

# Canopy tree growth responses following selection harvest in seven species varying in shade tolerance

Trevor A. Jones, Grant M. Domke, and Sean C. Thomas

**Abstract:** We used tree ring measurements to investigate the temporal response of basal area increment (BAI) of canopy trees following selection harvests by sampling across a chronosequence of stands with known harvest dates in tolerant hardwood (Great Lakes – St. Lawrence) stands in central Ontario. Seven tree species of various shade tolerances ranged widely in their responses to reduced competition. The more shade-tolerant species responded more positively: shade-tolerant species showed an average increase in BAI of 35% 4–15 years postharvest compared with 16% for mid-tolerant species and –7.5% for intolerant species. All species showed a time-lag in postharvest growth responses, with maximum growth responses occurring between 3 and 15 years postharvest. Tree size was the most important factor determining the magnitude of BAI response, with smaller trees consistently responding more than larger trees. We suggest that higher growth responses to selection harvests among shade-tolerant species may contribute to declines in mid-tolerant species abundance in selection-managed stands. More broadly, interspecific variability in canopy tree responses to forest disturbance appears to follow patterns distinct from seedling and sapling responses, with important implications to forest community dynamics in both managed and unmanaged forests.

**Résumé :** Nous avons utilisé des mesures d'anneau de croissance pour étudier la réaction temporelle de l'accroissement en surface terrière (AST) d'arbres dominants à la suite de coupes de jardinage en échantillonnant une chronoséquence de peuplements de feuillus tolérants à l'ombre du centre de l'Ontario (région des Grands-Lacs et du St-Laurent) pour lesquels l'année de récolte était connue. La réaction des arbres à une diminution de la compétition a grandement varié parmi sept espèces d'arbre dont la tolérance à l'ombre est différente. Les espèces plus tolérantes à l'ombre ont réagi plus positivement avec une augmentation moyenne de l'AST de 35 %, de 4 à 15 ans après la coupe, comparativement à une augmentation moyenne de 16 % pour les espèces de tolérance intermédiaire et de –7,5 % pour les espèces intolérantes. Un délai de réaction en croissance a été observé pour toutes les espèces à la suite de la coupe et la réaction maximale est survenue entre 3 et 15 ans après la coupe. La taille des arbres était le facteur le plus important pour déterminer l'amplitude de la réaction de l'AST, les plus petits arbres réagissant invariablement davantage que les plus gros arbres. Nous croyons que les plus fortes réactions de croissance aux coupes de jardinage des espèces tolérantes à l'ombre peuvent contribuer au déclin de l'abondance des espèces de tolérance intermédiaire dans les peuplements jardinés. Plus généralement, la variation interspécifique de la réaction des arbres dominants aux perturbations forestières semble suivre un patron distinct de celui des semis et des gaules, ce qui a des implications importantes pour la dynamique des communautés forestières dans les forêts aménagées et non aménagées.

[Traduit par la Rédaction]

## Introduction

Tree growth response to disturbance is an important aspect of forest dynamic processes in both natural and managed forest ecosystems. Canopy gap formation, in particular, is thought to be a major factor influencing eventual species com-

position because gaps strongly affect the availability of light and other plant resources (Runkle and Yetter 1987; McClure and Lee 1993; Bazzaz and Wayne 1994), with critical implications for species regeneration (Pacala et al. 1994; Kobe et al. 1995). While the responses of tree seedlings and saplings of various species to gap formation associated with partial stand harvests have received considerable research attention (Beaudet and Messier 1998; Beaudet et al. 2000; Wright et al. 2000), much less information is available on the temporal responses of mature trees near or adjacent to gaps created by such harvests (e.g., Jones and Thomas 2004, 2007; Wisser et al. 2005).

Selection system silviculture, in which individual trees or small groups of trees are removed diffusely across an area and in which an effort is made to maintain a target diameter distribution, is the most widespread form of uneven-aged forest management. Selection silviculture is prevalent in the tolerant hardwood forests (Great Lakes – St. Lawrence forest region) of eastern North America (Ontario Ministry of Natural Resources 1998) and is currently being promoted in

Received 25 July 2008. Accepted 9 October 2008. Published on the NRC Research Press Web site at [cjfr.nrc.ca](http://cjfr.nrc.ca) on 10 February 2009.

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a wide variety of forest ecosystems (O'Hara 1998; Nyland 2007). Selection silviculture is thought to emulate important aspects of natural gap phase dynamics that occur as a result of small-scale disturbance events and tree senescence (McCarthy 2001). However, the disturbance regime associated with selection silviculture also differs from natural gap dynamics, since selection harvests concentrate disturbance temporally (Beaudet and Messier 2002) and commonly truncate the age and size class distribution, resulting in few old and senescent trees in selection-managed stands. Single-tree selection also may result in the homogenization of light environments, which has been suggested to favour more shade-tolerant species at the expense of mid-tolerant or intolerant species (Miller and Kochenderfer 1998; Webster and Jensen 2007). Both environmental homogenization and size-distribution truncation may contribute to continuing declines in mid-tolerant and intolerant species abundance in selection harvested forests (Schwartz et al. 2005; Neuendorff et al. 2007). Several recent studies have evaluated growth responses of mature trees to partial stand harvests, with the general finding that postharvest growth responses in mature trees can be large but with a time-lag to peak postharvest growth that varies from 3 to 20+ years (e.g., Groot and Hökka 2000; McDowell et al. 2003; Jones and Thomas 2004; Thorpe et al. 2007). From these studies, it is apparent that growth responses following partial harvesting generally involve multiyear time lags and that both the magnitude and temporal pattern of response are likely to depend on the species, the type of harvest involved, and the size and position of trees within the canopy.

Growth responses of canopy trees adjacent to gaps may have important consequences for forest community dynamics, depending on patterns of interspecific variation. Based on growth responses of seedlings and saplings (Orwig and Abrams 1995; Walters and Reich 1996, 2000; Beaudet and Messier 1998), it might be expected that the more shade-intolerant species will be more responsive to increased light. It has been argued that adult canopy trees are less likely to respond to changes in resources than are smaller, fast-growing saplings (Ryan et al. 1997); however, comparative physiological studies have found that adults of temperate deciduous trees generally show increased photosynthetic capacity and related traits compared with saplings, even when comparisons are made across similar light levels (Cavender-Bares and Bazzaz 2000; Thomas and Winner 2002). High photosynthetic capacity is generally associated with higher saturating light intensities (Walters et al. 1993b) and capacity for photosynthetic acclimation (Valladares et al. 2002), suggesting that mature temperate deciduous trees may show large gains in growth in response to increased light levels. This line of reasoning would predict higher growth responses to canopy openings in intolerant and mid-tolerant species than in shade-tolerant species. However, growth responses would also likely be strongly influenced by differences in tree morphology and possibly by responses to resources other than light. In particular, shade-tolerant species generally maintain deeper crowns than shade-intolerant or mid-tolerant species (Pacala et al. 1993; Canham et al. 1994; Cole and Lorimer 1994) and so may experience greater increases in light levels lower in the canopy following gap creation (Jones and Thomas 2007). Wiser et al. (2005) examined postharvest

growth responses of two *Nothofagus* species in New Zealand and found that the growth of the more shade-tolerant is more responsive to gap formation.

The present study was designed to evaluate the temporal growth responses of tree species with various shade tolerances in a managed northern hardwood forest following selection harvests. We address the questions, (i) Do different species show a similar temporal pattern of increment response to gap creation?, (ii) Which species respond most to gap creation, and does the magnitude of response differ systematically between shade-tolerance classes?, and (iii) How does growth response vary among trees of different size classes and are patterns of size dependence consistent across shade-tolerance classes?

