

The time course of diameter increment responses to selection harvests in *Acer saccharum*

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Abstract: We used dendroecological techniques to analyze the temporal pattern in diameter growth following selection harvests in stands dominated by *Acer saccharum* Marsh. in central Ontario and examined differences in growth responses related to tree size, damage, and orientation relative to canopy gaps. While dendroecological studies have commonly assumed that trees show immediate growth responses to gap creation (i.e., within 1–2 years), we found that the growth enhancement in *A. saccharum* was gradual and did not reach a peak until 3–5 years following gap creation. Trees of intermediate size showed the largest proportional growth increases after gap creation, with the largest responses observed in trees on the north side of gaps. Trees with visible damage to the crown or bole had significantly lower preharvest basal area increments than trees with little or no damage, but showed greater proportional growth responses to gap creation. Both the long observed time delay in tree growth response to canopy opening and the variability in response relative to tree size and damage have important implications for attempts to reconstruct disturbance history using dendroecological methods and to sustainable forest management under selection system silviculture.

Résumé : Nous avons eu recours à la dendroécologie pour analyser le comportement temporel de la croissance en diamètre après une coupe de jardinage dans des peuplements dominés par *Acer saccharum* Marsh. dans le centre de l'Ontario et nous avons étudié les différentes réactions des arbres selon leur dimension, leurs dommages et leur orientation par rapport aux ouvertures dans le couvert. Alors que les études dendroécologiques prennent généralement pour acquis que les arbres réagissent immédiatement (i.e., en dedans de 1 à 2 ans) après la création d'une trouée, nous avons découvert que l'augmentation de croissance chez *A. saccharum* était graduelle et atteignait un sommet seulement 3 à 5 ans après la création d'une trouée. Proportionnellement, les arbres de dimension intermédiaire ont connu la plus forte augmentation de croissance après la création d'une trouée et la plus forte réaction a été observée chez les arbres situés du côté nord des trouées. Les arbres avec des dommages évidents dans la cime ou au tronc avaient un accroissement en surface terrière significativement plus faible avant la récolte que les arbres peu ou pas endommagés mais ils ont proportionnellement le plus réagi à la création de trouées. Autant le long délai observé dans la réaction des arbres après une ouverture du couvert que la variabilité dans la réaction selon la dimension et l'état des arbres ont d'importantes implications pour les tentatives de reconstitution de l'historique des perturbations à l'aide de la dendroécologie et pour l'aménagement forestier durable dans le contexte d'une futaie jardinée.

[Traduit par la Rédaction]

Introduction

The predominant silvicultural system in tolerant hardwood stands of eastern Canada is selection management, which emulates aspects of gap phase dynamics and is designed to produce an uneven-aged or multicohort stand. Many dendroecological studies have examined growth response of trees to natural disturbance events (Canham 1985, 1990; Merrens and Peart 1992; Digregorio et al. 1999; Naidoo and Lechowicz 2001), and a few studies have also examined tree growth responses to shelterwood cuts (Youngblood 1991; Latham and Tappeiner 2002) or to crown release, selective (high-grading), or structural retention harvests (Orwig and

Abrams 1994; Wood et al. 1996; Singer and Lorimer 1997; Bebbler et al. 2004). However, surprisingly little is known about how canopy trees respond to selection management per se, in which the gaps created are relatively small and a balanced distribution of tree sizes is maintained (Smith et al. 1997).

Understanding how trees respond to gap creation is of particular importance to developing a more detailed, mechanistic understanding of growth processes within selection-managed forests. Within each harvest cycle, up to one third of the trees may be removed, and most remaining trees will experience some degree of exposure to gaps. The division of trees into size, damage, and form categories is a common practice in the marking and removal of trees in selection management, but tree growth responses to gap creation have not, to our knowledge, been studied with respect to these management criteria. It is generally accepted that there will be a growth increase after gap creation and that this increase is due to reduced competition and increased resource availability (Lorimer and Frelich 1989; Abrams et al. 1995; Nowacki and Abrams 1997; Oguchi et al. 2003). However,

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the temporal pattern and magnitude of this increase has not been well documented in uneven-aged, single tree or small group selection silvicultural systems.

Studies on the physiological and growth responses of tree species to gap creation have usually focused on seedlings and saplings. Generally, young trees respond positively to increased light availability through increased photosynthetic carbon uptake (Naidu and DeLucia 1997; Tognetti et al. 1997; Yamashita et al. 2000), which ultimately results in greater height and diameter growth over time (Orwig and Abrams 1995; Peterson et al. 1997). However, trees of some species experience negative responses to canopy opening because of a lag in light acclimation and (or) photoinhibition and photodamage effects (Lovell et al. 1994). Likewise, understory vegetation responses to canopy gap creation may also show lagged responses as a result of time delays in the release of nutrient resources or because of the lagged effects of recovery from physical disturbance (Thomas et al. 1999). Large canopy trees might similarly be expected to show lagged responses as a result of photoinhibition, physical damage responses, or slow soil dynamic processes.

