to reconstruct, reference time periods on the order of several centuries appear to be useful benchmarks because: a) they

are long enough to have included some degree of natural climate variability; but b) not so long to have spanned major ecological shifts associated with inter-millenial climate variability.

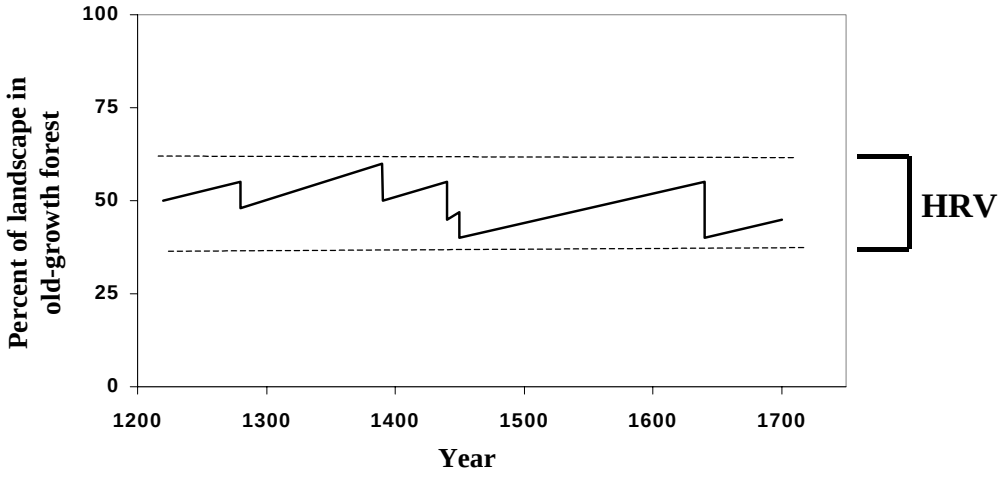


Figure 2. Conceptual diagram of Historic Range of Variability. An example is provided showing old-growth forest (defined by age class distributions only) abundance in northern hardwood systems at ecoregional scales. Data are hypothetical but consistent with regional disturbance dynamics (Seymour et al. 2002). Note the oscillation of forest age class distributions over time in response to high-intensity natural disturbances (inflection points) and resulting successional development. Figure is modified from Aplet and Keeton (1999).

Practical application of HRV to many of the indicators in the conceptual model will be challenging. Lack of available data from which to quantify ranges of variability, together with the difficulty in establishing "natural" ranges in landscapes heavily impacted by centuries of land-use, will limit the utility of HRV in some cases (Landres et al. 1999). Thus, benchmarks will need to be established based on multiple criteria and considerations, including management objectives, such as conservation of biological diversity and forest productivity, as well as social values, public input, and the well-informed judgment of forest managers.

It may be possible to develop historic ranges of variability for a subset of the indicators used at the Park. Benchmark ranges would be bounded by upper and lower thresholds of variability associated with ecosystem dynamics under low-levels of human disturbance (Figure 2). This would provide a more dynamic benchmark, compared to fixed or static benchmarks, against which to evaluate changes in ecological integrity caused by human-induced stresses. Even where actual ranges have not been accurately quantified, information on historic ecosystem conditions is a useful reference for understanding landscape change or altered dynamics associated with climate change. For instance, present day age class distributions in most of Vermont are outside the pre-European settlement HRV with respect to older age (e.g. >200 yr. old) classes (Foster et al. 1998). This is an artifact of 19th century land-use and subsequent reforestation, which has led to an overabundance, relative to HRV, of young to mature (e.g. <150 yr. old) forest stands.

Table 1. Conceptual model for forest monitoring at MBR. Note that stress responses and indicators sometimes correspond to multiple stressors, making it hard to determine causal relationships. Ecosystem drivers – such as succession, stand development, natural disturbances, and climate variability – interact with anthropomorphic stressors and, in some cases, result in similar responses. This further confounds accurate inferences regarding mechanistic linkages among variables.

Stressors	Stress Responses	Indicators
Tree disease infestation/ Pest insect outbreak	Weakened physiological vigor Increased production of defensive compounds Increased susceptibility to other natural disturbances	Crown dieback Crown density Foliage transparency Tree mortality Rates of tree growth Direct evidence of disease
Acid deposition	Weakened physiological vigor in less tolerant species Physiological responses to calcium depletion, such as changes in cold susceptibility Altered competitive dynamics Declines in fine root and mycorrhizal fungi production	Crown dieback Seedling mortality (e.g. sugar maple) Tree mortality Near-term shifts in community composition Soil pH* Live crown ratio
Climate change	Drought stress Altered reproductive phenology Altered allocation of resources by plants Altered competitive dynamics Altered susceptibility to natural disturbances Possible $C0_2$ fertilization effects and associated near-term increases in water-use efficiency Interactions with nitrogen deposition and tropospheric ozone	Crown density Crown dieback Tree growth rates Live crown ratio Seedling mortality/survival rates Tree mortality Long-term shifts in community composition
Invasive organisms	Shifts in community composition Altered nutrient cycling Altered pathways of energy flow	Percent cover: invasives vs. natives Plant diversity and dominance indexes
Intensive timber harvest	Altered availability of resources Altered competitive dynamics Increased rates of nutrient cycling and leaching Potential spread of invasive organisms Declines in species associated with negatively impacted habitats and forest structures Habitat fragmentation Variable belowground responses	Wildlife community composition* Relative abundance by species and life history strategy Invasive percent cover or dominance Structural metrics: canopy structure, gap frequency and sizes, large tree densities, coarse woody debris volumes and densities, etc. Patch metrics: edge to area, mean patch size, fractal dimension, etc.*
Recreational use and management	Reduction in habitat availability for human-averse and road-averse species Soil compaction and erosion Declines in fine-root production and associated productivity where soils are compacted Altered hydrologic regimes caused by roads/trails Fragmentation of interior habitats Vectoring of edge species and invasive organisms Loss of habitat structures (e.g. large snags)	Road and trail density* Core area/unroaded area patch metrics* Fine root density and turnover rate* Altered hydrograph: change in timing and magnitude of peak flows*

* Not currently assessed or monitored at MBR

Monitoring objectives

The monitoring program had several objectives. They were as follows:

1. establish a system of reference stands and permanent monitoring plots that is representative of the Park's diversity of plantations and semi-natural forest stands;

2. evaluate indicators of: a) forest structural and compositional development; b) tree regeneration; c) understory plant community composition; and d) forest health;

3. conduct periodic plot re-measurements;

4. maintain databases at the University of Vermont and MBR;

5. use statistical and data integration techniques to describe the current, near-term, and long-term attributes and dynamics of forest structure, composition, and health on the Park;

6. monitor key forest ecosystem processes, including growth, yield, and mortality; changes in wildlife habitat availability; the onset, spread, and effects of tree diseases and insect pests; and tree vigor trends and successional transitions in exotic and native timber plantations; and

7. coordinate with existing federal, state and regional programs, such as the Vermont Monitoring Cooperative and the NPS Inventory and Monitoring Program, to monitor forest ecosystem sustainability and responses to ecological stressors, such as airborne pollution and climate change.

METHODS

Data collection

The monitoring system is based on a statistical sample (i.e. multiple plots) within individual forest stands. However, because the Park has approxiamately 50 stands (depending on stand classification method) and many of these are very small (e.g. < 3 ha.), plots could not be established in all stands due to budgetary and experimental design constraints. Consequently, a subset of reference stands was selected for monitoring. The procedure for selecting reference stands was to stratify the stands delineated by Wiggin (1993) by species composition, age, plantation versus semi-natural, and silvicultural management history. The largest and/or most representative examples within each stratum were selected as reference stands. Sixteen reference stands were selected in this way, consisting of eight plantations and eight semi-natural stands (Figure 3).

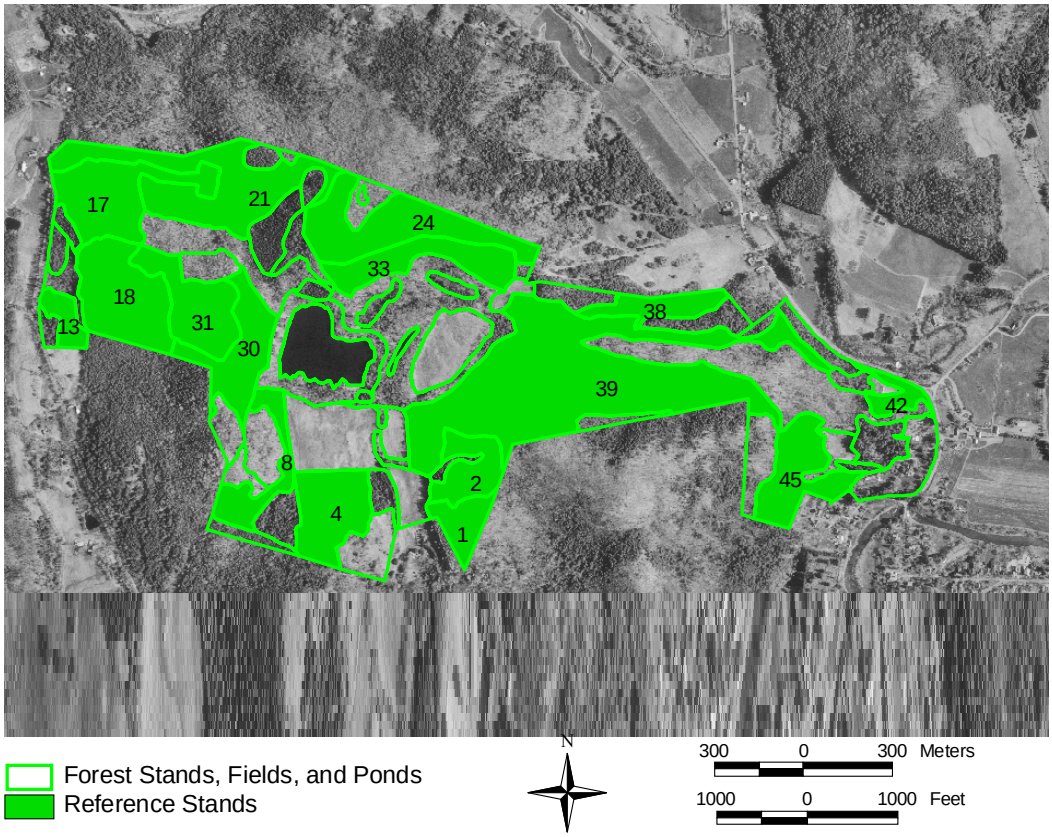


Figure 3. Reference stands selected for forest ecosystem monitoring. There are eight plantations and eight semi-natural stands. Stand identification numbers follow Wiggin (1993).

Permanent sampling plots were established within each reference stand. The number of plots in a stand is proportionate to the size of the stand, ranging from three to six plots, with the majority of stands having five plots. Stand 42 is an exception, having only one plot due to its particular dimensions; although statistical sampling was not possible it was selected for limited monitoring due to its unique combination of age and composition. A geographic information system was used to place the plots in a stratified random pattern to meet statistical sampling requirements while ensuring even dispersion within each stand. Pre-determined plot centers were located in the field using a Trimble Pro XRS Global Positioning System (GPS). A total of 62 monitoring plots were established in summer 2001 (Figure 4).

Each permanent plot consists of several nested square plots, line transects, and belt transects. Plot design and the corresponding attributes sampled are shown in Figure 5. Nested square plots are 0.1 ha, 0.05 ha, 0.02 ha, and 1 m^2 in size. There are thirteen m^2 quadrats used for estimating percent cover of all substrates (mineral soil, fine litter, rock, and coarse woody debris), understory plants by species (vascular and non-vascular plants), lichens, and above-ground fungal fruiting bodies. Canopy closure is measured at the center point of each quadrat using a spherical densitometer; litter layer depth is also measured at these points.

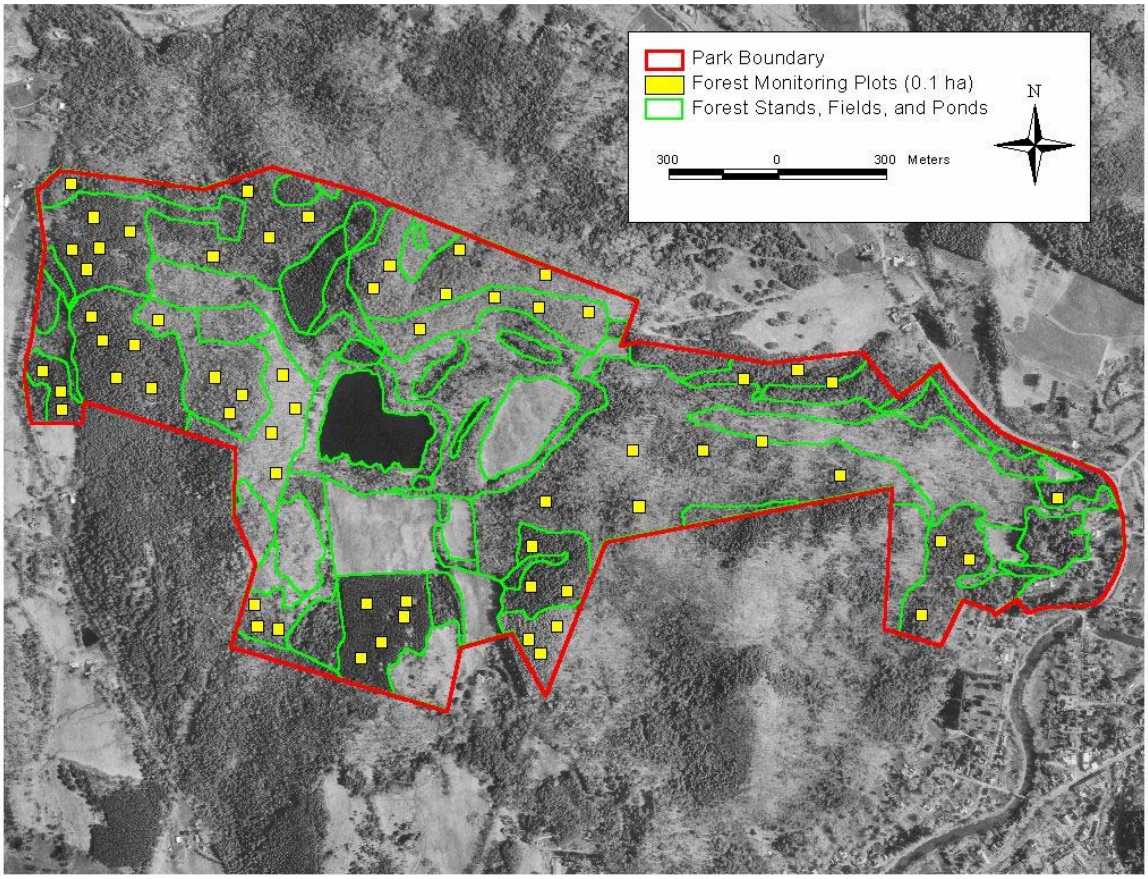


Figure 4. Location of permanent monitoring plots. The number of plots per reference stand is proportionate to the size of the stand. Plot distribution is based on a stratified random design. Plot sizes are shown to scale.

In the 0.05 ha. plot, all live and dead trees > 5 cm dbh and > 1.37 m tall are permanently tagged, measured, and recorded by species, diameter, height, and decay class (snags only). Tree heights and crown depth on each tagged tree are measured using an Impulse 200 laser range finder. Assessments of tree health include coding of crown and bole condition, presence of disease and disturbance indicators, and presence of natural excavations and cavities. Additional forest health indicators assessed include crown dieback, crown density, and foliage transparency, which are estimated by percentage class for all dominant canopy trees (Twardus et al. 1993). Beech bark disease (*Nectria coccinea* var. *faginata*) is assessed using a three class system developed for this project: BBD0 = no visible beech bark disease; BBD1 = light beech scale insect (*Cryptococcus fagisuga*) infestation; BBD2 = heavy scale insect infestation, but no *Nectria* fungal infection apparent; and BBD3 = *Nectria* infection.

The 0.1 ha plot size is used to record the same information described above for trees over 50 cm dbh and snags over 1 m tall with upper diameters >10 cm. The cross sectional area of canopy gaps within the 0.1 ha plots is surveyed using an integrated GPS/laser range finder/digital electronic compass surveying system. Density and size class of tip-up mounds are measured within this plot size. The 0.02 ha. plot is used for tallying saplings (by species) that are > 1 m tall but < 5 cm dbh. Evidence of deer browse is also recorded by stem. Coarse woody debris (downed logs ≥ 10 cm diameter at intercept) volume by decay class (1-5) is estimated using a line intercept method. Tree seedlings (regeneration < 1 m height) are sampled by species within two belt transects that are each 1 m wide and 31.62 m long.

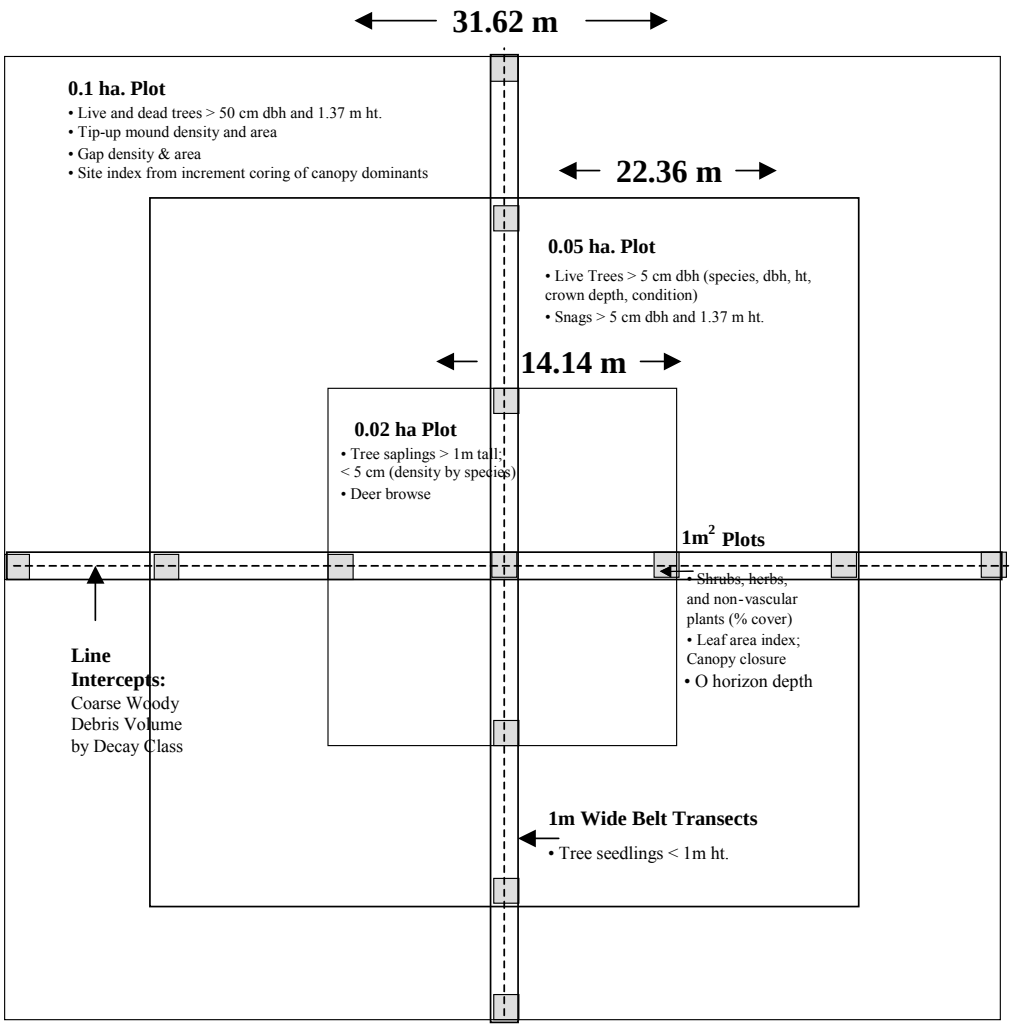


Figure 5. Design and parameters sampled in permanent plots. There are 62 of these plot systems distributed throughout the MBR National Historical Park.

The center point of each plot unit is mapped to within 1 - 30 cm horizontal precision using the GPS. Plot unit center points and the position of understory quadrats and line transects are permanently monumented. Two dominant canopy trees are cored at breast height to allow subsequent laboratory determination of tree age and site index. Data are collected on slope, aspect, topographic position, and shape of topographic cross section.

Data analysis

The monitoring program relies on a suite of metrics generated from plot data. These metrics were selected as robust indicators of forest structure, composition, and function, as well as for their usefulness in generating silvicultural prescriptions as per the Park's stewardship program. Each metric can be used explicitly to track changes over time because they are linked directly to processes of stand development, health, and productivity, and because they respond to perturbations, such as stress or disturbance.

To generate basic forest inventory metrics, including growth and yield data, plot data were entered into the Northeast Decision Model (NED) (Simpson et al. 1996). Stand comparison statistics in Tables 1 and 2 are the output of NED calculations. Exceptions include stand age, which were based on laboratory analysis of increment cores, and natural community typing. The later was determined on a plot by plot basis through GIS analysis using natural community data provided by Lautzenheizer (2002) (Figure 6). Coarse woody debris volumes were calculated following Warren and Olsen (1964) as modified by Shivers and Borders (1996). Mortality percentages were calculated by basal area and stem density for each stand.

A number of methods were used to analyze forest compositional development. First, I programmed an MS Excel spreadsheet to sort overstory data by species and diameter class. The latter followed USDA Forest Service timber-based diameter classes specific to northeastern U.S. conifers or hardwoods. These classes were used to facilitate conventional timber management planning. Diameter classes were as follows: sub-pole = 5 to 12.7 cm; pole = 12.7 to 27.7 cm (conifers) or 12.7 – 22.6 cm (hardwoods); small sawlogs = 27.7 to 37 cm (conifers) or 22.6 to 37 cm (hardwoods); and large sawlogs = 37 to 50 cm diameter at breast height (dbh). I also added classes (not included in the USDA Forest Service system) for seedlings (trees < 1 m height), saplings (trees > 1m height, < 5 cm dbh), and very large sawlogs (trees > 50 cm dbh). This made full use of all plot data and better represented the full spectrum of tree demography or age/size-based cohorts. I then calculated density by species within diameter classes as well as the proportion of total density represented by individual species. The proportions were graphed for each stand to provide a visual depiction of stand-specific tree demography, including responses to silvicultural management.

To quantify the observed differences in species composition and relative abundance among cohorts, I calculated the Simpson's Dominance Index for each diameter class by plot. I aggregated plot-level dominance index values to the stand level and generated mean values and estimators of variance (standard deviation and standard error). The dominance index assesses the relative predominance of one or more species, with a value = 1 representing complete dominance by a single species and a lower value representing a more even distribution of individuals among multiple species. The index is especially useful for monitoring compositional changes in plantations initially dominated by a single tree species.

A second method used to analyze compositional and structural development employed linear regression analysis of diameter distributions. Density data were pooled for each plot and aggregated to the stand level. I used linear regression analysis to test for statistically significant negative exponential diameter distributions indicative (in the absence of abundant suppression) of stands developing uneven-aged structure. Alternate curves (e.g. exponential, logarithmic, linear, polynomial, etc.) were fitted using transformations of the independent variable. Based on the statistical strength of alternate curves, I determined if distributions were approaching a "balanced" negative exponential form versus a uni-modal or bi-modal form indicative of even or two-aged structure.

A final method used to assess compositional development focused on tree reproduction, quantified as the density of seedlings < 1 m height. This analysis determined whether trees in the overstory are reproducing and re-establishing in the understory. Conversely, tree regeneration might consist more significantly of species not found in the overstory that are colonizing the site. Regeneration data were segregated by overstory species or colonizing species for each plot. In semi-natural hardwood and hardwood-hemlock stands, colonizing vegetation was defined as non-native species, white or red pine, or early-successional species, such as cherries and poplars, not currently present in the overstory. In pure hemlock groves, any species other than hemlock was considered to be a colonizer. Plot data were sorted and aggregated by natural community type, plantation vs. semi-natural, and silvicultural management. Aggregation in this case was not based on reference stands, resulting in larger

sample sizes and greater statistical power. Seedling densities were converted to proportions to normalize the overstory/colonizing regeneration ratios across all plots. Tukey tests assuming unequal variance were used to test for statistically significance differences in regeneration densities among the aggregate plot groupings.

crown condition data I created a series of Excel-based programs that 1) sorted data and calculated descriptive statistics by plot, species, and crown indicator; 2) aggregated descriptive statistics to the stand level by species and indicator; and 3) assessed indicators across all stands by species. Output of these programs were plotted as cumulative percentage distributions for each species by indicator for the Park and individual

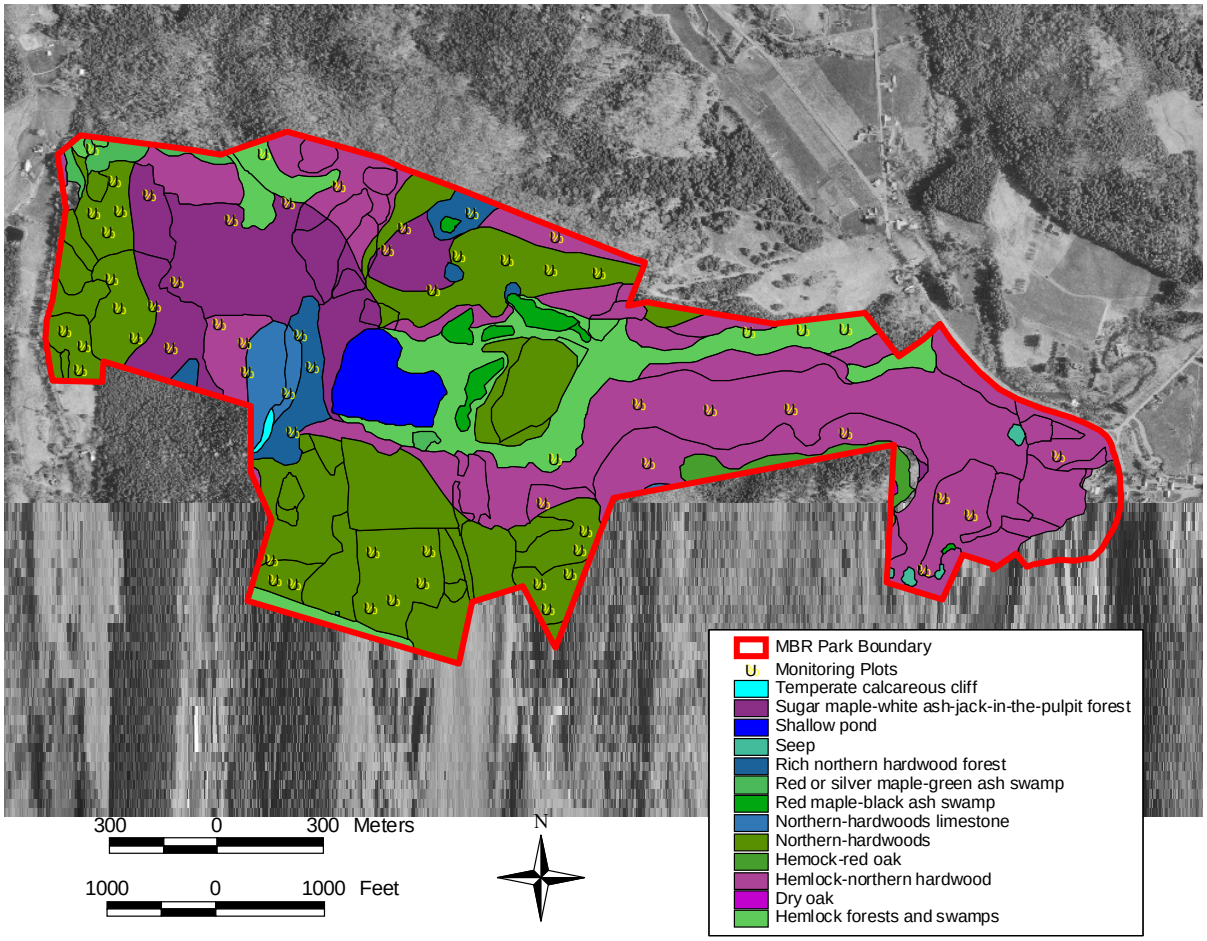


Figure 6. Permanent plot locations by natural community type. Natural community spatial data were provided courtesy of Tom Lautzenheizer, University of Vermont. Segregating plots by natural community, rather than current cover type or reference stand, provided a method for analyzing recolonization and successional trends. Tree demography and recruitment were analyzed relative to successional trajectories indicating development toward or away from a given natural community (or future potential vegetation).

Forest health evaluation was based on several indicators, including crown density, foliage transparency, crown dieback, tree regeneration, and mortality processes following protocol established by the USDA Forest Service National Forest Health Monitoring Program. To analyze

stands. Percentage thresholds for determining unacceptable crown condition followed Twardus et al. (1993) and VMC (2004). Beech bark disease and regeneration trends were evaluated using linear regression analysis with alternate curve fitting.

Analyses of mortality were focused on identifying the predominant mortality processes (e.g. density dependent competition vs. density independent exogenous factors) now operating across the Park's diversity of forests. Diameter and cumulative frequency distributions were generated for live vs. dead trees on a per stand basis. Kolmogorov-Smirnov two sample goodness of fit tests (Zar 1996) were used to test for statistically significant differences between live vs. dead cumulative frequency distributions. As a check on this analysis I tested differences between quadratic mean diameter for live vs dead trees using *t*-tests (paired two sample for means) and single factor Analysis of Variance. Linear regression analysis with alternate curve fitting (transformation) was used to evaluate mortality as a function of stand age by cover type. These tests also were used to compare deer browse intensities (by tree species) among forest vegetation cover types.

