VEGETATION DYNAMICS AND TREE RADIAL GROWTH RESPONSE IN HARVEST GAPS, NATURAL GAPS, AND CLOSED CANOPY CONDITIONS IN MAINE'S ACADIAN FOREST

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An Abstract of the Thesis Presented
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The creation of natural canopy gaps is an important ecological process in the Acadian forest. Designing harvest gaps that emulate natural gap dynamics may be important for maintaining structural and biological diversity, as well as naturally regenerating desired tree species. We used a controlled study to 1) compare vegetation dynamics among and within harvested gaps, natural gaps, and under a closed canopy, and 2) examine the growth response of mature overstory edge trees of harvests gap and saplings inside of gaps as possible methods for dating natural gaps in the Acadian forest.

For the vegetation dynamics study (objective 1), we compared plant abundance, diversity, and composition in 45 harvested gaps (four growing seasons after harvest), 23 natural gaps, and 23 closed canopy transects. The percent cover of each species was measured in 4 m^2 plots located every 2 m along a north/south transect across each gap. Total plant cover was greatest in harvested gaps ($p < 0.001$) and was highest in the center of the larger harvested gaps (672 – 2,106 m^2) ($p < 0.003$). *Abies balsamea* was the most abundant species in all conditions. Diversity (i.e., number of species per sample area)

was greatest in harvested gaps and least under the closed canopy ($p<0.001$). Species evenness (measured as the slope of dominance diversity curves) indicated that harvested gaps had greater evenness than natural gaps and closed canopy conditions. One hundred twelve of the 195 plant species identified occurred only in harvested gaps, and a detrended correspondence analysis indicated that plant composition in harvest gaps was different from natural gap and closed canopy plant composition.

Tree regeneration was abundant under all conditions but was not correlated to gap origin ($p = 0.15$) or location within the gap. Seedlings (< 0.5 m tall) were the most abundant form of regeneration, and saplings (0.5 – 2.0 m tall) were most abundant in harvested gaps. *A. balsamea* was the most abundant tree species regenerating in natural gaps and closed canopy conditions, while *Acer rubrum* was most abundant in harvested gaps.

In the gap dating study (objective 2), we examined the growth response of *Tsuga canadensis*, *Acer rubrum*, and *Betula papyrifera* at the edge of 20 harvested gaps as well as *A. balsamea* and *T. canadensis* saplings at the center of the harvested gaps and 23 natural gaps. Radial growth increment after harvest and percent growth response were assessed as release criteria in edge trees and saplings seven years before and after harvest. For edge trees, a 50% growth response provided the best release criterion for dating gaps. Gap size ($\chi^2 = 7.560$, $p<0.006$) and the interaction of gap size and species ($\chi^2 = 4.39$, $p<0.036$) were the best variables predicting release using this criterion. For saplings, a 200% growth response provided the best release criterion for dating harvested gaps. Gap size also was correlated with sapling growth response ($\chi^2 = 8.187$, $p< 0.004$). Using a

200% sapling growth response as a criterion underestimated the formation date of natural gaps. A 100% or more growth response provided the best results for dating natural gaps.

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LITERATURE REVIEW

1.1. Ecological Forestry and Biodiversity

The concept of ecological forestry, which prescribes a harvesting design that incorporates both timber and non-timber values, has been proposed for the management of Maine's managed forests (Seymour and Hunter1999; Seymour and Day 1997; Seymour et al. 2002). Ecological forestry involves harvesting according to the common natural disturbance regime within the spatial and temporal limits of Maine's natural forest structure. The goals of this management practice are to maintain the legacy of Maine's forests, defined as the presettlement forest structure, to maintain the presettlement forest composition, and to enhance the biological diversity within the forest landscape. These goals of ecological forestry are currently thought to be achieved by creating a range of gap sizes up to 0.2 ha (as would be witnessed after a natural disturbance) within the managed forest leaving large residual trees (both live and dead) throughout the harvesting rotations (Seymour et al. 2002; Seymour and Hunter 1992). These gaps and residual trees are proposed to achieve a presettlement structural diversity by creating an array of tree ages and sizes as witnessed in natural forests as opposed to simplified single cohort plantation forests in the industrial forest (Roberts and Gilliam 1995; Seymour and Hunter 1992). This landscape structural diversity in the Northeast promotes the most suitable habitat for plants and wildlife where many types of organisms occupy the full sere of young and old forest structures (Hansen et al. 1991). Furthermore, this forest management design will ensure the regeneration of commercially valuable, late succession species, since these species initially established under the natural disturbance conditions in the Acadian forest (Seymour and Hunter 1999).

The concepts of ecological forestry are based on two hypotheses: 1) disturbance is a natural process in forest ecosystems, and 2) the resulting canopy gaps create a diverse forest stand structure that fosters not only wildlife habitat and diversity, but also plant species diversity across a forested landscape. If canopy gaps are utilized in forest management, the forester needs to emulate the complex interactions of several ecological elements present in natural gaps. These ecological elements included not only a missing canopy, but also the presence of downed woody material, standing snags, and undergrowth vegetation including established trees, shrubs, and herbs (Lundquist and Beatty 2002). The following sections review the dynamics governing these hypotheses in northern forest ecosystems. We examine the natural disturbance regime of the Acadian forest and how this process may influence stand regeneration and species diversity within gaps and across landscapes.

1.2. Disturbances and the Acadian Forest Structure

Disturbance is a common occurrence in forest ecosystems, and often has crucial implications in the development of stand structure, wildlife habitat, and species diversity. Disturbances are often defined as events that provide available growing space for regeneration within a forest landscape (Runkle 1985; Oliver and Larson 1996). They can be classified as either stand-replacing disturbances that remove all the overstory and existing trees in a landscape, or minor disturbances that impact a stand to varying degrees leaving resistant trees within the disturbed area (Oliver and Larson 1996). Anthropogenic disturbances including forest harvesting and land clearing for development often occur more frequently than natural disturbances. Both anthropogenic and natural disturbances have important implications for forest management and long-term productivity of forest resources.

1.2.1 *Disturbance Frequency*

Stand-replacing disturbances in the Acadian forest do occur but with long recurrence rates. For example, analysis of the presettlement forests of Maine indicate three large-scale fires in the early 1800s, but the estimated return interval of such events was 1000 years (Lorimer 1977). Other stand-replacing disturbances in this region include catastrophic wind storms, like hurricanes or northeasters, but the return interval for such fire and wind disturbances occur between 806 - 14,300 years (Seymour et al. 2002). More common are minor disturbances creating canopy gaps in northern forests with a frequency of 1% per year (Runkle 1982). Tree mortality, windthrow, ice storms, cyclic disease and insect infestation like the spruce-bud worm, and partial harvesting comprise the frequent disturbance regime in the Acadian forest (Oliver and Larson 1996). These disturbances have various effects on stands, and they may predetermine a secondary disturbance event within the canopy structure (Lieberman et al. 1989). However, Frelich and Lorimer (1991) argue a continuum of disturbance in a forest landscape rather than differentiating between stand replacing or multiple disturbances since both largely determine the stand structure over a landscape. Consequently, frequency of disturbance can be viewed in terms of canopy turnover, or the rate in which a canopy is replaced by a new stand.

Defining the natural rotation of forest canopies, or canopy turnover, in relation to disturbance regimes is useful when prescribing ecological forest management for long-term productivity. In a mixed hardwood-conifer old-growth forest in Maine, broad-scale minor disturbances occurred every 60-70 years, but when a few minor disturbances, such as single-treefall gaps are included in the disturbance history, the disturbance frequency changes to every 30-40 years (Chokkalingam 1998). A study of the disturbance regimes in a hemlock-hardwood forest of the Great Lakes region determined canopy turnover of 69 years for disturbances that removed ≥10% of the canopy and 1920 years recurrence for ≥60% canopy removal (Frelich and Lorimer 1991). Disturbance frequency seems to differ with different forest types, but understanding this frequency is important. For example, if disturbance rates were too high, the tree life form would not be viable where the stand is replaced only by shrubs and herbs (Runkle 1985). Therefore, disturbances are important for the development of vertical and horizontal stand structure in the forest landscape.

1.2.2. Stand Structure After Disturbance

Minor and stand-replacing disturbances in northeastern forests determine stand regeneration. Both minor and stand-replacing disturbances have created a multiple cohort stand structure in non-plantation Acadian forests. A multiple cohort stand refers to component trees that arise after multiple disturbances including many age classes of one year to several decades (Oliver and Larson 1996). A minor disturbance may only replace one or two canopy trees within a canopy gap causing many age classes across a stand (Hibbs 1982). Stand-replacing disturbances initially do not create multiple cohort stands, but ultimately the regenerating stand becomes a multiple cohort structure since the low frequency of such an event far exceeds tree mortality, and tree falls occur continuously. The Acadian forest structure contains at least four canopy strata, each of which may contain four different tree crown classes. Canopy emergents (A stratum), the continuous canopy (B stratum), a non-continuous canopy underlying the continuous canopy (C stratum), and the forest floor (D stratum) comprise a multiple cohort forest structure. For example, in a northern hardwood forest, 10 different age classes were present in the forest structure, and 60% of the canopy trees were the result of tree fall gaps (Frelich and Lorimer 1991). Understanding these strata is important in predicting stand development as well as protecting the biological integrity of the forest. Since single cohort stand structures have no ecological significance in natural forests, managing forests for multiple cohorts sustains the biological integrity as well as the historical structural diversity of the Acadian forest.

1.2.3. *Stand Susceptibility*

Characteristics of a forest ecosystem, including stand age and stand composition will predetermine the magnitude of impact by disturbance events. Young even-aged stands that are not ecologically well adapted are often susceptible to disturbance (Seymour and Hunter 1999) as well as old-growth stands with very old trees approaching natural mortality. For example, a study on gap formation in a northern forest showed 40-year-old stands had a greater gap formation rate and larger mean gap size than old-growth hemlock forests, mature hardwood, and mature hemlock forests because of the infestation of Dutch Elm Disease (Dahir and Lorimer 1996). Old growth forests, containing very large trees, are also susceptible. Large trees tend to have proportionally greater aboveground biomass than the root system can support and massive crowns rendering them more susceptible to windthrow (Runkle 1985). The result is more frequent tree falls and larger gap areas (Dahir and Lorimer 1996).

Particular species of trees are more susceptible to disturbance and will be more frequent gap makers. A study in the Allegheny northern hardwood forests found that American beech (*Fagus grandifolia* Ehrh.), which is susceptible to beech bark disease, represented more than half of all the gap makers in the study. Red maple (*Acer rubrum* L.) was the most important uprooting gap maker (Krasny and Whitmore 1992). The species and frequency of gap makers may characterize the type of disturbance especially when a particular species is directly related to elevation. For example, in a New Hampshire spruce-fir forest, balsam fir (*Abies balsamea* (L.) P. Mill.), which is susceptible to root and butt rot, was one of the most important gap makers at lower elevations whereas, yellow birch was the most important gap maker at 885 m at the upper limit of its elevation distribution where windthrow and stem decay were the causes of mortality (Worrall and Harrington 1988).

1.3. Patterns of Natural Gap Regeneration

There are two common types of natural gaps in forest environments. A treefall gap is one where a tree has fallen or uprooted; a snag gap is one where the stem has broke or significant branch loss has occurred (Runkle 1992). The significance of the two gaps is the amount of soil disturbance. A treefall gap will create exposed mineral soil, whereas a snag gap will disturb the soil minimally if at all. The amount of exposed mineral soil often accounts for the patterns of succession following a gap event.

1.3.1. *Stand Regeneration*

In both old-growth forests and second growth forests, the most dominant trend for tree succession is the release of advance regeneration within the gap that develops into the future canopy (Mladenoff 1990; Dahir and Lorimer 1996; Clinton et al. 1994;

Kimball et al. 1995). In many eastern forests, gap events are the only means by which advance regeneration saplings are able to attain canopy status. For example, in a spruce-fir forest of New Hampshire, spruce and fir grew 2-3 times faster in gaps than under closed canopy (Battles and Fahey 2000). In an oak-pine forest of Maine, advance regeneration was the most dominant vegetation in tree fall gaps (Schumann et al. 2003). The stand composition surrounding the gap is often correlated to the sapling species or advance regeneration composition in the understory. Hence, the surrounding canopy often determines the future composition of the gap canopy. Furthermore, the differential growth of individual species in advance regeneration may determine which species attain canopy status in the future gap stand development (Runkle 1981; Canham 1988a). In a study of gaps in a spruce-fir forest, *Betula alleghaniensis* Britt. , *Betula papyrifera* Marsh., and *Abies balsamea* (L.) P. Mill. had the greatest growth in gap environments in comparison to spruce growth rates in gaps (Battles and Fahey 2000). In a northern hemlock-hardwood forest, *Betula nigra* L. in gaps had the greatest height growth after disturbance followed by *Acer rubrum* L., *B. alleghaniensis*, *Tsuga canadensis* (L.) Carr. and *Quercus rubra* L. (Hibbs 1982).

When advance regeneration is minimal or absent, natural gap tree succession allows shade tolerant or intermediate tolerant species to colonize and succeed into the canopy in some forests. In older forests, the death of individual trees is the only means that allow shade tolerant species to perpetuate themselves through the process of gap phase development (Pickett and White 1985). For example, in a mature oak forest with gaps created by gypsy moth infestation tree succession in all the gaps tended to recruit species with greater shade tolerance. *A. rubrum*, an intermediate shade tolerant species, was the most important tree in large gaps; *Fagus grandifolia* Ehrh., a shade tolerant species, was most important in small gaps 7 years after the gypsy moth disturbance, and the greatest density of *Fraxinus* seedlings occurred in gap environments (Ehrenfeld 1980). In an eastern old-growth forest, *Acer saccharum* Marsh. and *Ostrya virginiana* (P. Mill.) K. Koch, both shade tolerant species, were the only seedlings regenerating in significant numbers in gaps (Mladenoff 1990).

Some gaps will recruit specialists, but this dynamic is highly dependent on gap size. In a spruce-fir forest of New Hampshire, *B. papyrifera*, *Acer spicatum* Lam., and *Fraxinus americana* L. were only present in gaps in the forest landscape (Battles and Fahey 2000). In a study of gaps in a northern hardwood forest, *B. alleghaniensis*, *Fraxinus pennsylvanica* Marsh., and *Tilia americana* L. were classified as gap-phase species because their colonization and survival success were limited to gap areas (Dahir and Lorimer 1996). However, according to several studies, trees require an area >10-50 m^2 for tree recruitment in the gap before lateral extension closes the canopy (Kimball et al. 1995, Runkle 1982, Mladenoff 1990). A study of gaps in a hemlock-hardwood forest suggests that few or no new tree seedlings reached the canopy level in gaps with a radius <5 m (i.e. area approximately 78.5 m^2); the study further suggests that gaps with a 5 m radius surrounded by *Q. rubra* will fully close in 19 years if maximum lateral growth rates occur (Hibbs 1982).

Finally, as mentioned previously, the means by which the gap was created, by either tree fall or stem break, may influence the species composition of tree succession. In a spruce-fir forest of New Hampshire, tree fall gaps with significant exposed mineral soil limited tree succession to paper birch (Battles and Fahey 2000). The amount of woody material that decays after a gap event also has a significant impact on tree succession. In a spruce-fir forest of New Hampshire, decaying wood was the most preferred substrate for seedlings of all species in gaps (Battles and Fahey 2000).

1.3.2. *Herb and Shrub Recruitment*

Few studies mention a significant increase in herb diversity with the occurrence of natural gaps. In a mature beech-maple forest, herb species richness was largely unaffected by gap dynamics, but total herb cover increased with gap formation (Moore and Vankat 1986). In snag gaps of a mature oak forest, there was no significant difference in species richness among the gaps sizes that ranged from a single-canopy-tree snag gap to a 5-canopy tree snag gap (Ehrenfeld 1980). Furthermore, in an old-growth northern hardwood forest, a lack of annual opportunistic herbs, which contribute greatly to natural gap diversity, was noted in the smaller gaps; however, this response may be due to the lack of soil disturbance that opportunistic species favor (Mladenoff 1990). Finally, any increase in herb diversity in natural gaps is mostly a result of seed dispersal by vertebrates of fleshy-fruited seeds (Thompson 1980).

These studies mentioned illustrate the most significant trend in herb succession for natural gaps: an increase in abundance in early succession and then a gradual decline. For example, treefall gaps in a hemlock forest demonstrate a definitive trend in succession for the most common understory species. *Mitchella repens* and *Viola blanda* reached peak cover during first 2 years, *Medeola virginiana* and *Dryopteris spinualosa* reached peak cover during 2nd and 3rd years, and *Tiaraella cordifolia*, *D. noveboracensis*, and *Rubus allegheniensis* reached peak cover during 4th and 5th years of succession. Total understory cover returned to pre-gap levels 11-14 years following gap formation

(Rankin and Tramer 2002). A study of previous natural gaps (i.e., mean age 47 years old with a closed canopy) in a hemlock forest demonstrate a higher total percent cover of understory herbs and shrubs in the previous natural gap then under the closed canopy (Rankin and Tramer 2002). Increase in herb abundance in natural gaps may also be dependent on gap size. In a mature oak forest, herbaceous communities in snag gaps increased in abundance only if the gap opening was greater than the predisturbance understory assemblage (Ehrenfeld 1980).

Some shrub species demonstrate a positive response to natural gap formation in colonization and abundance. For example, in a Maine oak-pine forest, *Vaccinium* spp. and *Kalmia angustifolia* dominated the species composition in treefall gaps (Kimball et al. 1995). *Viburnum lantinoides* was also an abundant shrub in gaps in a spruce-fir forest although its abundance declined with canopy closure (Battles and Fahey 2000). In an old-growth northern hardwood forest, *Sambucus* spp., a gap colonizer, was very abundant in treefall gaps with disturbed soil although this species was not very abundant throughout the forest study area (Mladenoff 1990). However, natural gaps in a spruce-fir forest of New Hampshire indicate that gap specialist shrubs like *Rubus* spp. and *Sambucus* spp. were rare in natural gaps (Battles and Fahey 2000). In a northern hardwood forest, *Rubus* spp. was present in the seed bank but failed to germinate after the occurrence of a natural gap (Mladenoff 1990).

1.4. Patterns of Harvest Gap Regeneration

Little research has been performed on the succession of harvested gaps in eastern forests. Some studies on silviculture based on natural disturbance processes have predicted harvested gap regeneration, but these predictions are often based on natural gap tree succession (Seymour and Hunter 1992.). However, the following section will discuss the dynamics of harvested gap succession based on available studies.

1.4.1. *Stand Regeneration*

The greatest influences on tree succession for harvested gaps are the size of the gap, the level of soil disturbance, and the method of tree regeneration. According to the few studies available, the most significant trend in tree succession within harvested gap is the regeneration of shade intolerant trees. Regeneration of shade intolerant tree species is likely a combination of all the factors mentioned above. For example, a study of harvested gaps in an oak-pine forest of Maine, the investigators suggests that logging produced significantly greater soil disturbance than natural gaps and encouraged the establishment of more ruderal species than natural gaps. This trend was especially true for larger gaps. This data was collected 5 years after harvest (Kimball et al. 1995). A study on harvested gaps in the Southern Appalachians concurs with this same process. When advance regeneration was not present in the harvested gaps, shade intolerant species were the most dominant form of regeneration in large gaps the first and second growing season after harvest (i.e., 2.0 ha). Furthermore, stump and root sprouts were the major mechanism of tree regeneration in all gap sizes. However, shade tolerant species were present in the harvested gap regeneration; they were either more abundant in small gaps (i.e., 0.016 ha – 0.4 ha) or distributed evenly throughout all gaps (Philips and Shure 1990). The regeneration of intolerants is not always undesirable. In the same oak-pine forest of Maine, 10 years after harvest, harvested gaps effectively increased the white pine component in the forest. *Q. rubra* also regenerated well in the harvested gaps but was equally abundant in gaps and closed canopy (Schumann et al. 2003).

Schumann et al. (2003) suggests that this process of harvested gap succession where shade intolerants dominate is fairly short-lived. In the same oak-pine forest of Maine, 10 years after harvest, harvest gaps did not create patches that were vastly different from the forest in which they were embedded. *B. papyrifera* and *Hamamelis virginiana* both shade intolerant species, were more abundant in harvested gaps than under closed canopy, but their abundance decreased 10 years after harvest. A study by Philips and Shure (1990) in the Southern Appalachians also agrees with this conclusion. The investigators suggest that harvested gap succession involves the opportunistic growth of sprouts or seedlings of primary tree (i.e. dominant species in the surrounding forest overstory) species until canopy status is achieved. Then the gradual dieback of sprouts of pioneer species occurs and creates localized gaps that allow canopy accession of shade tolerant species. Gap size greatly influences this process where lateral growth of canopy trees may prevent the pioneer species from dominating the gap at any particular time.

The studies on harvested gaps in this review have not extended past 10 years after harvest. Most are performed a few growing seasons after harvest. Therefore, definitive long-term patterns of vegetation succession in harvest gaps have not yet been documented. A better understanding is important in determining the success of gap-based silviculture.

Most studies agree that harvested gaps promote diversity, abundance, and growth of plant species within a forested environment. This process is beneficial for advance regeneration present in the gap. In the oak-pine forest of Maine, species diversity was greater in harvested gaps than closed canopy for both 5 and 10 years after harvest (Schumann et al. 2003). In the Southern Appalachians, increase in biomass production was directly correlated with gap size and growing season after harvest. In the second growing season after harvest, there was two-fold more productivity for all vegetation in harvested gaps compared to preharvest conditions (Philips and Shure 1990). In a temperate conifer forest, planted seedlings rapidly increased diameter growth in gaps with an area of 10-2000 m^2. There was little improvement in average diameter growth rates after this gap size up to 5000 m^2 (Coates 1999).

1.4.2. *Herb and Shrub Recruitment*

The most significant trends in herb succession following gap harvesting include an increase in vegetation diversity and abundance, loss of some herb species, and a correlation with gap size and consequential microenvironment changes with herb composition in succession (Schumann et al. 2003). Patterns vary with forest type and level of soil disturbance. Regardless, herbs respond positively to the harvested gap with an increase in species diversity and abundance during early succession. The increase in richness is mostly attributed to the recruitment of opportunistic species such as asters and goldenrods. For example, in experimental canopy gaps of the Allegheny forest of Pennsylvania, *Aster acuminatus* was present after the gaps were harvested but not before (Collins and Pickett 1998a). In a Maine oak-pine forest, two species, *Lysimachia quadrifolia* and *Solidago rugosa*, were only present in harvested gaps, and *Anemone quinquefolia* increased in abundance in harvested gaps and decreased in abundance in control areas over time. Furthermore, 5 species of ferns and fern allies were more abundant in harvest gaps both 5 and 10 years after harvest (Schumann 1999). In the Allegheny forest, after canopy removal creating large gaps, *Lycopodium lucidulum*, *Uvularia* spp. and *M. repens* had the greatest increase in abundance (Collins and Pickett

1998b). In the oak-pine forest, common understory forest herbs, including *Maianthemum canadense*, *Gaultheria procumbens*, and *Mitchella repens,* present before the harvest significantly decreased in abundance after gap creation, but increased in abundance in control areas (Schumann 1999).

Species diversity and abundance often decline with age of the harvest gaps. The decline is mostly attributed to extensive lateral growth by canopy edge trees reducing available sunlight, and extensive tree regeneration within the harvested gap out-competing the opportunistic herbs (Philips and Shure 1990). In harvested gaps of the Allegheny forest, the number of herbs per plot increased over the study area up to three years after harvest, but after 3 years, no significant difference was found in the number of herbs between gaps and control areas (Collins and Pickett 1998b). The two gap specialists in a Maine oak-pine forest mentioned previously significantly declined in abundance 10 years after harvest (Schumann 1999). However, species diversity and abundance still increase in early succession. In a southern Appalachian forest, species richness was greater the second year after harvest than the first year and the most significant net primary productivity (NPP) was attributed to the increase in herb species during this time (Philips and Shure 1990).

Opportunistic species are often recruited in harvest gaps. This process is the most prominent for increasing herbaceous plant diversity in harvested gaps. However, some studies suggest that the predisturbance communities have a greater influence on herb succession in gaps than the recruitment of opportunistic species. In a study of various levels of canopy disturbance through harvest in New Hampshire, pre-harvest herbaceous communities were typical of the closed-canopy understory. After canopy removal, the same species occurred in the gap through the survival of stems and expansion of existing patches rather than by seedling development. The investigators further suggest that the spatial pattern of herb communities in gaps will persist for many years unless a more dramatic disturbance than harvesting occurs (Hughes and Fahey 1991). Alternatively, Collins and Pickett (1988a) suggest a species-specific reaction to harvested gaps because the herb layer response is directly correlated with the autecology of the herb and the change in the physical environment. Other studies support this suggestion. In the oak-pine forest, five species, including *A. quinquefolia*, *L. quadrifolia*, *M. canadense*, *P. paucifolia*, and *Viola cucullata*, were significantly correlated with gap size both 5 and 10 years after harvest. Furthermore, six species were significantly correlated with measured light levels (Schumann 1999). In the Allegheny forest, the presence *Erythronium* spp. was significantly correlated with gap position where it occurred predominantly towards the edge of the gap (Collins and Pickett 1988b).