We propose three general hypotheses as to how canopy tree growth may respond to gap creation. The first hypothesis, which has been implicitly assumed by prior dendroecological studies (Canham 1985, 1990; Lorimer and Frelich 1989; Orwig and Abrams 1995, 1999), is that there will be an immediate growth increase because of increased resource availability after harvest, but this increase can only be sustained for a short period of time before declining to some lower level (Fig. 1). The second hypothesis is that there will be a brief period of reduced growth (gap shock), due to photoinhibition or drought stress, followed by a gradual increase in growth to some maximum rate before a return to some lower growth rate (Fig. 1). The third hypothesis suggests that both the first two processes are involved, but that the effects of gap shock responses and the immediate growth response offset each other, resulting in a slow increase in growth to some maximum level several years after gap creation (Fig. 1). Such a lagged response is also expected to result from slow nutrient release dynamics. None of these hypotheses have been rigorously tested in selection management systems, either in terms of physiological process or with respect to the temporal pattern of tree growth response.

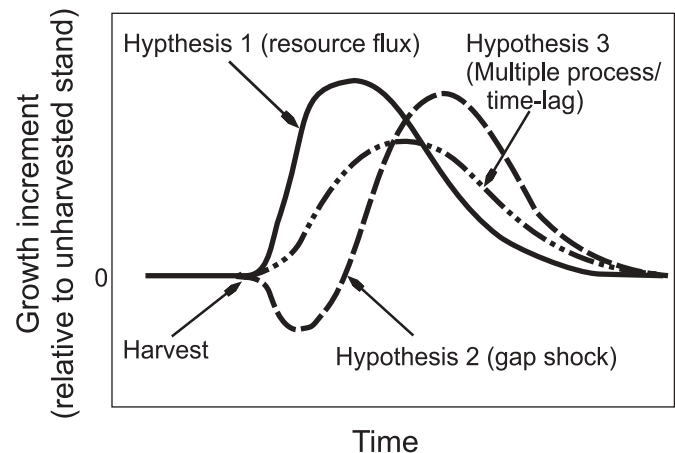
This study was designed to examine how gap creation affects tree basal area increment (BAI) growth over the first 5 years after harvest. By examining BAIs of trees that were released at known times, we are able to quantify the temporal growth response to gap creation. In addition, we examine tree responses relative to commonly used management criteria, including size, damage, bole quality, and position relative to gaps. We thus address the following questions: (i) What is the temporal pattern of BAI growth response to selection harvesting in *Acer saccharum* Marsh.? (ii) How do trees differ in growth response according to size, observable damage, and orientation relative to gap openings?

Materials and methods

Site description

Work was conducted at Haliburton Forest and Wildlife Reserve, a 25 000-ha, privately owned forest in Ontario,

Fig. 1. Hypothetical growth responses of canopy trees to harvest gap creation. Changes in growth are expressed as a proportion of the unharvested growth increments. The solid line represents hypothesis 1, corresponding to an immediate increase in growth driven by increased resources. The dashed line represents hypothesis 2, which postulates a gap shock effect, in which tree growth is initially reduced after gap formation. The double-dashed line (hypothesis 3) is intermediate between hypotheses 1 and 2 and represents that case in which both resource flux and gap shock effects occur (and (or) that resource fluxes are lagged).



Canada (45°13'N, 78°35'W). Tolerant hardwood forests in this area have been managed by selection harvest silviculture for the past 40 years and were selectively harvested for yellow birch (*Betula alleghaniensis* Britt.) and white pine (*Pinus strobus* L.) prior to that time. Large sections of the forest are now experiencing their second or third stand entry. Harvest locations and dates have been recorded and mapped for the last 20 years, making it possible to identify and accurately date when gaps in specific harvesting blocks were created. The dominant species in the forest is *A. saccharum*, representing over 60% of the basal area and frequency of stems, but *Fagus grandifolia* Ehrh., *Prunus serotina* Ehrh., *Quercus rubra* L., *B. alleghaniensis*, *Ostrya virginiana* (Mill.) K. Koch., and *Fraxinus americana* L. are also present in varying amounts (S.C. Thomas, unpublished data). This study was restricted to *A. saccharum* because of its high relative abundance in all harvest locations.

Site selection

In August 2002, 12 cutblocks from six different harvest dates were sampled, including cutblocks from 1992, 1994, 1996, 1998, 2000, and 2002. Two separate cutblocks were examined for each harvest year, and sampled areas were chosen to be of similar site quality and productivity. Within each cutblock, five gaps were located by following skidder trails through the forest and randomly choosing gaps from either side of the trail. A gap was defined by the presence of a harvested stump from the harvest year in question and by the ring of trees surrounding the stump. If more than one stump was present inside the gap, then the largest stump in the gap was designated as the middle of the gap. The average gap was formed by the harvest of 1.8 (± 0.5 SD) canopy trees and had an average project area of 172 (± 235 SD) m² at the time of measurement. For each gap, all trees larger

than 10 cm in diameter at breast height (DBH) surrounding the stump, with crowns adjacent to the gap opening, were included in the study.

