

# Hydraulic limitation on maximum height of *Pinus strobus* trees in northern Minnesota, USA

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## Abstract

**Key message** Using comparisons within and between trees, the authors show evidence for hydraulic limitation of tree height in a humid-climate species that is far from the global maximum tree height.

**Abstract** We measured water status and two indicators of drought stress as a function of height within the canopies of four tall (32–35 m) eastern white pines (*Pinus strobus*) at an old-growth site in northern Minnesota, USA. Pre-dawn and midday xylem pressure potential measured on terminal shoots ( $\Psi_{\text{shoot}}$ ), needle length, and foliar carbon isotope discrimination ( $\delta^{13}\text{C}$ ) all showed within-canopy gradients consistent with increasing drought stress with height. Midday  $\Psi_{\text{shoot}}$  near tree tops was  $-1.8$  MPa, close to values associated with stomatal closure for other temperate conifers. Pre-dawn  $\Psi_{\text{shoot}}$  decreased with height at  $>2\times$  the gradient in gravitational potential.  $\delta^{13}\text{C}$  was strongly correlated with height and weakly correlated with light. Needles were 15–25 % shorter at canopy top compared to the bottom of the canopy. Midday  $\Psi_{\text{shoot}}$  and needle length showed significant differences in regression model coefficients from tree to tree. The patterns are consistent with hydraulic constraints on height growth of white pine at this site.

**Keywords** Hydraulic limitation · *Pinus strobus* · Xylem pressure potential · Carbon isotope discrimination

## Introduction

Light competition in forests puts a premium on height growth in trees, in both evolutionary and successional time (King 1990). In spite of the strong competitive advantage of being tall, height growth slows down as it approaches a maximum that is characteristic of the species and the site (Ryan et al. 2006). A number of causes of height limitation have been proposed, including increased respiratory burden, structural instability, and hydraulic limitation (Friend 1993, Ryan and Yoder 1997). Of these, hydraulic limitation—decreasing water supply with height—has the broadest empirical support (Ryan et al. 2006). As height increases, water supply is increasingly limited by two factors: the difference in gravitational potential between the soil and the top of the canopy (purely a function of height), and the frictional resistance of water flow in xylem (which depends on the total length of xylem pathways in trunk and branches).

Water supply could limit maximum tree height by three distinct but not mutually exclusive mechanisms. In the first mechanism, if xylem pressure potential at the leaves or terminal shoots ( $\Psi_{\text{shoot}}$ ) falls below a critical value, stomata close, limiting carbon uptake, and thereby limiting either whole tree assimilation or at least local assimilation at the top of the canopy. This is the mechanism of hydraulic limitation originally proposed by Friend (1993) and Ryan and Yoder (1997). Critical  $\Psi_{\text{shoot}}$ , at which complete or substantial partial stomatal closure occurs, ranges from  $-1.5$  to  $-2.2$  MPa for a range of temperate conifers (Bond and Kavanagh 1999; Graham and Running

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1984; Lopushinsky 1969; Pavlik and Barbour 1991; Teskey et al. 1987). To the extent that extension growth is dependent on locally assimilated carbon, stomatal closure could limit height growth directly, or height growth could be regulated in relation to the overall carbon balance of the tree (Sala et al. 2012). Evidence in support of this mechanism includes within-tree gradients of foliar carbon isotope discrimination ( $\delta^{13}\text{C}$ ), and maximum assimilation rate  $A_{\text{max}}$  (Koch et al. 2004; Ryan et al. 2006; Ishii et al. 2008; but see Sala and Hoch 2009). In the second mechanism, if stomata do not close at extreme xylem tensions, runaway embolism may occur, causing crown dieback (Tyree and Sperry 1989). This may be difficult to distinguish from other causes of damage in the upper canopy, such as wind. In the third mechanism, lowered  $\Psi_{\text{shoot}}$  in the top of the canopy could directly limit leaf and shoot growth by lowering turgor pressure below the elastic yield limit, thereby limiting cell wall expansion (Friend 1993). Both turgor pressure and cell wall elastic yield are biochemically regulated (Morgan 1984; Van Volkenburgh 1999), so the possibility of a simple and general relationship stemming from the turgor pressure mechanism seems remote, but Woodruff et al. (2004) observed height-related gradients of turgor and organ expansion in Douglas-fir trees, and Koch et al. (2004) found strong vertical gradients of leaf morphology in redwoods that were consistent with turgor-limited leaf expansion.

Drought stress indicators may be measured in relation to height in two distinct study designs: comparisons between trees of different heights (usually based on measurements at the tops of canopies), and comparisons within individual tree canopies. Each design controls for different sets of potential confounding variables. Measurements at the tops of different trees, especially when the trees are all canopy dominants, control for within-canopy differences in light availability and wind—both of which can affect correlates of drought stress (Ambrose et al. 2009). Measurements within individual canopies control for genetic differences, variations in soil conditions, and variations in root architecture (Ryan et al. 2006). Measurements at multiple canopy positions within multiple trees allow assessment of both sources of variation.

Hydraulic limitation is easiest to measure on older trees, which have had sufficient time to approach their maximum height, and is probably most likely in the tallest species within a given region. Eastern white pine, *Pinus strobus*, is the tallest tree species in eastern North America, capable of exceeding 45 m in height, and commonly lives for more than two centuries (Burns and Honkala 1990), with some trees exceeding four centuries. It is moderately shade tolerant, but persists in many forests for long periods as a canopy emergent.

This study tested predictions of the hydraulic limitation hypothesis in *P. strobus* trees growing near the

northwestern range limit of this species in northern Minnesota, USA. We measured gradients of growing season water status (pre-dawn and midday  $\Psi_{\text{shoot}}$ ) and two potential signatures of drought stress—needle length and carbon isotope discrimination ( $\delta^{13}\text{C}$ )—within the canopies of four tall white pine trees. The trees were close to the maximum height reported for *P. strobus* in the region. We also measured two possible complicating variables: soil water potential ( $\Psi_{\text{soil}}$ ) around the study trees, and the light environment at needle sampling points. Two predictions of the hydraulic limitation hypothesis were tested: (1) shoot xylem pressure potential, needle length, and  $\delta^{13}\text{C}$  will all indicate increasing drought stress with height within the canopies; and (2)  $\Psi_{\text{shoot}}$  and  $\delta^{13}\text{C}$  will approach extreme values near the canopy tops.

## Methods

### Study site and sample trees

The study was carried out in the lost 40 Scientific and Natural Area, an old-growth forest preserve in northern Minnesota (47°46'N, 94°5'W). The preserve has some of the oldest and tallest eastern white pine (*P. strobus*) in Minnesota, approaching the regional maximum height of ca. 40 m (Lee Frelich, pers. comm.). White pines in this area are within 150 km of the western range limit and 350 km of the northern range limit of the species (Burns and Honkala 1990). The stand is dominated by large canopy-emergent white pines and red pines (*P. resinosa*), over a mixture of *Acer rubrum*, *Populus tremuloides*, *Abies balsamea*, *Betula papyrifera*, and small numbers of other species. Based on data from ten 10 × 10 m plots (M. Johnson, unpublished), red and white pines (mean dbh = 59 cm) have a basal area density of 76 m<sup>2</sup> ha<sup>-1</sup> and a stem density of 230 trees ha<sup>-1</sup>. The remaining species (dbh <35 cm) have a total basal area density of 17 m<sup>2</sup> ha<sup>-1</sup> and a stem density of 690 trees ha<sup>-1</sup> (for stems >5 cm dbh). Climate is continental, with a mean annual temperature of 4 °C, and annual precipitation of 669 mm (data for the period 1971–2000 from weather station at Big Falls, MN, USA located 55 km NNE of the study site, [www.ncdc.noaa.gov](http://www.ncdc.noaa.gov)). Soils are developed on glacial moraine deposits, with a sandy loam texture class (69–81 % sand, 13–17 % clay), and 2–7 % organic matter in the surface horizons. Topography is gentle, with slopes of <8 % throughout the area sampled.

We selected four trees for sampling by the following criteria: height  $\geq 32$  m (approaching the regional maximum height of ca. 40 m), a crown ratio  $\geq 0.4$  (to ensure an adequate range of sampling heights within a tree), and mechanical integrity (to ensure safety in canopy access). One of the four trees was found to have a large fracture in

the trunk, making it unsafe to climb in windy conditions, and was only sampled for pre-dawn and midday xylem pressure potential. Canopy access for sampling employed standard rope-assisted methods (Moffett and Lowman 1995), which do not damage the tree. We measured heights of sample points by dropping a weighted end of a fiberglass tape to the ground. During measurement of midday  $\Psi_{\text{shoot}}$ , we also measured the distance from the sample point to the base of the branch on which it was located; in the analysis that follows, the sum of this distance and the height to the branch base (“path length”) was taken as an approximation of the length of the xylem pathway from soil surface to shoot.

Pre-dawn and midday  $\Psi_{\text{shoot}}$ , and  $\Psi_{\text{soil}}$

Xylem pressure potentials ( $\Psi_{\text{shoot}}$ ) were measured on terminal shoots (Boyer 1969) using a PMS Model 1000 pressure bomb (PMS Industries, Albany, OR, USA). *Pinus strobus* retains needles for 2–3 years, with most needles retained for at least 2 years (Ewers and Schmid 1981, pers.obs.). Shoots were cut 1–2 cm proximal to (toward the tree trunk in relation to) the oldest needles. Sampling was done at 1–2 m intervals from the highest accessible point (generally within 1–2 m of the top) to the bottom of the canopy of each tree. Shoots were placed in plastic bags, lowered to the ground, and measured within 3 min of sampling. Shoots of white pine contain resin ducts, which complicate determination of the pressure endpoint, so a modification of a procedure by McGilvray and Barnett (1988) was used. The resin was wiped repeatedly with a piece of paper towel during pressurization (using fresh surfaces of the paper towel for each wipe), and the endpoint was detected when water visibly penetrated the towel. Pre-dawn measurements were done between 90 and 30 min before dawn, and midday measurements were done between 11 A.M and 3 P.M. All measurements were done in late June and early July, after needle expansion was complete but before the onset of late summer water deficits that commonly occur in this climate.

To account for possible tree to tree differences in  $\Psi_{\text{shoot}}$ , we measured soil water potential ( $\Psi_{\text{soil}}$ ) around each tree using a Quickdraw 2900 tensiometer (Soilmoisture Equipment Corp., Santa Barbara, CA, U.S.A.). Measurements of  $\Psi_{\text{soil}}$  were taken in the four cardinal directions around the base of each tree at distances of 1, 2, and 3 m from the trunk; and at depths of 2, 10 and 30. The average of these values was taken as an estimate of  $\Psi_{\text{soil}}$  in the main rooting volume of the tree, although we recognize that large trees have access to deeper soil layers as well. Analyses of  $\Psi_{\text{shoot}}$  described below were repeated on  $\Psi_{\text{shoot}} - \Psi_{\text{soil}}$ , and model fit statistics were compared to determine if  $\Psi_{\text{soil}}$  explained any variation in  $\Psi_{\text{shoot}}$ .

Needle length and  $\delta^{13}\text{C}$ , GSF

Near the end of the growing season, terminal shoot samples were taken in the three mechanically sound trees for determination of needle length and carbon isotope determination. Samples were taken over the entire range of the canopy at 1–2 m intervals. Two terminal shoots were taken within a few centimeters of each other on the same branch, and cut 1–2 cm proximal to the oldest (2–3 year old) needles. Needle samples were air dried before further measurements. To estimate differences in growing season light environment, a canopy hemispherical photo was taken at each sample location using a Nikon Coolpix 950 digital camera with fisheye lens.

Air-dried distal (current year) needles from one of the shoot samples at each location were ground, packed into capsules, and sent to the stable isotope laboratory of North Carolina State University (Raleigh, North Carolina, USA) for determination of  $\delta^{13}\text{C}$ .

For needle length measurements, two fascicles were taken from the distal end (current year needles) and two from the proximal end (previous year needles) of each air-dried shoot. All 5 needles from each fascicle were measured, and an average length for distal and proximal needles was calculated for each shoot.

Each canopy photograph was processed to extract the blue color channel (this gave the strongest contrast between sky and canopy), and the brightness threshold for sky/canopy was determined using the edge-detection algorithm of Nobis and Hunziker (2005). The global site factor (GSF), an estimate of the proportion of total direct and indirect solar radiation at a point (relative to full sun), was calculated using the program HemiView (version 2.1, Dynamax Inc., Houston, Texas, USA). GSF is intended to be a measure of the light environment of a point integrated over the growing season (Rich et al. 1993).

Data analysis

We used regression analysis, with model selection (Johnson and Omland 2004) to choose the best combinations of predictor variables. For pre-dawn and midday  $\Psi_{\text{shoot}}$ , possible predictor variables included height, estimated path length, and tree ID. Tree ID was treated as a random effect, so the models including it were fitted as mixed models, with tree ID treated as an additive factor (affecting the intercept) or an interactive factor (affecting both the slope and intercept). The analysis was repeated on  $\Psi_{\text{shoot}} - \Psi_{\text{soil}}$ , to account for possible differences in soil water potential in the rooting zone of each tree. For needle length and  $\delta^{13}\text{C}$ , possible predictor variables included height, GSF, and tree ID. As above, tree ID was considered as either an additive or interactive factor with height.

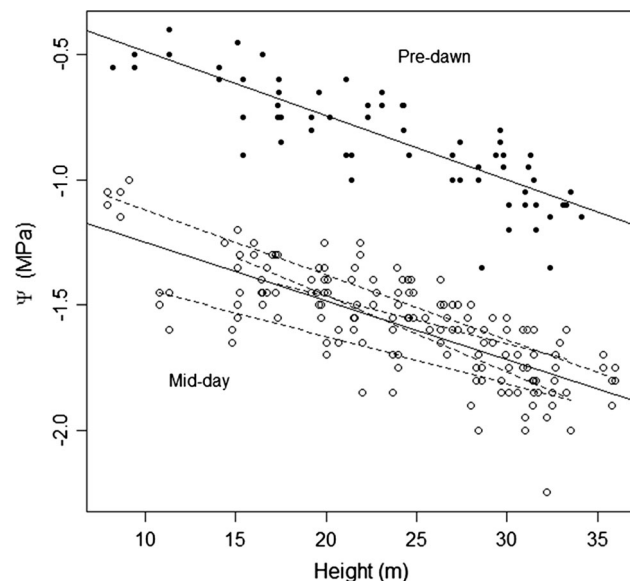
Models were compared using the Akaike Information Criterion, or AIC (Hilborn and Mangel 1997; Johnson and Omland 2004), which balances model fit and complexity. Inferences about model performance are based on differences between AIC among models of a given data set, not the absolute magnitude of AIC (Burnham and Anderson 2002), so we report  $\Delta(\text{AIC})$  values, which are obtained by subtracting the lowest AIC from the AIC of all the models. The model with the best empirical support then has a  $\Delta(\text{AIC})$  of 0, models with a high degree of empirical support have  $0 \leq \Delta(\text{AIC}) < 2$ , and models with essentially no empirical support have  $\Delta(\text{AIC}) > 10$ .

Analyses were carried out using the R statistical software package (R version 2.15.0, R Development Core Team 2005). Linear mixed-effects models were fitted with the R package lme4, using the default REML (restricted maximum likelihood) criterion.

## Results

Water status: pre-dawn and midday  $\Psi_{\text{shoot}}$

Pre-dawn  $\Psi_{\text{shoot}}$  was strongly related to height, and midday  $\Psi_{\text{shoot}}$  was strongly related to height and path length for (Fig. 1; Table 1). Average pre-dawn  $\Psi_{\text{shoot}}$  ranged from  $\sim -0.5$  MPa in the lower tree canopies, to  $\sim -1.0$  MPa in



**Fig. 1** Midday (open circles) and pre-dawn (filled circles)  $\Psi$  as a function of height. The best model for pre-dawn  $\Psi$  was a simple linear function of height (upper line). The best model of midday  $\Psi$  was a mixed model of height (shown) or path length (fig. 2); the fixed effect is indicated by the solid line, and the dashed lines show the predictions for the individual trees

**Table 1** Statistics for model fits of (a) pre-dawn and (b) midday xylem water potential

Model	<i>df</i>	$\Delta(\text{AIC})$	RMSE
(a) Pre-dawn $\Psi$ ( $N = 80$ )			
Null model	2	98.30	0.2160
Height	3	0	0.1154
Height + (1   tree ID)	4	8.71	0.1017
Height + (height   tree ID)	6	6.58	0.0942
(b) Midday $\Psi$ ( $N = 163$ )			
Null model	2	180.45	0.2127
Height	3	42.60	0.1385
Path	3	45.12	0.1396
Height + path	4	43.32	0.1380
Height + (1   tree ID)	4	5.09	0.1112
Path + (1   tree ID)	4	3.55	0.1106
Height + (height   tree ID)	6	0.29	0.1056
Path + (path   tree ID)	6	0	0.1054

The predictor variables height (above ground surface in m) and path (height plus distance from trunk in m) are treated as fixed effects. Tree ID is treated as a random effect, so that the models including it are mixed-effects models. In the “height + (1 | tree ID)” and “path + (1 | tree ID)” models, the slope is the same for all trees, but the intercept varies by tree ID. In the “height + (height | tree ID)” and “path + (path | tree ID)” models, both slope and intercept vary with tree ID.  $\Delta(\text{AIC})$  is the difference between model AIC and the lowest AIC for the candidate models; the model best supported by the data has a  $\Delta(\text{AIC})$  of 0, and models with  $\Delta(\text{AIC})$  of  $>10$  are considered to have essentially no empirical support. RMSE is the root mean square error, in units of  $\Psi$  (MPa). For pre-dawn  $\Psi$ , the best supported model is height alone. For midday water potential the best supported models include height or path length, with slope and intercept varying with tree ID

the canopy tops. Midday  $\Psi_{\text{shoot}}$  was  $\sim 0.77$  MPa lower for a given height than pre-dawn  $\Psi_{\text{shoot}}$ , ranging from  $\sim -1.2$  MPa in lower parts of the canopies, to  $\sim -1.8$  MPa in the canopy tops.

