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Factors controlling plasticity of leaf morphology in *Robinia pseudoacacia*: III. biophysical constraints on leaf expansion under long-term water stress

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In this article, we measured the relative growth rate (RGR) of leaves of *Robinia pseudoacacia* seedlings under well-watered and water-stressed conditions (mid-day Ψ_w = leaf water potential estimated with a pressure bomb of −0.48 and −0.98 MPa, respectively). Pressure–volume (PV) curves were done on growing leaves at 25, 50 and 95% of the mature size (growth stage) in order to compute solute potential (Ψ_π) and turgor pressure (Ψ_P) as a function of Ψ_w. The PV curves and diurnal measurements of Ψ_w and RGR allowed us to evaluate the parameters (cell wall extensibility m and growth turgor threshold Y) of the Lockhart equation, $RGR = m(\Psi_P - Y)$, at each growth stage. Our data showed that m and Y did change with leaf age, but the changes were slow enough to evaluate m and Y on any given day. We believe this is the first study to provide evidence that the Lockhart equation adequately quantifies leaf growth of trees over a range of time domains. The value of m linearly declined and Y linearly increased with growth stage. Also, mild drought stress caused a decline in m and increase in Y relative to controls. Although water stress caused an osmotic adjustment which, in turn, increased Ψ_P in stressed plants relative to controls, the RGR and final leaf sizes were reduced in water-stressed plants because of the impact of water stress on decreased m and increased Y.

Introduction

Leaf morphology can be quantified by leaf size (length, width, area and thickness), leaf density, leaf mass per unit area, or by cell sizes (epidermal, guard cell, palisade mesophyll or spongy mesophyll). There are large gradients in leaf morphology in mature leaves within the canopy of individual trees (Koch et al. 2004, Oldham et al. 2010). Several recent papers have described plasticity of leaf morphology in tall trees and have variously ascribed the cause of variable morphology to be because of light (Sack et al. 2006), height (hydrostatic gradient) (Cavaleri et al. 2010, Oldham et al. 2010), or to some measure of water stress or turgor pressure (Meinzer et al. 2008, Woodruff et al. 2004). While some studies have used statistical correlations to get at the 'cause' of observed morphological variation (Cavaleri et al. 2010, Oldham et al. 2010), others have used an approach that addresses possible mechanisms. In a mechanistic approach, it is necessary to quantify environmental conditions, while leaves are growing and the forces causing leaf expansion in the context of some kind of equation or quantitative theory. A good example of a mechanistic study is that shown by Meinzer et al. (2008), where a tower crane was used to access tall

Abbreviations – PV, pressure–volume; RGR, relative growth rate; RWC, relative water content.

Douglas-fir trees during the season of needle growth, and mechanical devices were used to estimate whole needle plasticity and elasticity during growth. While such measures are arguably related to the coefficients of the Lockhart equation (m and Y), they are not direct measurements of these parameters. In the Lockhart equation (Lockhart 1965), turgor pressure (Ψ_P) is seen as the driving force of instantaneous relative growth rate (RGR): $RGR = m(\Psi_P - Y)$, where m is a measure of wall extensibility and Y is the yield pressure for wall extension. When $\Psi_P < Y$, the RGR is assigned a value of zero.

Both m and Y are influenced by the rate of insertion of newly synthesized wall polymers (Cosgrove 2000, 2005). The growth rate is controlled by the extensibility, m, which depends on the cell wall properties, such as cell wall looseness or stiffness. On a molecular level, one might view m as being controlled by the viscous drag of polymers across each other as the force of turgor pressure causes plastic stretching of the cell wall. Growth ceases when cross-polymer linkages (covalent or ionic bonds) prevents slippage of polymers past each other (Cosgrove 2005). Cross-polymer linkages raise Y and lower m. The value of Y can also be viewed as a static coefficient of friction at the cell-wall scale and at a molecular scale Y can be viewed as the force required to break cross linkages, so polymers can slip past each other. Because the Lockhart equation was developed to describe short-term growth of individual cells, ambiguities and uncertainties, such as m and Y measuring methods, might arise when applying it to the growth of complex tissues such as needles and shoots (Meinzer et al. 2008). Nevertheless there is a long-term effect on RGR of tissues caused by changes in water stress during long-term experiments (Matthews et al. 1984, Van Volkenburgh and Boyer 1985).

In the first paper of this series (Zhang et al. 2011a), we described the range of morphological parameters of leaves in mature *Robinia pseudoacacia* trees and hypothesized that some of the observed changes might be caused by water stress. In the second paper, we investigated temporal changes in leaf morphological parameters during growth of seedling *Robinia* leaves grown in a controlled environment under two water stress conditions, control well-watered ($\Psi_w = -0.5$ MPa) and stressed ($\Psi_w = -1.0$ MPa). Stress was maintained by daily quantitative irrigation of exactly the mass of water evaporated the day before as determined by gravimetric measurements. In both papers, we discussed the complex dependence of Ψ_w and Ψ_P on several factors that combine to influence their values including Ψ_{soil}, height, path-length hydraulic resistance from soil to growing leaves, evaporative flux from leaves and how the latter depends on net irradiance and stomatal physiology. Given these complex interactions, it is no surprise that statistic analysis alone could not yield consistent conclusions between studies when only some of the possible variables were included in the statistical models. As cell-level growth is described by the Lockhart equation, detecting how complex environmental conditions influence cell growth through variation of m and Y might be considered a practical and direct method to quantify environment effects.

We hypothesize that the Lockhart equation describes instantaneous RGR of whole leaves in terms of instantaneous values of m, Ψ_P and Y. However, the ultimate size a cell or leaf will reach will depend on the duration of growth, the diurnal changes in Ψ_P during growth and how m and Y might change during the days of growth. The final size and morphology a leaf can reach at maturity will depend on the time integral of the Lockhart equation over the entire period of growth that can equal 30–40 days in the case of *Robinia* leaves.

The objective of this study was to quantify the parameters of the Lockhart equation (m and Y) in *Robinia* leaves and to determine how the parameters are influenced by water stress and leaf age during the growth of leaves.

Materials and methods

The conceptual approach

As long-term water stress can influence the entire growth process during leaf expansion (Meinzer et al. 2008), we quantified RGR at 2-h and daily intervals and used the pressure bomb methods to assess water stress (Ψ_w) diurnally. We used pressure–volume (PV) curves to assess osmotic potential (Ψ_π) and turgor pressure (Ψ_P) at three stages of leaf growth. At any given time of day, measurements of Ψ_w can be used to estimate Ψ_P from PV curves. The m and Y parameters should change considerably over the growth period of a leaf. We assumed that m and Y would change slowly enough on any given day that it would be possible to estimate the Lockhart parameters from diurnal changes in RGR and Ψ_P on any given day.

Although the Lockhart equation has been used in the past to describe whole tissue or organ growth, the equation was first introduced to describe growth at the cell level. An organ level application of the Lockhart equations is justified if experimental data fits an equation of the Lockhart-form; however, the authors and anonymous reviewers are not aware of any attempt to explain the theoretical implications of scaling up from the cellular to organ level hence a few comments are justified.

At a cellular level relative growth rate of the i-th cell (r_i) is given by $r_i = (1/l_i)\dot{l}_i$, where l_i is some measured dimension and $\dot{l}_i = dl_i/dt$ = the absolute rate of growth of the dimension. Hence scaling up to an entire leaf relative growth rate would be given by $RGR = \sum(l_i r_i)/\sum l_i$, i.e. the organ level RGR = the dimensional weighted mean of the sum of the cell growth rates (r_i) in the entire leaf in the direction of measurement. In our opinion, cell division does not need to be accounted for in any explicit manner (see Zhang et al. 2011a,b). If we use a pressure bomb to estimate the whole tissue turgor pressure (Ψ_P), then the pressure bomb produces a volume averaged turgor pressure (see Tyree and Hammel 1972, for the derivation): $\Psi_P = \sum(v_i P_i)/\sum v_i$, i.e. the individual cell turgor pressures (P_i) are weighted by the volume of each individual cell. The RGR of the entire leaf will stop only when the r_i of the last growing cell stops so we must view Y as equal to or close to the yield point of the last remaining growing cells. The value of m will scale up in some undefined way from some kind of weighted average of the m_i values of individual cells.