Analysis of vertical structure (e.g. the vertical distribution of foliage and canopy layering) included the generation of several metrics, including dominant canopy height, the number of canopy layers, and foliage height diversity index. I created a program in MS Excel that calculates the vertical area occupied by individual tree crowns. Individual crown occupancies within increments of 1 m along a vertical gradient were then pooled for each plot, with individual tree contributions weighted by their respective basal area. A proportion was calculated for each strata representing its share of the stand's total foliage. These were aggregated to the stand level, allowing variance to be estimated. The vertical distribution of foliage was graphed for each stand, allowing determination of canopy height and layering. A foliage height diversity index was calculated from the pooled data based on the formula for the Shannon-Wiener Diversity Index. The index yields an estimate of both the diversity of canopy strata occupied by tree crowns and the evenness with which foliage is distributed among these. I used *t*-tests that assumed unequal variance to test for statistically significant differences in foliage height index among stand types.

Another important indicator of stand development, response to management, visitor impacts, and forest ecosystem health is the abundance and diversity of understory plants. To evaluate this indicator I sorted quadrat data for each plot by species. The mean percent cover for woody shrubs, herbaceous plants (including herbs, ferns and allies, grasses, and sedges), and bryophytes was calculated by averaging quadrat data (N=13 per plot). Percent cover data were then transformed into proportions of total cover on an individual species basis. Using these proportions, I calculated the Shannon-Wiener Diversity Index for each plot. Species richness also was calculated for each plot. Plot values for mean percent cover, diversity index, and species richness were aggregated to the reference stand level. The fist two variables thus represent mean values throughout each reference stand, whereas the later represents mean richness at a scale of 0.1 ha; minimum and maximum species richness values were also calculated relative to this spatial scale. I compared understory plant variables for stand groupings using *T*-tests assuming unequal variance. In one instance, a *T*-test assuming equal variance was used, but a test of homogeneity of variance confirmed the equal variance assumption.

RESULTS

Stand inventory metrics

General stand inventory analysis results are presented in Tables 2 and 3. These results describe current and potential vegetation types (natural communities) where monitoring plots are located. They also provide basic metrics on stand structure and composition.

Current forest conditions are highly diverse, with the mosaic of stands providing a number of different canopy architectures, ranging from single to multi-layered. Dominant canopy height varies widely, but is highest in old plantations. For instance, a European larch stand, reference stand #1, represents the Park's second highest canopy, due to stand density and the growth form and rates exhibited by that species. The Park's tallest primary canopy and tallest individual second growth trees are found in the 1880 white pine plantation (reference stand #45) at the base of Mt. Tom.

Other indicators suggest that forest structure varies widely throughout the Park, providing a diversity of wildlife habitats, carbon sequestration potential, and other ecological functions. For instance, live basal area in reference stands ranges from 28.9 to 68.3 m^2/ha; highest basal areas are reached in the Park's oldest coniferous plantations. Relative density (a metric that integrates basal area with stem density) also varies widely, suggesting a diversity of stocking densities and overstory growth rates. The Park's forests are fully stocked, with stocking levels near, above, or well above the B line (optimal stocking for tree growth) in all cases. This represents a significant opportunity for continued forest stewardship.

The diversity in stocking densities also represents a diversity of wildlife habitats, such as hiding and resting cover versus foraging habitats, that are associated with differences in stand density and composition (DeGraaff and Yamasaki 2001). The juxtaposition of diverse patches over relatively small spatial scales represents a high quality habitat configuration for many wildlife species, especially generalists and those requiring multiple habitat types. This pattern may reduce habitat quality for some species, however, such as those associated with the interiors of specific forest types.

The metrics presented in Tables 2 and 3 will provide an efficient and ecologically meaningful system for monitoring changes in these forest characteristics and functions over time.

Table 2. General description of reference stands.

Stand ID[1]	Establ-ishment Year [2]	Size (ha)	Stand Type	USDA For. Ser. Cover Type	Potential Natural Communities Within Plots[3]	Hard Mast	Fruit & Nut Trees	Canopy Height (m)	Canopy Structure
1	1887	2.70	Plantation	European larch	Northern-hardwoods	present	0%	38	Multi-Layered
2	1911	4.13	Plantation	Eastern white pine	Northern-hardwoods, Hemlock-northern hardwood	present	0%	37	Two-Layered
4	1952	6.61	Plantation	Red pine	Northern-hardwoods	present	0%	25	Single-Layered
8	1940	3.94	Semi-Natural	Mixed white pine-hardwoods	Northern-hardwoods	present	0%	28	Single to Two-Layered
13	1950	1.79	Plantation	Norway spruce	Northern-hardwoods	present	1%	26	Single-Layered
17	1917	8.48	Plantation	Red pine	Northern-hardwoods	present	0%	35	Two-Layered
18	1905	8.98	Plantation	Eastern white pine	Northern-hardwoods, Sugar maple-white ash-jack-in-the-pulpit forest	present	0%	37	Two-Layered
21	1890	12.60	Semi-Natural	Hemlock-hardwoods	Sugar maple-white ash-jack-in-the-pulpit forest, Hemlock-northern hardwood, Hemlock forests and swamps, Red or silver maple-green ash swamp	present	0%	32	Two to Multi-Layered
24	1890	9.85	Semi-Natural	Maple	Northern-hardwoods, Hemlock-northern hardwood, Sugar maple-white ash-jack-in-the-pulpit forest	present	0%	28	Multi-Layered
30	1900	6.35	Semi-Natural	Maple	Rich northern hardwood forest, Northern-hardwoods limestone	present	0%	29	Multi-Layered
31	1890	6.54	Semi-Natural	Spruce-northern hardwoods	Northern-hardwoods limestone, Hemlock-northern hardwood, Sugar maple-white ash-jack-in-the-pulpit forest,	present	0%	32	Two to Multi-Layered
33	1890	6.00	Semi-Natural	Oak-northern hardwoods	Northern-hardwoods, Sugar maple-white ash-jack-in-the-pulpit forest	present	1%	28	Two to Multi-Layered
38	1890	3.57	Semi-Natural	Hemlock	Hemlock forests and swamps	present	0%	30	Two to Multi-Layered
39	1910	33.73	Semi-Natural	Hemlock-hardwoods	Hemlock-northern hardwood, Hemlock forests and swamps	present	2%	27	Multi-Layered
42	1882	2.07	Plantation	Norway spruce	Hemlock-northern hardwood	present	0%	44	Multi-Layered
45	1880	8.84	Plantation	Eastern white pine	Hemlock-northern hardwood	present	0%	37	Two-Layered

[1] from Wiggin (1993); [2] based on Wiggin (1993) or dominant tree ages; [3] based on Lautzenheiser (2002)

Table 3. Forest inventory metrics for reference stands.

Reference Stand	Year	q factor	Total Basal Area (m^2/ha)	Live Basal Area (m^2/ha)	Merch. Volume (m^3/ha)	Total Stand Volume (m^3)	Medial DBH (cm)	Merch. DBH (cm)	Avg. DBH (cm)	Quad. DBH (cm)	Relative Density (%)	Trees #/ha	Live Trees #/ha	Dead Trees #/ha
1	**2001**	1.09	54.3	51.0	359.2	968.50	34.09	34.79	21.53	24.84	65.5	1159.95	1053.29	106.66
	2002	1.09	55.1	51.6	365.4	985.22	34.36	35.05	21.88	25.13	66.2	1159.95	1039.96	119.99
	2003	1.08	55.3	52.2	369.2	995.46	34.57	35.25	22.11	25.37	67.0	1153.29	1033.29	120.00
2	**2001**	1.05	51.9	50.7	407.4	1682.25	48.44	49.82	22.55	29.53	99.2	773.30	739.97	33.33
	2002	1.07	53.9	52.8	424.2	1751.62	48.45	49.80	23.13	30.00	103.6	779.97	746.64	33.33
	2003	1.07	54.9	53.8	431.4	1781.35	48.59	50.06	22.02	29.13	105.5	833.30	806.63	26.67
4	**2001**	1.05	52.9	47.3	349.7	2312.13	47.21	47.49	24.97	27.87	117.1	819.97	775.97	44.00
	2002	1.06	53.9	48.2	358.4	2369.66	47.33	47.58	25.59	28.34	118.7	815.97	763.97	52.00
	2003	1.07	54.6	48.8	364.1	2407.34	47.23	47.48	25.76	28.53	119.6	815.97	763.97	52.00
8	**2001**	1.08	58.8	55.8	426.4	1679.16	59.95	61.25	20.96	27.30	122.1	1093.29	953.30	139.99
	2002	1.07	61.7	58.1	449.7	1770.91	63.17	64.31	21.21	27.96	125.8	1099.96	946.63	153.33
	2003	1.07	62.4	59.2	459.5	1809.50	62.78	63.73	21.33	28.03	128.6	1106.62	959.96	146.66
13	**2001**	1.04	54.5	45.9	356.3	636.37	35.29	35.29	31.13	31.93	71.5	593.31	573.31	20.00
	2002	1.02	55.8	47.1	367.4	656.20	35.57	35.57	31.40	32.35	72.8	599.98	573.31	26.67
	2003	0.95	56.2	47.5	369.9	660.66	35.79	35.80	30.98	32.29	73.0	606.64	579.98	26.66
17	**2001**	1.05	40.9	39.9	286.4	2427.72	34.44	37.20	14.71	19.70	97.2	1335.95	1307.95	28.00
	2002	1.10	41.7	40.7	289.4	2453.15	34.38	37.32	14.87	19.72	99.7	1355.95	1331.95	24.00
	2003	1.10	43.0	41.6	294.5	2496.38	34.43	37.47	14.80	19.62	97.7	1407.94	1375.94	32.00
18	**2001**	1.08	54.5	52.1	417.2	3744.71	50.10	52.69	16.65	24.56	108.8	1203.95	1099.96	103.99
	2002	1.08	56.0	53.9	431.1	3869.48	50.16	52.89	16.48	24.45	112.7	1247.95	1147.95	100.00
	2003	1.07	57.5	55.1	440.7	3955.65	51.00	53.82	16.74	24.73	115.6	1267.95	1147.95	120.00
21	**2001**	1.14	37.5	34.0	218.7	2756.33	35.48	36.69	19.97	23.79	99.0	863.97	763.97	100.00
	2002	1.14	38.5	35.3	228.8	2883.62	35.88	37.02	20.40	24.24	102.3	847.97	763.97	84.00
	2003	1.13	39.2	35.9	233.8	2946.64	36.02	37.10	20.80	24.54	104.1	839.97	759.97	80.00
24	**2001**	1.06	33.7	33.5	233.5	2300.29	39.03	40.04	22.20	26.65	100.6	631.97	599.98	31.99
	2002	1.09	33.5	33.2	226.6	2232.32	39.16	40.22	21.92	26.47	88.4	631.97	603.98	27.99
	2003	1.08	34.7	34.0	240.5	2369.25	39.96	40.97	22.27	26.97	102.9	631.97	595.98	35.99
30	**2001**	1.13	30.6	26.9	186.5	1183.36	36.70	37.82	20.04	24.00	86.6	669.97	594.98	74.99
	2002	1.12	31.2	27.5	189.9	1204.93	37.10	38.25	20.49	24.26	100.1	669.97	594.98	74.99
	2003	1.12	31.5	28.9	201.8	1280.44	38.18	39.37	20.65	24.56	92.5	659.97	609.98	49.99
31	**2001**	1.18	35.2	33.6	189.5	1239.03	31.76	33.54	15.87	18.93	106.7	1324.95	1194.95	130.00
	2002	1.17	36.3	34.8	195.7	1279.57	31.97	33.73	16.14	19.24	109.8	1319.95	1194.95	125.00
	2003	1.17	37.1	35.4	202.6	1324.68	32.20	33.94	16.40	19.49	110.6	1319.95	1184.95	135.00
33	**2001**	1.10	35.9	33.8	239.4	1435.46	40.88	41.98	21.06	26.04	111.8	674.97	634.97	40.00
	2002	1.11	36.8	34.9	248.7	1491.23	41.41	42.47	21.57	26.56	115.1	664.97	629.97	35.00
	2003	1.09	37.2	34.1	242.8	1455.85	41.15	42.34	21.05	26.24	112.1	674.97	629.97	45.00
38	**2001**	1.05	52.8	50.5	363.4	1295.88	46.42	47.12	27.72	32.54	120.0	646.64	606.64	40.00
	2002	1.04	52.8	51.3	371.3	1324.05	46.61	47.24	28.37	33.19	122.0	619.98	593.31	26.67
	2003	1.04	54.2	52.0	378.7	1350.44	46.99	47.63	28.69	33.60	126.7	619.98	586.64	33.34
39	**2001**	1.11	38.6	36.6	239.2	8068.87	40.42	41.41	21.12	25.55	103.4	806.63	713.30	93.33
	2002	1.12	39.3	37.3	244.9	8261.15	40.74	41.71	21.40	25.80	105.5	806.63	713.30	93.33
	2003	1.12	40.0	37.8	250.2	8439.93	41.03	41.92	22.25	26.59	106.0	803.30	679.97	123.33
42	**2001**	1.01	66.1	66.1	568.6	1176.14	57.78	58.58	32.82	41.01	102.3	519.98	499.98	20.00
	2002	1.03	69.6	67.9	585.1	1210.27	58.80	59.65	33.53	41.58	104.4	519.98	499.98	20.00
	2003	1.04	69.9	68.3	586.6	1213.37	58.90	59.88	31.61	40.11	105.6	559.98	539.98	20.00
45	**2001**	1.04	63.4	58.3	487.7	4311.09	67.40	68.05	29.97	38.77	113.1	599.98	493.31	106.67
	2002	1.05	64.3	59.4	498.4	4405.02	67.75	68.44	30.27	39.15	115.2	593.31	493.31	100.00
	2003	1.04	65.1	59.6	502.2	4438.61	68.71	69.30	30.76	39.76	115.5	599.98	479.98	120.00

Productivity, growth, and yield

Reliable detection of growth trends usually requires 5 or more years of growth and yield data. However, the monitoring data over a three year period do provide a general indication of whether growth is positive or negative, though the absolute values (e.g. growth increments) should be regarded having a degree of uncertainty.

Timber volumes reported for reference stands are based on NED estimations using plot data. However, plot data – which were collected following ecological inventory protocol rather than timber cruise methods – do not discriminate between acceptable growing stock (AGS) vs. unacceptable growing stock (UGS) for live trees. Volumes are thus liberal estimates: actual AGS values are likely to be 80% or more lower than the volumes reported here due to stem defects and unacceptable growth forms. In addition, NED volumes are based on sawlog and pulplog heights estimated using allometric equations relating these to stem diameter. In the absence of actual saw/pulplog heights, volumes are likely to be further overestimated. Finally, some plots include very large legacy trees (open grown "wolf trees" or remnant old-growth trees) that occur at low frequencies in actuality. With a relatively low sample size of plots per stand, the presence of even a single legacy tree can increase volume estimates in a manner not truly representative of the majority of a stand. Due to these limitations, volume calculations from monitoring data will be useful for tracking growth trends and biomass accumulations, but should be used in conjunction with, or validated by, cruise data or supplemental timber inventories when planning timber harvests.

Growth trends over three years of monitoring have been generally positive. Volume production (total merchantable tree volume) averages 7.5 m^3/ha but ranges very widely among stands (Table 4, left). Values range from 1.7 to 16.6 m^3/ha of annual increment.

Production in board feet (sawlogs only) was more variable (Table 4, right). The net change over three years was positive, with the Park's forests increasing in board foot volume by about 1.15% annually. However, three reference stands experienced deficits in board feet production due to mortality in high quality stems. For example, one of the Park's oldest white pine plantations, Stand 45, lost board foot volume due to windthrow. These figures contrast with total volume where sawtimber loss was compensated by production in pulp logs. Board feet yields are within the range that should be expected in mature forests over a short period of time. The death of only one or two large trees in a plot can result in a temporary net loss of standing volume but should not interpreted as unacceptable mortality or a long-term decline in productivity. Several of the stands that accrued board foot deficits (e.g. Stands 8, 30, and 45) are otherwise healthy, with vigorous, rapidly growing trees. Short-term losses resulting from individual tree mortality (usually small blow-downs) will likely be compensated over the longer term by continued growth in standing live trees.

Assessing growth and yield using basal area increment gives a slightly different picture of productivity in the Park. Since basal values encompass all trees, not just merchantable size classes, Table 5 shows there to be net positive productivity in all reference stands when smaller trees, excepting in-growth into measurable sizes, are included. Change in dead tree basal area was more variable throughout the Park. Some stands showed an increase in snag basal area, whereas in other stands snag basal area declined through loss of bole integrity, breakage, and falling. In the latter cases (e.g. Stands 1, 2, 21, 30, and 38) snag loss was not balanced or exceeded by new mortality.

Table 4. Growth and yield over three year period by reference stand. Values do not include in-growth and are for merchantable size classes only. "Volume" is total tree volume (sawlogs plus pulp-logs), whereas "board feet" includes sawlogs only.

	Volume (cubic meters per hectare)					Board Feet (per acre)				
	2001	2002	2003	Net % change	Annual Increm.	2001	2002	2003	Net % change	Annual Increm.
Stand 1	359.2	365.4	369.2	2.71	5.0	16738.8	16974.0	17187.7	2.61	224
Stand 2	407.4	424.2	431.4	5.56	12.0	22566.1	23260.1	23919.4	5.66	677
Stand 4	349.7	358.4	364.1	3.95	7.2	10063.1	10294.0	10813.6	6.94	375
Stand 8	426.4	449.7	459.5	7.20	16.6	22709.9	23272.1	19659.9	-15.51	-1525
Stand 13	356.3	367.4	369.9	3.68	6.8	15159.0	16460.3	17064.2	11.17	953
Stand 17	286.4	289.4	294.5	2.75	4.1	15231.8	15651.8	15958.0	4.55	363
Stand 18	417.2	431.1	440.7	5.33	11.8	23582.6	24480.8	25424.8	7.25	921
Stand 21	218.7	228.8	233.8	6.46	7.6	8815.8	9454.0	9574.1	7.92	379
Stand 24	233.5	226.6	240.5	2.91	3.5	10052.9	9734.6	10655.8	5.66	301
Stand 30	186.5	189.9	201.8	7.58	7.7	7118.0	7336.5	5756.1	-23.66	-681
Stand 31	189.5	195.7	202.6	6.47	6.6	5944.2	6325.6	6534.1	9.03	295
Stand 33	239.4	248.7	242.8	1.40	1.7	11166.5	11559.1	11246.5	0.71	40
Stand 38	363.4	371.3	378.7	4.04	7.7	17828.1	18265.8	18728.5	4.81	450
Stand 39	239.2	244.9	250.2	4.40	5.5	9761.2	9922.8	10357.2	5.75	298
Stand 44	568.6	585.1	586.6	3.07	9.0	36610.5	38563.7	38662.9	5.31	1026
Stand 45	487.7	498.4	502.2	2.89	7.3	29275.9	29919.7	28881.6	-1.37	-197
Mean	333.1	342.2	348.0	4.4	7.5	16414.0	16967.2	16901.5	2.30	244

Table 5. Change in basal area. Includes in-growth. All trees > 5 cm dbh.

	Live Tree Basal Area					Dead Tree Basal Area				
	2001	2002	2003	Net % change	Annual Increment	2001	2002	2003	Net % change	Annual Increment
Stand 1	51	51.6	52.2	2.30	1.2	3.3	3.5	3.1	-6.45	-0.2
Stand 2	50.7	52.8	53.8	5.76	3.1	1.2	1.1	1.1	-9.09	-0.1
Stand 4	47.3	48.2	48.8	3.07	1.5	5.6	5.7	5.8	3.45	0.2
Stand 8	55.8	58.1	59.2	5.74	3.4	3	3.6	3.2	6.25	0.2
Stand 13	45.9	47.1	47.5	3.37	1.6	8.6	8.7	8.7	1.15	0.1
Stand 17	39.9	40.7	41.6	4.09	1.7	1	1	1.4	28.57	0.4
Stand 18	52.1	53.9	55.1	5.44	3	2.4	2.1	2.4	0.00	0
Stand 21	34	35.3	35.9	5.29	1.9	3.5	3.2	3.3	-6.06	-0.2
Stand 24	33.5	33.2	34	1.47	0.5	0.2	0.3	0.7	71.43	0.5
Stand 30	26.9	27.5	28.9	6.92	2	3.7	3.7	2.6	-42.31	-1.1
Stand 31	33.6	34.8	35.4	5.08	1.8	1.6	1.5	1.7	5.88	0.1
Stand 33	33.8	34.9	34.1	0.88	0.3	2.1	1.9	3.1	32.26	1
Stand 38	50.5	51.3	52	2.88	1.5	2.3	1.5	2.2	-4.55	-0.1
Stand 39	36.6	37.3	37.8	3.17	1.2	2	2	2.2	9.09	0.2
Stand 42	66.1	67.9	68.3	3.22	2.2	0	1.7	1.6	100	1.6
Stand 45	58.3	59.4	59.6	2.18	1.3	5.1	4.9	5.5	7.27	0.4
Mean	44.75	45.87	46.51	3.79	0.88	2.85	2.9	3.04	6.17	0.09

Live basal area increment trends were fairly consistent among different types of stands, regardless of species composition or management history. There was no statistically significant difference in average growth rates between plantations vs. semi-natural stands from 2001 to 2002 (Figure 7, top) based on net live growth across merchantable and non-merchantable size

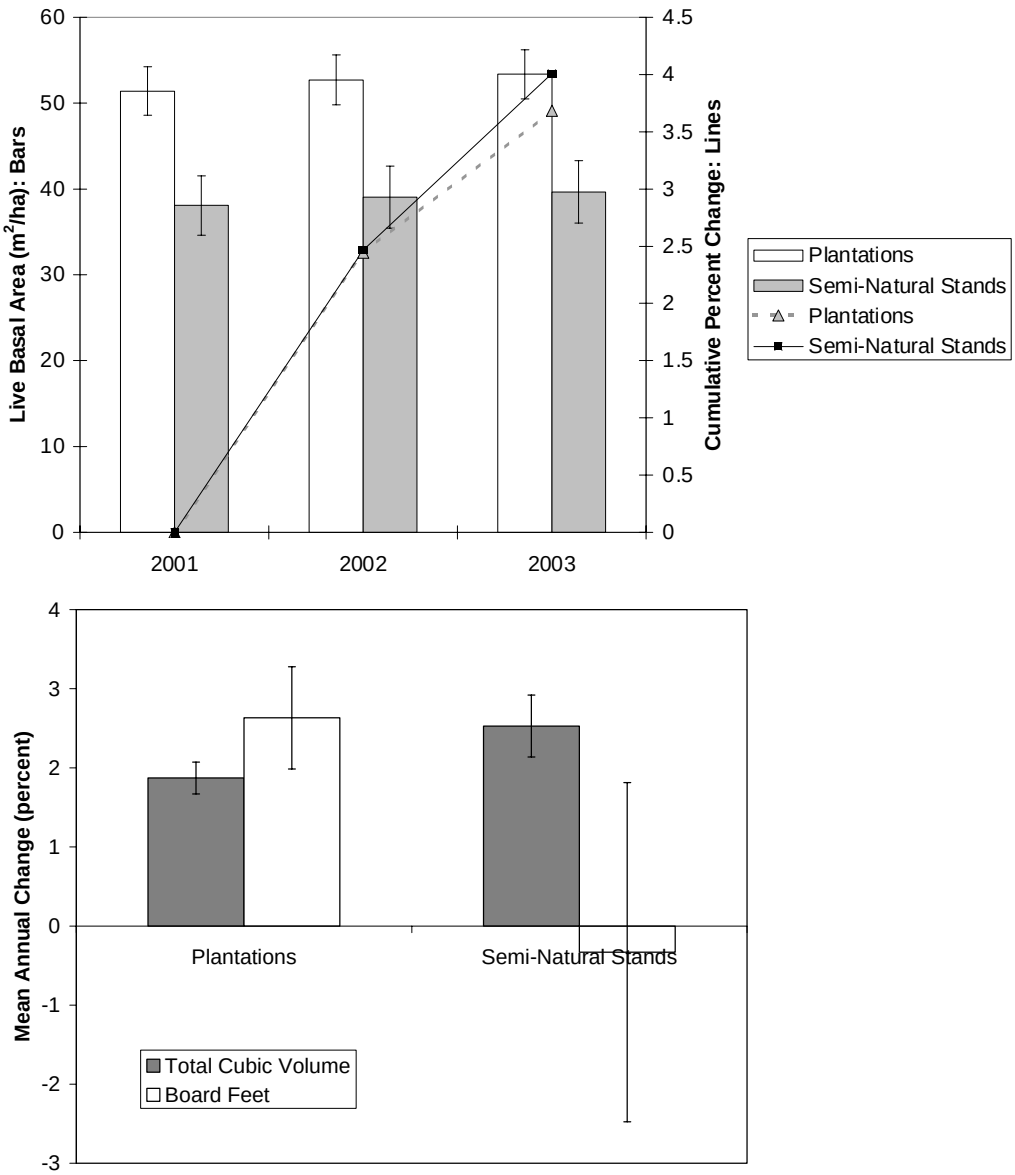


Figure 7. Basal area growth increment and volume production trends. Live tree basal area increment is compared between plantations and semi-natural reference stands (above). Yield (in cubic volume and board feet) is shown for plantations vs. semi-natural stands from 2001 to 2003 (below). Yield has been normalized as a percent change from one year to the next. Error bars are +/- one standard error of the mean.

classes. Semi-natural stands grew at a slightly more rapid rate on average from 2002 to 2003, although this difference was not statistically significant (Figure 7, top).

Plantations differed from semi-natural stands with respect to merchantable volume production and yield (Figure 7, bottom). Total annual volume production was slightly higher in semi-natural stands (7.9 cu m/ha) compared to plantations (7.1 cu m/ha) on average, whereas annual board feet production was substantially higher in plantations (543 bdft/acre) compared to semi-natural stands (-55 bdft/acre). It is not surprising that board feet production is greater in the Park's conifer plantations, irregardless of mortality, due to the

prevalence of larger mean diameters and higher quality growth forms in those stands and among those species. Board feet production was in deficit in some semi-natural stands due to mortality over the three year monitoring period. This resulted in an average negative value for that group, although the wide range of variability (error bars) should be noted. Board feet production was even more variable between different plantations, due primarily to age, species, and site differences.

The Park's forests are growing at a rate that will compensate for any short term net losses of sawtimber, due to localized natural disturbances, where those have occurred over the monitoring period. Growth rates are indicative of moderate to highly productive sites and will provide ample opportunity for sustainable forest management. Growth rates have been especially robust considering that 2001-2002 was a severe drought, although the slight decline in growth rates during the 2002-2003 time interval (Figure 7, top) may represent a lagged response to drought-stress. There was no statistically significant relationship between growth rates and stand age among either plantations or semi-natural stands based on linear regression analysis with alternate curve fitting. Thus, MBR's forests show little or no reduced vigor due to age, although culmination of mean annual increment has probably occurred in the oldest plantation. All stands, however, continue to have vigorous and positive periodic annual increments, presenting opportunities for extended rotations (Curtis 1997) and a range of either intermediate, regeneration, or alternative (i.e. hybrid) harvesting systems (Franklin et al. 1997; Tappeiner et 1997; Keeton 2005).

Stand dynamics

Size class distributions and species dominance

The results clearly show that stand development pathways and rates differ throughout the Park as a function of management history. There are distinct differences in community diversification within size classes, as indicated by the dominance index values presented in Table 6 for individual reference stands. Rates of successional development, with faster rates indicated by lower dominance values, vary between plantations and semi-natural forests. In un-thinned and lightly thinned plantations (e.g. precommercially thinned, thinned-from-below-the-canopy, or thinned to residual stocking above the B line), planted species continue to dominate most size classes, with little regeneration of other species, including native hardwood species endemic to most of the Park's plantation sites (Figure 8, top). As a result, dominance index values remain high, often close to 1 (or complete dominance) across both large and small size classes (Figure 9, top).

Plantations that have been moderately to intensively thinned (e.g. commercially thinned, thinned-from-above-the-canopy, or thinned to residual stocking at or lower than the B line) show successional development that is markedly different from less intensively managed plantations. Heavier thinning has increased light availability, allowing other species to recolonize the site. As a result, species dominant in the overstory are being almost entirely replaced by recruitment of native hardwoods into the understory and mid-canopies (Figure 8, bottom). The effect of this development to date has been reduced dominance and increased community diversity in seedling to sub-pole classes (Figure 9, bottom). Over time, as mortality in the overstory continues to open up growing space, native hardwoods will move into larger size classes, ultimately replacing overstory conifers. The results show that Simpson's dominance index, measured for discrete size classes, will be an efficient metric for monitoring this process of recovery.

Table 6. Simpson's dominance index by tree size class for selected reference stands. An index value of 1.00 means that only one species occupies a size class, implying complete dominance of that size class.