The most significant trend for shrub succession in eastern forests is the recruitment and abundance of *Rubus* spp. in harvested gaps. For example, in harvested gaps in an oak-pine forest, *R. allegheniensis* and *R. idaeus* were both abundant in harvested gaps 5 and 10 years after harvest. *R. allegheniensis* began to decline 10 years after harvest, but *R. idaeus* continued to increase in abundance 10 years after harvest. Furthermore, *R. idaeus* abundance was significantly different between harvested gaps and controls (Schumann 1999). In harvested gaps of New Hampshire, *R. idaeus* was one of the most common shrubs after overstory removal and remained abundant 3 years after harvest whereas other shrubs showed a decline in abundance. Furthermore, *R. idaeus* was not present in intact forest (i.e., control) or in the predisturbance communities

(Hughes and Fahey 1991). In gaps of the Allegheny forest, *Rubus* spp. was not present before the harvest (Collins and Pickett 1998b). Several factors influence *Rubus* recruitment and succession into harvested gaps. Highly viable, buried seeds are the most prominent form of *Rubus* recruitment, and the level of soil disturbance also influences their presence. Their increase in abundance through early to mid succession is dominated by their prolific seeding (Hughes and Fahey 1991; Collins and Pickett 1988b). Other shrubs are also associated with harvested gaps. In an oak-pine forest, *Juniperus communis* and *Spiraea latifolia* was more abundant in harvested gaps than in controls both 5 and 10 years after harvest; however, *Kalmia angustifolia* was more frequent in controls after harvest (Schumann 1999). In New Hampshire, *Viburnum lantanoides* was also a common shrub after canopy removal, but its abundance decreased 3 years after harvest (Hughes and Fahey 1991).

1.5. Canopy Gaps and Plant Species Diversity

The importance of disturbance in the development of forest structure is widely recognized and well documented. Studies have indicated that canopy gaps opened by disturbance not only create a diverse stand structure, but also enhance plant species diversity across a forest landscape. This section examines some of the major hypotheses describing the processes of increased diversity in forest landscapes from canopy gap formation.

1.5.1. *Gap Partitioning Hypothesis*

The gap-partitioning hypothesis, introduced by Ricklefs in 1977, states that various microenvironments (microsites) exist in a canopy gap as a result of the changes in the physical environment (e.g., downed woody material, bare soil, etc.) caused by a disturbance. These microsites will determine the distribution of a species existence or colonization not only along a gap gradient (e.g., from the center of the gap to the edge), but also across a landscape. This hypothesis assumes that certain species are limited only to a gap environment or to a position within a gap environment. A study of plant diversity in the montane forests of western Canada verifies this assumption. Plots with the most open canopy of the study area contained Arnica (*Arnica angustifolia* spp. *Tomentosum*), an herbaceous species not located in plots with closed canopies (Pharo and Vitt 2000). A study of plant diversity in harvested gaps in an oak-pine forest of Mid-coast Maine also documents two annual herbaceous species, whorled loosestrife (*Lysimachia quadrifolia* L.) and rough-stemmed goldenrod (*Solidago rugosa* P. Mill.), which occurred only in gap environments (Schumann 1999). Gray and Spies (1997) confirm the gap-partitioning hypothesis for seedling establishment of western hemlock (*Tsuga heterophylla* (Rafn.) Sarg.) in the coniferous forests of the Pacific Northwest. Western hemlock was sensitive to microsite heterogeneity within canopy gaps, requiring well-decayed logs and shade from the understory or other logs to establish successfully in the gap. Therefore, gap specialists contribute to forest landscape diversity as well as stand diversity with the occurrence and regeneration of a gap area. However, a study performed in the temperate forests of the Great Smoky Mountains demonstrated that there were few gap plant specialists, and that there were no strong differences in species composition along the gap gradients (Busing and White 1997).

1.5.2. *Density Hypothesis*

The density hypothesis describes species diversity within gaps as a function of frequency and density of seedling establishment. According to Denslow (1995), who suggested the hypothesis, gap interiors are important areas for species diversity where the primary regeneration occurs (Connell 1989; Denslow 1995). High sapling density in a gap is the primary cause of species diversity within a gap. In the Great Smoky Mountains, Busing and White (1997) confirm the density hypothesis where stem density and species richness increased in canopy gap openings as compared to closed canopy shaded areas. In an essay on tree fall gaps and forest dynamics in 1989, Connell supports this hypothesis as well, stating that the species composition of the canopy is a function of the densest colonizing population within a canopy gap. However, a long-term study in an eastern deciduous forest of Michigan discovered that the local environmental conditions predicted diversity in the gap rather than the density of plant species increasing the total diversity (Poulson and Platt 1989).

1.5.3. *Resource Allocation in Gaps*

As Poulson and Platt suggest (1989), plant species diversity will increase in gap areas according to localized environmental conditions. Resources (i.e., light, soil, water, nutrients) for plant establishment and growth become available after a disturbance. The disturbance event offers space that would otherwise be utilized by plants acquiring soil nutrients, water, and light. For example, after examining fine root hairs in gap species in a temperate forest, Canham et al. (1990) suggest that an increase in soil resources was more of a determining factor for regeneration than light availability. However, the light resource is the most documented reason for increasing plant diversity in canopy throughout canopy gap literature.

Some studies indicate conflicting results on the amount of photosynthetically active radiation (PAR) that influences species composition and diversity in gaps. In a study of temperate forest gaps by Canham et al. (1990), PAR in gaps and under a closed canopy had an even distribution of diffuse and direct solar radiation. Gaps received only brief periods of high light. However, a study of gaps in a northern hardwood forest in Michigan demonstrate that species with intermediate shade tolerance were more successful in tree fall gaps than shade tolerant trees, suggesting that PAR does increase in canopy gaps (Dahir and Lorimer 1996). In northern forests, the location where a species colonizes in a gap may be an important factor determining light availability and diversity. Poulson and Pratt (1989) found rapid initial growth of saplings, herbs, and shrubs occurring on the northern edge of a gap and a greater diversity of species in comparison to species composition on the southern edge.

Several factors influence the amount of light reaching the forest floor after a disturbance. Seasonality and the time of day the measurements are recorded often limit methods for measuring light availability (Canham et al. 1990; Schumann 1999). Other factors also influence PAR in gaps. A more developed understory within the gap forest structure will significantly limit sunlight to the forest floor. A study of sapling density in the Southern Appalachians indicated that high *Rhododendron maximum* density clearly inhibited the establishment of new seedlings in intermediate size harvest gaps (Beckage et al. 2000). Also, gap size and gap age will influence PAR for species regeneration.

1.5.4. *Gap Size and Plant Diversity*

The actual occurrence of a gap infers an influx of resource availability in both harvested and natural gaps. The physical changes in the environment can substantially influence gap succession by the amount of resources that become available. Plant species that require a significant amount of sunlight and space (i.e., ruderal species) to establish may be more prevalent in the early successional stages of gap regeneration. It seems logical then to suggest that the greater the gap area, the more resources available. Larger gaps have more available growing and colonization space, less competition for resources because of downed trees providing resources otherwise utilized before the disturbance, and more area to receive direct sunlight (Krasny and Whitmore 1992). The area of disturbance by tree mortality varies in size according to forest stand age. An old-growth forest with large trees and tree canopies will create much larger gaps than a younger stand 60-80 years old. In eastern forests, small gaps have an area of 50-100 m^2, and large gaps in old growth forests can be larger than 2000 m^2 (Runkle 1982).

As stated previously, frequent minor disturbances dominate the Acadian forest dynamic; however, these disturbances are rarely a restricted to one event (Worrall and Harrington 1988). Multiple disturbances create larger, expanding gap areas that increase overall species diversity (Hansen et al. 1991). Several studies have indicated that larger gaps allow pioneer tree species not only to establish but also to survive into canopy status (Foster 1988; Poulson and Platt 1989). A study of gaps in the southern Appalachians indicated that total tree net primary production (NPP) was greatest at the gap center, particularly for larger gaps where lateral extension of edge trees had less of an influence on succession than in smaller gaps (Philips and Shure 1990). Furthermore, large gaps permit less common herbaceous species (i.e. to the forest landscape) to be dispersed and established due to the increase in growing space and direct sunlight (Schumann 1999; Poulson and Platt 1989) thereby increasing the diversity of the overall forest landscape.

Alternatively, intermediate size harvest gaps between 150 – 400 m^2 did not effectively increase species diversity in a Southern Appalachian forest landscape (Beckage et al. 2000) indicating a threshold of gap size for increasing species diversity.

1.5.5. *Competitive Ability*

Variation in seed dispersal efficiencies and seedling competitive abilities can greatly influence the successional patterns in gaps (Denslow 1980). Survival and canopy recruitment in gaps is a function of the density and frequency of colonizing species, growth rate, heights, and germination success (Canham 1989). For example, basal sprouts from hardwood trees after disturbance rapidly occupy space and utilize resources within a disturbed environment. Also, rapid colonization of opportunistic herb species in disturbed areas can create high nutrient sequestering, thus limiting the succession of other non-opportunistic species (Muller 1990). However, species with viable buried seed can have greater success establishing in a gap than species that colonize the gap. Buried seed gap specialists are able to respond quicker to the canopy opening; their establishment limits space and nutrients for later colonizers (Connell 1989).

The future canopy composition of a gap environment is also dependent on the density and size of colonizing species and advance regeneration. Densely established advance regeneration will respond with increased growth after a canopy disturbance limiting the recruitment and/or establishment of pioneer tree species. Taller seedlings or saplings established in the gap area before canopy disturbance have a greater advantage depending on how fast the trees respond to the available light after suppression (Connell 1989). However, the advantage of advance regeneration is negated in gap tree succession when slower growing species (i.e., that persist into the upper canopy) or species with higher rates of mortality (i.e., creating space for more colonization) dominate the gap environment. Established herbaceous communities that survive the disturbance have a competitive advantage as well, particularly species that reproduce vegetatively (Muller 1990). Furthermore, the greater growth rate of the established community will preclude the succession of other forest herbs. When less common species are able to colonize into the established communities of trees and/or herbs, their abundance with the slower growing species will approach equilibrium in the future stand composition (Connell 1989).

1.6. Natural Gap Dating Methodologies

Understanding the gap dynamics of the Acadian forest is vital to developing silvicultural approaches that are based on patterns of natural disturbance (Seymour and Day 1997). A major limitation to quantifying vegetation dynamics in natural gaps is a lack of methods for accurately determining when a gap was created. Many studies comparing plant diversity and/or stand regeneration in recent natural gaps utilize several non-destructive techniques for dating the natural gaps. These methods include evaluation of conditions of the treefall, soil and litter disturbance, damage to adjacent vegetation (Mladenoff 1990), changes in the lateral growth of trees as indicated by the distance between bud scale scars (Rankin and Tramer 2002), and aging seedlings growing on tip-up mounds (Battles and Fahey 2000). These methods are often subjective and can be inaccurate.

A study performed by Dynesius and Jonsson (1991) evaluated eight different methods for obtaining the best date of natural gaps in a northern Sweden boreal forest. According to their results, initial growth of surrounding canopy trees and the growth release of suppressed saplings evaluated by radial growth of the stem provided the best method for dating natural tree fall gaps. Trees form an abrupt and sustained increase in height and/or radial growth when exposed to higher light intensities after being suppressed by larger trees and/or branches (Frelich 2002; Lorimer 1985). The date of formation of natural gaps in a forest landscape can be defined by the year in which the tree indicates a release from suppression. However, assigning a formation date for natural gaps is sometimes problematic since increases in stem radial growth are also indicative of climate changes and/or tree vigor. Furthermore, radial growth responses to increased light by canopy openings will vary by a tree's position in the canopy, location relative to the gap, species, shade tolerance, the magnitude of the disturbance (i.e. slow gap formation over long period), and whether a tree was injured during the disturbance.

Many studies have shown that saplings within the gap have provided accurate results in dating natural gaps. In the northern Sweden boreal forest, the growth release of suppressed saplings measured by the cross-section at the base of the tree provided an accurate age of the natural gap where 17 of 22 gaps supported the best obtainable results for dating the gaps (Dynesius and Jonsson 1991). In spruce-fir forests of the Rocky Mountains, suppressed saplings responded to partial overstory removal with a 4-fold increase in growth, but growth was sometimes depressed 1-2 years following harvest (McCaughey and Schmidt 1982). A study on recent natural gaps in a northern hardwood forest indicated that trees within the gap demonstrated a greater response in radial increment than trees at the gap edge. Not only was tree position important, but also different species had greater responses than others. Sugar maple responded to a greater degree than eastern hemlock, red maple, and yellow birch (Dahir and Lorimer 1996).

Northern hardwood gap capture in New Hampshire demonstrated that after gap formation, sugar maple and red maple grew more rapidly than American beech (McClure et al. 2000). However, in an old growth forest of Maine, smaller trees in natural gaps showed the same likelihood of response irrespective of their location within the gap (i.e. gap edge or center), and tree species response was only significantly different for a moderate release criterion, the preferred criterion (Chokkalingam 1998).

Because different tree species, ages, and location within a stand influence radial growth after disturbance, many different release criteria to indicate a disturbance event have been established. The suitability of a release criterion often varies by with region, species, site, and other environmental factors (Chokkalingam 1998). The majority of the release criteria cited in the literature were reviewed and summarized by Chokkalingam (1998). Although many studies often assign an arbitrary release criterion, most studies use an increase in radial growth of between 50% and 100% during a specified growth period before and after the disturbance to indicate a major release or a minor release depending on the characteristics of the tree species (Frelich and Lorimer 1991; Frelich and Graumlich 1994; Frelich 2002).

Not only are the magnitude of the release important, but also the duration of the response. The duration of an abrupt and sustained release discriminates disturbances from growth changes due to climatic variation (Frelich 2002; Canham et al. 1990). Lorimer (1985) suggests a 15-year consecutive growth release from suppression screens out growth releases that are climatically related. Some studies deviate from these standards. For example, Dahir and Lorimer (1996) used an average of 40% radial growth increase from eight years predisturbance and five years post-disturbance to estimate the probable date of gap formation. This low value was selected because the canopy gaps were < 50 m^2 in size, and it was successful in this study only because the researchers had data on the initial size and growth rate of all the trees studied. Hence, climatic responses in radial growth could be excluded.

Chokkalingam (1998) compared three different release criteria in a disturbance study in an old-growth forest of Maine. Her release criteria ranged from a moderate release (≥ 100% increase in growth 10 years duration before disturbance and after disturbance) to absolute release (three years of radial growth < 0.5 mm following four years of > 0.5 mm radial growth). Although all the criteria produced similar numbers of responses, the lenient criterion overestimated disturbance intensity. Frelich (2002) suggests that percentage growth increase is a more valuable indicator of disturbance than a fixed growth rate (i.e., 0.5 mm/yr) because many tree species have a high growth rates before a disturbance event.

Because of the considerable variation in tree response to canopy disturbance due to differences in species, shade tolerance, gap size, and other environmental conditions, the best method for dating recent natural gaps in the Acadian forest is difficult to determine. Furthermore, assigning an arbitrary release criterion for tree response in natural gaps in the Acadian forest type may not determine the best formation date. Most disturbance chronology studies usually identify a disturbance event within a ten-year period (Lorimer 1985) because there are many factors that influence tree growth response to release from suppression. Therefore, understanding how particular species in various positions of a forest structure and in various gap sizes react to a known disturbance (i.e., both spatially and temporally) can benefit natural disturbance chronological studies where the disturbance patterns of the forest structure are unknown.

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Chapter 2

VEGEATATION DYNAMICS IN HARVEST GAPS, NATURAL GAPS, AND CLOSED CANOPY CONDITIONS IN MAINE’S ACADIAN FOREST

2.1. Abstract

The creation of canopy gaps through natural disturbance is an important ecological process in the Acadian forest. Designing harvest gaps that emulate natural gap dynamics may be important for maintaining structural and biological diversity, as well as the natural regeneration of desired tree species. To better understand this process, we used a controlled study in central Maine to compare the abundance, diversity, and composition of plants among and within harvested gaps, natural gaps, and under a closed canopy in the Acadian forest. We evaluated 45 harvested gaps, 23 natural gaps, and 23 closed canopy transects. The percent cover of each species was recorded in 4 m^2 plots located at 2 m intervals along a north/south transect across each gap. Harvested gaps were measured four growing seasons after harvest.

Total plant cover in all gaps (60.4% mean cover per gap) was 83% greater than under the closed canopy (10.6%) ($p < 0.001$). Cover was 27% greater in harvested gaps (34.9%) than in natural gaps (25.5%) ($p < 0.005$). *Abies balsamea* was the most abundant species among harvested gaps, natural gaps, and closed canopy conditions. Total cover was correlated with distance from the gap center of the largest harvest gaps (1,170 – 2,106 m^2) with the highest cover occurring in the gap centers ($r^2 = 0.27$, $p < 0.001$). Species richness (# of plant species) per sample area was greater in harvest gaps > natural gaps > closed canopy ($p < 0.001$), but species richness was not correlated with location within the gap. Species evenness (measured as the slope of the dominance

diversity curves) indicated that 1) neither gaps nor closed canopy conditions had an even distribution of plant species ($p < 0.001$) and 2) that plant cover was less evenly distributed under the closed canopy than in both harvested and natural gaps.

One hundred ninety-five plant species were identified in all plots. One hundred twelve species were found only in harvest gaps, and 35% of the 112 were classified as early successional, shade-intolerant species. Detrended correspondence analysis on the presence and absence of plant species indicated that the composition of natural gaps and closed canopy conditions were more similar to each other than to that of harvested gaps.

Tree regeneration was abundant under all conditions but was not correlated to gap origin ($p = 0.15$) or location within the gap. Seedlings (<0.5 m tall) were the most abundant form of regeneration, and saplings (0.5 – 2.0 m tall) were most abundant in harvested gaps. *A. balsamea* was the most abundant tree species regenerating in natural gaps and closed canopy conditions, while *Acer rubrum* was most abundant in harvested gaps.

2.2. Introduction

Maine is 90% forested, and 96% of the forest landscape is used in productive timberland mostly owned by large landowners both industrial and non-industrial. Although the current forest inventory in Maine remains stable, the Maine Forest Service has found a slight decline in inventory that is projected to continue for the next 5 years (Laustsen and Griffith 2002). Furthermore, harvesting practices and spruce-budworm epidemics have changed the composition of the most abundant forest type in northern Maine (i.e. where most of the managed forests are located) from a spruce-fir forest typical of the presettlement forest structure (Lorimer 1977) to a maple/beech/birch forest type (Laustsen and Griffith 2002). Maine's forests are the largest contributor to Maine's economy with forest-based manufacturing and forest-related tourism contributing over $6.5 billion (z NESFA 2001). In 1993, Maine wood products, lumber, and paper industries produced goods and services totaling $4.7 billion (MCSFM 1996). Because of great social concern and the multiple-use nature of the industrial and non-industrial forest, managing forests for long-term productivity as well as non-timber values, such as wildlife habitat, biodiversity, and recreation, is crucial.

The concept of ecological forestry, which prescribes a harvesting design that incorporates both timber and non-timber values, has been proposed for the management of Maine's managed forests (Seymour and Hunter1999; Seymour and Day 1997; Seymour et al. 2002). Ecological forestry involves harvesting according to the common natural disturbance regime within the spatial and temporal limits of Maine's natural forest structure. The goals of this management practice are to maintain the legacy of Maine's forests, defined as the presettlement forest structure and composition, and to enhance the biological and structural diversity within the forest landscape. These goals of ecological forestry are currently thought to be achieved in Maine by creating a range of gap sizes up to 0.2 ha (as would be witnessed after a natural disturbance) within the managed forest leaving large residual trees (both live and dead) throughout the harvesting rotations (Seymour et al. 2002; Seymour and Hunter 1992; Hansen et al. 1991). These gaps and residual trees are proposed to achieve a presettlement structural diversity by creating an array of tree ages and sizes as witnessed in natural forests as opposed to simplified single cohort plantation forests in the industrial forest (Roberts and Gilliam 1995; Seymour and Hunter 1992). This landscape structural diversity in the Northeast promotes the most suitable habitat for plants and wildlife where many types of organisms occupy the full sere of young and old forest structures (Hansen et al. 1991). Furthermore, this forest management design can ensure the regeneration of commercially valuable, late succession species. In Maine, commercially valuable tree species like *Picea rubens* Sarg., *Pinus strobus* L., and *Betula alleghaniensis* Britt naturally initiated their populations under the natural disturbance regime in this forest type (Seymour and Hunter 1999). Therefore, the regeneration of these species could be maintained through canopy gap formation.

The concepts of ecological forestry are based on two hypotheses: 1) disturbance is a natural process in forest ecosystems, and 2) canopy gaps create a diverse forest stand structure that fosters not only wildlife habitat and diversity, but also plant species diversity across a forested landscape (Seymour and Hunter 1999). If canopy gaps are utilized in forest management, the forester needs to emulate the complex interactions of several ecological elements present in natural gaps. These ecological elements included not only a missing canopy, but also the presence of downed woody material, standing snags, and undergrowth vegetation including established trees, shrubs, and herbs (Lundquist and Beatty 2002).

Minor disturbances, including windthrow and tree mortality, are characteristic of the Acadian forest, a sub-boreal transition zone forest, with a 0.5 - 1% annual frequency (Runkle 1981; Seymour and Hunter 1992). This disturbance regime creates tree fall canopy gaps and a multiple cohort stand structure with an uneven distribution tree ages and sizes (Seymour and Hunter 1992; Oliver and Larson 1996). Several studies indicate that natural disturbances creating canopy gaps are important to the structural and biological diversity of a forest ecosystem (Busing and White 1997; Hansen et al. 1991; Whitmore 1989). Location within a gap, available growing space, and the success of gap capture by plant species can determine the level of vegetation diversity within a disturbed area. Some species of herbaceous plants, shrubs and trees are limited primarily to gap environments, and their establishment can enhance the overall diversity of the forest stands with the frequent occurrence of canopy gaps (Poulson and Platt 1989; Runkle 1982). The development of commercially valuable tree species in forest stands may depend on the occurrence of a canopy gap and the species response to increased available light and other resources (Foster 1988; Runkle 1985; Seymour and Hunter 1992). Since most of Maine's forests are utilized for timber extraction, understanding vegetation diversity and patterns of forest regeneration within canopy gaps in managed forests is crucial.

In order to implement the principles of ecological forestry in Maine, we must better understand the dynamics of canopy gaps in the Acadian forest. The Forest Ecosystem Research Program (FERP) at the University of Maine is a long-term, interdisciplinary research effort examining the ecological effects of an expanding-gap silvicultural system. Harvests gaps created as part of this study provide an opportunity to evaluate vegetation dynamics four years after harvest, and compare the results to the vegetation dynamics in natural gaps and under the closed canopy. In this study, we examine the following hypotheses:

1) There is no difference in plant abundance, diversity, and composition among and within harvest gaps, natural gaps, and closed canopy conditions

2) Plant abundance, diversity, and composition are not correlated with the following gap characteristics:

    a. Gap origin
    b. Gap age
    c. Gap size
    d. Canopy openness
    e. Location within the gap

2.3. Methods

2.3.1. *Study Area*

The study area is located in the University of Maine's Penobscot Experimental Forest (PEF) in the towns of Bradley and Eddington, Penobscot County, Maine (44 50'N, 68 35'W). The PEF encompasses 1,600 hectares and is part of the Acadian forest type. The dominant tree species in the PEF include *Tsuga canadensis* (L.) Carr., *Acer rubrum* L., *P. rubens*, *P. strobus*, *Thuja occidentalis* L, *Abies balsamea* (L.) P. Mill, *Populus tremuloides* Michx, and *Betula papyrifera* Marsh.. The PEF has a complex history of repeated cuttings resulting in relatively even-aged stands dating from the late seventeenth century. Forest soil structure is variable, but principally Aquic or Typic Haplorthods or Podzols; slope is generally less than 8% (Brissette and Kenefic 1999).

2.3.2. *Experimental Design*

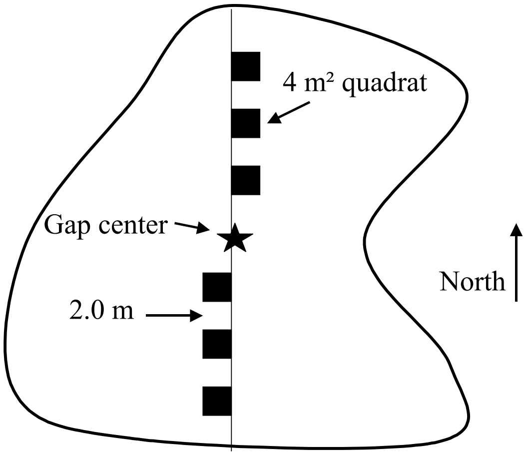
Using current information about natural disturbance regimes in the Acadian Ecoregion (Runkle 1981; Seymour and Hunter 1992), an expanding-gap silvicultural system with permanent reserve trees was developed (Seymour and Day 1997). Based loosely on the German "Femelschlag" system (Seymour and Day 1996), the treatment prescriptions include: 1) 20:10 treatment - 20% canopy removal on a 10-year cutting cycle for 50 years (creating 0.2 ha openings) following 50 years regeneration with 10% of the basal area remaining in permanent reserve trees for, and 2) 10:30 treatment - a 10% canopy removal level on a 10-year cutting cycle for 100 years (creating 0.1 ha openings) with 30% of the basal area remaining in permanent reserve trees. These treatments are being compared to control areas that receive no harvesting.

Both harvest treatments are designed to provide a 1% annual disturbance rate in 100 years regeneration similar to that estimated for presettlement forests in Maine (Lorimer 1977). The 20:10 treatment will hypothetically enhance the development of mid-succession species and produce five different cohorts within the managed stand. The 10:30 treatment is intended to accelerate the development of late successional species and produce ten cohorts within the managed stand. These treatments also were designed to maintain the economic advantages of even aged methods, yet provide many of the structural features found in uneven aged stands. The maintenance of permanent reserve trees is intended to provide structural diversity and control species composition.

The treatment areas are approximately 10 ha in size, and replicated three times in a randomized complete block design. The first harvest entry (i.e., gap creation) occurred in 1995 for Block 1 (Research areas 1, 2, and 3), 1996 for Block 2 (Research areas 4, 5, and 6) and 1997 for Block 3 (Research areas 7, 8, and 9). As a result of this initial harvest, between seven and 10 gaps were produced in each of the six treated plots creating approximately 52 gaps between 0.1 and 0.2 ha in size.