The details

The materials and treatments for this study have been described in detail in paper II of this series, so in this section only a summary will be presented.

All experiments were performed in a climate controlled growth chamber. Maximum photosynthetic photon flux density was 350 μmol m^{-2} s^{-1}. Temperature was kept at 22/18°C (day/night) and relative humidity at 75%. Two watering regimes were imposed on 24 seedlings of *Robinia* for 90 days in the growth chamber: (1) well-watered (mid-day Ψ_w was around −0.45 MPa), (2) water-deficit (mid-day Ψ_w was kept around −1.00 MPa). Twelve replicate seedlings of *Robinia* were used in each treatment.

Measurement of leaf growth and water relations

All lateral branches were removed as soon as they became visible. Hence, all the growth measurements were taken on leaves from the main stem. The leaf of *Robinia* is an odd-pinnate compounded leaf; length was taken as the distance from the base of the petiole to the base of the terminal leaflet and was measured to ±0.1 mm with a digital caliper. A mark with a pen was made quite near the base to provide a well-defined point for repeated measurements. Length data were collected from leaves at three growth stages: 25, 50 and 95% of final leaf length, when the mean lengths were 66, 131 and 251 mm long in controls, respectively, and when the mean lengths were 47, 98 and 178 mm long in stressed plants. These growth-stage lengths were assessed from preliminary experiments. According to the measured data in paper II of this series, the absolute length growth rate at these three growth stages were 19, 29 and 3.7 mm day^{-1} for controls, and 8.6, 13.2 and 1.6 mm day^{-1} for stressed plants. Every 2 h, leaf growth was measured on 12 plants per treatment as increases in leaf length with a digital slide caliper to ±0.1 mm. The growth increment every 2 h was on average 0.87–2.18 mm during the day and night for controls, and on average 0.14–1.41 mm during the day and night for stressed plants. Relative growth rate (RGR) of leaf length was calculated using RGR = [d(ln(L))/dt], where L is the instantaneous length of leaf, t, the time (Pereyra-Irujo et al. 2008).

Leaf water potential (Ψ_w) was measured on mature leaves with a pressure bomb (Soil Moisture Equipment Corp., Santa Barbara, CA) every 2 h as a proxy for the growing leaf Ψ_w, which could not be destructively sampled. The difference of Ψ_w between mature leaves and growing leaves was less than ±0.011 MPa (SE ± 0.003) based on total 15 measurements in preliminary experiment (data not shown). During growth experiments, Ψ_P (turgor pressure) was estimated from the proxy Ψ_w and PV curve analysis is explained below.

Six to eight leaves at the three growth stages: 25, 50 and 95% (of final leaf length) per treatment were harvested for PV curve measurements. The leaf was cut off from the tree under water and rehydrated for 8–12 h in the dark with only the petiole immersed in the water. PV curves were initiated by first measuring the Ψ_w of rehydrated shoots with a pressure bomb and then determining the corresponding fresh weight with an analytical balance to ±0.1 mg (Mettler Toledo, XP205 Columbus, OH, USA). Consecutive determinations of Ψ_w and fresh weight were repeated during slow dehydration in the air on the laboratory bench until values of Ψ_w reached −3.5 MPa. The inverse of Ψ_w was plotted against relative water content (RWC) to create a PV curve and analyzed by standard methods (Tyree and Hammel 1972). The saturated weight of each sample, necessary for calculating tissue RWC, was estimated by fitting a linear regression to a plot of sample fresh weight against Ψ_w for points above the turgor loss point and extrapolating to zero Ψ_w. Values of Ψ_P were estimated from the difference between values of Ψ_w and the values of Ψ_π derived from the PV curve. Maximum volumetric elastic modulus (ε^{max}; MPa) was computed from the standard definition of $\varepsilon = dP/dRWC$ evaluated a full turgor. Osmotic potential at full turgor (Ψ_π^{100}) was the osmotic potential at full hydration (100% RWC), and osmotic potential at zero turgor (Ψ_π^0) was the Ψ_w at the

inflexion of linear portion and curvilinear portion in the PV curve.

Results

The mean predawn Ψ_w in control plants was −0.35 MPa, and mean predawn Ψ_w in stressed plants was −0.51 MPa, which was approximately 0.16 MPa more negative than controls ($P < 0.001$). The mean mid-day Ψ_w in control plants was −0.46 MPa, and mean mid-day Ψ_w in stressed plants was −0.98 MPa, which was −0.52 MPa more negative than controls ($P < 0.001$) (Fig. 1A). At the 25% growth stage, the mean predawn Ψ_π was −0.99 and −1.39 MPa for controls and drought, respectively. From predawn to mid-day, Ψ_π decreased −0.031 and −0.091 MPa for control and drought plants, respectively, and Ψ_π reached the lowest value of −1.025 and −1.48 MPa at the mid-day for control and stressed plants, respectively (Fig. 1B). The value of Ψ_P under water stress was higher than controls, except around mid-day (Fig. 1C). Predawn RGR was similar between controls and drought, however, during the day, RGR was lower under water stress than controls and it reached the lowest (0.0003 ± 0.00017) around midday (Fig. 1D).

At 50 and 95% of final leaf length, daily Ψ_π and Ψ_P followed the similar pattern to that at 25% growth point (the detailed data not shown). 24-h averaged Ψ_π increased a bit at 50% and then dropped markedly at 95%, while stressed plants always had more negative Ψ_π (Fig. 2A). The 24-h averaged Ψ_P increased with leaf age, while stressed plants had even higher average Ψ_P than controls (Fig. 2B).

There was a nonlinear negative relationship between RGR and Ψ_w (Fig. 3). Values of RGR measured at 2-h intervals followed the Lockhart equation, i.e. were linearly correlated with Ψ_P (Fig. 4). However, the slopes (m) and x-axis intercepts (Y) changed with growth stage and with water stress. During leaf growth, m decreased and Y increased with leaf age. However, m was always smaller under water stress than controls, and Y was always higher in drought plants compared to controls (Fig. 5). Leaf RGR was positively correlated with m for both controls and stressed plants (Fig. 6).

During leaf growth, there were both elastic and osmotic adjustments (Fig. 7). The maximum volumetric elastic modulus (ε^{max}) increased with leaf age, while it was always greater under water stress than controls (Fig. 7A). Osmotic potential at full turgor and at zero turgor were significantly decreased at the 95% growth stage, although they did not differ significantly at the 25 and 50% growth stages (Fig. 7B, C). At the three growth stages, osmotic potential at full turgor and at zero turgor were always lower under water stress.

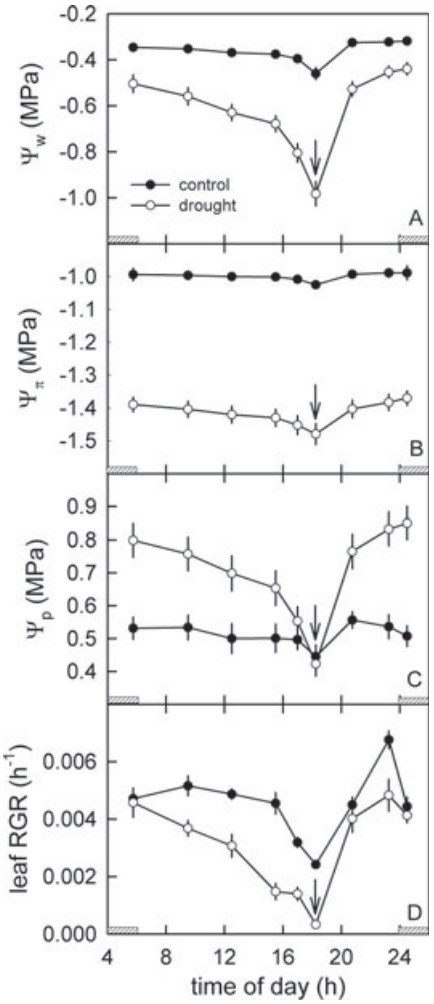

Fig. 1. Daily pattern of water potential (Ψ_w) (A), osmotic potential (Ψ_π) (B), turgor pressure (Ψ_P) (C) and leaf relative growth rate (RGR) (D) at 25% growth stage in the two treatments. Ψ_w was measured with a pressure bomb, and Ψ_π was attained from the linear part of PV curves. Ψ_P was computed as the difference between Ψ_w and Ψ_π at each time. The downward arrowhead marks the time when water was added for water-stressed and control plants. Hatched area on 'x-axis' indicates darkness, which was from midnight to 06:00 h. Each mean value was the average value of 12 plants per treatment. Bars indicate SE.