## Materials and methods

### Site description

The study was conducted at Haliburton Forest and Wildlife Reserve, a 25 000 ha privately owned forest in Ontario, Canada (45°13'N, 78°35'W). Forests in this area have been managed using selection silviculture for the past 40 years and, prior to that time, were selectively harvested for yellow birch (*Betula alleghaniensis* Britt.) and white pine (*Pinus strobus* L.). Large sections of the forest are now undergoing their second or third stand entry. Harvest locations and dates have been recorded and mapped for the last 25 years, making it possible to identify and accurately date when gaps in specific harvesting blocks were created. Although some winter harvesting does occur, harvest operations in Haliburton forest typically occur throughout the summer. In all cases, the year of harvest refers to the calendar year of the growing season, for example, stands that were harvested in March of 1998 were included in the 1997 harvest areas. The dominant species was *Acer saccharum* Marsh., representing nearly 60% of basal area and stem frequency. Other important canopy tree species in the study included *Acer rubrum* L., *B. alleghaniensis*, *Fagus grandifolia* Ehrh., *Picea glauca* (Moench) Voss, *Prunus serotina* Ehrh., and *Tsuga canadensis* (L.) Carrière. Common subcanopy trees and shrubs included *Ostrya virginiana* (Mill.) K. Koch., *Acer pensylvanicum* L., and *Viburnum alnifolium* Marshall. Preharvest stand basal areas were typically between 24 and 30 m<sup>2</sup>·ha<sup>-1</sup> and were reduced to between 15 and 18 m<sup>2</sup>·ha<sup>-1</sup> postharvest. The majority of merchantable stems harvested were the shade-tolerant *A. saccharum* and *F. grandifolia*, although *T. canadensis*, which is typically nonmerchantable as saw timber, was also frequently harvested for log cabin construction.

### Site selection

In the summer of 2004, cutblocks representing nine harvest years (1984, 1989, 1992, 1994, 1997, 1998, 2001, 2002, and 2003) across a 20 year chronosequence were selected for study. Up to 20 plots (16–20), in each of the nine harvest years, were selected in upland forest areas with low-lying poorly drained sites systematically avoided to reduce the plot-specific differences in growth rates. Where possible, plots were divided between at least two harvest locations (cutblocks) from each harvest year. In cases where only one cutblock per harvest year was available, multiple transects

were established so that at least half of the plots were located as far from the other half as possible. Within each cutblock, we located primary skid trails and ran transects along their length. Plots were established on each side of the transect, 100 m apart, at 100 m intervals along the length of the transect. Harvesting within and around the plots was confirmed by systematically searching for and identifying stumps from the harvest operations. At each plot, we extracted a single short (~8–15 cm) core from every tree greater than 8 cm in diameter at breast height (DBH) within a 10 m radius. In total, 174 plots were established and 4127 trees were cored. Within each plot, tree DBH and species were recorded. Stumps were measured for diameter at the highest point; species was recorded and diameters were scaled to DBH using species-specific taper equations.

### Tree cores

Cores were mounted on plywood boards and sanded with progressively finer grit sandpaper until rings were clearly visible and all surface defects were removed. Ring widths were measured to within 0.001 mm using WinDendro (versions 2003a, 2003b). For samples with extremely narrow rings or for species with faint rings, ring width series were verified under a dissecting microscope and in some cases were remeasured with a table-mounted tree-ring increment measurement system. One consequence of taking short cores was that we were unable to cross-date effectively with the program COFECHA (Grissino-Mayer 2001). Ring series were typically ~20–50 years and exhibited large stand- and tree-level variance in growth increment caused by harvesting and other natural disturbances. Consequently, tree cores were cross-dated using two other visual methods. The first method involved comparing individual cores, using skeleton plots, with a cutblock-specific local chronology. Any discrepancies in growth pattern were noted, and cores with apparent shifts in ring series were double-checked for missing or extra rings. In the second method, cores were cross-dated using skeleton plots against a regional master chronology. Cores with slight variation (i.e., 1 or 2 years difference in either large or small rings) were also checked for missing or extra rings. In total, 665 (16%) of the cores were removed from the analysis for one of three reasons: (i) cross dating was inconclusive or not possible, (ii) sample size was inadequate ( $n < 15$ ) for that species, and (iii) trees were calculated to be less than 8 cm DBH at harvest.

### Analysis

Many previous studies have used radial increment instead of basal area increment (BAI) to evaluate growth responses to management or natural disturbance. To provide context to previous studies with respect to mean growth rate and growth response, we used a general linear model (proc GLM, SAS version 9.0) to test for absolute differences in log-transformed growth increments between the mean 5 year preharvest growth interval and the mean 4–15 year postharvest growth interval for each of the seven species studied. Owing to drastically different sample sizes and heteroscedasticity, a separate model was required for each species. All subsequent analyses were conducted on the calculated BAI, which tends to be more meaningful than radial increment from a forest growth and yield perspective.

BAIs for up to 20 years pre- and post-harvest for each stand were sorted into pre- and post-harvest categories. For example, the first postharvest year (+1 post) for a stand harvested in 1992 was 1993, while the first postharvest year (+1 post) for a stand harvested in 1998 was 1999. By comparing BAIs across many cutblocks, regardless of year of harvest, the year-to-year variation in climatic growth trends was reduced, and growth trends owing to harvest could be more easily identified. All analyses were based on the year pre- and post-harvest temporal scale rather than on actual calendar years. The pre- and post-harvest scale was then separated into one of four temporal groups: 5 years preharvest, the year of harvest, 1–3 years postharvest, or 4–15 years postharvest. Partial rings from the summer of 2004 were not included in the analysis.

Trees were subsequently divided into one of three size categories: small (8–15 cm DBH), medium (15–25 cm DBH), and large (>25 cm DBH) based on the back-calculated diameters at the time of harvest. Back calculation of DBH was accomplished by subtracting twice the measured post-harvest radial increments from the diameter of the tree at the time of coring.

Relative growth change was calculated on a per-tree basis based on the average preharvest growth rate from the 5 years prior to harvest; the relative proportional increase or decrease in growth rate was determined for each pre- and post-harvest increment year. Preharvest growth rates were subsequently separated into three preharvest growth rate categories relative to the average preharvest growth rate of all trees in a given size class. These categories included slowly growing (below the first growth rate quartile), moderately growing (between the first and third growth rate quartiles), and fast-growing (above the third growth rate quartile) trees.

To test for the effect of harvesting, tree size, and preharvest growth rate on the continuous growth response patterns observed in canopy trees, a mixed model (proc MIXED, SAS version 9.0) was used. A separate model was fit to each of the seven species because of drastically uneven sample sizes and owing to the fact that not all species were distributed evenly between plots and cutblocks. BAIs were log transformed to meet assumptions of normality within species. Categorical fixed effects in the model were included in a stepwise function, and improvement in model fit was determined by comparing Akaike's information criterion (AIC: Burnham and Anderson 2002) values among submodels. The most parsimonious models included categorical fixed effects for size class, a pre- vs. post-harvest term, and a preharvest growth rate term, as well as a continuous fixed-effect term for the relative time since harvest. Interaction terms between all categorical and the continuous pre- and post-harvest terms were also included. To account for serial autocorrelation within individual trees, a first-order autoregressive moving average covariance structure was used. A random unstructured covariance plot term was specified to account for plot-level spatial autocorrelations, and a random unstructured covariance year-of-harvest term was included to account for cutblock-level autocorrelation.

To further test for the effects of species, tree size (DBH), year of harvest, and preharvest growth rate on the postharvest BAI response, we used a repeated measures analysis of

**Table 1.** Relative contribution, by size class, of different species to cutblock- and forest-level residual basal areas at the time of harvest in the Haliburton Forest, Ontario, Canada.

