CrossMark

ORIGINAL ARTICLE

Reproductive costs in *Acer saccharum*: exploring size-dependent relations between seed production and branch extension

Shaik Md. Yousuf Hossain[1] · John P. Caspersen[1] · Sean C. Thomas[1]

Abstract

Key message **Branch extension of *Acer saccharum* is negatively correlated with seed production, with no independent effect of tree size, consistent with reproductive allocation as the main driver of the age-related decline in tree canopy growth.**

Abstract Life-history theory predicts that reproductive allocation should increase with age and size once plants reach reproductive maturity. This suggests that there may also be a subsequent decline in somatic growth as plants become larger or older. However, few studies have examined how the relationship between branch extension growth and reproduction varies with size or age in the longest-lived plants: trees. Using a mobile lift for canopy access, we retrospectively measured branch extension growth before, during and after two (between 2011 and 2013) *Acer saccharum* mast events (the synchronous production of many seeds at long intervals), quantifying seed production per internode and internode length. Branch extension was reduced by 24 and 36%, respectively, in 2011 and 2013 relative to non-mast years, consistent with the expectation that increased reproductive allocation comes at the cost of allocation to growth. Internode length decreased from 8 to 3 cm year^{-1} as seed production increased from zero to 17 seeds year^{-1}; a similar decrease was observed at the whole-tree level using average internode extension rates and seed production per tree. Seed production alone was the most parsimonious predictor of branch extension growth, with no independent effect of tree size, suggesting that it is the increase in reproductive allocation, rather than an increase in tree size per se, that drives the decline in branch extension rates. The slope of the relationship between branch extension and reproduction did not vary with tree size, suggesting that there was no increase in the somatic cost of reproduction with tree size. We also found no evidence for lag effects of reproduction on extension growth in subsequent years. Overall, these results suggest that reproductive allocation assessed at the shoot level increases with tree size and is a major driver of the ontogenetic decline in branch extension growth.

Keywords *Acer saccharum* · Allocation · Branch extension · Cost of reproduction · Haliburton Forest · Internode · Trade-offs

Introduction

Numerous studies have examined whether and why tree growth declines later in ontogeny (Bond and Ryan 2000; Choi et al. 2001; Cole and Lorimer 2005; Ryan et al. 2006; Bond et al. 2007; Stephenson et al. 2014). Two principal hypotheses have emerged from the ecophysiology literature (Ryan et al. 1997). On the one hand, the largest body of literature focuses on biophysical processes as the main drivers of growth decline. For example, both height growth and branch extension have been hypothesized to be limited by hydraulic conductance because the combined forces of gravity and friction increase as trees grow taller and branches grow longer, thereby reducing hydraulic conductance and increasing the risk of xylem cavitation (Koch et al. 2004). This in turn forces stomatal closure and limits carbon dioxide diffusion into leaves, which leads to

✉ Shaik Md. Yousuf Hossain
  shaikhossain812@gmail.com

[1] Faculty of Forestry, University of Toronto, Toronto, ON, Canada

reduced photosynthesis and potentially reduced growth (Barnard and Ryan 2003; Yoder et al. 1994; Gower et al. 1996). Alternatively, xylem tension may constrain the turgor pressure of the uppermost leaves, thereby limiting cell expansion, intercellular diffusion of carbon dioxide, and ultimately shoot extension (Woodruff et al. 2004; Ryan et al. 2006).

Although biophysical processes have received more attention, there is a smaller body of literature that focuses on the role of reproduction in driving ontogenetic patterns of tree growth. Life-history theory provides an important basis for predicting growth declines based on the recognition that allocation of resources to competing biological functions changes throughout ontogeny (Iwasa and Cohen 1989; Thomas 1996, 2011; Iwasa 2000). In particular, life-history theory asserts that reproductive allocation increases with plant size due to switching of resources from vegetative tissues to reproductive structures (King and Roughgarden 1982; Thomas 1996; Kelly and Sork 2002; Obeso 2002; Genet et al. 2010). As a result, plants are expected to exhibit a developmental trade-off between reproduction and growth, whereby growth declines as reproduction increases (Gross 1972; Fox and Stevens 1991; Weiner and Thomas 2001; Monks and Kelly 2006). Specifically, one would expect to observe a tradeoff at the level of individual branches (Sanchez-Humanes et al. 2011), such as reduced growth of branches that produce seeds during mast years, particularly if branches are independent from other parts of the tree with regard to translocation of resources such as carbon and nutrients (Dick et al. 1990; Sprugel et al. 1991; Despland and Houle 1997).

Reproductive costs have commonly been dismissed as playing an important role in age-related growth decline, based on the argument that reproduction is often sporadic, and thus unlikely to explain the continuous decline in tree growth (Gower et al. 1996; Ryan et al. 1997; Bond and Ryan 2000; Bond et al. 2007; Kutsch et al. 2009). However, several studies have reported that reproduction in prior years may have a significant carry-over effect on the current year's growth and survivorship (Gross 1972; Woodward et al. 1993; Silvertown and Dodd 1999). This suggests that despite being sporadic, reproduction may entail a substantial reduction in tree growth as trees grow older (Thomas 2010), particularly if seed production increases in frequency or intensity through ontogeny (Thomas 2011), resulting in continual carry-over effects between successive reproductive events.

Two lines of reasoning indicate that allocation to reproduction increases over the lifespan of a tree. First, many species do not reproduce until they reach a threshold size, even when light is not limiting, so there is no initial trade-off between reproduction and growth (Thomas 2011, 2015). Second, once reproductive maturity is attained,

the frequency and output of reproduction often increase with tree size (Thomas 2011), suggesting an ontogenetic increase in allocation to reproduction as predicted by life-history theory. Indeed, allocation of annual fixed carbon to reproductive structures is reported to increase from 5% in small diameter (<20 cm DBH) trees to over 40% in large diameter trees (>20 cm DBH) of mature forests (Genet et al. 2010). This increase in allocation to reproduction could be one of the primary drivers of the decline in tree growth, including stem growth and branch extension (Obeso 2002).