For pre-dawn  $\Psi_{\text{shoot}}$ , model selection strongly favored the model with height as the single predictor variable (Table 1; Fig. 2). The fitted equation was:

$$\text{Pre-dawn } \Psi_{\text{shoot}} = -0.026 * \text{Height} - 0.23$$

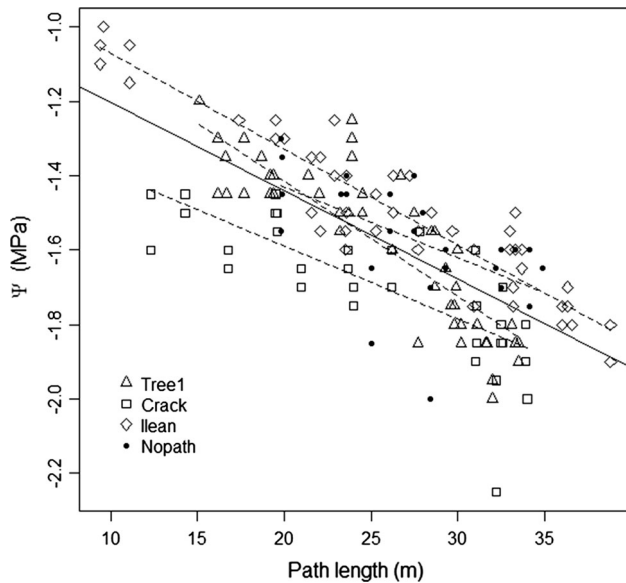
( $\Psi_{\text{shoot}}$  is in units of MPa and height is in m)

The pre-dawn slope was  $>2\times$  the gradient due to gravitational potential of  $-0.01 \text{ MPa m}^{-1}$  (Friend 1993). For midday  $\Psi_{\text{shoot}}$ , model selection strongly favored models with height or path length as predictors (fixed effects), with tree ID included as an interactive random effect (slope and intercept varying as a function of tree ID). Path length was a very slightly better predictor of midday  $\Psi_{\text{shoot}}$  than height, but both models are equally supported by the data (Table 1b). The crowns of our study trees are fairly narrow, so the values of path length are dominated by height. Distinguishing the effects of path length vs. height

alone would be easiest in a species with a broader crown than *P. strobus*. The fixed effect portion of the best supported model was:

$$\begin{aligned} \text{Midday } \Psi_{\text{shoot}} = & -0.024 * \text{Path} \\ & - 0.96(\Psi_{\text{shoot}} \text{ is in units of MPa,} \\ & \text{path is in } m). \end{aligned}$$

The model using height as a predictor had nearly identical parameter values:



**Fig. 2** Midday  $\Psi$  as a function of path length and tree ID; the best model by  $\Delta(\text{AIC})$ . The *solid line* shows the fixed effect, the *dashed lines* show differences in *fitted lines* by tree ID (fitted as a random effect). This model was only marginally better than the model of midday  $\Psi$  as a function of height and tree ID (Table 1)

$$\begin{aligned} \text{Midday } \Psi_{\text{shoot}} = & -0.023 * \text{Height} \\ & - 1.013 \text{ (units as above)} \end{aligned}$$

The variability associated with tree ID (random effects) is shown in Figs. 1 and 2. Air temperatures ranged from 16 to 26 °C during measurements of midday  $\Psi_{\text{shoot}}$ , with generally clear conditions. We did not formally analyze weather conditions in relation to  $\Psi_{\text{shoot}}$ , but did not see any interpretable difference between measurements taken on sunny and cloudy days.

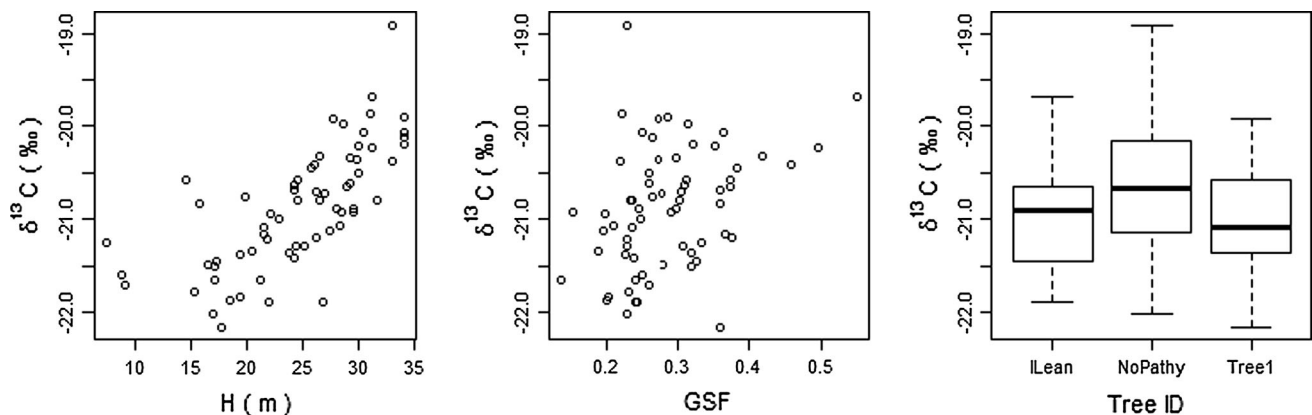
To allow for the possibility that some of the tree-to-tree variability in  $\Psi_{\text{shoot}}$  might be due to variations in  $\Psi_{\text{soil}}$  around each tree, we also fitted models for  $\Psi_{\text{shoot}} - \Psi_{\text{soil}}$  (where  $\Psi_{\text{soil}}$  was the mean of measurements around each tree). Mean  $\Psi_{\text{soil}}$  varied over a very small range between trees, from  $-0.05$  to  $-0.013$  MPa. Model fits as measured by RMSE were very close to RMSE for the comparable models of  $\Psi_{\text{shoot}}$  alone, from which we inferred that tree-to-tree differences in  $\Psi_{\text{soil}}$  as measured had little power to account for differences in  $\Psi_{\text{shoot}}$ .

Tree responses:  $\delta^{13}\text{C}$  and needle length

Both height and GSF were correlated with  $\delta^{13}\text{C}$ , while there was small variability in  $\delta^{13}\text{C}$  among trees (Fig. 3). The model of  $\delta^{13}\text{C}$  with only height and GSF as predictors (Table 2) was much more strongly supported by the data than any other model (Table 2a). None of the models including tree ID was supported by the data.  $\delta^{13}\text{C}$  increased with increasing height and GSF (Fig. 4); the fitted model was:

$$\delta^{13}\text{C} = 0.70 * \text{Height} + 2.33 * \text{GSF} - 23.26.$$

( $\delta^{13}\text{C}$  is dimensionless in units of ‰, height is in m, and GSF is dimensionless).



**Fig. 3**  $\delta^{13}\text{C}$  plotted as a function of height (H), global site factor (GSF), and tree ID. Both height and GSF show a negative correlation with  $\delta^{13}\text{C}$  ( $r = -0.71$  and  $r = -0.35$ , respectively). The *box* and

*whisker plot* on the right shows the small variation among trees in median, interquartile range, and extreme values of  $\delta^{13}\text{C}$

**Table 2** Statistics of model fits for  $\delta^{13}\text{C}$  (a) and needle length (b)

Model	<i>df</i>	$\Delta(\text{AIC})$	RMSE
(a) $\delta^{13}\text{C}$ ( <i>N</i> = 65)			
1. Null model	2	52.26	0.656
2. Height	3	8.56	0.465
3. GSF	3	45.62	0.619
4. Tree ID	4	53.34	0.652
5. Height + GSF	4	0	0.432
6. Height + (1   tree ID)	4	49.64	0.458
7. GSF + (1   tree ID)	4	73.92	0.576
8. Height + GSF + (1   tree ID)	5	54.08	0.421
9. Height + (height   tree ID)	6	43.61	0.405
Needle length ( <i>N</i> = 65)			
1. Null model	2	44.98	0.959
2. Height	3	13.90	0.750
3. GSF	3	46.88	0.966
4. Tree ID	4	16.86	0.761
5. Height + GSF	4	14.51	0.748
6. Height + (1   tree ID)	4	1.20	0.571
7. GSF + (1   tree ID)	4	23.65	0.731
8. Height + GSF + (1   tree ID)	5	1.10	0.569
9. Height + (height   tree ID)	6	0	0.531

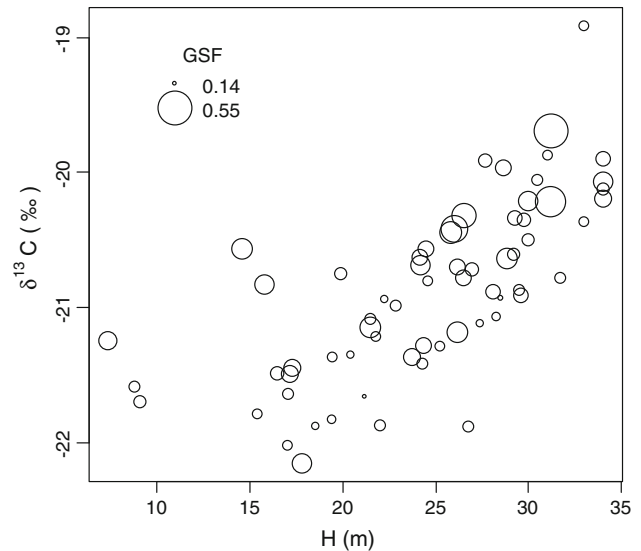
Predictor variables are height (*m*), GSF (a measure of growing season light environment), and tree ID. Tree ID is treated as a random factor, so the models in which it appears are mixed-effects models with tree ID affecting the slope or slope/intercept as in Table 1. RMSE is the root mean square error. Except for the last model in each table, when tree ID is included as a predictor variable it only appears as an additive constant. In the interactions models (model 9 in both tables), both slope and intercept vary by tree ID. For  $\delta^{13}\text{C}$ ,  $\Delta(\text{AIC})$  strongly favors the model with both height and GSF as predictors, with no effect of tree ID. The best models of needle length all include both height and tree ID; with  $\Delta(\text{AIC}) < 2$  the three models (6, 8, 9) have nearly equal empirical support

Height and GSF were slightly correlated ( $r = 0.115$  at the level of the whole data set), but the variance inflation factor was only 1.014.  $\delta^{13}\text{C}$  at the tops of the trees was  $\sim 20$  ‰, the value chosen by Koch et al. (2004) to correspond with height limitation by  $\text{CO}_2$  uptake limitation.

Needle length was highly correlated with height and tree ID, and uncorrelated with GSF (Fig. 5). The only models of needle length with any empirical support in this data set included both height and tree ID as predictors, and the interaction model (slope and intercept vary with tree ID) was the best supported (Table 2b). The fixed effect portion of this model was:

$$\text{Needle length} = -0.090 * \text{Height} + 9.32 \text{ (needle length is in cm and height is in } m \text{)}.$$

Needle length decreased by 15–25 % from the bottom to the top of the canopy for all three trees sampled, but there



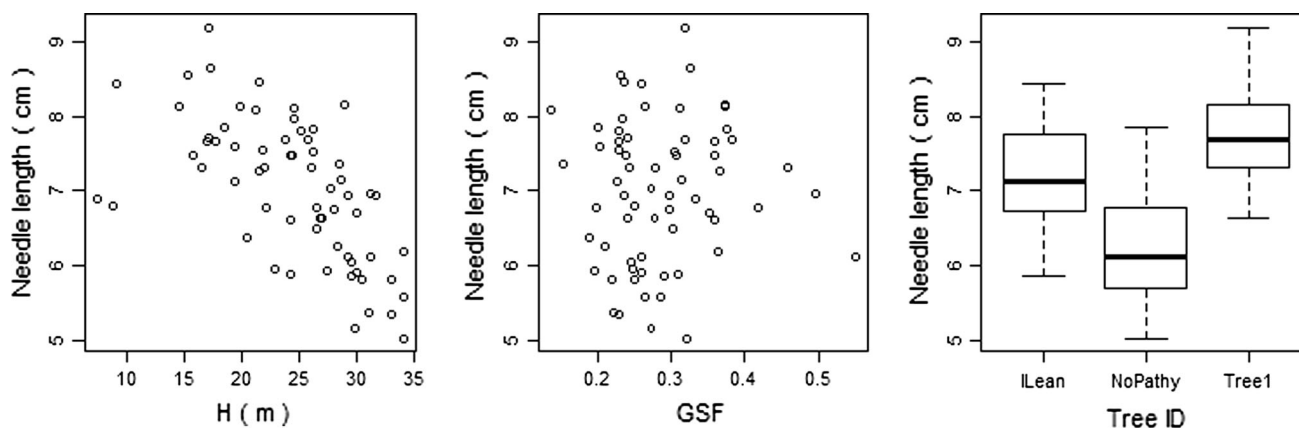
**Fig. 4**  $\delta^{13}\text{C}$  as a function of height (*x* axis) and GSF (size of circles). Size of plotted circles indicates GSF, from a minimum of 0.136 (smallest circle) to a maximum of 0.55 (largest circle)

was substantial tree-to-tree variability in the relationship as shown by the model comparisons (Table 2b) and Fig. 6.

## Discussion

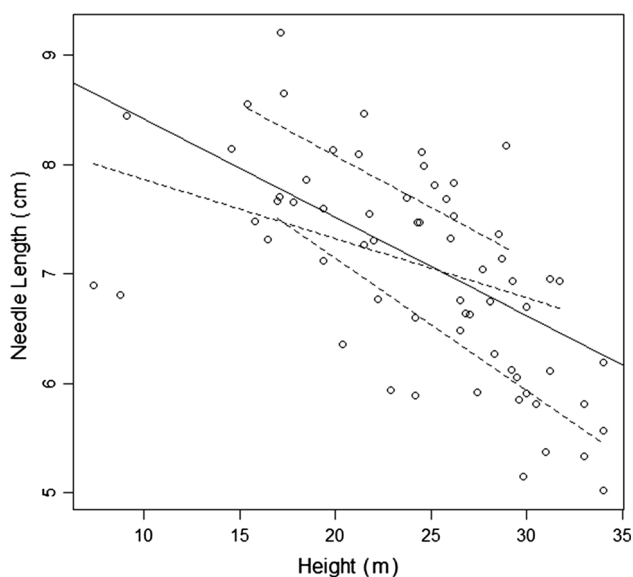
The patterns of variation with height of  $\Psi_{\text{shoot}}$ ,  $\delta^{13}\text{C}$  and needle length are consistent with a role for water supply in limitations of height growth for *P. strobus* at this site.  $\Psi_{\text{shoot}}$  and needle length decreased with height, and  $\delta^{13}\text{C}$  increased with height. Height (or path length) was the strongest predictor for all four variables measured, and was a component of all models with strong empirical support.