Size class (cm DBH)	Basal area (m <sup>2</sup> ·ha <sup>-1</sup> ) in year of harvest									
	1984	1989	1992	1994	1997	1998	2000	2002	2003	Mean
<i>Prunus serotina</i>										
>25	—	—	—	—	0.05	0.36	—	—	0.18	0.07±0.04
15–25	—	—	—	0.08	0.18	0.04	—	0.05	—	0.04±0.02
8–15	—	—	—	0.03	0.01	—	—	—	0.05	0.01±0.01
<i>Picea glauca</i>										
>25	—	0.13	0.34	0.06	0.49	0.30	—	—	0.15	0.16±0.06
15–25	—	0.06	0.17	—	0.29	0.07	—	0.02	0.11	0.08±0.03
8–15	—	0.01	0.01	—	0.13	0.02	—	—	0.07	0.03±0.02
<i>Acer rubrum</i>										
>25	0.07	0.51	0.42	0.11	0.82	—	0.65	—	0.51	0.34±0.10
15–25	—	0.14	0.02	0.03	0.22	0.02	0.2	—	0.18	0.09±0.03
8–15	—	0.07	—	0.01	0.07	—	0.01	—	0.02	0.02±0.01
<i>Betula alleghaniensis</i>										
>25	0.08	0.82	0.79	0.19	1.61	1.53	1.08	0.55	0.75	0.82±0.18
15–25	0.06	0.17	0.05	0.22	0.16	0.16	0.15	0.06	0.28	0.15±0.03
8–15	0.13	0.11	0.02	0.11	0.07	0.03	0.04	0.06	0.08	0.07±0.01
<i>Acer saccharum</i>										
>25	3.41	3.77	9.06	11.52	5.63	8.08	6.93	10.16	6.99	7.28±0.91
15–25	1.77	1.04	2.57	1.49	2.07	2.68	1.36	2.58	1.96	1.95±0.20
8–15	0.64	0.4	0.79	0.73	0.83	0.69	0.34	0.72	0.54	0.63±0.06
<i>Fagus grandifolia</i>										
>25	0.22	1.84	0.93	1.5	0.62	0.97	2.48	1.82	1.28	1.30±0.23
15–25	0.30	0.93	0.58	0.9	0.27	0.39	0.22	0.28	0.65	0.50±0.09
8–15	0.12	0.19	0.10	0.27	0.06	0.29	0.2	0.12	0.19	0.17±0.03
<i>Tsuga canadensis</i>										
>25	—	3.67	0.90	1.48	4.15	2.81	4.64	0.94	5.33	2.66±0.63
15–25	—	0.57	0.07	0.03	0.06	0.16	0.27	—	0.23	0.15±0.06
8–15	—	0.04	—	0.01	0.02	0.01	0.03	—	0.02	0.01±0.00
Other species										
>25	0.05	0.53	—	0.09	0.13	—	—	0.34	—	0.13±0.06
15–25	0.26	0.15	0.02	—	0.49	0.12	0.08	0.13	0.34	0.18±0.05
8–15	0.04	0.06	0.03	0.06	0.21	0.11	—	0.15	0.28	0.10±0.03
Number of plots	18	19	20	16	20	19	20	20	19	
Stump basal area	6.16	7.53	6.05	12.81	6.91	11.24	8.81	10.16	7.00	8.51±0.80
Postharvest basal area	7.56	15.19	16.88	17.47	18.65	19.83	18.69	17.97	21.25	17.00±1.32

variance (proc GLM, SAS version 9.0), with the four temporal categories specified as the repeated variable. Only harvest blocks that included BAI values in each of the four categories were included in the analysis (i.e., harvest years 1984, 1989, 1992, 1994, 1997, and 1998). To test for specific differences among categorical variables and temporal groups, we used polynomial orthogonal contrasts relative to the preharvest BAI value.

Classification of species into shade-tolerance classes followed Burns and Honkala (1990). For these species, the classifications correspond closely to quantitative measures of shade tolerance based on estimates of whole-plant light compensation points (Baltzer and Thomas 2007).

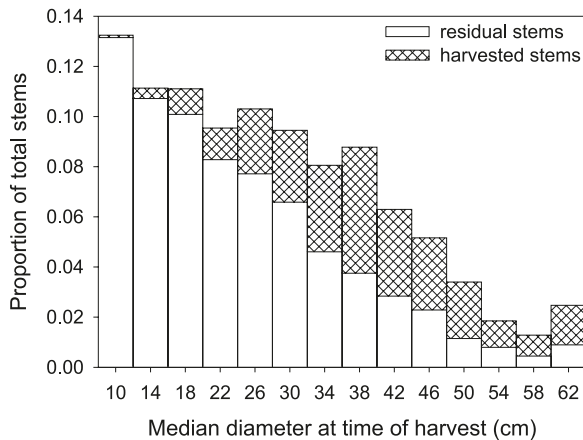
## Results

For the 174 plots evaluated in this study, the average (mean ± SE) residual basal area at the time of harvest was 17.0 ± 1.3 m<sup>2</sup>·ha<sup>-1</sup>, with an average of 8.5 ± 0.8 m<sup>2</sup>·ha<sup>-1</sup> basal

area removed during harvesting (Table 1). The majority (58% of the basal area or 59% of the stem frequency) of the residual forest species composition was *A. saccharum*, with large trees (>25 cm DBH) contributing 42% of the average stand basal area. The other abundant shade-tolerant species (*T. canadensis* and *F. grandifolia*) accounted for another 28% of the residual basal area and 24% of the residual stem frequency (Table 1). The mid-tolerant deciduous tree species were less abundant, with *B. alleghaniensis* and *A. rubrum* contributing 6% and 3%, respectively, to the residual stand basal area. *Prunus serotina* was uncommon in the forest in general, occurring in only five of the nine cutblocks (28 trees in total), and contributed less than 1% of the stand basal area and stem frequency (Table 1). The residual size distribution of all species combined followed an approximate negative exponential distribution (Fig. 1), and most of the harvested stems were from the larger size classes (Fig. 1).

Significant increases in tree ring growth increments as a result of selection management were evident for the more

**Fig. 1.** Mean relative plot-level frequency distribution of harvested and residual trees, by 4 cm size classes, for all species combined.



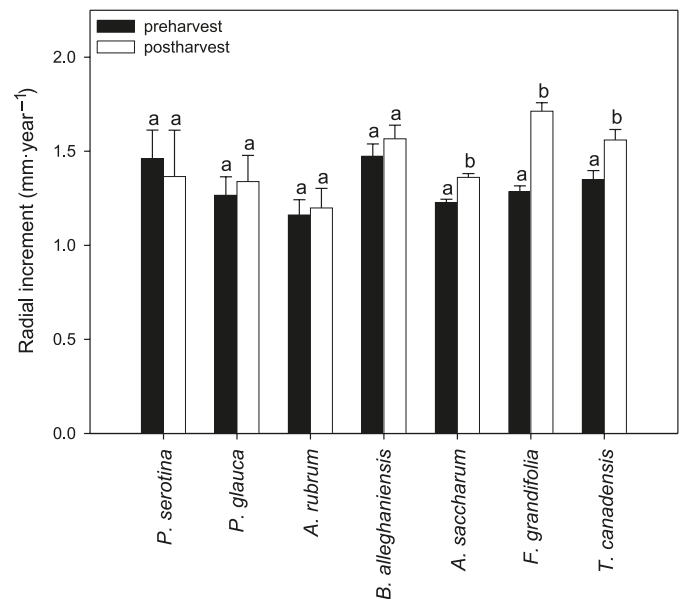
shade-tolerant species (*T. canadensis*, *F. grandifolia*, and *A. saccharum*) (Table 2, Pre/Post effect), with an average increase in BAI of 35.4%, and with *F. grandifolia* exhibiting the highest average growth increase at 55.1% (Table 3; Fig. 2). Although there were also significant growth increments for the less shade-tolerant species (Table 2, Pre/Post effect), the average response of mid-tolerant and intolerant species was 14.5% and -7.5%, respectively (Table 3; Fig. 3).