	Seedlings		Saplings		Sub Pole-sized		Pole-sized		Small Sawlogs		Large Sawlogs		Very Large Sawlogs	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Stand 2	0.42	0.24	0.23	0.14	0.57	0.33	0.44	0.25	0.62	0.36	1.00	0.58	0.00	0.00
Stand 4	0.72	0.32	1.00	1.00	0.80	0.46	0.83	0.37	0.94	0.42	1.00	1.00	1.00	0.71
Stand 8	0.68	0.39	1.00	0.71	0.75	0.43	0.72	0.41	0.69	0.40	1.00	0.58	0.69	0.40
Stand 13	0.94	0.54	0.00	0.00	0.00	0.00	0.43	0.17	0.95	0.55	0.64	0.37	1.00	0.71
Stand 17	0.46	0.20	0.36	0.16	0.27	0.12	0.79	0.46	0.90	0.40	0.95	0.43	0.00	0.00
Stand 18	0.95	0.43	0.29	0.13	0.37	0.16	0.70	0.31	0.81	0.36	1.00	0.50	1.00	0.45
Stand 21	0.49	0.22	0.65	0.33	0.43	0.19	0.44	0.20	0.57	0.26	0.70	0.31	0.92	0.46
Stand 24	0.66	0.30	0.53	0.30	0.71	0.32	0.81	0.36	0.72	0.32	0.88	0.39	0.75	0.33
Stand 30	0.91	0.46	0.75	0.43	0.74	0.37	0.83	0.41	0.68	0.34	0.80	0.40	0.70	0.41
Stand 31	0.74	0.37	0.88	0.44	0.42	0.21	0.39	0.19	0.72	0.36	0.78	0.39	0.85	0.49
Stand 33	0.71	0.35	0.73	0.37	0.50	0.25	0.55	0.28	0.48	0.24	0.91	0.45	0.67	0.34

There also are differences in successional rates among semi-natural stands based on the data. The Park's semi-natural stands appear to vary with respect to overstory self-perpetuation through conspecific recruitment versus community diversification through recruitment of additional mid- to late-successional species. Examination of size class distributions (by species) consistently showed un-managed (i.e. little or no evidence of timber harvest within the last 2-3 decades or longer) stands to have lower rates of diversification (Figure 10, top), and thus higher dominance values across most size classes (Figure 11, top). Stands which have had intermediate silvicultural treatments (i.e. thinning) and low intensity regeneration harvests (e.g. single-tree selection) appear to have greater diversification across multiple size classes. As a result, dominance values are lower in the size classes that have diversified (Figure 11, bottom). Other factors, such as differences in seed source availability, site productivity, and dominant species composition may co-vary with management history. Thus while low intensity silviculture appears to have increased rates of successional development in semi-natural stands, pathways and rates of development are variable. Differences between stands are likely due to multiple factors.

Regression analysis of size class distributions for semi-natural stands resulted in negative exponential relationships that were statistically significant (α = 0.05). Negative exponential trend lines generally had tighter fits than other curves, explaining 50 to 90% of the variability in residuals (Figure 12). Some younger, more structurally simple stands, however, had uni- or bi-modal tendencies (Figure 12, lower left). In general, however, the regression results suggest that the Park's maturing semi-natural stands are developing or have developed uneven-sized class distributions characteristic of uneven-aged forests. Field data and increment coring confirmed that these distributions are not an artifact of suppression in small to mid-sized trees. Rather, they represent multiple age cohorts, although some degree of suppression is always present. This is another indication that semi-natural stands are developing the structural complexity associated with late-successional forests. Silvicultural management may have accelerated this process in some stands (Figure 12 upper left), although the Park's most productive, un-managed semi-natural stands show similar rates of structural development (Figure 12, upper right).

The more intensively thinned plantations also are developing uneven-aged diameter distributions, with very high q ratios (e.g. > 1.9, includes saplings < 5 cm dbh) as a result of prolific recruitment of hardwoods into the smallest size classes (Figure 12, lower right). Q ratios in plantations are shallow (1.1) to flat (1.0) when ratio calculations do not include the pulse of saplings and sub-pole sized trees established after thinning. To some degree, however, thinned plantations are developing characteristics indicative of late-successional structure, albeit in this case an unusual mix of sometimes non-endemic conifers in one canopy layer and native hardwoods in the other canopy layers.

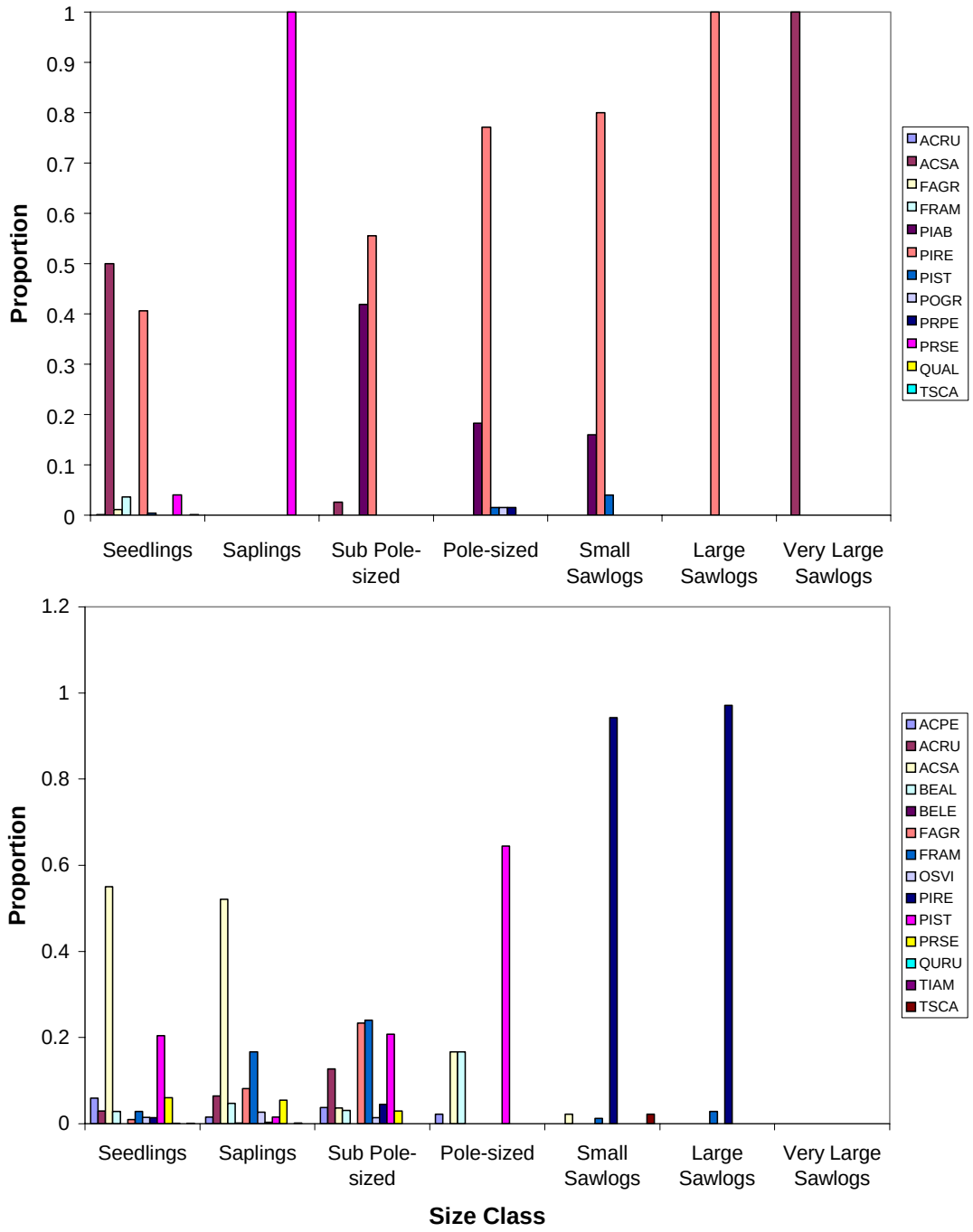


Figure 8. Timber size class distributions segregated by tree species code (first two letters of genus and species) in reference plantations. A lightly thinned red pine plantation (reference stand #4) planted in 1953 (above) is compared with a more intensively thinned 1917 red pine plantation (reference stand #18) (below). Note the static dominance across most size classes of red pine (PIRE) in the lightly thinned plantation. While the species is regenerating, no seedlings are surviving into the sapling stage, which is exclusively dominated by suppressed, transient black cherry (PRSE). Note the contrast with the more heavily thinned plantation, in which recruiting and mid-sized cohorts are now dominated by a diversity of native hardwood species, which are recolonizing the site, developing vertically, and ultimately replacing the overstory red pine. The "very large sawlogs" in the top figure are open-grown (or "wolf"), legacy sugar maple, now embedded within the younger plantation.

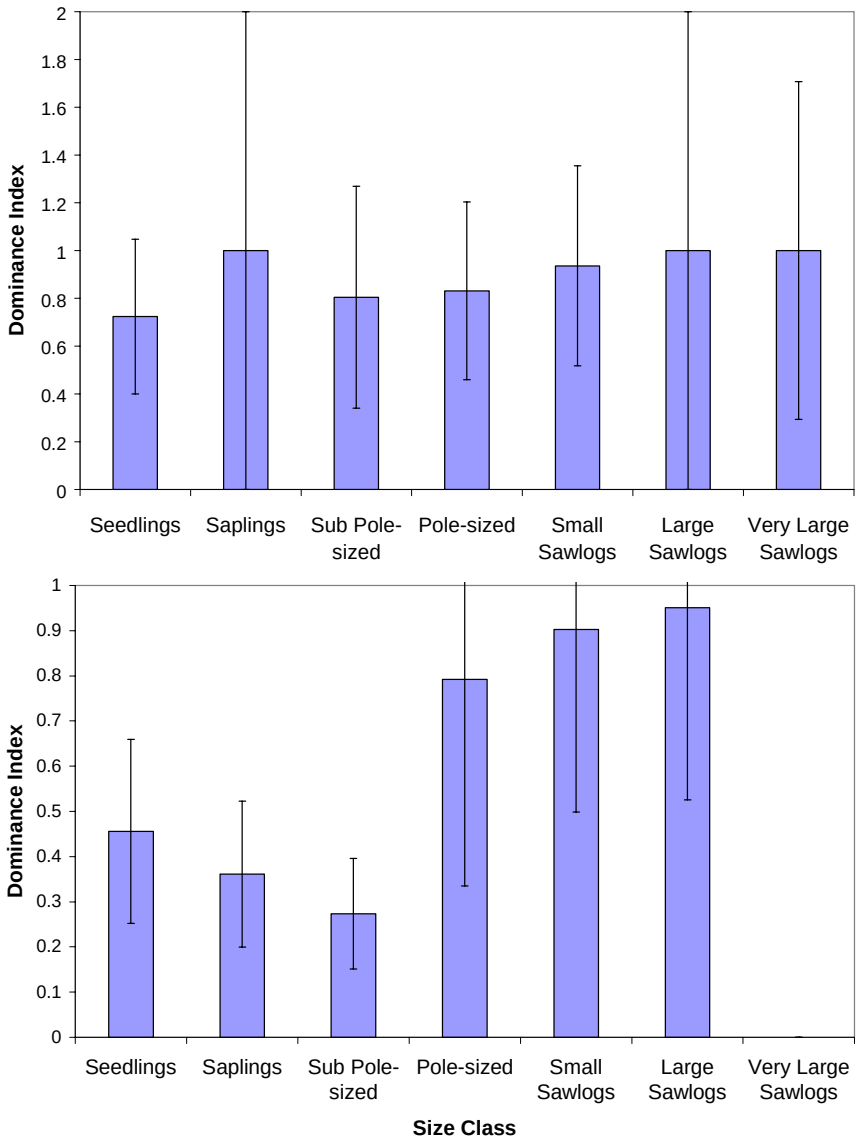


Figure 9. Simpson's Dominance Index for timber size classes in reference plantations. A lightly thinned red pine plantation planted in 1953 (above) is compared with a more intensively thinned 1917 red pine plantation (below). In the latter, note the reduced single species dominance in the smaller size classes due to recruitment of site-endemic species, resulting in diversified species composition. Error bars show +/- one standard error of the mean.

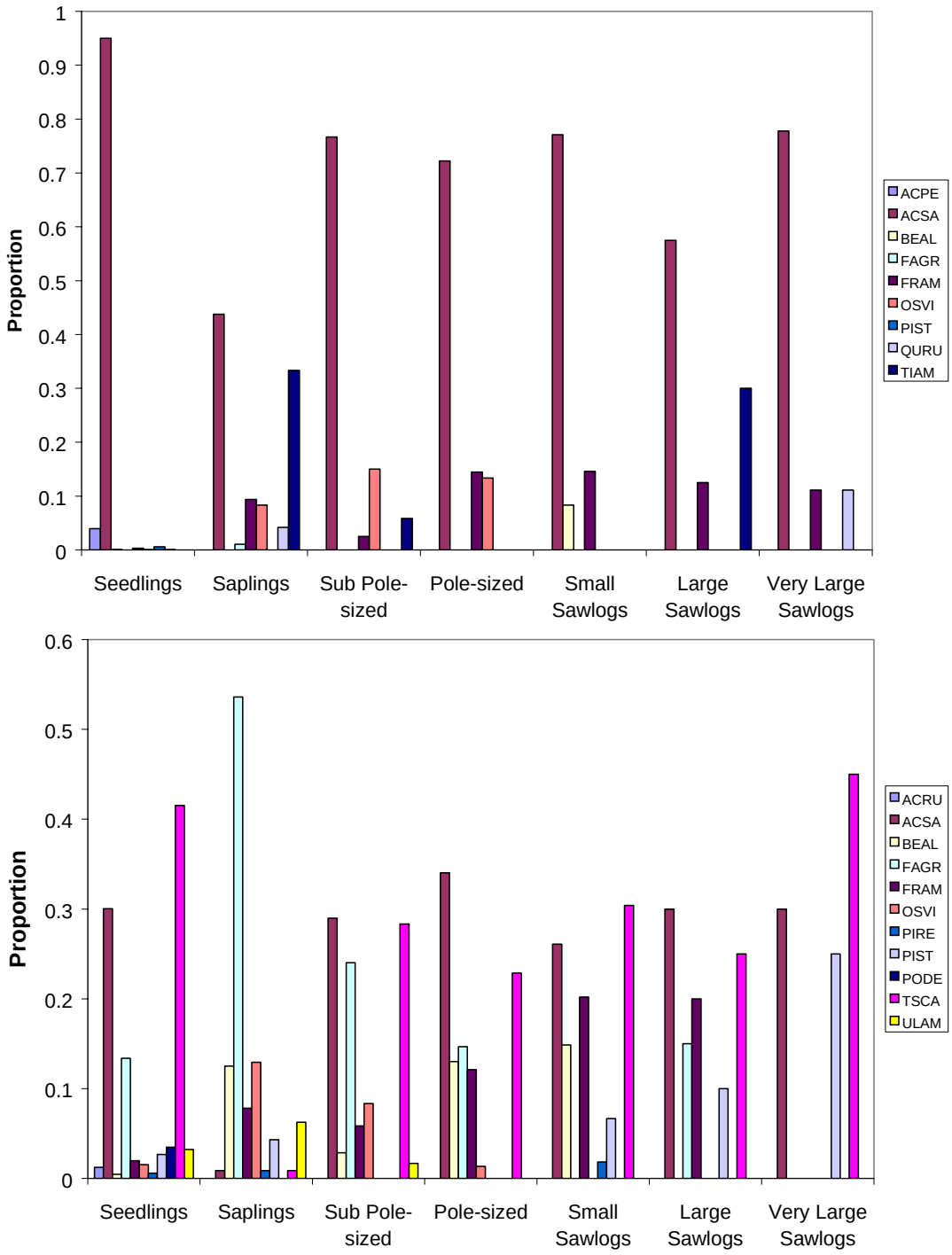


Figure 10. Timber size class distributions segregated by tree species code (first two letters of genus and species) in reference semi-natural stands. A rich northern hardwood stand that has had little or no silvicultural management (reference stand #30) is shown above, and a northern hardwood-hemlock stand (reference stand #21) that has been silviculturally managed is shown below. Note the self-perpetuation of the dominant sugar maple (ACSA) above, versus the more diverse species composition below. These trends may reflect natural differences in successional dynamics and/or they may have been influenced by management differences.

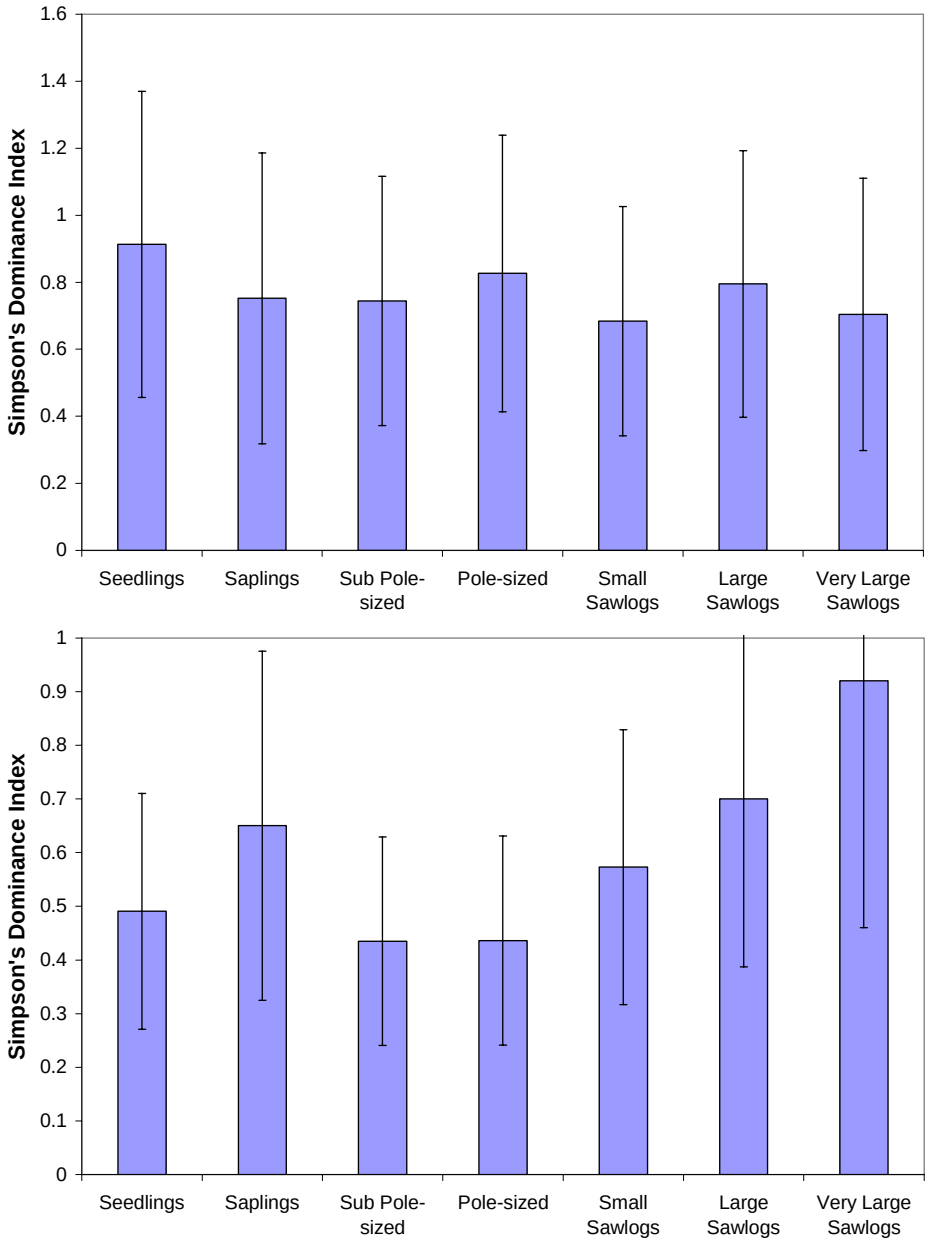


Figure 11. Simpson's Dominance Index for timber size classes in reference semi-natural stands. A rich northern hardwood stand that has had little or no silvicultural management is shown above, and a northern hardwood-hemlock stand that has been actively managed is shown below. Note the lower index values for seedling through pole-sized classes in the silviculturally managed stand (below). Error bars show +/- one standard error of the mean.

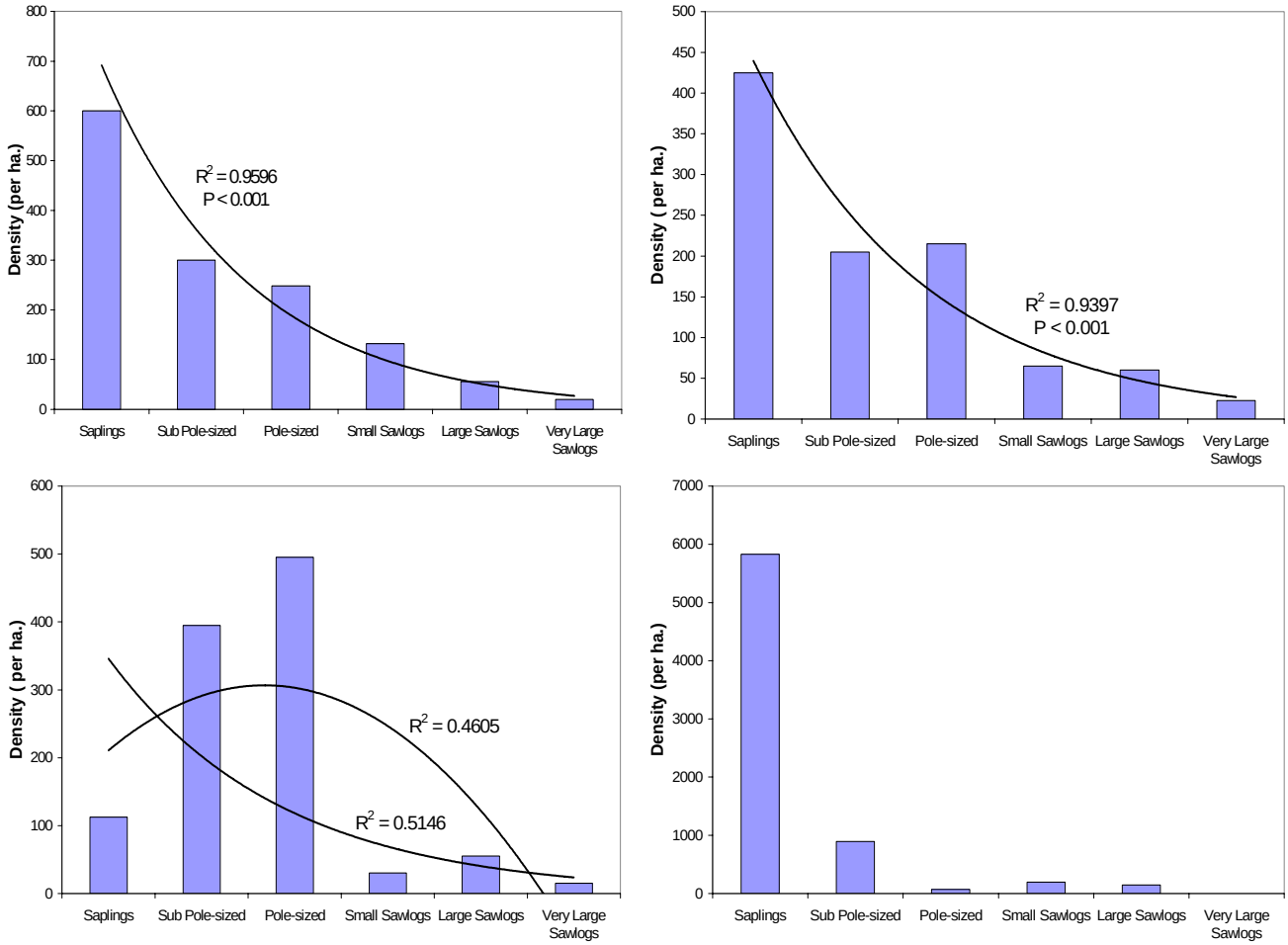


Figure 12. Size class distributions and regression curves for A) a silviculturally managed, semi-natural stand (reference stand #21); B) a highly productive though un-managed, semi-natural stand (reference stand #30); C) a lightly managed, lower productivity semi-natural stand (reference stand #31); and D) a thinned 1917 red pine plantation (reference stand #17). In each case, succession and/or management has moved stand structure toward an un-even size (and potentially age) class distribution. A possible exception, indicative of the Park's slower developing hardwood forests, is Example C, which has uni-modal, even-aged characteristics, despite a stronger regression fit to a negative exponential curve.

Mortality processes and self-thinning

Tree mortality in the Park is strongly concentrated in sub-dominant, relatively smaller sized trees. Dead tree diameter distributions are compared against live tree distributions in Figures 13 and 14. Visual inspection of these indicates that dead tree diameter distributions are weighted towards smaller trees for the majority of reference stands. This inference is validated by the results of Kolmogorov-Smirnov goodness of fit tests (Table 7), from which it can be concluded that the differences between dead and live tree cumulative frequency distributions are statistically significant at the 95% confidence level for most reference stands. There were exceptions, however. Statistical tests did not support a hypothesis of small tree mortality tendencies for reference stands 18, 21, and 33. In these stands the size range for dead trees is either not statistically different than live trees (stands 18 and 21) or is concentrated in the largest, dominant trees (stand 33).

Further support for the conclusion that mortality is concentrated in relatively smaller, less-competitive growing stock, for at least the majority of stands, is provided by a comparison of quadratic mean diameters (QMD) for live and dead trees. QMD serves as a useful indicator metric for this purpose. Representing the diameter of a tree of average basal area (measured on an individual tree basis), QMD adjusts mean stand

diameter to compensate for the inverse relationship between tree density and size, such that larger trees are weighted more heavily than smaller trees. Thus, dead tree QMD yields a clearer picture of overstory mortality because it is not overly reflective of the high levels of mortality in saplings and pole-sized trees that we would normally expect to see in most types of forests. Plotting the ratio of dead to live tree QMD (Figure 15) cross-validates the diameter distribution analyses. The QMD of dead trees is smaller than the QMD of live trees in the majority of reference stands (Figure 15). Again there are exceptions. Three stands have dead tree QMDs higher than that for live trees. However, it should be noted that this analytical method identifies only one "large tree mortality" stand in common with the previously discussed results: that is reference stand 33. Stands 30 and 17 also have significant levels of large tree mortality according to the QMD results. QMD differences are statistically significant for stands with QMD ratios (dead to live) <1.0 ($F = 16.3$, $F_{crit} = 4.6$, $p = 0.0005$). For the Park overall dead tree QMD is also significantly smaller than live tree QMD based on *T*-tests ($p = 0.0002$).

The results can be readily interpreted with respect to likely mortality processes. Stands where mortality is occurring predominantly in smaller trees are undergoing natural competitive processes, leading to decline and death in less vigorous, potentially genetically inferior trees. Variably termed "stem exclusion" (Oliver and Larson 1996) or "self-thinning" (Spies 1997; Franklin et al. 2002) this type of morality is similar to "thinning-from-below-the-canopy" from a silvicultural perspective. It is generally density-dependent and not associated with external environmental stresses, natural disturbances, or disease (Franklin et al. 2002). Smaller, weaker trees are removed, leaving healthier more rapidly growing trees and an overall stand condition that is generally improved. There is a downside from a wildlife management perspective in that this type of mortality does not produce high levels of large snags for associated species. From a more conventional "forest health" or timber management standpoint, however, evidence of self-thinning from below-the-canopy is a positive signal.

Both analytical approaches suggested that at least of few stands are undergoing a very different mortality process. Mortality appears to be density-independent in these cases and most probably related to wind disturbance, slope instability, and/or disease. The results are consistent with our field observations. Stand 30, while stocked primarily with healthy sugar maple, has had a number of large trees blow down in recent years. Some trees have partially uprooted and died. This mortality is clearly related to slope steepness and soil instability, which makes stand 30 highly prone to windthrow. Managers should not conclude that stand 30 is unhealthy. Rather, mortality trends are further evidence of the site's extreme sensitivity. Consequently, timber management of any type is not recommended in stand 30.

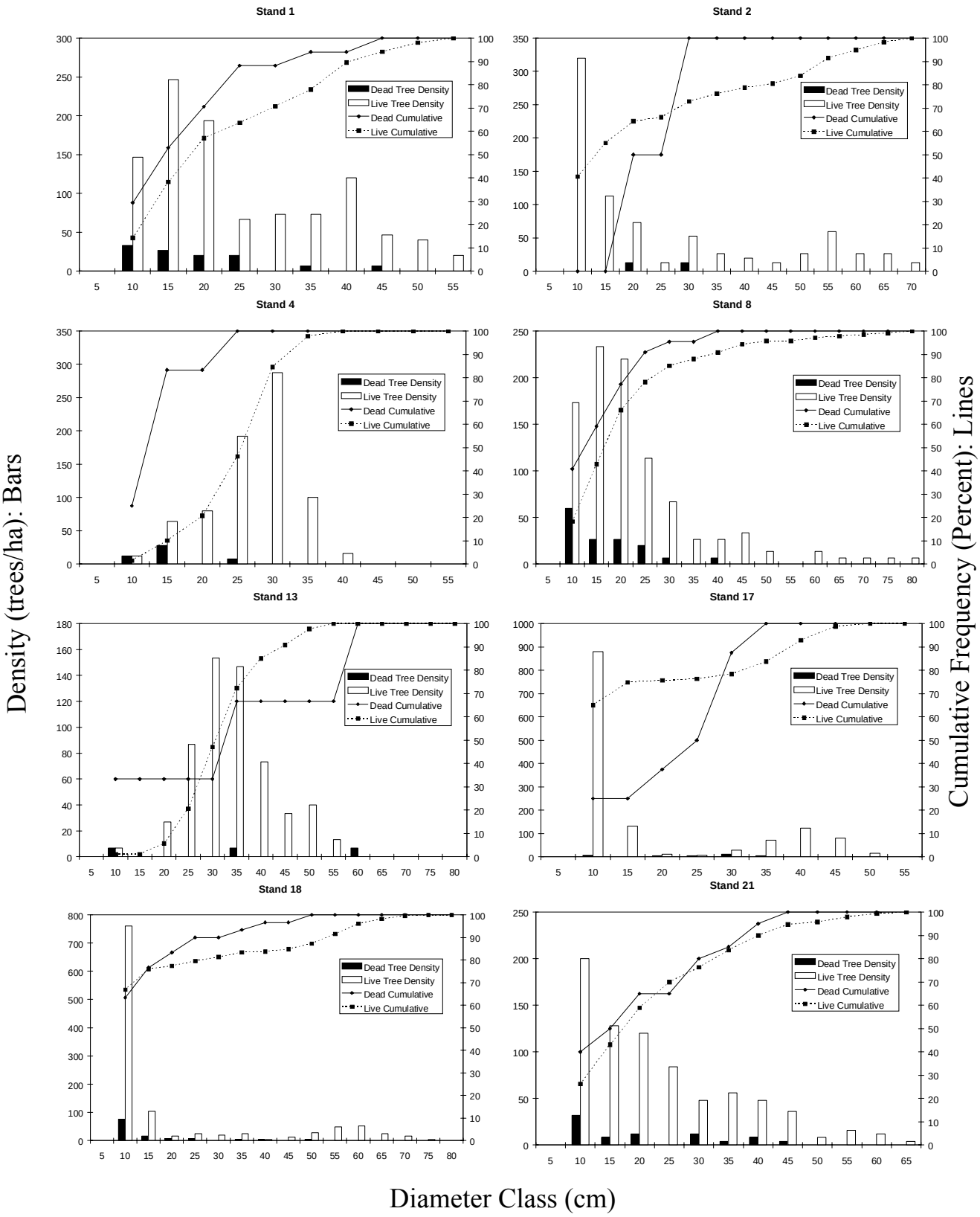


Figure 13. Live and dead tree diameter distributions (bars) for eight reference stands. Density (trees/ha) per diameter class is plotted on the left Y axis. Lines represent the cumulative frequency (percent) of trees in each successive diameter class. Values for these are plotted on the right Y axis.

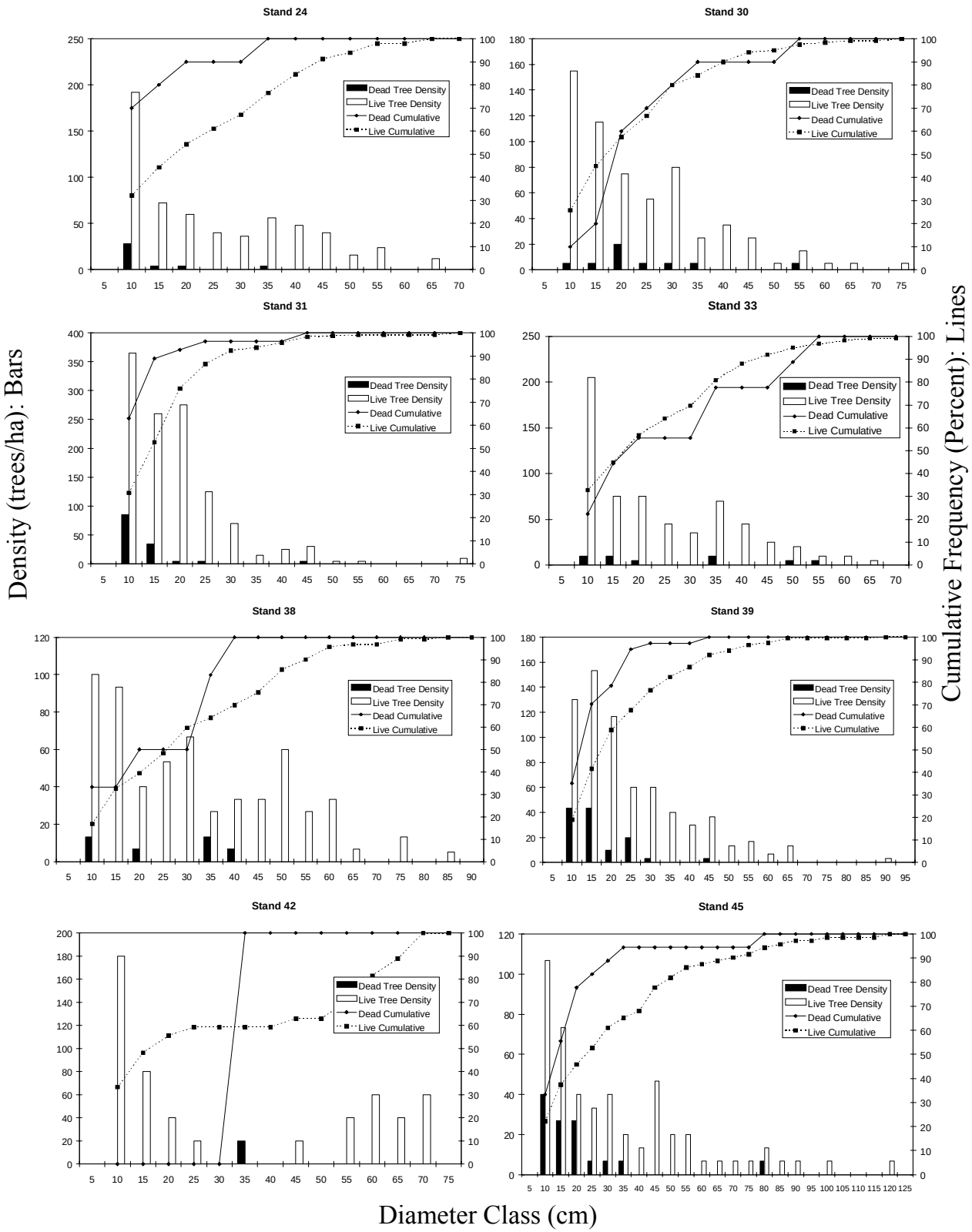


Figure 14. Live and dead tree diameter distributions (bars) for eight reference stands. Density (trees/ha) per diameter class is plotted on the left Y axis. Lines represent the cumulative frequency (percent) of trees in each successive diameter class. Values for these are plotted on the right Y axis.

Table 7. Results of Kolmogorov-Smirnov Goodness of Fit tests comparing dead tree and live tree diameter distributions. The hypothesis is tested that dead tree cumulative frequency distributions are more weighted towards smaller diameter trees than are live tree distributions.

Reference Stand	D_{max}	$D_{crit, 0.05}$	*P*-value	Conclusion
1	0.245	0.134	< 0.05	Mortality is concentrated in smaller diameter classes relative to the stand's diameter distribution.
2	0.551	0.268	< 0.05	ibid
4	0.732	0.202	< 0.05	ibid
8	0.226	0.120	< 0.05	ibid
13	0.333	0.308	< 0.05	ibid
17	0.499	0.243	< 0.05	ibid
18	0.129	0.130	Not Significant	Diameter distribution of dead trees is not significantly different from the stand's diameter distribution.
21	0.137	0.160	Not Significant	ibid
24	0.378	0.222	< 0.05	Mortality is concentrated in smaller diameter classes.
30	0.250	0.200	< 0.05	ibid
31	0.361	0.123	< 0.05	ibid
33	0.142	0.210	Not Significant	Mortality is concentrated in larger diameter classes.[1]
38	0.301	0.222	< 0.05	Mortality is concentrated in smaller diameter classes.
39	0.286	0.133	< 0.05	ibid
42	0.593	0.309	< 0.05	ibid
45	0.319	0.139	< 0.05	ibid

[1] Based on the statistical test and the form of the dead tree frequency distribution relative to the live tree distribution.

It is noteworthy that stand 33 was twice identified as having high levels of large tree mortality. These results are clearly related to that stand's very high levels of beech bark disease (see page 45). Stand 33 is the only beech-dominated reference stand. Most of its large diameter beech are dead or dying as a result of the disease. This signals the severe effect the disease is having on the Park's beech trees. Mortality results for stands 17, 18, and 21 reflect deaths of individual medium and large diameter trees in sample plots, resulting from disease and stem breakage. Stands 17 and 18 may have slightly elevated susceptibility to density-independent mortality due to stand structure, plantation history, and tree age, although mortality for those was similar to the live tree distributions (Table 7).

For the Park's plantations there is a statistically significant (90% confidence level only) relationship between the ratio of dead to live QMD and stand age. There was no statistically significant relation with age for semi-natural stands (Figure 16). For the Park as a whole, stand age is predictive ($R = 0.60$, $P = 0.014$) of shifts in mortality processes from "thinning-from-below" to "thinning-from-above" the canopy. This is consistent with our understanding of natural stand dynamics (Franklin et al. 2002). This relationship represents an important aspect of how stands develop structurally and compositionally over time and does not necessarily indicate a decline in "health" or exposure to a stressor. Such determinations must be based on additional information used to attribute mortality to specific stressors.

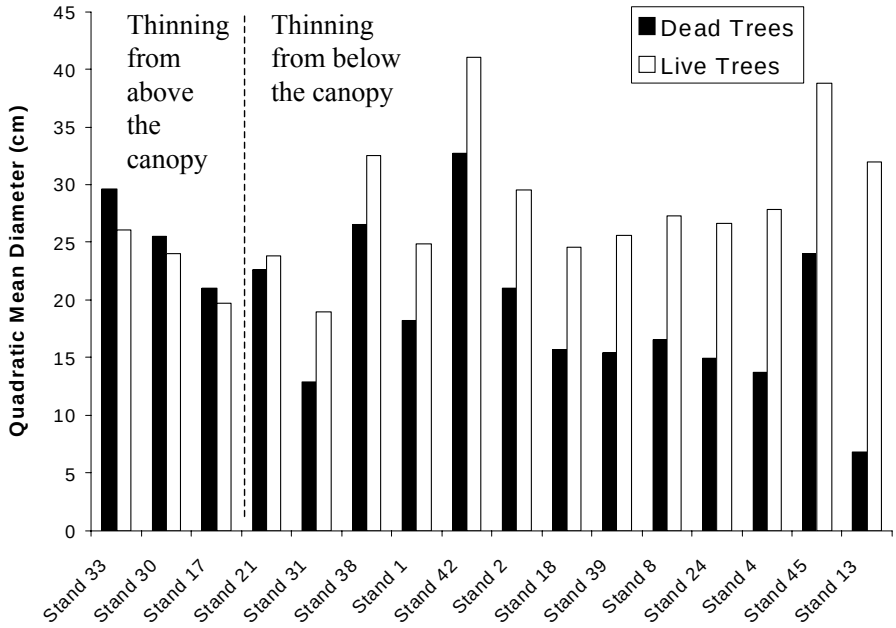


Figure 15. Comparison of dead to live tree quadratic mean diameters (cm) for reference stands. Where dead tree QMD is lower than live tree QMD it is inferred that mortality is coming off the low end of trees sizes and is thus predominately the result of competitive self-thinning (e.g. thinning from below the canopy).

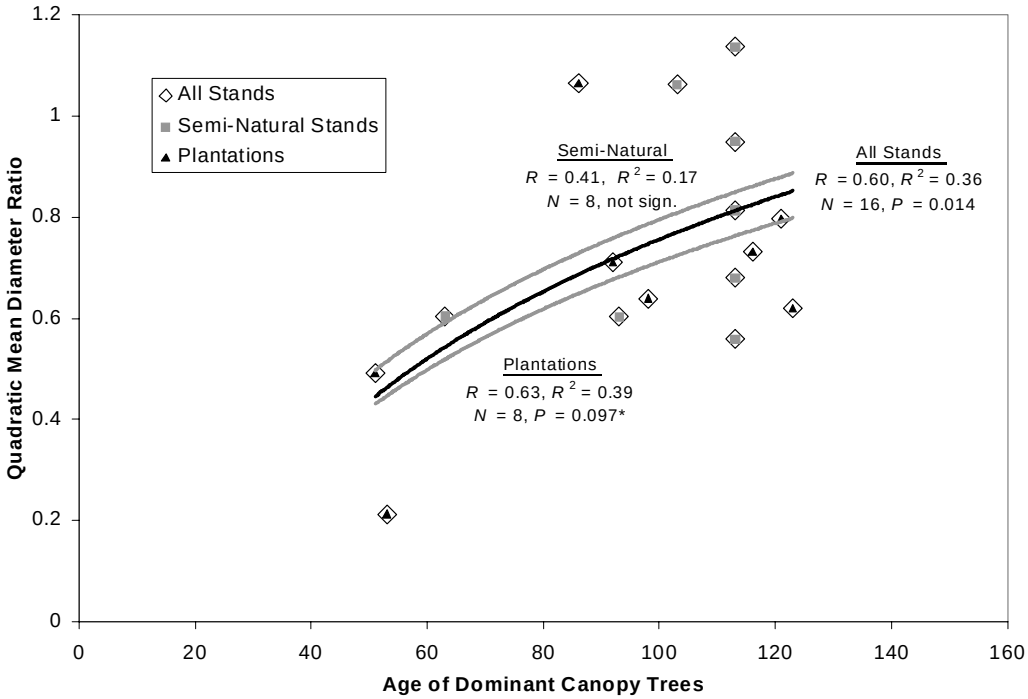


Figure 16. Relationship between (a) the ratio of dead to live quadratic mean diameter and (b) age of dominant canopy trees for reference stands. Regression curves are based on a log transformation of the independent variable.

Compositional dynamics and regeneration demography

Analysis of tree regeneration data resulted in significant differences between plot groupings. These differ by natural community type and management history (Table 8). In hardwood and mixed-wood forests as a whole, reproduction by overstory species is significantly ($P<0.0001$) more abundant than is colonizing reproduction by exotic species or species not currently represented in the stand (Figure 14, upper left). The only natural community type represented in semi-natural stands that does not show this trend is hemlock forests and swamps. In those patches, reproduction by hemlock is minimal, with the majority of regeneration consisting of non-overstory species. Non-overstory seedlings are more abundant in hemlock groves, but this relationship is only statistically significant at a 90% probability level (Figure 14, lower right).

Table 8. Tree regeneration data by seed source, plot, natural community, and stand management.

Plot	Natural Community (Potential Veg.)	Plantation	Thinned Plantation	Managed Hardwoods	Overstory Reproduction (Density per ha.)	Colonizing Reproduction (Density per ha.)	Notes
1	Rich Northern Hardwood Forest	No		No	207911.4	0	
2	Hemlock-northern hardwood	Yes	Yes		0	226582.2	
3	Hemlock-northern hardwood	Yes	Yes		0	53639.22	
4	Hemlock-northern hardwood	Yes	No		335442.9	18354.42	
5	Hemlock-northern hardwood	No		Yes	32911.38	0	
6	Hemlock forests and swamps	No		No	2689.873	25316.45	
7	Hemlock forests and swamps	No		No	632.9112	42879.73	
8	Hemlock forests and swamps	No		No	1424.05	5537.973	
9	Hemlock-northern hardwood	No		Yes	20569.61	0	
10	Hemlock-northern hardwood	No		Yes	41613.91	0	
11	Hemlock-northern hardwood	No		Yes	31962.02	0	
12	Hemlock forests and swamps	No		Yes	632.9112	30537.97	
13	Hemlock-northern hardwood	Yes	Yes		791.139	62025.3	
14	Northern-hardwoods	Yes	Yes		2531.645	23892.4	Anomalous due to legacy sugar maples
15	Northern-hardwoods	Yes	Yes		791.139	42721.51	
16	Northern-hardwoods	Yes	Yes		0	117405	
17	Northern-hardwoods	Yes	Yes		0	58227.83	
18	Northern-hardwoods	Yes	Yes		0	16930.37	
19	Northern-hardwoods	Yes	No		7278.479	349999.9	
20	Northern-hardwoods	Yes	No		2689.873	2056.961	
21	Northern-hardwoods	Yes	No		1740.506	300791	
22	Northern-hardwoods	Yes	No		1424.05	1424.05	
23	Northern-hardwoods	No		Yes	192246.8	632.9112	
24	Northern-hardwoods	No		No	33069.61	1107.595	
25	Northern-hardwoods	No		No	54746.82	632.9112	
26	Rich Northern Hardwood Forest	No		No	74208.84	0	
27	Rich Northern Hardwood Forest	No		No	108860.7	0	
28	Northern-hardwoods limestone	No		No	169145.5	316.4556	
29	Hemlock-northern hardwood	No		Yes	313132.8	316.4556	
30	Northern-hardwoods	No		Yes	94778.45	0	
31	Northern-hardwoods	No		Yes	64082.26	0	
32	Rich Northern Hardwood Forest	No		Yes	80063.27	158.2278	
33	Northern-hardwoods	No		Yes	270886	0	Anomalous due to legacy sugar maples
34	Northern-hardwoods	No		Yes	168829.1	0	
35	Sugar maple-white ash-jack-in-the-pulpit forest	No		Yes	61392.39	316.4556	
35	Sugar maple-white ash-jack-in-the-pulpit forest	No		Yes	61392.39	316.4556	
Plot	Natural Community (Potential Veg.)	Plantation	Thinned Plantation	Managed Hardwoods	Overstory Reproduction	Colonizing Reproduction	Notes

Table 8. (Continued)

					(Density per ha.)	(Density per ha.)	
36	Sugar maple-white ash-jack-in-the-pulpit forest	No		Yes	42721.51	86234.15	Anomalous due to proximity to Norway Spruce stand
37	Sugar maple-white ash-jack-in-the-pulpit forest	No		Yes	7436.707	4113.923	
38	Hemlock-northern hardwood	No		Yes	66455.68	158.2278	
39	Hemlock-northern hardwood	No		Yes	34018.98	0	
40	Sugar maple-white ash-jack-in-the-pulpit forest	No		Yes	21677.21	0	
41	Hemlock forests and swamps	No		Yes	32911.38	2215.189	
42	Sugar maple-white ash-jack-in-the-pulpit forest	No		Yes	13924.05	2689.873	
43	Hemlock-northern hardwood	No		Yes	46993.66	9018.985	
44	Hemlock-northern hardwood	No		Yes	178797.4	8227.846	
45	Northern-hardwoods limestone	No		Yes	117879.7	6170.884	
46	Northern-hardwoods	Yes	No		444936.6	16455.69	
47	Sugar maple-white ash-jack-in-the-pulpit forest	No		Yes	35284.8	178322.7	Anomalous due to proximity to white pine stand
48	Northern-hardwoods	Yes	No		299525.2	2689.873	
49	Sugar maple-white ash-jack-in-the-pulpit forest	Yes	No		466455.6	6962.023	
50	Northern-hardwoods	Yes	No		363449.3	17721.51	
51	Northern-hardwoods	Yes	No		302531.6	5379.745	
52	Northern-hardwoods	Yes	Yes		156803.7	12025.31	
53	Northern-hardwoods	Yes	Yes		62974.66	1582.278	
54	Northern-hardwoods	Yes	Yes		90031.62	474.6834	
55	Northern-hardwoods	Yes	No		33860.75	1424.05	
56	Northern-hardwoods	Yes	Yes		3481.012	46202.52	
57	Northern-hardwoods	Yes	Yes		0	42405.05	
58	Northern-hardwoods	Yes	Yes		0	10917.72	
59	Red or silver maple-green ash swamp	No		Yes	12816.45	0	
60	Northern-hardwoods	Yes	Yes		0	89556.93	
61	Sugar maple-white ash-jack-in-the-pulpit forest	Yes	Yes		19145.56	0	
62	Hemlock-northern hardwood	Yes	Yes		7911.39	24999.99	

Silvicultural management may have increased overstory reproduction rates, relative to colonizing species, based on the results (Figure 17, upper right). Overstory regeneration was significantly more abundant than colonizing seedlings in managed stands (P<0.0001). In un-managed hardwood and hardwood-hemlock stands, overstory reproduction was also greater than colonizing reproduction, but this relationship was not statistically significant (*P*=0.11). This fact explains the lack of a stronger statistical relationship when all semi-natural stands, managed and un-managed, are analyzed as one group (Figure 17, upper left).

Seedling recruitment in plantations showed similar dynamics, although weighted in the opposite direction (Figure 18). For plantations as a whole, species associated with natural communities may be recruiting slightly more abundantly than overstory conifers, but this relationship is not statistically significant (*P*=0.23). But when thinned plantations are compared with un-thinned plantations, a much stronger relationship emerges. In thinned plantations colonizing species are recruiting far more abundantly than overstory species (Figure 18, lower left) (*P*=0.047). Un-thinned plantations, by contrast, have significantly (P=0.005) higher densities of seedlings reproduced by the overstory, with only small amounts of colonizing

reproduction (Figure 18, lower right). Very dramatic exceptions to this can be found where legacy hardwood trees, either old-growth or open grown, are embedded within conifer plantations. Plot data showed that legacy trees are acting as seed sources for native hardwood species, resulting in prolific colonizing reproduction (see Table 8, stand # 4).

It can be concluded that thinning in plantations redirects successional pathways toward natural community recovery. It also significantly increases successional rates, defined as accelerated understory re-initiation leading to vertical development and differentiation of the canopy.

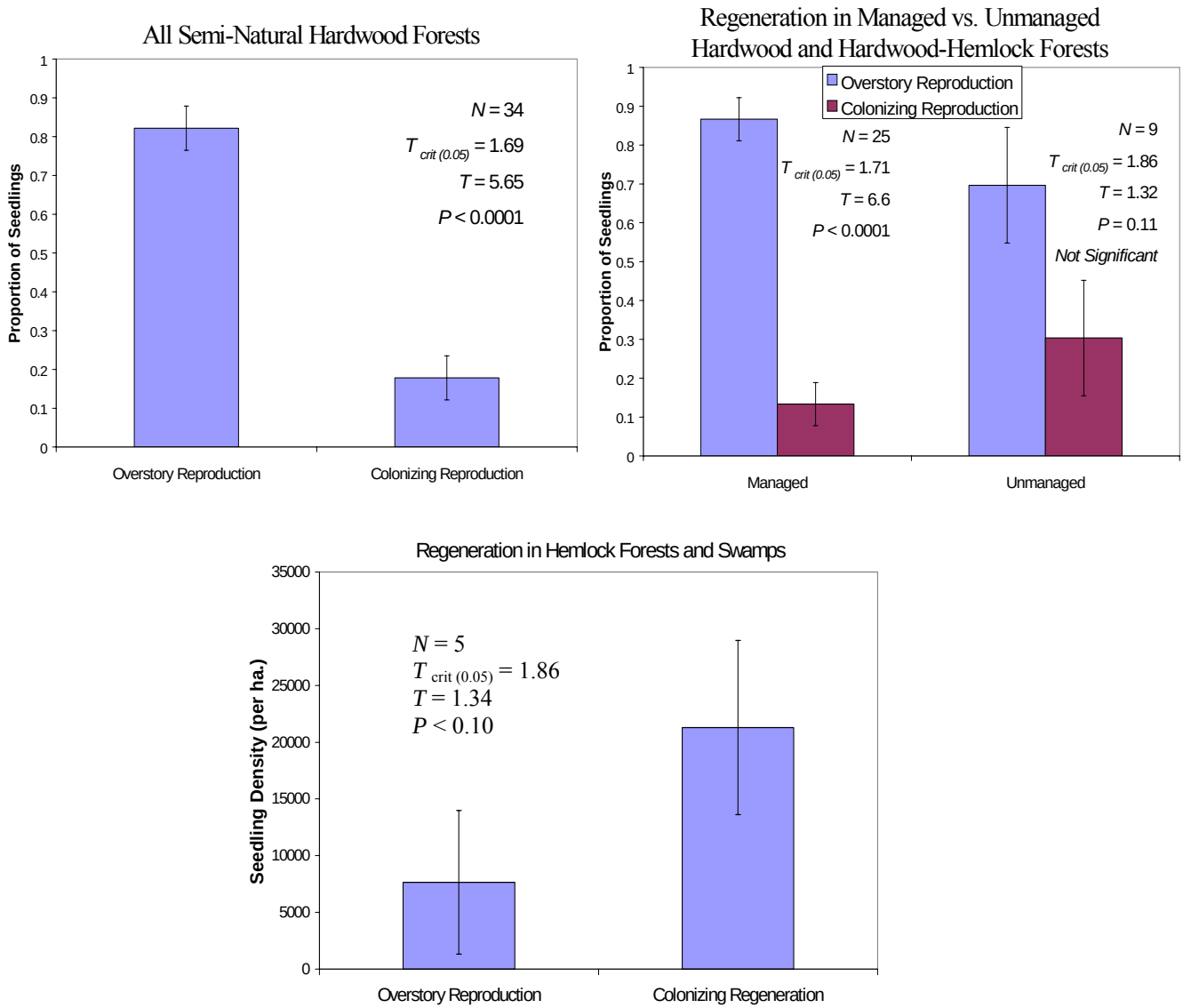


Figure 17. Tree regeneration ratios (overstory vs. colonizing reproduction) for all semi-natural stands (upper left), silviculturally managed vs. un-managed (upper right), and hemlock forests (bottom). Error bars show +/- one standard error of the mean.

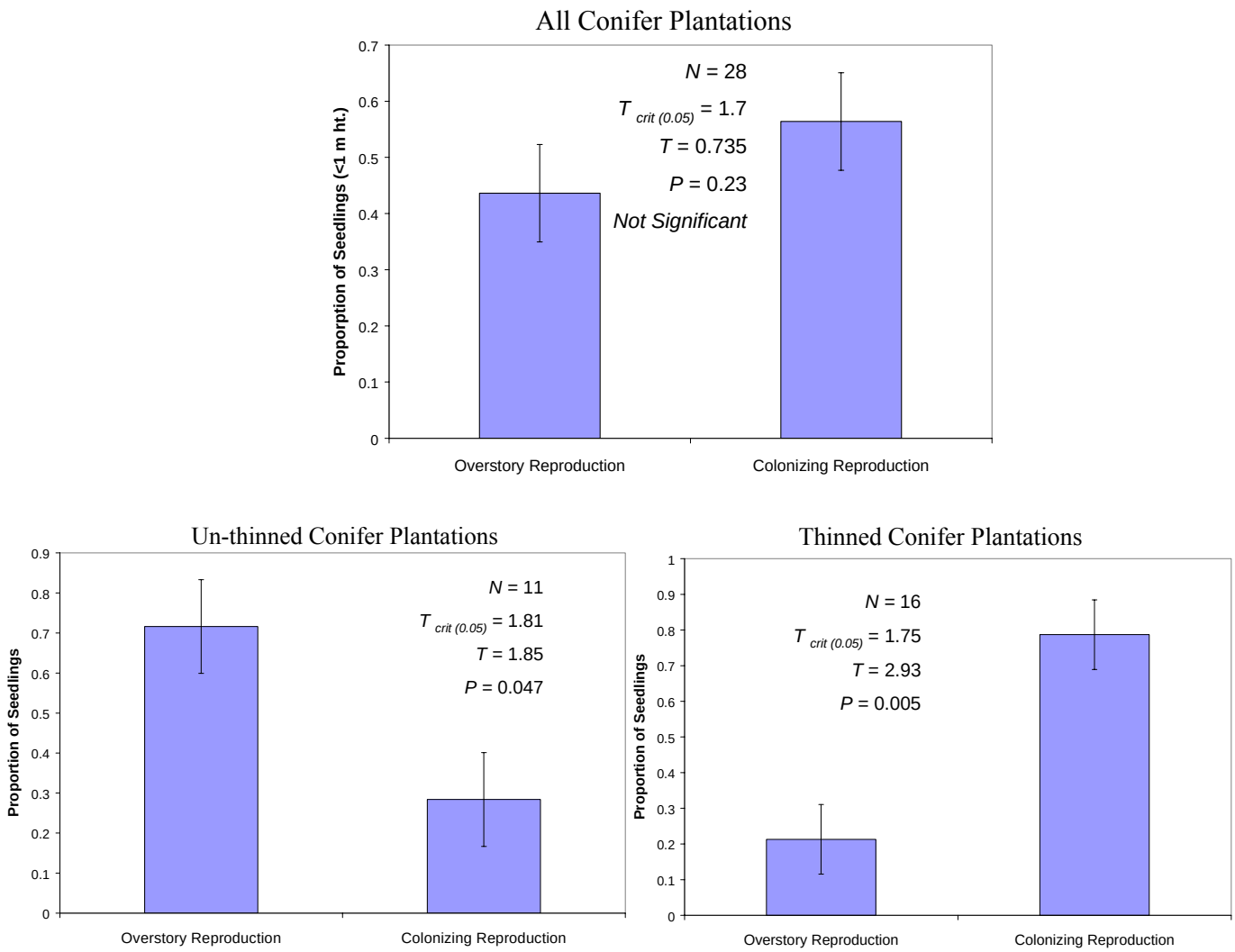


Figure 18. Tree regeneration ratios (overstory vs. colonizing reproduction) for all plantations (top), un-thinned plantations (bottom left), and thinned plantations (bottom right). Inverse relationships in the lower charts cancel one another in the upper chart. Error bars show +/- one standard error of the mean.

Deer browse impacts

Browsing by ungulates (primarily deer and, to a lesser extent, moose) is having a major effect on forest successional dynamics at MBR. While deer browse is heavily impacting regeneration for a number of tree species, the species-specific results were unexpected. Deer browse typically impacts the tree species that deer find most nutritious and palatable (Frelich and Lorimer 1985). These include sugar maple, oak, black cherry, hemlock, and others. The monitoring data for saplings (trees >1 m ht. and < 5 cm dbh), by comparison, showed beech to be the most heavily browsed species. Beech is not considered to be a species preferentially selected by deer. Over 55% of the Park's beech saplings have been browsed, whereas 33.1, 33.3, and 35.4% of sugar maple, red oak, and black cherry, respectively, have been browsed (Figure 19, top). When these percentages are normalized to density (Figure 19, bottom) we see that sugar maple is second only to beech in terms of browse. Surprisingly, hophornbeam and white ash are also heavily browsed despite the lower levels of palatability these species are generally assumed to offer. That such a large percent of oak and black cherry are browsed is of concern because these species are both rare at MBR and ecologically and economically valuable.