2.3.3. *Plot Establishment*

A subset of 45 harvest canopy gaps was selected for the study in order to establish equal gap samples per treatment. In addition, 23 natural gaps were selected from the three control areas. Gap boundaries of both natural gaps and harvest gaps were defined using a line connecting the bole of each tree whose canopy contributes to the edge of the gap (Runkle 1992). This approach provides a more meaningful assessment of the total area affected by increased light intensity as a result of the canopy opening (Dahir and Lorimer 1996). Natural gaps within the control plots were defined as follows: the area of the canopy opening that is large enough to expose to the sky the crowns of stems that would otherwise be in the understory and where those stems are no taller than 2 m. The canopy gap must have been created by at least two tree falls or stem breaks of canopy trees (gap maker) that are ≥25 cm at 1.4 m (Runkle 1992). Finally, natural canopy gaps were considered only if they were at least 30 m away from a road to eliminate any environmental factors caused by edge effects.



Gap Area

Figure 2.1: An example of the plot layout within a gap. Vegetation data were collected at each quadrat lain on the north/south transect line within the gap. The same layout for the transect and sample plots was used under the closed canopy.

Once all natural and harvested gaps were located, the length of the longest north/south transect from the gap center was measured. The transect was permanently marked with two lines of white paint where the transect intersects with the gap edge tree or on the two closest trees. We used yellow flagging to mark the precise point of intersection between the gap edge and the transect line. The gap center was located by measuring the center of the north/south transect line, and the center was permanently marked with a rebar. Square vegetation sample plots (2 m x 2 m in size) were established at 4 m intervals along each transect beginning at the gap center and extending to the north and south gap edge. For sample plots on the northern half of the gap, the southwest corner to the plot was placed on the 4 m interval point, and for plots on the southern half of the gap, the northeast corner of the plot was placed at the 4 m interval points along the transect (Figure 2.1). Twenty-three closed canopy transects were established in the control areas (7-10 plots in each of the three control research areas). Each transect contained a total of four sample plots (two north and two south) placed two meters apart creating a 16 m transect line. Closed canopy transects were placed under a continuous closed upper canopy that was at least 30 m away from a canopy opening.

2.3.4. *Independent Variables*

The following independent variables were used to examine the relation between gap characteristics and vegetation responses:

2.3.4.1. Gap Origin

Gap origin was determined by whether the gap was created by a harvest treatment, naturally by the death of two or more canopy trees in the control area, or no gap (i.e., by the continuous closed upper canopy).

2.3.4.2. Canopy Openness

The openness of a harvest gap, natural gap, and closed canopy was quantified using three methods including 1) gap area, 2) overstory basal area, and 3) gap fraction. Gap area was calculated by mapping each gap using both Trimble Pro XL™ and Trimble GeoExplorer® 3 GPS units. Satellite data were processed and exported in NAD83 datum, UTM Zone 19 coordinate system format using GPS Pathfinder Office v. 2.80 to ArcView 3.2 shapefiles. Harvest gap area was determined from these GIS maps and harvest gap size ranged from 108 m^2 to 2169 m^2. Gap area for the natural gaps was determined using the sampling protocol for estimating gap size described by Runkle (1992). Gap size was estimated by calculating the area of an ellipsoidal shape within the gap. Using the already established north/south transect line, a perpendicular east/west transect line was established for producing the ellipsoidal shape. The area for each gap was calculated from the length of these two transect lines using the formula for an ellipse:

$$\text{Area} = \pi LW/4 \tag{1}$$

where L is the length of the longer transect line and W is the length of the shorter transect line (Runkle 1992). Natural gap size ranged from115 m^2 to 511m^2.

Overstory basal area was also measured at each sample plot using a 5 factor wedge prism. Each tree considered as “in” using the prism measurement was identified and counted. Gap fraction (DIFN) was measured at each sample plot using a Licor LAI 2000 plant canopy analyzer at 1.4 m (i.e. breast height). A 180° view restrictor (i.e. covering half of the lens) was used to prevent the person recording from being in the image. When leaves from trees or shrubs were close to the lens, the leaves were moved away from the lens, but the trees remained in their original position. Each plot value was compared against a gap fraction value measured simultaneously (i.e., within 5 seconds) under open conditions. The LAI-2000 records the DIFN value from a hemispherical lens in front of five concentric rings, but only the inner 4 concentric rings were used for the analysis. The DIFN value indicates the fraction of sky that is not blocked by foliage (Gendron et al. 1998). All measurements were taken under uniformly cloudy or uniformly clear sky conditions.

Differences in canopy openness among harvest gaps, natural gaps, and closed canopy conditions as measured by canopy gap fraction and overstory basal area were analyzed using two different statistical tests. ANOVA with linear contrasts using PROC GLM in SAS System for Windows, Version 8.1 was used to determine differences in overstory basal area among harvest gaps, natural gaps, and closed canopy conditions. The Kruskal-Wallis test with linear contrasts, a non-parametric statistical test, was used to test the differences in canopy gap fraction among harvest gaps, natural gaps, and closed canopy conditions using PROC RANK and PROC GLM in SAS. The Kruskall-Wallis test assesses whether the observations in the sample population are all the same across locations. All observations are ranked from smallest to largest. The sum of the ranks for each sample is used to compute the test criterion and compare with tabulated values. Because the Kruskal-Wallis test is able to perform linear contrasts, this test was ideal for identifying differences among gaps and between natural conditions and harvest conditions. Linear regression analyses using PROC REG in SAS were performed to determine whether canopy openness measured by both overstory basal area and canopy gap fraction were correlated to gap size. Normal distribution and equality of variance of the data were tested using proc univariate and proc anova on the absolute value of the residuals (i.e., Levine's test) respectively in SAS.

2.3.4.3. Location Within the Gap

In a long-term study on vegetation responses to canopy gaps in Michigan, Poulson and Platt (1989) discovered that growth, regeneration, and species diversity differed between a northern gap edge and a southern gap edge. We hypothesized that vegetation composition would differ by location within each gap in our study. In this study, we used a distance along the north/ south transect to assess whether vegetation responses were correlated with locations within each gap. Spacing of sample plots at 2 m intervals along each transect was used as the measurement of distance from gap center.

3.4.4. Gap Age

Differing ages among gaps are likely to influence interpretations of vegetation response patterns. Harvest gaps were sampled four years after harvest (i.e., in 1999 for RA 1 and RA 2, in 2000 for RA 5 and RA 6, and in 2001 for RA 7 and RA 9). However, the age of the natural gaps was unknown. Therefore, natural gaps were aged using understory sapling tree ring analysis (See Chapter 3). Nine natural gaps were approximately five years old, five of the natural gaps were approximately 10 years old, and the remaining nine natural gaps could not be dated using this method for aging gaps.

2.3.5. *Dependent Variables and Analytical Approach*

The response variables used in the analysis included:

2.3.5.1. Vascular Plant Abundance

Vascular plants were identified to the species level using Haines and Vining (1995) for all herbs, shrubs, trees, and ferns within each sample plot. An ocular estimation of percent cover (to the nearest 1% for small species with low cover and to the nearest 10% for larger species with greater cover) was recorded for each species in every sample plot. These measurements were used to determine the species diversity, evenness of distribution, and species richness for each gap and species location within the gap. Overall percent cover estimate also was recorded by class for 1) dead wood; 2) rocks; 3) leaf litter; 4) all conifer species; 5) all hardwood species; 6) all shrub species; 7) all herbaceous species; 8) all fern species; 9) graminoids 10) mosses and 11) lichens.

Plant species abundance was evaluated as the average percent cover of each species per gap and per closed canopy transect. Two non-parametric statistical tests were used for testing differences in plant abundance because these data did not meet the assumptions of parametric statistics. The Kruskal-Wallis test with linear contrasts was used to test the differences in abundance among harvest gaps, natural gaps, and closed canopy conditions using PROC RANK and PROC GLM in SAS. However, the Kruskal-Wallis test is sensitive to normal distribution of data (Steele et al. 1997), and normality was not achieved with rank transformations for abundance data by species category (i.e., ferns, grasses, lichens, mosses etc.) Hence, a Multiple Response Permutation Procedure (MRPP) using PC-ord was used to detect differences abundance by plant type among harvest gaps, natural gaps, and closed canopy. MRPP is a non-parametric procedure that uses a weighting factor with a squared Euclidean distance to produce a statistical test equivalent to an ANOVA F-test. MRPP uses a random permutation of all the observations to perform the ANOVA equivalent test, and it is based on the assumption of equal dispersion of the data (McCune and Mefford 1999). However, linear contrasts cannot be used with this procedure. Multiple linear regression analysis was performed to test whether abundance of vascular plant species was correlated to gap characteristics (stand density, canopy openness, and location within the gap). This analysis was performed using PROC REG in SAS, and SYSTAT Version 10 (2000). Plant cover data were transformed using an inverse transformation.

2.3.5.2. Vascular Plant Composition

Composition of a gap was determined for tree regeneration and total species composition. An importance index was created for each species by origin to determine how important a species was in a given condition based on how frequently it occurred and how much space the species occupies (i.e., its cover in the sample plot). Frequency was calculated by the number of times a species occurred in a gap divided by the number of sample plots in the gap (i.e., because sample are was proportional to gap size).

Average cover of a species was calculated by the total cover of the species in the gap divided by the number of sample plots in the gap. Both mean cover and frequency were averaged over each condition to create a mean frequency and a mean cover of the species in harvest gaps, natural gaps, and closed canopy conditions. The importance index was calculated by multiplying the mean frequency of the species by its mean cover in harvest gaps, for example. Further, each species was categorized by its life history traits in Maine, including shade tolerance, lifespan, phenology, and habitat to determine its relative successional status in forest ecosystems.

A multivariate analysis was performed using overall community composition to determine the patterns and trends in the variation of the vegetation response (McGarigal et. al 2000). A detrended correspondence analysis (DCA) was used first to determine the similarity of all the research areas based on their location within ordination space. This test was performed to determine if differences in soil moisture were creating different environments among the research areas. DCA is an eigenanalysis ordination technique based on reciprocal averaging which ordinates both species and samples simultaneously based on a chi-square distance measure (McCune and Mefford 1999). Second, DCA was used to assess the compositional similarity among harvest gaps, natural gaps, and closed canopy transects based on the presence and absence of plant species. This analysis was performed to assess the similarity of harvest gaps to natural tree fall gaps based on the compositional changes that occur by gap origin.

2.3.5.3. Tree Regeneration

The species, density, and height of all regenerating tree species were recorded using stem counts by height class (≤ 0.5 m, > 0.5 - 1.0 m, > 1.0 - 2.0 m, and > 2.0 m) for each tree species in each sample plot. Tree regeneration (i.e., stems categorized by height class in each quadrat) was analyzed with chi-square test for independence using the SAS. Non-linear regression using Sigma Plot 2000 Version 6 was performed to determine whether tree regeneration was correlated to its location within the gap

2.3.5.4. Plant Species Diversity

Plant diversity was evaluated from the vascular plant assessment using species richness and the Shannon-Weiner index of diversity. Because sample area was proportional to gap size, and larger gaps had more opportunity to acquire plant species, species area curves were used as indicators of species richness. Separate species area curves were generated for harvest gaps, natural gaps, and closed canopy transects using PC-ord (Version 4). PC-ord generates the species-area curve by randomly subsampling all possible combinations of the maximum number of sample plots (500 at most as a limitation of PC-ord) to determine the mean number of species identified as a function of sample size (McCune and Mefford 1999).

To test whether the species area curves were derived from different populations for the harvest gaps, natural gaps, and closed canopy conditions, non-linear regression models were derived for each condition. The purpose of this test was to determine whether species richness (indicated by the species area curves) was different among harvest gaps, natural gaps, and closed canopy transects. Statistical differences among the three models were tested using the method described by Wagner and Ter-Mikaelian (1999). Using an *a priori* approach, the full model (i.e., the three separate species area curves for harvest gaps, natural gaps, and closed canopy plots) was compared with three reduced model forms that pooled the samples from gaps and closed canopy plots in various combinations. We tested sequentially to determine whether the full model accounted for more variation than 1) a reduced model of richness including all quadrats regardless of origin 2) a reduced model of gap richness versus closed canopy richness, and 3) a reduced model of natural gap and closed canopy richness versus harvest gap richness.

An insignificant result at any step of the comparison ($p > 0.05$) terminated any further model comparisons. Each model comparison was evaluated using an F-test. The F-statistic was calculated using the ratio of the difference between the residual sum of squares for the reduced and full models to the residual sum of squares for the full model divided by the appropriate degrees of freedom. The P-value was calculated as a percentile of the F-distribution with the respective degrees of freedom.

The Shannon-Weiner index of diversity (H), which measures the proportional abundance and distribution of species, was calculated for each gap in all conditions:

[2] $$H = -\sum_{i=1}^{s} p_i \ln p_i$$

where s is the species richness, p_i is the proportion of percent cover that belongs to species i. Analysis of variance with linear contrasts was used to detect differences by gap origin as measured by the Shannon-Weiner index using Proc GLM in SAS. T-tests were performed to test differences in plant abundance and diversity between natural gaps and harvest gaps within the same size range (~100-500 m^2). Isolating gaps of a similar size range allowed us to determine what variables were affecting abundance and diversity by eliminating the large range of gap sizes. Multiple regression analysis using a linear model was performed to test whether the Shannon-Weiner diversity was correlated to gap characteristics (stand density, canopy openness, and location within the gap) using PROC REG in SAS and SYSTAT Version 10 (2000).

2.3.5.5. Plant Species Evenness

Both species richness and the Shannon-Weiner diversity index do not differentiate between rare species and dominant species. Therefore, Whittaker's dominance-diversity curves (1975), and the Shannon-Weiner Equitability index were calculated to determine the evenness of plant diversity.

Based on Whittaker (1975), a dominance diversity curve was created for every gap and every closed canopy transect as a measure of species evenness independent of sample area. Each species in a gap were ranked from highest to lowest based on their proportional abundance (i.e., percent cover of a given species divided by the total percent cover in the gap). In each gap or transect, the species ranks were plotted against their proportional abundance in that gap, and a non-linear regression was performed using the log normal model $y=e^{-ax}$. These analyses were performed separately for all gaps and closed canopy transects. Hence, each gap and transect contained a separate curve and a corresponding slope ('a' in the model). The slope of each line was used as an indicator of the plant distribution in each gap or transect. For example, if the slope of the dominance diversity curve for gap y was equal to zero, then all species were of equal importance and were evenly distributed throughout the gap. The Kruskal-Wallis test with linear contrasts was used to test the differences in plant evenness (i.e., differences among the slopes of the dominance-diversity curves) among harvest gaps, natural gaps, and closed canopy transects using SAS because this data did not meet the assumptions of parametric statistics.

The Shannon-Weiner equitability index (E) was used to determine the extent of which distribution contributes most to diversity (Magurran 1988) [3].

$$E = H/H_{\max} = H'/\ln(s) \qquad [3]$$

$H_{\max}$ indicates the maximum diversity of the given condition. Analysis of variance with linear contrasts was used to detect differences in plant evenness by gap origin as measured by the Shannon-Weiner equitability index using Proc GLM in SAS.

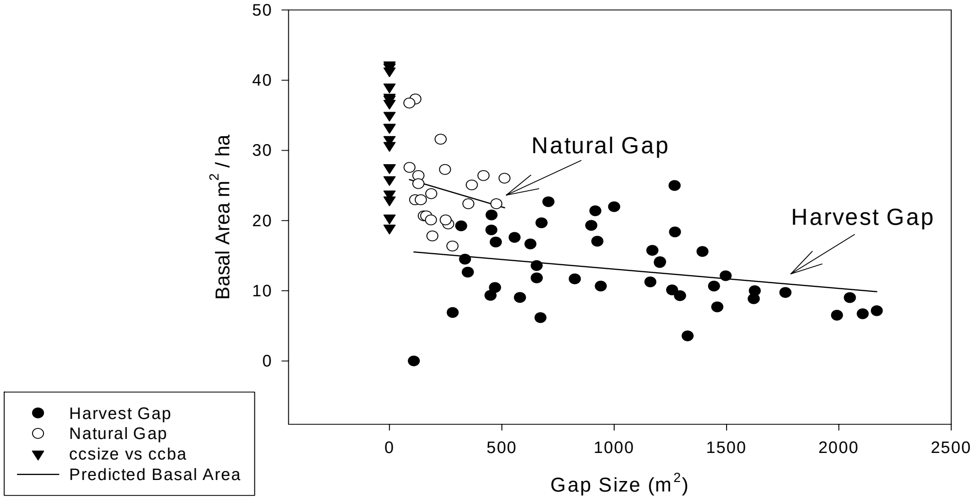
2.4. Results

2.4.1. *Canopy Openness*

Closed canopy plots had the highest stand density measured by basal area (mean 32 m^2/ha) ($p < 0.001$), and mean basal area in natural gaps (24 m^2/ha) was greater than mean basal area in harvest gaps (13 m^2/ha) ($p < 0.001$). Some natural gaps also had basal area values equivalent to those of closed canopy transects as well as those of harvest gaps (Figure 2.2a). The largest harvest gaps had the lowest basal area, and the relationship between gap size and basal area was weak but significant ($r^2 = 0.17$, $p < 0.03$). This was true for natural gaps as well where larger gaps had lower overstory stand density ($r^2 = 0.47$, $p < 0.001$). The relationship between closed canopy basal area and gap size could not be tested because no gap size exists.

Using MRPP, canopy gap fraction measured by DIFN values was highest in harvest gaps (0.57) indicating a more open canopy and mean DIFN was lowest under the closed canopy (0.30) indicating a heavy upper canopy ($p < 0.01$). Mean DIFN for natural gaps was 0.34. Although DIFN values increased with increasing gap size (Figure 2.2b), the relationship between canopy openness and gap size was not significant for harvest gaps ($r^2 = 0.03$, $p < 0.33$) and natural gaps ($r^2 = 0.08$, $p < 0.21$).

a.)



b.)

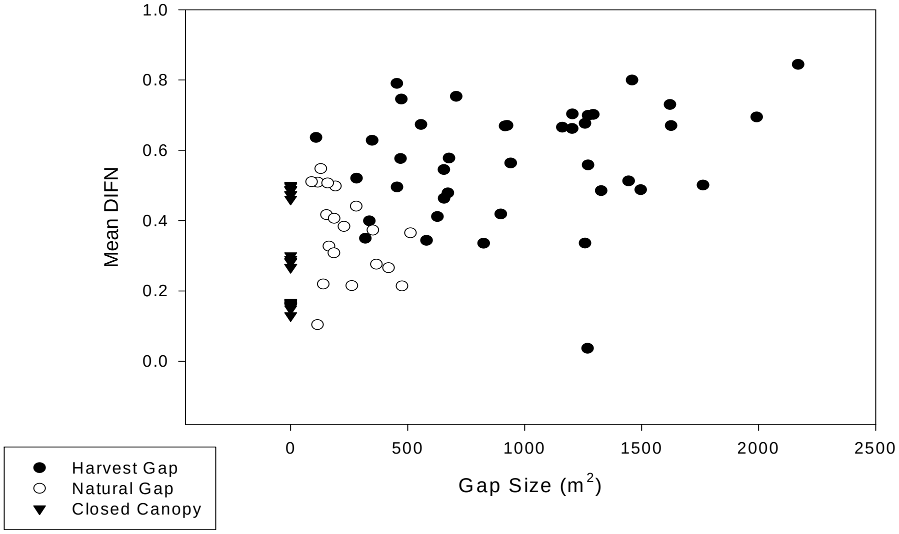


Figure 2.2: Relation between canopy openness measured by (a) basal area and (b) canopy gap fraction (DIFN) and gap size for all harvest gaps, natural gaps, and closed canopy conditions.

2.4.2. *Vegetation Differences Among Gap Conditions*

2.4.2.1. Plant Species Cover

Total mean plant cover was 83% higher in both harvest gaps (34.8% mean cover per gap) and natural gaps (25.5% mean cover per gap) combined than under the closed canopy (10.8% mean cover per transect) ($p < 0.001$), and 14% higher in harvest gaps than in natural gaps ($p < 0.048$). Total mean plant cover in natural gaps was 63% higher than under the closed canopy. The species most abundant in harvest gaps included (in order of abundance): *A. balsamea*, *A. rubrum, Aralia nudicaulis* L.*, T. canadensis,* and *Rubus occidentalis* L. (Table 2.1). Species most abundant in natural gaps included *A. balsamea, T. canadensis, Fraxinus americana* L.*, A. nudicaulis* and *Osmunda claytoniana* L. The

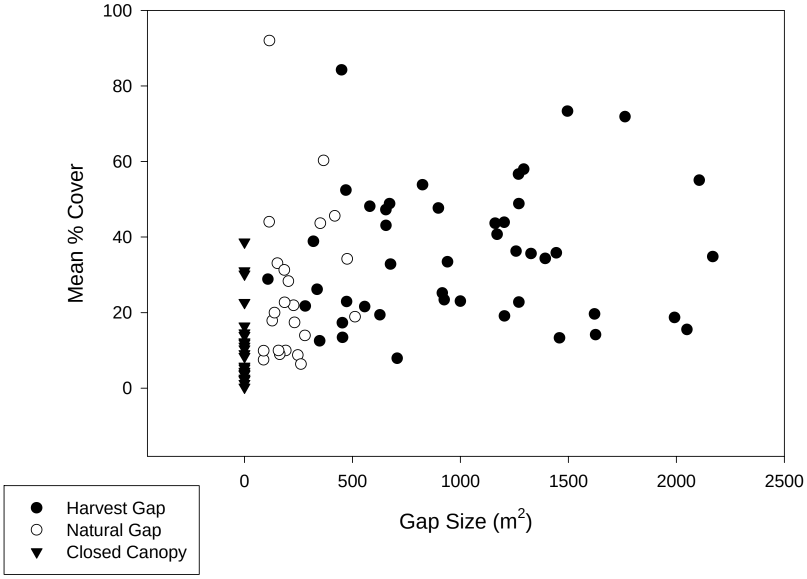


Figure 2.3: Mean total plant cover of all species for all natural gaps, harvest gaps, and closed canopy conditions by gap area.

Table 2.1. Mean cover for the 10 most abundant plant species in harvest gaps, natural gaps, and closed canopy conditions.

Plant Species	Harvest gap (%)	Natural gap (%)	Closed Canopy (%)
Abies balsamea	8.54	10.25	5.95
Acer rubrum	8.54	0.28	0.11*
Acer saccharum	--	--	0.18
Aralia nudicaulis	3.24	1.43	0.17
Betula papyrifera	0.78	0.01*	0.01*
Fraxinus americana	0.06*	1.86	0.22
Gymnocarpium dryopteris	--	--	0.13
Impatiens capensis	--	0.51	--
Osmunda claytoniana	--	0.45	0.27
Picea rubens	--	0.26	--
Pinus strobus	--	--	0.35
Polystichum acrostichoides	--	--	0.47
Populus tremuloides	0.99	0.03*	0.09*
Pteridium aquilinum	0.86	0.01*	0.01*
Rubus idaeus	0.66	0.01*	0.01*
Rubus occidentalis	1.26	0.01*	0.01*
Thuja occidentalis	--	--	0.16
Toxicodendron radicans	--	0.47	--
Trientalis borealis	0.54	--	--
Tsuga canadensis	2.20	6.64	1.71

"—" indicates that the species is not present
"*" indicates that the species is not among the10 most abundant

species most abundant under the closed canopy included *A. balsamea*, *T. canadensis, Polystichum acrostichoides* (Michx.) Schott, *P. strobus*, and *O. claytoniana.*

Because gap size was confounded with gap origin, the relationship between species abundance and gap size between harvest gaps and natural gaps were analyzed separately. Although plant cover in gaps tends to increase with increasing gap size (Figure 2.3), no relationship existed between plant cover and gap size for both harvest gaps ($r^2 = 0.02$, $p = 0.38$) and natural gaps ($r^2 = 0.01$, $p = 0.90$). Furthermore, when we restrict this analysis for harvest gaps and natural gaps of the same size range (~100 – 500m^2), gap size was still not correlated to plant cover ($r^2 = 0.08$, $p < 0.14$),

but there were significant differences in plant cover between natural gaps and harvest gaps ($p < 0.001$) within this gap range. Closed canopy transects could not be analyzed because gap size was zero for all conditions.

Overall, canopy openness was not an important variable in predicting plant abundance. Cover in harvest gaps increased with increasing canopy openness (as measured by canopy gap fraction), but the relationship was weak ($r^2 = 0.14$, $p = 0.02$)**.** No relationship was found between plant cover and canopy openness measured by canopy gap fraction in natural gaps ($r^2 = 0.03$, $p = 0.50$) and closed canopy transects ($r^2 = 0.001$, $p = 0.88$). Cover decreased with increasing stand density measured by basal area for all harvest gaps, natural gaps, and closed canopy, but this relationship was only significant for natural gaps (Harvest gaps $r^2 = 0.01$, $p = 0.61$, natural gaps $r^2 = 0.05$, $p = 0.02$, and closed canopy $r^2 = 0.14$, $p = 0.11$ closed canopy,).

Table 2.2: Mean percent cover per gap of different plant types for harvest gaps, natural gaps, and closed canopy conditions. The "*" indicates a significant difference ($p < 0.05$) among the three gap origins.

Plant Type	Harvest Gaps	Natural Gaps	Closed Canopy
Conifers	1.88	4.49*	1.72
Hardwoods	2.07*	0.82	0.17
Shrubs	0.40*	0.22	0.04
Herbs	0.52*	0.68	0.10
Ferns	0.22	0.33	0.24
Grasses	0.03	0.32	0.00
Sedges	0.06	0.08	0.01
Rushes	0.01	0.00	0.00
Mosses	0.44	3.57*	1.64
Lichens	0.06	0.29*	0.10

Using the MRPP test, herbaceous species ($p < 0.001$), hardwood trees ($p < 0.001$), and shrubs ($p < 0.001$) were more abundant in harvest gaps than in natural gaps and under the closed canopy (Table 2.2). Coniferous trees had the highest cover in natural gaps ($p < 0.01$), and all herbaceous, hardwood, coniferous, and shrub species were least abundant under the closed canopy. However, there was no difference in fern abundance among harvest gaps, natural gaps, and closed canopy ($p < 0.42$).

Other vascular species not identified to the species, but included in the overall percent cover estimation include: moss, lichens, grasses, sedges, and rushes. Natural gaps had the greatest average abundance of moss ($p < 0.01$) and lichens ($p < 0.00$) (Table 2.2). Harvest gaps had the least abundance of moss species, and closed canopy transects had the least abundance of lichen species. No differences occurred in mean cover of grasses, sedges, and rushes among all gaps and closed canopy ($p < 0.05$).

2.4.2.2. Species Diversity Among Gaps

Comparison of the regression models for the species area curves for harvest gaps, natural gaps, and closed canopy conditions indicated that the full model (i.e., accounting for each gap origin separately) provided the best model ($p < 0.001$). The full model was better than 1) pooling data from all three gap origins, 2) pooling both harvest and natural gaps versus closed canopy conditions, and 3) pooling natural gap and closed canopy conditions versus harvest gap. Since the full model best described the relation between species richness and sample plot area, we concluded that species richness differed significantly among gap origins. Therefore, species richness in harvest gaps > natural gaps > under a closed canopy (Figure 2.4).

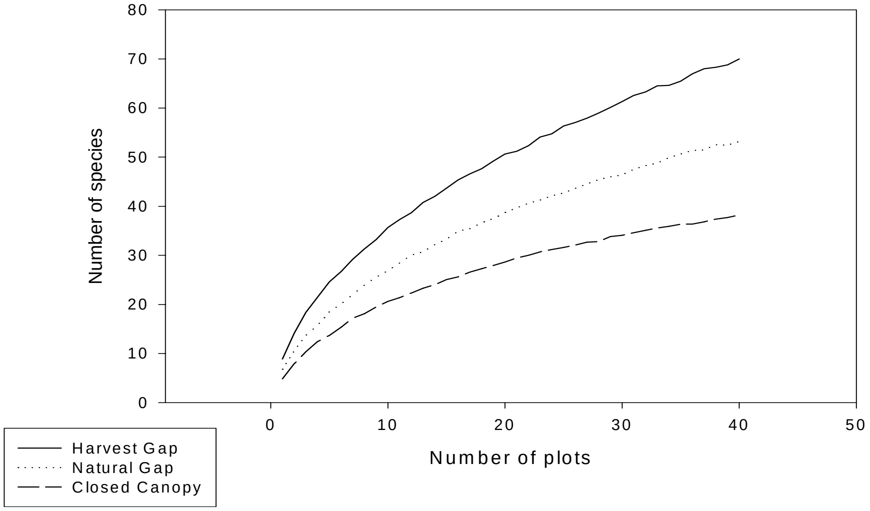


Figure 2.4: Species richness with increasing sample plot area for harvest gaps, natural gaps, and closed canopy conditions. Richness was calculated using all possible combinations of random subsampling of sample plots for each condition.

Plant evenness measured by the slope of the dominance diversity curves was different among harvest gaps, natural gaps, and closed canopy conditions ($p < 0.001$). Harvest gaps had the shallowest mean slope ($a = 57$), and the closed canopy had the steepest mean slope ($a = 23$). The natural gap mean slope was somewhat greater to closed canopy conditions ($a=37$) (Figure 2.5). Both gaps had a higher slope value than under the closed canopy ($p < 0.02$), and harvest gaps had a higher slope value than natural gaps ($p <0.003$). These results indicate 1) that neither gaps nor closed canopy conditions had an even distribution of plant species (i.e., $a=0$), 2) that the cover was less

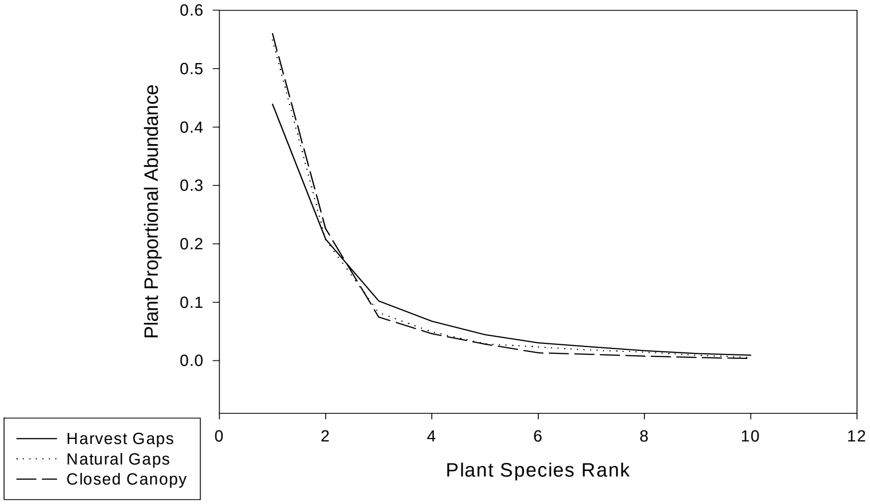


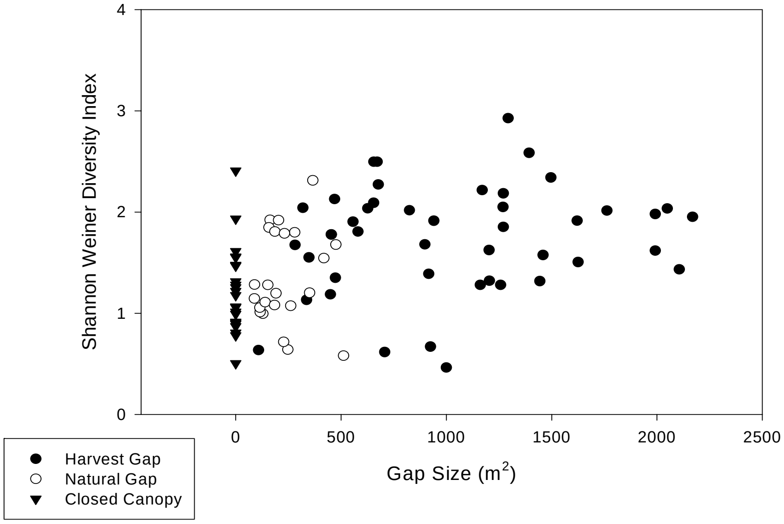
Figure 2.5: Mean dominance diversity curves truncated for the 10 most abundant plant species for harvest gaps, natural gaps, and under the closed canopy. Slope of the curves based on the model y= e $^{-ax}$, were used as an indicator of plant evenness among gaps and closed canopy conditions.

evenly distributed among species under the closed canopy than in the gaps, and 3) that the larger harvest gaps had greater evenness than the natural gaps. However, no relation was found between the slope of the curves and gap area for both harvest gaps ($r^2 = 0.01$, $p < 0.63$) and natural gaps ($r^2 = 0.05$, $p < 0.30$), nor was the slope of the curves correlated with canopy openness as measured by overstory basal area or canopy gap fraction for all harvest gaps, natural gas, and closed canopy conditions.

As stated before, the Shannon diversity indices (both diversity and evenness) are sensitive to species richness. Although sample area in this study was proportional to gap size, we may still evaluate these indices of diversity (albeit with caution), because we found that species richness (as determined by the species area curves) was independent of sample area (Figure 2.4). Nonetheless, to eliminate the large variation in sample area, we restricted harvest gaps and natural gaps of the same size range (~100-500m^2), and we found that there was no difference in Shannon-Weiner diversity index between natural gaps and harvest gaps ($p < 0.15$).

Differences in Shannon diversity for all gaps and closed canopy transects were similar to the results for species richness. Using ANOVA with linear contrasts, the Shannon-Weiner index was higher in gaps than under closed canopy conditions ($p = 0.0087$), and it was higher in harvest gaps than in natural gaps ($p = 0.0027$). Shannon-Weiner diversity was not correlated with canopy openness measured by canopy gap fraction in harvest gaps ($r^2 = 0.01$, $p = 0.31$), natural gaps ($r^2 = 0.07$, $p = 0.24$), and closed canopy ($r^2 = 0.17$, $p = 0.06$). Similarly, there was no relation between Shannon diversity and basal area for harvest gaps ($r^2 = 0.01$, $p = 0.67$), natural gaps ($r^2 = 0.12$, $p = 0.12$) and

a.)



b.)

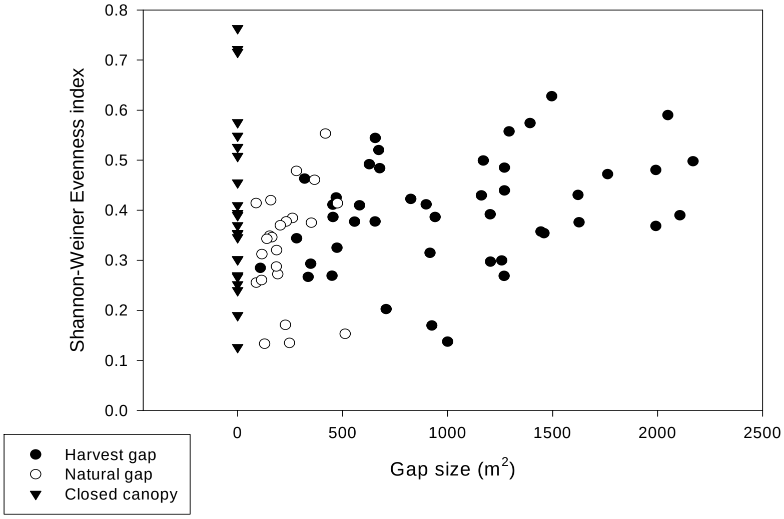


Figure 2.6: Relation between Shannon-Weiner index (a) and Shannon Equitability index (b) by gap size for harvest gaps, natural gaps, and closed canopy conditions.

closed canopy transects ($r^2 = 0.01$, $p = 0.82$). The Shannon-Weiner index was not correlated to gap size for both harvest gaps ($r^2 = 0.03$, $p < 0.228$) and natural gaps ($r^2 = 0.01$, $p < 0.71$) (Figure 2.6a). Similarly, when harvest gaps and natural gaps were isolated to the same size range, the Shannon diversity index showed no correlation to gap size ($r^2 = 0.08$, $p < 0.14$).

The closed canopy transects had the highest Shannon-Weiner evenness values compared to harvest and natural gaps as well as a large range of evenness values. As a result of the wide range of evenness values among the three conditions, there was no statistical difference in the Shannon evenness index among harvest gaps, natural gaps, and under the closed canopy ($p < 0.74$). When harvest gaps and natural gaps of the same size range are isolated, there was no difference in Shannon evenness index ($p < 0.36$) between harvest gaps, and natural gaps. Furthermore, no relationship between Shannon Evenness and gap size was found for harvest gaps ($r^2 = 0.01$, $p < 0.71$) and natural gaps ($r^2 = 0.01$, $p < 0.73$) (Figure 2.6b).

2.4.2.3. Tree Regeneration and Stand Composition

The average number of regenerating trees in each height class was independent of gap origin or closed canopy ($p < 0.15$). The greatest number of stems in all gap and closed canopy conditions were growing in the seedling (i.e., < 0.5 m) height class (Figure 2.7). Natural gaps had the greatest number of stems growing in this height class (57,961 stems / ha) and closed canopy transects had the least number of stems growing in this height class (28,967 stems / ha). Tree abundance decreased with increasing stem height, and the average number of stems > 0.5 m tall was less than 10,000 stems / ha.

Acer rubrum and *A. balsamea* had the greatest number of regenerating trees in the < 0.5 m height class for both gaps and closed canopy conditions (Table 2.3)

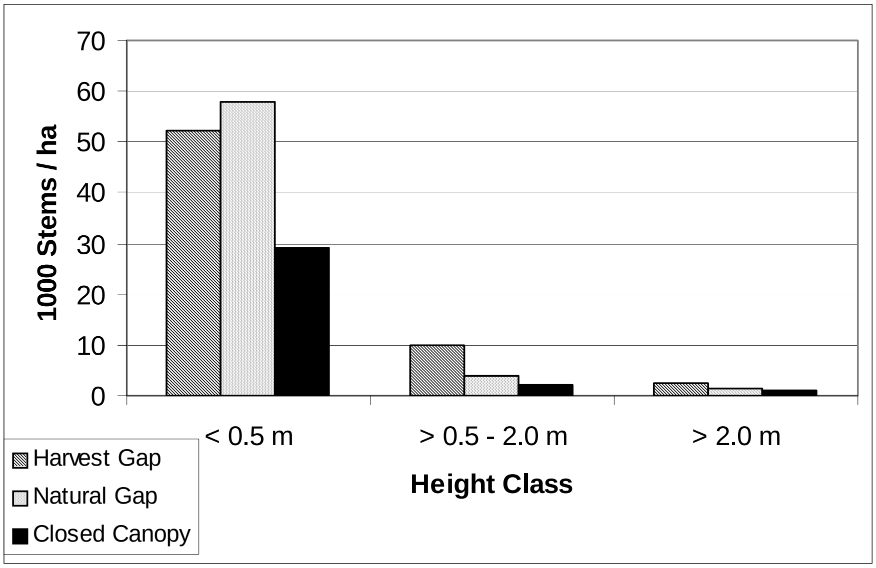


Figure 2.7: Tree regeneration by height class for all harvest gaps, natural gaps, and closed canopy conditions for all height classes.

B. papyrifera, *P. strobus*, and *T. canadensis* were also the most abundant species growing < 0.5 m height class for harvest gaps. These species were also abundant under natural conditions (i.e., natural gaps and closed canopy) with the exception *B. papyrifera*; instead of *B. papyrifera*, the natural conditions are regenerating *Ostrya virginiana* (Mill.)K. Koch (Table 2.3).

In natural gaps and closed canopy conditions, *A. balsamea* was the most abundant tree in the > 0.5 m to 2.0 m height class, whereas in harvest gaps, *A. rubrum* was most abundant tree species in this height class. After *A. rubrum*, the most abundant stems in

Table 2.3: Density of tree regeneration by species and height class for all harvest gaps, natural gaps, and closed canopy conditions.

HG = harvest gaps, NG = natural gaps, and CC = closed canopy transects.

	Tree Stems <0.5 m tall			**Tree Stems > 0.5 - 2.0 m tall**			**Tree Stems > 2.0 m tall**		
	1000 stems / ha			1000 stems / ha			1000 stems / ha		
Species	**HG**	**NG**	**CC**	**HG**	**NG**	**CC**	**HG**	**NG**	**CC**
Abies balsamea	7.44	17.62	6.41	0.64	1.18	0.55	0.37	0.42	0.57
Acer rubrum	25.83	18.22	7.83	1.55	0.82	0.31	1.27	0.06	0.03
Acer saccharum	**	0.57	1.85	**	**	0.05	**	0.03	0.11
Betula allegheniensis	**	**	**	0.03	0.01	**	**	**	**
Betula papyrifera	5.12	**	0.33	0.20	**	0.00	0.06	**	**
Fagus grandifolia	**	0.41	**	**	0.01	**	0.02	0.03	**
Fraxinus americana	**	1.56	**	**	0.07	0.02	**	0.11	**
Fraxinus species	1.52	**	4.40	0.10	**	**	**	**	**
Ostrya virginiana	**	2.11	0.84	**	**	**	**	0.03	**
Picea rubens	0.59	**	**	0.05	**	**	0.05	**	**
Pinus strobus	4.53	11.46	2.36	0.15	0.39	0.10	0.02	0.02	0.05
Populus grandidentata	**	**	0.27	0.06	0.02	0.01	0.09	**	0.03
Populus tremuloides	0.66	1.33	1.55	0.16	0.13	0.04	0.25	**	**
Prunus pennsylvanica	0.53	**	**	**	0.02	**	**	0.11	**
Quercus rubra	0.70	0.53	**	**	**	**	**	**	**
Thuja occidentalis	**	**	**	**	**	0.01	0.03	0.03	0.14
Tsuga canadensis	3.02	8.55	2.36	0.16	0.71	0.15	0.09	0.45	0.11

harvest gaps were *A. balsamea*, *B. papyrifera, P. tremuloides*, and *T. canadensis*. After *A. balsamea*, natural gaps were regenerating (in order of abundance) *T. canadensis*, *P. strobus*, and *P. tremuloides*. Under closed canopy conditions, only eight tree species were found in the > 0.5 m to 2.0 m height class, and the most abundant species, after *A. balsamea*, included *A. rubrum*, *T. canadensis*, *P. strobus,* and *Acer saccharum* L.

2.4.2.4. Plant Community Composition

One hundred ninety-five plant species were identified among all harvest gaps, natural gaps, and closed canopy conditions. Among these species, 82 were rare (i.e., occurring only once or twice). All species were categorized based on their life history characteristics in Maine such as habitat, shade tolerance, reproductive habits, and successional status (USDA, NRCS 2002). Of the 195 species identified, the majority (55) are classified as shade intolerant, and considered to be early successional species. Forty-two of the species are classified as intermediate in shade tolerance and found in both highly disturbed areas as well as mature forest, and 37 of the 195 species were classified as tolerant, late successional species. Additionally, 10 were obligate wetland indicator species, and 17 of these species were classified as exotic either nationally or in Maine (USDA, NRCS 2002; Haines and Vining 1998). Finally, 34 of these species did not have enough research available to be classified into categories or were identified only to the genus.

More than half (112 species) of the 195 species identified were found only in harvest gaps. Among the remaining species, 33 were common to all harvest gaps natural gaps, and closed canopy conditions, 16 were found only in natural gaps, and 5 were found only under the closed canopy. Finally, two species, *Maianthemum racemosum* (L.)

Link and *Pyrola chlorantha* Sw., were exclusive only to natural conditions (i.e., natural gaps and closed canopy).

There were 140 species that could be considered ‘gap specialists’ (i.e., only occur in gap environments). The two most important gap specialists were *Rubus* species. Among the 10 most important gap specialists, 8 species were classed as ruderal or early successional species, and four of these were *Rubus* species. Two exceptions, *F. grandifolia* (i.e. the fourth most important) and *Onoclea sensibilis* L., were shade tolerant, mid-to-late successional species.

Harvest and natural gaps of similar sizes (from 100 m^2 to 550 m^2) were examined to determine whether gap origin was correlated with species composition by eliminating gap size as a variable. One hundred twenty-one species were identified in natural gaps and harvest gaps in this size range. Among these species, 49% were found only in harvest gaps, 35% were found in both harvest and natural gaps, and 26% of the species are found only in natural gaps.

Most plant species that were found exclusively in harvest gaps were classed as early successional or shade intolerant species (35%). Eighteen percent of these species were exclusive to harvest gaps and classified as intermediate in shade tolerance, and 11% are considered shade tolerant or late successional species. Fourteen percent of these species were exotics (i.e., introduced to Maine). The greatest numbers of species (31%) exclusive to natural gaps were intermediate in tolerance (USDA, NRCS 2002; Burns and Honkala 1990). Thirteen percent of the natural gap species were shade intolerant, early successional, and thirteen percent were shade tolerant, late successional species. Twenty-

Table 2.4: Importance index, mean frequency, and mean cover for the ten most important species found in harvest gaps, natural gaps and under closed canopy conditions. Importance index for a species was calculated by multiplying the mean frequency of a species by its mean percent cover (i.e., cover (%) in table) in a gap. The symbol "**" indicates that the species is not important.

	Harvest Gaps			**Natural Gaps**			**Closed Canopy**		
Species	**Cover (%)**	**Freq (%)**	**Import**	**Cover (%)**	**Freq (%)**	**Import**	**Cover (%)**	**Freq (%)**	**Import**
Abies balsamea	8.42	77	648.17	10.25	91	932.78	5.95	73	434.43
Acer rubrum	8.93	95	848.35	0.28	80	22.06	0.11	65	6.99
Acer saccharum	0.13	2	0.26**	0.22	12	2.64**	0.18	20	3.50
Aralia nudicaulis	3.05	35	106.62	1.43	41	58.61	0.17	10	1.65
Betula papyrifera	0.75	46	34.5**	0.01	7	0.07**	0.01	9	0.09**
Fraxinus americana	0.06	8	0.48**	1.86	30	55.78	0.22	8	1.73
Impatiens capensis	0.00	0	0**	0.51	9	4.62	0.00	0	0**
Maianthemum canadense	0.44	65	28.43	0.23	60	14.00	0.08	30	2.28
Osmunda claytoniana	0.47	5	2.35**	0.45	3	1.35**	0.27	5	1.34
Pinus strobus	0.51	58	29.77	0.22	68	14.73	0.35	37	12.95
Polystichum acrostichoides	0.02	1	0.02**	0.11	10	1.10**	0.47	14	6.53
Populus tremuloides	0.97	28	27.27	0.03	14	0.42**	0.09	14	1.26**
Rubus idaeus	0.66	27	17.88	0.00	0	0**	0.00	0	0**
Toxicodendron radicans	0.14	3	0.42**	0.47	10	4.67	0.01	2	0.02**
Trientalis borealis	0.56	57	31.80	0.21	48	10.24	0.06	17	1.02**
Tsuga canadensis	2.20	48	105.56	6.64	67	445.04	1.71	52	89.13

five percent (4) of the species exclusive to natural gaps were wetland obligate species. Of the five species exclusive to closed canopy transects, two species of the five were wetland, obligate species, and the remaining three species were shade intolerant, intermediate, and shade tolerant (USDA, NRCS 2002; Burns and Honkala 1990).

Abies balsamea was the most important species for all harvest gaps, natural gaps, and closed canopy conditions. Five other species, *A. rubrum*, *A. nudicaulis*, *Maianthemum canadense* Desf., *P. strobus*, and *T. canadensis*, were important across all three conditions. Natural gaps and closed canopy conditions shared one other species that was not important in harvest gaps, *F. Americana*. Harvest gaps and natural gaps shared one important species, *Trientalis borealis* Raf., a common forest understory herb, which was not important under the closed canopy.

In harvest gaps, both shade intolerant, ruderal species comprised the remaining most important species. These species were (in order of importance): *A. rubrum*, *B. papyrifera, P. tremuloides*, and *Rubus idaeus* L. (USDA, NRCS 2002; Burns and Honkala 1990). In natural gaps, the remaining of the 10 most important species included *F. americana,* an intermediate- to shade tolerant species, *Impatiens capensis* Meerb, a species characteristic of moist conditions, and *Toxicodendron radicans* (L.) Kuntze, a robust species that grows under a variety of environmental conditions (USDA NRCS 2002*)*. Under the closed canopy, the remaining important species were adapted to more shaded conditions with intermediate- to shade-tolerant. They included: (in order of importance): *P. acrostichoides, A. saccharum*, *F. americana*, and *O. claytoniana*. *O. claytoniana* and *P. acrostichoides*, are common forest understory ferns, and *A. saccharum* is a shade tolerant tree (Burns and Honkala 1990).

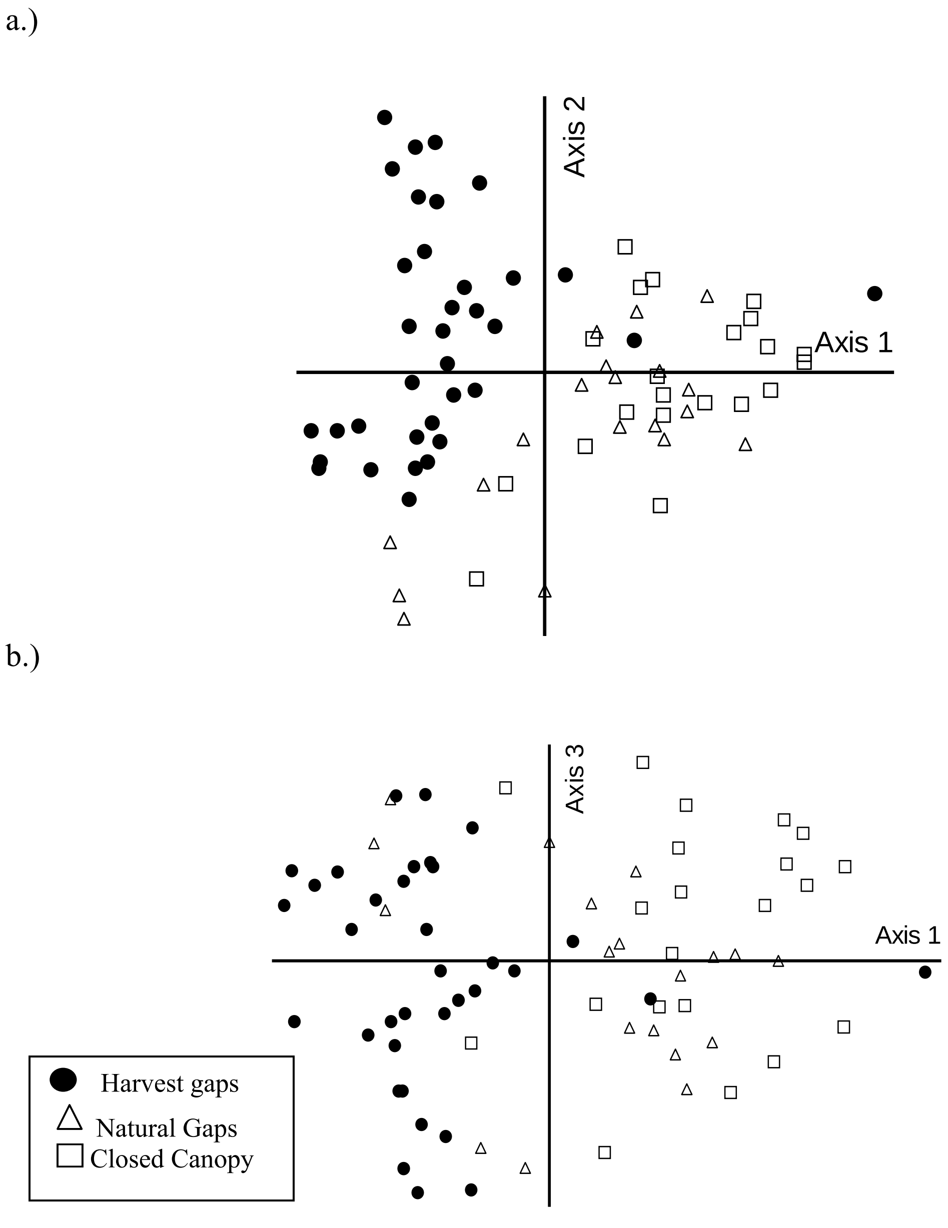


Figure 2.8: DCA (Detrended Correspondence Analysis) on the presence and absence of all species in all gaps and transects for harvest gaps, natural gaps, and closed canopy conditions. Plots close in ordination space are more similar in composition. Figures a and b represent two different viewpoints (i.e., axes in ordination space) of plot orientation.

Finally, because natural gaps and closed plots are the conditions for which we evaluate the success of emulating natural gaps, we performed a DCA on the presence or absence of plant species to examine the compositional similarity between harvest gaps and natural conditions. Rare species were down-weighted because 87 of the 112 species in harvest gaps occurred only once or twice, and the axes were rescaled. The large spread of the plots in ordination space suggested a high range of variation in species composition for all harvest gaps, natural gaps, and closed canopy conditions (Figure 2.8). More importantly, the distinct separation between harvest gaps and natural conditions around the second and third axes suggests that natural gaps and closed canopy transects were more similar in composition to each other, and that harvest gaps were less similar in composition than natural conditions.

2.4.3. Vegetation Differences Within Harvest Gaps

2.4.3.1. Abundance and Diversity

The objective of this analysis was to assess whether there were any patterns of vegetation abundance and diversity in the north-south transects within the harvest gaps. Because the number of sample plots or distance sampled within gaps was proportional to gap size, we conducted this analysis in stages, starting first with the largest gaps and then systematically examining within gap patterns for progressively smaller gaps. The assumption with this approach was that any patterns of within gap vegetation, abundance, and diversity would likely be most apparent in the largest gaps.

Due to the nature of this study, all gaps analyzed for this analysis were harvest gaps since these were the largest gaps. The largest gaps with at least 4 replicates ranged in size form 1,170 to 2,106 m^2 and contained ± 30 m transect length. The next largest gaps with sufficient replication (i.e., 10 replicates) ranged in size from 627 to 1,762 m^2, and contained ± 25 m transect length. The smallest gaps examined were 336 to 2,049 m^2 in size and had a ± 20 m transect length.

For the largest gaps (± 30m transect length), total mean cover was 49% greater within 10 m of the center of the gap than at the edge of the gap ($p < 0.03$), and species abundance was positively correlated with the location within the gap ($r^2 = 0.27$, $p < 0.0001$) (Figure 2.9). Furthermore, the north side of the gaps had higher cover than the south side of the gaps ($p < 0.02$).

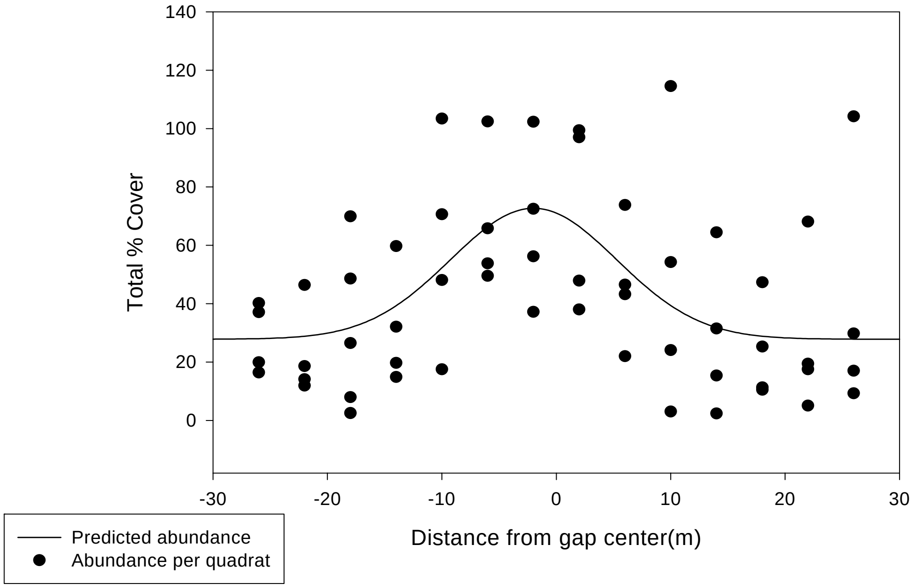


Figure 2.9: Mean cover of all plant species at various distances from the centers of the four largest harvest gaps (1,170-2,106 m^2). Negative distances denote southern plots, and ± 30 m indicate the ends of the transect. A four parameter Gaussian regression model was used.

In the next largest gaps (627 to 1,762 m^2), total mean cover was 52% greater in the center than at the edge of the gap ($p < 0.01$), but no relationship was found between species abundance and distance from the gap center ($r^2 = 0.60$, $p = 0.92$). The smallest gaps analyzed (336 to 2,049 m^2) did not show any differences in abundance ($p < 0.06$) between the center of the gap and the edge of the gap, and hence, further analysis of smaller gaps was terminated. Further, there was no difference in species abundance between the north side and the south side of the gap for these smaller gaps ($p < 0.01$).

There were no differences in species richness ($p < 0.38$), evenness ($p < 1.00$), and Shannon-Weiner diversity index ($p < 0.57$) between the north and the south side of the largest gaps (1,170 to 2,106 m^2). There was also no difference in richness ($p < 0.85$), evenness ($p < 0.78$), or Shannon-Weiner index ($p < 1.00$) between the center of the gap and the edge of the gap. Similar results were found for gaps 627 to 1,762 m^2 where there was no difference in cover ($p < 0.51$), richness ($p < 0.41$), evenness ($p < 0.31$), or Shannon-Weiner index ($p < 0.35$) between the north and south sides of the gap. Because there was no relationship between diversity and 1) location within the gap and 2) canopy openness for the largest gaps, we did not test these variables any further for the next largest gap size, 627 to 1,762 m^2

2.4.3.2. Tree Regeneration

Because we were looking for trends in tree species regeneration by their life history characteristics (i.e., ruderal or late successional species) relative to their location within the gap (i.e., gap center versus gap edge), we first restricted this analysis, again, to the largest gaps (i.e., 1170 - 2106m^2). We selected five tree species of various shade tolerance, *A. rubrum, P. tremuloides, P. rubens, T. canadensis*, and *P. strobus*, to determine if tree regeneration was correlated to the location within the gap. Although all of the selected tree species were abundant and/or more frequent in the southern side of the gap, there was no significant relationship between tree abundance of individual species and location within the gap. Furthermore, for the largest harvest gaps, there was no significant relationship between the numbers of seedlings (< 0.5 m tall), saplings (> 0.5 – 2.0 m tall), and trees (> 2.0 m tall) of all species and their location within the gap.

2.4.3.3. Plant Species Composition

In harvest gaps, the four most important species were *A. balsamea*, A. *rubrum*, *T. canadensis*, and *A. nudicaulis* up to 14 m north and 14 m south of the gap center. In the sample plots up to 18 m north and 14 m south of the gap center, the remaining most important include (in order of importance) *R. occidentalis*, *Rubus pubescens* Raf., *Pteridium aquilinum* (L.) Kuhn *ex* Decken, *P. tremuloides*, *P. rubens*, *B. papyrifera*, *Corylus cornuta* Marsh., *Alnus incana* (L.) Moench, and *P. grandidentata*. In natural gaps, *A. balsamea* and *T. canadensis* were the two most important species. *I. capensis*, *T. radicans* (L.) Kuntze, *D. intermedia*, and *O. virginiana* K. Koch. were important in natural gaps, but they were either not important or did not exist in harvest gaps. Overall, importance values for species in natural gaps were far less than importance values in harvest gaps. Similarly, in closed canopy transects, *A. balsamea* and *T. canadensis* were the two most important species in all quadrats. Other important species included were *O. claytoniana*, *P. acrostichoides*, *F. americana*, *P. strobus*, *A. saccharum*, *C. cornuta*, *Gymnocarpium dryopteris* (L.) Newman, *P. rubens*, *P. grandidentata*, and *T. occidentalis*.

We selected the three most frequent ruderal, early successional species, *P. tremuloides*, *R. idaeus*, and *P. aquilinum* (USDA NRCS 2002) within the largest gaps (1170 -2106 m^2) to determine if early successional species were more abundant in the centers of the largest gaps. Although both *P. tremuloides* and *R. idaeus* were more important on the south side of the gap, and *P. aquilinum* was more important in the north side of the gap, the importance of these species was not correlated with their location within the gap. Because no significant relationships existed, we terminated any further analysis of species composition and location within the gap for gaps smaller than this size range.

2.5. Discussion

2.5.1. *Plant Abundance*

Results from this study indicate that an expanding gap shelterwood harvest creating gaps openings from 0.10 to 0.20 ha in size increased the mean cover of plants by 69% (i.e., absolute cover including all species) compared to closed canopy conditions. Physical changes caused by gap harvesting may have substantially influenced gap regeneration by altering the microenvironment in the gap, and as a result of those physical changes, plant resources (light, soil moisture, and nutrients) become more abundant for the growth of plants within the gap. Although plant cover tended to increase with increasing gap size, the greater species abundance in harvest gaps was not correlated with gap size or overstory density within the gap, and only weakly correlated with canopy openness as measured by canopy gap fraction. Large permanent reserve trees occupying the upper canopy, and basal sprouting of *A. rubrum*, comprise a large amount of space both vertically and horizontally, and are likely to influence the canopy gap fraction measurements creating a weak relationship between plant abundance and canopy openness. Nonetheless, a biological relationship is apparent where the highest DIFN occurred in the largest harvest gaps indicating a large amount of light reaching the forest floor.

A study of harvest gaps in the Southern Appalachians indicated that plant biomass production was doubled two seasons after harvest compared to preharvest plant productivity (Philips and Shure 1990). Furthermore, a study in northeastern forests suggest that the spatial location in which a species colonizes in a gap may be more important than overall increase in light (Poulson and Pratt 1989). The size, shape, abundance, and distribution of standing dead and live trees, downed woody material and regenerating vegetation can influence humidity, light intensity, air temperature, and nutrient availability (Lundquist and Beatty 2002). We found greater plant abundance in the center of large (1,170 – 2,106 m^2 area) harvest gaps than on the north and south edges of the gaps. The presence of 39 shade intolerant or light-demanding species out of 141 species found only in the harvest gaps clearly suggests an overall increase in light as a resource. Therefore, the greater species abundance in harvest gaps is more likely related to changes in light, soil disturbance, and other microenvironmental factors.

There was little overlap between natural gap area and harvest gap area, but natural gaps had only 19% difference in mean plant cover than harvest gaps, and 62% more cover than closed canopy conditions. This result suggests that canopy openings alone, regardless of gap size, provide an ample amount of light to greatly influence plant growth, particularly since mean plant abundance was not related to gap size. Mean plant cover was also not related to canopy openness, but natural gaps had higher mean DIFN values than under the closed canopy suggesting, again, a biological significance between light and plant growth. Because natural gap size is small, lateral extension of the upper canopy can greatly influence the amount of light reaching the forest floor reducing plant abundance, but lateral extension does not seem to be influencing plant abundance for natural gaps in this study. Furthermore, natural gaps are rarely limited to a single event where the death of a single canopy tree in one year, for example, can create the blow down of several surrounding trees in the following years. This condition defines an expanding gap (Runkle 1982). Hence, the continuous opening of the canopy by multiple events may have allowed plants to sustain high growth rates.

Other studies on natural gap regeneration report an increase in species abundance early in succession that gradually declines with the closing of surrounding overstory canopy. Treefall gaps in an eastern hemlock forest demonstrate a definitive trend in succession for the most common understory species up to five years after gap formation, but total understory cover returned to pre-gap levels 11-14 years following gap formation (Rankin and Tramer 2002). In a mature oak forest, herbaceous communities in natural gaps increased in abundance only if the gap opening was greater than the predisturbance understory assemblage (Ehrenfeld 1980). Some natural gaps in this study may still be in early stages of succession where many were aged near 1995. These younger natural gaps may be creating a higher mean of plant abundance where the older natural gaps are less abundant.

2.5.2. *Plant Diversity*

Results of the species area curves analysis indicated that species richness in canopy gaps, both harvest and natural, was higher under closed canopy conditions, and that harvest gaps were more diverse than natural gaps. The differences in the slopes of the dominance diversity curves indicate that the evenness of the plant diversity was not equal among all harvest gaps, natural gaps, and closed canopy conditions. Harvest gaps contained 112 new species that were not present in natural gaps or under the closed canopy. Although species richness was higher in harvest gaps, 82 of these species occurred only once or twice, indicating a low frequency and uneven distribution of these new species.

In contrast, the Shannon-Weiner Equitability index indicated no difference among plant evenness among harvest gaps, natural gaps, and closed canopy conditions. A wide range of evenness values were found under closed canopy conditions indicating an even distribution of abundance values for the small number of species found under relatively homogenous conditions. Hence, as a result of large evenness values under the closed canopy and large evenness values in harvest gaps (i.e., indicating a high diversity with an even distribution), no difference was detected among the three conditions.

The Shannon-Weiner diversity index indicated similar results to species richness where harvest gaps had the highest diversity. Because larger harvest gaps had more opportunity to acquire plant species, we would expect higher Shannon diversity values for harvest gaps with greater sample area. However, several natural gaps with smaller sample area had very high Shannon diversity indices comparable to values found in harvest gaps. In addition, our analysis using species area curves revealed that species richness was higher in harvest gaps, less in natural gaps, and lowest under closed canopy conditions. Therefore, despite the possible confounding between gap area and the

Shannon-Weiner index, our results indicate that the diversity index differences demonstrated here are supported.

Thus, all diversity indices examined in this study indicated that the creation of gaps, both harvest and natural, promoted the colonization of new species. High plant diversity among gaps was due to a combination of both gap size and canopy openness measured by canopy gap fraction, although these relationships were weak. Several studies on natural gaps report that species diversity increases with gap size (Busing and White 1997; Clinton et al. 1994; Phillips and Shure 1990; Runkle 1982), and many studies have indicated that intermediate size gaps (~300 m^2), both harvest and natural, have not increased diversity in second-growth forests (Beckage et al. 2000; Collins and Pickett 1988a; Hibbs 1982; Della-Bianca and Beck 1985). Therefore, the greater plant diversity in gaps is likely due to the change in microenvironment as a result of the disturbance creating enough light and temperature fluctuations to allow early successional species to colonize the gap. For example, of the total number of species found in both harvest gaps and natural gaps of the same size range (100 – 500 m^2), half of these species were present only in harvest gaps, suggesting that gap origin rather than gap size had a greater influence on plant species composition. Natural gaps had a greater species diversity than closed canopy transects but less than harvest gaps. This result suggests that in some natural gaps, the occurrence of a treefall (i.e., rather than the slow death of canopy trees) also created environmental conditions allowing the colonization of few new plant species.

2.5.3. *Plant Composition*

Increasing stand structural diversity to promote the full sere of young and old forest structure is a long-term goal for the expanding-gap treatments in this study. Enhancing structural diversity suggests creating early successional habitat to allow the colonization of new plant species. Four growing seasons after harvest, the forest structure is such that many early successional species have been introduced in the harvest gaps that were not present under the closed canopy, therefore increasing the overall plant diversity of the harvested research areas. The differences in age between harvest gaps and natural gaps likely account for the lower plant diversity in natural gaps. The majority of the natural gaps were five to eleven years old, and although the natural canopy opening allowed significant growth for plants present in the understory, lateral extension of the upper canopy may have prohibited the colonization of a large number of new species in the natural gaps.

Change in species composition as a result of increased diversity, however, may have significant implications on gap regeneration, especially potential competition with desired tree species and/or wildlife habitat. Although many studies indicate high plant diversity as a result of the influx of early successional species in forest gaps, diversity and abundance often decline as the these gaps get older. The decline is mostly attributed to extensive lateral growth by canopy edge trees reducing available sunlight, and extensive tree regeneration within the harvested gap outcompeting the opportunistic herbs (Philips and Shure 1990; Collins and Pickett 1998b). Runkle (1982) found that in old-growth mesic forests, edge trees responded to canopy disturbance with lateral extension rates of 8.3 cm / year for *A. saccharum* and 7.0 cm/ year for *T. canadensis.* Gap edge trees in a hemlock and hardwood stand had lateral extension rates from 14.03 to 6.10 cm/year for the following species (in descending order of extension rates) *Q. rubra*, *B. papyrifera*, *B. allegheniensis*, *T. canadensis*, *A. rubrum*, and *P. strobus* (Hibbs 1982).

2.5.3.1. Understory Composition

Many studies have shown that gap harvesting has reduced or eliminated the original forest understory. For example, a shelterwood harvest in an old-growth forest of Ontario eliminated 14 species present in the understory and introduced 10 species not present before harvest; four of these species were early successional and/or invasive species (Quinby 2000). In an oak-pine forest of Maine, common understory forest herbs, *M. canadense*, *Gaultheria procumbens* L., and *Mitchella repens* L., present before gap harvesting decreased in abundance significantly after gap creation, but increased in abundance in control areas. Furthermore, *Clintonia borealis* (Ait.) Raf. was recorded only in the control areas that were 60-80 years old and was absent from neighboring harvested gaps (Schumann et al. 2003). *C. borealis* is associated with late stages of forest succession (Pitelka et al. 1985).

In this study, the plant composition obtained under natural conditions was used as a comparison to evaluate the success of an expanding-gap harvest on emulating natural conditions. Although the harvest introduced many new species, common forest understory herbs with a higher shade tolerance such as *M. canadense*, *G. procumbens*, *M. repens*, *Cornus canadensis* L., *T. borealis*, and *C. borealis* were more important in harvest gaps than natural gaps and closed canopy, and *M. canadense* and *A. nudicaulis* were two of the most important species in harvest gaps. Furthermore, *G. procumbens* was absent under the closed canopy and *C. borealis* was absent in both natural gaps and closed canopy. A study of harvest gaps in an eastern hemlock forest by Rankin and Tamer (2002) demonstrated similar results. Of eight common forest understory species examined, all responded to harvest gap formation with a significant positive response except *Medeola virginiana* L., which reached its peak cover under the closed canopy. Hence, the expanding-gap harvest not only maintained the populations of species common in the forest understory, it also provided an environment for these species to become more abundant.

2.5.3.2. Gap Specialists

Gap specialists are species that are exclusive to gap environments. Some studies suggest that the predisturbance communities and/or the autecology of the predisturbance species have a greater influence on gap herb succession than the recruitment of opportunistic species (Hughes and Fahey 1991; Collins and Pickett 1988a). In this study, 141 species out of the 195 identified species are gap specialists including both harvest and natural gaps suggesting that the creation of early successional habitat had a greater influence on gap regeneration than the predisturbance plant communities.

Rubus idaeus, a gap specialist, was one of the most important species in harvest gaps, and of the four *Rubus* species identified, only *R. pubescens* was present in natural gaps. The dearth of *Rubus* species in natural gaps in this study is similar to natural treefall gaps in New Hampshire, where the recruitment of *Rubus* species was relatively rare (Battles and Fahey 2000). Although uncommon in natural gaps, several studies have indicated that *Rubus* species are the most important shrub regenerating in harvest gaps. In harvested gaps of an oak-pine forest of Maine, *R. allegheniensis* and *R. idaeus* were both abundant in harvested gaps five and 10 years after harvest. *R. allegheniensis* began to decline 10 years after harvest, but *R. idaeus* continued to increase in abundance 10 years after harvest. Furthermore, *R. idaeus* abundance was significantly different between harvested gaps and controls (Schumann et al. 2003). In harvested gaps of New Hampshire, *R. idaeus* was one of the most common shrubs after overstory removal and remained abundant three years after harvest, whereas other shrubs showed a decline in abundance. Furthermore, *R. idaeus* was not present in the intact forest (or unharvested control) or in the predisturbance communities (Hughes and Fahey 1991). Several factors influence *Rubus* recruitment and vegetation succession in harvested gaps. Highly viable, buried seeds are the most prominent form of *Rubus* recruitment, and the level of soil disturbance also influences their presence. Not only is it the most abundant species regenerating after harvest, but also its abundance continues to increase throughout the stages of early succession, often taking over a gap area. Many studies indicate that *Rubus* spp. can stop the early succession of trees if management actions are not taken. For example, a study on *Rubus* and spruce competition in Maine indicates that *Rubus* biomass production was positively correlated with an increase in nutrients, light, moisture, and growing space. Further, spruce seedling biomass production decreased with interspecific competition mostly with *Rubus* species (Lautenschlager 1999).

2.5.4. *Tree Regeneration*

2.5.4.1. Tree Abundance

The greatest numbers of stems regenerating in all gaps and closed canopy are seedlings (i.e., < 0.5 m tall), but natural gaps were regenerating more seedlings than harvest gaps. Natural gap sizes range from 100 to 500m^2 indicating that this range of gap sizes is large enough to generate a new cohort. Harvest gap sizes in this study ranged from 100 to 2,100m^2, and have introduced many new species that may be competing for resources with establishing tree seedlings. The differences in gap environment caused by the different disturbance regimes (i.e., harvesting vs. treefall) that allowed the introduction of ruderal species (i.e., the abundance of *Rubus* species in harvest gaps) may account for the deficit of seedling regeneration in harvest gaps. Some studies have demonstrated that regenerating seedling densities are low with dense understories in gaps (Ehrenfeld 1980; Huenneke 1983) because of light attenuation by the dense shrub understory (Beckage et al.2000). Nonetheless, harvest gaps are regenerating more seedlings than the closed canopy, and sapling abundance is greatest in harvest gaps indicating that the harvest is creating a new cohort within these stands.

Differences in tree regeneration among harvest gaps, natural gaps, and closed canopy is likely due to several factors. First, trees within the same height class among gaps and closed canopy may contain different age classes. For example, seedlings (i.e. trees < 0.5m tall) in the closed canopy could be significantly older than those in harvest gaps since their existence in this height class could be caused by the suppression of the heavy upper canopy. Second, between harvest gaps and natural gaps, gap age could be a significant source of variation between seedling and sapling abundance where natural gaps were between one to seven years older than harvest gaps. A study of tree regeneration in harvest gaps in a hemlock-hardwood forest found tree biomass production was significantly greater in younger gaps where gap ages ranged from 1-55 years (Webster and Lorimer 2002). Natural gaps were smaller than harvest gaps, and the lateral extension of the gap edge trees may have suppressed the growth release of trees in the understory reducing the number of stems in higher height classes. Further, seedlings in harvest gaps may have advanced to the sapling stage faster. Third, differential growth of species by gap capture as well as shade tolerance would account for differences in species abundance in each height class. Abundant saplings in harvest gaps, *A. rubrum*, *P. tremuloides*, *B. papyrifera*, *P. strobus*, and *Q. rubra* may have advanced into the sapling height class faster because of available light and space more limited in natural gaps.

2.5.4.2. Tree Species Composition

The tree species, particularly seedlings, in gaps most abundantly regenerating were *A. rubrum* and *A. balsamea*. The abundance of these two species is likely a result of several factors. First, some of the harvest gaps were established on previous treefall gaps where natural gap regeneration was already established before harvest, thus confounding interpretations about regeneration in the harvest gaps. Second, advance regeneration, comprised mostly of *A. balsamea*, in the harvest gaps also would contribute to the abundance of this regenerating tree. Third, both *A. balsamea* and is a prolific seeder, and *A. balsamea* and *A. rubrum* seedlings have few germination requirements allowing their germination with very little light and some moisture. Finally, *A. rubrum* also is a vigorous stump sprouter (Burns and Honkala 1990) producing several stems per stump accounting for its greater stem abundance in gaps.

T. canadensis, *A. balsamea*, *A. rubrum*, *P. strobus*, and *P. rubens*, and *T. occidentalis* (i.e., only under the closed canopy) were the most dominant trees in the overstory as measured by basal area for all gaps and closed canopy. The abundance of these species found in all height class in all harvest gaps, natural gaps, and closed canopy illustrate the importance of the upper canopy in providing a seed source for natural regeneration, as well as dominating regeneration that will become the composition of the future canopy. Tree species most abundant in natural gaps and closed canopy for all height classes included more shade to mid-tolerant species such as *A. balsamea*, *T. canadensis*, *A. rubrum*, and *P. strobus*. However, in all height classes, harvest gaps were regenerating in great numbers (i.e., excluding *A. rubrum*, *A. balsamea*, and *T. canadensis*) two early successional species, *P. tremuloides* and *B. papyrifera*, that are scarce in natural gaps and closed canopy. The difference in tree species regeneration between natural gaps and closed canopy are the abundance of *P. tremuloides* in natural gaps and *A. saccharum* in closed canopy.

Seymour and Hunter (1992) suggest that clearcut and high-grade harvesting have reduced economically important tree species such as *P. strobus*, *P. rubens*, and *B. alleghaniensis.* This statement provides the rationale for gap harvesting since canopy gaps are the conditions in which these species originally established. Furthermore, a study on canopy structure and development of a multi-cohort stand in Maine indicated that partial disturbances are important mechanisms for shade tolerant species to dominate the canopy (Favjan and Seymour 1993). Although this data represents growth four years after harvest, *A. rubrum* and *A. balsamea* were the most abundant regenerating tree species. More desired species, such as *P. strobus* and *P. rubens* are regenerating in greater numbers in harvest gaps in both seedling and sapling height classes, and these species are producing more stems per hectare in harvest gaps than in natural gaps. In natural gaps, *P. rubens* saplings are regenerating 50 stems/ha whereas *P. rubens* saplings in harvest gaps are regenerating 590 stems/ha. Under the closed canopy *P. rubens* is not an abundant species. These results indicate the preliminary success of natural regenerating economically valuable tree species by harvesting in an expanded gaps shelterwood harvest four years after harvest. However, one interesting result is the scarcity *A. saccharum* and *B. alleghaniensis* regeneration in harvest gap and natural gaps. Both species are of equal shade tolerance and are considered gap phase species (Mladenoff 1990). Their lack of regeneration may be accounted by their lack of representation in the stand measured by basal area in the gaps.

2.5.4.3. Predicting Canopy Status

Although many studies on harvest gap regeneration have not exceeded 10 years, many studies indicate that shade intolerant species often dominates harvest gap tree regeneration in the early stages of succession (McClure 2000; Kimball et al. 1995; Schumann 1999; Philips and Shure 1990). This dominance may be short-lived. The opportunistic growth of sprouts and seedlings after gap formation produces localized gaps from their gradual dieback allowing canopy accession of shade tolerant species (Philips and Shure 1990). Both *A. balsamea* seedlings and *A. rubrum* basal sprouts were the most abundant species regenerating in gaps, but these species are highly susceptible to competition. *A. balsamea* growth is directly related to site index, and in the PEF, its periodic annual volume in growth greatly exceeds its representation in the original stands before shelterwood harvest. However volume mortality of balsam fir also greatly exceeds its original representation in the PEF stands (Frank and Blum 1978). As a result of their inability to outcompete other species, *A. rubrum* and *A. balsamea* may attain canopy statues, but their abundance in the future canopy is likely to be diminished.

Other seedlings that are regenerating in high numbers that are more shade tolerant and economically valuable include *P. strobus*, *Q. rubra*, and *P. rubens*. This result is important for predicting the future canopy structure within harvest gaps where a study on natural gaps in New Hampshire indicated that all tree species that reached the 44 to 48 year old gap canopy established within 4 years after gap formation (McClure et al. 2000). These species, particularly *P. strobus* and *P. rubens* are also likely to be well represented in the future canopy because of their tolerance levels and competitive advantage. Canopy stratification patterns in a multi-cohort stand in Maine (i.e., as a result of partial disturbances) indicate that *P. rubens* dominate the intermediate crown class, and *P. strobus* as well as *P. rubens* were the species that comprised the dominant canopy class present. Furthermore, *P. strobus* was the only species present as an emergent (Favjan and Seymour 1993). A gap dynamics study in a spruce-fir forest in New Hampshire indicated that both *P. rubens* and *A. balsamea* grew 2-3 times faster in gaps than under closed canopy (Battles and Fahey 2000). Therefore, based on the presence of regenerating stems in harvest gaps and the species stratification of stand development in gaps based on studies of similar forest types, we can predict the dominant species composition of the future gap canopy to be (i.e., not in any order of importance) *A. rubrum*, *A. balsamea*, *P. rubens*, and *P. strobus*.

2.5.5. *Conclusion*

The primary objective of the expanding-gap harvest strategy is managing the Acadian forest in a manner that is more consistent with the natural disturbance regime of this region. The expanding-gap strategy strives to 1) increase species diversity, 2.)

diversify the forest structure, 3) naturally regenerate commercially valuable tree species, and 4) promote the presettlement forest structure and composition. Several of these objectives have been accomplished within four years after harvest. Gap harvesting successfully increased the abundance and diversity of plant species, regenerated more tree saplings than any other condition indicating the addition of a new cohort, and regenerated in significant abundance commercially valuable tree species such as *P. rubens* and *P. strobus*.

Natural gap canopy openings effectively allowed enough light for high plant abundance values similar to harvest gap plant abundance values, but canopy openings were not large enough to introduce a large number of new species as witnessed in harvest gaps. The dissimilarity in composition between the composition of harvest gaps and natural gaps as well as the large number of species only occurring in harvest gaps indicated that the expanding gap harvesting system is initiating a different pattern of vegetation dynamics than the natural gaps. There are three possible explanations for this result. First, many natural gaps are formed by the slow death of a canopy tree producing a standing snag with minimal disturbance to the forest floor and/or the upper canopy. The slow forming natural nature of these gaps did not create an abrupt change in habitat to introduce many early successional species. Second, the lateral extension of the natural gap canopy trees quickly reduces the opportunity for early successional species to exist. Third, the older age of the natural gaps, five to eleven years and possibly older, may be exhibiting vegetation conditions that have had more time to develop than the harvest gaps. Therefore, the greatest differences between natural gaps and harvest gaps were the magnitude of the disturbance.

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Chapter 3

RELEASE RESPONSE OF SAPLINGS AND EDGE TREES IN HARVEST GAPS AS A METHOD FOR DATING NATURAL TREEFALL GAPS IN MAINE'S ACADIAN FOREST

3.1. Abstract

Understanding the dynamics of natural gaps in the Acadian forest is crucial for developing forest management practices that are based on patterns of ecological disturbance. A major limitation to quantifying vegetation dynamics in natural gaps is a lack of methods for accurately determining when a gap was created. Tree radial growth response has been a successful means for dating natural tree fall gaps in disturbance chronological studies. Because different tree species, ages, and location within a stand structure influence radial growth after disturbance, many different release criteria to indicate a canopy disturbance event have been established. We examined the growth response of saplings and edge trees to harvest gaps of a known age and compared the release response patterns of several tree species, gap sizes, and tree sizes. The relative response patterns were used to determine the best release criteria for dating natural gaps in the Acadian forest of Maine.

We examined the radial growth response of *Acer rubrum* L., *Tsuga canadensis* (L.) Carr., and *Betula papyrifera* Marsh. overstory trees at the edge of 20 various-sized harvest gaps as well as *Abies balsamea* (L.) P. Mill and *T. canadensis* saplings in these harvest gaps. *A. balsamea* and *T. canadensis* saplings were also sampled in 23 natural gaps as a test of the best release criteria determined in harvest gap trees. All overstory trees were cored at breast height, and sapling cross-sections were made at the base of the

tree. Both average gap growth after harvest and percent growth response were examined in harvest gap trees to determine the best method for dating natural gaps using a duration of 7 years pre- and post-harvest (i.e., harvest gaps were 7 years old).

For overstory trees at the edge of harvest gaps, a 50% growth response provided the most accurate date of gap formation. Gap size ($\chi^2 = 7.560$, $p<0.006$) and the interaction of gap size and species ($\chi^2 = 4.39$, $p<0.036$) where *T. canadensis* indicated the most frequent response were the best variables predicting a response using this criterion. In saplings from the harvest gaps, a 200% growth response provided the most accurate date of gap formation. Only gap size ($\chi^2 = 8.187$, $p< 0.004$) was a significant variable predicting a sapling response to canopy disturbance. Based on the results from the harvest gaps, a 200% growth response as a criterion was selected for dating natural gaps. We found, however, that this criterion underestimated gap formation dates since the harvest created a more abrupt disturbance than the slow-forming natural gaps. A more conservative release criterion, 100% growth response, provided more natural gap formation dates than the 200% growth response, and it was the best release criteria for dating natural gaps in this study.

3.2. Introduction

Understanding the gap dynamics of the Acadian forest is vital to developing silvicultural approaches that are based on patterns of natural disturbance (Seymour and Day 1997). A major limitation to quantifying vegetation dynamics in natural gaps is a lack of methods for accurately determining when a gap was created. Many studies comparing plant diversity and/or stand regeneration in recent natural gaps utilize several non-destructive techniques for determining the date of gaps. These methods include evaluation of conditions of the treefall, soil and litter disturbance, damage to adjacent vegetation (Mladenoff 1990), changes in the lateral growth of trees as indicated by the distance between bud scale scars (Rankin and Tramer 2002)**,** and aging seedlings growing on tip-up mounds (Battles and Fahey 2000). These methods are often subjective and can be inaccurate.

A study performed by Dynesius and Jonsson (1991) evaluated eight different methods for obtaining the best date of natural gaps in a northern Sweden boreal forest. According to their results, initial growth of surrounding canopy trees and the growth release of suppressed saplings evaluated by radial growth of the stem provided the best method for dating natural tree fall gaps. Trees form an abrupt and sustained increase in height and/or radial growth when exposed to higher light intensities after being suppressed by larger trees and/or branches (Frelich 2002; Lorimer 1985). The date of formation of natural gaps in a forest landscape can be defined by the year in which the tree indicates a release from suppression. However, assigning a formation date for natural gaps is sometimes problematic since increases in stem radial growth are also indicative of climate changes and/or tree vigor. Radial growth responses to increased light by canopy openings will vary by a tree's position in the canopy, location relative to the gap, species, shade tolerance, the magnitude of the disturbance (i.e., slow gap formation over long period), and whether a tree was injured during the disturbance. Further, natural gaps are rarely formed by one event, often making the spatial and temporal boundary of the natural gap indiscernible, especially in radial growth patterns. Hence, assigning a single year to natural gap formation does not accurately characterize when the gap was created.

Many studies have shown that saplings within the gap have provided accurate results in dating natural gaps. In the northern Sweden boreal forest, the growth release of suppressed saplings measured by the cross-section at the base of the tree provided an accurate age of formation for the natural gaps where 17 of 22 gaps were dated using this method (Dynesius and Jonsson 1991). In spruce-fir forests of the Rocky Mountains, suppressed saplings responded to partial overstory removal with a 4-fold increase in growth, but growth was sometimes depressed 1-2 years following harvest (McCaughey and Schmidt 1982). A study on recent natural gaps in a northern hardwood forest indicated that trees within the gap demonstrated a greater response in radial increment than trees at the gap edge. Not only was tree position important, but also different species had greater responses than others. Sugar maple responded to a greater degree than eastern hemlock, red maple, and yellow birch (Dahir and Lorimer 1996). Gap capture in a northern hardwood forest of New Hampshire indicated that after gap formation, sugar maple and red maple grew more rapidly than American beech (McClure et al. 2000). However, in an old growth forest of Maine, smaller trees in natural gaps showed the same likelihood of response irrespective of their location within the gap (i.e. gap edge or center), and tree species response was only significantly different for a moderate release criterion, the preferred criterion (Chokkalingam 1998).

Because different tree species, ages, and location within a stand influence radial growth after disturbance, many different release criteria to indicate a disturbance event have been established. The suitability of a release criterion often varies by with region, species, site, and other environmental factors (Chokkalingam 1998). The majority of the release criteria cited in the literature were reviewed and summarized by Chokkalingam

(1998). Although many studies often assign an arbitrary release criterion, most studies use an increase in radial growth of between 50% and 100% during a specified growth period before and after the disturbance to indicate a major release or a minor release depending on the characteristics of the tree species (Frelich and Lorimer 1991; Frelich and Graumlich 1994; Frelich 2002).

Not only are the magnitude of the release important, but also the duration of the response. The duration of an abrupt and sustained release discriminates radial growth changes due to disturbance events from changes due to climatic variation (Frelich 2002; Canham et al. 1990). Lorimer (1985) suggested a 15-year consecutive growth release from suppression screens out growth releases that are climatically related. Some studies deviate from these standards. For example, Dahir and Lorimer (1996) used an average of 40% radial growth increase from eight years predisturbance and five years post-disturbance to estimate the probable date of gap formation. This low value was selected because the canopy gaps were < 50 m^2 in size, and it was successful in this study only because the researchers had data on the initial size and growth rate of all the trees studied. Hence, climatic responses in radial growth could be excluded.

Chokkalingam (1998) compared three different release criteria in a disturbance study in an old-growth forest of Maine. Her release criteria ranged from a moderate criterion (≥ 100% increase in growth from 10 years prior to disturbance and sustained 10 years) to lenient criterion (≥ 100% mean increase in growth from 5 years prior to disturbance and sustained for 5 years), and absolute criterion (three years of radial growth < 0.5 mm following four years of > 0.5 mm radial growth). Although all the criteria produced similar numbers of responses, the lenient criterion overestimated disturbance intensity. Frelich (2002) suggests that percentage growth increase is a more valuable indicator of disturbance than a fixed growth rate (e.g., 0.5 mm/yr) because many tree species have a high growth rates before a disturbance event.

Because of the considerable variation in tree response to canopy disturbance due to differences in species, shade tolerance, gap size, and other environmental conditions, the best method for dating recent natural gaps in the Acadian forest is difficult to determine. Furthermore, assigning an arbitrary release criterion for tree response in natural gaps in the Acadian forest type may not determine the most accurate formation date. Most disturbance chronology studies usually identify a disturbance event within a ten-year period (Lorimer 1985) because there are many factors that influence tree growth response to release from suppression. Therefore, understanding how particular species in various positions of a forest structure and in various gap sizes react to a known disturbance (i.e., both spatially and temporally) can benefit natural disturbance chronological studies where the disturbance patterns of the forest structure are unknown.

We examined the growth response of saplings and edge trees to harvest gaps of a known age and compared the release response patterns of several tree species, gap sizes, and tree sizes. The relative response patterns were used to determine the best release criteria for dating natural gaps in the Acadian forest of Maine. Hence, we examined the following hypotheses: 1) there is no difference in growth response to canopy disturbance between gap overstory edge trees and gap saplings, 2) there is no difference in the growth response to canopy disturbance for gap overstory edge trees in relation to their position in the canopy, and 3) there is no difference in the growth response to canopy disturbance by trees species for both gap overstory edge trees and gap saplings.

3.3. Methods

3.3.1. *Study Area*

The study area is located in the University of Maine's Penobscot Experimental Forest (PEF) on the Forest Ecosystem Research Project (FERP) lands in the towns of Bradley and Eddington, Penobscot County, Maine (44 50'N, 68 35'W). The PEF encompasses 1,600 hectares and is part of the Acadian forest type. The dominant tree species in the PEF include eastern hemlock (*Tsuga canadensis* (L.) Carr.), red maple (*Acer rubrum* L.), red spruce (*Picea rubens* Sarg.), eastern white pine (*Pinus strobus* L.), northern white cedar (*Thuja occidentalis* L.), balsam fir (*Abies balsamea* (L.) P. Mill), trembling aspen (*Populus tremuloides* Michx.), and paper birch (*Betula papyrifera* Marsh.). This forest has a complex history of repeated cuttings resulting in relatively even-aged stands dating from the late seventeenth century. Forest soil structure is variable, but principally Aquic or Typic Haplorthods or Podzols; slope is generally less than 8% (Brissette and Kenefic 1999).

Using current information about natural disturbance regimes in the Acadian Ecoregion (Runkle 1981; Seymour and Hunter 1992), an expanding-gap silvicultural system with permanent reserve trees was developed (Seymour and Day 1997). Based loosely on the German "Femelschlag" system, the treatment prescriptions include: 1) 20:10 treatment - 20% canopy removal on a 10-year cutting cycle for 50 years and 50 years regeneration (creating 0.2 ha openings) with 10% of the basal area remaining in permanent reserve trees, and 2) 10:30 treatment - a 10% canopy removal level on a 10-year cutting cycle for 100 years (creating 0.1 ha openings) with 30% of the basal area remaining in permanent reserve trees. These treatments are being compared to control areas that receive no harvesting.

Both harvest treatments were designed to provide a 1% annual disturbance rate over 100 years of regeneration similar to that estimated for presettlement forests in Maine (Lorimer 1977). The 20:10 treatment will hypothetically enhance the development of mid-succession species and produce five different cohorts within the managed stand. The 10:30 treatment is intended to accelerate the development of late successional species and produce ten cohorts within the managed stand. These treatments also were designed to maintain the economic advantages of even-aged methods, yet provide many of the structural features found in uneven-aged stands. The maintenance of permanent reserve trees is intended to provide structural diversity and control species.

Using the gaps created in this study, the response of stem radial growth was examined in two of the FERP plots. Research Area one (RA1) contains the 20:10 treatment providing large gaps with a size range of 940 m^2 – 2,169 $m^2$and RA2 contains the 10:30 treatment providing small gaps with a size range of 108 m^2 - 472 m^2. The harvest gaps were created in the winter of 1994 / 1995 providing seven growing seasons for saplings and mature edge trees to respond to the creation of the harvest gap (i.e., data collected at the end of the growing season 2001). RA 3 is the untreated control, and trees in this plot were sampled to provide a climatic baseline for comparison with trees in the harvested gaps. All tree samples were collected during October and November of 2001. The most frequently occurring tree species in the forest overstory and understory (i.e., saplings) in RA 1-3 were selected based on data collected from sample plots before the site was harvested in 1995.

3.3.2. *Harvest Gap Edge Tree Response*

The three most abundant species in the overstory were *T. canadensis*, *A. rubrum*, and *B. papyrifera*. Gap edge trees that had between 50% and 75% of their crown circumference exposed to the harvest gap were cored at breast height (1.4 m). Cores were extracted to indicate at least 20 years of growth and taken on the side of the stem exposed to the gap opening. The following measurements were collected from each cored tree: total height, live crown height, diameter, crown exposure, and azimuth to the harvest gap center. Total height and live crown height were measured using a Haglöf hypsometer and crown exposure was measured using an ocular estimation of percent crown circumference exposed to the gap opening. Ten cores of each of the three species were collected from trees in the A/B and the C canopy stratum, in the 20:10 treatment and 10:30 treatment, and under the closed canopy conditions in the control plot providing a total of approximately 180 cores. The A/B stratum includes trees both above the highest continuous canopy and within the upper continuous canopy, and the C stratum includes trees within the lower canopy strata below the B strata (Oliver and Larson 1996). It was not always possible to collect all replications for the conditions for a tree core (e.g., *B. papyrifera* in the A/B strata under the closed canopy).

All tree cores were mounted and sanded using a radial sander beginning with 100 grit and finishing with 600 grit using 100 grit increments. Both *A. rubrum* and *B. papyrifera* cores were finished up to 1000 grit in order to make the growth rings were more visible. All cores were scanned into a computer and the tree rings were measured using WINDendro version 2001 up to at least 20 years of growth from the last growing season. Because trees were not cored to the pith, there were an inadequate number of growth rings to perform cross dating.

3.3.3. *Harvest Gap Sapling Tree Response*

The most abundant understory tree species (i.e., saplings less < 10 cm DBH) were *A. balsamea* and *T. canadensis*. Twenty saplings (10 *A. balsamea* and 10 *T. canadensis*) were selected within the gaps of each treatment including under the closed canopy in the control plot providing a total of 60 saplings. Saplings were chosen if they 1) were at least 14 years old (i.e., 7 years post- and pre-harvest) determined by counting yearly nodal growth, 2) were dominant among saplings in the gap to reduce the confounding effects of competition with neighboring saplings, 3) had 100% of their crown exposed to the gap opening, and 4) were no farther from the gap center than one half of the gap radius.

Sapling growth response was measured using ring width analysis of stem cross-sections. Because we were unable to precisely determine specific years of nodal growth before the harvest treatment due to the suppressed nature of the balsam fir saplings, we could not examine nodal growth, both from crown release and the ratio of lateral to vertical nodal growth as done by Duchesneau et al. (2001). Saplings were cut 10 cm from the base of the tree and a cross-section removed for analysis. Tree height and diameter at breast height (i.e., 1.4 m) were also recorded for each sapling. All sapling cross-sections were prepared and analyzed as the cores described above. Four equidistant radii were marked on all sapling cross-sections, and all radii were analyzed to determine an average yearly growth.

3.3.4. *Natural Gap Sapling Response*

A total of 23 natural gaps were identified in the control plot. A natural gap was chosen if it 1) was caused by the death of at least two canopy trees with ≥ 25 cm diameter (Runkle 1992), 2) had a maximum of 2 m understory height within the gap (i.e., regeneration), and 3) was at least 30-40 m away from other canopy openings to minimize edge effects. Area of each natural gap was estimated by the expanded gap area of an ellipse based on the method defined by Runkle (1992). Gap area ranged from 110-510 m^2. In every natural gap, five dominant saplings (or at least three dominant saplings if five were not found) located no farther than from the gap center than one half the gap radius were selected providing a total of 105 saplings. Due to the restrictions of sapling frequency in natural gaps, all conifer species including *A. balsamea*, *T. canadensis*, *P. strobus*, and *P. rubens* were used for the analysis. However, only four *P. strobus* saplings and two *P. rubens* saplings were collected. Each sapling was cut 10 cm from the base to collect a stem cross section for tree growth analysis. Height, diameter (either at breast height or basal diameter depending on height of the sapling), and distance from the gap maker(s) were noted for each sapling. Cross-sections were prepared and analyzed as described above for harvest gap saplings.

3.3.5. *Harvest Gap Release Response Criteria*

In order to establish the best criteria for determining release response in harvest gaps, we evaluated stem growth of harvest gap saplings and edge trees in three ways: 1) mean ring width from 1995-2001, 2) percent growth response based on the release criteria created by Lorimer (1980) using 7-year growth pre-harvest and 7-year growth post-harvest [1], and 3) both mean ring width and percent release.

[1] % Response = [Ave. post growth - Ave. pre growth] / [Ave. pre growth] x 100

The mean ring width from 1995-2001 (i.e., post harvest) release criterion was used to differentiate growth patterns under the closed canopy from the growth patterns of trees in canopy openings. For example, *Acer saccharum* Marsh. saplings in the understory of a northern hardwood forest average 0.22 mm/ year, whereas *A. saccharum* saplings in even the smallest canopy openings average 0.69 mm/year (Canham 1985). The justification for using both percent growth response and mean radial growth after gap formation (i.e., number three above) is the radial growth patterns of highly suppressed trees. Because of small radial growth patterns, highly suppressed trees might have indicated a large percent growth response that may not have been attributed to canopy gap formation producing a false release. Hence this release criterion is very strict. Thresholds for release were determined by the maximum number of harvest gap trees that met the specified criterion and by the exclusion of closed canopy trees that produced a false positive release to the specified criterion.

Logistic regression was used to investigate what predictive variables (i.e., tree species, gap size, and diameter) accounted for the probability of harvest gap edge trees and harvest gap saplings to indicate a release. Dummy indicator variables were used for tree species within the logistic model. Using the maximum likelihood estimation, logistic regression is appropriate for estimating parameters with both categorical and continuous variables with binary response indicator variables (i.e., release or no release in this study) (Neter et. al 1996). Using backward elimination in proc logistic (SAS system for

Windows v. 8.01 2000), the fit of a full model with both main effects and interactions was tested for the release criteria that produced the best obtainable formation date results. The backward-elimination calculates the statistics for the full model including all independent variables; variables from the model are eliminated until all remaining variables and interactions produce a significant (i.e., $p < 0.05$) statistic.

3.3.6. *Natural Gap Release Response Criteria*

The three release criteria for each harvest-gap edge-tree and sapling were analyzed to determine the best release criterion for dating natural gaps in the untreated control plots. After choosing the best release criterion for natural gaps, the first year where the natural gap sapling reached a determined growth response indicated the time when the natural gap formed, and at least 3 saplings with corresponding release years (i.e., within 3-5 years) in a given natural gap were needed to date the gap. All releases in natural gaps were categorized into periods of 3-5 years to account for potential lag in sapling response.

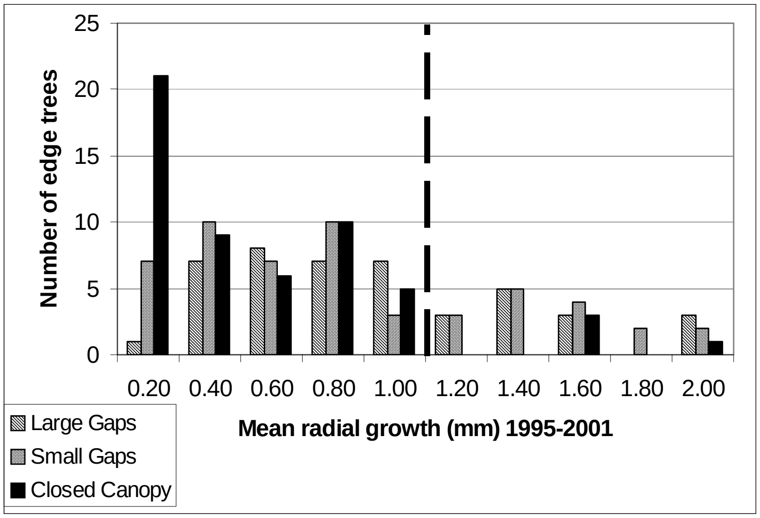
3.4. Results

3.4.1. *Harvest Gap Tree Response*

3.4.1.1. Harvest Gap Edge Trees

Based on the distribution of growth patterns for trees under the closed canopy, the minimum release threshold for harvest gap edge trees was positioned at 50% growth response (Figure 3.1b) and 1.0 mm average growth after harvest (Figure 3.1a). These thresholds were chosen based on the growth patterns of the closed canopy trees. The

a.)



b.)

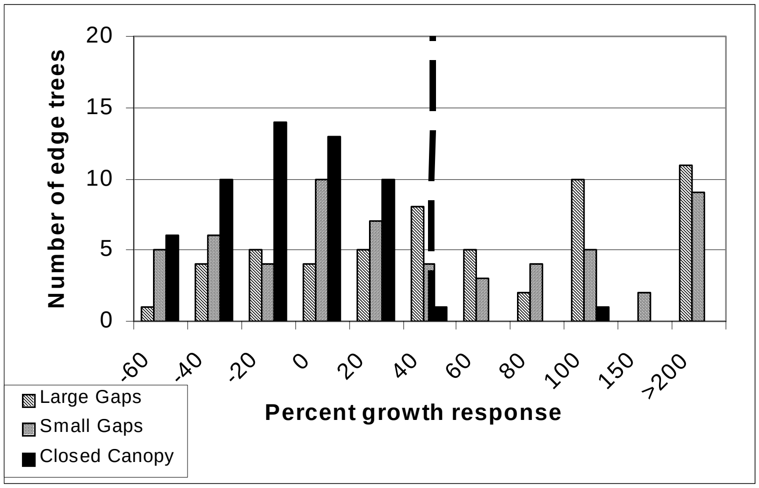


Figure 3.1: The distribution of response for harvest-gap edge-trees by (a) average stem radial growth from 1995-2001 and (b) percent response using 7 years pre- and post-disturbance average growth. The heavy dashed line indicates the threshold used for judging whether a release had occurred.

closed canopy radial growth patterns illustrate the typical growth rates of trees in the closed canopy. Although these thresholds exclude some harvest gap edge trees (i.e., individuals showing no response according to our criterion), these thresholds reduce the possibility of identifying false positive releases in closed canopy trees.

Only 31% of harvest gap edge trees demonstrated a release of ≥ 50% growth response after harvest. Of the edge trees that responded by percent release, 54% were in large gaps, 44% were in small gaps, and 2% were under the closed canopy. *T. canadensis* responded most frequently (42%), and *B. papyrifera* responded the least frequently (23%). *A. rubrum* responded 35% of the time. Similarly, 32% of harvest gap edge trees showed a release of ≥ 1.0 mm average gap growth from 1995-2001. Of the trees that demonstrated a response by this criterion, 52% were in large gaps, 41% percent were in small gaps, and 7% were under the closed canopy.

For the ≥ 1.0 mm mean gap growth, *T. canadensis* responded most frequently (48%) and *B. papyrifera* responded least frequently (15%); *A. rubrum* responded 37% of the time. Using both 50% response and ≥1.0 mm average gap growth (1995-2001) release criterion, only 19% of harvest gap edge trees demonstrate a release. Of these release trees, 53% percent were in large gaps, 47% percent were in small gaps, and none were under the closed canopy. Thirty-four percent of the release trees were *A. rubrum*, 16% were *B. papyrifera*, and 50% percent were *T. canadensis*. Table 3.1 summarizes the number of harvest gap edge trees indicating a release for each release criteria.

Logistic regression indicated that for the ≥ 50% response release criteria, *B. papyrifera* ($\chi^2 = 7.560$, $p < 0.006$) showed the lowest rate of response among the three

Table 3.1: The number of harvest-gap edge-trees indicating a release for the three release criterion using 7 year pre-and post-harvest duration for percent growth response and 7 year average gap growth

Release Criteria	**Gap Type**	*Acer rubrum*		*Betula papyrifera*		*Tsuga canadensis*	
		Released	**Total Sampled**	**Released**	**Total Sampled**	**Released**	**Total Sampled**
≥50% Growth response	Large Gaps	8	20	10	18	10	18
	Small Gaps	10	18	2	18	11	19
	Closed Canopy	0	20	0	21	1	18
1.0 mm+ mean gap growth	Large Gaps	9	20	8	18	13	18
	Small Gaps	11	18	1	18	10	19
	Closed Canopy	0	20	1	21	3	18
≥50% and 1.0 mm+ response	Large Gaps	5	20	4	18	9	18
	Small Gaps	6	18	2	18	8	19
	Closed Canopy	0	20	0	21	0	18

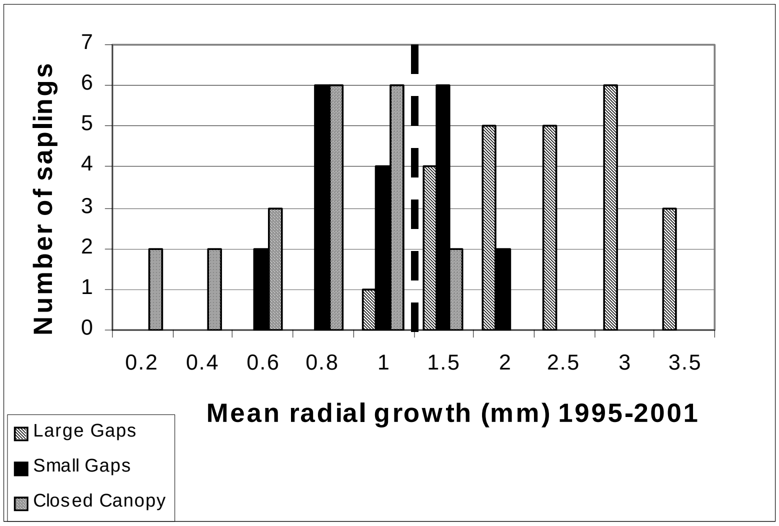
species. Gap size ($\chi^2 = 5.024$, $p < 0.025$) and the interaction of gap size and tree species (*B papyrifera*) provided the best model for predicting a harvest gap edge tree response ($\chi^2 = 4.39$, $p < 0.036$). Hence, *A. rubrum* and *T. canadensis* in the large harvest gaps provided the strongest release response among edge trees in the harvest gaps.

3.4.1.2. Harvest Gap Sapling Response

Based on the distribution of closed canopy tree growth patterns, the maximum release threshold for saplings in the harvest gaps was positioned at 200% response (Figure 3.2b) and 1.0 mm mean radial growth after harvest (Figure 3.2a). The 1.0 mm radial growth criteria excluded many of the small gap saplings, suggesting that saplings in small gaps produced less of a release response than saplings in large gaps. This threshold, however, minimizes the number of closed canopy trees producing a false positive release response. The 200% release threshold maximizes the number of large and small gap saplings indicating a response and minimizes the number of closed canopy saplings showing a false positive response.

Overall, saplings in harvest gaps had a greater growth response to gap harvesting than did the mature trees at the edge of the gaps (i.e., 200% growth response versus 50% growth response). Fifty-one percent of harvest gap saplings demonstrated ≥ 200% growth response. Among the gap saplings that responded by ≥200% release, 48% occurred in large gaps and 42% were in small gaps. Fifty-five percent of saplings showing ≥ 200% release were *A. balsamea* and 45% were *T. canadensis*. For the ≥ 1.0 mm mean radial growth release criteria, 57% of saplings indicated a release. Of the saplings that showed a release, 57% were in large gaps, 25% were in small gaps, and

a.)



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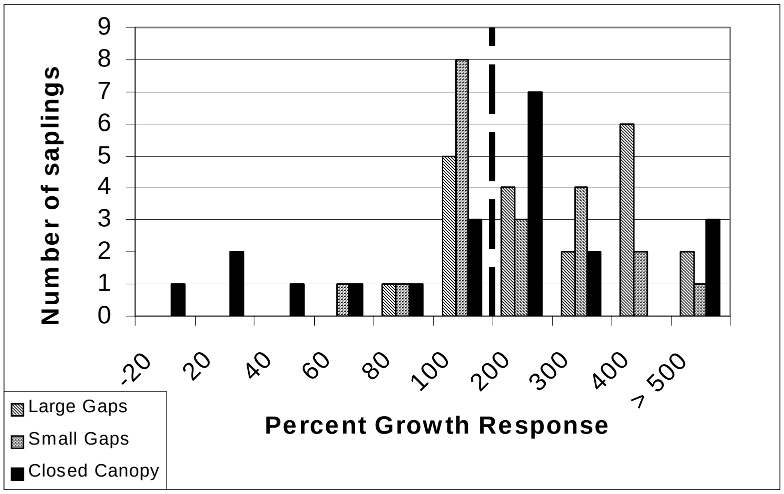

Figure 3.2: The distribution of response for harvest gap saplings by (a) mean radial growth from 1995-2001 and (b) percent response using 7 years pre- and post-harvest average growth. The heavy dotted line indicates the threshold for release criterion.

17% were under the closed canopy. *T. canadensis* responded more frequently (65%) than *A. balsamea* (35%).

Using both ≥ 200% release and ≥ 1.0 mm average gap growth as an absolute indicator of release, only 37% of harvest gap saplings showed a release. Among these released saplings, 68% were from large gaps, 27% from small gaps, and 5% from under the closed canopy. Forty-five percent of the released saplings were *A. balsamea*, and 55% percent were *T. canadensis*. Table 3.2 summarizes the number of harvest gap saplings indicating a response for each criterion.

Finally, logistic regression indicated that gap size ($\chi^2 = 8.187$, $p < 0.004$) was the only variable predicting ≥ 200% release. This result indicates that the saplings in the large gaps had a higher probability of release than saplings in the small gaps, and species (*A. balsamea* and *T. Canadensis*) was not an important variable predicting the likelihood of release.

3.4.2. *Formation Dates of Natural Gaps*

Radial growth response of saplings in harvest gaps was found to be a better indicator of harvest gap creation than using mature trees at the edge of harvest gaps. In addition, the ≥ 200% release response criterion provided the most sensitive indicator of sapling release. Fifty-one percent of sapling population in harvest gaps showed a ≥ 200% release response. Although 57% of the harvest gap saplings demonstrated a release with a response ≥1.0 mm mean gap growth, this criterion had a higher number of closed canopy saplings than the ≥ 200% response (i.e., 17% versus 10%). Based on the growth response results obtained with the harvest gap saplings, the 7 year pre-growth and 7 year

Table 3.2: The number of harvest gap saplings indicating a release for the three release criterion using 7 years pre- and post-harvest duration for percent growth response and 7 years average gap growth.

Release Criteria	**Gap Type**	*Abies balsamea*		*Tsuga canadensis*	
		Released	**Total Sampled**	**Released**	**Total Sampled**
200% Growth Response	Large Gaps	9	10	6	10
	Small Gaps	7	10	2	11
	Closed Canopy	1	10	2	10
1.0 mm+ Mean Gap Growth	Large Gaps	10	10	10	10
	Small Gaps	1	10	8	11
	Closed Canopy	1	10	5	10
200% and 1.0mm+ Response	Large Gaps	9	10	6	10
	Small Gaps	1	10	5	11
	Closed Canopy	0	10	1	10

post-growth ≥ 200% percent response was used in determining release for saplings in natural gaps. Only 16 out of 105 (15%) natural gap saplings demonstrated a ≥200% response, and only five natural gaps had more than one sapling meeting this release criterion. Of these five natural gaps, only four had saplings with corresponding release periods, and all showed a response at 1995 ± 3 years (Table 3.3). However, because a minimum of three release saplings of the same period were required to confirm a date of natural gap formation, only one natural gap could be dated using this absolute criteria (Figure 3.3). The formation date of the gap was determined to be between 1993 and 1996 to account for variation in growth response by species and tree size.

Because only one natural gap could be dated using the ≥ 200% growth response release criterion, we applied a more conservative release criterion, ≥ 100% growth response for 7 years pre-and post-disturbance. The justification for applying a more conservative criterion is 1) that gap harvesting created a more abrupt disturbance than the formation of natural gaps by the death of a canopy tree and 2) that the natural gap is known to exist because we chose a natural gap with an open canopy caused by the death of at least two canopy trees. Therefore, saplings in natural gaps that demonstrated a release response of at least 100% at the year where the sapling first reach this threshold were considered to be gap creation events.

Sixty-three saplings (60%) indicated a release of ≥100% growth response at least once in a core sequence. Fourteen of the 22 natural gaps (63%) were dated using this moderate release criterion. Nine of the natural gaps had a formation date of 1995 ± 3 years (Table 3.3). Three of the natural gaps contained saplings with growth response, but

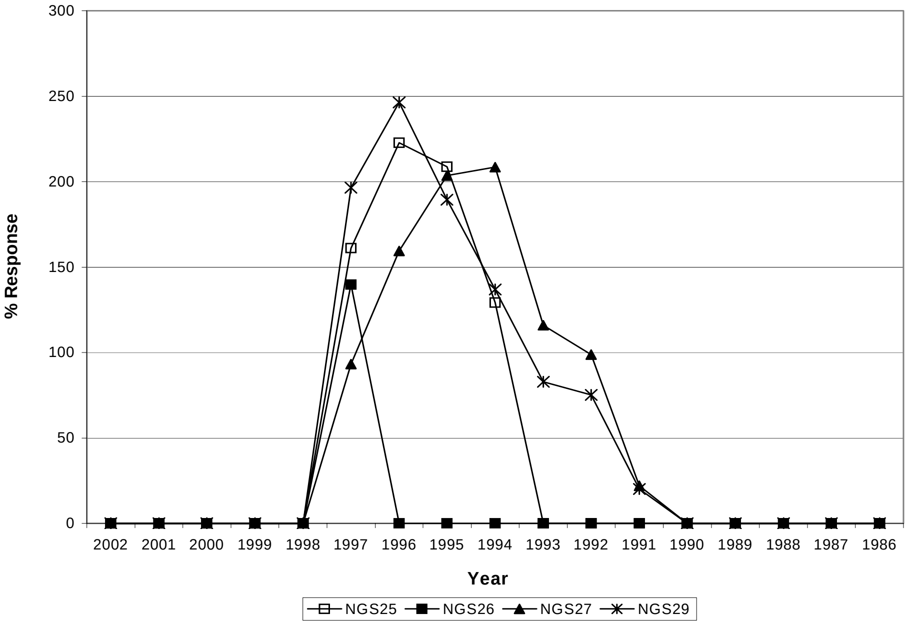

Figure 3.3: Example of release response for three saplings in a natural gap (3-C4) where three of four saplings had ≥ 200% release response. This was the only natural gap measured where a creation date was established using an absolute release criterion. The formation date of the gap was determined to be between 1993 and 1996 to account for variation in growth response by species and tree size.

Table 3.3: Summary of natural gap formation dates using both the ≥ 100% growth response and ≥ 200% growth response. "None" indicates that no saplings in the gap had a growth response, and "**" indicates no corresponding release period.

Natural Gap	**Gap Size (m^2)**	**Formation Date** *≥ 100% growth response*	 *≥ 200% growth response*
3-A3	350.7	1993-1995	None
3-C4	280.1	1993-1994	1994-1996
3-D4	191.1	1981-1986 &1993-1995	**
3-E3	152.6	1990-1993	**
3-E4	163.3	1996-1997	None
3-J2	246.9	1978-1982	None
3-J4	511.9	None	None
4-A7	128.6	1994-1996	None
4-C3	88.1	None	None
4-C4	157.8	1989-1994	None
4-C5	88.9	**	None
4-D3	227.7	None	None
4-D4	114.1	**	None
8-B8	418.3	1992-1996	None
8-C1	261.5	1992-1993	**
8-C2	139.1	None	None
8-D4	185.7	None	None
8-D5	475.6	1992-1995	None
8-E3	184.5	1992-1995	None
8-E6	231.5	**	None
8-H7	203.6	1994-1997	None

the year of the growth response did not correspond. Five of the natural gaps had no growth response at all.

3.5. Discussion

3.5.1. *Release Response To Harvest Gaps*

3.5.1.1. Release Criteria

For harvest gaps created in this study, the best criterion for determining the date of gap creation was the percent growth response from a given period pre- and post-disturbance (i.e., Equation 1). The percent growth response release criteria produced the best results for both harvest gap edge trees and saplings with the least number of closed canopy trees demonstrating an erroneous release. However, the magnitude of percent response as a release criterion differs between harvest gap edge trees and harvest gap saplings because of the differences in growth rates of the trees. As a result, saplings in harvested gaps provided more reliable measure of release response than did mature trees at the edge of harvest gaps.

This result is consistent with the release of trees of an old-growth forest of Maine where smaller trees (≤ 11 cm DBH) appeared to respond more to natural gap disturbances, and there was little change in radial growth patterns of larger trees in response to recent natural gaps (Chokkalingam 1998). In oak forests of Pennsylvania, understory trees responded more to thinning (50-100% radial growth increase) than mature canopy oaks (25% radial growth increase) (Nowak and Abrams 1997). The harvest gap saplings in this study were chosen if they were dominants in an area of “clumped” regeneration and hence, had maximum exposure to the new growing space created by the gap. In contrast, mature trees at the edge of the gaps had only a portion of their crowns exposed to the new gap, with significant portions of their crowns still competing with neighboring trees, thus possibly reducing any potential release response relative to saplings. Tree growth increases in proportion to the amount of growing space available to each tree; when growing space is fully occupied, then tree growth resumes to its original rate of growth (Oliver and Larson 1996). In addition, saplings must maximize their growth for successful accession into the canopy, which they achieve by their ability to capture belowground resources and maintaining foliage. Whereas, overstory trees, who have successfully established in the canopy, do not need to maximize their growth but maintain resistance to biotic stresses, reproductive output, and conservation of mineral resources (Day et al. 2002).

Many studies in natural disturbance history use the release criteria established by Lorimer and Frelich (1989) of a major growth response of 100% and a moderate growth response of 50% for 15 years pre- and post-disturbance (Chokkalingam 1998). This criterion was also applied to a study on the radial growth response of trees in a selectively logged old-growth forest in the Allegheny plateau, where the majority of the sample trees in the study showed a moderate release of 50% with 15 years pre- and post-disturbance rather than a major release (100%). The dominant trees in this forest included *Fagus grandifolia* Ehrh., *T. canadensis*, *A. rubrum,* and *Quercus* species (Orwig and Abrams 1999). The results of our study indicate that 50% growth response with seven years pre- and post-disturbance in overstory gap edge trees provided the best indicator of gap creation in our study. The duration of the growth response in this study was limited to seven growing seasons after harvest, but many of the trees indicated a decrease in growth in the last two growing seasons. Hence, a seven-year duration of growth response was an adequate time period for identifying a release response to a gap creation event.

However, a study of the radial growth response of *Picea abies* (L.) Karst. to different thinning intensities utilized a ring-area series as a release criterion rather than annual ring increment (Misson et al. 2003); this criterion was used to differentiate the effects of climate and the tree physiological response to environmental variation from a growth release due to thinning. Their results indicate that the duration of growth increases due to thinning (4 to 15 years) was related to structural adaptation of the tree (such as crown enlargement) and the physiological acclimation (such as respiration) of the tree to the open canopy area (Misson et al. 2003).

3.5.1.2. Predictive Variables for Release

T. canadensis responded most frequently for both harvest gap edge trees and saplings for all release response criteria, except for the ≥200% response in harvest gap saplings, but this species was not a statistically significant variable in predicting the probability of release. *B. papyrifera* provided the least number of releases in harvest gap edge trees, and logistic regression indicates that *B. papyrifera* was a significant variable in not producing a release. Hence, *T. canadensis* and *A. rubrum* were more likely to indicate a canopy disturbance in harvest gap edge trees, because both *A. rubrum* and *T. canadensis* respond well to canopy thinning after a period of suppression (Burns and Honkala 1990). Because *B. papyrifera* is a shade-intolerant tree and establishes dominance early in the life of a stand (Burns and Honkala 1990), the *B. papyrifera* in this study may not have been able to release because of a long period of suppression prior to gap harvesting. Furthermore, allocation of photosynthates to leaf and root production may have inhibited an increase in stem growth after release (Pothier and Maroglis 1990). A study on growth rates in *B. papyrifera* after commercial thinning (although not producing true gaps) support these results where *B. papyrifera* responded to the harvest in the first growing season, but the release was not sustained in the second growing season (Pothier and Margolis 1990). Harvest gap *T. canadensis* saplings responded more frequently than *A. balsamea* saplings, but tree species was not a significant variable in predicting a release in saplings. Both *T. canadensis* and *A. balsamea* are very shade-tolerant, and respond well with an increase in stem growth after new canopy openings (Pothier and Margolis 1990; Burns and Honkala 1990).

Edge trees and saplings in large harvest gaps (941 m^2 – 2,169 m^2) responded more frequently than edge trees and saplings in small gaps (108 m^2 – 472 m^2), and logistic regression indicated that trees in larger gaps were an important variable in predicting a release than trees in smaller gaps. This result was statistically significant for all release response criteria. Because of the high number of saplings not showing releases in small harvest gaps, perhaps the release threshold criterion used for larger gaps was too high for detecting a release response in small gaps. The number of closed canopy trees not showing a release determined the threshold for the release criteria. However, as mentioned previously, many closed canopy trees exhibited an erroneous release due to high growth rates after 1995. Therefore, the release response threshold we used was biased towards large harvest gaps since the trees in small harvest gaps and under the closed canopy were demonstrating similar growth results for the period 1995-2001. This pattern is discussed in more detail in section 3.4.3.

Harvest gap saplings responded more frequently for all three release criteria than harvest gap edge trees, indicating that sapling radial growth is a better indicator of gap formation dates than edge tree radial growth. However, the size of the saplings and edge trees in harvest gaps did not predict the probability of response. This result is inconsistent with Dahir and Lorimer (1996). In their study of canopy gap formation in northern hardwood forests, they collected some cores in large trees (i.e., 40 to 60 cm dbh), but they assumed that smaller trees (i.e., < 40 cm dbh) would provide a better indication of canopy disturbance. Hence, the probability of a tree responding to the harvest gap is likely due to 1) the species ability to respond to a canopy disturbance, 2) the competitive position to acquire available growing space, and 3) the amount of damage both belowground and aboveground caused by the harvest or the falling of a canopy tree in the gap.

3.5.2. *Release Response to Natural Gaps*

The best release criterion for dating natural gaps was a 100% growth response (i.e., Equation 1). The 200% growth response only dated one natural gap where at least three saplings indicated a corresponding release. These gaps were known to exist because they were selected for this study only if at least two canopy trees were downed or standing dead, and the≥ 200% growth response release criteria did not adequately detect natural gap formation. Nonetheless, other studies in other forest types have shown that ≥ 200% growth response was adequate for detecting natural gap formation dates. In a study with *T. canadensis*, current and former natural gaps were identified in overstory trees by a four-fold increase in radial growth (i.e., 200% growth response) for three or more years from the mean radial growth three years prior to disturbance (Rankin and Tramer 2002). The area of the gaps ranged form 8 to 632 m^2, but the mean gap size was 162 m^2. Similarly, in a northern hardwood forest, a 250% growth response identified natural gap formation (Henry and Swan 1974). The success of these release criteria in their study suggests that the duration for release in this study (i.e., seven years pre- and post-disturbance) may have been too large to detect a date of natural gap formation.

Regardless of other studies' success with the ≥ 200% growth response, a 100% growth response release criteria is a well-accepted and successful means for dating natural gaps, especially in the Acadian forest. Typically, in the literature for disturbance history studies, a conservative release has been defined as ≥100% growth increase for 15 years pre- and post-disturbance and a moderate release has been defined as ≥ 50% release for 15 years pre- and 10-15 years post-disturbance (Lorimer and Frelich 1989; Frelich and Lorimer 1991; Frelich and Graumlich 1994). Dahir and Lorimer (1996) found that 40% growth response for eight years pre-disturbance and five years post-disturbance was sufficient to indicate the probable date of natural gap formation, particularly because the gaps in this study were <50 m^2 and were formed in the last 11 years before the study. These criteria have allowed an accurate estimation of canopy accession for a tree within a natural gap.

The differences in the growth response between harvest gaps saplings and natural gap saplings also can be explained by differences in the origin of the disturbance. There are two common types of natural gaps, defined as the death of at least two canopy trees, in this study. A tree fall gap is one where a tree has fallen or uprooted; a snag gap is one where the stem has broke or the tree slowly died standing due to natural mortality. The significance of the two types of natural gaps is the magnitude of the disturbance and the area of canopy opening caused by the mortality. Furthermore, a gap is rarely limited to one event, because multiple disturbance agents may occur in the same gap and/or on the same tree (Worrall and Harrington 1988). Therefore, the slow, natural death of the canopy trees produced a much smaller growth response in natural gap saplings than the harvest gap saplings. Our gap harvesting of more than two canopy trees created a more abrupt disturbance and generally a larger canopy opening than occurred with the natural gaps.

3.5.3. *Erroneous and Absent Releases*

The majority of erroneous releases in closed canopy trees were found using an average gap radial growth release threshold (≥ 1.0 mm average radial growth 1995-2001). Forty-six percent of the closed canopy saplings and 32% of closed canopy overstory trees had ≥ 1.0 mm radial growth during the same growing period as the post-harvest growing period in harvest gaps (1995-2001). Although the number of closed canopy overstory trees demonstrating a response with this criterion was relatively low, 32% of large harvest gap edge trees also indicated a release using this criterion. This result creates some difficulty in differentiating what is a release response from a gap creation and what is an increase in growth due to a shift to more favorable climatic conditions.

The short duration for defining a release (seven years pre- and post-harvest) may account for this discrepancy. Having a long period of sustained increase in radial growth would screen out patterns caused by short-term climatic fluctuations (Frelich 2002; Lorimer et al. 1988). Although mean temperatures for the growing season from 1996-1998 in Maine were below average, mean precipitation for the growing season for this period in Maine was above average (NCDC 2003; NADP 2003). The cool, moist growing seasons may account for the high growth rates for closed canopy trees during this period. Furthermore, below average mean precipitation for the year of 1995 following above average mean precipitation from 1996-1998 may indicate a growth response following a drought in the closed canopy trees.

Many harvest gap saplings and edge trees did not indicate any release response, especially saplings in small harvest gaps. More than half of the saplings did not show a release using all three release criteria. There are several possible reasons to account for these absent releases. First, gap size was a significant variable in predicting whether a tree showed a release for all harvest gap saplings and edge trees for all release criteria. Second, logging damage to the saplings (e.g., root or crown damage), which was no longer apparent at time of data collection, may account for the absence of release. Finally, trees that were in the canopy at the time of coring may have been in a poor competitive position and unable to allocate photosynthate to the growth of stemwood (Frelich 2002).

The greatest number of trees in harvest gaps not showing releases were found using both percent response and average post-disturbance growth (i.e., gap growth) release criterion, where only 19% of harvest gap edge trees and 37% of harvest gap saplings indicated a release at the time of harvest. Although it effectively eliminated erroneous releases by closed canopy trees, this criterion appears to be too strict, since it excludes many trees known to have shown a growth response in harvest gaps. Since the formation date and origin of the disturbance is known for the trees in harvest gaps, using this criterion would provide misleading results by underestimating the formation dates of natural gaps.

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Chapter 4

EPILOGUE

4.1. Introduction

Gap harvesting as a means of forest management that strives to emulate the natural disturbance patterns of the Acadian forest achieves several goals in the forest landscape. The Forest Ecosystem Research Program (FERP) strives to manage the Acadian forest in a manner that is more like the natural disturbance regime by harvesting in an expanding gap shelterwood harvest with reserve trees. The objectives of the expanding-gap harvest treatments include 1) increasing species diversity, 2) diversifying the forest structure, 3) naturally regenerating commercially valuable tree species, and 4) maintaining the presettlement forest structure. These objectives were effectively accomplished four years after harvest based on the study of vegetation dynamics presented here. In our study, expanded-gap shelterwood harvesting 1) increased stand structural diversity by introducing a significant number of new seedlings and saplings in harvest gaps, 2) increased plant diversity by introducing 112 species found only in harvest gaps, 3) encouraged the regeneration of commercially valuable tree species such as *Picea rubens* and *Pinus strobus,* and 4) maintained common forest understory plant species, such as *Maianthemum canadense* and *Trientalis borealis*, after the harvest. Nonetheless, several ruderal, highly competitive species were introduced after the harvest possibly compromising the successful regeneration of commercially valuable tree species.