Midday  $\Psi_{\text{shoot}}$  in the tree tops were within the range of values that cause stomatal closure in many temperate conifers ( $< -1.8$  MPa), even when the soil was not especially dry.  $\delta^{13}\text{C}$  in the tree tops was  $\sim 20$  ‰, considered by Koch et al. (2004) to be consistent with partial or complete midday stomatal closure in coastal redwood trees during the growing season. Even if simple carbon starvation at the tree top does not limit height growth in this circumstance, carbon limitation can still limit growth. There is evidence that trees, especially large trees, maintain large pools of stored carbon for long-term survival (Sala et al. 2012), so that slowed photosynthesis could limit growth even if non-structural carbon is not exhausted. The caveat is that tissue  $\delta^{13}\text{C}$  most directly indicates  $\text{CO}_2$  concentrations within leaves, so possible interpretations of the  $\delta^{13}\text{C}$  gradient are not limited to water stress. Duursma and Marshall (2006) have shown that  $\delta^{13}\text{C}$  can also be strongly correlated with leaf N. We found that the light environment, as estimated by GSF, was a significant predictor of  $\delta^{13}\text{C}$  in conjunction



**Fig. 5** Needle length plotted as a function of height (H), global site factor (GSF), and tree ID. Height is strongly negatively correlated with needle length ( $r = -0.63$ ). The *box and whisker plot* on the right

shows appreciable differences among trees in the median, interquartile range, and extreme values of needle length



**Fig. 6** The best supported model of needle length was a mixed model with height treated as a fixed effect and tree ID treated as a random effect, with tree-to-tree variability in slope and intercept. The fixed effect of height is shown by the *solid line*, and tree-to-tree variability in the slope and intercept is shown by the *dashed lines*

with height; the pattern of  $\delta^{13}\text{C}$  with GSF is consistent with a lower  $\text{CO}_2$  concentration in well-illuminated leaves. However, height was by far the strongest single predictor of  $\delta^{13}\text{C}$  in our data, which is most consistent with water supply limiting carbon uptake.

While the cell wall stretching that underlies leaf expansion is strongly regulated by biochemical mechanisms, turgor pressure plays a short-term role in the timing of leaf expansion (turgor will be highest at night when transpiration demands are at a minimum), and water status is one of the exogenous factors that regulates leaf expansion on a longer time scale (Van Volkenburgh 1999). The

gradients of decreasing pre-dawn  $\Psi_{\text{shoot}}$  and needle length with height are both consistent with a role for water stress in needle expansion, although direct measurements of both turgor pressure and shoot extension growth early in the growing season would provide the strongest test of this mechanism in limiting height.

The gradient of pre-dawn water potential was  $>2\times$  the gradient that would have resulted from gravitational potential alone. There are two possible explanations. First, it has long been assumed that transpiration ceases at night, allowing plant and soil water potential to come into equilibrium, but there is now extensive evidence for nocturnal transpiration in a variety of plant communities, including conifer forests (Dawson et al. 2007; Kavanagh et al. 2007). Second, the stems of large trees can have significant capacitance for water, and this storage can slow the approach to equilibrium between tree and soil water potential (Cermák et al. 2007). These two mechanisms are not mutually exclusive, but both would need to be measured simultaneously in any attempt to determine their relative magnitude.

Some authors have attempted, by direct calculation from simple assumptions (Friend 1993) or extrapolation of empirical trends (Koch et al. 2004), to establish an absolute ‘physiological ceiling’ (Burgess and Dawson 2007) for tree height, close to the current observed maximum height, although some constants assumed in the models may not be constant (Becker et al. 2000; Burgess and Dawson 2007). Whether or not there is an absolute ceiling, there are a number of species far from the global maximum height that still show strong evidence of hydraulic limitation (Ryan et al. 2006) including—on the basis of this study—*P. strobus*.

Limitation of water supply functions within a web of physiological and anatomical plasticity operating in the context of environmental variation. One step toward

disentangling this web consists of identifying general vs. situation-specific relationships. In this study, we found substantial tree-to-tree variation in midday  $\Psi_{\text{shoot}}$  and needle length regressions with height, indicating that these relationships may have large situation-specific components. Midday  $\Psi_{\text{shoot}}$  is controlled partly by fine-scale variations in illumination and microclimate; and needle length variation may be controlled by the genetics of individual trees and the timing of water potential variations in relation to leaf expansion. On the other hand, the relationship between  $\delta^{13}\text{C}$  with height did not depend on tree ID, but solely on a combination of height and light environment (GSF), with height as the strongest predictor. Burgess and Dawson (2007) found that trends in  $\delta^{13}\text{C}$  seemed to predict absolute heights more consistently than other physiological and anatomical trends. It would be of interest to compare tree top  $\delta^{13}\text{C}$  levels across a range of species, site conditions, and proximity to regional maximum height.

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