Tree size was the best predictor of BAI, with the larger trees having the greatest BAI and the smaller trees having progressively smaller BAIs (Table 3). On average, the largest trees (>25 cm DBH) grew  $13.0 \pm 0.2 \text{ cm}^2\cdot\text{year}^{-1}$ , while the smallest trees (8–15 cm DBH) grew  $2.4 \pm 0.1 \text{ cm}^2\cdot\text{year}^{-1}$  prior to harvest (Table 3). Although the largest trees had greater BAIs both before and after harvest, the relative BAI growth of the smallest tree size classes was greater in response to forest management than that of the largest tree size classes (Table 3; Fig. 3).

Trees of differing sizes responded to selection management more or less positively depending on their species (Table 2). In the shade-tolerant *A. saccharum* and *F. grandifolia*, the smaller trees responded most positively to gap creation and the larger trees showed little response (Fig. 3). *Tsuga canadensis*, the other abundant shade-tolerant species, exhibited a significant size-related difference in growth rate but no significant size-related differences in response to gap creation (Table 2). The shade-intolerant *Prunus serotina* exhibited significant size-related differences in growth rate but no significant increase in growth in response to selection management (Table 2). All three mid-tolerant species (*Picea glauca*, *B. alleghaniensis*, and *A. rubrum*) exhibited size-related differences in growth rate and in growth response to gap creation, with small trees responding more positively than large trees (Table 2; Fig. 3).

The increase in growth increment and BAI as a result of selection management was not immediate; temporal lags in growth response of 2–15 years were observed before the maximum postharvest growth rates were achieved. The temporal pattern varied markedly among species. For example, small *B. alleghaniensis* trees exhibited a linear increase in percentage of growth change for the entire 15 year postharvest growth interval, while small *A. saccharum* and *F. grandifolia* exhibited an asymptotic pattern of growth re-

**Fig. 2.** Radial increment in the 5 years before and the 4–15 years after selection harvesting for seven species with various shade tolerances. Different letters above adjacent bars indicate significant change in growth rate at  $P < 0.05$  from a Tukey–Kramer's test. Error bars are  $\pm$  one standard error.



sponse, where near-maximum growth rates were achieved within 5–10 years of harvest (Fig. 3). *Acer rubrum* and *T. canadensis* on the other hand exhibited unimodal growth responses, where the maximum growth rate was achieved within 5 years before declining again (Fig. 3).

When trees were further subdivided into size-class-specific preharvest growth rate categories, it was evident that trees that were growing slowly prior to harvest showed the greatest proportional increase in postharvest growth rate (Fig. 4). The magnitude of the increase was extremely species-specific, with slowly growing *A. saccharum*, *F. grandifolia*, and *B. alleghaniensis* exhibiting the largest (300%–500%) increases (Fig. 4). Furthermore, shade-tolerant species under 25 cm DBH and with moderate growth rates showed significant proportional increases postharvest (Fig. 4). Trees with high preharvest growth rates, regardless of species or size, did not show significant increases in postharvest growth rates (Fig. 4).

## Discussion

Previous studies examining canopy tree growth responses to partial harvest have found that the residual trees generally respond positively, but with a time lag before maximum postharvest growth is reached (Youngblood 1991; Digregorio et al. 1999; Latham and Tappeiner 2002; Bebbler et al. 2004). The present study documents significant increases in radial growth increment postharvest, particularly for more shade-tolerant species, with a magnitude of response similar to that found in prior studies of dominant species in the region (Jones and Thomas 2004; Forget et al. 2007). The most pronounced increases in growth occurred over the first 1–3 years postharvest until a maximum growth rate was reached 5–15 years postharvest (Fig. 3).

**Table 2.** Results of the most parsimonious MIXED model, by species, describing the fixed, random and repeated effects of selection harvests on basal area increment of residual trees in Haliburton Forest.

Attribute assessed	df	<i>Prunus serotina</i>	<i>Picea glauca</i>	<i>Acer rubrum</i>	<i>Betula alleghaniensis</i>	<i>Acer saccharum</i>	<i>Fagus grandifolia</i>	<i>Tsuga canadensis</i>
<b>Fixed effects</b>								
Year <sup>a</sup>	1	5.78 (0.017)	—	3.12 (0.077)	—	0.10 (0.755)	—	—
Size <sup>b</sup>	2	25.46 (<0.001)	72.15 (<0.001)	69.77 (<0.001)	159.88 (<0.001)	1868.73 (<0.001)	377.19 (<0.001)	168.44 (<0.001)
Pre/Post <sup>c</sup>	3	3.15 (0.030)	9.08 (<0.001)	2.04 (0.107)	5.34 (0.001)	61.78 (<0.001)	15.69 (<0.001)	7.01 (0.001)
PH growth <sup>d</sup>	2	21.38 (<0.001)	59.36 (<0.001)	99.88 (<0.001)	189.15 (<0.001)	1066.85 (<0.001)	249.28 (<0.001)	179.25 (<0.001)
Year × size	2	5.47 (0.005)	7.97 (<0.001)	—	47.44 (<0.001)	31.52 (<0.001)	19.15 (<0.001)	9.77 (<0.001)
Year × PH growth	2	4.65 (0.010)	27.61 (<0.001)	4.85 (<0.001)	37.39 (<0.001)	—	14.97 (<0.001)	31.75 (<0.001)
Pre/Post × size	6	—	—	—	—	3.38 (0.003)	5.32 (<0.001)	—
Pre/Post × PH growth	4	0.38 (0.772)	—	—	5.14 (<0.001)	3.12 (0.014)	—	4.64 (0.001)
Year × size × PH growth	6	—	—	2.31 (0.032)	—	130.65 (<0.001)	6.90 (<0.001)	—
Year × size × PH growth	4	—	—	—	—	—	—	5.05 (<0.001)
<b>Random covariance effects</b>								
Harvest year <sup>e</sup>	—	—	—	0.87 (0.192)	—	1.70 (0.044)	1.55 (0.061)	—
Plot <sup>f</sup>	—	—	1.09 (0.138)	—	2.28 (0.011)	5.88 (<0.001)	3.37 (<0.001)	2.96 (0.002)
<b>Repeated covariance effects</b>								
Individual tree (ρ) <sup>f</sup>	—	13.06 (<0.001)	24.25 (<0.001)	29.22 (<0.001)	43.56 (<0.001)	95.51 (<0.001)	77.41 (<0.001)	41.33 (<0.001)
Individual tree (γ) <sup>f</sup>	—	12.46 (<0.001)	22.12 (<0.001)	25.33 (<0.001)	39.48 (<0.001)	115.47 (<0.001)	69.28 (<0.001)	48.07 (<0.001)
AIC	—	529.0	876.4	1695.8	3468.5	39132.6	8865.6	4822.0
No. of trees	3289	28	64	94	229	2041	535	298

**Note:** Values for fixed effects are *F* values (*P* values follow in parentheses), while values for random and repeated effects are *Z* values (*P* values follow in parentheses).

<sup>a</sup>Years in tree ring series.

<sup>b</sup>Categorical size class (DBH): small (8–15 cm), medium (15–25 cm), and large (>25 cm).

<sup>c</sup>Categorical time intervals relative to the year of harvest: 5 years preharvest, harvest year, 1–3 years postharvest, or 4–15 years postharvest.

<sup>d</sup>Categorical preharvest (PH) growth rate per tree size class: slow (below the first growth rate quartile), moderate (between the first and third growth rate quartiles), and fast (above the third growth rate quartile).

<sup>e</sup>Random unstructured covariance term for plot- and cutblock-level growth autocorrelations.

<sup>f</sup>Autoregressive moving average covariance terms for serial autocorrelation in growth rings.

**Table 3.** Basal area increments (BAI; cm<sup>2</sup>·year<sup>-1</sup>) for residual trees following selection harvests, classified by species, tree size, year of harvest, and preharvest growth rate.