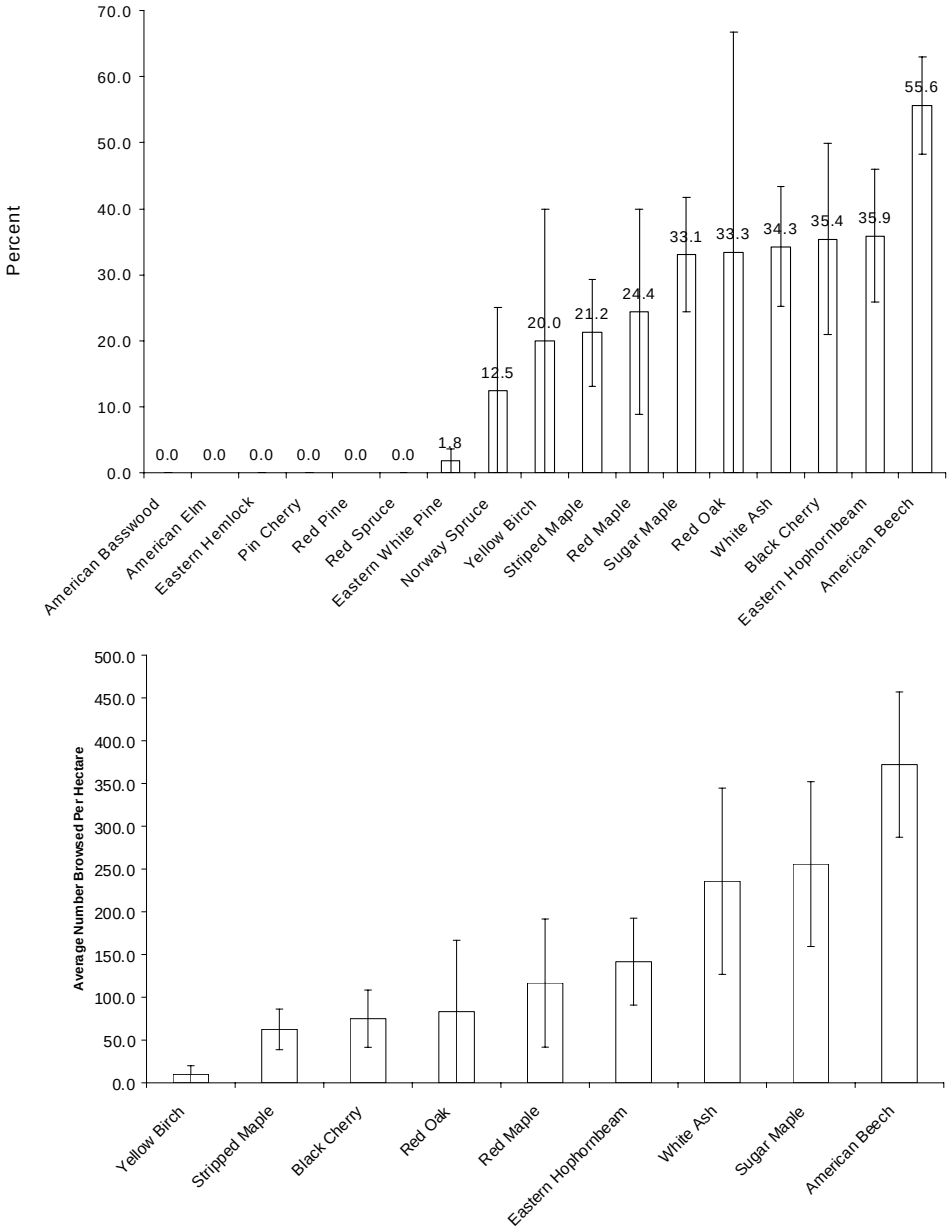
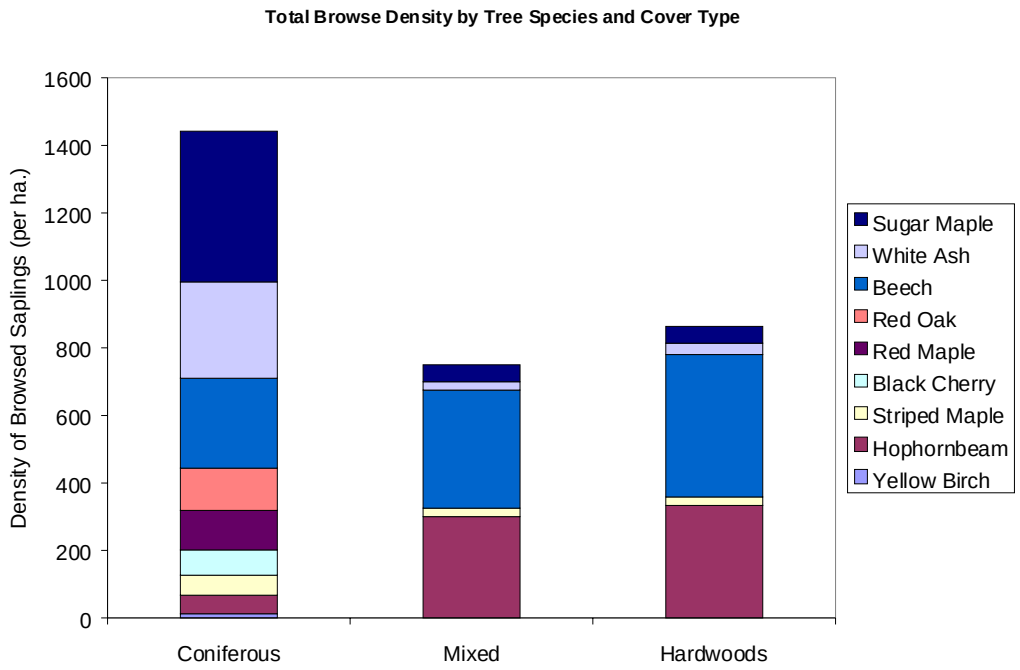


Figure 19. Deer browse on saplings by species. Browse as a percentage of individuals is shown on top, whereas browse normalized to density (per ha) is shown on the bottom. Species are ranked in order of degree browsed. Error bars are +/- one standard error of the mean.

It is likely that the statistically higher browse on beech does not adequately reflect species-species differences in browse intensity. In other words, the sampling design did not categorize browse by intensity on a per sapling basis. Beech might be widely browsed, but with only light damage done to individual plants. Individual sugar maples might be browsed more intensively, resulting in greater tissue damage. Field observations suggest this as a possibility, but browse intensity was not directly measured. Future plot remeasurements could assign browse intensity classes on a plant-by-plant basis. Another caveat is that the data do not reflect

seedling browse. Species-specific browse rates may be different for seedlings. It is possible, therefore, that browse rates on saplings are an artifact of differentials in survivorship: i.e. more beech surviving means there are more of them to be grazed later. What is clear is that the Park's heavy browse rates are influencing successional trajectories, especially where browse intensities are high enough to reduce sapling growth rates and thus alter competitive dynamics.



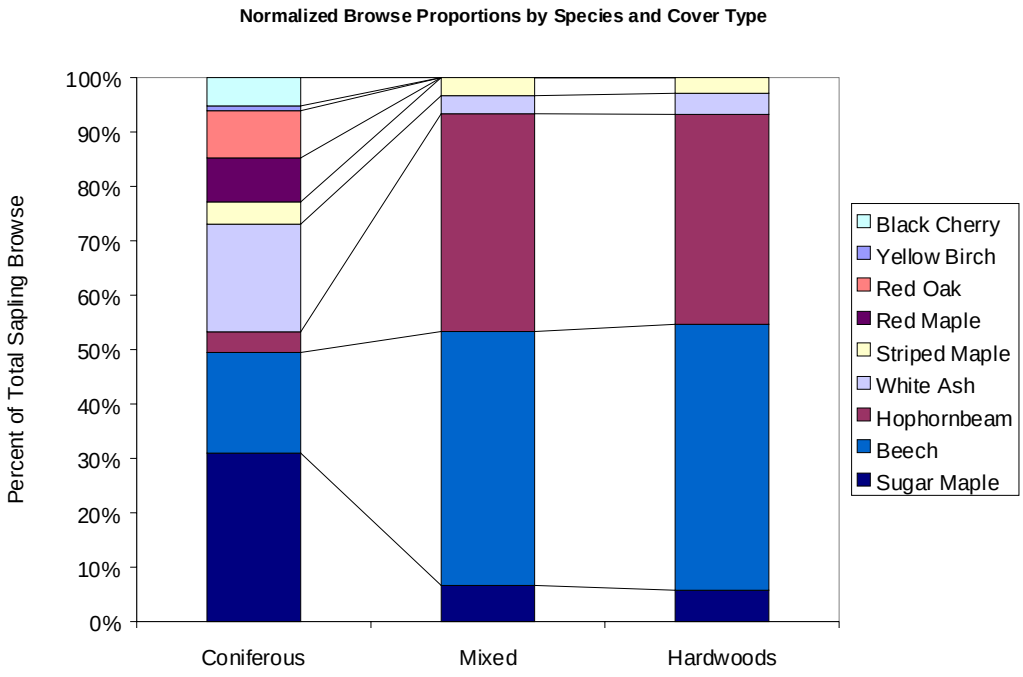


Figure 20. Deer browse effects by species as a function of browse density (top) and proportion of total browse (bottom).

Deer browse is having a significantly larger effect in coniferous stands (e.g. plantations and hemlock stands) than in mixed woods and hardwood stands (Figure 20, top). Total browse density in mixed woods and hardwood stands was only 52 and 60%, respectively, of that found in coniferous stands. A significantly greater proportion of sugar maple is browsed in coniferous stands than in mixed or hardwood stands ($P = 0.029$). Beech is browsed significantly (90% confidence level only) less frequently in coniferous stands ($P = 0.077$). There were significant differences for hophornbeam, ash, oak, and cherry as well (Figure 20, bottom). As a percentage of total browse density, sugar maple, beech, and white ash, in their respective order, were the most heavily browsed species in coniferous stands. Beech, sugar maple, and hophornbeam were the most heavily browsed in mixed woods and hardwood stands. As a percentage of individuals on a per species basis, beech (57.2%), red oak (50.0%), black cherry (35.4%), sugar maple (31.8%), and white ash (30.6%) were most heavily browsed in conifer stands. In hardwood stands the same ranking included white ash (66.7%), hophornbeam (59.7%), striped maple (50.0%), beech (48.5%), and sugar maple (48.1%).

It is not clear precisely why there are such distinct differences in browse selection among cover types. It is possible that preferential selection of sugar maple in conifer stands relates to the use of those stands as cover by deer at night and during cold weather. Saplings, especially those of higher nutritional content, may be a more important food source where deer congregate and under thermal cover provided by conifer stands, since the saplings would be at least partially accessible over snow. The overall higher levels of browse in conifer stands is very probably due to concentration of deer activity. In those areas deer browse impacts on successional dynamics may be especially pronounced. Sugar maple may be at a competitive disadvantage in coniferous cover types due to browse effects.

Deer browse effect on forest successional dynamics at MBR may or may not be within the historic range of variability, depending on the density of the local deer population. Herbivory is intrinsic to these ecosystems and is an important element of natural successional dynamics. However, if deer populations are elevated over their HRV, then more intense herbivory will alter or redirect successional pathways (Whitney 1984; Frelich and Lorimer 1985), resulting in a forest composition that is outside the HRV.

Forest health

Crown condition

Tree health in MBR is generally good, with some notable exceptions. “Healthy trees” are defined here as having >20% crown density, ≤50% foliage transparency, or ≤21% crown dieback. Unacceptable or “significant” levels of decline are defined as >10% of individuals for a given species classified as unhealthy. Beech are in severe decline due to beech bark disease, but are evaluated using other indicators. Their condition is treated separately in this report (see page 45). Among other species and for MBR as a whole, the monitoring data indicate significant levels of defoliation, decline, or physiological stress for only five species, butternut, green ash, white ash, red maple, and American basswood (Figure 21).

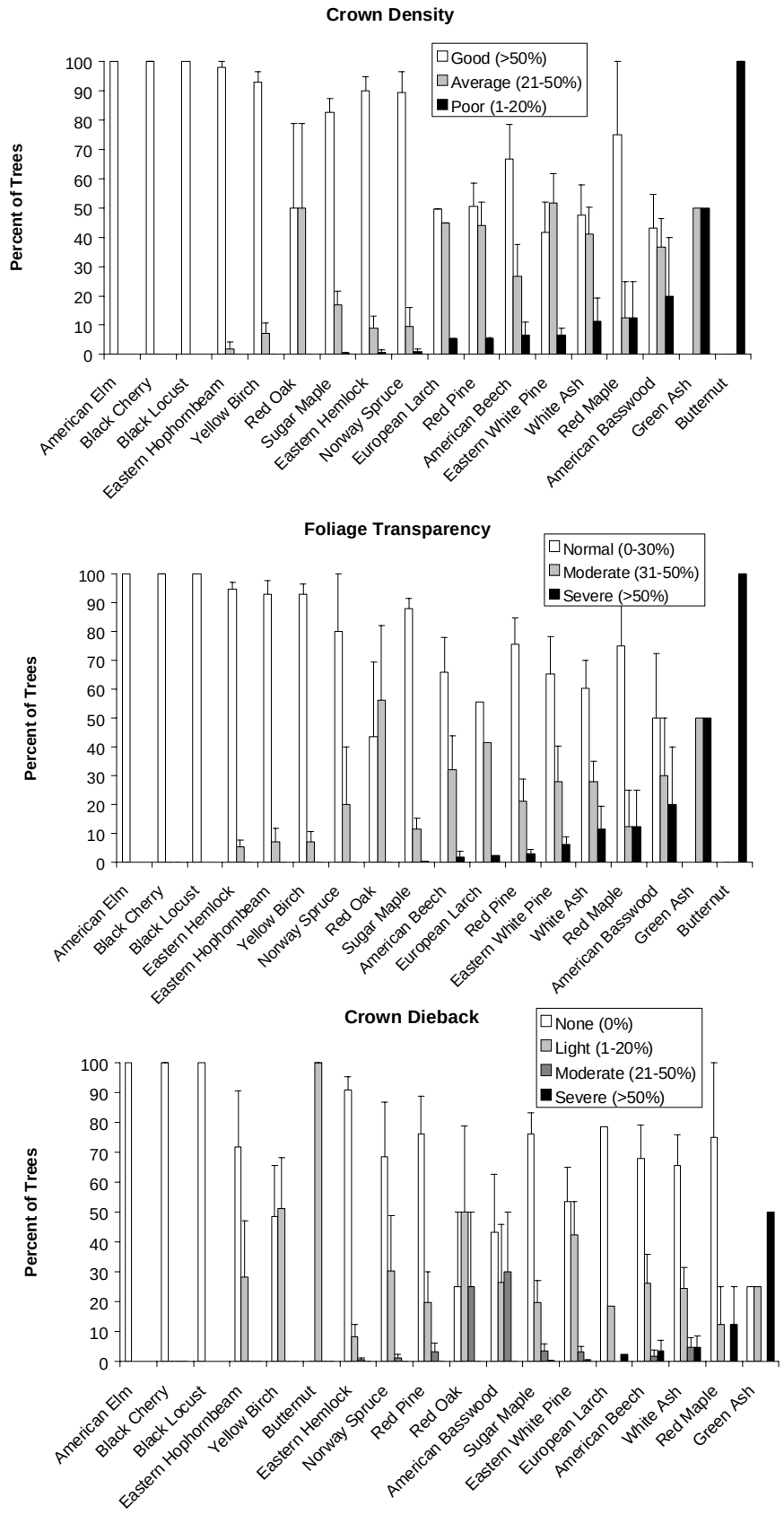


Figure 21. Crown condition ratings for three tree health indicators by tree species across all reference stands

At the other end of the spectrum, black locust, black cherry, and the Park's few American elm are given a clean bill of health. For elm this is perhaps surprising given the ubiquity of Dutch elm disease (*Ophiostoma ulmi*), although the elms monitored are of only small to medium diameter and thus of low susceptibility to the disease. It is also possible that the remaining few individuals are exhibiting some degree of resistance to the disease. Important species such as sugar maple, yellow birch, and eastern hemlock have only light levels of crown condition decline. These are most probably within the historic range of variability and thus not indicative of ecological stress. Those species should be considered to be currently "healthy" at MBR.

Poor health in American basswood and, possibly, red maple cannot be attributed to specific causative factors at this time. Crown condition for these species may reflect physiological stress experienced during the 2001-2002 drought, although other species would have been expected to respond in a similar fashion if that were the case. Further monitoring and research is needed to determine (a) if these species are truly declining over the longer term and (b) the causes of decline.

Butternut are relatively rare at MBR. However, the few individuals present rate poorest in health of any species at the Park. Their severe decline is due to the butternut canker (*Sirococcus clavigignenti-juglandacearum*), a now widespread disease of unknown origin. It is not possible to control infected trees, although dead or severely declining butternut should be removed to lower inoculum loads. Trees should be removed if dead crown volume exceeds 30% and > 20% of the main stem is cankered. It is possible to retain trees with up to 50% crown dieback if there is little or no cankering.

The data indicate significant levels of crown density loss, foliage transparency increase, and crown dieback for both green and white ash. Poor health for white ash is most evident in reference stands #2 (a European larch plantation) and #39 (a northern hardwood hemlock forest with isolated wet, ash patches) (Figures 22-23). Green ash are monitored only in stand 21, where they occur near the extreme western boundary of the Park in a forested wetland with low overall overstory vigor. White ash decline may be due to "ash yellows," a disease caused by mycoplasmalike organisms. These invade trees through phloem sieve tubes; leafhoppers and related insects are believed to be the transmission vectors. The results suggest that additional research should be conducted to determine if ash yellows are indeed the source of the problem at MBR.

There are light to moderate declines in crown condition affecting the Park's plantation conifers, including European larch, Norway spruce, eastern white pine, and red pine. These can be attributed to several possible factors, including (a) reduced vigor with age (e.g. larch); (b) poor adaptability to site conditions (e.g. larch and possibly red pine); and (c) plantation densities resulting in high levels of competition and growing space limitations (e.g. red pine, Norway spruce, and white pine). Appropriate silvicultural management to increase crown health for these species would include pre-commercial and commercial thinning.

Results presented in Figures 22-23 focus on a subset of species selected for comparative purposes. The results show that, for a given species, crown condition as an indicator of forest health varies widely by stand and by indicator. Data for only those stands where a focal species occurs are presented. These data highlight the stands where moderate or severe species-specific health declines are occurring. Managers should consult Figures 22-23 to pinpoint areas needing forest health related management and/or further investigation to determine causative factors.

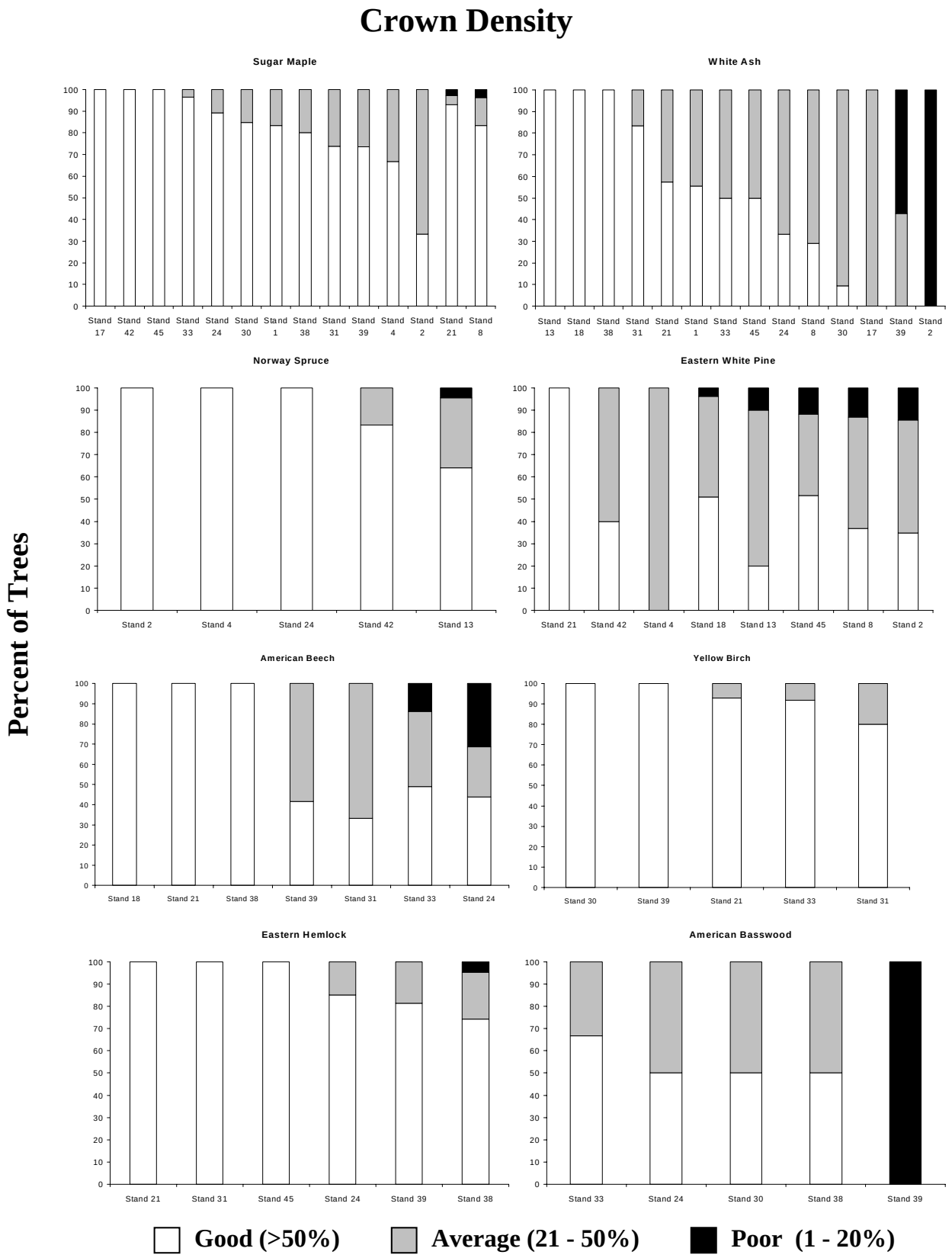


Figure 22. Crown density by reference stand for selected species. Distributions are the cumulative percentage of dominant canopy trees in each crown density class. They are ranked in order of decreasing crown health.

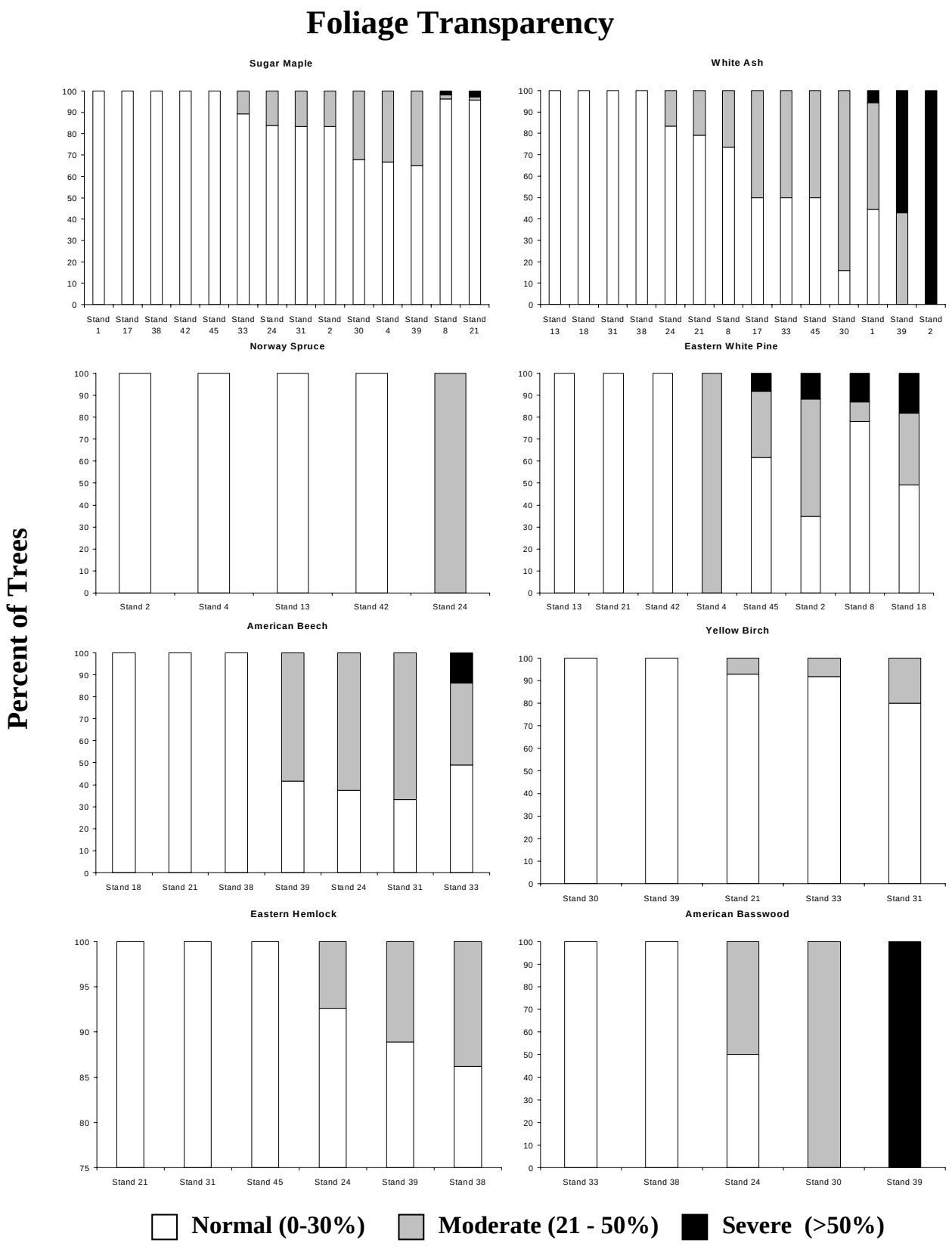


Figure 23. Foliage transparency by reference stand for selected species. Distributions are the cumulative percentage of dominant canopy trees in each foliage transparency class. They are ranked in order of decreasing crown health.

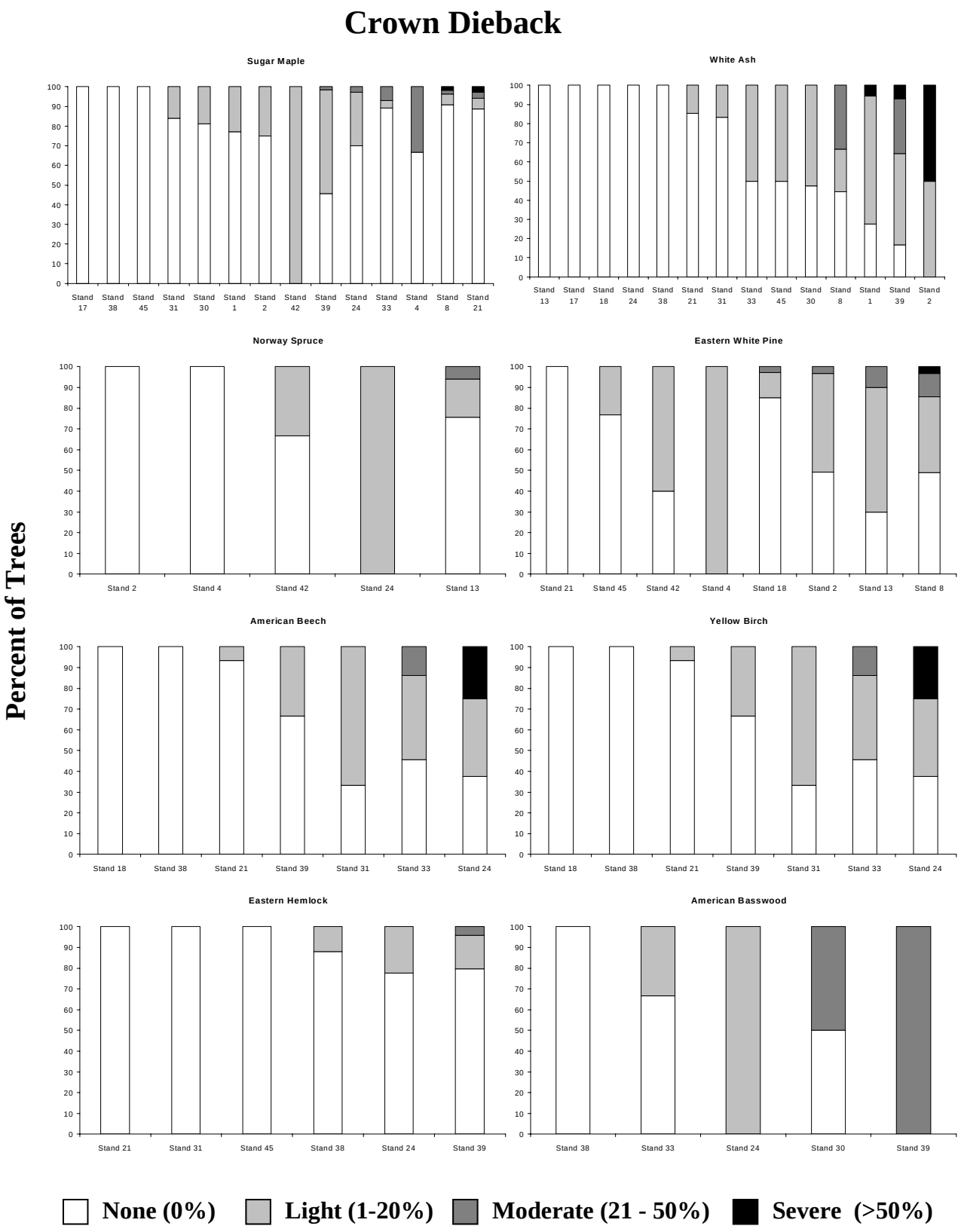


Figure 24. Crown dieback by reference stand for selected species. Distributions are the cumulative percentage of dominant canopy trees in each crown dieback class. They are ranked in order of decreasing crown health.

Beech bark disease

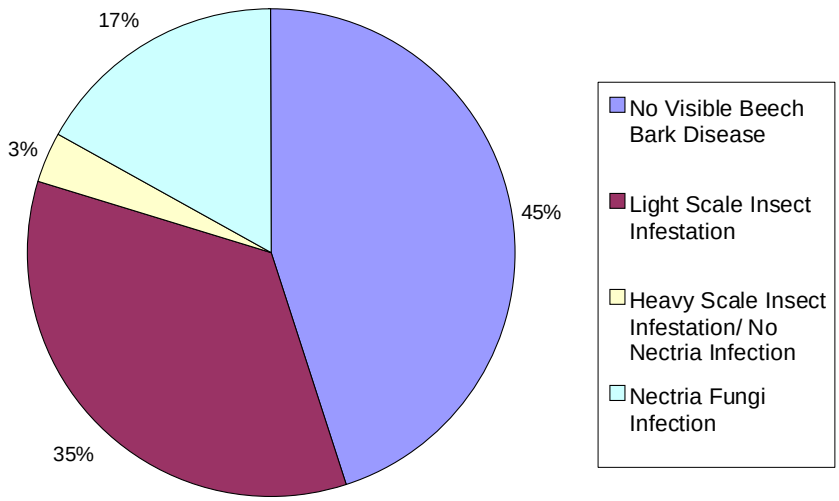


Figure 25. Percent of beech trees at MBR infested with beech scale insect and *Nectria* fungus.

MBR's beech trees are heavily infected with beech bark disease. Beech bark disease is caused by two exotic organisms, the beech scale insect (*Cryptococcus fagisuga*) and a fungus, primarily *Nectria coccinea* var. *faginata* but sometimes *N. galligena*. The disease results from a predicable pattern: first the bark is altered by the scale insect, then the tree is invaded by *Nectria* fungi. On average, 17% of the Park's beech are infected with *Nectria* and another 38% have been attacked by the beech scale insect with fungal infection not yet apparent (Figure 25). These levels are higher in beech dominated areas, however. For instance, in the beech dominated slope of reference stand 33 (plots 31, 34, and 35), 42 % of beech are infected with *Nectria* and another 30% have beech scale only. Most of the large beech in stand 33 are dead or dying, which explains the large dead tree quadradic mean diameter (29.6 cm) for that stand reported previously in Figure 15. These infection levels suggest that portions of the Park are within a "killing front" of heavy beech bark disease related mortality (Houston et al. 1979; Gavin and Pert 1993). Over time, as mortality takes its toll, infection rates may recede into an "aftermath" stage, in which only a few residual, resident large beech survive (probably < 10% of the population). Beech in the aftermath stage will be mostly small stems, many of root-sprout origin (Houston 1975; Houston et al. 1979).

Beech bark disease infestation at MBR follows a size-related trend similar to that reported more widely (Gavin and Pert 1993). Larger diameter trees are strongly associated with higher incidences of both heavy scale insect infestation and *Nectria* infection (Figure 26, top). Infection percentages increase linearly with tree diameter ($P = 0.001$) and tree size explains 78% of the variability in *Nectria* infection rates (Figure 26, bottom). In the monitoring plots, 100% beech trees > 55 cm dbh were heavily infected, but the sample size in this size range was very low; it remains possible that large resistant trees may occur in the Park. A large portion (>55%) of even very small beech at MBR are heavily infested with beech scale and/or *Nectria* (Figure 26, top), affecting small to medium sized trees to a magnitude not previously reported (Gavin and Pert 1993). It can be concluded that beech bark

disease will significantly weaken, and ultimately decimate, the Park's population of large diameter beech based on these results. This will not only limit the abundance of important late-successional forest structural characteristics provided by this species, but also will reduce the availability of beech nut, an important food source for wildlife.

Management actions are advised that favor and retain resistant beech and promote recolonization of resistant beech propagules. All large sized (e.g. >30 cm dbh) beech believed to be resistant should be marked for permanent retention as seed trees, a restoriation approach now advocated regionally.

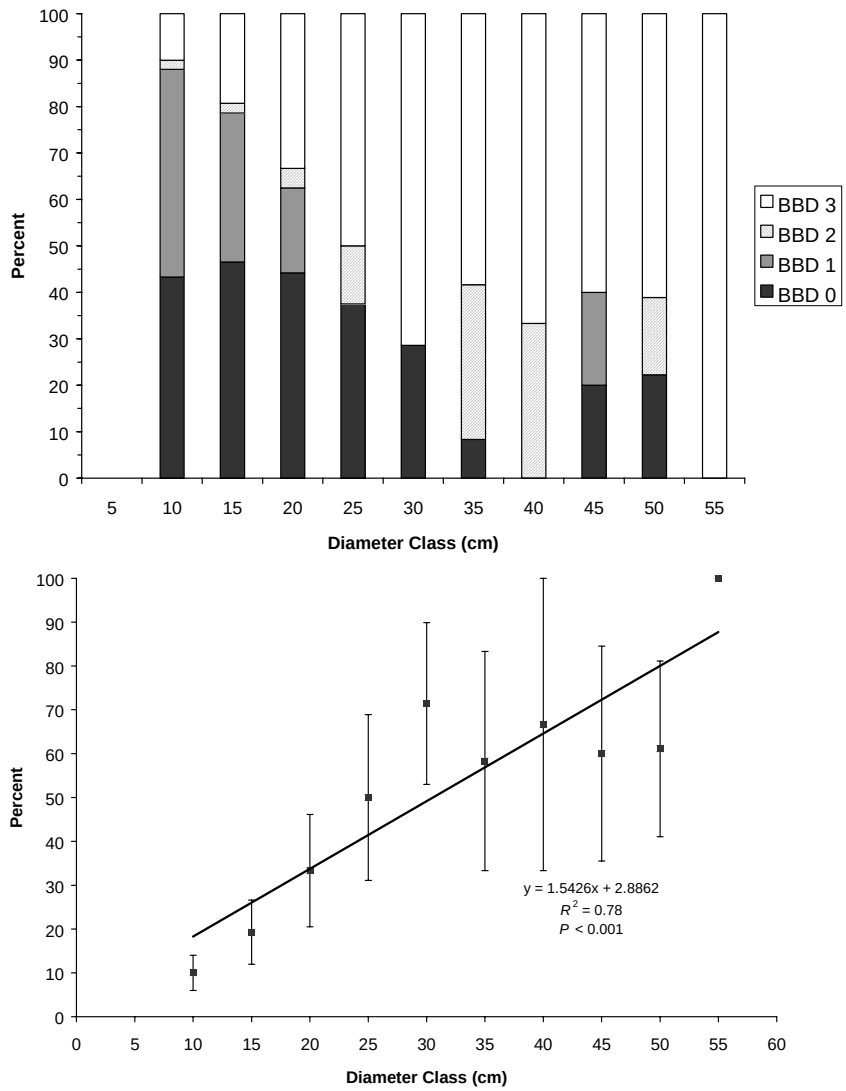


Figure 26. Beech bark disease as a function of tree diameter. Proportions by disease class are shown on the top: BBD0 = no evidence of scale or fungus; BBD1 = light beech scale; BBD2 = heavy scale, but no *Nectria* fungal infection; and BBD3 = *Nectria* infection. BBD3 regressed against tree diameter is shown on the bottom (*N*=13 plots).

Regeneration trends

Tree seedlings (regeneration < 1m ht.) at MBR declined precipitously over the three year monitoring period (Figure 27). Hardwood and conifer seedlings declined 60 and 74%, respectively, from 2001 to 2003 for the Park as a whole. Declines were especially severe for certain species, such as sugar maple (73%) and eastern white pine (87%).

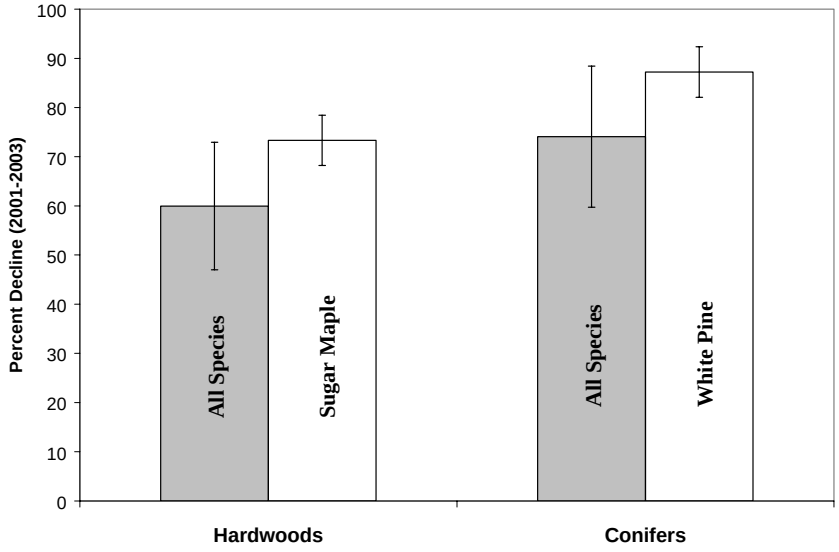


Figure 27. Percent decline for tree seedlings from 2001 to 2003. Error bars show +/- one standard error of the mean.

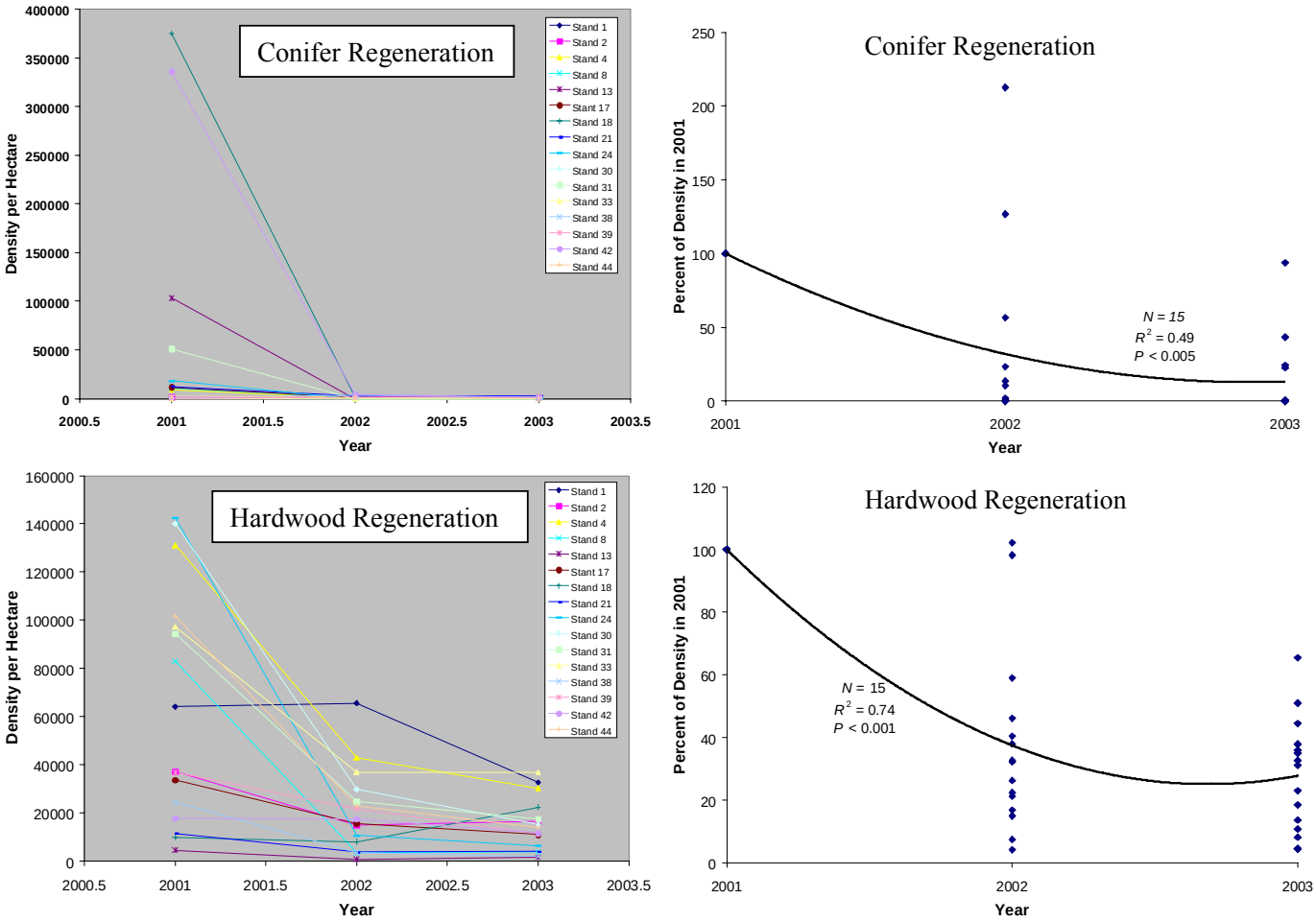


Figure 28. Conifer (top) and hardwood (bottom) regeneration trends from 2001 to 2003.

Hardwood seedlings declined fairly consistently across all stands (Figure 28, bottom left), whereas conifer decline was more variable between stands for the 2001-2002 time interval (Figure 28, top left; conifer seedling increased in two stands over that period. Net conifer seedling decline varied between stands from only 7% (i.e. 93% left after three years) to 99.8%. Net hardwood decline varied between stands from 35% percent to 95% over three years. Regeneration declines across all stands were statistically significant for conifers ($P < 0.005$) and hardwoods ($P < 0.001$). These trends were also statistically significant for sugar maple and *Pinus* sp. ($P < 0.0001$), used here as examples of species and genera that experienced the most severe declines and are of particular interest to forest managers (Figure 29).

The most likely explanation for regeneration declines during the monitoring period is summer drought. The summer (June-August) of 2001 was the 5th driest on record since 1895. Precipitation in summer 2002 was also below normal. Seedling survivorship is directly influenced by drought stress, although the almost 100% seedling mortality rates observed in some stands are severe even for drought related dieback. That seedlings continued to dieback during the 2002-2003 interval is typical of lagged reductions in physiological vigor and increased susceptibility to secondary stressors, such as pathogens, herbivores, and acid deposition. Thus, while it is possible that anthropogenic stressors (i.e. acid deposition) were a contributing factor, it is most likely that the regeneration declines are within the historic range of variability as driven by natural climate variability.

The possibility of altered drought dynamics as a function of global climate change is beyond the scope of this study to evaluate. However, the results do suggest that wide fluctuations in regeneration survivorship rates are to be expected as a function of climate variability. The results also highlight the sensitivity of seedling survivorship to drought stress, which may be of increasing concern into the future if the climate warms. Decreased summer precipitation, leading to increased frequency and intensity of drought, is consistently predicted for New England under a range of climate change scenarios spanning the next century (National Assessment Synthesis Team 2000). If repeated and persistent regeneration failure occurs in the future this could dramatically influence successional dynamics, comprise the ability of Park managers to regenerate and manage desirable species, and facilitate migration into the MBR of drought-adapted species including central hardwoods and invasive exotics (Iverson and Prasad 1998; DeHayes et al. 2000).

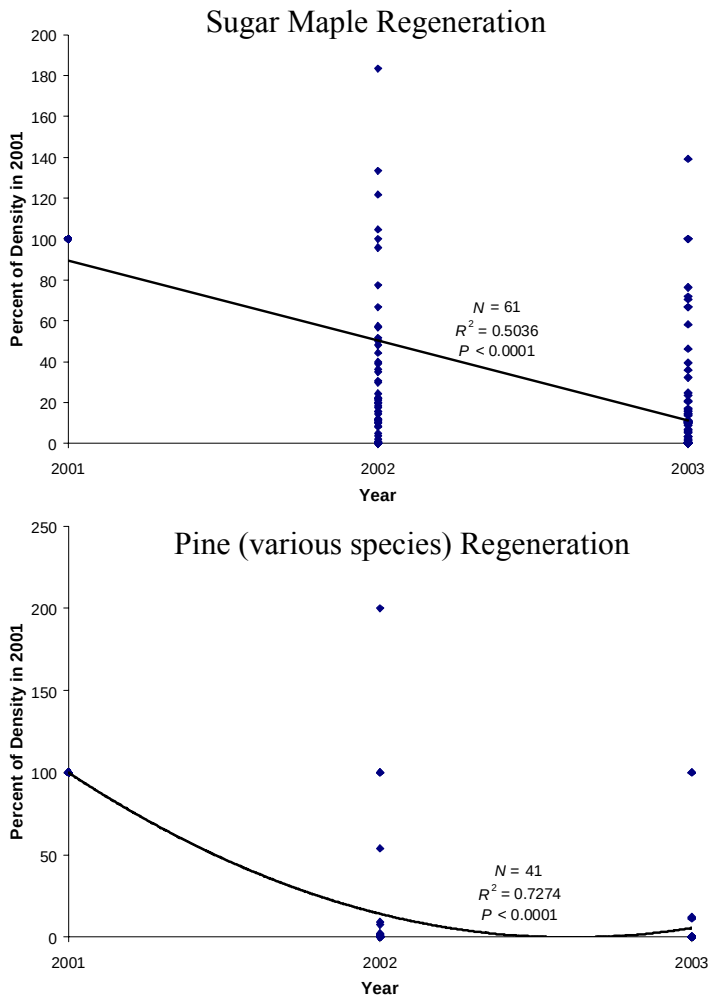


Figure 29. Regeneration trends for sugar maples and *Pinus* (primarily white pine but includes some red pine) over the monitoring period.

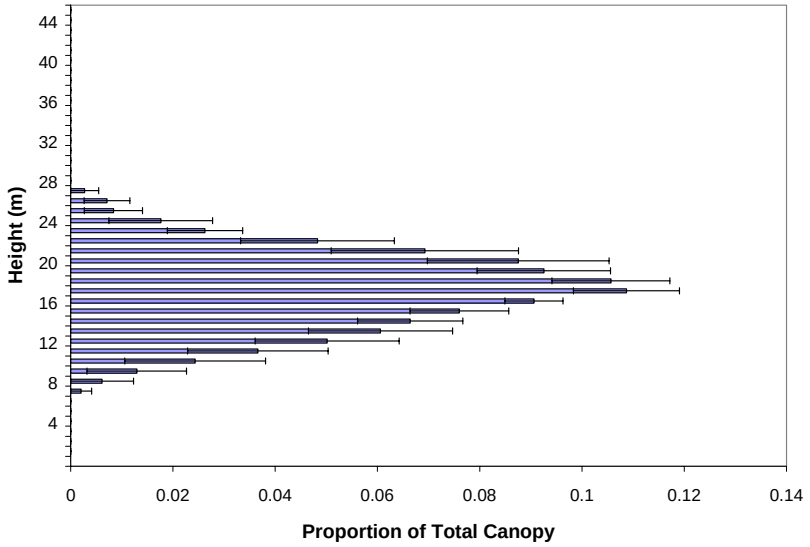
Biodiversity and habitat structure

Vertical structure: foliage height distribution and diversity index

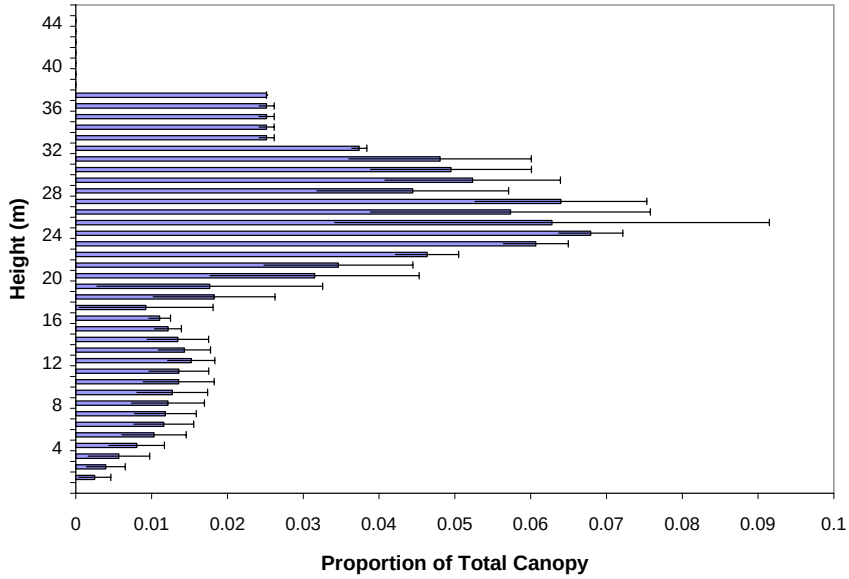
MBR's forests include a range of vertical conditions as defined by canopy layering, based on analysis of foliage height distributions for all reference stands. Figure 30 shows three such conditions, a single-layered un-thinned plantation, a two-layered plantation, and a multi-layered mature hardwood forest. These are representative of the Park's diversity of canopy structures, although reference stands fall along a continuous spectrum, ranging from single to multi-layered, making finer distinctions regarding canopy architecture unclear in some instances.

A trend shared by several stands was the initiation of canopy differentiation (i.e. development of sub-canopies) caused by disturbances, either anthropogenic in the case of thinned plantations or natural in the case of stand #45 (Figure 30, middle). Under both scenarios, reduction in overstory density increased light levels near the ground, leading to accelerated understory re-initiation of shade-tolerant species and subsequent vertical development of two or three layered canopies. Thus, low intensity forestry in the Park appears to have mimicked natural disturbance effects to some degree, especially in terms of the vertical response. It is also noteworthy that at least some of the Park's oldest plantations are now rapidly developing late-successional structural complexity without human intervention, thanks to natural disturbances and natural stand development processes.

Single-Layered:
un-thinned plantation



Two-Layered:
naturally disturbed,
older plantation



Multi-Layered:
un-managed, highly
productive
hardwood stand

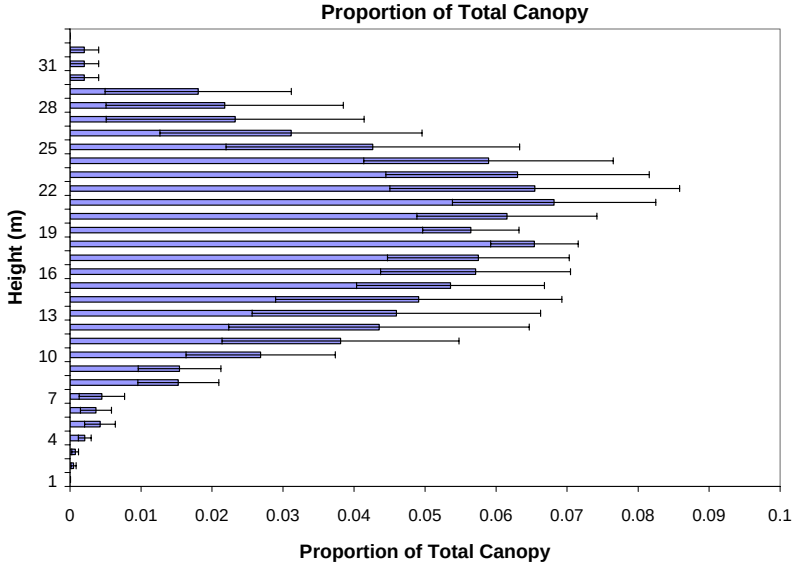


Figure 30. Foliage height distributions for an un-thinned 1950 Norway Spruce plantation (stand #13) (top), an 1880 white pine plantation (stand #45) disturbed by low intensity windthrow (middle), and an unmanaged, uneven-aged, rich northern hardwood stand (stand #30) (bottom). Error bars show +/- one standard error of the mean.

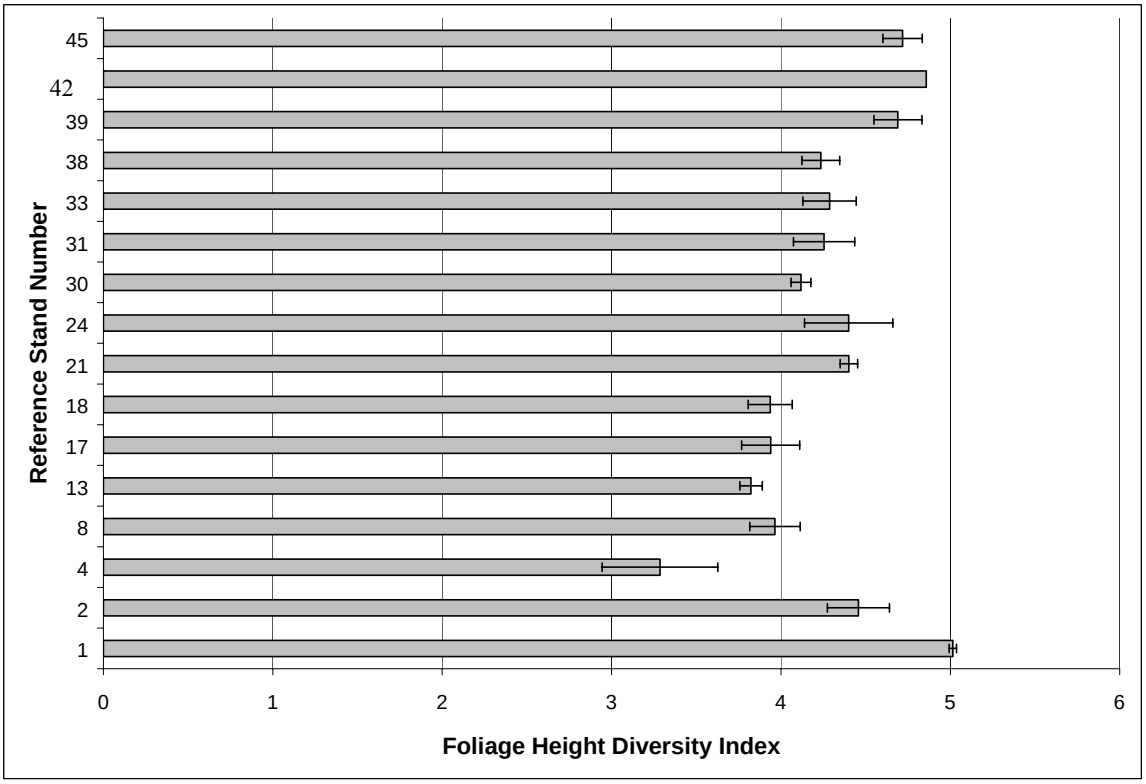


Figure 31. Foliage height diversity index values for all reference stands. Error bars show +/- one standard error of the mean.

Calculation of foliage height diversity index based on the above mentioned distributions provided a means of empirically comparing stands and testing the relationships inferred above. Foliage height diversity index values for reference stands are presented in Figure 31.

There are significant relationships between foliage height diversity and forest management history. Foliage height diversity is significantly higher in stands that have had low intensity silvicultural management (Figure 32), either thinning in the case of plantations (P=0.038) or uneven-aged harvests in the case of semi-natural stands (P=0.038). This relationship holds also when all reference stands are aggregated (P=0.021). Thus, the results suggest that low intensity forestry in the Park has mimicked fine-scale natural disturbances, increasing regeneration rates, releasing advanced regeneration, and generally promoting vertical development.

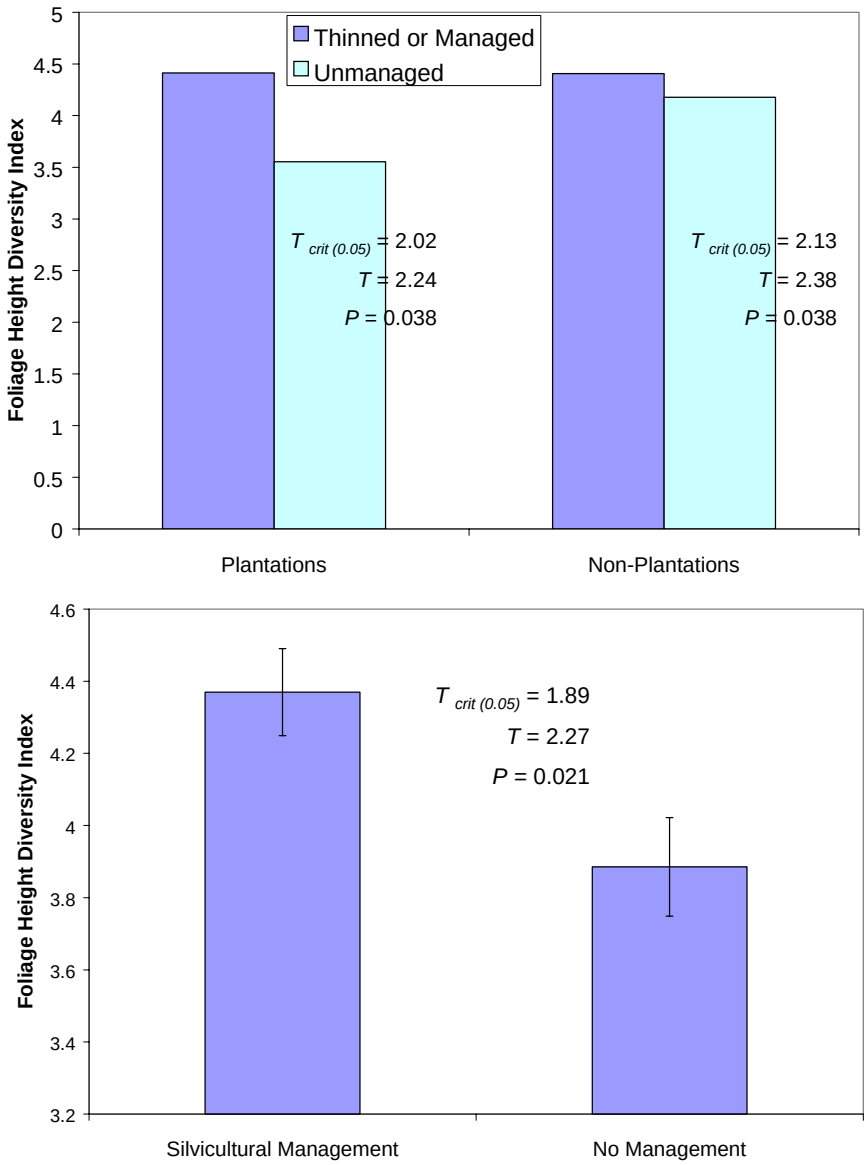


Figure 32. Comparison of foliage height diversity index for plantations and semi-natural stands by silvicultural management regime (above) and for all reference stands (combined) by management regime (bottom). Error bars show +/- one standard error of the mean.

Downed coarse woody debris

Monitoring results specifically include measures of CWD because it is an important structural feature that influences wildlife habitat, nutrient cycling, tree regeneration, below-ground communities, and other ecological functions associated with forest ecosystem health (Keddy and Drummond 1996; Hunter 1999; Franklin et al. 2002). Coarse woody debris (CWD) volumes vary substantially throughout the Park. Mean volume and variability data are presented in Table 9.

Table 9. Downed coarse woody debris (>10 cm diameter) data by reference stand.

	Mean Volume (m^3/ha)	Variability (One Standard Error of the Mean)
Stand 1	40.64	17.13
Stand 2	234.98	88.28
Stand 4	13.14	4.78
Stand 8	24.56	10.00
Stand 13	39.17	14.68
Stand 17	31.60	12.44
Stand 18	26.20	8.59
Stand 21	53.77	17.08
Stand 24	14.83	13.53
Stand 30	71.28	24.22
Stand 31	16.93	7.05
Stand 33	5.85	3.80
Stand 38	64.62	26.96
Stand 39	21.45	7.04
Stand 42	11.24	4.59
Stand 45	40.14	24.58

CWD volumes are highest in stand # 2 (Figure 33). This reflects windthrow of large diameter white pine as well as significant accumulation of logging slash from past thinning activity in some areas. Data for that stand significantly bias average volumes estimated for plantations as a group (Figure 34), although volumes are indeed higher in general in the Park's conifer plantations. This may be due to the larger mean diameters in some of the older plantations and the slower decay rates associated with conifer boles. It also may be due to elevated soil acidity in conifer stands, which allows CWD to persist on the ground longer and, thus, accumulate.

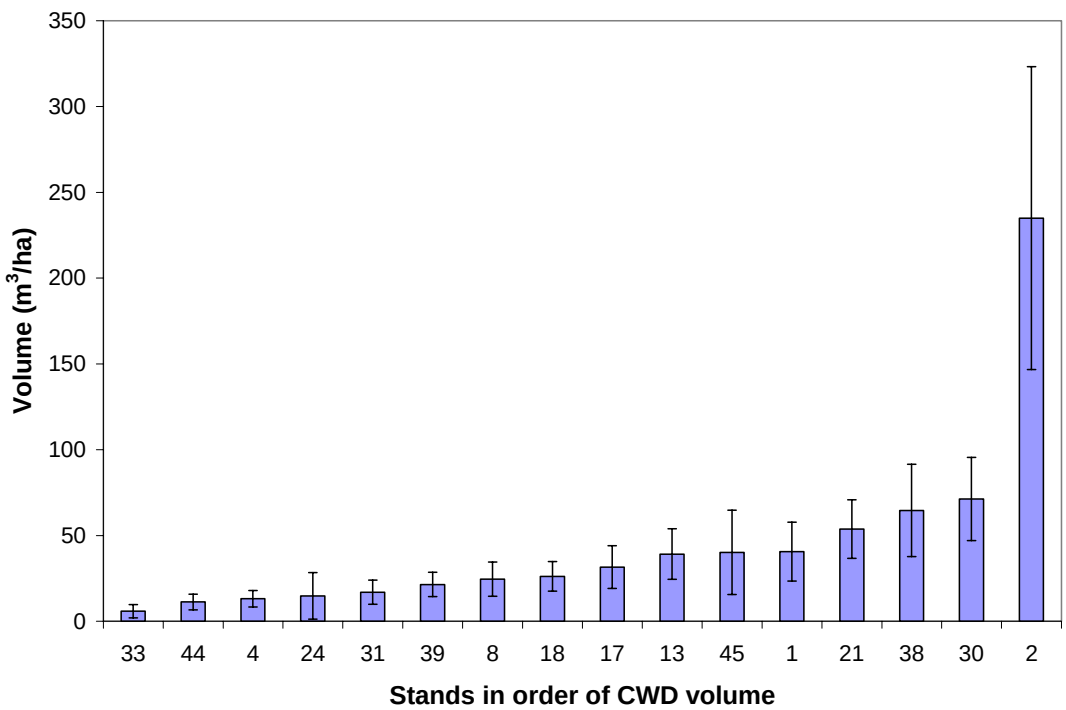


Figure 33. Reference stands ranked by downed coarse woody debris volume.

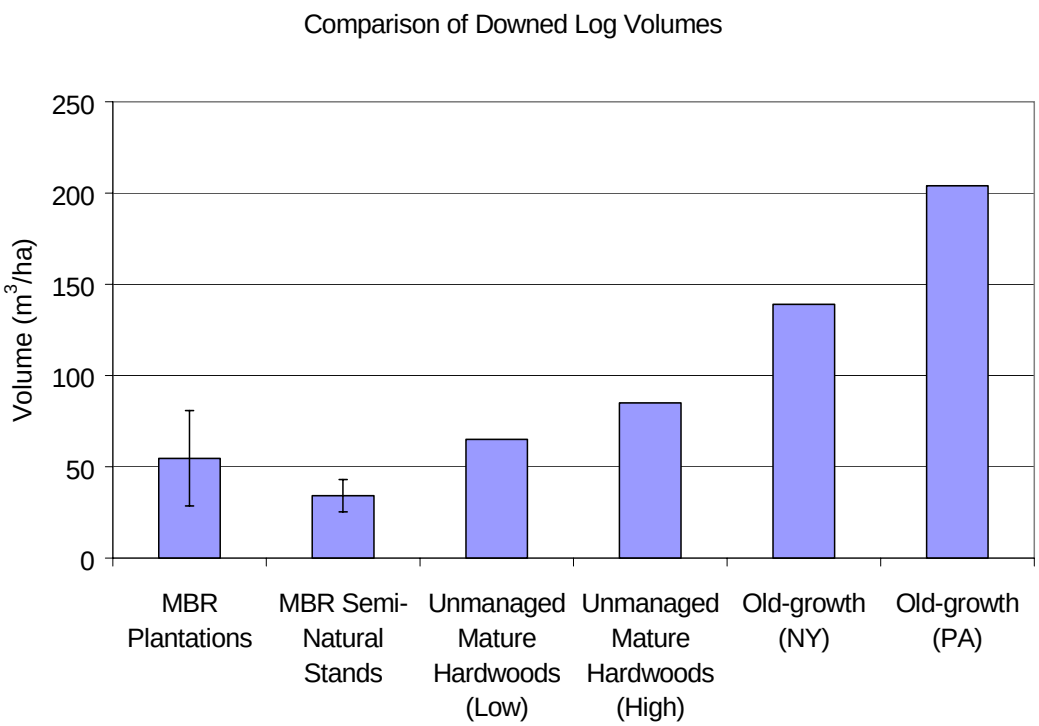


Figure 34. Downed coarse woody debris volumes at MBR as compared to benchmark values for mature and old-growth northern hardwoods in the northeastern United States (benchmark data are from Tyrrell and Crow 1994a; 1994b; Haney and Schaadt 1996; and McGee et al. 1999).

CWD volumes in semi-natural stands may be below their potential based on comparisons with reference data for mature and old-growth northern hardwood stands in the northeastern U.S. (Tyrrell and Crow 1994a; 1994b; Haney and Schaadt 1996; and McGee et al. 1999). CWD volumes in MBR are less than half the mean values recorded for moderate to highly productive, lightly managed to unmanaged, mature northern hardwood forests throughout the region (Figure 34).

Dead tree structure

Standing dead trees (snags) and dying trees are an important habitat structure required by many cavity excavators, cavity nesters, and a host of other species guilds (Hunter 1999; DeGraaff and Yamasaki. 2001). Monitoring snag abundance is, therefore, essential for adaptive biodiversity management (Hunter 1999). Snag density and basal area data are presented in Table 10 and graphed in Figure 35. Snag recruitment (i.e. creation) rates vary widely among the Park's forest stands. As a percentage of basal area, recruitment rates are highest in reference stands 4, 13, and 30. This metric correlates with larger diameter trees, suggesting that those stands have experienced higher levels of mortality in overstory trees. There is likely to be intense competition and self-thinning in dense plantations (e.g. stands 4 and 13). This contrasts with density-independent mortality processes (e.g. wind throw and pathogens) operative in low density, mature hardwood stands, such as stand 30. Both would result in overstory tree mortality but there is a key difference with respect to habitat structure. Stands undergoing predominately density-dependent thinning will recruit primarily small to medium diameter snags of less value to cavity-dependent species. Conversely, stands undergoing density-independent mortality tend to provide more abundant large diameter snags of high wildlife habitat value.

Standing snag abundance as a percentage of stem density is highest in a range of stand types, most of which have dense sapling-sized and mid-canopy layers. The data suggest, therefore, that Park stands in this structural condition will have elevated levels of competition and self-thinning from-below-the-canopy, resulting in mortality among sub-dominant and suppressed size classes.

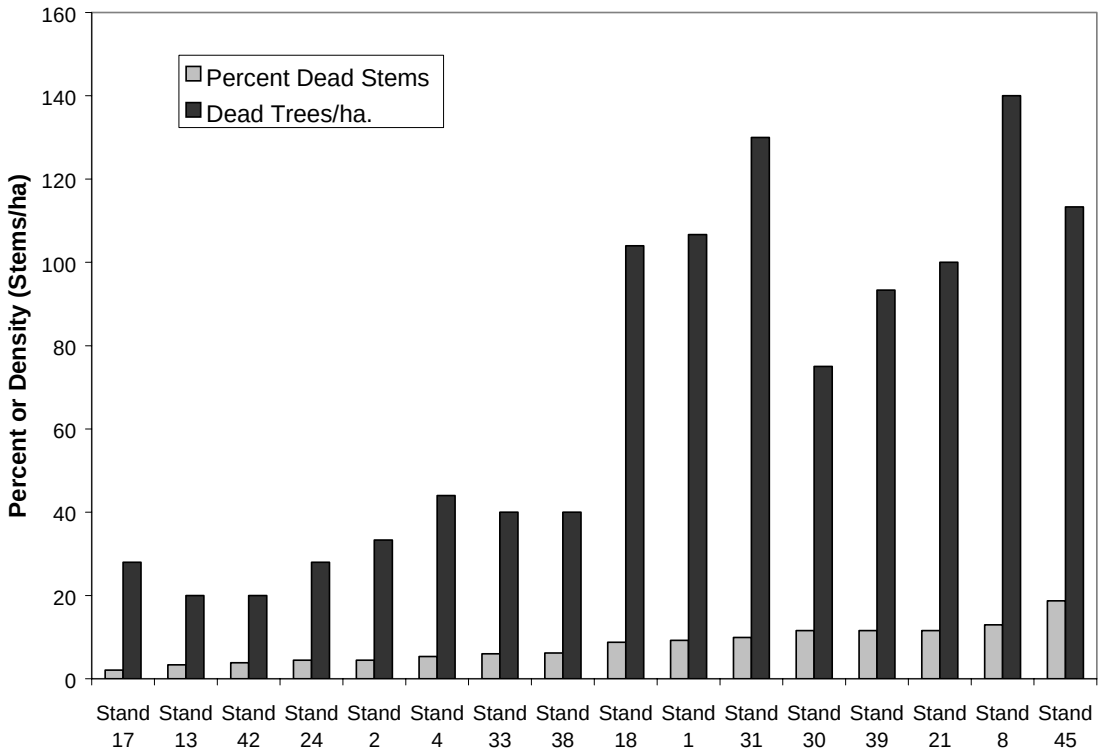


Figure 35. Reference stands ranked by dead tree densities and mortality as a percentage of total stems.

Table 10. Snag availability data: densities and basal area.

	Percent Dead Stems	Dead Trees/ha.	Dead Tree Basal Area	Percent Dead Basal Area
Stand 1	9.25	107	3.20	5.93
Stand 2	4.47	33	1.20	2.34
Stand 4	5.34	44	5.50	10.24
Stand 8	12.96	140	3.10	5.25
Stand 13	3.37	20	8.70	15.85
Stand 17	2.11	28	1.00	2.45
Stand 18	8.78	104	2.40	4.36
Stand 21	11.57	100	3.60	9.52
Stand 24	4.46	28	0.30	0.92
Stand 30	11.54	75	3.70	12.13
Stand 31	9.92	130	1.60	4.56
Stand 33	6.02	40	2.10	5.88
Stand 38	6.19	40	2.40	4.52
Stand 39	11.57	93	2.00	5.14
Stand 42	3.85	20	1.70	2.50
Stand 45	18.68	113	5.60	8.71

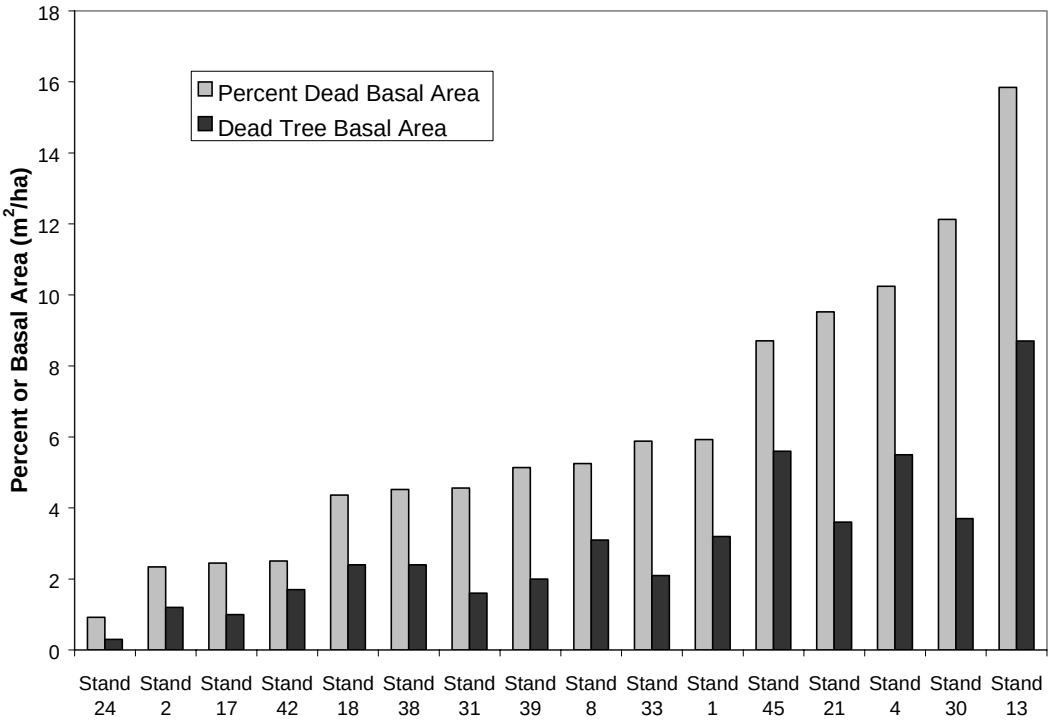


Figure 36. Reference stands ranked by dead tree basal area and mortality as a percentage of total basal area.

Wildlife habitat values provided by snags are directly related to decompositional status and the degree of stem integrity. The decay class system used here integrates all aspects of snag degradation over time (i.e. decomposition, breakage, etc.). As a snag decomposes, fragments, and physically degrades, the suite of associated species (vertebrates, invertebrates, vascular plants, non-vascular plants, lichens, fungi, and microorganisms) that might potentially use the snag changes accordingly (Hunter 1999). Thus, providing an abundance of snags spanning a range of decay classes maximizes snag-associated biodiversity in a managed forest. It is important, therefore, to monitor snag decay class distributions. These are provided for reference stands in Figure 37 and are normalized to percent of dead tree basal area. Normalized basal area distributions in this case facilitate stand comparisons and weight distributions towards snags of larger diameter, which captures the greater biodiversity value associated with larger snags.

The results show that MBR's forests provide snags encompassing a full range of decay stages. However, decay class distributions vary considerably among stands (Figure 37). Several stands provide primarily less decayed material resulting from recent mortality. Other distributions are weighed towards moderate or well decayed material, while several stands have fairly even distributions of snag among decay classes. We can conclude that MBR in aggregate is providing a full range of decay-class associated snag biodiversity values. However, these vary spatially across the Park, which will limit population sizes of territorial, snag-associated wildlife, such as most woodpecker species. In addition, the Park is providing few large snags (e.g. >50 cm dbh); most of the snags are concentrated in smaller diameter classes (see Figures 13 and 14). Only five reference stands (stand #'s 13, 18, 30, 33, and 45) have snags ≥ 50 cm dbh. Management approaches that (a) promote and retain large diameter snags well-distributed throughout the Park, and (b) allow snags to progress through the full range of decay stages, will help correct these limitations over time.

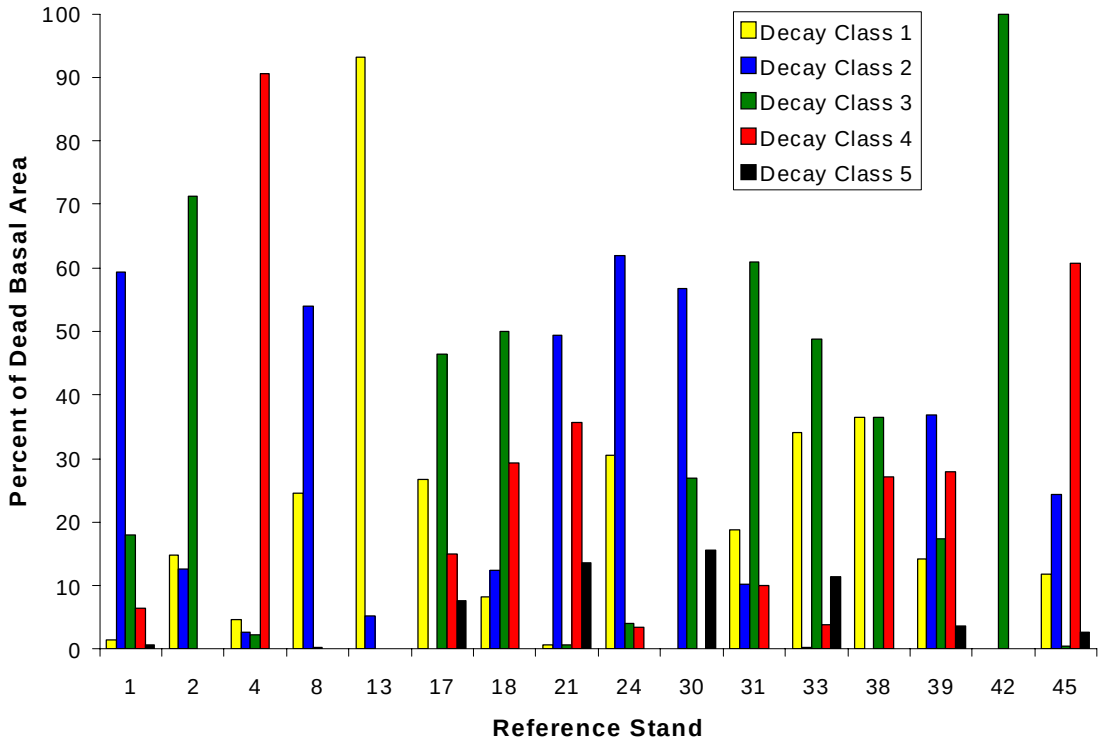


Figure 37. Snag basal area distributions (percent of total dead tree basal area) by decay class. Decay class 1 is least decomposed and decay class 5 is the most decomposed.

Understory plant assemblages

The diversity, abundance, and mix of understory plants serve as key indicators of ecosystem integrity. They respond to important stressors, such as off-site impacts from roads and trails, recreational use, acid deposition, exotic earthworms, and noxious invasive plants. The forest monitoring program, therefore, tracks several key understory metrics. They are percent cover, Shannon-Wiener Diversity Index, and species richness at the scale of individual plots.

The forest monitoring system spans a diversity of understory plant communities. A list of species currently found in the monitoring plots is provided as an Appendix (page 70). Data on the three metrics are provided in Table 11. Mean percent cover for all vascular and non-vascular understory plants ranges from 1.97 % (in a dense red pine plantation, stand #4) to 23.27 % (in a 110 year old northern hardwood-hemlock forest, stand #21). The second highest percent cover is in stand #30, an enriched northern hardwood site previously noted for its sensitive and unique (within the Park) botanical attributes (Lautzenheiser 2002; Wiggin 1993). Interestingly, while stand #30 has a high diversity index (2.18), the data suggest that it is second in this regard to stand #42. This may be an artifact of the non-statistical sample in stand #42 and the stand's narrow shape and adjacency to a clearing, which exposes most of the stand to edge effects. Species richness was highest in stand #30, but was almost as high in a thinned and rapidly developing 1911 white pine plantation (stand #2).

Statistical comparisons of stand groups based on management history indicated that there are strong correlations between low intensity silviculture and both percent cover and diversity index. Percent cover was significantly greater in thinned than in un-thinned plantations (P=0.02).

This disparity held true for managed compared to un-managed semi-natural stands as well (*P*=0.05). Interestingly, while there was a slight, though not statistically significant (*P*=0.18), difference between plantations and semi-natural stands, there was no difference between thinned plantations and semi-natural stands (*P*=0.41). Collectively, these results suggest that thinning in plantations has enhanced understory plant abundance and biomass (Figure 38).

Shannon-Wiener Diversity Index values showed similar relationships, with the index higher in thinned vs. un-thinned plantations (*P*=0.03). The index also differed in comparisons of managed to un-managed semi-natural stands and plantations to semi-natural stands, but these were only significant with $\alpha = 0.10$ (Figure 39).

Exotic plants represented only a small portion of the total percent cover sampled. Exotic species found in the monitoring plots included Japanese honeysuckle, tatarian honeysuckle, Japanese barberry, and common (or "European") buckthorn. However, in plots where these species occurred, their mean percent cover was < 1% per species. Their distribution appears to be limited and isolated based on plot data. They do not pose a significant threat to native plant communities in the Park at this time. Nevertheless, it will be important to monitor occurrences of exotic species to determine whether their populations expand in the future. This will be particularly important in light of stewardship activities and recreational uses that may or may not facilitate further spread of exotic species.

Table 11. Understory plant data by reference stand. Percent cover data are for all vascular and non-vascular understory plants, but do not include tree seedlings. Shannon-Wiener Diversity Index and Species Richness are for vascular understory plants only.

Reference Stand	**Percent Cover**		**Diversity Index**		**Species Richness at 0.1 ha**	
	Mean	Std. Error	Mean	Std. Error	Mean	Std. Error
1	2.24	0.92	1.23	0.35	6	3
2	22.35	4.18	1.36	0.26	18	5
4	1.97	0.64	1.14	0.15	5	1
8	5.06	2.22	1.78	0.33	16	5
13	3.08	1.74	0.56	0.30	3	2
17	12.58	2.05	1.43	0.15	11	2
18	15.79	2.52	1.20	0.23	13	3
21	23.27	11.83	1.72	0.36	15	5
24	4.85	2.11	1.23	0.12	8	1
30	22.53	3.65	2.18	0.14	19	4
31	5.28	1.50	1.67	0.21	12	3
33	5.98	2.66	0.82	0.27	9	1
38	17.61	2.94	1.53	0.13	6	4
39	16.69	6.11	1.34	0.24	9	2
42	5.64	na	2.25	na	13	na
45	10.13	6.02	1.74	0.16	12	2

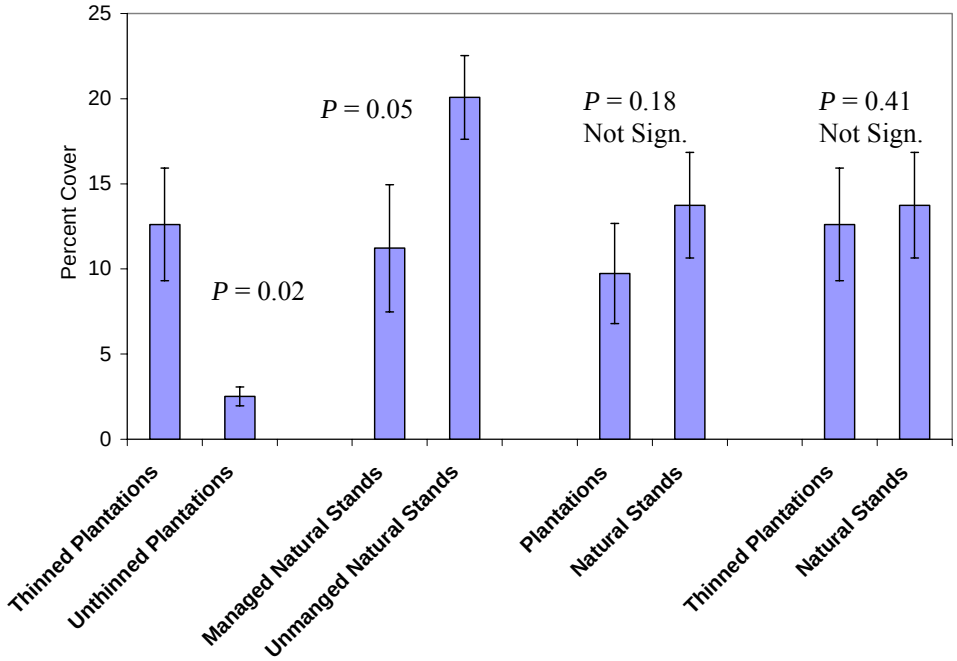
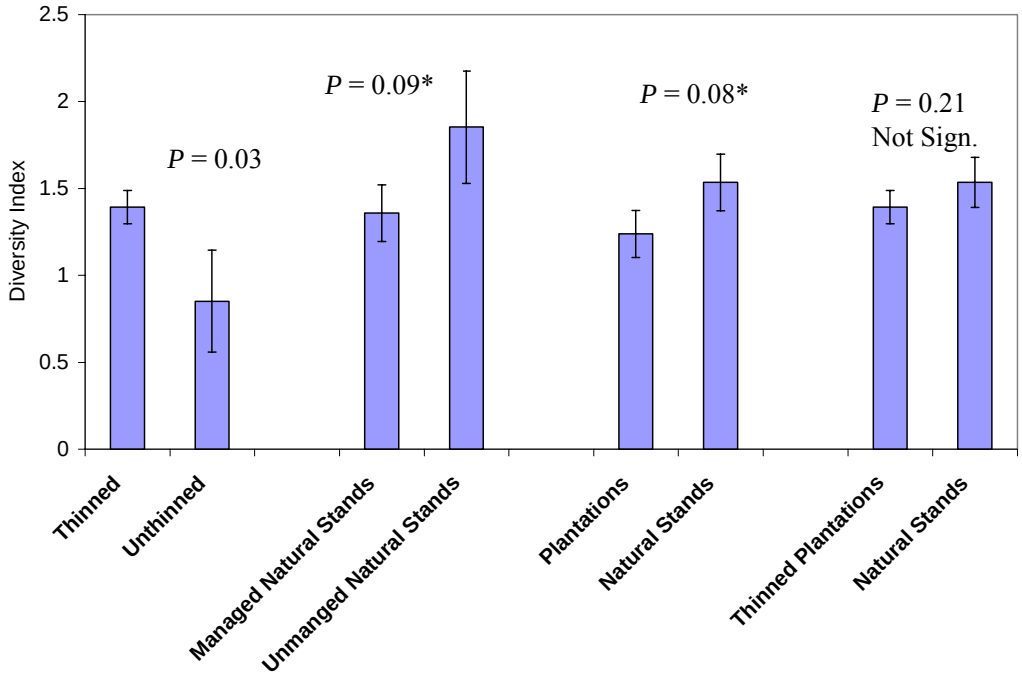


Figure 38. Mean percent cover for understory vascular (shrubs, herbs, and graminoids) and non-vascular (mosses and clubmosses) plants. Lichens and fungi, although sampled, were not included in this analysis. Errors bars show +/- one standard error of the mean. Statistical results are based on T-tests assuming unequal variance. Significance determined at the 95% probability level.



* Significant difference only at the 90% probability level.

Figure 39. Mean Shannon-Wiener Diversity Index, integrating species richness and relative abundance, for understory vascular plants (shrubs and herbs). Errors bars show +/- one standard error of the mean. Statistical results are based on T-tests assuming unequal variance.

Legacy trees: remnant old-growth and "wolf" trees

MBR is unique in Vermont in that it has a large concentration of remnant old-growth trees and old, open-grown "wolf" trees. The remnant old-growth trees pre-date 19th century forest clearing: many of them are 350-400 years based on cross-sectional dating. A well-distributed cohort of remnant old-growth hemlock, for example, date to ca. 1600. The Park also has many trees that established in open fields during the 19th century. These open-grown wolf trees are now embedded in secondary forests that developed around them on abandoned agricultural land. Scattered widely throughout the Park, remnant old-growth and wolf trees help tell the story of MBR's cultural and ecological history; they are a living testament to the land use changes that have occurred. When visitors come across these legacy trees they catch a glimpse of what the forests might have looked like before European settlement and better appreciate the history of agricultural use and subsequent ecosystem recovery.