It remains uncertain whether ontogenetic increases in reproductive allocation are important in driving growth trends in mature trees. To date, direct evidence that increased reproductive allocation reduces growth is largely limited to herbaceous plants (e.g., Worley and Harder 1996), because it is relatively easy to conduct experiments on small plants with shorter lifespans to study ontogenetic trends in growth and reproduction. Although direct evidence for tradeoffs between reproduction and growth for trees is scant, a tractable observational method that has been employed is to examine relationships between branch extension growth and reproduction. Branch extension is critical to tree resource capture and competition (Hibbs 1982; Cole and Lorimer 2005; Purves et al. 2007; Thorpe et al. 2010), and, therefore, of at least comparable ecological importance as stem diameter growth or biomass accumulation. A recent review found that every prior study collecting such data showed a negative correlation between reproduction and extension growth (Thomas 2011), suggesting that this pattern is pervasive. However, most studies have not distinguished between branch-level and whole-tree-level effects, and we are not aware of any prior research that has utilized observations on shoot extension—reproduction patterns to investigate age- and/or size-related reproductive costs and their role in plant ontogeny.

In the present study we utilized a mobile canopy lift for canopy access to retrospectively quantify seed production and branch extension in mature *Acer saccharum* trees before, during, and after two mast events. These data are used to address the following questions: (i) Is there a negative correlation between seed production and branch extension? (ii) Does seed production per internode increase with tree size? (iii) Does variation in seed production contribute independently to decreased internode extension growth when one accounts for size-dependent growth? (iv) Does the relationship between seed production and branch extension vary with tree size, such that large trees show a higher apparent somatic cost of reproduction than smaller trees? and (v) Is there evidence for temporally lagged effects of seed production on extension growth? We addressed each of these questions at the level of individual branches, and also at the level of entire trees, to determine whether the

relationship between growth and reproduction is mediated by local resource allocation.

Methods

Study area and species

The study area is located in south central Ontario at Haliburton Forest and Wildlife Reserve (45º15′N, 78º34′W), a 32,000 ha privately owned forest. The climate is characterized by warm, wet summers and cold winters, with a mean annual precipitation of 1000 mm and mean monthly temperature ranging from 18.9 in July to −10.9 °C in January (Environment Canada 2004). Sugar maple is the dominant tree species in this tolerant hardwood forest, representing nearly 60% of basal area; other common species include yellow birch (*Betula alleghaniensis* Britt.), American beech (*Fagus grandifolia* Ehrh.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), and balsam fir (*Abies balsamea* L.). The forest has an uneven-aged structure, having been managed by selection silviculture over last 40 years, with basal area and canopy height ranging from 15 to 30 m² ha⁻¹ and 20–25 m, respectively.

Sampling occurred in 2011 and 2013, both of which were mast years when most sugar maple trees produced seeds, with a smaller sample collected in 2015, a non-mast year. Sugar maple exhibits sequential dichogamy, a reproductive system in which trees are monoecious but with protandrous and protogynous morphs; apparently trees producing only male flowers also occur (Renner et al. 2007). At the study site flowers are produced in May to early June after leaf emergence; female flowers develop into a pair of winged seeds (samaras) during summer that mature and disperse in the fall. In the northern part of its range sugar maple exhibits masting, producing fruit crops at 2- to 5-year interval depending upon climatic conditions (Godman et al. 1990; Luzadis and Gossett 1996). The production of samaras in years between successive masting events (i.e. non-mast years) is generally negligible (USDA 2008).

Bud-break in sugar maple is followed by the expansion of twigs in late May to June (McGee 1986; Watson et al. 1986). Sugar maple twigs may have both determinate and indeterminate patterns of growth depending on age and vigor of the tree as well as position in the crown. While both determinate and indeterminate growth patterns can be observed in the same tree, indeterminate twigs are fairly abundant in the branches of young vigorous trees, but rare in slow growing older trees (Steingraeber 1982). After the initial flush, sugar maple twigs elongate with a terminal bud located at their ends. The growth in new twigs usually peaks in June or July and culminates in July or August. Sugar maple generally demonstrates apical dominance—a

phenomenon whereby the main stem of the branch grows more strongly than side branchlets, particularly at the young age (Bonser and Aarssen 1994).

Care was taken to distinguish long shoots from short shoots. Long shoots are the branches with long internodes that grow at the outer edge of the crown, while short shoots are the lateral buds that grow along the long shoot with no distinct internodes (Kozlowski and Clausen 1966). By selecting branches with longer internodes we were able to avoid short shoots, and thus the difficulty of measuring the growth of indistinct internodes.

Site and tree selection

In the summer of 2011, sugar maple trees spanning a wide size range (20–55 cm DBH), all above the size threshold for reproduction (~14 cm DBH: Thomas 2010), were located in one stand that had even topography and was accessible by the canopy lift (Scanlift 240 manufactured by Kesla of Finland). A total of 31 trees located in close proximity of primary skid trails were sampled, with a roughly equal number of trees in each of four diameter classes: 20–30 cm, 30–40 cm, 40–50 cm, and >50 cm diameter at breast height (DBH). Among the selected trees, 26 were reproductive (i.e., with samaras) and 5 were non-reproductive (i.e., without samaras). Trees were permanently marked with aluminum tags and diameter at breast height (DBH) measured. The effect of slope position and topography on the selected variables was assumed to be minimal since the study site was almost flat (slope < 2%).

Branch selection and measurement

In 2011, three branches ~1 cm in diameter were harvested from each tree using an all-terrain canopy lift. The lift was first raised to a pre-determined portion of the crown (upper, mid, or lower), then one of the peripheral branches accessible from that point was chosen at random. Thus, the branches were evenly spaced around the periphery of the upper crown, where most of the seeds are produced. We conducted sampling on the main axis of each branch. A total of 93 branches were harvested from the 31 trees, each with sufficient length to measure rates of branch extension for several years prior to the mast event in 2011. Of these, 30 branches were non-reproductive.

Another three branches were sampled from 24 of the same trees in the summer of 2013 (of which 20 were reproductive and 4 were non-reproductive), for a total additional 72 branches. Of these, 26 branches were non-reproductive. The second sample included trees with similar range of diameter classes (DBH ranged between 20 and 50 cm) as those sampled in 2011. In 2015 (a non-mast year), a more extensive sample of 40–50 branches per tree was collected

from 6 additional trees adjacent to the study site that were felled prior to sampling. In all three years, sampling took place in July or August when annual extension growth is complete but seeds have not yet dispersed. All harvested branches were tagged, placed in plastic bags, and brought to the laboratory for measurement.

The number of samaras (pairs of winged seeds) on the terminal internode of each branch was counted: the terminal internode was identified by finding the distal bud scale scar that marks the start of the current year's growth. For this measurement, only the terminal internode of the main axis of each sample branch was considered. Seed production in non-mast years was not assessed, but assumed to be zero since no *Acer saccharum* seeds were found in a set of 60, 0.5 m^2 litter traps located nearby in the years 2008–2010, 2012, 2014 and 2015 (S.C. Thomas, unpublished data).

The relationship between reproduction and branch extension was examined at both the level of individual branches and at the level of entire trees. Thus, to enable tree-level analyses, seed production was averaged across all six of the branches collected from trees that were sampled in both 2011 and 2013. For the 7 trees that were not resampled in 2013, this average was calculated across the three branches collected in 2011, so the average would be influenced by any difference in seed production between 2011 and 2013.

The length of annual internodes was measured retrospectively to quantify the annual variation in extension rates of each branch (cm year^{-1}), including growth during non-mast years. The non-terminal internodes were identified by the presence of successive bud scale (cataphyll) scars representing the start and end of each year's growth. Multiple flushing does occur exceptionally in *Acer saccharum* (Filewod and Thomas 2014), but is recognizable from bud scale morphology and was not encountered during sampling. Due to the difficulty of correctly identifying older internodes, the measurement of annual extension rates only extended back 3 years prior to the year of collection. Terminal internode lengths were averaged across all six of the branches collected from trees that were sampled in both 2011 and 2013.

Statistical analysis

Non-linear regression models were used to determine whether extension rates decline as a negative exponential function of seed production and/or stem diameter (Tables 1, 2). Categorical variables were also used to test whether masting reduces growth in subsequent years: a "pre-/post-mast" categorical variable (0 for 2008–2011, 1 for 2012–2013) allows the intercept of the negative exponential function to be lower after the first mast year (resulting in two parallel curves), as would be expected if the

Table 1 Branch-level analyses of the relationship between seed production and branch extension. G_b is the extension rate of an individual branch, S_b is the seed production of the branch, and S_t is the seed production averaged across all branches sampled in a tree

Model	AICc	ΔAICc
$Gb = \phi + \alpha e^{(-\beta Sb)}$	2597.51	0.00
$Gb = \phi + \alpha e^{(-\beta Sb - \gamma St)}$	2599.87	2.36
$Gb = \phi + \alpha e^{(-\beta Sb - \theta DBH)}$	2599.89	2.38
$Gb = \phi + \alpha e^{(-(\alpha + \delta D1)Sb)}$	2600.12	2.61
$Gb = \phi + (\alpha + \lambda D2) e^{(-\beta Sb)}$	2602.05	4.54
$Gb = \phi + \alpha e^{(-\theta DBH)}$	2604.11	6.60
$Gb = \phi$	2604.16	6.65

D1 (pre-/post-mast) and D2 (first/second mast) are categorical variables used to test whether masting reduces growth in subsequent years (see "Methods")

depletion of stored reserves reduces growth in subsequent years. The "first/second mast" categorical variable (0 for 2011 and 1 for 2013) allows the slope of the exponential function to be steeper for the second mast year, as would be expected if the depletion of stored reserves reduces growth in subsequent mast years, but not in the intervening years.

The regression analyses were conducted at both the level of individual branches and at the level of an entire tree, using the averages taken across all three branches in a tree. Mixed-effects models were used for the branch-level analysis, since the observations were not independent. In particular, a random covariance term was included in the mixed-effects models to account for any unmeasured variances associated with nested data (i.e., branches nested within trees) (Pinheiro and Bates 2000).

To assess the significance of each predictor variable, reduced models were fit that excluded one or more of the predictor variables. An interaction term between the predictor variables was included in each analysis, but interactions were found to be non-significant (not shown). The best regression model was selected from this set of predictors using Akaike's Information Criteria (AIC). Since the sample size in this study was small ($n = 31$), AICc (a variant of AIC) was calculated and used instead of AIC to correct for small sample size (Burnham and Anderson 1998). Finally, we also conducted a power analysis to assess whether a small sample of branches would suffice to estimate average leader extension throughout the tree crown (see Appendix A).

Results

There was considerable variation in seed production among branches (0–20 seeds year^{-1} with 2.31 standard deviation (SD); Fig. 1) and among trees (0–12 seeds year^{-1} with

Table 2 Tree-level analyses of the relationship between seed production and branch extension

Model	AICc	ΔAICc
$Gt = \phi + \alpha e^{(-\gamma St)}$	126.31	0.00
$Gt = \phi + \alpha e^{(-\gamma St - \theta DBH)}$	128.89	2.58
$Gt = \phi + \alpha e^{(-\theta DBH)}$	131.26	4.95
$Gt = \phi$	134.48	8.17

G_t is the average extension rate of all the branches in a tree, and S_t is the average seed production of all the branches in a tree

1.21 SD; Fig. 2a). While most trees produced seed in both mast years, some did not: among the 26 trees that set seed in 2011, four did not reproduce in 2013, while three of the five trees that did not reproduce in 2011 set seed in 2013. Average seed production per year was 5.29 (SD = 0.53) in 2011 and 4.31 (SD = 0.27) in 2013.

Branch extension was reduced by 24 and 36% (respectively in 2011 and 2013) relative to non-mast years (2010 and 2012, respectively), consistent with the expected negative correlation between growth and seed production (Fig. 3; Table 1). However, masting did not exhibit any relationship with growth in subsequent years (Table 1): neither categorical variable improved the fit of the regression model, indicating that a single intercept and a single slope were sufficient to characterize the relationship between seed production and branch extension. Thus, growth in 2013 was not significantly lower (5.63 ± 0.33 (SD) cm year^{-1}) than growth in 2011 (6.71 ± 0.74 (S.D.) cm year^{-1}),

even after accounting for the fact that seed production was 23% lower in 2013 (Fig. 3; Table 1).

Branches that produced many seeds grew significantly slower than those that did not (Table 1): terminal internode length decreased from 8 to 3 cm year^{-1} as seed production increased from zero to 17 seeds year^{-1} (Fig. 1). Seed production on other branches had no significant effect on a branch's growth rate (Table 1), as indicated by the fact that the most parsimonious model (i.e., the model with the lowest AIC) did not include the average number of seeds year^{-1} (S_t). These results suggest that the correlation between growth and reproduction is mediated by local resource allocation.

Trees that produced many seeds also grew significantly slower than those that did not (Table 2): average internode length (at the whole-tree level) decreased from 10 to 4 cm year^{-1} as the average number of seeds year^{-1} increased from 0 to 12 (Fig. 2a). Much of this tree-to-tree variation in seed production is correlated with tree size: the average number of seeds year^{-1} increased from 0 to 8 as stem diameter increased from 20 to 55 cm DBH (Fig. 2b). Thus, large trees that produce many seeds grew less than small trees that produce fewer seeds: average branch extension declined from about 10 to 4 cm year^{-1} as stem diameter and seed production increased from 20 to 55 cm and 0–8 seeds year^{-1}, respectively (Fig. 2b, c).

The most parsimonious model for branch extension growth included seed production, but no other predictors (Table 1). This suggests that it is the ontogenetic increase in reproductive allocation (in mast years), rather than an

Fig. 1 Seed production and extension rates of all internodes ($n = 165$), including non-terminal internodes formed in non-mast years. The *trend line* is a negative exponential function that was fit to the data using mixed-effects regression. This model was selected as the most parsimonious because it had the lowest AIC score (ΔAIC = 0, Table 1). The *black* and *white circles* represent terminal internodes formed in mast years (2011 and 2013, respectively), while those in *gray* represent non-terminal internodes formed in non-mast years (2008–2010 and 2012). Note that non-terminal internodes had no seed set
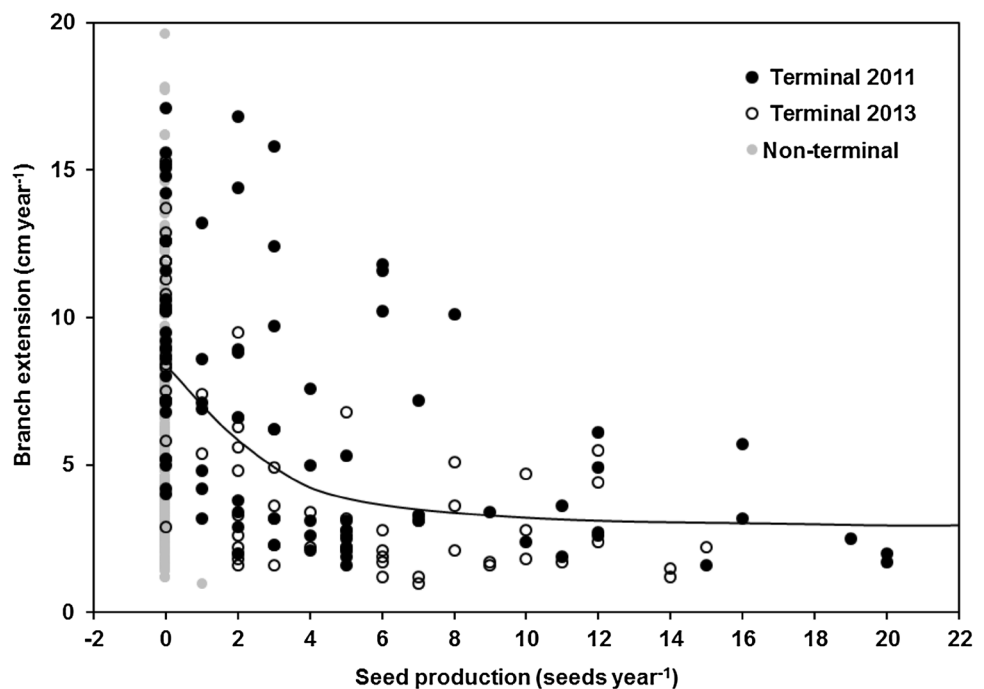
Fig. 2 Average seed production and branch extension of each sugar ▶ maple tree, including all the terminal internodes collected in 2011 and 2013 ($n = 31$; **a**). Data points are means taken across the terminal internodes of three or six branches per tree. The trend line is a negative exponential function that was fit to the data using standard regression (Table 2). This model was selected as the most parsimonious because it had the lowest AIC score ($\Delta AIC = 0$, Table 1). The *dotted lines* (above and below the *solid line*) represent regression trends that were fit to a subset of the data from trees that are below and above, respectively, the average seed production (~5 seeds year^{-1}). In both cases, the negative exponential model was significant (Table A1 in Appendix A), and the lines are parallel, indicating that, regardless of stem diameter, trees with lower than the average seed production had higher branch extension, and vice versa

increase in tree size per se, that drives the decline in branch extension rates. Including a seed production-by-stem diameter interaction did not improve the fit to the data either (not shown), indicating that the slope of the relationship between growth and reproduction (the rate that growth declines with reproduction) is the same for both larger and smaller trees.

Discussion

This study provides two important insights into the relationships between extension growth and reproduction. First, branch extension varied with the number of seeds produced during mast years (2011 and 2013), such that branches that produced many seeds grew less in that mast year than those that produced few or no seeds. Since most branches produced reproductive structures, this resulted in reduced tree-level average branch extension in mast years. Second, although both seed production and branch extension varied with tree size, the most parsimonious model only included seed production as a predictor of branch extension. These results suggest that increasing reproductive allocation largely determines ontogenetic trends in branch extension growth, with the frequency of mast years controlling growth rates over shorter time scales. The results also suggest that sugar maple branches are somewhat independent from other parts of the tree and that masting does not reduce extension growth in subsequent years (see discussion below).

Surprisingly few studies have examined ontogenetic trends in both reproduction and growth of plants, and most of these studies have utilized small plants with short lifespans. Mendez and Obeso (1993) and Worley and Harder (1996) have documented an ontogenetic increase in reproductive allocation and a concomitant decline in growth in two herbaceous perennial species. Our results similarly show a decline in branch extension growth that parallels an increase in reproduction in sugar maple: average branch extension declined from about 10 to 4 cm year^{-1} as stem
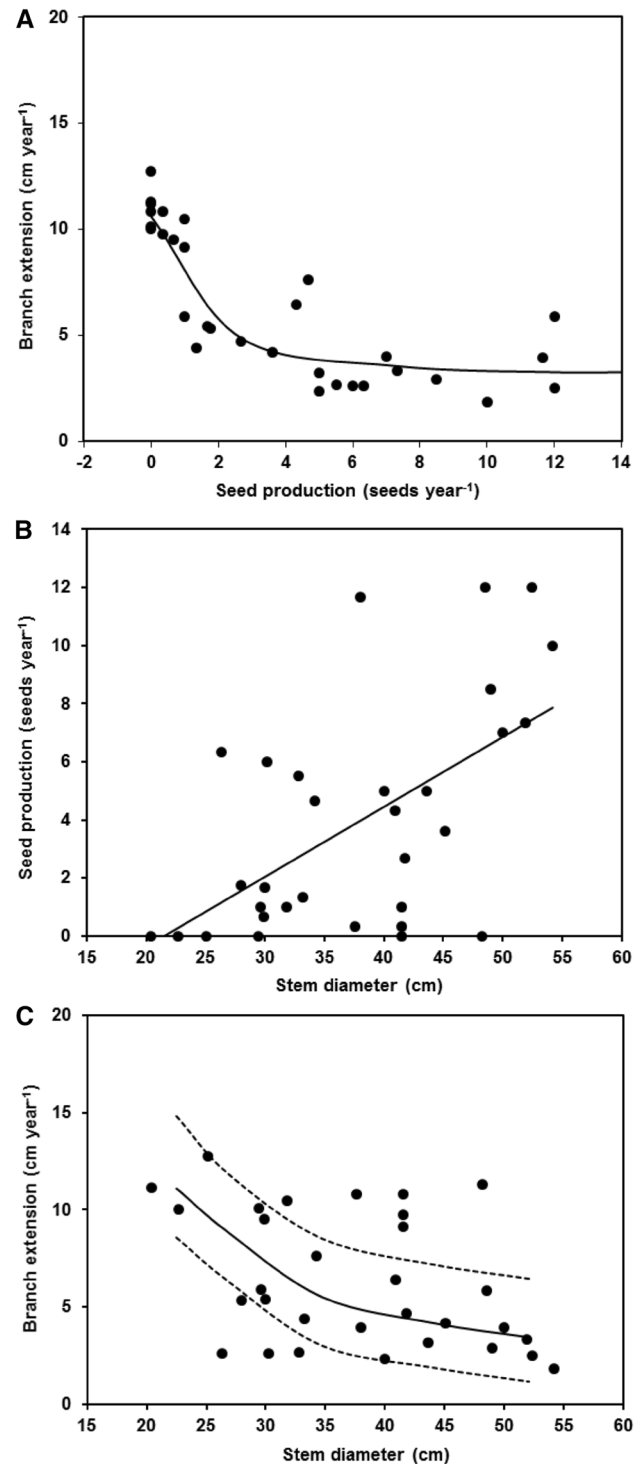
diameter increased from 20 to 55 cm (Fig. 2c), while seed production increased from 0 to 8 seeds year^{-1} (Fig. 2b). Moreover, we found no statistical effect of tree size on branch extension independent of reproduction. These results are thus consistent with prior studies of herbaceous species, and suggest a dominant role of reproductive

Fig. 3 Annual variation in the extension rate of all internodes. The years 2011 and 2013 were mast years. *Bars* on each data point indicate ± two standard deviations
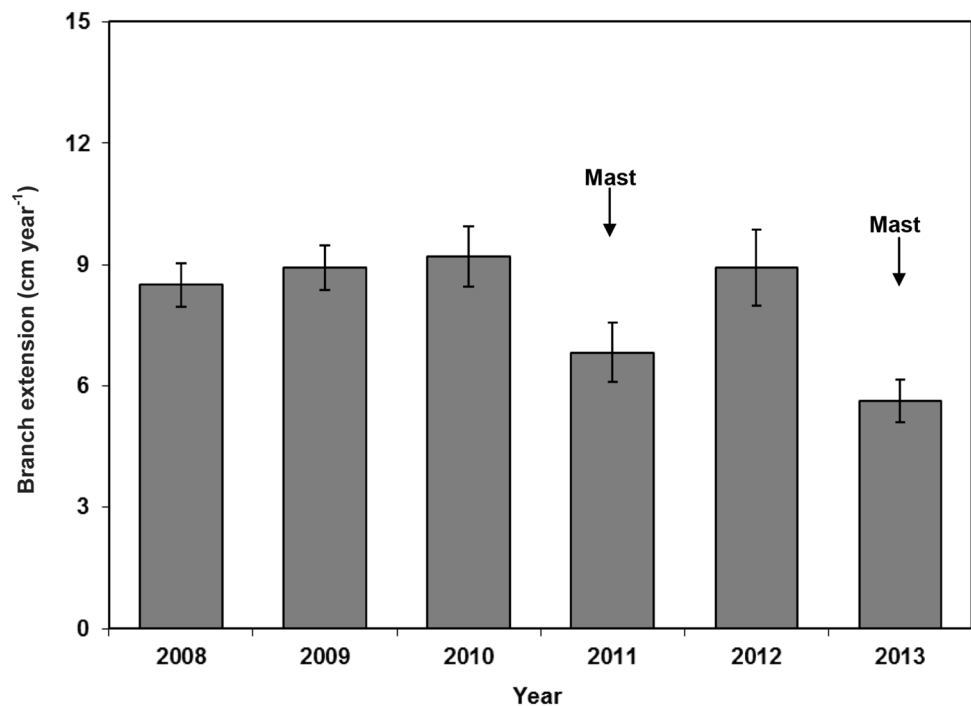
allocation in driving ontogenetic trends in branch extension growth. Our results are also consistent with data from dioecious tree species, where female trees exhibit a steeper ontogenetic decline in stem growth compared to male trees, associated with higher resource allocation to production of fruits and seeds (Wheelwright and Logan 2004; Thomas 2011).

Studies of herbaceous plants also suggest that the extent to which reproduction affects growth is often size-dependent: i.e. the "somatic cost of reproduction" (Bazzaz et al. 2000) increases through ontogeny. In their experimental manipulations of reproduction in two herbaceous perennials (e.g., *Plantago rugelii* and *P. major*), Reekie and Bazzaz (1992) found that the reduction in growth per unit of seed production increased with plant size for *P. major*. This observation is consistent with the hypothesis that the costs of reproduction are higher for large plants than for smaller plants because transportation of metabolites to reproductive structures requires more energy due to longer delivery path-lengths (Thomas 2011; Woodruff et al. 2004). However, in the present study we found that the negative correlation between growth and reproduction was size independent: the seed production-by-stem diameter interaction term was not significant, and thus not consistent with a size-dependent somatic cost of reproduction.

Height-dependent increases in hydraulic limitation have been considered as one of the primary drivers of age- or size-related declines in tree growth in contemporary

literature (Ryan et al. 2006; Bond et al. 2007). We found that controlling for seed production, stem diameter did not have any effect on branch extension (Table 2), suggesting that size-related biophysical factors (hydraulic limitation) are not responsible for the decline in extension rates as the trees get larger. Indeed, large diameter (~50 cm DBH) trees that had zero seed production (Fig. 2b) showed identical branch extension rates (~10 cm year^{-1}) to smaller diameter (~20 cm DBH) trees (Fig. 2c). If there were hydraulic limitation effects of tree size on branch extension, large trees that are non-reproductive would be expected to grow more slowly than small, non-reproductive trees. To further substantiate this inference, we fit two separate regressions for branch extension~stem diameter for trees with above and below the average seed production (~5 seeds year^{-1}), respectively. Regression analyses result in two nearly parallel lines, one higher and one lower, indicating that trees with lower than the average seed production had higher branch extension and vice versa (Fig. 2c). Note that although DBH is not a direct measure of transport distance, which could be better reflected by tree height, we found a reasonably high correlation between DBH and tree height ($R^2 = 0.62$, results not shown) in our study system. This led us to choose DBH as a surrogate for transport distance in a tree. Future research could consider tree height as a direct measure of path length.

The results presented here are correlational, not experimental: it is thus critical to consider possible alternative

explanations to observed patterns. Reduced extension growth with tree size could potentially be driven by senescence (e.g., the progressive decline in the physiological functioning of an organism through time: see Day et al. 2001, 2002; Thomas 2010), or by other age-related ontogenetic processes such as increased investment in defenses to combat with pathogens and herbivores (Gross 1972; Tappeiner 1969; Boege and Marquis 2005; Loehle 1988). However, these mechanisms would neither explain an association between reproduction and extension growth at the branch level, nor a recovery in branch extension rates in non-mast years. The reduction in branch growth observed in mast years is instead consistent with a wide range of observations that suggest masting involves large changes in resource allocation from vegetative tissues to reproductive structures (Wallace and Rundel 1979; Tuomi et al. 1982; Norton and Kelly 1988; Obeso 2002; Monks and Kelly 2006).

Annual variation in growth may also reflect confounding variation in environmental factors (temperature and precipitation) that could cause spurious correlations between growth and reproduction (Woodward et al. 1993; Knops et al. 2007; Sanchez-Humanes et al. 2011). For example, in a dendrochronological study of Californian oaks, Knops et al. (2007) found that an apparent negative correlation between acorn output and ring width was driven by opposite responses of growth and reproduction to climatic variables. However, Woodward et al. (1993) reported that environmental factors had positive effects on both growth and reproduction in two conifers (*Abies lasiocarpa* and *Tsuga mertensiana*), which enhanced the relationships (negative correlations) between growth and reproduction. A similar pattern was reported by Monks and Kelly (2006) in a study of *Nothofagus truncata*. Moreover, a meta-analysis of similar studies found no difference in correlations between ringwidths and reproductive measures based on direct correlations, and those correcting for climate variables (Thomas 2011).

The present study focuses on branch extension growth, rather than growth of the main stem or biomass increment of the whole tree. From the perspective of tree resource access and competition, crown extension is critical, determining light interception and lateral capture of canopy gaps (Hibbs 1982; Cole and Lorimer 2005; Purves et al. 2007; Thorpe et al. 2010). Crown extension depends not only on branch extension, but also branch dieback, which we have recently found to increase with tree size in *Acer saccharum* (Hossain and Caspersen 2012). Thus, while we did not directly examine whole-tree diameter or biomass increment in the present study, it seems likely that the net decrease in crown extension would ultimately contribute to decreased whole-tree carbon gain. It is thus reasonable to hypothesize that reduced branch extension growth goes along with reduced growth of main stems.

Masting appeared to have no influence on extension rates in subsequent years, as branch extension rebounded immediately after masting to a level that is similar to pre-mast extension rates (Fig. 3). This result contrasts with some prior findings from dendrochronological studies that masting results in both reduced growth in the mast year and a lagged growth reduction in subsequent years (Kelly and Sork 2002; Monks and Kelly 2006; Silvertown and Dodd 1999). The lack of a lagged growth response in the present study suggests that branch extension in sugar maple does not depend upon resources stored over previous years (Monks and Kelly 2006). As a result, ontogenetic decline in growth may be dependent upon the frequency of masting, which generally increases monotonically with tree size (Thomas 2011, 1996; Kelly and Sork 2002; Obeso 2002; Genet et al. 2010). Over shorter time scales, however, declining growth may not be observed given variability in masting.

In addition, we found that the extension rate of a branch was influenced by the seed production of the branch itself (Fig. 1), but not by seed production on other branches (Table 1), suggesting that the trade-off between growth and reproduction is mediated by resources that are allocated locally. This trade-off is also manifest at the tree level (Fig. 2) simply because the average extension rate of a tree is proportional to the fraction of reproductive branches (regardless of their level of integration), and the amount of reproduction per branch. These findings suggest some degree of independence of individual branches from other parts of the tree in terms of carbon translocation (Sprugel et al. 1991; Despland and Houle 1997; Yasumura 2006).

Reproductive costs have long been considered of central importance in understanding life-history evolution (Stearns 1992), but the physiological mechanisms that result in tradeoffs between reproduction and growth have only recently received closer scrutiny (Harshman and Zera 2007). In short-lived plant species, reproductive effects on growth have not only been recognized to be pervasive, but also to have practical significance for enhancing growth and yield by reducing reproductive costs via genetic engineering (Mouradov and Teasdale 1999; Strauss et al. 1995). The emphasis in the literature on biophysical constraints on tree growth has likely contributed to a lack of research on reproductive costs and possible applications in trees (Strauss et al. 1995; Brunner et al. 2007).

Author contribution statement SMYH, JPC and SCT originally conceptualized the study. SMYH, JPC, and SCT designed the sampling and data collection methods. SMYH conducted fieldwork, including measurement of branch extension growth and seed production, and performed the statistical analyses and result interpretation with JPC and SCT. SMYH wrote the initial draft of the manuscript, which was revised by JPC and SCT.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Appendix 1

A power analysis was conducted to determine the minimum sample size per tree in order to detect a significant trend. First we pulled out data for the largest and smallest tree, and then resampled with replacement to calculate proportion of statistically significant comparisons by a simple t test (results not shown). This analysis showed that a sample of 3–6 branches would provide one a 10% chance of detecting a significant trend, with an assumed effect size value of 0.5 (coefficient of determination). However, the minimum sample size should have been ~40 to achieve a statistical power of 0.8 (Table 3).

Table 3 Tree-level analyses of the relationship between seed production and branch extension, conducted using a subset of the data from trees that are below and above, respectively, the average seed production (~5 seeds year^{-1})

Subset	Model	AICc	ΔAICc
Above	$G_t = \phi + \alpha e^{(-\gamma S_t)}$	107.42	0.00
Above	$G_t = \phi$	112.37	4.95
Below	$G_t = \phi + \alpha e^{(-\gamma S_t)}$	108.26	0.00
Below	$G_t = \phi$	111.44	3.18

G_t is the average extension rate of all the branches in a tree, and S_t is the average seed production of all the branches in a tree

References

Barnard HR, Ryan MG (2003) A test of the hydraulic limitation hypothesis in fast-growing *Eucalyptus saligna*. Plant Cell Env 26: 1235–1245

Bazzaz FA, Ackerly DD, Reekie EG (2000) Reproductive allocation and reproductive effort in plants. In: Fenner M (ed) Seeds: the ecology of regeneration in plant communities, 2nd edn. CAB International, Oxford, pp 1–37

Boege K, Marquis RJ (2005) Facing herbivory as you grow up: the ontogeny of resistance in plants. Tren Ecol Evol 20:520–526

Bond BJ, Ryan MG (2000) Comment on 'Hydraulic limitation of tree height: a critique' by Becker, Meinzer & Wullschleger. Funct Ecol 14:137–140

Bond BJ, Czarnomski NM, Cooper C et al (2007) Developmental decline in height growth in Douglas-fir. Tree Physio 27: 441–453

Bonser SP, Aarssen LW (1994) Plastic allometry in young sugar maple (*Acer saccharum*): adaptive responses to light availability. Am J Bot 81:400–406

Brunner AM, Li JY, DiFazio SP et al (2007) Genetic containment of forest plantations. Tree Gen Geno 3: 75–100

Burnham KP, Anderson DR (1998) Model Selection and Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York

Choi J, Lorimer CG, Vanderwerker J et al (2001) A crown model for simulating long term stand and gap dynamics in northern hardwood forests. For Ecol Manage 152:235–258

Cole WG, Lorimer CG (2005) Probabilities of small-gap capture by sugar maple saplings based on height and crown growth data from felled trees. Can J For Res 35:643–655

Despland E, Houle G (1997) Climate influences on growth and reproduction of *Pinus banksiana* (Pinaceae) at the limit of the species distribution in Eastern North America. Am J Bot 84:928–937

Dick JM, Leakey RRB, Jarvis PG (1990) Influence of female cones the vegetative growth of *Pinus contorta* trees. Tree Physio l6: 151–163

Environment Canada (2004). Canadian Climate Normals 1971–2000. Accessed in 2005.

Filewod B, Thomas SC (2014) Impacts of a spring heat wave on canopy processes in a northern hardwood forest. Glob Chan Bio 20: 360–371

Fox JF, Stevens GC (1991) Costs of reproduction in a willow: experimental responses vs. natural variation. Ecology 72:1013–1023

Genet H, Bréda N, Dufrêne E (2010) Age-related variation in carbon allocation at tree and stand scales in beech (*Fagus sylvatica* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.) using a chronosequence approach. Tree Physio 30: 177–192

Godman RM, Yawney HW, Tubbs CH (1990) *Acer saccharum* (Marsh.) sugar maple. *Silvics of North America. Vol. 2. Hardwoods Agric. Handb. 654* (Burns, Russell M.; Honkala, Barbara H., technical coordinators), Washington DC, U.S. Department of Agriculture, Forest Service, pp 78–91

Gower ST, McMurtrie RE, Murty D (1996) Aboveground net primary production decline with stand age: potential causes. Tren Ecolog Evol Res 11: 378–382

Gross HL (1972) Crown deterioration and reduced growth associated with excessive seed production by birch. Can J Bot 50:2431–2437

Harshman LG, Zera AJ (2007) The cost of reproduction: the devil in the details. Tren Ecol Evol 22:80–86

Hibbs DE (1982) Gap dynamics in a hemlock-hardwood forest. Can J For Res 12:522–527

Hossain SMY, Caspersen JP (2012) In-situ measurement of twig dieback and regrowth in mature *Acer saccharum* trees. For Ecol Manage, 270: 183–188

Iwasa Y (2000) Dynamic optimization of plant growth. Evol Ecol Res 2:427–455

Iwasa Y, Cohen D (1989) Optimal growth schedule of a perennial plant. Am Nat 133:480–505

Kelly D, Sork VL (2002) Mast seeding in perennial plants: why how where? Ann Rev Ecol Sys 33:427–447

King D, Roughgarden J (1982) Graded allocation between vegetative and reproductive growth for annual plants in growing seasons of random length. Theor Pop Biol 21: 1–16

Knops JMH, Koenig WD, Carmen WJ (2007) Negative correlation does not imply a tradeoff between growth and reproduction in California oaks. Proc the Nat Aca Sci, USA 104: 16982–16985

Koch GW, Sillett SC, Jennings GM et al (2004) The limits to tree height. Nature 428:851–854

Kozlowski TT, Clausen JJ (1966) Shoot growth characteristics of heterophyllous woody plants. Can J Bot 44:827–843

Kutsch WL, Wirth C, Kattge K et al (2009) Ecophysiological characteristics of mature trees and stands – consequences for old-growth forest productivity. In: Wirth C, Gleixner G, Heimann M (eds) Old growth forests: function, value and fate. Springer, Berlin, pp 57–69