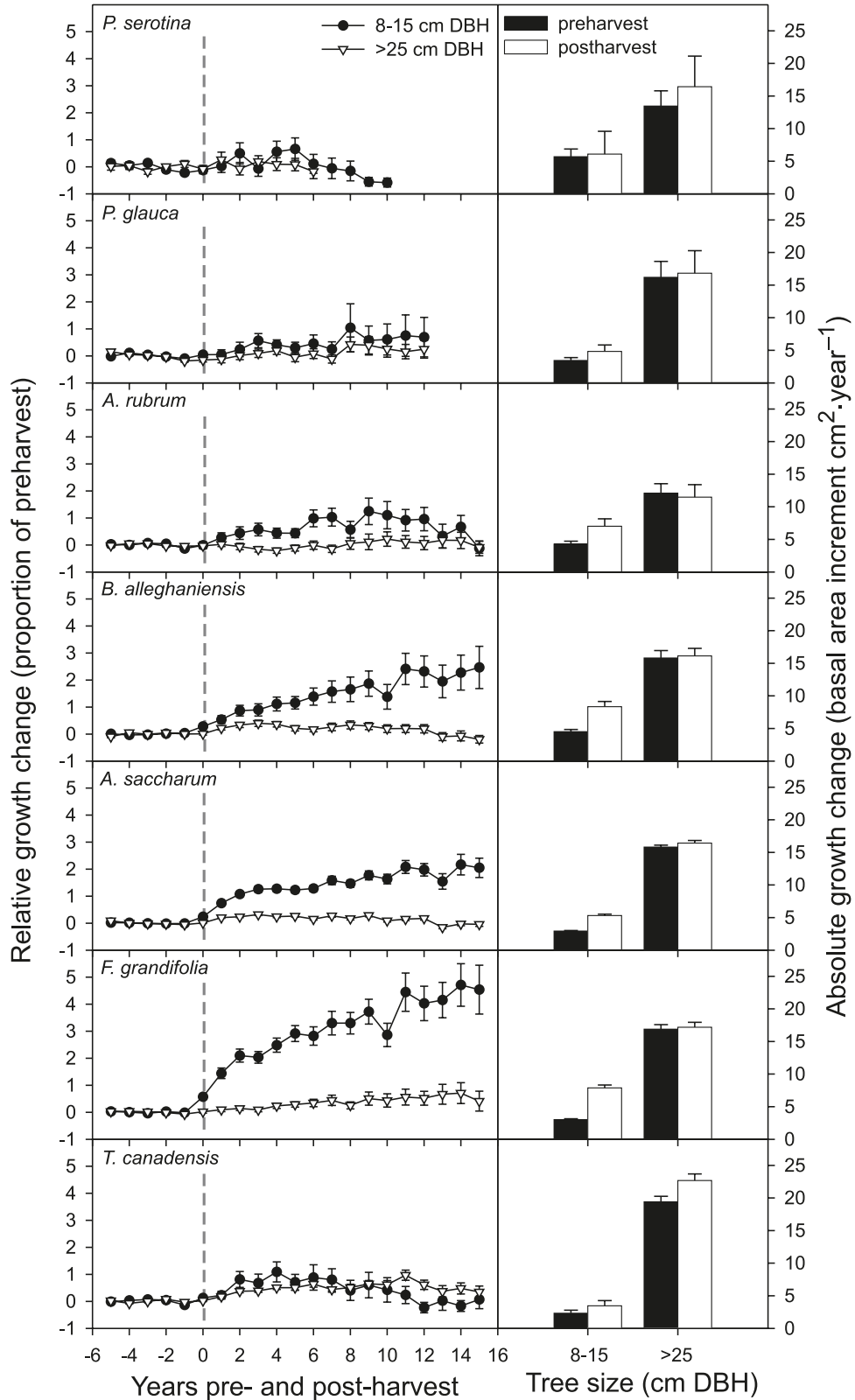
Classes	Postharvest			Repeated measure analysis of variance				
	Preharvest	Harvest	1–3 years	4–15 years	% Relative BAI change <sup>†</sup>	Source	df (error df)	F value (P value)
<b>Species*</b>								
<i>Prunus serotina</i>	6.9 (1.0, 0.8)	6.2 (1.1, 0.9)	6.6 (1.4, 1.2)	6.4 (1.9, 1.5)	-7.2	Species	6 (2187)	13.89 (<0.001)
<i>Picea glauca</i>	5.2 (0.7, 0.6)	4.9 (0.7, 0.6)	4.4 (0.7, 0.6)	5.9 (1.0, 0.9)	+13.5	Time	3 (6561)	27.02 (<0.001)
<i>Acer rubrum</i>	5.7 (0.5, 0.5)	5.5 (0.5, 0.5)	5.8 (0.5, 0.5)	6.0 (0.7, 0.6)	+5.3	Time × species	18 (6561)	7.65 (<0.001)
<i>Betula alleghaniensis</i>	6.9 (0.4, 0.4)	7.1 (0.5, 0.4)	7.9 (0.5, 0.5)	8.6 (0.5, 0.5)	+24.6			
<i>Acer saccharum</i>	6.0 (0.1, 0.1)	6.1 (0.1, 0.1)	7.3 (0.2, 0.1)	7.5 (0.2, 0.2)	+25.0			
<i>Fagus grandifolia</i>	5.8 (0.2, 0.2)	6.5 (0.3, 0.3)	6.8 (0.3, 0.3)	9.0 (0.4, 0.4)	+55.1			
<i>Tsuga canadensis</i>	10.8 (0.6, 0.6)	11.0 (0.6, 0.6)	12.4 (0.7, 0.7)	13.6 (0.8, 0.8)	+26.0			
<b>Contrasts<sup>†</sup></b>								
Mean difference	—	21.63 (<0.001)	27.01 (<0.001)	38.72 (<0.001)				
Species difference	—	11.45 (<0.001)	5.30 (<0.001)	2.29 (0.033)				
<b>Size*</b>								
>25 cm DBH	13 (0.2, 0.2)	12.5 (0.3, 0.2)	13.3 (0.3, 0.3)	13.5 (0.3, 0.3)	+3.8	Size	2 (2191)	962.77 (<0.001)
15–25 cm DBH	5.7 (0.1, 0.1)	5.9 (0.1, 0.1)	6.9 (0.2, 0.2)	7.8 (0.2, 0.2)	+36.9	Time	3 (6573)	303.88 (<0.001)
8–15 cm DBH	2.4 (0.1, 0.1)	2.8 (0.1, 0.1)	3.5 (0.1, 0.1)	4.2 (0.1, 0.1)	+75.0	Time × Size	6 (6573)	57.54 (<0.001)
<b>Contrasts<sup>†</sup></b>								
Mean difference	—	350.37 (<0.001)	269.91 (<0.001)	252.03 (<0.001)				
Size class difference	—	112.59 (<0.001)	13.34 (<0.001)	1.04 (0.355)				
<b>Harvest year*</b>								
1984	6.2 (0.4, 0.4)	6.5 (0.4, 0.4)	6.6 (0.4, 0.3)	8.3 (0.4, 0.4)	+33.9	Harvest	5 (2188)	5.17 (<0.001)
1989	7.5 (0.4, 0.4)	7.7 (0.4, 0.4)	9.2 (0.5, 0.4)	10.2 (0.5, 0.5)	+36.0	Time	3 (6564)	251.85 (<0.001)
1992	5.3 (0.3, 0.3)	5.6 (0.3, 0.3)	8.9 (0.4, 0.4)	8.9 (0.4, 0.4)	+68.0	Time × harvest	15 (6564)	27.62 (<0.001)
1994	6.0 (0.3, 0.3)	7.9 (0.4, 0.4)	9.9 (0.5, 0.5)	9.1 (0.4, 0.4)	+51.7			
1997	6.1 (0.3, 0.3)	6.1 (0.3, 0.3)	8.2 (0.4, 0.4)	6.9 (0.3, 0.3)	+13.1			
1998	6.5 (0.3, 0.3)	6.9 (0.3, 0.3)	8.3 (0.4, 0.4)	6.4 (0.3, 0.3)	-1.5			
<b>Contrasts<sup>†</sup></b>								
Mean difference	—	302.61 (<0.001)	195.18 (<0.001)	212.02 (<0.001)				
Harvest year difference	—	32.59 (<0.001)	24.18 (<0.001)	21.12 (<0.001)				
<b>Preharvest growth rate (PHGR)*</b>								
Slow	1.8 (0.1, 0.1)	2.3 (0.1, 0.1)	3.4 (0.1, 0.1)	3.8 (0.1, 0.1)	+111.1	PHGR	2 (2191)	419.24 (<0.001)
Moderate	6.8 (0.1, 0.1)	7.1 (0.1, 0.1)	8.7 (0.2, 0.2)	8.3 (0.2, 0.2)	+22.1	Time	3 (6573)	267.62 (<0.001)
Fast	20.9 (0.3, 0.3)	19.8 (0.4, 0.4)	21.3 (0.5, 0.5)	18.5 (0.4, 0.4)	-11.5	Time × PHGR	6 (6573)	84.04 (<0.001)
<b>Contrasts<sup>†</sup></b>								
Mean difference	—	302.49 (<0.001)	250.38 (<0.001)	220.25 (<0.001)				
Growth rate difference	—	154.70 (<0.001)	31.21 (<0.001)	9.89 (<0.001)				