4.2. Management Implications of Gap Harvesting

Given the results of the effects of expanding gap shelterwood harvest on vegetation dynamics and tree regeneration, a forester interested in forest management based on natural disturbanceshould consider two important objectives and their management implications, the size of the harvest gap and the regeneration of desired species.

4.2.1. *Gap Size*

Harvest gaps in the vegetation dynamics study ranged in size from 100 m^2- 2100 m ^{2}, whereas natural gaps ranged in size from 115 m^2 – 518 m^2. The differences in gap size suggest that the harvest treatments created larger gaps than are found in natural gaps in this forest type. Because the harvest treatment was designed according to old-growth gap dynamics, the differences between harvest gap and natural gap size are likely due to the size of trees. Younger forests generally contain smaller trees with smaller crowns in comparison to old-growth forests, and the natural mortality of these trees in younger forests create smaller canopy openings. Although a more precise harvest history of the Penobscot Experimental Forest (PEF) does not exist in the areas of this study, the PEF has a history of repeated cuttings beginning in the late 17th century indicating that this forest is a mature, secondary forest. According to the literature, old-growth natural tree fall gaps in eastern forests range in size from 37 m^2- 2000 m^2 (Dahir and Lorimer 1996; Runkle 1982; Battles and Fahey 200), whereas natural tree fall gaps in mature stands (i.e., about 60 years old) range from 9 – 209m^2 (Dahir and Lorimer 1996; Krasny and Whitmore 1992; Kimball et al.

1995). Furthermore, a study of natural gaps in a northern hardwood forest suggested that harvested gaps > 200 m^2 in this forest type rarely emulate natural treefall gap size, but gaps in this study were large enough to regeneration economically valuable shade tolerant tree species (Dahir and Lorimer 1996). Therefore, if the forester's goal is to create harvest gaps that are most similar to natural tree fall gaps, then the size of the harvested gap should be considered given the surrounding forest matrix. The design of the harvest gaps should be based on the species composition of the forest landscape to determine the type of species creating the natural gaps, the size of the largest trees to determine the average size of a gap if several were to fall naturally, and the frequency of gap occurrence in natural systems to determine how frequently harvest gaps should be formed on a yearly basis.

4.2.2. *Desirable Species*

If particular species are desired for regeneration in harvest gaps, both economically valuable tree species as well as any possible endangered forest plants, then gap size, again, is important to consider. Overall, in this study, the magnitude of the disturbance played a significant role in creating differences in the species composition between harvest gaps and natural gaps. Natural gap canopy openings effectively allowed enough light for high plant abundance values similar to harvest gap plant abundance, but canopy openings were not large enough to introduce a large number of new species as witnessed in harvest gaps (i.e., 112 species out of 195 identified species only in harvest gaps). Furthermore, three *Rubus* species, a highly competitive and robust plant, were of the 10 most important species in harvest gaps whereas, natural gaps had one *Rubus* species present, *R. pubescens*, and it was of little importance to natural gap regeneration.

There two possible explanations for this result. First, many natural gaps are formed by the slow death of a canopy tree producing a standing snag with minimal disturbance to the forest floor and/or the upper canopy. The slow forming natural nature of these gaps did not create an abrupt change in the microenvironment (i.e., influx of resources and soil disturbance) to introduce many early successional species. Harvest gaps in this study were significantly larger than natural gaps, and they were formed by an abrupt single disturbance causing a significant influx of resources. Second, the lateral extension of the natural gap canopy trees quickly reduces the opportunity for early successional species to exist. Therefore, the combination of large gap area as well as the magnitude of the harvest certainly contributed to the differences in species composition between harvest and natural gaps, and the presence of many early successional, ruderal species could potentially inhibit the growth of commercially valuable tree species.

Large harvest gaps in this study effectively regenerated commercially valuable tree species, but the success of these tree species accessing the canopy is yet to be determined. Hence, if the forester wants to harvest in large gaps (i.e., > 500 m^2) (likely a simpler and more economically feasible option), then further management of highly competitive species is likely to be required in order to ensure canopy accession of valuable tree species. Nonetheless, large harvest gaps did effectively increase the plant diversity of the forest landscape, and large canopy openings could be maintained if plant diversity is the goal. However, smaller gaps (i.e. < 500 m ^{2}) have effectively regenerated valuable tree species in this study and others (Dahir and Lorimer 2000; Pickett and White 1985; Mladenoff 1990; Runkle 1981), and little management of the forest understory is required since most highly competitive species were not able to colonize in smaller gaps. Nonetheless, the forester must consider whether harvesting larger gaps and managing undesirable species as a result of the larger gap area is economically viable when compared to the cost and benefits managing smaller gaps with less further management. Finally, harvest during the winter period with adequate snow cover minimizes soil disturbance in the harvest gap, this method both reduces the colonization of ruderal, highly competitive species that require highly disturbed soils and sustains the present composition of the forest understory in the harvest gap.

4.3. Improvements

Based on the results and limitations encountered in this study, I suggest three improvements to the future researcher. For examining the vegetation dynamics study in the future, I suggest two changes in vegetation sampling. First, when estimating plant percent cover in the sample plots, it would be helpful to differentiate height classes for the species. For example, *Cornus canadensis* often forms large mats on the ground encompassing a potential large percent cover in the data collection, whereas *Aralia nudicaulis*, a much taller and larger bodied herbaceous species, encompasses a potential large percent cover in the data collection for the same sample plot. Differentiating between the height of these two species by collecting the percent cover of a species in a given height class would allow better qualitative interpretation on the importance of each species in the sample area. Second, I suggest sampling in a method that creates equal sample area for every gap and transect. We now know that plant diversity and composition was not correlated to the location within the gap, and that plant abundance was greatest in the gap center for only the largest gaps. Furthermore, the presence of reserve trees likely confounded any trend that may have occurred. Equal sample size could be accomplished by establishing sample plots at the two extreme environments of the gap, the center and the edge. Unequal sample area provided a great deal of difficulty in assessing species diversity and evenness and made interpretations of the data difficult.

In the tree growth response to harvest gaps (i.e., chapter three), I suggest two improvements. First, tree cores that were collected should have been cored to the pith. Because an incomplete core was taken, cross dating could not be performed preventing more accurate results in establishing gap formation dates in the natural gaps. Furthermore, tree age may be a factor in determining a growth response to canopy openings, and this variable could have been easily addressed if trees were cored to the pith. Second, when measuring tree core and cross-section growth rings, I suggest using the Velmex microscope. Although WINDendro is a widely-used and accepted means of measuring growth rings, much time was wasted correlating measurement results from the Velmex to the measurement results in all the hardwood trees, many of which were very difficult to discern. I used WINDendro because of its familiarity, ease of use, and consistency with my other softwood cores and cross-sections. The Velmex microscope is better at detecting the hard-to-see hardwood growth rings.

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Appendix: The mean cover and mean frequency of all species by gap origin. Mean cover is calculated by the mean percent cover in a gap averaged over all harvest gaps, for example. Mean frequency is the frequency of a species in a gap (number of times a species occurred in a gap divided by the number of sample plots) averaged over all harvest gaps, for example.

	Harvest Gaps		**Natural Gaps**		**Closed Canopy**	
Species	**Mean % Cover**	**Mean Frequency**	**Mean % Cover**	**Mean Frequency**	**Mean % Cover**	**Mean Frequency**
Abies balsamea	8.418	0.772	10.250	0.908	5.951	0.728
Acer pennsylvanicum	0.001	0.001	0.002	0.007	0.009	0.022
Acer rubrum	8.936	0.953	0.276	0.801	0.108	0.652
Acer saccharum	0.125	0.019	0.222	0.123	0.175	0.196
Acer spicatum	0.002	0.002	0.000	0.000	0.000	0.000
Actaea rubra	0.000	0.000	0.000	0.000	0.018	0.022
Alnus incanca	0.288	0.049	0.000	0.000	0.000	0.000
Amelanchier laevis	0.000	0.002	0.000	0.000	0.000	0.000
Amelanchier species	0.002	0.014	0.002	0.022	0.002	0.022
Anapahlis margaritacea	0.006	0.005	0.000	0.000	0.000	0.000
Aralia hispida	0.029	0.018	0.000	0.000	0.000	0.000
Aralia nudicaulis	3.046	0.354	1.430	0.415	0.165	0.098
Aralia spinosa	0.005	0.012	0.000	0.000	0.000	0.000
Arisaema triphyllum	0.007	0.002	0.019	0.020	0.004	0.033
Asplenium species	0.000	0.004	0.000	0.000	0.000	0.000
Asplenium trichomanes	0.000	0.004	0.000	0.000	0.000	0.000
Aster radula	0.004	0.002	0.000	0.000	0.000	0.000
Aster species	0.001	0.010	0.000	0.000	0.000	0.000
Athyrium filix-femina	0.087	0.063	0.011	0.011	0.000	0.000
Betula alleghaniensis	0.026	0.042	0.000	0.000	0.000	0.000

Appendix cont’d

	Harvest Gaps		**Natural Gaps**		**Closed Canopy**	
Species	**Mean % Cover**	**Mean Frequency**	**Mean % Cover**	**Mean Frequency**	**Mean % Cover**	**Mean Frequency**
Betula papyrifera	0.750	0.458	0.014	0.072	0.000	0.087
Betula populifolia	0.002	0.003	0.000	0.000	0.011	0.000
Betula species	0.005	0.017	0.000	0.000	0.000	0.000
Calystegia sepium	0.000	0.000	0.054	0.022	0.000	0.000
Circaea alpina	0.000	0.000	0.011	0.007	0.000	0.000
Clintonia borealis	0.014	0.032	0.000	0.000	0.000	0.000
Coptis trifolia	0.107	0.049	0.004	0.011	0.000	0.000
Cornus canadensis	0.402	0.116	0.004	0.022	0.000	0.033
Corylus americana	0.057	0.020	0.152	0.011	0.000	0.000
Corylus cornuta	0.119	0.025	0.135	0.087	0.007	0.022
Cypripedium acaule	0.001	0.002	0.000	0.000	0.122	0.000
Cystopteris species	0.000	0.004	0.000	0.000	0.000	0.000
Dennstaedtia punctilobula	0.006	0.018	0.000	0.000	0.000	0.000
Diervilla lonicera	0.007	0.012	0.000	0.000	0.000	0.000
Doellingeria umbellata	0.001	0.006	0.000	0.000	0.000	0.000
Doellingeria umbellata	0.004	0.002	0.000	0.000	0.000	0.000
Dryopteris cristata	0.000	0.002	0.201	0.071	0.000	0.000
Dryopteris intermedia	0.036	0.016	0.252	0.109	0.000	0.000
Dryopteris marginalis	0.004	0.006	0.000	0.000	0.000	0.000
Dryopteris species	0.008	0.049	0.048	0.038	0.000	0.043
Epilobium angustifolium	0.001	0.009	0.000	0.000	0.071	0.000
Epilobium ciliatum	0.000	0.004	0.000	0.000	0.000	0.000
Epilobium leptophyllum	0.001	0.002	0.000	0.000	0.000	0.000
Epipactis heeleborine	0.000	0.002	0.000	0.000	0.000	0.000
Equisetum arvense	0.002	0.006	0.000	0.000	0.000	0.000
Equisetum pratense	0.001	0.003	0.013	0.022	0.000	0.000

Appendix cont'd

	Harvest Gaps		**Natural Gaps**		**Closed Canopy**	
Species	**Mean % Cover**	**Mean Frequency**	**Mean % Cover**	**Mean Frequency**	**Mean % Cover**	**Mean Frequency**
Erechtites hieraciifolia	0.002	0.002	0.000	0.000	0.000	0.000
Erysimum cheiranthoides	0.000	0.002	0.000	0.000	0.000	0.000
Euphorbia species	0.000	0.002	0.000	0.000	0.000	0.000
Euthamia graminifolia	0.012	0.031	0.000	0.000	0.000	0.000
Euthamia tenuifolia	0.006	0.019	0.003	0.011	0.000	0.000
Fagus grandifolia	0.400	0.062	0.343	0.098	0.000	0.000
Fallopia convolvulus	0.001	0.001	0.000	0.000	0.000	0.000
Fallopia scandens	0.000	0.004	0.000	0.000	0.000	0.000
Fragaria virginiana	0.000	0.000	0.013	0.036	0.036	0.000
Fraxinus americana	0.060	0.079	1.859	0.304	0.000	0.076
Fraxinus nigra	0.036	0.012	0.000	0.000	0.216	0.000
Fraxinus species	0.141	0.123	0.000	0.000	0.000	0.217
Galium asprellum	0.004	0.009	0.000	0.000	0.000	0.000
Galium palustre	0.000	0.000	0.011	0.040	0.000	0.000
Galium trifidum	0.000	0.000	0.001	0.007	0.000	0.000
Gaultheria hispidula	0.001	0.004	0.000	0.000	0.000	0.000
Gaultheria procumbens	0.067	0.114	0.014	0.076	0.000	0.000
Geranium species	0.000	0.002	0.000	0.000	0.000	0.000
Gratiola neglecta	0.000	0.004	0.000	0.000	0.000	0.000
Gymnocarpium dryopteris	0.059	0.020	0.055	0.034	0.000	0.076
Hieracium aurantiacum	0.001	0.004	0.000	0.000	0.127	0.000
Hieracium caespitosum	0.002	0.003	0.000	0.000	0.000	0.000
Hieracium lachenalii	0.001	0.012	0.000	0.000	0.000	0.000
Hieracium pilosella	0.001	0.002	0.000	0.000	0.000	0.000
Hieracium piloselloides	0.000	0.001	0.000	0.000	0.000	0.000
Hieracium species	0.000	0.002	0.002	0.011	0.000	0.000
Hydrocotyle americana	0.000	0.000	0.002	0.007	0.000	0.000
Hypericum species	0.000	0.004	0.000	0.000	0.000	0.000
Ilex species	0.001	0.003	0.000	0.000	0.000	0.000
Ilex verticillata	0.001	0.002	0.000	0.000	0.000	0.000
Impatiens capensis	0.000	0.000	0.514	0.094	0.000	0.000

Appendix cont'd

	Harvest Gaps		Natural Gaps		Closed Canopy	
Species	**Mean % Cover**	**Mean Frequency**	**Mean % Cover**	**Mean Frequency**	**Mean % Cover**	**Mean Frequency**
Kalmia angustifolia	0.009	0.010	0.004	0.011	0.010	0.011
Krigia virginica	0.001	0.007	0.000	0.000	0.000	0.000
Lactuca canadensis	0.001	0.007	0.000	0.000	0.000	0.000
Lactuca sativa	0.002	0.002	0.000	0.000	0.000	0.000
Leontodon autumnalis	0.001	0.003	0.000	0.000	0.000	0.000
Linaria vulgaris	0.000	0.002	0.000	0.000	0.000	0.000
Linnaea borealis	0.129	0.024	0.002	0.011	0.000	0.000
Lobelia inflata	0.000	0.002	0.000	0.000	0.000	0.000
Lonicer morrowii	0.006	0.018	0.000	0.000	0.000	0.000
Lonicer species	0.000	0.001	0.000	0.000	0.000	0.000
Lonicera canadensis	0.088	0.078	0.013	0.069	0.005	0.033
Lycopodium clavatum	0.001	0.005	0.000	0.000	0.000	0.000
Lycopodium hickeyi	0.001	0.007	0.000	0.000	0.001	0.011
Lycopodium obscurum	0.010	0.047	0.029	0.076	0.009	0.033
Lycopus uniflorus	0.004	0.004	0.049	0.022	0.000	0.000
Lysimachia quadrifolia	0.001	0.002	0.000	0.000	0.000	0.000
Maianthemum canadense	0.437	0.645	0.233	0.603	0.076	0.304
Maianthemum racemosum	0.000	0.000	0.011	0.011	0.023	0.033
Medeola virginiana	0.016	0.043	0.013	0.054	0.002	0.011
Melampyrum lineare	0.001	0.003	0.000	0.000	0.000	0.000
Mitchella repens	0.013	0.065	0.075	0.167	0.009	0.054
Mitella nuda	0.000	0.002	0.000	0.000	0.000	0.000
Moneses uniflora	0.000	0.004	0.000	0.000	0.000	0.000
Nemopanthus mucronatus	0.003	0.009	0.000	0.000	0.000	0.000
Oclemena acuminata	0.044	0.073	0.005	0.011	0.000	0.000
Onclemena acuminata	0.018	0.014	0.000	0.000	0.000	0.000
Onoclea sensibilis	0.269	0.061	0.071	0.047	0.000	0.000
Orthilia secunda	0.002	0.002	0.000	0.000	0.000	0.000
Osmunda cinnamomea	0.121	0.019	0.027	0.011	0.009	0.011
Osmunda claytoniana	0.471	0.055	0.451	0.027	0.268	0.054
Ostrya virginiana	0.001	0.008	0.062	0.076	0.000	0.109

Appendix cont’d

	Harvest Gaps		**Natural Gaps**		**Closed Canopy**	
Species	**Mean % Cover**	**Mean Frequency**	**Mean % Cover**	**Mean Frequency**	**Mean % Cover**	**Mean Frequency**
Oxalis corniculata	0.000	0.004	0.000	0.000	0.000	0.000
Oxalis montana	0.002	0.007	0.000	0.000	0.000	0.011
Oxalis species	0.000	0.002	0.000	0.000	0.000	0.000
Oxalis stricta	0.020	0.009	0.000	0.000	0.000	0.000
Phegopteris connectilis	0.000	0.002	0.000	0.000	0.000	0.000
Photinia melanocarpa	0.010	0.020	0.000	0.000	0.000	0.000
Potentilla norvegica	0.038	0.028	0.000	0.000	0.000	0.000
Picea abies	0.000	0.000	0.005	0.011	0.000	0.000
Picea glauca	0.011	0.004	0.000	0.000	0.000	0.000
Picea rubens	0.530	0.207	0.256	0.114	0.122	0.033
Picea species	0.141	0.013	0.000	0.000	0.000	0.000
Pinus resinosa	0.030	0.019	0.000	0.000	0.000	0.000
Pinus strobus	0.513	0.576	0.217	0.683	0.350	0.370
Polygala species	0.000	0.004	0.000	0.000	0.000	0.000
Polygala viridescens	0.006	0.005	0.000	0.000	0.000	0.000
Polygonatum pubescens	0.000	0.000	0.028	0.065	0.000	0.000
Polystichum acrostichoides	0.017	0.006	0.109	0.098	0.466	0.141
Populus grandidentata	0.373	0.122	0.043	0.022	0.057	0.033
Populus species	0.000	0.004	0.002	0.007	0.001	0.011
Populus tremuloides	0.974	0.279	0.029	0.141	0.092	0.141
Potentilla simplex	0.007	0.003	0.000	0.000	0.000	0.000
Potentilla vorvegica	0.005	0.008	0.000	0.000	0.000	0.000
Prunella vulgaris	0.001	0.005	0.000	0.000	0.000	0.000
Prunus pennsylvanica	0.028	0.117	0.098	0.011	0.000	0.000
Prunus virginiana	0.002	0.002	0.000	0.000	0.000	0.000
Pteridium acquilinum	0.852	0.122	0.001	0.011	0.000	0.000
Pyrola americana	0.002	0.002	0.000	0.000	0.000	0.000
Pyrola chlorantha	0.000	0.000	0.002	0.007	0.001	0.011

Appendix cont'd

	Harvest Gaps		Natural Gaps		Closed Canopy	
Species	**Mean % Cover**	**Mean Frequency**	**Mean % Cover**	**Mean Frequency**	**Mean % Cover**	**Mean Frequency**
Pyrola elliptica	0.000	0.002	0.007	0.011	0.000	0.000
Quercus rubra	0.259	0.220	0.105	0.138	0.010	0.054
Ranunculus abortivus	0.000	0.000	0.006	0.018	0.000	0.000
Ranunculus acris	0.003	0.003	0.000	0.000	0.000	0.000
Ranunculus hispidus	0.001	0.004	0.000	0.000	0.000	0.000
Rhus hirta	0.106	0.047	0.000	0.000	0.000	0.000
Ribes lacustre	0.002	0.008	0.000	0.000	0.000	0.000
Ribes species	0.000	0.000	0.011	0.007	0.000	0.000
Rosa virginiana	0.006	0.004	0.000	0.000	0.000	0.000
Rubus allegheniensis	0.195	0.069	0.000	0.000	0.000	0.000
Rubus dalibarda	0.005	0.003	0.000	0.000	0.000	0.000
Rubus flagellaris	0.003	0.002	0.000	0.000	0.000	0.000
Rubus hispidus	0.171	0.013	0.000	0.000	0.000	0.000
Rubus ideaus	0.662	0.272	0.000	0.000	0.000	0.000
Rubus occidentalis	1.260	0.141	0.000	0.000	0.000	0.000
Rubus pubescens	0.456	0.051	0.029	0.007	0.000	0.000
Scutellaria lateriflora	0.000	0.000	0.037	0.022	0.000	0.000
Silene species	0.000	0.002	0.000	0.000	0.000	0.000
Smphyotrichum nvi-belgii	0.003	0.002	0.000	0.000	0.000	0.000
Solidaga altissima	0.003	0.008	0.000	0.000	0.000	0.000
Solidaga gigantea	0.015	0.005	0.000	0.000	0.000	0.000
Solidaga nemoralis	0.000	0.002	0.015	0.033	0.000	0.000
Solidaga puberula	0.000	0.001	0.000	0.000	0.000	0.000
Solidaga rugosa	0.013	0.038	0.000	0.000	0.000	0.000
Solidago hispida	0.000	0.003	0.000	0.000	0.000	0.000
Solidago species	0.005	0.006	0.000	0.000	0.000	0.000

Appendix cont'd

Species	**Harvest Gaps** **Mean % Cover**	 **Mean Frequency**	**Natural Gaps** **Mean % Cover**	 **Mean Frequency**	**Closed Canopy** **Mean % Cover**	 **Mean Frequency**
Solidao canadensis	0.004	0.012	0.000	0.000	0.000	0.000
Streptopus landeolatus	0.002	0.007	0.013	0.043	0.008	0.033
Symphyotrichum lateriflorum	0.000	0.000	0.001	0.011	0.000	0.000
Symphyotrichum novi-belgii	0.004	0.005	0.000	0.000	0.000	0.000
Symphyotrichum puniceum	0.006	0.012	0.000	0.000	0.000	0.000
Symphyotrichum racemosum	0.002	0.002	0.000	0.000	0.000	0.000
Taraxacum officinale	0.001	0.004	0.000	0.000	0.000	0.000
Thelypteris noveboracensis	0.018	0.021	0.013	0.043	0.017	0.043
Thelypteris simulata	0.000	0.000	0.000	0.000	0.003	0.011
Thelypteris species	0.000	0.000	0.000	0.000	0.014	0.011
Thuja occidentalis	0.037	0.062	0.184	0.042	0.163	0.043
Tilia americana	0.000	0.000	0.000	0.000	0.002	0.022
Toxicodendron radicans	0.001	0.001	0.000	0.000	0.000	0.000
Toxicodendron radicans	0.136	0.028	0.467	0.100	0.011	0.022
Trientalis borealis	0.558	0.567	0.213	0.482	0.064	0.174
Trifolium hybridum	0.001	0.003	0.000	0.000	0.000	0.000
Trifolium species	0.000	0.000	0.000	0.000	0.005	0.011
Trillium undulatum	0.006	0.002	0.000	0.000	0.018	0.033
Tsuga canadensis	2.199	0.484	6.642	0.668	1.714	0.500
Uvularia sessilifolia	0.000	0.000	0.008	0.011	0.000	0.000
Vaccinium angustifolium	0.089	0.056	0.000	0.000	0.012	0.033
Vaccinium myrtilloides	0.005	0.007	0.000	0.000	0.000	0.000
Vaccinium oxycoccos	0.001	0.008	0.000	0.000	0.000	0.000
Vaccinium species	0.133	0.044	0.000	0.000	0.000	0.000
Veronica officinalis	0.005	0.017	0.000	0.000	0.000	0.000
Viburnum nudum	0.008	0.008	0.009	0.022	0.000	0.000
Vicia tetrasperma	0.000	0.002	0.000	0.000	0.000	0.000
Viola species	0.000	0.159	0.000	0.011	0.000	0.000

BIOGRAPHY OF THE AUTHOR

Darci Schofield was born and raised in Sterling, Massachusetts on January 8, 1975. Following graduation from Notre Dame Academy High School, she attended Boston University where she received a Bachelor's degree in Environmental Science and Geology. During her college career, Darci also studied abroad in Vancouver Island, British Columbia where she studied temperate rain forest ecology and forest economics.

Following her college education, Darci became a volunteer with the Non-Government Organization, Operation Crossroads Africa, in Tanzania, Africa. Working in a rural village, Darci performed agricultural services and helped establish an irrigation system for the people in the village. After returning from Africa, Darci enjoyed various jobs working in the outdoors including teaching rock climbing to children, leading backpacking trips in the mountains of Maine and New Hampshire, as well as teaching environmental education in an experiential setting in New Hampshire. She was also the naturalist for Borestone Mountain Wildlife Sanctuary in Elliotsville Plantation Maine. Here Darci also performed forestry research on their (now defunct) Long-Term Ecological Research Plot. Darci entered graduate school in the Department of Forest Ecosystem Science in January of 2001. She is a candidate for the Master of Science degree in Forestry from The University of Maine in December, 2003.