Loehle C (1988) Tree life-history strategies: the role of defenses. Can J For Res 18:209–222

Luzadis VA, Gossett ER (1996) Sugar Maple. In: Lassoie, JP, Luzadis VA, Grover DW (eds) Forest Trees of the Northeast, Cooperative Extension Bulletin 235, Cornell Media Services, University of Cornell, pp 157–166

McGee CE (1986) Budbreak for Twenty-Three Upland Hardwoods Compared Under Forest Canopies and in Recent Clearcuts. For Sci 32(4): 924–935

Mendez M, Obeso JR (1993) Size-dependent reproductive and vegetative allocation in *Arum italicum* (Araceae). Can J Bot 71:309–314

Monks A, Kelly D (2006) Testing the resource-matching hypothesis in the mast seeding tree *Nothofagus truncata* (Fagaceae). Aust Ecol 31: 366–375

Mouradov A, Teasdale RD (1999) Genetic engineering of reproductive incompetence in radiata pine. Protoplasma 208(1–4):13–17

Norton DA, Kelly D (1988) Mast seeding over 33 years by *Dacrydium cupressinum* Lamb (rimu) (Podocarpaceae) in New Zealand: the importance of economies of scale. Func Ecol 2: 399–408

Obeso JR (2002) The costs of reproduction in plants. New Phyto 155: 321–348

Pinheiro JC, Bates DM (2000) Mixed-effects models in S and S-PLUS. Springer, New York

Purves DW, Lichstein JW, Pacala SW (2007) Crown plasticity and competition for canopy space: a new spatially implicit model parameterized for 250 North American tree species. PLoS One 2:e870

Reekie EG, Bazzaz FA (1992) Cost of reproduction as reduced growth in genotypes of two congeneric species with contrasting life histories. Oecologia 90:21–26

Renner SS, Beenken L, Grimm GW et al (2007) The evolution of dioecy, heterodichogamy, and labile sex expression in Acer. Evolution Int J org Evolution 61:2701–2719

Ryan MG, Binkley D, Fownes JH (1997) Age-related decline in forest productivity: Pattern and Process. Adv Ecol Res 27:214–262

Ryan MG, Phillips N, Bond BJ (2006) The hydraulic limitation hypothesis revisited. Plant Cell Env 29: 367–381

Sanchez-Humanes B, Sork VL, Espelta JM (2011) Trade-offs between vegetative growth and acorn production in *Quercus lobata* during a mast year: the relevance of crop size and hierarchical level within the canopy. Oecologia 166:101–110

Silvertown J, Dodd M (1999) The Demographic Cost of Reproduction and Its Consequences in Balsam Fir (*Abies balsamea*). Am Nat 154:321–332

Sprugel DG, Hinckley TM, Schaap W (1991) The theory and practice of branch autonomy. Ann Rev Ecol Sys 22:309–334

Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford

Steingraeber DA (1982) Heterophylly and Neoformation of leaves in sugar maple (*Acer saccharum*). Am J Bot 69(8):1277–1282

Stephenson NL et al (2014) Rate of tree carbon accumulation increases continuously with tree size. Nature 507:90–93

Strauss SH, Rottmann WH, Brunner AM et al (1995) Genetic engineering of reproductive sterility in forest trees. Mol Breed 1:5–26

Tappeiner JC (1969) Effect of cone production on branch, needle, and xylem ring growth of Sierra Nevada Douglas-fir. For Sci 15: 171–174

Thomas SC (1996) Reproductive allometry in Malaysian rain forest trees: biomechanics versus optimal allocation. Evol Ecol 10:517–530

Thomas SC (2010) Photosynthetic capacity peaks at intermediate size in temperate deciduous trees. Tree Physio 30: 555–573

Thomas SC (2011) Age-related changes in tree growth and functional biology: the role of reproduction. In: Meinzer FC, Dawson T, Lachenbruch BJ (eds) Invited chapter for Size- and age-related changes in tree structure and function, tree physiology, Springer-Verlag, pp 33–64

Thomas SC, Martin AR, Mycroft EE (2015) Tropical trees in a wind-exposed island ecosystem: height-diameter allometry and size at onset of maturity. J Ecol 103:594–605

Thorpe HC, Astrup R, Trowbridge A et al (2010) Competition and tree crowns: a neighborhood analysis of three boreal tree species. For Ecol Manage 259: 1586–1596

Tuomi J, Neimela P, Mannila R (1982) Resource allocation on dwarf shoots of birch (*Betula pendula*) – reproduction and leaf growth. New Phyto 91: 483–487

United States Department of Agriculture (USDA) (2008) Woody Plant Seed manual. USDA Forest Service, Agriculture Handbook 727

Wallace CS, Rundel PW (1979) Sexual dimorphism and resource allocation in male and female shrubs of *Simmondsia chinensis*. Oecologia 44:34–39

Watson GW, Himelick EB, Smiley ET (1986) Twig growth of eight species of shade trees following transplanting. J Arbori 12(10):241–245

Weiner J, Thomas SC (2001) The nature of tree growth and the age-related decline in forest productivity. Oikos 94:374–376

Wheelwright NT, Logan BA (2004) Previous-year reproduction reduces photosynthetic capacity and slows lifetime growth in females of a neotropical tree. Proc Nat Aca Sci USA 101: 8051–8055

Woodruff DR, Bond BJ, Meinzer FC (2004) Does turgor limit growth in tall trees? Plant Cell Env 27: 229–236

Woodward A, Silsbee DG, Schreiner EG et al (1993) Influence of climate on radial growth and cone production in subalpine fir (*Abies lasiocarpa*) and mountain hemlock (*Tsuga mertensiana*). Can J For Res 24:1133–1143

Worley AC, Harder LD (1996) Size-dependent resource allocation and costs of reproduction in *Pinguicula vulgaris* (Lentibulariaceae). J Ecol 84:195–206

Yasumura Y, Hikosaka K, Hirose T (2006) Resource allocation to vegetative and reproductive growth in relation to mast seeding in *Fagus crenata*. For Ecol Manage 229: 228–233

Yoder BJ, Ryan MG, Waring RH et al (1994) Evidence of reduced photosynthetic rates in old trees. For Sci 40: 513–527