Discussion

Zhang et al. (2011b) argued that soil water potential, height and light all influence Ψ_w and RGR. The quantitative expression that describes the functional dependence of Ψ_w on the combined influence of Ψ_{soil}, light and height is the soil–plant continuum model (see Eqns 1 and 2 in paper II of this series). Studies that use only a statistical test to determine the relative importance of light vs height fail to address the underlying mechanisms controlling the process of growth. The unifying concept that allows us to see

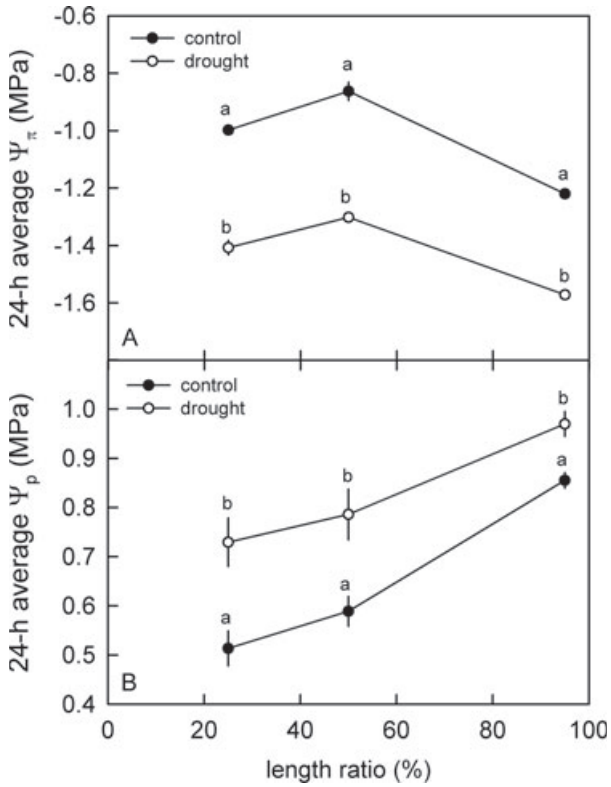

Fig. 2. Values of 24-h averaged Ψ_π (A) and Ψ_P (B) are plotted vs leaf length ratio. Leaf length ratio (= growth stage) is the ratio of the length of growing leaf to the final leaf length. Each mean value was the average of 12 plants per treatment. Bars indicate SE. Different letters above the bars indicate significant difference between control and drought treatment ($P < 0.05$).

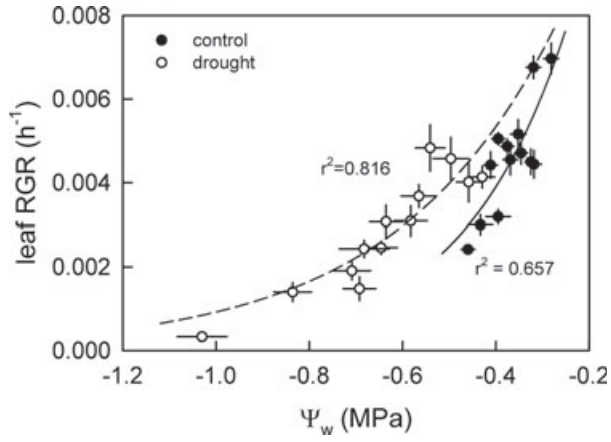

Fig. 3. Daily average RGR is a nonlinear function of daily average leaf Ψ_W in the two treatment: control and drought. Values of r^2 of the nonlinear regression of RGR vs Ψ_W are shown next to each plot. Each mean value was the average value of 12 plants per treatment. Both 'x'- and 'y'-bars indicate SE.