\*Numbers in parentheses following means are asymmetrical upper and lower standard error values back transformed from log-transformed basal area increments.

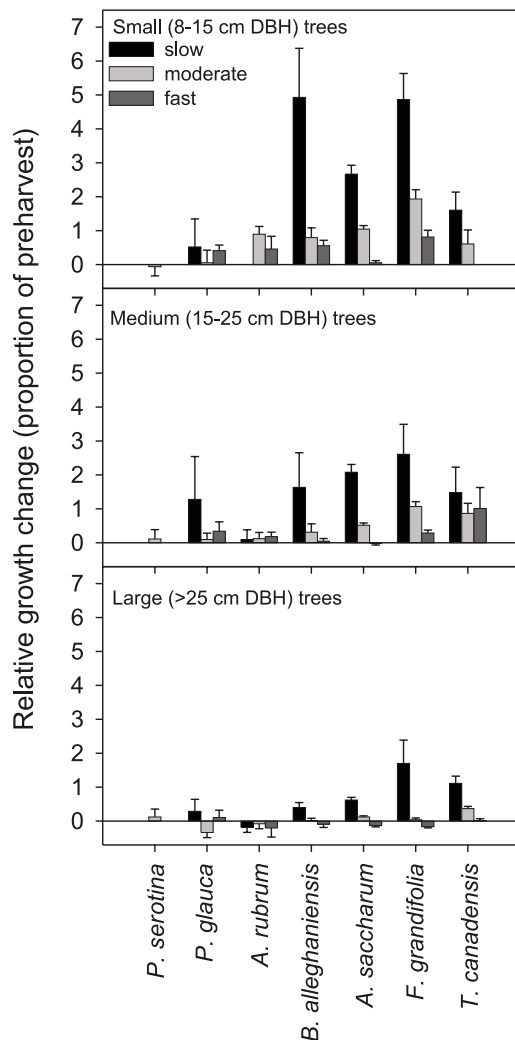
<sup>†</sup>Significant F values (P values) presented below means are polynomial orthogonal contrasts relative to preharvest growth rates, as determined by a repeated measures general linear model (proc GLM, SAS version 9.0).

<sup>‡</sup>Percentage of change is the percentage increase or decrease in growth between the preharvest BAI and the 4–15 years postharvest BAI.

**Fig. 3.** Yearly relative growth change in basal area increment for seven species, from large (>25 cm DBH) and small (8–15 cm DBH) trees (left panels). Vertical broken bar indicates year of harvest; relative growth change was calculated as described in methods. Mean basal area increment of seven species (right panels) for the 5 years prior to harvest and the 3–15 years postharvest for two size classes of trees. Error bars are  $\pm$  one standard error.



**Fig. 4.** Relative basal area increment change for seven species of trees with various shade tolerances (from least (left) to greatest (right)), and with slow, moderate, and fast preharvest growth rates (as described in methods) for three size classes. Error bars are  $\pm$  one standard error.



Our results point to a number of factors that can dramatically affect tree growth response to forest management activities. Smaller size classes of trees with slower preharvest growth generally had greater proportional growth increases following harvest (Fig. 4). A similar pattern of larger growth response among trees that were slow growing prior to harvest was also observed by Black and Abrams (2003) who examined radial growth responses of *T. canadensis* to harvest. The postharvest growth responses also varied strongly among species. For example, growth of the shade-tolerant *A. saccharum* and *F. grandifolia* increased following partial harvest, whereas the only mid-tolerant trees to show a significant postharvest growth response were small, slowly growing individuals of *B. alleghaniensis* and *Picea glauca* (Fig. 3). Growth increment of the shade-intolerant *Prunus serotina* did not increase significantly postharvest. These findings agree with those of Schuler (2006) who observed that the radial growth in pole-sized *Prunus serotina* increased briefly as a result of crop tree harvest but returned to growth rates similar to those of control trees within 5–

10 years. Conversely, the mid-tolerant *Quercus rubra* showed prolonged radial growth increases, above those of reference trees, immediately postharvest, and maintained that level of growth for up to 10 years postharvest.

From previous studies that examined the response of seedlings and saplings to increased light availability, mid-tolerant and intolerant species were expected to respond more to gap creation because of higher growth capacity in high light (Beaudet and Messier 1998; Reich et al. 1998a), higher photosynthetic rates (Walters et al. 1993a; Niinemets 1997; Reich et al. 1998b), and greater ability to acclimate physiologically and morphologically to increased light availability (Naidu and Delucia 1997; Kursar and Coley 1999). Our results document precisely the opposite pattern: the more shade-tolerant species showed larger, longer-term BAI responses to management and gap creation than intolerant and mid-tolerant species. Similar trends of more shade-tolerant species having more positive and longer term growth responses to release were found in recent studies comparing two *Nothofagus* species in New Zealand (Wiser et al. 2005) and also *Prunus serotina* and *Q. rubra* in West Virginia (Schuler 2006), suggesting that this pattern may be widespread. Although the present study was not designed to rigorously evaluate alternative explanations for this unexpected trend, we present several alternative hypotheses below.

One important systematic difference between shade-tolerant and intolerant species may have been their relative position within the canopy prior to gap creation. Intolerant and mid-tolerant species generally suffer greater mortality when subjected to suppression than do shade-tolerant species (Kobe et al. 1995). If residual stems of mid-tolerant and intolerant species were present because they had already captured canopy positions, with high crown exposure, then their growth rate would already be high and thus further harvest may not result in a dramatic increase in growth. Knowing that small, slower-growing species respond more positively to gap creation (Fig. 4), one would expect suppressed or partially suppressed shade-tolerant species to show the greatest response to gap creation relative to intolerant and mid-tolerant species, which may have already been growing in less competitive environments. To evaluate this hypothesis, direct measures of light availability or suitable proxies (neighbourhood competition or crown exposure indices) for individual trees prior to release would have to be estimated.

Another possible explanation for the lack of responsiveness of mid-tolerant and intolerant species could be differences in their ability to take advantage of additional light resources. Shade-tolerant species typically have much deeper and wider crowns than shade-intolerant and mid-tolerant species (Pacala et al. 1993; Canham et al. 1994; Cole and Lorimer 1994). By displaying leaves lower in the canopy, late-successional, shade-tolerant species may experience a larger increase in intercepted light than do species with leaves displayed only in the upper canopy. Although this hypothesis has not been directly tested, crown depth has been shown to be important in the growth response of trees following thinning (Brown et al. 2004). This pattern would suggest that intolerant and mid-tolerant species would not be subject to a dramatic change in light availability following moderate canopy disturbance and, thus, would not show the same increase in net carbon gain possible for shade-tolerant species.

