

# Relationship between growth and xylem hydraulic characteristics of clones of *Eucalyptus* spp. at contrasting sites

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**Summary** To assess relationships between hydraulic characteristics and growth efficiency (expressed as trunk volume increment per unit leaf area per year), we measured xylem specific conductivity, leaf specific conductivity and the vulnerability of xylem to cavitation in branches of 7–8-year-old trees of four closely related *Eucalyptus* clones growing in plantations on mesic and xeric sites. Growth was influenced more by site than by clone. Hydraulic conductivities were higher in trees on mesic sites than in trees on xeric sites, but within a site, conductivity did not differ among clones. Huber values (functional xylem cross-sectional area:leaf area) were similar across clones and between sites. Vulnerability of xylem to cavitation differed among clones but not between sites. We conclude that, within these genetically related clones, hydraulic conductivity is determined predominantly by environmental conditions, whereas vulnerability to cavitation is more closely associated with genotype. The clone most vulnerable to cavitation showed considerable aboveground die-back during a severe drought and there was a positive correlation between growth efficiency and maximum xylem specific conductivity.

**Keywords:** cavitation, drought tolerance, embolism, hydraulic conductivity, vulnerability, water relations.

## Introduction

Demands by the forestry industry for improved productivity and the introduction of plantation trees into marginal areas have created a need for a detailed understanding of the water relations of commercially grown *Eucalyptus* clones (Mulin and Park 1992). A recent drought in South Africa caused severe mortality of some clones, whereas other clones survived the drought.

Water stress is a major factor limiting terrestrial plant productivity (Pyrke and Kirkpatrick 1994), because a wide variety of growth-related processes are affected by water deficits (Tyree and Jarvis 1982). The hydraulic properties of a tree influence the supply of water to the leaves, and hence possibly growth (Tyree and Ewers 1991). The ability of water in the xylem to withstand the tensions developed by high rates of transpiration, or brought about by soil water deficits, can also have a significant bearing on the susceptibility of trees to drought (Boyer 1982). Cavitation is influenced by the structure

of the xylem, and the ability of the xylem to prevent, or at least limit, cavitation could have a marked influence on the response of a tree to drought.

The aim of this investigation was to test the hypotheses that, for four *Eucalyptus* clones grown on sites of differing water availability, growth is related to leaf specific conductivity and drought survival is related to vulnerability of the xylem to cavitation.

## Material and methods

### *Experimental material and study sites*

Two *Eucalyptus grandis* W. Hill *ex* Maiden. × *camaldulensis* Dehnh. hybrids, GC1 and GC2, a *Eucalyptus grandis* × *urophylla* S.T. Blake hybrid, GU, and a pure *Eucalyptus grandis* clone, GG, were chosen on the basis of their observed drought susceptibilities. Clone GG is more drought susceptible, in terms of both growth and survival, than the GC clones. The drought tolerance of the GU hybrid was unknown because it has been planted only at sites with non-limiting water availability (B. Verbizier, Tree Improvement Research, Mondi Forests, South Africa, personal communication).

Branches from 7–8-year-old trees of the four clones were collected from clonal competition trials (one xeric and two mesic sites) in the coastal region of KwaZulu-Natal, South Africa during winter 1995 (June–July) and summer 1996 (January). Because the trials were not designed for the purpose of these experiments, all four clones were not found at the same sites; hence it was necessary to sample from two mesic sites. At each site, the sampled plots comprised three rows of 10 trees planted at a spacing of 3 m × 3 m. All of the sampled plots were located among other trial plots so that there were no edge effects. At all three sites, the soil is sandy. Descriptions of the three sites from which material was sampled are given in Table 1.

Total annual rainfall and mean temperature at the three sites were estimated from data collected from surrounding weather stations (R. Kunz, Institute for Commercial Forestry Research, Pietermaritzburg, South Africa, personal communication). Temperatures at the three sites are similar. At a weather station positioned between the trial sites (28°26' S; 32°11' E), mean summer maximum and winter minimum temperatures are 30.5

Table 1. Details of the trial sites from which plant material from the 7–8-year-old *Eucalyptus* trees was collected. Estimates of rainfall and temperature were calculated from nearby weather stations.

	Xeric site	Mesic site A	Mesic site B
Location	28°31' S, 32°08' E	28°33' S, 32°16' E	28°25' S, 32°14' E
Altitude (m)	220	50	30
Soil depth (cm) <sup>1</sup>	> 150	> 120	> 150
Underlying rock <sup>2</sup>	Basalt	Coastal sand	Coastal sand
Topography	Hill top	Valley/wetland	Valley/wetland
Planting date <sup>1</sup>	Aug 23, 1988	Oct 18, 1988	July 30, 1987
Total annual rainfall (mm) <sup>3</sup>	812	1057	958
Mean temperature (°C) <sup>3</sup>	21.8	21.8	21.9

<sup>1</sup> Unpublished data courtesy of Tree Improvement Research, Mondi Forests.

<sup>2</sup> From Geological Survey of South Africa (1985), 1:250 000 Geological Series Map of St. Lucia. Government Printer, Pretoria.

<sup>3</sup> Data courtesy of the Institute for Commercial Forestry Research, Pietermaritzburg.

and 12.3 °C, respectively, and mean rainfall for February and July is 140 and 35 mm, respectively. Although the difference in rainfall between the xeric and mesic sites was less than 250 mm, the xeric site was situated on a hill top, whereas the mesic sites were in valley bottoms. Both the lower rainfall and location contributed to the reduced availability of water at the xeric site. During the last decade, 1987 was recorded as the wettest year. This coincides with the period when the trials were planted (Table 1). Since then, 1992 was recorded as the driest year with a total rainfall of 504 mm. During all field experiments, the rainfall was above average.

### Growth

From the age of 3 years, trunk diameter at breast height (DBH, cm) and tree height ( $H$ , m) of all clones were measured annually on the central row of trees at each site by the Mondi Forests Tree Improvement Research team. From these data, trunk volumes ( $V$ , m<sup>3</sup>) were calculated as (Bredenkamp 1982):

if DBH < 20 cm

$$V = 10^{(-11.162 + 3.652 \log((DBH/10) + 100) + 1.148 \log H)},$$

if DBH > 20 cm but < 40 cm

$$V = 10^{(-4.982 + 1.328 \log((DBH/10) - 70) + 1.1783 \log H)}.$$

There was considerable die-back of Clone GG at the xeric site during the 1992 drought (B. Verbizier, personal communication). At the time of our study, 27 of the 30 trees in the GG plot had died aboveground, and similar mortality was observed in other GG plots at the xeric site. During the past few years, coppice shoots have started to grow from the bases of these dead trunks, most of which have remained standing. The productivity of this clone is thus considerably less than that of the other clones at the xeric site. No other mortalities were observed.

Leaf area per tree was calculated from leaf area index ( $L$ ) and planting density. The  $L$  values were calculated from plant area indices (PAI), measured with an LAI-2000 Plant Canopy

Analyzer (Li-Cor, Inc., Lincoln, NE), based on the linear relationship between  $L$  and PAI derived for *Eucalyptus nitens* (Deane & Maiden.) Maiden. and *E. globulus* Labill. growing in plantations over a range of sites and planting densities (Battaglia et al. 1998). Readings from the fourth and fifth rings of the sensor were ignored to reduce the influence of neighboring trial plots. Because the trees had been felled at two of the sites before PAI was measured, the LAI-2000 measurements were made at comparable sites in the vicinity. Growth efficiencies (m<sup>3</sup> wood m<sup>-2</sup> leaf area year<sup>-1</sup>; Waring 1983), were calculated from the  $L$  and  $V$  data.

### Hydraulic conductivity and the vulnerability curves

Hydraulic conductivity and xylem vulnerability to embolisms were measured by a modification of the dehydration technique of Sperry et al. (1988), as described by Pammenter and Vander Willigen (1998). Five to seven comparable branches (distal end diameters of 15 to 30 mm) from different trees were selected from the lower third of the canopy, about 15 m above ground. Because of the aboveground die-back of Clone GG at the xeric site, measurements were made on coppice shoots of similar dimensions. Hydraulic conductivity was determined by measuring the water mass flow through a branch connected to a constant pressure reservoir. Vulnerability curves were measured on excised branches that were allowed to dehydrate over a period of two to three days. During dehydration, five to seven measurements of water potential and the corresponding hydraulic conductivity were taken. After a dehydration period, water in the tissue was allowed to equilibrate for 1 to 1.5 h. At the end of the experiment, the branch was flushed at a pressure of approximately 200 kPa for 20 min. After measurement of maximum conductivity, functional xylem was stained by passing safranin dye (0.05%) through the distal end of the branch. Functional xylem cross-sectional area and the area of leaves distal to the excised branch were measured. Conductivity data were then expressed as xylem specific conductivity ( $k_s$ ) and leaf specific conductivity ( $k_l$ ).

The exponential sigmoidal equation,  $PLC = 100/(1 + \exp(a(\Psi - b)))$  was fitted to the vulnerability curve data (Pammenter and Vander Willigen 1998); where PLC is the percent

loss of conductivity,  $\Psi$  is water potential, and  $a$  and  $b$  are constants. Coefficient  $a$  is related to the gradient of the curve or the water potential range over which conductivity is lost and  $b$  affects the lateral position of the vulnerability curve on the  $\Psi$  axis and gives the water potential corresponding to 50% loss of conductivity ( $PLC_{50}$ ). Fitting an equation to the data permitted evaluation and statistical comparison of the coefficients of the equation, thus providing objective comparisons of the vulnerability curves.

#### Field measurements

Branches were collected from the crowns of the trees before dawn and at midday on calm, sunny days, as described by Pammenter and Vander Willigen (1998). Water potentials were measured on minor shoots with a Scholander pressure chamber and initial and maximum hydraulic conductivities of the excised branches were measured by the technique described above.

## Results

#### Growth

At the time of the study, the trees were approximately 7 years old. There was a significant effect of site on trunk volume ( $P < 0.001$ ), with trees at the mesic sites having greater trunk volumes than trees at the xeric site (Figure 1A). When Clone GU, which had the greatest trunk volume, was excluded from the two-way ANOVA, because it was not grown at the xeric site, there were no clonal effects on trunk volume. A one-way ANOVA across clones within the mesic and xeric sites separately showed that the GC clones exhibited the poorest growth, with trees of Clone GU having significantly greater trunk volumes than trees of Clone GG at the mesic site (Figure 1A). There were no significant differences in  $L$  between xeric and mesic sites, within a clone, or among clones within sites (Figure 1B).

#### Hydraulic characteristics

Because there were no significant seasonal differences in any of the hydraulic characteristics measured, winter and summer data were combined for each clone and site. A two-way ANOVA revealed significant site effects on  $k_s$  and  $k_l$ , with trees growing at mesic sites having higher conductivities than trees

growing at the xeric site (Figure 2). (Because Clone GU occurred only at a mesic site, this clone was excluded from the two-way ANOVA.) There was no site effect on the Huber value (HV, ratio of functional xylem area to leaf area supplied). Although the two-way ANOVA did not indicate a significant clonal effect on any of the measured hydraulic parameters, a one-way ANOVA across clones within mesic and xeric sites independently indicated a small but significant clonal effect on the hydraulic properties of trees at the xeric site (Figure 2). The two-way ANOVA showed a significant site  $\times$  clone interaction on the measured hydraulic parameters.

There was a positive correlation between growth efficiency and maximum  $k_s$  (Figure 3,  $R^2 = 0.68$ ,  $P = 0.011$ ) that was based primarily on site effects rather than on clonal differences. Because Huber values were not significantly different across clones and sites,  $k_l$  should vary in parallel with  $k_s$ ; however, the correlation between  $k_l$  and tree growth was not significant ( $R^2 = 0.48$ ,  $P = 0.125$ ). An explanation for the lack of correlation between  $k_l$  and tree growth is that Clone GG at the mesic site was an outlier, having the highest  $k_l$  but lowest trunk volume. When this datum point was removed from the analysis, the correlation between  $k_l$  and trunk volume was significant ( $R^2 = 0.97$ ,  $P < 0.0005$ ).

#### Vulnerability to cavitation

Because there were no effects of season or site on the vulnerability curves for each clone (Pammenter and Vander Willigen 1998), data for each clone were pooled to assess clonal differences in the vulnerability of the xylem to cavitation. The coefficients of the vulnerability curves of each clone are given in Table 2 and the fitted lines are illustrated in Figure 4.

The gradient of the vulnerability curves (coefficient  $a$ ) was steeper for Clone GU than for Clone GG, which, in turn, was steeper than for the two GC clones. The water potential corresponding to 50% loss of conductivity (coefficient  $b$ ) was significantly higher in Clone GG than in the other clones, which did not differ from each other (Table 2). Clone GG suffered cavitation events at higher water potentials, and conductivity was lost over a narrower range of water potentials compared with the GC clones (Figure 4), which initiated loss of conductivity at lower water potentials and lost their ability to conduct water over a much wider range of water potentials (Figure 4). Losses of conductivity measured in branches excised at mid-

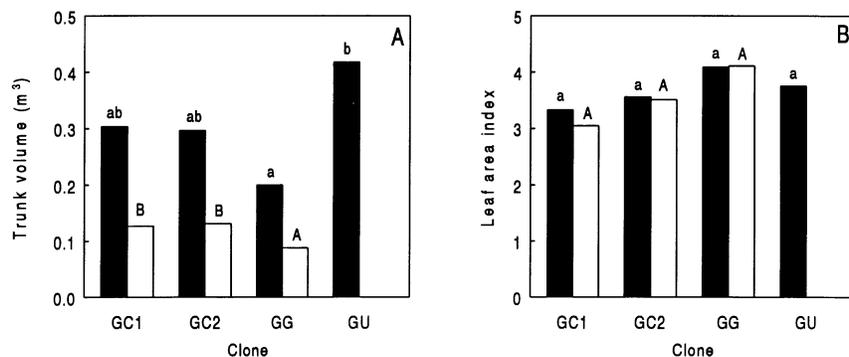


Figure 1. (A) Trunk volumes of four *Eucalyptus* clones, calculated from DBH and height measured for the center row of trees within each plot at the mesic (filled bars) and xeric (open bars) sites. (B) Leaf area indices of the four *Eucalyptus* clones measured at comparable mesic (filled bars) and xeric (open bars) sites. Letters represent mean separation by Scheffé's multiple range tests and show comparisons within the mesic (lower case letters) and xeric (upper case letters) sites separately ( $P < 0.05$ ,  $n = 3-10$ ).

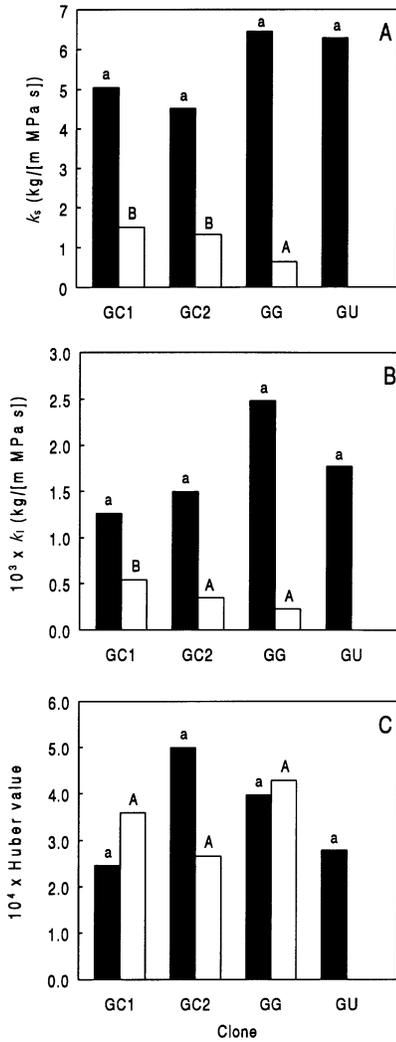


Figure 2. Maximum xylem specific conductivity,  $k_s$  (A), maximum leaf specific conductivity,  $k_1$  (B) and Huber values (C) of branches from four *Eucalyptus* clones at the mesic (filled bars) and xeric (open bars) sites. Data from the summer and winter sampling periods were pooled. Letters represent the mean separation by Scheffé's multiple range tests and show comparisons within the mesic (lower case letters) and xeric (upper case letters) sites separately ( $P < 0.05$ ,  $n = 5-8$ ).

day were within 13% of those predicted from the vulnerability curves.

During water stress it is not so much the proportion of conductivity lost that is important, but the hydraulic conductivity that remains to supply the leaves with water. We used maximum  $k_1$  values (Figure 2B) and the relationship between conductivity loss and water potential, to model actual  $k_1$  values against decreasing water potentials (Figure 5). Predawn and midday water potentials measured in both summer and winter are shown in Table 3. There were no differences in  $k_1$  between season, site or among clones. Predawn  $k_1$  of branches of trees growing on the xeric site was considerably lower than midday  $k_1$  of branches of trees on the mesic site. The same proportional loss of  $k_1$  is likely to have more deleterious effects in trees on the xeric site than in trees on the mesic site.

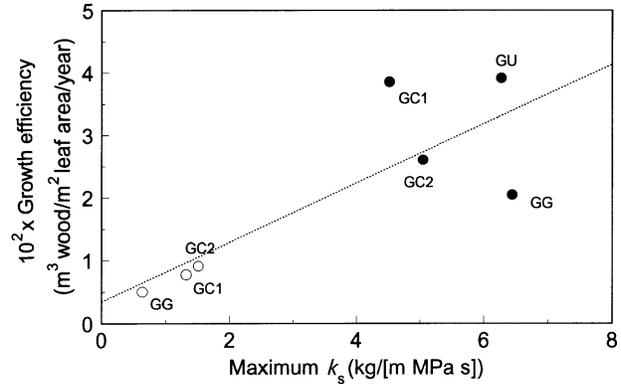


Figure 3. Relationships between maximum xylem specific conductivity,  $k_s$ , of branches and growth efficiency of 7–8-year-old trees of four *Eucalyptus* clones growing at the mesic (●) and xeric (○) sites. The correlation coefficient for the linear regression is 0.68 ( $P = 0.010$ ).

Table 2. Values of the coefficients of the exponential equation fitted to the vulnerability curves. Values followed by different letters are significantly different (Scheffé's multiple range tests,  $P < 0.05$ ).

Coefficient	Clone GC1	Clone GC2	Clone GG	Clone GU
<i>a</i>	1.94 a	1.76 a	2.25 b	2.80 c
<i>b</i>	-1.75 a	-1.77 a	-1.31 b	-1.50 a

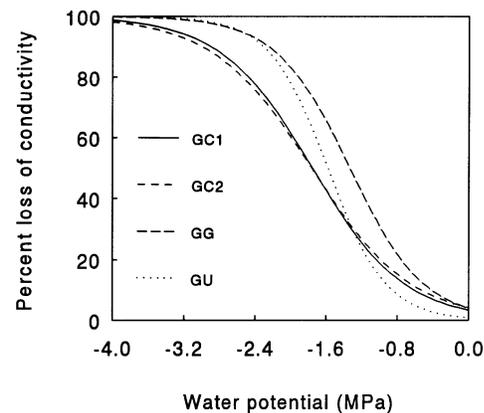


Figure 4. Vulnerability of xylem to cavitation in branches from 7–8-year-old trees of four *Eucalyptus* clones. Curves were calculated from the combined data for seasons and sites (Pammenter and Vander Willigen 1998).

### Discussion

We characterized the relationships between hydraulic characteristics and growth, and between vulnerability to cavitation and response to drought, in four closely related *Eucalyptus* clones. Differences in xylem specific and leaf specific conductivities were more closely related to water availability (mesic versus xeric site) than to genetic makeup (clone), conductivi-

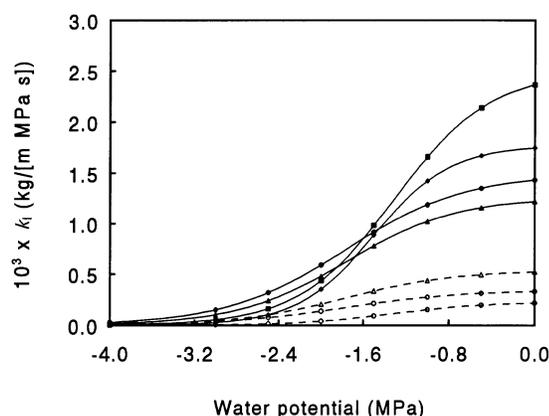


Figure 5. Modeled relationship between water potential and leaf specific conductivity,  $k_1$  of branches from 7- to 8-year-old *Eucalyptus* trees. Values of  $k_1$  were calculated from estimates of maximum conductivity (Figure 2) and the loss in conductivity with decreasing water potential (Figure 4). Symbols: GC1 =  $\blacktriangle$ ,  $\triangle$ ; GC2 =  $\bullet$ ,  $\circ$ ; GG =  $\blacksquare$ ,  $\square$ ; and GU =  $\blacklozenge$ ; data from mesic sites = closed symbols and solid lines; and data from xeric sites = open symbols and dashed lines.

ties being higher in trees at mesic sites than in trees at xeric sites (Figure 2). A similar trend in xylem specific conductivity has been found in other species (Shultze and Mathews 1988, Shumway et al. 1991, 1993).

In branches, the relative allocation of wood to leaves, as measured by the Huber value, was similar across clones and between sites (Figure 2), such that leaf specific conductivity followed a similar pattern to xylem specific conductivity. This observation contrasts with those of Shumway et al. (1991), Mencuccini and Grace (1995) and Kuuluvainen et al. (1996), who found that Huber values and  $k_1$  increased with decreasing water availability. Leaf area index and hence leaf area per tree, was also constant across clones and sites.

The values of xylem specific and leaf specific conductivities measured in this study were high compared with values reported for other trees and are in the same range as those of gap colonizers and some tropical tree species (Tyree et al. 1991, Machado and Tyree 1994, Patiño et al. 1995). Because the study clones have been highly selected for growth rates and wood properties, their hydraulic properties may bear little resemblance to the wild types.

Vulnerability curves differed among clones, but not between sites (Table 2, Figure 4, