Effects of above- and belowground partial harvest disturbance on growth and water status of residual sugar maple

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Summary Partial forest harvesting is known to modify both above- and belowground resource availability and may result in direct and indirect stress to the residual trees as a result of machinery traffic and sudden changes in irradiance. We studied sugar maple (*Acer saccharum* Marsh.) trees in stands that had undergone a selection harvest 11 years before sampling to verify whether sudden increases in light availability and soil disturbance caused by machinery influence growth rates and lead to water stress. We selected trees that had experienced either no disturbance from partial harvest, soil disturbance only, sudden increases in light availability only or both disturbances. We analyzed stem radial growth rates and stable carbon isotope composition ($\delta^{13}C$) of stem wood with an annual resolution from 10 years before partial harvest until 10 years after partial harvest. Disturbances from partial harvest did not negatively affect growth rates or tree water status. Although trees that experienced increased light availability had higher (less negative) $\delta^{13}C$ after harvest (indicating increased water-use efficiency), they also had higher growth rates, suggesting that they experienced no pronounced water stress. Trees subjected to soil disturbance showed no sign of water stress. These results may partly be associated with favorable growth conditions (abundant precipitation and mild temperature) in the years following harvest and could differ from results that would be observed under more severe climatic conditions.

Keywords: Acer saccharum, light availability, selection cut, soil disturbance, tree water status.

Introduction

Partial forest harvests remove varying proportions of canopy and understory trees to liberate resources, thereby improving growth conditions of the released residual trees (Smith et al. 1997). Increased growth rates of residual trees following partial harvest have been reported for trees of different species and ages (e.g., Drew and Flewelling 1979, Bodner 1984, Kneeshaw et al. 2002, Jones and Thomas 2004). Partial harvest results in higher growth rates of residual canopy trees through increases in light interception of the exposed tree crowns (Wyckoff and Clark 2005), accompanied by adjustments in the lower-canopy leaves to higher maximum area-based photosynthetic rates and higher stomatal conductances (Jones and Thomas 2007). Hence, increases in light interception can increase both photosynthetic rates and transpirational water demands.

Residual trees located close to skid trails may be subjected to root damage (Rönnberg 2000, Ouimet et al. 2005) and soil compaction (Kozlowski 1999), which may impair root development (Taylor and Brar 1991). Reduced water availability in compacted soils (Starsev and McNabb 2001) and decreased water uptake by damaged root systems both reduce the water supply to affected trees. Trees may mitigate effects of limited water availability by down-regulating transpiration either by decreasing canopy leaf area or by reducing stomatal conductance (Sperry 2000, Sperry et al. 2002).

Experimental studies of tree responses to stand thinning are often limited to a few measurements made during one or two growing seasons (e.g., Bréda et al. 1995, Stoneman et al. 1997, Jones and Thomas 2007). In contrast, tree rings provide an integrated reflection of environmental conditions at the time when the wood was deposited (Saurer et al. 1997). Tree rings can reveal not only growth responses, but also the photosynthetic behavior of trees for thousands of years, with an annual resolution (McCarroll and Loader 2004). Moreover, fluctuations in stable carbon isotope ratios ($\delta^{13}C$) of tree rings have been used to reconstruct past climate conditions (e.g., Lipp et al. 1991), and have proved useful in contemporary ecophysiological studies relating climatic variables to physiological processes such as respiration (e.g., Berninger et al. 2000, Bowling et al. 2002, 2003, Fessenden and Ehleringer 2003).

Variations in $\delta^{13}C$ may be caused by increases in photosynthetic rate at constant stomatal conductance. Scheidegger et al. (2000) used information on evaporative enrichment in the $\delta^{18}O$ of plant matter to distinguish between biochemical and stomatal limitations to photosynthesis in response to changes in environmental conditions (e.g., precipitation). Saurer et al. (1997) proposed linking growth rates with variations in $\delta^{13}C$ to

indicate whether photosynthetic rate or stomatal conductance caused variations in $\delta^{13}C$ in response to environmental conditions. (1) If enhanced photosynthetic rate at constant stomatal conductance (i.e., no water stress) increases $\delta^{13}C$, growth rates should increase simultaneously. (2) If increased stomatal conductance (i.e., decreasing water stress) increases CO_2 supply thereby increasing photosynthetic rate, $\delta^{13}C$ should decrease and growth rates increase. (3) If the plant controls stomatal conductance and photosynthetic capacity simultaneously, $\delta^{13}C$ may stay constant. In this scenario, growth rates may vary depending on the tree's ability to adjust to prevailing growth conditions (i.e., irradiance, water supply). Similarly, a constant photosynthetic rate and reduced stomatal conductance (due to reduced water supply) will yield higher $\delta^{13}C$ and lower growth rates.

We investigated the responses of radial growth rates and stable carbon isotope discrimination in stem wood of residual sugar maple trees (*Acer saccharum* Marsh.) following partial harvest. Trees were classified according to the degree of impact (soil disturbance, light increases) of the partial harvest. To interpret changes in radial growth and ^{13}C discrimination in response to harvest disturbance, application of the theoretical framework of Saurer et al. (1997) allowed us to formulate four hypotheses (*sensu* Saurer et al. 1997): (1) undisturbed trees (no light increase, no soil disturbance) should show no significant changes in either growth rates or $\delta^{13}C$ following harvest (constant photosynthetic rate at constant stomatal conductance and no water stress); (2) trees subjected to sharply increased irradiances, but no soil disturbance, should show higher growth rates and less negative $\delta^{13}C$ values following harvest; (3) trees experiencing soil disturbance but no increase in irradiance should have constant (or decreasing) growth rates and less negative $\delta^{13}C$ values following harvest, and (4) trees experiencing sharply higher irradiances and soil disturbance should have decreased growth rates and much less negative $\delta^{13}C$ values following harvest.

Materials and methods

Study site

The study sites are located in western Quebec (Canada, 46°43′ N, 79°04′ W). The region has a mean annual temperature varying from 2.5 to 5.0 °C. The growing season extends over 170 to 180 days. Mean annual precipitation ranges from 800 to 1000 mm, with snowfall comprising about 25% of the total (Gosselin et al. 2000). Soils are podzols with sandy to loamy texture, and are derived principally from glacial tills or fluvio-glacial deposits (Robitaille and Saucier 1998).

Study plots

In 2004 and 2005, 19 plots (26 × 56 m) were established in sugar maple stands located on level ground or on gentle slopes with good to moderate drainage. The stands experienced a severe outbreak of forest tent caterpillar (FTC, *Malacosoma disstria* Hubner) in 1988, and had been harvested by selection cuts in 1993 or 1994. The selection cut aimed to remove ~30% of stand basal area across age- and diameter classes while maintaining the preexisting species proportions. Mean preharvest basal area (BA) was reduced from 27 to 21 $m^2\ ha^{-1}$. Tree marking aimed mainly at removing low quality low vigor trees to increase overall post-harvest stand quality. Tree felling was done manually with chainsaws and whole trees were forwarded to forest roads with cable skidders. Skid trails were spaced about 15 m apart, but spacing was not constant along the trail path, so that some areas were more affected by machine traffic than others.