Measurements

Tree diameter was measured at 1.3 m DBH for all trees adjacent to the gap and at 0.5 m diameter at stump height (DSH) for all stumps and trees adjacent to or within the gap. Each tree was classified by damage, crown class, and stem quality using guidelines established by the Ontario Ministry of Natural Resources for assessing individual tree risk potential (OMNR 1998). It was not possible to determine if damage was caused at time of harvest or during an earlier disturbance event; therefore, damage was classified into three categories irrespective of wound age. Trees with no apparent damage were classified as damage class one; those with some damage (i.e., small bole scar less than 0.5 m², minor crown damage), although not enough to cause serious decline in the next cutting cycle, were classified as damage class two; trees with significant or severe damage (i.e., very large scar more than 0.5 m², visible rotting and cavities in bole, major crown damage), which may cause serious decline before the next harvest cycle were classified as damage class three (OMNR 1998). Quality of trees was also based on the OMNR classification scheme, in which class one represents trees with high- or mid-quality saw logs, class two represents high- or mid-quality saw logs that show signs of decline, and class three trees are cull trees with poor form and no potential to improve (OMNR 1998). Crown position was broken down into five categories: emergent, dominant, codominant, intermediate, and suppressed (OMNR 1998). There were no emergent *A. saccharum* and most of the suppressed trees fell below the 10-cm DBH category and were not included in the study. Crown aspect, relative to the center of the gap opening, was measured to the nearest degree.

Tree cores

Tree cores were taken at 0.5 m (corresponding to DSH measurements) to minimize damage to merchantable bole sections. Cores were mounted on plywood and sanded down with progressively higher grit sand paper until rings were clearly visible. Ring widths were measured to within 0.01 mm with a table-mounted tree ring increment measurement system. Tree cores were cross-dated using two methods. The first method involved comparing individual cores to the mean ring width series for each cutblock. Any large discrepancies in growth pattern were noted, and cores that showed apparent shifts in ring series were double-checked for missing or extra rings. Cores were then cross-dated by examining years with consistently large or small rings among all cores. Cores that showed slight variation (i.e., 1 or 2 years difference in either large or small rings) were also checked for missing or extra rings. If after both inspections a consistent pattern of ring widths could not be established, the core was removed from the results. Increments for the most recent 20 years of growth were used in the study.

Analysis

Calculation of proportional increases in growth after harvest was achieved using the 2002 cutblocks as a control and the 1992, 1994, and 1996 cutblocks to test for increases in

BAI after harvest. The 2002 cutblocks were used as a control stand because trees within that stand would not have experienced any release in the last 20 years. The control value (expected value) was calculated by obtaining the yearly mean for the 2002 cutblocks. This procedure removed much of the interannual variation in growth resulting from climatic variation and other environmental factors. The proportional increase in BAI (Δ BAI) was calculated using the formula

$$[1] \quad \Delta\text{BAI} = (O - E)/E$$

where expected (E) is the mean value per year for the 2002 cutblocks and observed (O) is the BAI per year per gap and core. Significance testing for the Δ BAI was performed with a general linear model, with comparisons between the control and harvested stands examined using a Tukey–Kramer post hoc test. Statistical analyses were conducted using SAS v. 8.1. (SAS Institute Inc., Cary, N.C.).

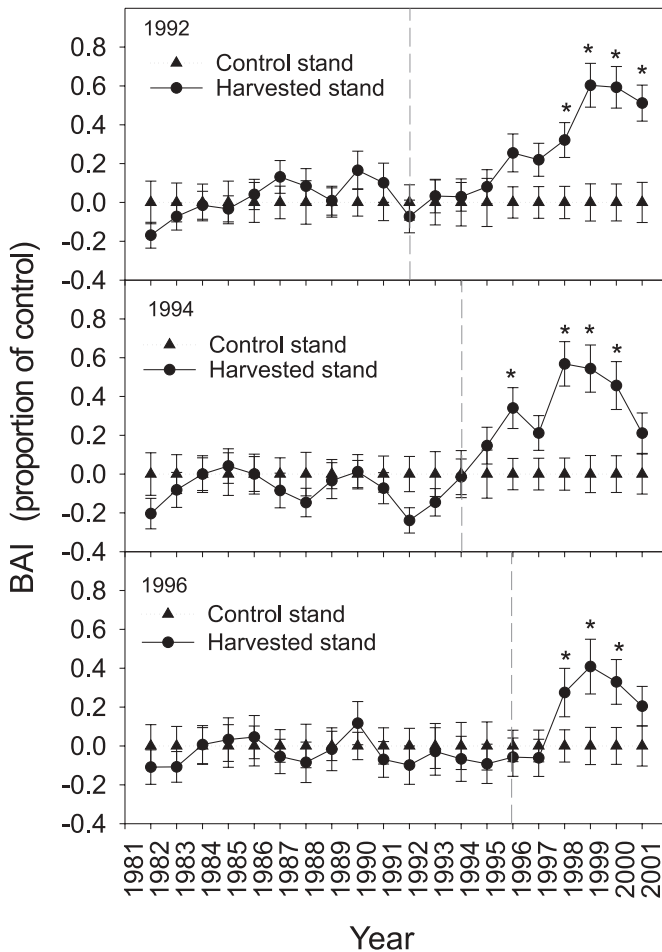
For the remaining analyses, BAI for the 5 years prior to and after harvest for each stand were sorted into pre- and post-harvest categories. For example, the first year post-harvest (+1 post) for a stand harvested in 1992 is 1993, whereas the first post-harvest year (+1 post) for a stand harvested in 1996 was 1997. Only the 5 years before and after harvest were used in the analysis because of inadequate replication across harvest years, since there were only two harvest dates that would allow us to examine more than 5 years of growth response post-harvest. By comparing BAIs across many cutblocks, irrespective of year of harvest, the year-to-year variation in climatic growth trends were reduced, and growth trends due to harvest could be easily identified. A general linear model procedure was used to test the significance of all independent variables and interactions, with BAI of the cores as the dependent variable. Terms and interactions, such as damage class and tree form, were added sequentially to the basic model until the higher order interaction terms failed to significantly explain additional variation within the data. Significant terms such as tree and stand identity are not reported, although they accounted for much of the variation in growth response. The data met criteria for homoscedasticity and normality, so no transformation was necessary. If the general linear model indicated a significant difference for a class variable or interaction term, then a Tukey–Kramer post hoc test was employed.

