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Age-class differences in shoot photosynthesis and water relations of Fraser fir (*Abies fraseri*), southern Appalachian Mountains, USA

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Abstract: Fraser fir (*Abies fraseri* (Pursh) Poir.) is an endemic tree species found only in refugial mountain-top forests in the southern Appalachian Mountains, USA. Very few studies have investigated the ecophysiology of this species in its natural environment. We measured and compared photosynthetic gas exchange and water relations of understory germinating seedlings (<3 cm height), older seedlings (>3 years old and ~0.15–1 m tall), and saplings (>10 years old and ~1–2 m tall) on a leaf-level basis. No significant differences in gas exchange were found among the age classes, although midday xylem water potentials were significantly different among the age classes. Differences in maximum photosynthesis (A_{\max}) were <13%, ranging between 2.4 and 2.7 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ($P = 0.26$). Maximum leaf conductances (g_{\max}) were between 0.16 and 0.18 $\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, varying less than 13% ($P = 0.15$). Midday xylem water potentials were similar between SE and SA (–1.2 to –1.4 MPa), but GS values were significantly less negative (–0.2 to –0.5 MPa). Thus, gas exchange and water relations in these understory age classes appeared similar, indicating no particular limitation to advanced regeneration between age classes.

Résumé : Le sapin de Fraser (*Abies fraseri* (Pursh) Poir.) est une espèce d'arbre endémique dans les forêts refuges sur le sommet des montagnes dans la partie sud des Appalaches, aux États-Unis d'Amérique. Très peu d'études se sont intéressées à l'écophysologie de cette espèce dans son environnement naturel. Nous avons mesuré et comparé les échanges gazeux liés à la photosynthèse et les relations hydriques sur la base des aiguilles des semis en voie de germination (GS, hauteur <3 cm), des semis plus vieux (SE, >3 ans et ~0,15–1 m de haut) et des jeunes tiges (SA, >10 ans et ~1–2 m de haut) dans le sous-bois. Aucune différence significative dans les échanges gazeux n'a été observée entre les différentes classes d'âge malgré les différences significatives entre les différentes classes d'âge dans le cas du potentiel hydrique du xylème à midi. Les différences dans la photosynthèse maximum (A_{\max}) étaient inférieures à 13% et variaient de 2,4 à 2,7 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ($P = 0,26$). La conductance foliaire maximum (g_{\max}) variait de 0,16 à 0,18 $\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, soit une variation de moins de 13% ($P = 0,15$). Le potentiel hydrique du xylème à midi des SE et des SA était semblable (–1,2 à –1,4 MPa) mais les valeurs des GS étaient significativement moins négatives (–0,2 à –0,5 MPa). Par conséquent, les échanges gazeux et les relations hydriques dans ces classes d'âge en sous-bois semblent similaires indiquant qu'il n'y a aucune contrainte particulière chez la régénération préétablie quelle que soit la classe d'âge.

[Traduit par la Rédaction]

Introduction

Fraser fir (*Abies fraseri* (Pursh) Poir.) is an endemic tree species found only in seven mountain-top populations occurring from southwestern Virginia to southern North Carolina, USA (Ramseur 1960). Over the past half century, substantial mortality has been reported for adult Fraser fir and is attributed to a variety of factors, such as acidic deposition, climate change, logging, fires, and (or) introduced pests, such as the balsam woolly adelgid (*Adelges piceae* (Ratzeburg)) (White

1984; Arthur and Hain 1986; Bruck and Robarge 1988; Busing et al. 1988; McLaughlin et al. 1990; White and Cogbill 1992). This mortality has caused long-term changes in community composition and ecosystem dynamics.