Regardless of the causes of the differences in growth response to reduced competition, it is clear that the two shade-tolerant tree species *A. saccharum* and *F. grandifolia* as well as the mid-tolerant *B. alleghaniensis* gain a competitive advantage over other species in selection-managed forests owing to postharvest growth responses. This pattern is likely to contribute to the widely observed decline in mid-tolerant and intolerant species under selection management (Webster and Jensen 2007). The competitive advantage of shade-tolerant species may be linked to a change in the natural gap phase dynamic processes, where smaller and more frequent gaps are created. Selection management also alters a suite of stand dynamic processes through life-cycle truncation and removal of senescing trees (McGee et al. 1999), harvesting effects on tree mortality (Caspersen 2006), reduction in mineral soil exposure and creation of pit-and-mound topography (Caspersen and Sapruff 2005; Shields et al. 2007), and accelerated gap closure (Angers et al. 2005; Domke et al. 2007) caused by changes in age structure. Although we are not aware of a simple way to distinguish between these effects, a greater understanding of the temporal dynamics of tree growth response is an important step towards understanding how tree-level growth responses may contribute to the shifts in species composition in managed tolerant hardwood forests.

## Acknowledgements

We thank Haliburton Forest and Wildlife Reserve for their support, and Lisa Buse, Sheelah Griffith, Rachel Mayberry, Justin Morgenroth, and Charles Nock for assistance with field data collection and tree ring observations. John Caspersen provided valuable input on the project as well as the manuscript at various stages. This research was supported by the National Sciences and Engineering Research Council of Canada, the Ontario Premier's Research Excellence Award program, and a University of Toronto Faculty of Forestry Grant-in-Aid.

## References

- Angers, V.A., Messier, C., Beaudet, M., and Leduc, A. 2005. Comparing composition and structure in old-growth and harvested (selection and diameter-limit cuts) northern hardwood stands in Quebec. *For. Ecol. Manage.* **217**: 275–293. doi:10.1016/j.foreco.2005.06.008.
- Baltzer, J.L., and Thomas, S.C. 2007. Physiological and morphological correlates of whole-plant light compensation point in temperate deciduous tree seedlings. *Oecologia (Berl.)*, **153**(2): 209–223. doi:10.1007/s00442-007-0722-2.
- Bazzaz, F.A., and Wayne, P.M. 1994. Coping with environmental heterogeneity: the physiological ecology of tree seedling regeneration across the gap-understorey continuum. In *Exploitation of environmental heterogeneity by plants*. Edited by M.M. Caldwell and R.W. Pearcy. Academic Press, San Diego, Calif., USA. pp. 349–390.
- Beaudet, M., and Messier, C. 1998. Growth and morphological responses of yellow birch, sugar maple, and beech seedlings growing under a natural light gradient. *Can. J. For. Res.* **28**(7): 1007–1015. doi:10.1139/cjfr-28-7-1007.
- Beaudet, M., and Messier, C. 2002. Variation in canopy openness and light transmission following selection cutting in northern hardwood stands: an assessment based on hemispherical photographs. *Agric. For. Meteorol.* **110**(3): 217–228. doi:10.1016/S0168-1923(01)00289-1.
- Beaudet, M., Messier, C., Hilbert, D.W., Lo, E., Wang, Z.M., and Lechowicz, M.J. 2000. Leaf- and plant-level carbon gain in yellow birch, sugar maple, and beech seedlings from contrasting forest light environments. *Can. J. For. Res.* **30**(3): 390–404. doi:10.1139/cjfr-30-3-390.
- Bebber, D.P., Thomas, S.C., Cole, W.G., and Balsillie, D. 2004. Diameter increment in mature eastern white pine, *Pinus strobus* L., following partial harvest of old-growth stands in Ontario, Canada. *Trees*, **18**(1): 29–34. doi:10.1007/s00468-003-0274-y.
- Black, B.A., and Abrams, M.D. 2003. Use of boundary-line growth patterns as a basis for dendroecological release criteria. *Ecol. Appl.* **13**(6): 1733–1749. doi:10.1890/02-5122.
- Brown, P.L., Doley, D., and Keenan, R.J. 2004. Stem and crown dimensions as predictors of thinning responses in a crowded tropical rainforest plantation of *Flindersia brayleyana* R Muell. *For. Ecol. Manage.* **196**(2–3): 379–392. doi:10.1016/j.foreco.2004.03.029.
- Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York, USA.
- Burns, R.M., and Honkala, B.H. 1990. *Silvics of North America*. Vol. 2. Hardwoods. USDA For. Serv., Washington, D.C., USA.
- Canham, C.D., Finzi, A.C., Pacala, S.W., and Burbank, D.H. 1994. Causes and consequences of resource heterogeneity in forests — interspecific variation in light transmission by canopy trees. *Can. J. For. Res.* **24**(2): 337–349. doi:10.1139/x94-046.
- Caspersen, J.P. 2006. Elevated mortality of residual trees following single-tree felling in northern hardwood forests. *Can. J. For. Res.* **36**(5): 1255–1265. doi:10.1139/X06-034.
- Caspersen, J.P., and Sapruff, M. 2005. Seedling recruitment in a northern temperate forest: the relative importance of supply and establishment limitation. *Can. J. For. Res.* **35**(4): 978–989. doi:10.1139/x05-024.
- Cavender-Bares, J., and Bazzaz, F.A. 2000. Changes in drought response strategies with ontogeny in *Quercus rubra*: implications for scaling from seedlings to mature trees. *Oecologia (Berl.)*, **124**: 8–18. doi:10.1007/PL00008865.
- Cole, W.G., and Lorimer, C.G. 1994. Predicting tree growth from crown variables in managed northern hardwood stands. *For. Ecol. Manage.* **67**(1–3): 159–175. doi:10.1016/0378-1127(94)90014-0.
- Digregorio, L.M., Krasny, M.E., and Fahey, T.J. 1999. Radial growth trends of sugar maple (*Acer saccharum*) in an Allegheny northern hardwood forest affected by beech bark disease. *J. Torrey Bot. Soc.* **126**(3): 245–254. doi:10.2307/2997279.
- Domke, G.M., Caspersen, J.P., and Jones, T.A. 2007. Light attenuation following selection harvesting in northern hardwood forests. *For. Ecol. Manage.* **239**: 182–190. doi:10.1016/j.foreco.2006.12.006.
- Forget, E., Nolet, P., Doyon, F., Delagrangé, S., and Jardon, Y. 2007. Ten-year response of northern hardwood stands to commercial selection cutting in southern Quebec, Canada. *For. Ecol. Manage.* **242**(2–3): 764–775. doi:10.1016/j.foreco.2007.02.010.
- Grissino-Mayer, H.D. 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Res.* **57**(2): 205–221.
- Groot, A., and Hokka, H. 2000. Persistence of suppression effects on peatland black spruce advance regeneration after overstorey removal. *Can. J. For. Res.* **30**(5): 753–760. doi:10.1139/cjfr-30-5-753.
- Jones, T.A., and Thomas, S.C. 2004. The time course of diameter increment responses to selection harvests in *Acer saccharum*. *Can. J. For. Res.* **34**(7): 1525–1533. doi:10.1139/x04-034.

- Jones, T.A., and Thomas, S.C. 2007. Leaf-level acclimation to gap creation in mature *Acer saccharum* trees. *Tree Physiol.* **27**(2): 281–290. PMID:17241970.
- Kobe, R.K., Pacala, S.W., Silander, J.A., and Canham, C.D. 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecol. Appl.* **5**(2): 517–532. doi:10.2307/1942040.
- Kursar, T.A., and Coley, P.D. 1999. Contrasting modes of light acclimation in two species of the rainforest understory. *Oecologia (Berl.)*, **121**(4): 489–498. doi:10.1007/s004420050955.
- Latham, P., and Tappeiner, J. 2002. Response of old-growth conifers to reduction in stand density in western Oregon forests. *Tree Physiol.* **22**(2–3): 137–146. PMID:11830410.
- McCarthy, J. 2001. Gap dynamics of forest trees: a review with particular attention to boreal forests. *Environ. Rev.* **9**: 1–59. doi:10.1139/er-9-1-1.
- McClure, J.W., and Lee, T.D. 1993. Small-scale disturbance in a northern hardwoods forest — effects on tree species abundance and distribution. *Can. J. For. Res.* **23**(7): 1347–1360. doi:10.1139/x93-172.
- McDowell, N., Brooks, J.R., Fitzgerald, S.A., and Bond, B.J. 2003. Carbon isotope discrimination and growth response of old *Pinus ponderosa* trees to stand density reductions. *Plant Cell Environ.* **26**(4): 631–644. doi:10.1046/j.1365-3040.2003.00999.x.
- McGee, G.G., Leopold, D.J., and Nyland, R.D. 1999. Structural characteristics of old-growth, maturing, and partially cut northern hardwood forests. *Ecol. Appl.* **9**(4): 1316–1329. doi:10.1890/1051-0761(1999)009[1316:SCOOGM]2.0.CO;2.
- Miller, G.W., and Kochenderfer, J.N. 1998. Maintaining species diversity in the central Appalachians. *J. For.* **96**(7): 28–33.
- Naidu, S.L., and Delucia, E.H. 1997. Growth, allocation and water relations of shade-grown *Quercus rubra* L. saplings exposed to a late-season canopy gap. *Ann. Bot. (Lond.)*, **80**(3): 335–344. doi:10.1006/anbo.1996.0446.
- Neuendorf, J.K., Nagel, L.M., Webster, C.R., and Janowiak, M.K. 2007. Stand structure and composition in a northern hardwood forest after 40 years of single-tree selection. *North. J. Appl. For.* **24**(3): 197–202.
- Niinemets, U. 1997. Role of foliar nitrogen in light harvesting and shade tolerance of four temperate deciduous woody species. *Funct. Ecol.* **11**(4): 518–531. doi:10.1046/j.1365-2435.1997.00109.x.
- Nyland, R.D. 2007. *Silviculture*. 2nd ed. Waveland Press, Inc., Long Grove, Ill., USA. pp. 213–276.
- O'Hara, K.L. 1998. Silviculture for structural diversity: a new look at multiaged systems. *J. For.* **96**(7): 4–10.
- Ontario Ministry of Natural Resources. 1998. A silvicultural guide for the tolerant hardwood forest in Ontario. Ontario Ministry of Natural Resources, Peterborough, Ont., Canada.
- Orwig, D.A., and Abrams, M.D. 1995. Dendroecological and eco-physiological analysis of gap environments in mixed-oak understories of northern Virginia. *Funct. Ecol.* **9**(6): 799–806. doi:10.2307/2389977.
- Pacala, S.W., Canham, C.D., and Silander, J.A., Jr. 1993. Forest models defined by field measurements: I. The design of a north-eastern forest simulator. *Can. J. For. Res.* **23**: 1980–1988. doi:10.1139/x93-249.
- Pacala, S.W., Canham, C.D., Silander, J.A., and Kobe, R.K. 1994. Sapling growth as a function of resources in a north temperate forest. *Can. J. For. Res.* **24**(11): 2172–2183. doi:10.1139/x94-280.
- Reich, P.B., Tjoelker, M.G., Walters, M.B., Vanderklein, D.W., and Buschena, C. 1998a. Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and low light. *Funct. Ecol.* **12**(3): 327–338. doi:10.1046/j.1365-2435.1998.00208.x.
- Reich, P.B., Walters, M.B., Tjoelker, M.G., Vanderklein, D., and Buschena, C. 1998b. Photosynthesis and respiration rates depend on leaf and root morphology and nitrogen concentration in nine boreal tree species differing in relative growth rate. *Funct. Ecol.* **12**(3): 395–405. doi:10.1046/j.1365-2435.1998.00209.x.
- Runkle, J.R., and Yetter, T.C. 1987. Treefalls revisited: gap dynamics in the southern Appalachians. *Ecology*, **68**(2): 417–424. doi:10.2307/1939273.
- Ryan, M.G., Binkley, D., and Fownes, J.H. 1997. Age-related decline in forest productivity: pattern and process. *Adv. Ecol. Res.* **27**: 213–262. doi:10.1016/S0065-2504(08)60009-4.
- Schuler, T.M. 2006. Crop tree release improves competitiveness of northern red oak growing in association with black cherry. *North. J. Appl. For.* **23**(2): 77–82.
- Schwartz, J.W., Nagel, L.M., and Webster, C.R. 2005. Effects of uneven-aged management on diameter distribution and species composition of northern hardwoods in upper Michigan. *For. Ecol. Manage.* **211**(3): 356–370. doi:10.1016/j.foreco.2005.02.054.
- Shields, J.M., Webster, C.R., and Nagel, L.M. 2007. Factors influencing tree species diversity and *Betula alleghaniensis* establishment in silvicultural openings. *Forestry*, **80**(3): 293. doi:10.1093/forestry/cpm013.
- Thomas, S.C., and Winner, W.E. 2002. Photosynthetic differences between saplings and adult trees: an integration of field results by meta-analysis. *Tree Physiol.* **22**(2–3): 117–127.
- Thorpe, H.C., Thomas, S.C., and Caspersen, J.P. 2007. Residual-tree growth responses to partial stand harvest in the black spruce (*Picea mariana*) boreal forest. *Can. J. For. Res.* **37**(9): 1563–1571. doi:10.1139/X07-148.
- Valladares, F., Chico, J.M., Aranda, I., Balaguer, L., Dizengremel, P., Manrique, E., and Dreyer, E. 2002. The greater seedling high-light tolerance of *Quercus robur* over *Fagus sylvatica* is linked to a greater physiological plasticity. *Trees-Struct. Funct.* **16**(6): 395–403.
- Walters, M.B., and Reich, P.B. 1996. Are shade tolerance, survival, and growth linked? Low light and, nitrogen effects on hardwood seedlings. *Ecology*, **77**(3): 841–853. doi:10.2307/2265505.
- Walters, M.B., and Reich, P.B. 2000. Seed size, nitrogen supply, and growth rate affect tree seedling survival in deep shade. *Ecology*, **81**(7): 1887–1901.
- Walters, M.B., Kruger, E.L., and Reich, P.B. 1993a. Growth, biomass distribution and carbon dioxide exchange of northern hardwood seedlings in high and low light: relationships with successional status and shade tolerance. *Oecologia (Berl.)*, **94**(1): 7–16. doi:10.1007/BF00317294.
- Walters, M.B., Kruger, E.L., and Reich, P.B. 1993b. Relative growth rate in relation to physiological and morphological traits for northern hardwood tree seedlings: species, light environment and ontogenetic considerations. *Oecologia (Berl.)*, **96**(2): 219–231. doi:10.1007/BF00317735.
- Webster, C.R., and Jensen, N.R. 2007. A shift in the gap dynamics of *Betula alleghaniensis* in response to single-tree selection. *Can. J. For. Res.* **37**(3): 682–689. doi:10.1139/X06-267.
- Wiser, S.K., Allen, R.B., Benecke, U., Baker, G., and Peltzer, D. 2005. Tree growth and mortality after small-group harvesting in New Zealand old-growth *Nothofagus* forests. *Can. J. For. Res.* **35**(10): 2323–2331. doi:10.1139/x05-158.
- Wright, E.F., Canham, C.D., and Coates, K.D. 2000. Effects of suppression and release on sapling growth for 11 tree species of northern, interior British Columbia. *Can. J. For. Res.* **30**(10): 1571–1580. doi:10.1139/cjfr-30-10-1571.
- Youngblood, A.P. 1991. Radial growth after a shelterwood seed cut in a mature stand of white spruce in interior Alaska. *Can. J. For. Res.* **21**(3): 410–413. doi:10.1139/x91-052.