Percent increase in growth response for each class variable combination was calculated using the mean pre-harvest BAIs as the denominator and post-harvest BAIs as the numerator. Proportional increases of 25%, 50%, 75%, and 100% are commonly used to indicate ecologically significant increases in growth response and are more easily interpreted than post hoc lettering for higher order interaction terms. Since Tukey–Kramer post hoc tests were generally able to detect differences between means, which were equivalent to a 25% difference in BAI, any post-harvest proportional increase in growth of greater than 25% also generally indicates a significant increase at $P < 0.05$.

Results

There was a consistent pattern of increasing post-harvest BAI increase regardless of year of harvest (Fig. 2), but no

Fig. 2. Proportional changes in basal area increment (BAI) (\pm SE) for harvested and control stands. BAI change was calculated as described in eq. 1. Asterisks indicate significant differences between the control and the harvested stands ($P < 0.05$). Vertical dashed lines indicate year of harvest.



significant difference in BAI between the control and the cutblocks for pre-harvest years. Increases in post-harvest BAI were not significantly different from pre-harvest values for at least 2 years post-harvest, with the time lag in growth response between the time of harvest and significant increases in BAI varying by year of harvest (Fig. 2). Increases in BAI lasted for 3–5 years following the 2–5 year post-harvest lag period. The 1992 cutblock experienced no significant increase in BAI for 5 years post-harvest, though a general increasing trend can be seen after 3 years post-harvest. A maximum proportional increase in BAI of approximately 60% occurred 7 years post-harvest (Fig. 2, top panel). The 1994 cutblocks showed significant increases in BAI in the second year post-harvest and had a maximal increase of approximately 60% (Fig. 2, middle panel). The 1996 cutblock showed a lag in BAI response before showing significant increases in the second year. The maximum increase in BAI for the 1996 cutblock was approximately 40% and occurred 3 years post-harvest (Fig. 2, bottom panel). Analyses that pooled all harvest dates also indicate a significant difference in BAI pre- and post-harvest (Table 1). The BAI for all post-harvest dates beyond and including the

Table 1. Results of ANOVA describing effects on basal area increment of residual *Acer saccharum* trees following selection harvests at Haliburton Forest.

Source	df	SS	F	P value
Years ^a	12	3 657.7	4.48	<0.0001
Size ^b	3	33 069.8	175.10	<0.0001
Damage ^c	2	803.2	6.38	0.0017
Quality ^d	2	744.2	5.91	0.0027
Direction ^e	3	1 591.6	8.39	<0.0001
Years × Size	36	6 178.6	2.73	<0.0001
Years × Damage	24	2 144.3	1.42	0.0842
Years × Quality	24	1 927.7	1.28	0.1657
Years × Direction	36	2 560.2	1.13	0.2731
Size × Damage	6	4 591.7	12.16	<0.0001
Size × Quality	6	1 531.6	4.06	0.0005
Size × Direction	9	4 806.4	8.48	<0.0001
Years × Size × Damage	72	6 695.5	1.46	0.0056
Years × Size × Quality	72	4 670.9	1.03	0.5973
Years × Size × Direction	8	8 747.9	1.29	0.0253

Note: SS, sum of squares.

^aYears pre- or post-harvest.

^bTree size class as defined in Methods.

^cDamage class as defined in Methods.

^dTree quality as defined in Methods.

^eDirection of tree canopy relative to gap as described in Methods.

fourth year post-harvest were higher than all the pre-harvest years as well as the harvest year.

BAI varied with tree size (Table 1). The largest trees had the largest BAI, while the smallest trees had the smallest BAI. Post-hoc tests revealed that the BAI for the large (35–45 cm DBH) and the very large trees (45+ cm DBH) were not significantly different. However the BAI for the medium-sized trees (25–35 cm DBH) were significantly smaller than large trees, and BAI for small trees (less than 25 cm DBH) were significantly smaller than those for all the larger size classes (Table 2).