As part of the monitoring program a study of legacy trees was conducted to help the National Park Service protect and manage this distinctive resource. I used a methodology independent of plot-based monitoring for this purpose. Eleven survey transects were placed systematically at 100 meter intervals and running west to east across the Park. A GPS survey, using a Trimble Pro XRS receiver with real time differential correction, was then conducted by navigating along transects. All live and dead legacy trees within 50 meters either side of transects were mapped in this way (Figure 40). Data on legacy tree species, size, health, condition (crown and bole), and interesting habitat features (e.g. cavities by size class and distribution along tree boles) were also recorded.

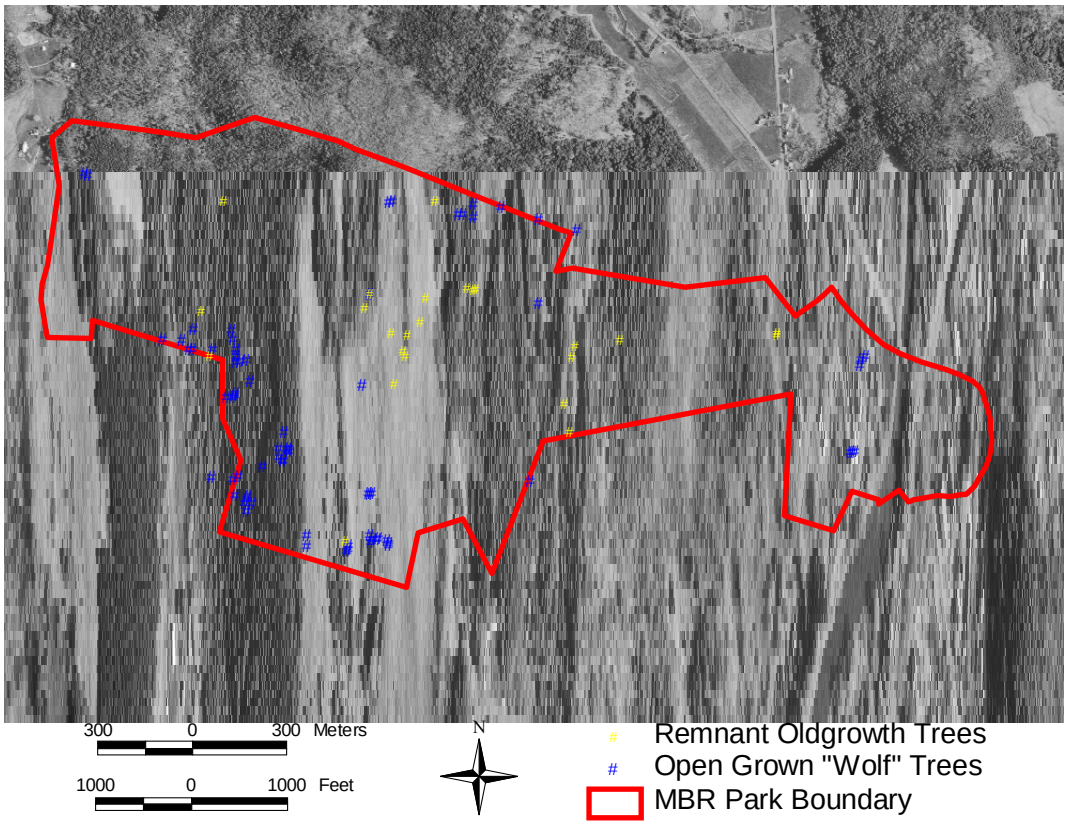


Figure 40. Position of remnant old-growth trees and open-grown wolf trees within (or immediately adjacent to) the MBR Park boundary. The data include three species of old-growth and four open-grown species.

Field data were post-processed through a second differential correction. This was performed in Trimble Pathfinder Office software using base station data downloaded from the National Geodetic Survey. Geo-referenced positions achieved horizontal precisions ranging from 0.1 to 1.0 meters, with the majority of trees positions accurate to < 50 cm. Data for continuous and discrete variables were converted to distributions for analysis. These were compared against published values for large tree densities in old-growth northern hardwood forests (McGee et al 1999) using *Z* tests (Zar 1996).

The survey located a total of 24 remnant old-growth trees and 70 wolf trees. Legacy trees biologically enrich MBR's forested ecosystems. This conclusion is based on several lines of reasoning. First, legacy trees include several different species of hardwoods and conifers (Figure 41). Old-growth trees were predominantly eastern hemlock and red oak, whereas wolf trees were primarily hardwoods, with the exception of a few open-grown white pines. Second, both old-growth and wolf trees increase the representation of large diameter trees in mature forests for which this structure is otherwise scare (with the notable exception of the oldest white pine and Norway spruce plantations). The average size of both open-grown and remnant old-growth trees at MBR is significantly ($P < 0.05$) larger than largest tree sizes reported for old-growth northern hardwood-hemlock forests in the northern forest region. Diameter distributions for remnant old-trees are weighted towards a size range encompassing trees two to three times larger in girth than the Park's dominant, mature conspecific trees (Figure 42). The remnant trees are often of great height (often > 40 meters for remnant hemlock), forming an emergent canopy layer above the dominant canopy of mature trees (generally between 25-35 meters in height for semi-natural stands). Wolf trees tend to be of comparatively enormous girth, although height tends to be no greater than dominant canopies due to the open-grown morphology (e.g. large spreading crown, multiple boles, squat appearance, etc.). Their diameter distributions extend well beyond the very largest trees sizes reported for natural hardwood forests in the Northeast (Figure 42).

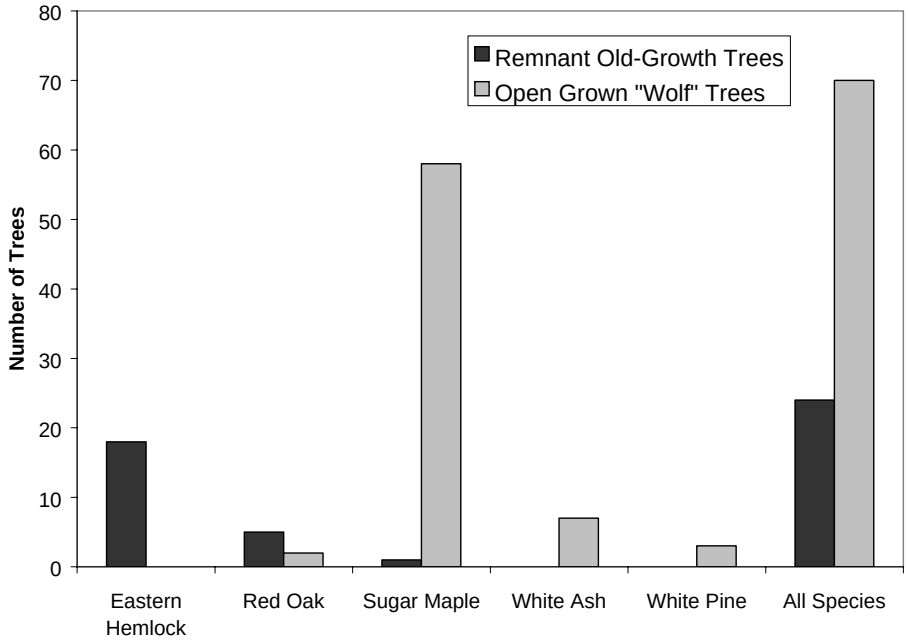


Figure 41. Legacy tree total, park-wide abundance by species.

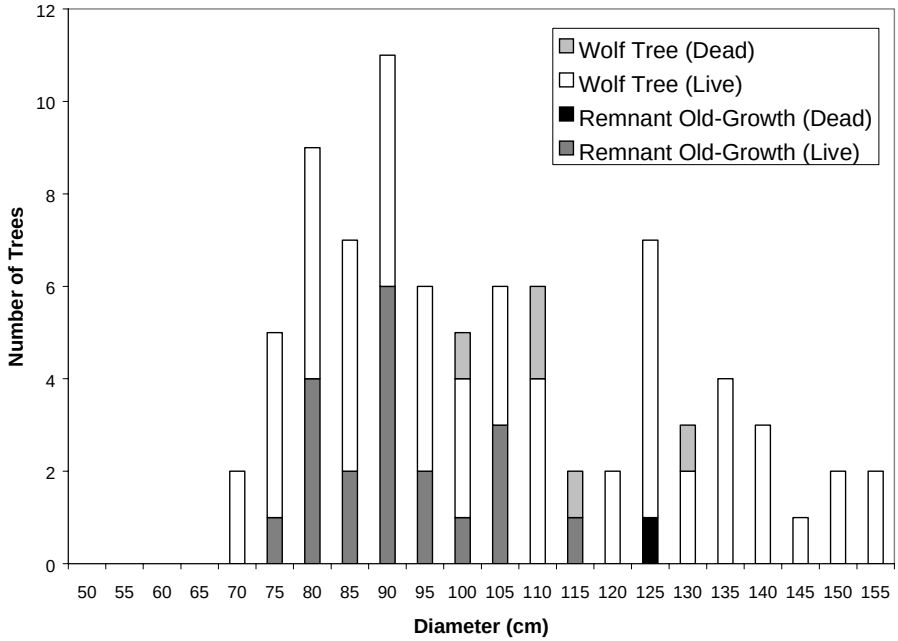
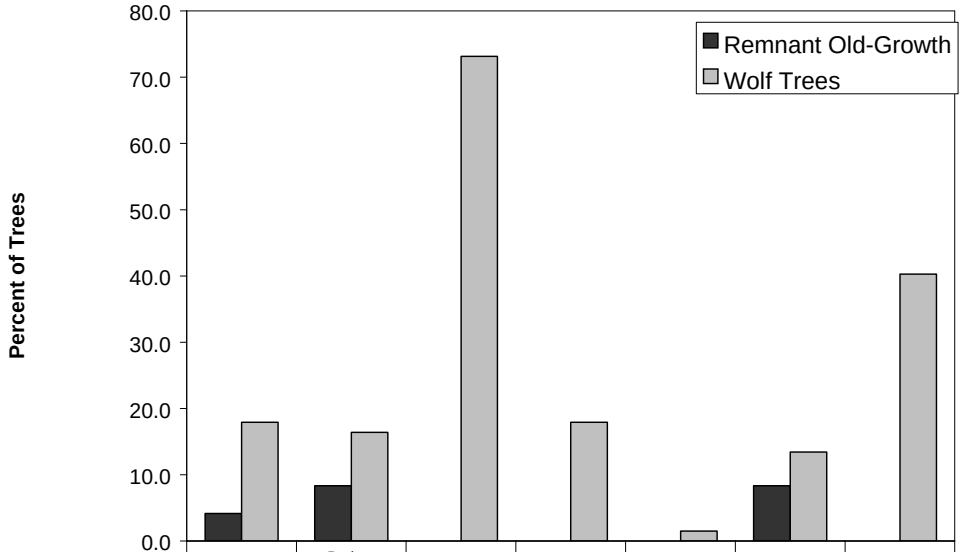


Figure 42. Park-wide diameter distributions for live and dead old-growth and open-grown wolf trees.

Another way in which legacy trees biologically enrich MBR is by dying and forming large snag structures (Figure 42). Large snags are ecologically important for a wide array of species (Hunter 1999). Large snags comprise a recruitment source for downed coarse woody debris of exceptional size. Based on field observations, these logs often have hollow boles formed over decades by heart rots affecting standing legacy trees. Large hollow logs provide denning sites for mesopredators. This structure would otherwise be in very low abundance within the Park based on our coarse woody debris data.



	> 20 % Crown Dieback	Broken Branches or Stem	Cankers	Wound	Dead Boles	Small Cavities	Large Cavities
Remnant Old-Growth	4.2	8.3	0.0	0.0	0.0	8.3	0.0
Wolf Trees	17.9	16.4	73.1	17.9	1.5	13.4	40.3

Figure 43. Crown dieback, bole condition, and habitat attributes of legacy trees.

Finally, living wolf trees provide an abundance of habitat attributes associated with decadence (but not necessarily decline) in older trees (Figure 43). They are abundant in cavities utilized by a host of species (Hunter 1999, DeGraaff and Yamasaki 2001, Lindenmayer and Franklin 2002). Over 40% of wolf trees have large cavities and 13.4% have small cavities. Despite this decadence (and an 18% wound rate), wolf trees show only moderate evidence of physiological decline or senescence. Only 18% of wolf trees have crown dieback in excess of 20%. Decline or senescence is even less evident in old-growth trees. Only 4.2% of remnant trees have crown dieback greater than 20%, none had open wounds or cankers, and only 8.3 % had broken branches or stems. Remnant old-growth trees appear to remain physiologically vigorous and healthy despite their age. This provides opportunities for continued retention, conservation, and stewardship of this ecologically and cultural significant resource.

Discussion and Conclusions

The forest monitoring program at MBR has been successfully initiated. Results are providing highly informative regarding forest ecosystem conditions and management efficacy. As data are collected, processed, and analyzed over subsequent years, broader time series will be constructed, allowing more robust assessment of trends, such as tree growth and forest productivity, and predictive modeling.

MBR's forests are highly diverse and provide multiple biological and ecological values based on the monitoring results. Mortality rates appear to be within acceptable ranges. However, regeneration declined precipitously during the monitoring period. Regeneration demonstrated a high degree of sensitivity to climate variability that may be of long-term concern to Park managers in light of climate change predictions. Growth and yield are positive for most stands. Growth increments are above average, especially considering climate conditions during the monitoring period. Stocking levels and other forest inventory metrics suggest considerable opportunity for continued demonstrations of sustainable, scientifically informed forest stewardship. However, deer browse is preferentially affecting certain species and may alter long-term successional dynamics.

Forest health is generally good except for moderate declines in ash and severe declines in butternut, mostly probably associated with known diseases (ash yellows and butternut canker). Stress related to the 2001-2002 drought may be a contributing factor to the light to moderate impairment of crown condition affecting some species. The most significant forest health problem facing the Park is a beech bark disease epidemic. This is causing severe decline and mortality in medium to large sized beech. Management approaches are warranted that retain and promote recolonization by disease-resistant beech.

Diameter distributions are distinctly multi- to uneven-aged in maturing semi-natural stands. Thus, these stands are appropriate for uneven-aged harvesting systems, including single-tree selection, group-selection, and recently developed approaches, such as structural complexity enhancement (Keeton 2005; Keeton et al. 2001). Coarse woody debris volumes appear to be in deficit and warrant management attention. The spatial distribution of large diameter snags for wildlife is also highly variable and could be improved through management efforts. Legacy trees (remnant old-growth and wolf trees) provide structures of exceptional biological value and should be managed accordingly.

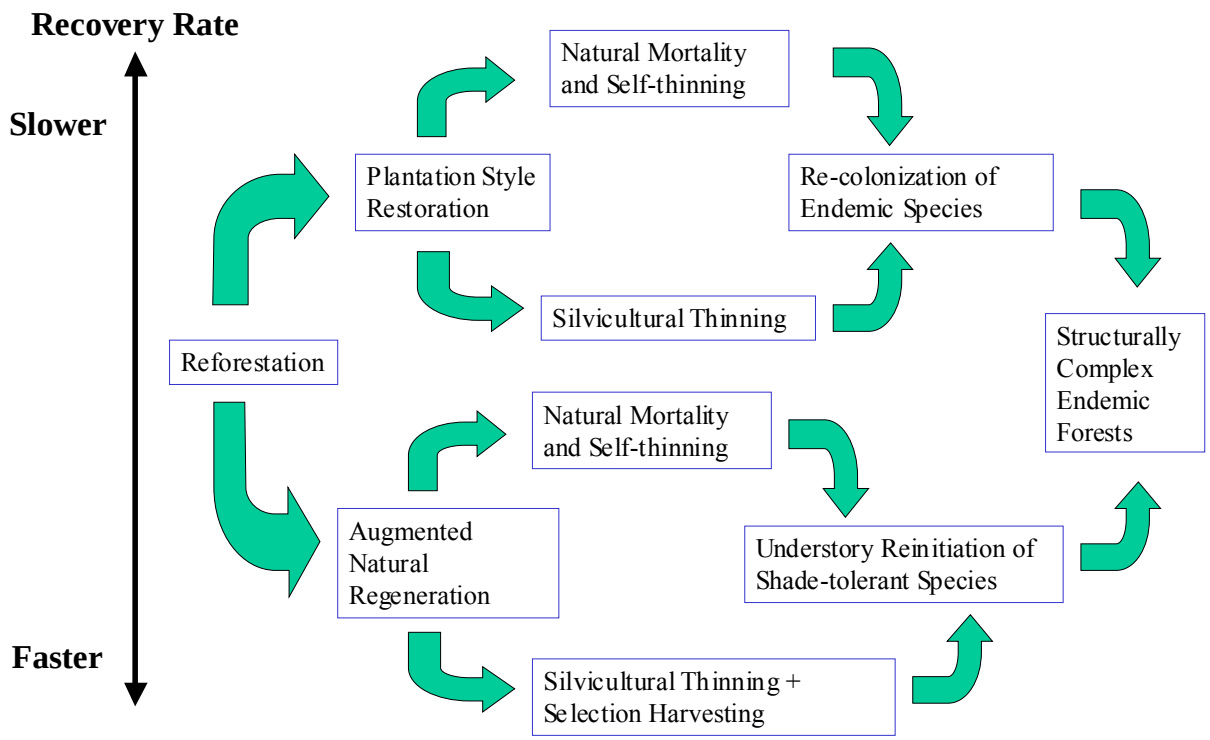


Figure 44. Conceptual stand development model for MBR. The model shows alternate pathways and rates of forest recovery as a function of initial reforestation approach and subsequent silvicultural management.

Overall, stand development processes – influencing myriad functions, such carbon sequestration, structural development and wildlife habitat, and understory plant communities – are robust throughout the Park. However, rates of stand development vary considerably by forest type and silvicultural history. A long history of low intensity forest management on Park lands has accelerated rates of structural development and compositional change. This is most dramatic in the case of plantation thinning, for which almost all monitoring metrics show a significant positive effect on stand development rates. Pathways of development, by contrast, are converging towards locally endemic plant assemblages and late-successional forest structure. This holds true regardless of initial restoration approach, such as conifer plantation versus augmented natural regeneration of mixed species (Figure 44). Figure 44 summarizes these findings in a conceptual model of long-term reforestation processes at MBR.

The monitoring results suggest that restorative silviculural treatments in plantations are highly likely to achieve management objectives where these call for restoration of native or site-endemic species. The results also show, however, that restorative treatments are not necessary in some of the older plantations under-going natural processes of stand development, including low intensity natural disturbances effects. These processes are rapidly moving some areas toward native species restoration.

Finally, it can be concluded from the monitoring results that maintenance of

existing plantation composition will be difficult where that continues to be a cultural, historic, or scenic management objective. Plantation maintenance will require careful planning and intensive management inventions, for example understory planting. An adaptive management approach will be essential to achieve this and other forest management and conservation objectives. Continued forest ecosystem monitoring will be an essential component of that approach.

Summary of Management and Monitoring Recommendations

Forest stewardship

- There are opportunities for many types of forest stewardship activities due to high stocking levels in most stands. Regeneration harvests should, in general focus on mature stands with the highest stocking levels and volumes. Intermediate treatments should focus on stands with lower merchantable volumes and higher densities of sub-merchantable trees.

- Where desired, an alternative that would perpetuate continued late-successional forest recovery (see figure 44) is to employ structure or disturbance based (Seymour et al. 2002) silvicultural approaches that promote and/or retain structural complexity, such as large diameter trees (live and dead) and downed woody debris (Singer and Lorimer 1997, O'Hara 1998, Keeton 2005).

- Un-manipulated control areas provide both conservation values and the potential for comparative research and monitoring over time. This helps to evaluate the effects of management activities and informs adaptive management accordingly. It is prudent, therefore, to retain a portion of each stand in an unmanaged condition for some period of time.

- Prohibit or restrict timber harvesting in sensitive and ecologically unique areas, including, but not limited to, Stand 30; steep, rocky portions of Stand 39; riparian areas (e.g. Stand 38), forested wetland areas within Stand 21 and east of the Pogue, and areas with high densities of legacy trees (in order to minimize windthrow risk).

Plantations

- Park managers have the opportunity to promote continued recolonization of, and successional development in, coniferous plantations through selection harvesting and thinning. This is appropriate where cultural/historical interpretation objectives do not otherwise require maintenance of the existing overstory species composition. It is recommended that monitoring be conducted to determine the long-term effectiveness of these approaches.

- A range of silvicultural techniques would be effective for plantation restoration, including high canopy thinnings and regeneration harvests. Regeneration harvests that retain residual plantation trees over multiple entries are recommended given the Park's mandate. These include techniques such as shelterwood with permanent reserves or variable retention forestry (Franklin et al. 1997), and selection systems (Nyland 1998) where plantations are now multi-aged.

- The monitoring data clearly show that maintenance of existing plantations would be very challenging. Such efforts will buck natural successional trends that are moving thinned plantations towards native or site-endemic species compositions. Where maintenance is desired, it will be necessary to employ aggressive silvicultural techniques in order to 1) regenerate overstory species and reduce

competition from endemic species. Thus, treatments need to both increase light availability and the distribution of exposed mineral soil. Underplanting with multiple, subsequent liberation thinnings may be necessary.

Forest health

- The monitoring results indicate that beech bark disease is the most serious near-term forest health concern facing the Park's forested resources. All large beech exhibiting disease resistance (e.g. clean, un-blistered bark) should be retained during forest stewardship activities.

- Park managers should remove dead or severely declining butternut trees to lower disease inoculum loads. As stated previously, trees should be removed if dead crown volume exceeds 30% and > 20% of the main stem is cankered. It is possible to retain trees with up to 50% crown dieback if there is little or no cankering.

- Monitoring is recommended to track the continued incidence and extent of ash yellows. Management should be adapted accordingly.

- Poor crown vigor in coniferous plantations may be due to a number of causative factors. In general, however, where retention of plantation trees is desired, managers should employ thinning techniques that increase growing space around relatively higher vigor crowns.

Deer browse

- Deer browse is having a dramatic effect on successional dynamics and species composition throughout the Park. These effects are especially severe in some of the plantations. It is recommended that Park managers develop a management strategy for reducing deer browse.

Recreation

- Recreational activities should be restricted in and around sensitive areas, including the herbaceously rich and unique Stand 30.

- Develop opportunities for visitor interpretation based on the Park's unique natural resources, such as forest stewardship demonstration areas, legacy trees, old plantations, and the diversity of successional conditions prevalent throughout the Park.

Biodiversity

- Promote continued vertical structural development in both semi-natural stands and plantations through the use of uneven-aged silvicultural systems that retain trees of all sizes, release advanced regeneration, and establish new cohorts.

- Volumes and densities of large downed logs are relatively low throughout the park. Management should identify opportunities for increasing these during forest stewardship activities, for instance by leaving slash and several boles per acre on the forest floor. It is highly recommended that debris chipping be curtailed or restricted in spatial extent.

- Increase the density and spatial availability of large (e.g. > 30 cm dbh) snags through 1) retention during harvesting; 2) girdling of selected diseased and or dying trees; and 3) conservative management of potential hazard trees along trails and roads.

- Exotic, invasive plants do not presently appear to be a major threat to the Park's biological diversity based on the monitoring data. Managers should continue to monitor for noxious species. It should be possible to control further spread in the Park by treating individual outbreak areas.

- Mangers should retain, wherever possible, open-grown wolf trees and remnant old-growth trees, including live, dead, and dying trees.

Climate change and other environmental stressors

- The monitoring data suggest that tree seedling survivorship in the Park is highly sensitive to climatic fluctuations, such as drought. This has significant implications for long-term successional dynamics and the Park's native biodiversity. Over the long-term it will be important to monitor species and ecosystem level responses to climatic variability and change as well as other stressors, such as acid deposition and exotic insects and pathogens. This will help inform adaptive responses to these threats.

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APPENDIX – Vascular Plant Species in Monitoring Plots

SCIENTIFIC NAME	COMMON NAME
Grasses	
Agrostis perennans	upland bentgrass
Bromus inermis	smooth brome grass
Cardamine pennsylvanica	common bitter cress
Deschampsia sp.	hairgrass
Glyceria sp.	manna grass
Poa sp.	bluegrass
Schizachne purpurascens	swallen grass
Sedges	
Carex debilis	weak sedge
Carex intumescens	swollen sedge
Carex pedunculata	pedunculed sedge
Carex platyphylla	broad-leaved sedge
Carex sp.	sedge species
Trees	
Acer negundo	box elder
Acer pennsylvanicum	striped maple
Acer rubrum	red maple
Acer saccharum	sugar maple
Acer spicatum	mountain maple
Betula populifolia	gray birch
Betula alleghaniensis	yellow birch
Betula lenta	black birch
Betula papyrifera	white birch
Carya cordiformis	Bitternut hickory
Fagus grandifolia	American beech
Fraxinus americana	white ash
Fraxinus pennsylvanica	green ash
Juglans cineria	butternut
Larix decidua	European larch
Ostrya virginiana	eastern hophornbeam
Picea abies	Norway spruce
Picea rubens	red spruce
Pinus resinosa	red pine
Pinus strobes	eastern white pine
Pinus sylvestris	Scots pine
Populus deltoides	eastern cottonwood
Populus grandidentata	bigtooth aspen
Populus tremuloides	quaking aspen
Prunus pensylvanica	pin cherry
Prunus serotina	black cherry
Quercus alba	white oak
Quercus rubra	northern red oak
Robinia pseudoacacia	black locust
Tilia americana	American basswood

Tsuga canadensis	eastern hemlock
Ulmus americana	American elm
Ulmus rubra	slippery elm

Woody Shrubs

Amelanchier laevis	allegheny service-berry
Berberis vulgaris	common barberry
Cornus alternifolia	alternate leaved dogwood
Cornus racemosa	gray dogwood
Cornus canadensis	bunchberry
Corylus cornuta	beaked hazelnut
Lonicera canadensis	american fly-honeysuckle
Lonicera japonica	japenese honeysuckle
Lonicera tatarica	tatarian honeysuckle
Prunus virginiana	chokecherry
Rhamnus cathartica	common buckthorn
Rhamnus frangula	glossy buckthorn
Rubus allegheniensis	common blackberry
Rubus odoratus	purple flowering raspberry
Rubus pubescens	dwarf raspberry
Rubus sp.	raspberry/blackberry species
Sambucus canadensis	elderberry
Vaccinium corybosum	highbush blueberry
Vaccinium myrtilloides	velvet-leaf blueberry
Viburnum acerifolum	maple-leaved viburnum
Viburnum alnifolium	hobblebush
Vitis riparia	river bank grape

Ferns and Allies

Adiantum pedatum	Maiden-hair fern
Athyrium filix-femina	lady fern
Dennstaedtia punctilobula	hay-scented fern
Deparia acrostichoides	silvery spleenwort
Dryopteris carthusiana	spinulose wood fern
Dryopteris filix-mas	male fern
Dryopteris intermedia	intermediate wood fern
Dryopteris marginalis	marginal wood fern
Equisetum sciroides	dwarf scouring rush
Equisetum sp.	horsetail species
Gymnocarpium dryopteris	oak fern
Matteuccia struthiopteris	ostrich Fern
Onoclea sensibilis	sensitive fern
Osmunda cinnamomea	cinnamon Fern
Osmunda claytoniana	interrupted fern
Osmunda regalis	royal fern
Phegopteris connectilis	long beech fern
Phegopteris hexagonoptera	broad beech fern
Polysticum acrostichoides	christmas fern
Pteridium aquilinum	bracken fern
Thelypteris noveboracensis	new york fern

Herbaceous Plants

Actaea pachypoda	white baneberry
Aquilegia canadensis	wild columbine
Aralia hispida	bristly sarsparilla
Aralia nudicaulis	wild sarsparilla
Arisaema atrorubens	jack-in-the-pulpit
Asarum canadense	wild ginger
Asclepias syriaca	common milkweed
Aster acuminatus	whorled aster
Aster sp.	aster species
Boehmeria cylindrica	false nettle
Caulophyllum thalictoides	blue cohosh
Circaea alpina	dwarf enchanter's nightshade
Clintonia borealis	yellow clintonia
Crepis capillaris	smooth hawksbeard
Dicentra candensis	squirrel corn
Eupatorium rugosum	white snakeroot
Fragaria vesca	wood strawberry
Fragaria virginiana	wild strawberry
Galium tinctorium	bedstraw
Galium triflorum	fragrant bedstraw
Geranium bicknellii	bicknell's cranesbill
Geranium robertianum	herb robert
Hepatica acutiloba	sharp-lobed hepatica
Hieracium aurantiacum	devil's paintbrush
Hieracium vulgatum	common hawkweed
Hypericum perforatum	common st. johnswort*
Impatiens capensis	jewel weed
Laportea canadensis	wood nettle
Maianthemum canadense	canada Mayflower
Mitchella repens	partridgeberry
Orchidaceaa unknown	unknown orchid
Oryzopsis asperifolia	white-fruited mountain rice
Osmorhiza claytonii	sweet cicely
Polygala paucifolia	fringed polygala
Polygonatum pubescens	hairy solomon's Seal
Potentilla simplex	common cinquefoil
Prenanthes alba	white lettuce
Pyrola asarifolia	pink pyrola
Pyrola elliptica	shinleaf
Pyrola secunda	one-sided pyrola
Rananculus fuscicularis	early buttercup
Ranunculus repens	creeping buttercup
Saxifraga virginiensis	early saxifrage
Solidago flexicaulis	broad-leaved goldenrod
Solidago sp.	goldenrod species
Streptopus amplexifolius	twisted stalk
Streptopus roseus	rosy twisted stalk
Taraxacum officinale	common dandelion
Tiarella cordifolia	heart-leaf foamflower
Trientalis borealis	starflower
Trillium erectum	red trillium
Trillium sp.	trillium species
Uvularia sessilifolia	sessile-leaved bellwort
Veronica officinalis	common speedwell
Viola sp.	violet species