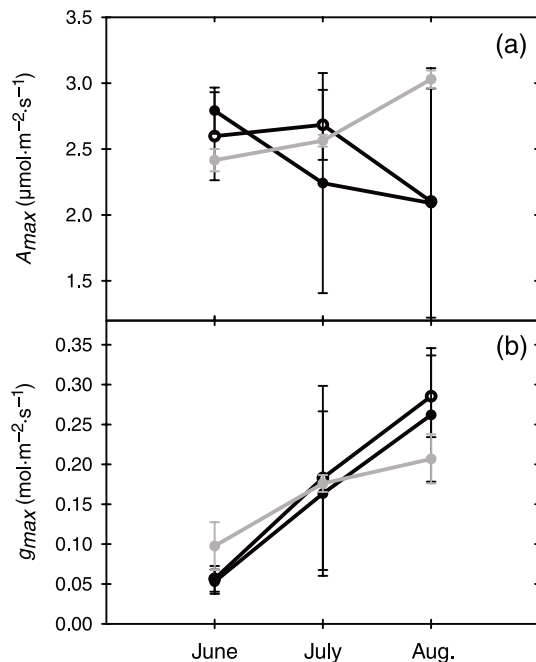
Most studies evaluating Fraser fir decline in the southern Appalachians have focused on population biology, emphasizing long-term changes in age-class distribution and community structure (Busing et al. 1988; Pauley and Clebsch 1990; Dale et al. 1991; Potter 2006). Very few studies have evaluated the ecophysiology of this species in natural stands

Received 2 October 2008. Accepted 17 October 2008. Published on the NRC Research Press Web site at cjfr.nrc.ca on 17 December 2008.

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Fig. 1. Daily (a) maximum photosynthesis (A_{\max}) and (b) maximum leaf conductance (g_{\max}) on measurement days for germinant seedlings (gray circles), seedlings (black circles), and saplings (open circles). Vertical bars are 95% confidence intervals.



(Johnson and Smith 2005, 2006; Reinhardt and Smith 2008a, 2008b), and no studies that we know of have investigated differences between age classes of this species. Understanding the differences in physiological response to the environment at the age-class level is critical to identifying current limitations to successful natural regeneration in this potentially vulnerable species.

The goal of the present study was to quantify differences in photosynthetic gas exchange and water relations in Fraser fir for three juvenile sizes and (or) age classes (germinant seedlings, older seedlings, saplings). Because juvenile age classes may be more sensitive to environmental stress than mature trees (Kohyama 1983; Smith et al. 2003; Howe et al. 2004; Greenwood et al. 2008), understanding the direct ecophysiological impacts on plant productivity may help to identify potential life-stage bottlenecks and enable early predictions about ultimate regeneration. This particular approach has important implications for successful forest regeneration in these relic spruce–fir forests because of the continuing attacks by the balsam woolly adelgid on more mature trees (Eagar 1984). Finally, these forests may be particularly vulnerable to global climate change effects, such as warming temperatures and altered precipitation regimes.

Materials and methods

Photosynthetic gas exchange and water relations were compared for three of the smallest (youngest) size classes of understory Fraser fir under natural conditions. These measurements were used to evaluate the maximum photosynthetic performance and possible water stress throughout the growing season. Data for adult understory trees reported in the literature (K. Reinhardt and W.K. Smith, unpublished

data; Bernier et al. 2001) were compared with that of the youngest life stages, e.g., current year to <3 years old.

Study sites

The data reported here were compiled from two different field seasons. In the first field season (2004), one 25 m² study site was established at Roan Mountain, North Carolina (Pisgah National Forest, 36°5'N, 82°8'W, 1900 m). In 2006, two study sites (25 m² each) were established in Pisgah National Forest and Mount Mitchell State Park at the summits of Richland Balsam (35°22'N, 82°59'W, 1847 m) and Mount Mitchell (35°46'N, 82°16'W, 2028 m), respectively. All of these field sites are predominately red spruce (*Picea rubens* Sarg.) and Fraser fir (*A. fraseri*) forest, with fir the dominant species at all sites. These sites were selected as representative of the most common stand structure found in these forests (Pitillo and Smathers 1979; Bruck and Robarge 1988; Goelz et al. 1999), i.e., with tree ages ranging from young seedlings (<0.05 m tall and <5 years old) to mature, old-growth spruce trees (diameter at breast height >0.3 m, and >200 years old) within a relatively open canopy (<25% overstory canopy, determined from hemispherical photographs).

Photosynthesis and water relations

Diurnal gas exchange measurements were made on randomly selected individuals ($N = 5$ for each measurement time) on the previous year's shoots at mid-tree height (for nongerminant seedlings). Study trees were divided into three size classes: germinant seedlings (GS, 1st year, <3 cm), seedlings (SE, 0.15–1 m), and saplings (SA, 1–2 m). Photosynthetic gas exchange of understory trees was measured with a LI-COR LI-6400 model portable photosynthesis system (LI-COR Inc., Lincoln, Nebraska) and was calculated on a total leaf area basis, even under full-sun exposure, because of the high silhouette to projected area ratio of the shoots of these understory plants (Smith et al. 1991). For GS (1st year), an LED chamber was used (LI-COR Model 6400-02B) as a light source; for the larger size classes (SE and SA) a clear conifer chamber was used with ambient sunlight conditions (LI-COR Model 6400-05). Gas exchange measurements using the LED chamber in a greenhouse were comparable to those using the conifer chamber under ambient sunlight (within $\pm 4\%$). Natural orientation of shoots was maintained during measurements, and air temperature and relative humidity inside the leaf chamber were maintained within $\pm 5\%$ of ambient values.

Diurnal photosynthesis measurements were combined to create integrated light response curves for photosynthesis for all three size classes. Photosynthetic light response parameters (e.g., photosynthesis at saturating light levels, apparent quantum efficiency (AQE, and light saturation point for photosynthesis) were calculated using Photosyn Assistant (ver. 1.1.2, Dundee Scientific, Dundee, UK). Maximum photosynthesis (A_{\max}) and leaf conductance (g_{\max}) were calculated as the mean of the five highest values at saturating sunlight levels.

Midday xylem water potentials (Ψ) were measured with a Scholander-type pressure chamber (Model 1000, PMS Instrument Co., Corvallis, Oregon) on individuals adjacent to those used for gas exchange measurements ($N = 10$ for each

Table 1. Comparison of leaf gas exchange measurements for different life stages of understory trees.

Life stage	A_{\max} ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	g_{\max} ($\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Afternoon Ψ (MPa)
Germinant seedling	2.3 – 2.4	0.11 – 0.21	–0.2 – –0.5
Older seedling	2.2 – 2.8	0.09 – 0.23	–1.3 – –1.4
Sapling	2.2 – 2.7	0.13 – 0.15	–1.2 – –1.4
Adult	3.0 \pm 0.2*, 4.3 \dagger		

Note: A_{\max} , maximum photosynthesis; g_{\max} , maximum leaf conductance; and Ψ , water potential. In this study germinant seedlings are defined as <1 year old, seedlings are <1 m tall, saplings are 1–2.5 m tall, and adults are >2.5 m. Numbers are ranges, except for the adult life stage.

*From K. Reinhardt and W.K. Smith (unpublished).

\dagger From Bernier et al. 2001.

Table 2. Photosynthetic light response of understory trees.

Month	Age class	A_{sat} ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	AQE	LSP ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)
June	Germinant seedling	2.40	0.0340	96
	Seedling	2.30	0.0172	194
	Sapling	2.20	0.0116	213
July	Germinant seedling	2.40	0.0246	98
	Seedling	2.80	0.0154	174
	Sapling	2.20	0.0100	249
August	Germinant seedling	2.60	0.0329	95
	Seedling	2.40	0.0080	365
	Sapling	2.30	0.0072	334

Note: A_{sat} , saturation photosynthesis; AQE, apparent quantum efficiency; and LSP, light saturation point to achieve A_{sat} . All parameters were computed using the best-fit light response equation $y = a(1 - e^{-bx})$, where y is photosynthesis (A), x is photosynthetic photon flux density, and a and b are fitted constants (see Table 2). $N = 19$ to 41 for all regressions. $P < 0.001$ for all regressions.

species) at 1400 hours on the same days as photosynthesis measurements. For measurements, 10 cm shoot tips were excised from the previous year's shoots at mid-tree height for SE and SA, while entire seedlings (excised at the soil surface) were used for GS water potential measurements.

Statistics

All data sets were tested for statistical assumptions of normality and equality of variance. Monthly gas exchange measurements and shoot water potentials were averaged by time of measurement. Best-fit regression analysis was used to generate response curves of photosynthesis to photosynthetic photon flux density values measured throughout the day. Age-class differences in gas exchange measurements were averaged by day and evaluated using single-factor ANOVA methods, with significance set at $P < 0.05$. Statistical analyses were performed using JMP Statistical Analysis Software (ver. 3.2.2, SAS Institute Inc., Cary, North Carolina).

Results

Photosynthetic gas exchange

For all months, the daily (A_{\max} values for SA (2.2–2.7 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) were not significantly different from that of SE or GS (Fig. 1a). The mean A_{\max} values during the

study were 2.5 ± 0.2 , 2.4 ± 0.2 , and 2.7 ± 0.2 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for SA, SE, and GS, respectively (Table 1; $P = 0.26$). There was also no significant difference in the daily g_{\max} values among the three size classes (0.09–0.25 $\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for SA compared with 0.09–0.23 $\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for SE and 0.10–0.21 $\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for GS; Fig. 1b) across all months ($P = 0.15$). The mean g_{\max} values during the study period were 0.18 ± 0.06 , 0.16 ± 0.06 , and 0.16 ± 0.03 for SA, SE, and GS, respectively (Table 1). The mean light saturation point of the photosynthetic light response curve was 265 ± 36 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for SA, 244 ± 71 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for SE, and 96 ± 1 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for GS (Table 2; Fig. 2). Mean photosynthesis at saturating light levels (A_{sat}) was 2.2 ± 0.01 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, 2.5 ± 0.02 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, and 2.5 ± 0.01 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for GS, SE, and SA, respectively (Table 1; Fig. 2).

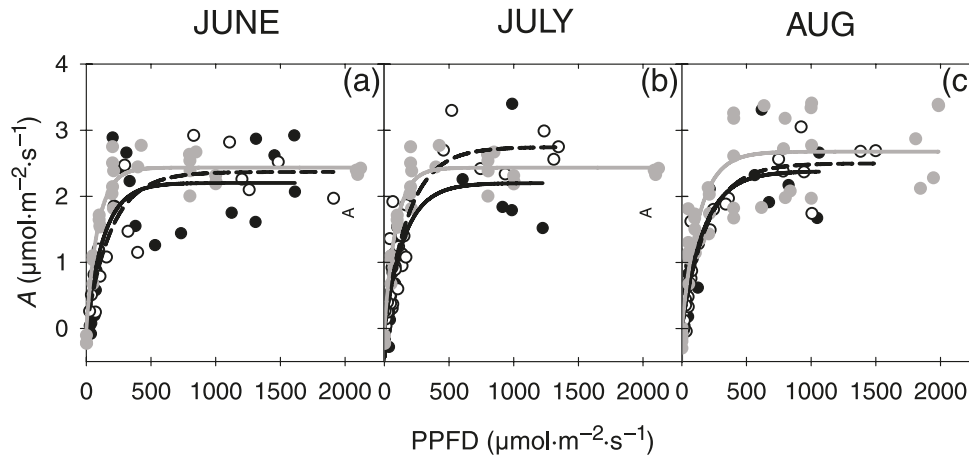
Plant water status

Midday Ψ of GS were significantly less negative than that of SE and SA throughout the summer ($P < 0.01$; Table 1). GS Ψ ranged from –0.2 to –0.5 MPa, while SE Ψ and SA Ψ were between –1.2 and –1.4 MPa.

Discussion

Few studies have investigated the ecophysiology of Fraser

Fig. 2. Photosynthetic light response curves for June (a), July (b), and August (c) measurement days of germinant seedlings (gray circles), older seedlings (black circles), and saplings (open circles). Regression lines: germinant seedlings (solid gray line), older seedlings (solid black line), and saplings (broken black line). $P < 0.0001$ for all regressions.



fir in natural stands (Johnson and Smith 2005; Reinhardt and Smith 2008a, 2008b). Additionally, little is known about the relative physiological performance of younger understory life stages, e.g., germinant seedlings, seedlings, and saplings. Physiological differences may exist among different age classes of trees because of ontogenetic and environmental changes as individuals mature. For example, very young seedlings can lack fully expanded lateral branches and may devote most assimilation to new needle growth (Kohyama 1983). Also, there are usually substantial differences in natural sunlight regimes and, therefore, in shade tolerance between seedlings and adult trees (Kobe et al. 1995). It has also been shown that in general, leaf-level photosynthetic capacity (on a leaf mass basis) and hydraulic capabilities appear to decrease with tree age class (Ryan and Yoder 1997; Niinemets 2002; Thomas and Winner 2002; Winner et al. 2004). Most previous studies have only compared saplings with adults, with less research focusing on the physiology of younger, smaller life stages (Thorton et al. 1994; Germino and Smith 1999; Johnson and Smith 2005, 2008; Greenwood et al. 2008).

In Fraser fir, we found no significant differences in photosynthetic gas exchange among GS, SE, and SA size classes when measured at the leaf level. A_{\max} , A_{sat} , and g_{\max} were similar for all size classes for all months, except for A_{\max} and A_{sat} in GS in August (Figs. 1 and 2, Tables 1 and 2). However, differences in photosynthetic performance were evident. The apparent quantum efficiency of GS was as much as threefold greater than that of SE and SA, and the light saturation point of GS was 55%–75% lower than that of SE and SA (Table 2), underscoring important differences in photosynthetic mechanisms among age classes of understory fir. These differences in photosynthetic performance may be due to differences in sunlight interception among the age classes or may be indicative of developmental or physiological (for example, sun versus shade needles) differences between cotyledons and primary needles, which no research has addressed, to our knowledge.

While there were no significant differences in photosynthetic gas exchange at the shoot level, differences in plant water status were evident. Midday Ψ were higher (less negative) for GS during all summer months (Table 1). Since hydraulic demands with increased tree size would be

insignificant among these size classes of trees (~ 0.01 MPa·m⁻¹; hydraulic limitation hypothesis, Ryan and Yoder 1997), the increased Ψ for GS was most likely related to the reduced sunlight exposure of trees of the smaller age class in the study. Reinhardt and Smith (2008a) showed that the low vapor pressure deficit and the often cloudy conditions of southern Appalachian forests exert a strong positive influence on photosynthetic gas exchange and water relations of understory Fraser fir saplings. The humid conditions and low solar radiation at ground level may have lowered transpirational demand and, combined with wet soils, may have allowed GS plants to maintain a higher water status than trees of the taller size classes.

Comparing our results with previous research on other life stages of Fraser fir, we know of no published studies that have measured the photosynthetic gas exchange of adult Fraser fir understory trees in natural stands. However, Bernier et al. (2001) reported an A_{\max} of $4.3 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for adult understory balsam fir (*Abies balsamea* (L.) Mill.), which is greater than an A_{\max} of $3.0 \pm 0.2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for adult Fraser fir understory trees (K. Reinhardt and W.K. Smith, unpublished data) and $1.5 \pm 0.2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for 3- to 5-year-old seedlings (Johnson and Smith 2008) (Table 1). Additionally, Thomas and Winner (2002) reported A_{\max} values ranging from 2.4 to $7.0 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for adult understory western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and $4.1 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for saplings. Thus, the values reported here appear similar to the few previous findings.

Differences in gas exchange and water relations among size classes may provide insight to identifying specific physiological bottlenecks to advanced regeneration and corresponding environmental limitations important for understanding future forest sustainability, especially, within the context of current global change scenarios, such as warming temperatures and changing precipitation patterns. More research is also underway to elucidate the environmental variables that may be limiting to specific life stages on an intra- and inter-annual basis. Identifying life stage vulnerability, as indicated by low photosynthetic carbon gain, may enable early detection of future regeneration bottlenecks.

Acknowledgments

This research was supported by a grant from the William and Flora Hewlett Foundation to WKS. We thank the National Park Service (Blue Ridge Parkway) and Mount Mitchell State Park for permission to conduct research in their areas. We are especially grateful to Dr. Robert Browne for discussion and insightful comments.

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