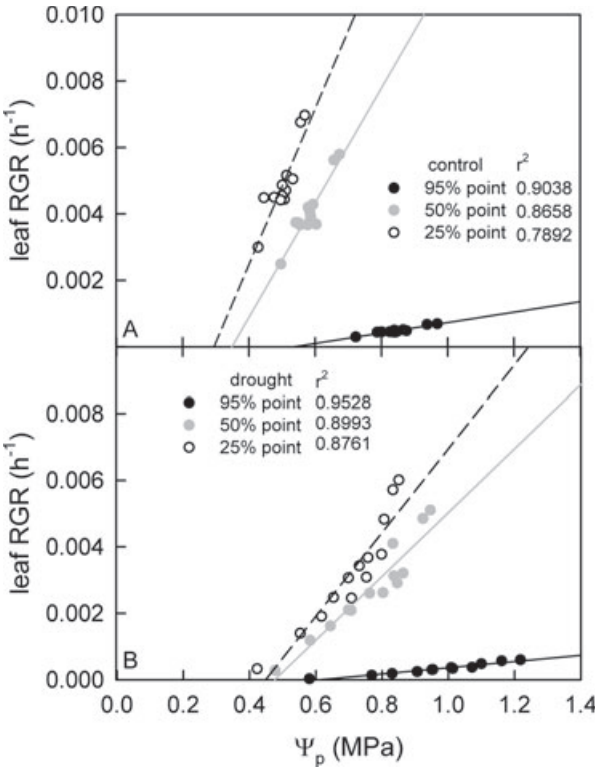

Fig. 4. Leaf RGR at three growth stages (25, 50 and 95%) at various leaf Ψ_P in the two treatments: control (A) and drought (B).The r^2-values are for the linear regression of RGR vs Ψ_P.

beyond this debate of the importance of light vs height in influencing leaf morphology is the Lockhart equation, which provides the causative connection between RGR and Ψ_P, which in turn is a function of Ψ_W. In this paper, the connection between Ψ_W and RGR is established in *Robinia* (Fig. 3). The data in Fig. 4 provides credible evidence that the Lockhart equation applies on any given day during leaf expansion in *Robinia*. Finally, the data in Fig. 5 show how values of m and Y are influenced by water stress and how m decreases with leaf age and how Y increases with leaf age. Although our method of evaluating m and Y differs with that used by Meinzer et al. (2008), both studies come to qualitatively similar conclusions on quite different species (broad- vs needle-leaf species).

Although the Lockhart equation (Lockhart 1965) was originally formulated to model the irreversible expansion of single cells, it has been discussed in the growth of complex plant tissues and organs (Matthews et al. 1984). The values m and Y are represented as constants for short-term analyses of growth rates; however, Ψ_P usually exhibits large diurnal changes and m and Y are likely to change in other species in response to water stress (Lu and Neumann 1998, Meinzer et al. 2008, Roden et al.

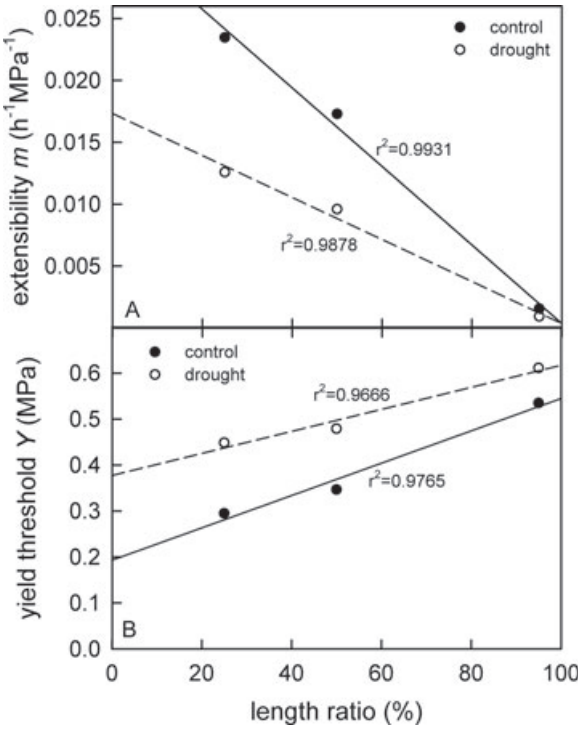

Fig. 5. Values of leaf extensibility (m) (A) and yield threshold (Y) (B) determined on any given day are strongly correlated with length ratio (growth stage). Leaf length ratio is the ratio of the length of growing leaf to the final leaf length. Values of r^2 of linear regression function of m and Y vs length ratio is shown in the plot.

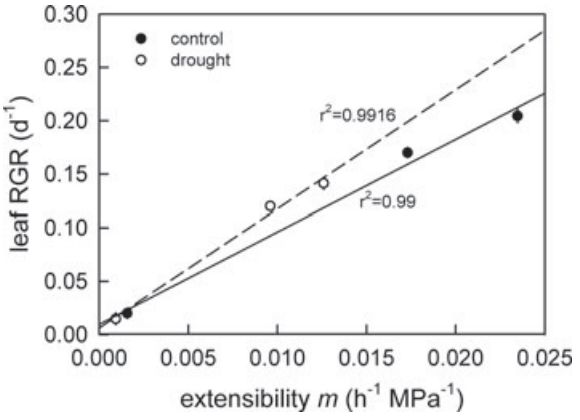

Fig. 6. Daily values of leaf RGR are dependent on daily values of extensibility (m) for the two treatments. Each regression consists of three points corresponding to three growth stages. Values of r^2 of linear regression of leaf RGR vs m is shown in the plot.

1990, Fig. 5) and leaf age (Meinzer et al. 2008, Fig. 5). So far no other study seems to quantify how m and Y change with both leaf age and water stress (Fig. 5).

We observed short-term inhibition of growth around mid-day in drought-leaves (Figs 1 and 5) when Ψ_P dropped lower than Y. During leaf growth, pronounced osmotic adjustment resulted in Ψ_P gradually increasing during leaf maturation (Fig. 2), consistent with previous studies (Meinzer et al. 2008). Despite increasing Ψ_P with leaf age, RGR decreased with leaf age because m decreased and Y increased (Lu and Neumann 1998, Roden et al. 1990). The increase in Ψ_P is a consequence of the osmotic adjustment in response to drought documented in Fig. 7. Hence, although the driving force on RGR increased in response to drought, the RGR decreased and mature leaf size decreased because

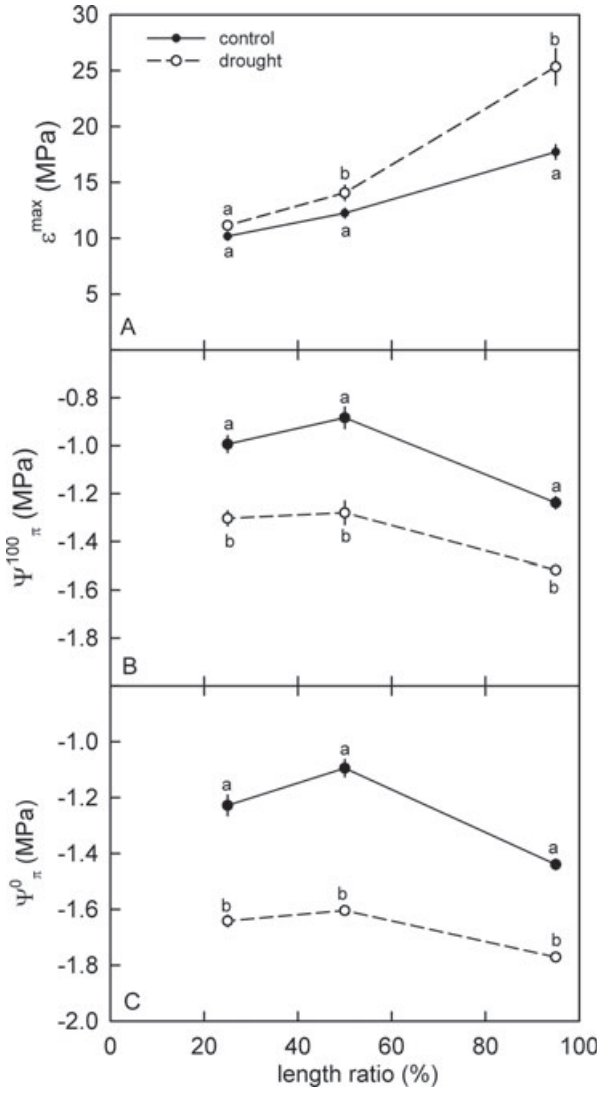

Fig. 7. Values of maximum volumetric elastic modulus (ε^{max}) (A), osmotic potential at full turgor (B) and at zero turgor (C) are functions of length ratio (growth stage) in two treatments: control and drought. Each mean value was the average of 12 plants per treatment. Bars indicate SE. Different letters above the bars indicate significant difference between control and drought treatment ($P < 0.05$).

drought has some direct influence on m and Y. The biochemical and genetic mechanisms that explain the influence of drought on m and Y are beyond the scope of this paper.

The rapid decline and slow recovery of osmotic solute content in leaves concurrent with phenological cycles of bud flushing and expansion and maturation of new foliage in Douglas-fir (Meinzer et al. 2008, Figs 2 and 7B, C) is suggestive of significant physiological constraints on the availability and supply of solutes to generate Ψ_P sufficient to drive expansive growth at maximal rates. Scarcity of organic solutes such as sugars is likely to have a synergistic negative impact on growth because of their dual role as both osmotic and raw material for cell wall synthesis. For example, when buds swell in conifers, sugars are metabolized more rapidly than they are produced and therefore tend to be limited (Billow et al. 1994). Nevertheless, our results indicate that constraints on the leaf growth increase with increasing leaf age because m decreased and Y increased. Although osmotic adjustments in water-stressed plants increased Ψ_P for much of the day (Fig. 1), it was not sufficient to increase RGR in stressed plants to control levels because water stress caused a large decrease in m and an increase in Y (Fig. 4) relative to controls. Others have reported that osmotic adjustment is insufficient to maintain high RGR (Van Volkenburgh and Boyer 1985), and our study explains why in terms of the parameters of the Lockhart equation.

Some studies have discussed the dominant roles of m and Y in regulating leaf expansion, but only under conditions in which water stress is rapidly or transiently imposed by altering the external osmotic environment or transpiration rate for minutes to an hour (Hsiao and Xu 2000, Lu and Neumann 1998, Roden et al. 1990, Shackel et al. 1987). Experiments in which transient water stress is rapidly imposed to study mechanisms underlying dynamic perturbations in growth rates do not create conditions analogous to the permanent vertical gradient of Ψ_w in tall trees. Hence our results provide more insight into the mechanisms that might explain gradients of leaf morphology in tall trees. In our study, long-term water stressed plants always had lower Ψ_w (Fig. 1) than control plants, and the constant Ψ_w gradient between control- and stressed plants was the sole distinguishable factor for the two treatments. We suggest that our study might mimic the stress levels found in tall trees, while leaves are growing. In most previous studies water potential gradients were measured after leaves have matured and when soils might be dry. Hence, the conditions reported in Sack et al. (2006), Oldham et al. (2010), Cavaleri et al. (2010), paper I of this series, probably overestimate the range and magnitudes of water stress that occur during leaf growth. However, more work is needed to confirm this.

Previous studies conducted on Douglas-fir demonstrated a highly significant linear decline in annual branch elongation with increasing height (Woodruff et al. 2004) and decreasing leaf expansion with height (Meinzer et al. 2008). It is likely that biophysical constraints on stem and leaf expansion in Douglas-fir are similar to those in our study. According to our data collected in China (paper I of this series) and experimental data from seedlings grown in a growth chamber (paper II of this series), the plasticity of leaf traits with height in *Robinia* is mainly attributed to decreasing water status along height, and this study explains how water stress affects leaf growth via its effects on biophysical constraints (parameters in the Lockhart equation). This study might provide insights into the underlying causes of the well-known decline in height growth rate as tall trees increase in size.

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