There was a difference in how trees of different sizes responded to harvest as evidenced by a highly significant year × tree size interaction (Table 1). Small-sized trees (<25 cm DBH) and medium-sized trees (25–35 cm DBH) responded more positively after harvest than either of the larger size classes (Fig. 3). There was a 25% increase in growth by the small- and medium-sized trees in the first years post-harvest, which continued over time, so that by the fourth year the small-sized trees (<25 cm DBH) had increased by 50%. In contrast, medium-sized trees (25–35 cm DBH) required 5 years to achieve a 50% increase in BAI (Fig. 3). The larger size classes (>35 cm DBH) never showed a proportional increase in BAI greater than 50% and took between 1 and 5 years to reach a 25% increase in growth (Fig. 3).

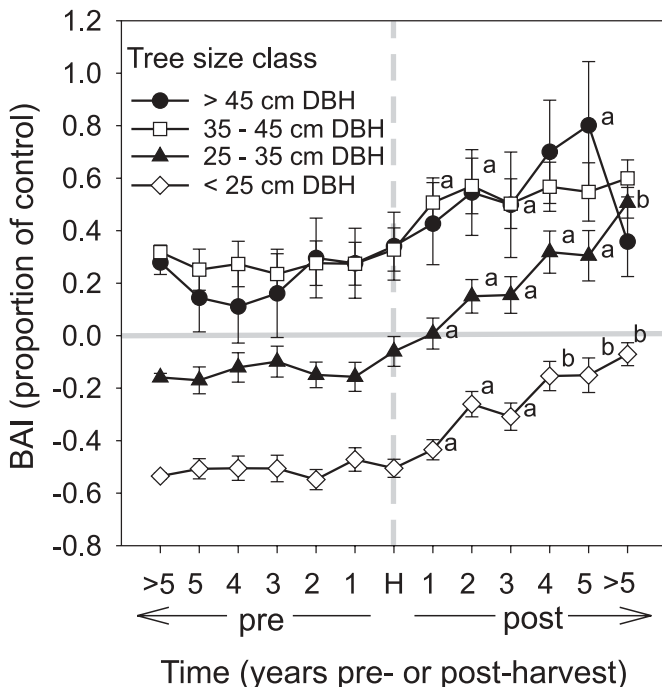
The orientation of trees relative to canopy openings also had a significant effect on BAI. Trees with gaps formed on the south side of their canopies had lower pre-harvest BAI than trees with gaps formed on the north side (Table 2). We infer that this difference is due to the fact that most harvested trees were canopy dominants, implying that prior to harvest, trees with gaps formed to the south suffered from higher competition for light than did trees with gaps formed

Table 2. Basal area increments (cm²·year⁻¹; mean ± SE) for residual *Acer saccharum* trees following selection harvests, classified by tree size, orientation relative to gaps, damage, and bole condition.

Classes	Pre-harvest	Harvest	Post-harvest	
			1–2 years	3–5 years
Tree size (cm, DBH)				
<25	7.60±0.3a	7.65±0.53a (1.01)	10.27±0.50a (1.35)	11.59±0.46a (1.53)
25–35	13.06±0.3b	14.04±0.79b (1.08)	16.96±0.70b (1.30)	18.80±0.70b (1.44)
35–45	18.72±0.5c	19.42±1.18c (1.04)	24.33±1.12c (1.30)	23.11±0.85c (1.23)
>45	20.48±1.01c	20.07±1.78c (0.98)	22.23±1.71c (1.09)	23.67±1.68c (1.16)
Direction of gap relative to tree				
North	14.33±0.52a	14.97±1.16a (1.04)	17.70±0.90a (1.24)	19.40±1.04a (1.35)
South	13.06±0.45b	13.71±0.98b (1.05)	17.25±0.87b (1.32)	17.53±0.71b (1.34)
West	15.89±0.5a	15.61±1.22a (0.98)	18.55±1.15a (1.17)	19.48±1.01a (1.23)
East	14.16±0.54a	15.32±1.22a (1.08)	18.21±1.18a (1.29)	20.36±0.99a (1.44)
Damage				
None	16.30±0.43a	16.77±0.90a (1.02)	20.57±0.84a (1.26)	21.13±0.72a (1.30)
Moderate	13.66±0.41a	14.33±0.95a (1.05)	17.62±0.84a (1.29)	17.89±0.73a (1.31)
Severe	11.12±0.42b	11.70±0.98b (1.05)	12.70±0.70b (1.14)	16.31±0.93b (1.47)
Condition				
No defects	15.27±0.42a	15.54±0.89a (1.02)	19.69±0.78a (1.29)	20.28±0.72a (1.33)
Minor defects	13.75±0.40a	15.35±1.03a (1.12)	17.35±0.94a (1.26)	18.91±0.76a (1.38)
Cull	12.80±0.48b	12.31±0.85b (0.96)	14.72±0.78b (1.15)	16.51±0.90b (1.29)

Note: Numbers in brackets following means are proportional increases calculated by dividing post-harvest interval mean by the pre-harvest mean for each class variable. Different letters indicate significant differences at $P < 0.05$ from a Tukey–Kramer test.

Fig. 3. Proportional changes in basal area increment (BAI) (±SE) for different tree size classes as compared with the control stand. BAI change was calculated as described in eq. 1. Points marked “a” represent a >25% increase in growth compared with the pre-harvest BAIs, while points marked “b” represent a >50% increase in growth compared with the pre-harvest increments. Vertical dashed line indicates year of harvest.



to the north. Trees of different sizes responded differently to gap orientation, as indicated by a significant time × tree size × direction interaction term. Specifically, large trees facing south into the gap responded slightly more positively to gap creation than large north-facing trees, while small south-facing trees responded much more positively to gap creation than small north-facing trees (Fig. 4).

Visible damage to trees also was significantly related to BAI (Table 1). Trees with severe damage generally had the lowest BAI, while those with little or no damage had higher BAI (Table 2). There was also a significant year × damage ($P < 0.1$) (Table 1), indicating that trees of different damage classes showed different temporal patterns of growth response to gap creation. Trees with no damage or moderate amounts of damage responded quickly to gap creation and had a 25% increase in growth in the first and second years post-harvest but never showed proportional increases beyond 50%. In contrast, severely damaged trees showed no significant increase in growth until the third year post-harvest, but these trees did obtain a 50% proportional growth increase by years 4–5 post-harvest (Fig. 5).

Trees of differing bole quality, as assessed by regional guidelines for selection-managed forests (OMNR 1998), showed significant differences in BAI (Table 1) but did not differ in response to harvest, as indicated by a nonsignificant year × condition interaction term (Table 1). Although the bole quality effect on average BAI was highly significant, closer examination revealed that differences in BAI between trees with good form and those with poor form were explained by damage severity and not by condition alone. BAIs from trees that had good form and severe damage were not significantly different from trees that were classified as

Fig. 4. Proportional changes in basal area increment (BAI) (\pm SE) for large (35–45 cm DBH) and small (<25 cm DBH) tree size classes facing either south or north into gaps. BAI change was calculated as described in eq. 1. Points marked “a”, “b”, “c”, and “d” represent a >25%, 50%, 75%, and 100% increase in growth compared with the pre-harvest BAIs, respectively. Vertical dashed line indicates year of harvest.

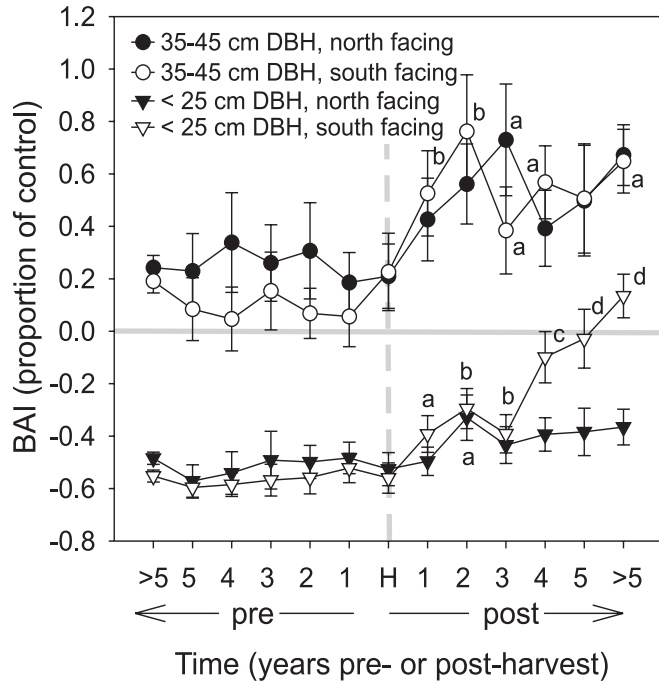
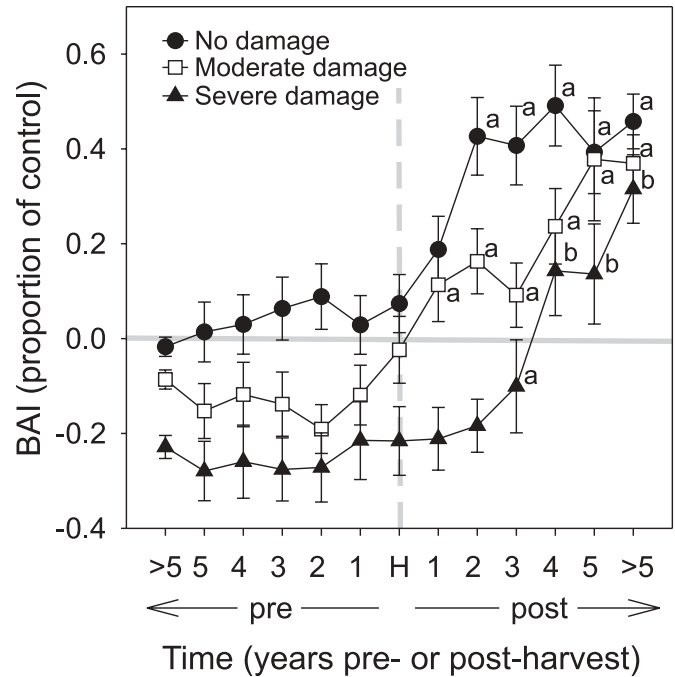


Fig. 5. Proportional changes in basal area increment (BAI) (\pm SE) for trees classified by damage class. BAI change was calculated as described in eq. 1. Points marked “a” represent a >25% increase in growth compared with the pre-harvest BAIs, while points marked “b” represent a >50% increase in growth compared with the pre-harvest increments. Vertical dashed line indicates year of harvest.



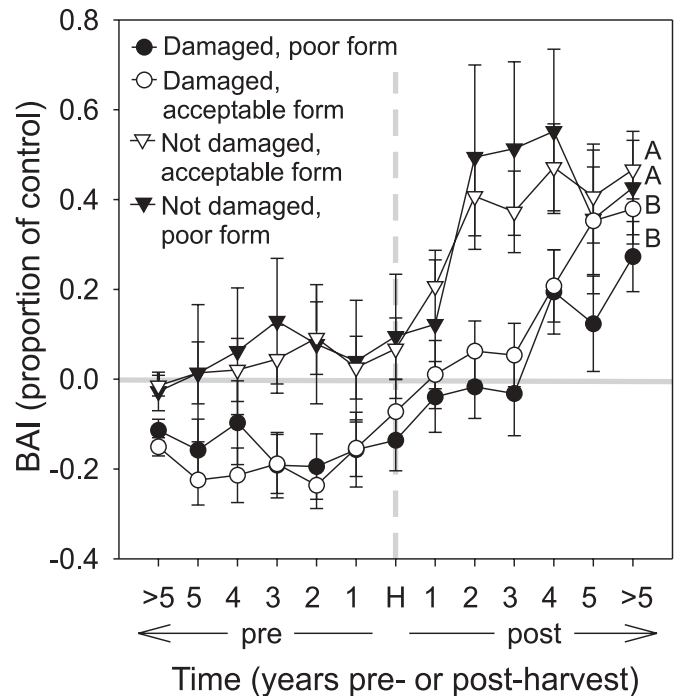
cull and severely damaged. Likewise, undamaged cull trees showed no significant difference in growth from the undamaged trees with good form (Fig. 6).

Discussion

In the introduction, we proposed three possible patterns of growth response of residual trees to selection harvests: (i) immediate large increases in growth, (ii) a period of reduced growth followed by gradual increases, and (iii) the gradual increase over time without any initial decline. Our findings support the third hypothesis, with growth increasing slowly over the first 3–5 years following gap creation. Responses to gap creation varied according to tree size, orientation relative to gaps, and prior history of tree damage. Of these factors, size was the single most important predictor of tree growth responses to gap formation; however, orientation and damage effects, as well as interactions between these factors, also had pronounced effects on the magnitude and temporal pattern of observed growth responses (Tables 1 and 2).

Although no previous studies have examined temporal patterns of BAI response to selection harvests, the general pattern of a lagged, gradual increase in growth increments has also been found in other types of partial stand harvest. Youngblood (1991) examined the growth response of residual white spruce (*Picea glauca* (Moench) Voss) to a shelterwood cut and found that there was a 2-year lag period in growth response followed by an increase in growth incre-

Fig. 6. Proportional changes in basal area increment (BAI) (\pm SE) for trees classified by damage and growth form classes. BAI change was calculated as described in eq. 1. Lines with the same letters are not significantly different at the $P < 0.05$ confidence level. Vertical dashed line indicates year of harvest.



ment for 8 years after harvest. Digregorio et al. (1999) studied the response of sugar maple trees to diffuse disturbance caused by a disease outbreak and found increased growth of subcanopy trees, with a lag in growth of at least 2 years (although this was not tested explicitly). A recent study by Bebbler et al. (2004) showed that there was a 4-year lag in growth response of white pine (*Pinus strobus*) after a structural retention harvest, a pattern similar to that found here for sugar maple. Latham and Tappeiner (2002) found that there was a lag period of between 5 and 25 years following either shelterwood or light thinning treatments in growth responses of old-growth ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*).

In the present study, one of the most important factors affecting growth response was tree size. Large trees had the greatest BAI both before and after harvest, but they showed relatively small responses to gap creation and never showed proportional increases of 50% or more (Fig. 3). The smallest trees examined (10–25 cm DBH) gained the most from gap creation, with an average 50% increase in growth 4 years post-harvest (Fig. 3). These results are similar to DiGregorio et al. (1999), who also found that larger trees responded less positively to natural gap creation than did subcanopy trees. A possible explanation for this differential response may be that larger trees do not experience as dramatic a change in light environment, since larger trees already have much of their canopies exposed to high light environments. Smaller diameter trees are more likely to be suppressed and (or) heavily shaded by large individuals and will experience a proportionally greater increase in resource availability upon gap creation. Although the response of smaller trees to gap creation was larger, they still did not achieve the same BAI as the large trees (Fig. 3). This may be because smaller trees are still under competition for light and other resources with larger trees on the closed-forest sides of their canopies and are still somewhat limited in their growth because of this competition.

Tree damage also contributed greatly to variation in observed growth responses. Overall, damaged trees had smaller BAI and took longer to respond to gap creation than undamaged trees (Fig. 4). Severely damaged trees showed a greater proportional growth response than undamaged or moderately damaged trees, after an initial lag period (Fig. 5). We offer the following hypothesis for this unexpected pattern. Most types of damage have been shown to reduce growth and increase mortality (Clark and Clark 1991; Guariguata 1998; Ickes et al. 2003). This may commonly be driven by fungal infection and the disruption of sapwood function (Shigo 1985). If the tree is able to compartmentalize the damaged area, it may be able to recover from the damage without noticeable decline. However, compartmentalization of damaged sections has been shown to reduce growth potential in trees (Shigo 1985) by reducing functional sapwood area, which is strongly correlated to canopy productivity and leaf area index (O'Hara et al. 1999). As functioning sapwood area increases after initial reductions due to the compartmentalization, growth potential may sharply increase under high resource conditions. Studies of sap flux of damaged and undamaged trees under varying in-canopy exposure are needed to test this sapwood recovery hypothesis.

Regardless of the cause of growth rate differences between damaged and undamaged trees or the variability in the length of time required to respond to gap openings, the difference in growth is substantial and should be accounted for in silvicultural management. Damage should be explicitly factored into growth and yield calculations and stand management criteria, particularly if optimizing stand growth is the objective. In this study, no attempts were made to quantify differences in damage type or determine when the damage occurred. However, it may be important to quantify specific damage types and the tree's response to this damage over time. For example, loss of crown area may affect tree growth differently than a large bole wound. In future work, damage type should be considered to explain more of the variation in growth response post-damage and also to determine how to best improve growth by minimizing certain damage types.

Tree condition or quality is also an important consideration for the operational management of stands (OMNR 1998). We found that trees with good form (Anderson and Rice 1993) had higher BAIs (Table 2), but that there was not a significant difference in how trees of differing quality responded to harvesting and gap creation (Table 1). However, it was apparent that the difference in tree BAI was due to damage rather than the form of the tree per se. Trees with no damage and poor form do not have different BAI from trees with no damage and good form, while trees that were damaged had significantly lower BAI regardless of tree form (Fig. 5). There is little evidence to support the idea that trees with defective form are physiologically inferior or have lower growth rates compared with trees with better growth form (Zobel and Talbert 1984). Typical malformations that would be classified as cull are vertical seams, leaning or bending of the bole, low crotches, or a high degree of taper in the bole (Nyland 1996; OMNR 1998). Since it is damage to trees and not tree form itself that reduces BAI over time, managers and tree markers may want to target previously damaged trees for removal first, because they may be at risk of further decline in both health and value, and then remove trees with poor form afterwards. However, because non-damaged cull trees show surprisingly strong responses to gap creation, it may be important to remove such trees to reduce the potential competitive interactions between low-value trees and suppressed trees with higher potential value.

Studies on the dynamics of natural disturbance in hardwood stands have often used proportional increase to identify release events. Nowacki and Abrams (1997) used a 25% increase in radial growth as a cut-off for the detection of minor releases, such as those created by single tree removal, while Lorimer and Frelich (1989) used 50% as their threshold for determining release. The present study suggests that growth enhancement due to gap creation is delayed by several years or not present at all, depending on the size of the tree and the presence or absence of damage. For example, very large trees showed little response to gap creation, only showing a 25% increase in BAI after 5 years (Fig. 3). Further, damaged trees took at least 3 years to show a 25% increase in BAI, while less damaged trees responded within 1 or 2 years (Fig. 5). Only very small trees exhibited a consistent 50% increase in BAI within the 5-year period of examination (Figs. 3, 4, 5). Because of the variability in growth

response of trees, the dating of disturbance events through dendrochronological techniques may either be temporally unreliable, since the date at which the tree shows a detectable (>25%) increase in growth may at least 3 years past the harvest date, or may not be detectable at all. A growth response of 25% may be a suitable threshold for *A. saccharum* in central Ontario, so long as it is acknowledged that detection of growth increases due to gap creation depends on tree size and status both before and after gap formation and that there is a variable time lag of ~2–5 years.

Studies of temporal growth responses to gap creation also have important implications to forest simulation models (Pacala et al. 1993; Menard et al. 2002). At present, forest simulation models generally assume an immediate increase in growth after a disturbance event. This assumption is not supported by our results and could result in as much as a 25% overestimation of growth over each harvest interval in selection-managed, tolerant hardwood stands. One relatively simple modeling approach to incorporate the temporal dynamics of gap responses described here may be to explicitly include a time lag in tree responses to resource changes. With better information regarding tree responses to gap creation, models should be better able to simulate tree- and stand-level growth dynamics.

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