Sugar maple is the most frequent species in most plots (about 70% of total BA), followed by yellow birch (*Betula alleghaniensis* Britton, 18%), red oak (*Quercus rubra* L., 3.0%). American beech (*Fagus grandifolia* Ehrh., 2.3%), eastern hemlock (*Tsuga canadensis* (L.) Carr., 1.8%), eastern white cedar (*Thuja occidentalis* L., 1.6%), and red maple (*Acer rubrum* L., 1.5%). Other species occur in minor proportions (= 1% of total BA, Table 1), and included balsam fir (*Abies balsamea* (L.) P. Mill.) and white spruce (*Picea glauca* (Moench) Voss). Mean post-harvest diameter at breast height (DBH, 1.3 m above ground) ranged between 155 mm for balsam fir and 422 mm for eastern hemlock. Canopy height reached 19.2 m in eastern white cedar and up to 23.8 m in red oak (Table 1).

Within the plots, the DBH of all live and dead trees > 9.1 cm DBH, and the diameter at stump height (dsh) of all stumps

Table 1. Minimum, maximum and mean tree diameter at breast height (DBH) at time of sampling (2004–2005), tree height and mean tree density per species in the sample plots.

Species	DBH (mm)			Height (m)			Mean density	
	Min	Max	Mean	Min	Max	Mean	(trees ha^{-1})	(m^2 ha^{-1})
Yellow birch	92	849	271	5.8	31.1	19.3	49	4.85
Red oak	91	685	405	11.2	30.8	23.8	4	2.30
White spruce	91	370	196	6.1	25.7	15.2	6	0.58
Red maple	93	720	299	7.1	33.3	21.9	3	1.46
Sugar maple	91	792	230	5.3	35.8	18.3	269	18.75
American beech	91	542	203	4.9	31.0	15.4	11	1.18
Eastern hemlock	225	631	422	14.9	24.3	20.1	3	1.49
Balsam fir	91	270	155	6.1	19.6	12.4	10	0.47
Eastern white cedar	173	575	416	2.5	26.4	19.2	2	2.31

(stump height ≅ 0.5 m above ground) from the 1993–1994 harvest were measured and their positions mapped. Mapping was accomplished by laying out a virtual grid on the forest floor for which the plot center line served as the *Y*-axis. The *X*-coordinates were determined by measuring (with a Vertex III hypsometer, Haglöf Sweden AB) the perpendicular distances of tree positions from the center line. Orientation (magnetic azimuth) of the plot center line was measured with a standard forester's compass.

Skid trails from the 1993–1994 harvest were also measured. Because regeneration and litter accumulation since harvest (about 11 years) made skid trail identification difficult, we used several indicators as evidence: (1) linear openings in the canopy; (2) ruts and tire (or skid) wounds at tree bases; (3) dense undergrowth of light- and soil-disturbance-dependent species (e.g., yellow birch, pin cherry (*Prunus pensylvanica* L.f.), poplars (*Populus* spp.)); (4) stumps in the proximity to the proposed skid trail path; (5) absence of obstacles (e.g., boulders, escarpments); (6) conformity with machinery constraints (e.g., turning radius); and (7) general concordance with the trail network and stand features. Only when all of these criteria were satisfied were skid trails considered for further analysis.

We drew the skid trail paths as the estimated center of the skid trails on the tree maps using tree positions as landmarks. We could not directly measure trail width because of forest floor vegetation and litter accumulation and so we assumed that the skid trails were 2-m wide on either side of the central path, based on an approximate but realistic machine width of 4 m.

We evaluated the impact of machine traffic on soil bulk density by measuring penetration resistance with a dynamic penetrometer (PEM-1, Roctest Inc., Montreal, QC, Canada). We measured the penetration depth after 10 blows and computed the ratio of penetration depth per blow. In each plot, we took five measurements at about 1-m intervals across each of three transects on the skid trails and three transects in the undisturbed forest floor. For the skid trail measurements, we selected only trail sections with clearly defined trail features (wheel tracks, inter-wheel space, off trail). Transect locations were chosen randomly, and the five measurement points on the skid trails were made such that Measurements 1 and 5 were off-trail, Measurements 2 and 4 were on wheel tracks, and Measurement 3 was in the inter-wheel space.

Tree-ring width data

In the mapped plots, increment cores (three cores per tree) were taken from all sugar maple trees between 19.1 and 49.0 cm DBH as a retrospective measure of radial growth. Trees with DBH < 19.1 cm were not sampled to avoid the juvenile effect in ¹³C discrimination (Freyer 1979, Francey and Farquhar 1982) and to avoid trees with heavily suppressed growth. Trees with DBH > 49.0 cm were not sampled, to avoid trees with declining growth rates. We sampled a total of 321 sugar maple trees.

Increment cores were progressively sanded down to grain 400 to allow unambiguous identification of tree rings. We measured tree rings with a microscope equipped with a computer-assisted micrometer (0.001 mm precision). At least two cores per tree were readable in most cases, and we took mean ring widths among cores to account for intra-tree variability in radial increment (Kienholz 1930, Peterson and Peterson 1995). This yielded a single growth chronology per tree.

We took radial growth measurements of dominant canopy trees to construct a master chronology by adding progressively highly correlated ($r = 0.3$, Tardif et al. 2001) tree-ring series to the existing series and obtained a final master chronology containing 29 individual tree-ring series with an overall cross-correlation coefficient of 0.479.

We cross-dated (matched tree rings with calendar years) the remaining tree-ring series based on (1) visual examination of marker years (severe growth declines in 1971 and 1988) and (2) cross-correlation coefficients of chronology segments with the master chronology. We ran the computer software program COFECHA (Holmes 1983, Grissino-Mayer 2001) to detect missing or false rings in individual segments of tree-ring series. In suspect cases, we identified false or missing rings on the cores or cross sections and added tree rings with zero width or removed these from the series. We then reran COFECHA on these series to verify improvements of the cross-correlations with the master chronology.

Only trees whose ring-width series showed strong cross-correlations ($r > 0.4$) with the master chronology were retained for further analysis. To exclude harvest disturbance unrelated to sudden increases in irradiance or soil disturbance from influencing the growth and carbon isotope responses, data from trees with severe harvest damage (e.g., uprooting, bole breakage) were excluded from the analysis.

We standardized each individual tree-ring series by dividing it by its long-term growth trend, which was estimated with a cubic smoothing spline over the entire series. The resulting dimensionless ring-width indices could be more adequately compared among trees of different ages and from different sites. This standardization procedure was performed with the i.detrend function in the R software progam dplR (Bunn 2007) in the R software environment for statistical computing and graphics (Version 2.6.0).

Because stable carbon analysis was limited to the period 1983–2003 (see below), the growth series were truncated for further analysis during these years. To reduce inter-tree differences in ring-width indices before harvest, we rescaled each series individually by dividing each ring-width series by its pre-harvest (1983–1993) mean. These rescaled values could be more adequately compared and averaged over treatment groups than series of raw ring-width indices.

Measures of harvest disturbance

Sudden changes in light conditions Because the partial harvest took place 11 years before sampling, changes in light conditions could not be measured directly and had to be estimated retrospectively. Based on spatial information on trees and stumps from the last harvest, we simulated pre-harvest stand conditions. To achieve this, we converted diameters at stump height of tree stumps to DBH values with existing conversion

tables (MRNFP 2003), and these were considered the DBH measurements of cut trees before harvest. When external criteria for dead trees such as the presence of bark and fine branches, stem wood decay or crown deterioration (Sénécal et al. 2003) indicated that these trees died only after harvest, we considered these trees as being alive in the pre-harvest stands (2.9% of all trees). The DBH measurements and estimates of all trees present before harvest (live trees + cut trees + trees that died after harvest) and of trees present after harvest (live trees only) were then loaded into the forest dynamics simulator SORTIE to estimate light availability for individual trees. Deutschman et al. (1997) have provided a comprehensive overview of SORTIE's structure and simulation procedure.

We parameterized SORTIE with regional parameters of tree species allometry and tree canopy light extinction coefficients (Canham et al. 1994, Poulin and Messier 2007, Lefrançois et al. 2008, M. Beaudet, unpublished data). Based on these parameters, SORTIE modeled tree dimensions and estimated light availability for each individual tree in the stand as the seasonally averaged percentage of full sun (Canham 1988). Estimates of light availability for each individual tree, in the center of simulated crowns at 0.75(crown height), were made for pre- and post-harvest plots. Dividing post-harvest light availability by pre-harvest light availability yielded our measure of changes in light conditions.

Soil disturbance in close proximity to trees　Assuming that tree crown dimensions can be predicted from tree diameter, and that tree crown dimensions are a proxy for tree root system coverage (Tubbs 1977), a circular influence zone was estimated around each tree based on species-specific parameters of diameter–crown relationships. This yielded diameter-dependent influence zones with radii (m) = 0.100(DBH) (cm) for sugar maple (Beaudet et al. 2002). By overlapping the influence zones of the mapped trees with the mapped skidding trails, we obtained an estimate of the proportion of the influence zone that had been disturbed by machinery traffic. The ratio of the area of the influence zone disturbed by machinery traffic, divided by the total area of the influence zone, served as our measure of soil disturbance in close proximity to trees.

Disturbance classes　All trees retained in the analysis were grouped into four disturbance classes: (1) trees not subjected to sudden increases in irradiance or soil disturbance (no disturbance class), (2) trees subjected to sharp sudden increases (> 100%) in irradiance following harvest, but not subjected to soil disturbance (light class); (3) trees not subjected to sudden increases in irradiance, but subjected to soil disturbance (> 30% of influence zone) (soil class), and (4) trees subjected to both a sharp sudden increase (> 100%) in irradiance following harvest and soil disturbance (> 30% of influence zone) (light + soil class). For each disturbance class, we randomly selected five trees for growth and stable carbon isotope analyses. Sample sizes were limited because of the large number of carbon isotope analyses (20 trees × 21 years = 420 analyses) and their associated costs.

The threshold for soil disturbance in each disturbance class was set assuming that disturbance to > 30% of the forest floor surrounding trees had an effect on tree growth and water status, through its effects on soil compaction and root damage (Kozlowski 1999, Rönnberg 2000, Ouimet et al. 2005). The threshold for sudden increases in irradiance was set at > 100% because increases up to about 40% can still allow a gradual acclimation of leaf-level photosynthetic rate in mature sugar maple trees (Jones and Thomas 2007).

Stable carbon isotope analysis

The isotopic composition of a carbon compound ($\delta^{13}C$, ‰), i.e., the proportional deviation of the $^{13}C/^{12}C$ ratio from the Vienna PeeDee belemnite (VPDB) carbonate standard, is defined as:

$$\delta^{13}C = \left(\frac{^{13}C/^{12}C_{sample}}{^{13}C/^{12}C_{VPDB}} - 1 \right) 1000 \qquad (1)$$

The trees selected for $\delta^{13}C$ analysis were felled and cross sections of the trunk were taken at 1.3 m height. To avoid carbon contamination from chainsaw lubricants, small rectangular pieces were cut from the interior of these cross sections with a band saw. The sections were then further cut to cover a 10-year period before and after the year of harvest, yielding a sampling period spanning from 1983 to 2003.

To prevent mobile substances and handling contamination from interfering with stable carbon isotope measurements, the wood sections were extracted with a 2:1 (v/v) toluene:methanol solution for several hours in a heated ultrasonic bath and oven-dried at 70 °C overnight (Loader et al. 1997). Single tree rings were then shaved from the wood sections with a surgical scalpel. These shavings were ball-milled to ensure that there was a homogeneous distribution of latewood and earlywood in the sample. Three of the wood sections had tree rings so tightly spaced that shaving with annual precision and subsequent milling was not feasible. These sections were therefore cut to dimensions that allowed their measurement by laser ablation combustion gas chromatography isotope ratio mass spectrometry (LA-C-GC-IRMS) (Schulze et al. 2004). All other milled wood samples were weighed into tin cups and assayed with a conventional elemental analyzer, (EA)-IRMS. Because the laser ablation technique necessitated the use of whole wood sections, conventional isotope ratio analysis was also based on whole wood samples. Moreover, it has been shown that undecayed whole wood and extracted cellulose have consistent $\delta^{13}C$ signatures, with whole-wood samples having slightly less negative $\delta^{13}C$ values (Loader et al. 2003). Laser trajectories spanned the entire ring width so that ablated wood material contained both early- and latewood. Thus, averaged $\delta^{13}C$ values were considered representative of entire tree rings.

Sequential isotopic analyses of milled wood samples were made with a Finnigan MAT DeltaPlus XL EA-IRMS (ThermoFinnigan GmbH, Bremen, Germany), coupled to an autosampler. For the laser ablation technique, wood dust was ablated from the samples with a frequency quadrupled Nd:YAG 266 nm UV-laser (New Wave Research Merchantek;

GeoLasArF, MicroLas, Göttingen, Germany). After combustion of the ablated wood dust, CO_2 was separated from other combustion gases and analyzed by mass spectrometry (Finnigan DeltaPlus XL EA-IRMS). Measurement precision of $\delta^{13}C$ analyses was < 0.1‰ for the milled wood samples and < 0.25‰ with the laser ablation technique, based on measurements of an internal lab standard (NBS 22: −30.03‰ on VPDB scale). All isotope measurements were made in the Iso-Lab of the Max-Planck-Institute for Biogeochemistry, Jena, Germany.

For consistency with ring-width measurements and to reduce differences in $\delta^{13}C$ between individual trees, we rescaled $\delta^{13}C$ values by dividing individual time series by their pre-harvest (1983–1993) mean. This rescaling implied that values below 1 are indicative of post-harvest increases in $\delta^{13}C$ (less negative) and, therefore, are indicative of constrained post-harvest water status. Values above 1 indicated improvements in water supply or decreases in water use, and therefore, were indicative of releases of the pre-harvest water status of trees.

We did not correct $\delta^{13}C$ values for time trends due to CO_2 enrichment of the atmosphere. The time series spanned only 21 years and comparisons were made between disturbance classes for which atmospheric enrichment was identical.

Climate–growth and climate–$\delta^{13}C$ relationships

Mean monthly climate data (precipitation, temperature) were obtained from the Canadian National Climate Data and Information Archive of Environment Canada (http://climate.weatheroffice.ec.gc.ca). Weather stations that were closest to our study sites (within about 60 km) were Barrage Temiscaming (46°42′36″ N, 79°06′00″ W, 181 m a.s.l.) and Rapide des Joachims (46°12′00″ N, 77°42′00″ W, 137 m a.s.l.). Acquisition of monthly climate data from Barrage Temiscaming was discontinued from 1995 onward. Therefore, we amended the dataset by adding data from Rapide des Joachims and mean values in overlapping years (1983–1995).

To quantify climate–growth and climate–$\delta^{13}C$ relationships, we performed correlation and response function analyses with the program Dendroclim2002 (Biondi and Waikul 2004). The correlation function gives univariate estimates of Pearson's product-moment correlation (r) between ring-width indices (or $\delta^{13}C$ indices) and climate variables, whereas the response function is a principal component regression model of the multivariate climate data with ring-width indices (or $\delta^{13}C$ indices) as the response variables. To account for multicollinearity in climate data and to increase the accuracy of correlations and the response function analysis, Dendroclim2002 computes bootstrapped confidence intervals of the parameter estimates for both functions (Biondi and Waikul 2004). Only climate variables with consistently positive or negative parameter estimates within the 95% bootstrapped confidence interval were considered significant.

Statistical analysis

We tested for differences in the rescaled ring-width indices and rescaled $\delta^{13}C$ between disturbance classes by performing a year-by-year analysis. Because of small sample sizes (5 trees per class × 4 classes per year = 20 measurements per year) and heteroscedasticity (differing variances) among groups, we did not use conventional parametric analysis of variance (ANOVA). Instead, we performed permutational analysis of variance (Anderson 2001, McArdle and Anderson 2001), with the program PERMANOVA (Anderson 2005). PERMANOVA tests assume that individual observations can only be exchanged under a true null hypothesis. The program provides a partitioning of variation, based on distance measures and according to treatment factors, and applies permutations to test for differences between groups (factor levels). First, the program estimates a distribution of the test statistic F under a true null hypothesis (i.e., no differences between groups) by randomly shuffling group labels among observations. For each permutation, PERMANOVA computes the test statistic F^*. Probabilities for the tests under a true null hypothesis are computed as the proportion of all permutational F^* values that are greater than or equal to the value of F observed for the real data (Anderson 2005). Similarly, pairwise comparisons are based on the permutational test statistic t^* and probabilities for the test under a true null hypothesis are estimated as the proportion of all permutational t^* values that are greater than or equal to the value of t observed for the real data. For both test procedures, we used 4999 permutations to estimate F^* and t^* distributions as recommended by Anderson (2005). The significance level of permutational ANOVA was $\alpha = 0.05$, but this was adjusted for multiple comparisons using the Tukey correction which, for six comparisons, yields an α threshold of 0.0085.

We compared pre- versus post-harvest values in rescaled ring-width indices and in rescaled $\delta^{13}C$ within classes to test whether harvest caused a change in these variables within a given class. Significance tests of these comparisons were made with paired t-tests after confirming normality of the sample distributions with Kolmogorov-Smirnov tests.

Results

Mean DBH at the time of sampling (2004–2005) ranged from 241 mm (light + soil class) to 379 mm (soil class). Trees in the light class ($n = 5$) had a mean increase in light availability of more than 10 times the preharvest value. Mean soil disturbance of trees in the soil class ($n = 5$) was 48.2% of the tree's influence zone, whereas for trees that experienced soil disturbance and increased light availability (light + soil class; $n = 5$), mean soil disturbance was 46.1% with a mean irradiance increase of 9.55 times preharvest light availability (Table 2).

Estimates of the impact of machine traffic on soil bulk density showed that, even 11 years after harvest, penetration ratios (soil penetration per blow) were significantly lower in wheel tracks and in the inter-wheel space than off-trail or in the undisturbed forest floor (Figure 1).

Ring-width indices showed a marked decline across all disturbance classes in 1988, the year of the FTC outbreak (Figure 2A). Pre-harvest growth rates in trees in the no distur-

Table 2. Mean diameter at breast height (DBH, at time of sampling), soil disturbance, the change in light availability (before versus after harvest) and height of trees in the no disturbance class and in the light, soil and light + soil disturbance classes. Values in parentheses are minima and maxima ($n = 5$ trees per class).

Disturbance class	DBH (mm)	Soil disturbance (%)		Light change ratio		Height (m)
No disturbance	310 (215–456)	0	–	1	–	22.4 (17.2–25.8)
Light	282 (237–360)	0	–	10.6 (2.5–26.3)		19.4 (16.9–23.4)
Light + soil	241 (197–337)	46.1 (31.3–68.4)		9.6 (2.1–16.8)		18.1 (13.5–22.2)
Soil	379 (344–410)	48.2 (37.0–52.6)		1	–	22.4 (18.1–29.5)

bance class were higher than in trees in the other classes, especially in the period following the insect outbreak. Growth rates increased after harvest in all classes, but only briefly for the trees in the no disturbance class where growth rate increases leveled off by 2001 (Figure 2A). The $\delta^{13}C$ showed some increase in 1988 in trees in all classes except the soil class (Figure 2B). From 1988 to 1990, $\delta^{13}C$ declined and then increased until 1993–1994 in trees in all classes. From 1994 onward, $\delta^{13}C$ either declined (light and soil classes) or remained constant (no disturbance and light + soil classes) over time until 2003 (Figure 2B).

Rescaled ring-width indices declined below the pooled (all classes) pre-harvest mean twice within the 1983–2003 period. In 1988, which was the year of the FTC outbreak, rescaled growth indices of trees in all disturbance classes declined below the 1983–1993 mean (Figure 3A). However, trees in the different classes responded differently to the effects of partial harvest disturbance. Mean rescaled ring-width indices of trees in the light and the light + soil classes increased and stayed above pre-harvest values until 2003 (except for 2002, when the index for trees in the light class fell briefly and slightly below the mean). Mean rescaled ring-width indices of trees in the soil class showed a one-year lag in response, but increased in 1995 and stayed above the pre-harvest mean until 2002. Trees in the
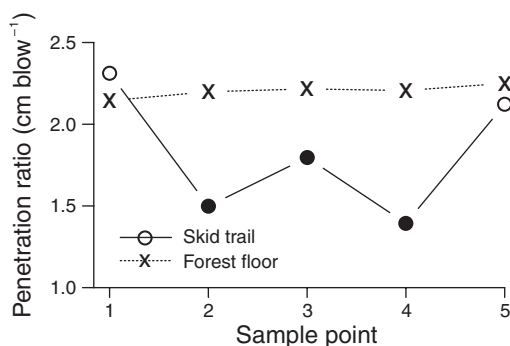
no disturbance class showed only a brief increase in 1995 but fell below the pre-harvest mean immediately afterward and remained there until 2003 (Figure 3A). Standard errors of rescaled ring-width indices increased from harvest onward and were similar among trees in the no disturbance, light and soil classes, and highest in trees in the light + soil class (Figure 3B).

From 1993 onward, rescaled $\delta^{13}C$ stayed below the pre-harvest mean in trees in all disturbance classes, except for the soil class, where it increased above the pre-harvest mean from 1998 onward (Figure 4A). Below-average values in rescaled $\delta^{13}C$ were equivalent to post-harvest increases in $\delta^{13}C$ (i.e., less negative) relative to pre-harvest values, and therefore were indicative of water stress. Thus, mean rescaled post-har-

Figure 1. Penetration ratios (cm blow^{-1}), an estimate of soil compaction, taken 11 years after harvest across skid trails or on the undisturbed forest floor. Skid-trail Measurements 1 and 5 were off-trail, Measurements 2 and 4 were on wheel tracks, and Measurement 3 was in the inter-wheel space. Measurements 1 through 5 on undisturbed forest floor were spaced ~1 m apart. Filled circles indicate significant differences ($P < 0.05$, Mann-Whitney U-test) between skid-trail and forest-floor measurements at a given sample point.
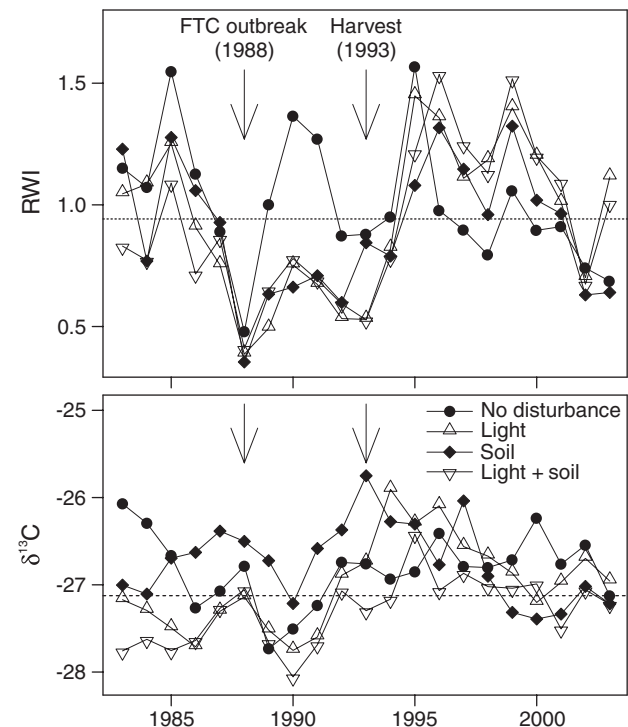

Figure 2. Mean (A) ring-width indices (RWI) and (B) $\delta^{13}C$ for trees in the no disturbance class and in the light, soil and light + soil disturbance classes from 1983 to 2003. Horizontal lines are pooled means of all 1983–2003 values. Note the negative effect of the forest tent caterpillar (FTC) outbreak in 1988 on RWI in trees in all disturbance classes.

vest $\delta^{13}C$ values were indicative of water stress in trees in the light and light + soil classes until 1998, after which they leveled off. Rescaled post-harvest $\delta^{13}C$ values in trees in the no disturbance class were quite constant throughout the period and values in trees in the soil class even increased (i.e., alleviation of water stress) from 1998 onward. Standard errors of rescaled $\delta^{13}C$ were generally higher in the post-harvest period than in the pre-harvest period, except for trees in the soil class, for which standard errors were higher at the beginning and end of the 1983–2003 period and lower in the interim (Figure 4B).

Summer precipitation was variable in the study region throughout 1910–2003, with a long-term mean of 78.10 mm. Most abundant summer precipitation was in 1970, and the driest summer was in 1975 (Figure 5). During the period of growth and $\delta^{13}C$ sampling (1983–2003), the forests received a maximum of almost 120 mm of precipitation per summer month in 1984; mean monthly summer precipitation was lower than average in 1987, 1989, 1999 and 2001, and lowest overall in 2002 (Figure 5). Mean monthly summer temperature was above the long-term mean (13.65 °C) for almost the entire 1983–2003 period, except in 1984 and 1992. However, in the years following partial harvest, mean monthly summer temperatures were close to the long-term mean (Figure 5).

Climate–growth relationships were similar in trees in all disturbance classes (Figure 6). Both correlation and response function coefficients showed a similar pattern for current-year precipitation, although the positive correlation between July precipitation and growth was significant only in the no disturbance class ($r = 0.48$). August precipitation was negatively correlated with growth ($r = -0.62$) and had significant regression parameters in the no disturbance and soil classes. This pattern was also evident in the other disturbance classes, but the coefficients were not significant. Prior fall and winter (November and January) precipitation had a positive influence on growth of trees in the no disturbance class, but not in the other classes for which prior October precipitation had a negative influence on growth (Figure 6A). Prior October temperature had a significant positive effect on growth of trees in all disturbance classes, whereas June temperature was positively correlated with growth only in trees in the light and light + soil classes ($r = 0.38$ and 0.53, respectively) (Figure 6B).

Climate–$\delta^{13}C$ relationships were less obvious than the climate–growth relationships. No clear pattern could be established for precipitation correlation or regression coefficients in the no disturbance class (Figure 7). Although we predicted that rescaled $\delta^{13}C$ values would be consistently positively correlated with any form of precipitation (i.e., precipitation would cause post-harvest $\delta^{13}C$ to be lower and more negative than the pre-harvest mean), this was not necessarily the case. Although winter (December) and spring (March) precipitation was positively correlated with rescaled $\delta^{13}C$ in the light class ($r = 0.34$ and 0.39, respectively), and summer (June) precipitation was correlated with $\delta^{13}C$ in the soil class ($r = 0.45$), no significant relationship was detected in the light + soil class (Figure 6A). Temperature was not correlated with rescaled $\delta^{13}C$ in the no disturbance class. In the light + soil and soil classes, December temperatures were negatively correlated with rescaled $\delta^{13}C$
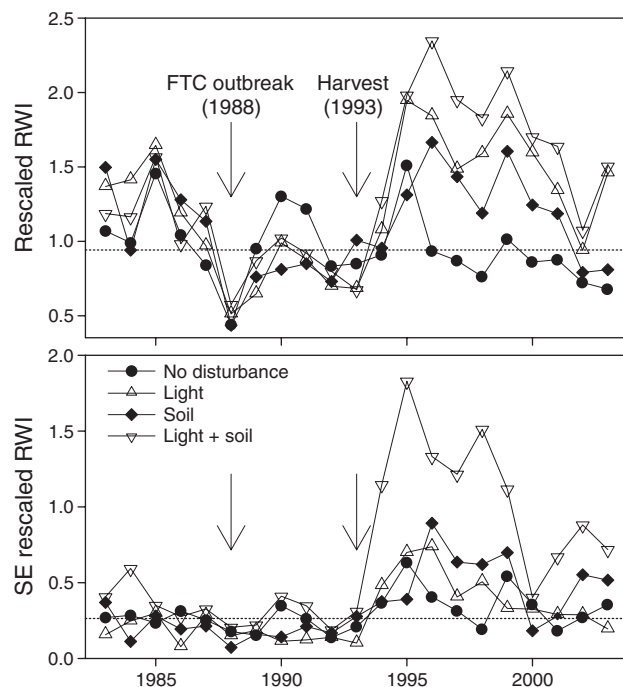

Figure 3. (A) Mean rescaled ring-width indices (RWI) and (B) standard errors of rescaled RWI for trees in the no disturbance class and in the light, soil and light + soil disturbance classes from 1983 to 2003. Horizontal lines are pooled (all classes) pre-harvest (1983–1993) values. Note the negative effect of the forest tent caterpillar (FTC) outbreak in 1988 on standardized RWI in trees in all disturbance classes.
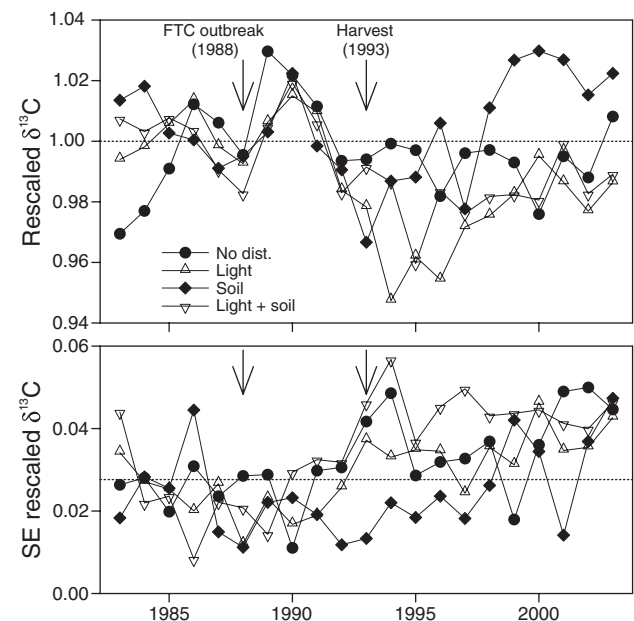

Figure 4. Mean (A) rescaled $\delta^{13}C$ and (B) standard errors of $\delta^{13}C$ for trees in the no disturbance class and in the light, soil and light + soil disturbance classes from 1983 to 2003. Horizontal lines are pooled means (all classes) of rescaled pre-harvest (1983–1993) values.
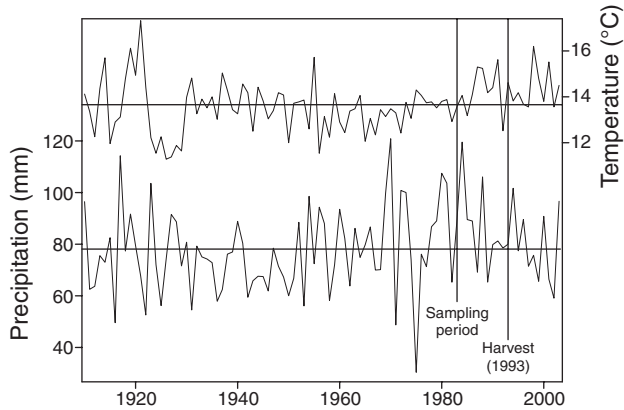
Figure 5. Mean monthly summer (April–August) precipitation and temperature from 1910 to 2003. Horizontal lines are long-term means across these years. Vertical lines indicate the start of growth and δ^{13}C sampling (1983) and the year of partial harvest (1993).

trees in the no disturbance and light classes, and only in 2003 ($P = 0.0054$). However, rescaled ring-width indices were significantly different between trees in the no disturbance and the light classes in 1991 and 1998 (both $P = 0.0054$), even though PERMANOVA did not indicate significant difference overall (Table 3). Rescaled δ^{13}C values were not statistically different in any years from 1983 to 2003.

Contrasting pre-harvest (1983–1993) versus post-harvest (1994–2003) values of rescaled ring-width indices within disturbance classes showed statistically significant increases in growth rates in trees in the light ($P < 0.001$), light + soil ($P < 0.001$) and soil ($P = 0.025$) classes, but not in the no disturbance class ($P = 0.228$, Table 4). Rescaled δ^{13}C decreased significantly in trees in the light ($P < 0.001$) and light + soil ($P = 0.007$) classes, but not in the no disturbance class ($P = 0.299$). Rescaled δ^{13}C increased in trees in the soil class but these increases were not statistically significant ($P = 0.377$, Table 4).

($r = -0.66$ and -0.38, respectively) and had significant regression parameters, whereas June temperatures were negatively correlated with rescaled δ^{13}C in the light class ($r = -0.39$). In contrast, February temperature was positively correlated with rescaled δ^{13}C in the light and soil classes ($r = 0.45$ and 0.43, respectively), whereas April temperature was positively correlated with δ^{13}C in the light and light + soil classes ($r = 0.46$ and 0.43, respectively) (Figure 7B).

Multivariate analysis indicated that rescaled ring-width indices differed significantly between classes in 2000 ($P = 0.0036$), 2001 ($P = 0.0324$) and 2003 ($P = 0.0302$). Multiple comparisons based on permutation tests in these years were, after Tukey correction, significantly different only between

Discussion

Our data support Hypotheses 1 and 2, which state, respectively, that undisturbed trees do not experience any changes in growth rates or δ^{13}C, and that trees that experienced a sharp increase in irradiance but no soil disturbance have higher growth rates and less negative δ^{13}C values following harvest. However, our data did not support Hypothesis 3 that trees with soil disturbance experience increases in δ^{13}C and decreases in growth rates. Hypothesis 4, that the light + soil class causes significant decreases in growth rates and significant increases in δ^{13}C indicating water stress, was also refuted.

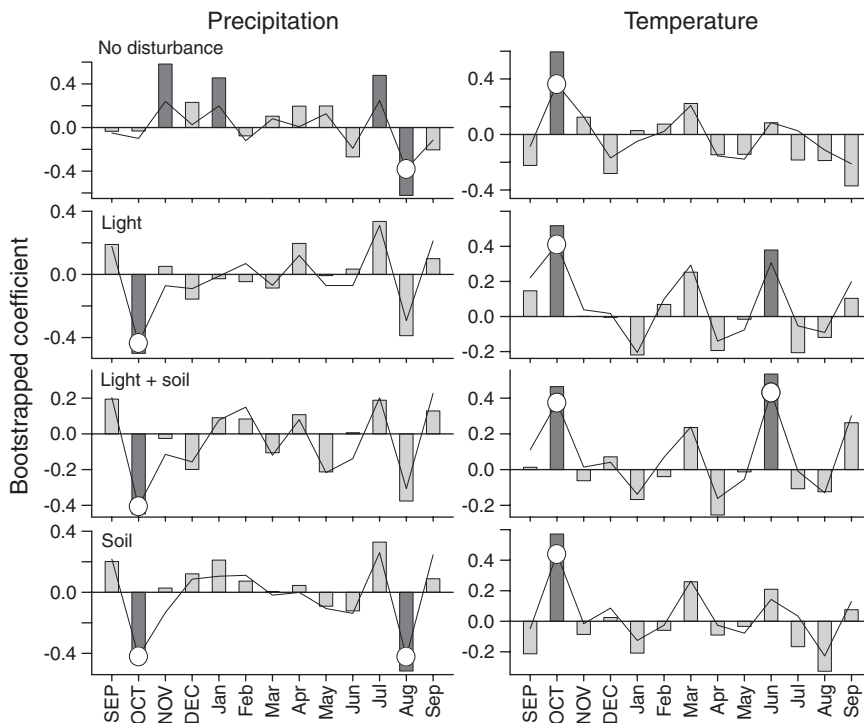Growth and stable carbon isotope analyses following partial

Figure 6. Correlation (bars) and response function (lines) analyses of rescaled ring-width indices and climate data. Monthly precipitation (left) and temperatures (right) from the previous (upper case) September to the current (lower case) September (1983–1994) were used to explain variances in rescaled ring-width indices of trees in the no disturbance class and in the light, soil and light + soil disturbance classes. Significant correlation and response function coefficients ($P < 0.05$) are indicated with dark gray bars and white circles, respectively.

Figure 7. Correlation (bars) and response function (lines) analyses of rescaled $\delta^{13}C$ and climate data. Monthly (A) precipitation and (B) temperature from prior (upper case) September to current (lower case) September (1983–1994) were used to explain variances in rescaled $\delta^{13}C$ of trees in the no disturbance class and in the light, soil and light + soil disturbance classes. Significant correlation and response function coefficients ($P < 0.05$) are indicated with dark gray bars and white circles, respectively.
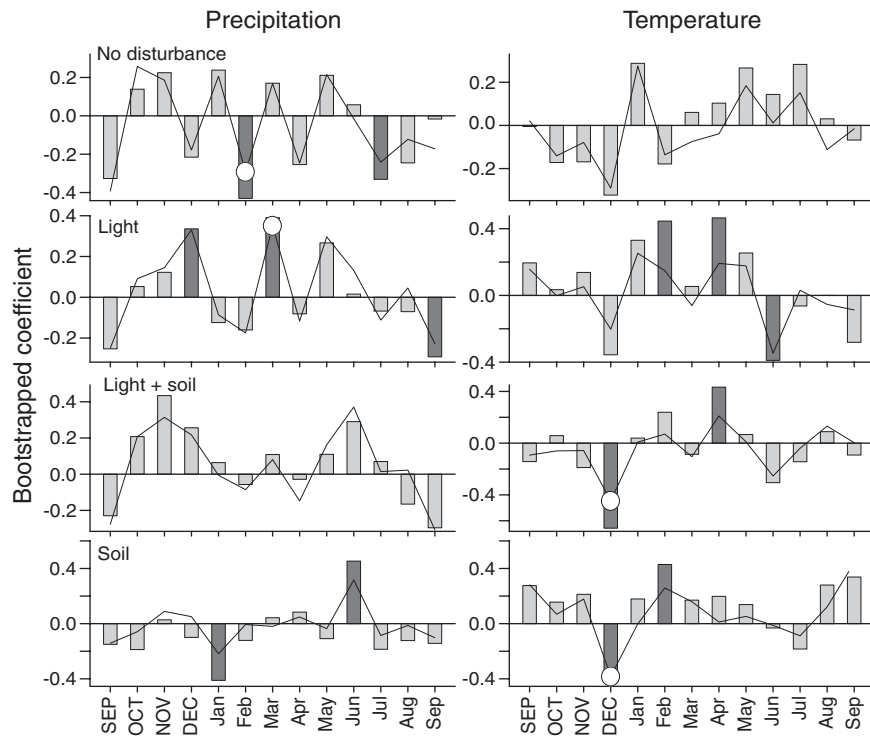
harvest indicated no negative effects of harvest disturbance on growth rates or water status of the residual sugar maple trees. Rescaled growth indices increased after harvest in trees in all

but the no disturbance class (Figure 3, Table 4), whereas rescaled $\delta^{13}C$ decreased only with sudden increases in light availability but increased slightly with soil disturbance five years after harvest (Figure 4, Table 4), indicating that none of the studied disturbances caused by partial harvest resulted in water stress in the residual sugar maple trees.

We are aware of the potential pitfalls associated with limited sample sizes in factorial analytical designs. Also, we acknowledge that SORTIE relies on a simplification of the complex canopy structure in uneven-aged deciduous forests. Similarly, our measure of soil disturbance was indirect and relied on several assumptions (e.g., negative impact of machine traffic on soil bulk density and tree root systems, uniform distribution root systems within influence zones) that are unavoidable in a retrospective study. However, we showed that soil compaction

Table 3. Summary of PERMANOVA (degrees of freedom (df), sum of squares (SS), mean squares (MS)) for years with significant ($P < 0.05$) differences in rescaled ring-width indices among all disturbance classes (no disturbance and the light, soil and light + soil disturbance classes) and with significant ($P < 0.0085$) differences in pairwise comparisons between disturbance classes (only light class versus no disturbance class were significant). Tests were based on 4999 data permutations using Euclidean distances. Significant P-values for annual PERMANOVA ($P < 0.05$) and for multiple comparisons after Tukey correction ($P_{mc} < 0.0085$) are in bold.

Year	df	SS	MS	F	P	t	P_{mc}
1991	3	0.4337	0.1446	2.3208	0.1112	2.6129	**0.0054**
Resid.	16	0.9967	0.0623				
Total	19	1.4304					
1998	3	3.2861	1.0954	1.4785	0.2254	3.4097	**0.0054**
Resid.	16	11.8539	0.7409				
Total	19	15.14					
2000	3	2.1691	0.723	6.7271	**0.0036**	3.3896	0.0128
Resid.	16	1.7197	0.1075				
Total	19	3.8888					
2001	3	1.5103	0.5034	3.1188	**0.0324**	3.0287	0.0128
Resid.	16	2.5827	0.1614				
Total	19	4.0929					
2003	3	2.7749	0.925	3.9047	**0.0302**	4.313	**0.0054**
Resid.	16	3.7901	0.2369				
Total	19	6.565					

Table 4. Paired t-tests of differences (post-harvest – pre-harvest) of rescaled ring-width indices and rescaled $\delta^{13}C$ within disturbance classes. There were 49 degrees of freedom in all cases.

Disturbance class	Difference	t	P
Rescaled ring-width indices			
No disturbance	−0.100	1.22	0.228
Light	0.482	−5.39	< 0.001
Light + soil	0.713	−4.67	< 0.001
Soil	0.220	−2.31	0.025
Rescaled $\delta^{13}C$			
No disturbance	−0.007	1.05	0.299
Light	−0.028	4.52	< 0.001
Light + soil	−0.019	2.77	0.007
Soil	0.006	−0.89	0.377

from machine traffic persisted for at least 11 years (Figure 1). In addition, our results on growth responses to harvest disturbances corroborated the findings of Hartmann and Messier (2008), who analyzed the impact of insect defoliation and harvest disturbances on radial growth and survival probabilities of residual sugar maple trees. Hartmann and Messier (2008), who used the same disturbance measures but larger samples sizes per disturbance class compared with our study, found that harvest disturbances had either no effect (soil disturbance) or a positive effect (sudden exposure to higher irradiances) on growth compared with trees in the no disturbance class (Hartmann and Messier 2008). Their observed increases in growth in response to higher irradiances corroborate our method of estimating light availability with SORTIE.

In our study, harvest disturbances had little influence on the climate–growth relationships, except that the positive correlation of precipitation in the previous November and the previous January with growth vanished in all trees affected by harvest disturbance. However, precipitation in the previous October was significantly negatively correlated with growth in trees in all but the no disturbance class (Figure 6). The positive correlation of current January precipitation with growth may by linked to increased protection of fine roots against freezing damage by deeper snow cover (Tierney et al. 2001), but the reason for the shift in correlation from precipitation in the previous October and the previous November to current January precipitation remains unclear. Several other studies on climate–growth relationship of sugar maple either failed to detect these correlations (e.g., Ryan et al. 1994, Yin et al. 1994, He et al. 2005) or were not designed to explain these causal relationships (Goldblum and Rigg 2005). The absence of a correlation between summer precipitation and growth rates may be associated with the humid climate at our research area where variations in summer precipitation explain little of the variation in growth rates.

The positive correlation of temperature during the previous October with growth indices may be linked to freezing damage. Yin et al. (1994) used regression analysis to identify a threshold temperature of 6.4 °C during the previous October on sugar maple growth indices. They argued that temperatures below 6.4 °C may expose trees to frost damage, whereas temperatures above this value may result in high maintenance respiration (Yin et al. 1994) and that both high and low temperatures may reduce the amount of carbon reserves for growth in the upcoming spring (Wong et al. 2003).

In our study, current June temperature was positively correlated with growth indices in the light and light + soil classes (Figure 6), and seemed to be indicative of favorable growth conditions. Trees with increased crown exposure as a result of partial harvest (light and light + soil classes) had increased growth rates, which was not the case for trees that experienced no change in crown exposure (no disturbance and soil classes).

Although $\delta^{13}C$ variations have been shown to be correlated with climate variables, such as air temperature and precipitation (e.g., Mazany et al. 1980, Saurer et al. 1995, Robertson et al. 1997, Hemming et al. 1998) and radiation (e.g., Smith et al. 1976, Leavitt and Long 1986, Geßler et al. 2001, Jäggi et al.

2002), we found no consistent and intuitive climate–$\delta^{13}C$ relationship in our data. Summer precipitation had no strong negative effect on $\delta^{13}C$ in our study, even in trees subjected to increased light availability (light and light + soil classes) or in trees subjected to assumed reductions in water availability and uptake (soil class).

McDowell et al. (2003) observed that carbon isotope discrimination increased in *Pinus ponderosa* (C. Lawson) following stand thinning as a result of increases in water availability, with maximum discrimination occurring 6 years after thinning. It is possible that post-harvest decreases in rescaled sugar maple $\delta^{13}C$ in the light and light + soil classes were mitigated by increases in water availability as a result of thinning, such that no differences between classes in individual years immediately after harvest were detected. Also, Vesala et al. (2005) found little influence of thinning on transpiration in Scots pine (*Pinus sylvestris* L.). Abundant growing season precipitation and moderate summer temperatures in the immediate post-harvest period (1994–1996) could have intensified this effect and may have contributed to further mitigating $\delta^{13}C$ responses to disturbance following the partial harvest.

The absence of a response in $\delta^{13}C$ to soil disturbance may be explained by an interplay of root turnover and favorable growth conditions. Fine root turnover in northern hardwoods is estimated to be about 8 months in the uppermost soil layer (< 30 cm) and 5.5 months in deeper soil horizons (> 30 cm, Hendrick and Pregitzer 1992). Given the stimulating effect of root pruning on root growth (Geisler and Feree 1984, Hipps et al. 1999), potential root damage from machinery traffic may have accelerated the replacement of damaged roots. Abundant precipitation during the post-harvest period and rapid root replacement following disturbance may have mitigated water deficits of trees subjected to soil disturbance, thereby preventing substantial increases in $\delta^{13}C$ (i.e., significant decreases in rescaled $\delta^{13}C$).

Nevertheless. despite abundant summer precipitation in 1988 (Figure 5), $\delta^{13}C$ increased (Figure 2). The forest tent caterpillar outbreak reached its climax in 1988 and reallocation of reserves for refoliation of defoliated crowns may have caused this increase. Starch reserves stored in woody tissue during winter are enriched in ^{13}C compared with other metabolites such as sucrose and hexoses, and their mobilization during heterotrophic leaf development in spring causes increases in stem wood $\delta^{13}C$ (Helle and Schleser 2004). Refoliation following herbivory should have the same effect on $\delta^{13}C$.

In conclusion, our results indicated that the redistribution of resources for individual trees following partial harvest was balanced, i.e., increases in water availability through thinning outweighed increased water demands associated with increased light interception. This redistribution of resources may have counteracted potential decreases in water availability and uptake caused by soil compaction and root damage, respectively, and prevented the development of water deficits in affected trees. In addition, mean growing season precipitation and temperature were favorable for growth for at least 3 years following partial harvest in the studied stands (Figure 5). Effects of harvest disturbances on the climate–growth relation-

ship could be different if climatic conditions in the first few years following harvest were less favorable, causing the redistribution of resources resulting from the partial harvest to become imbalanced.

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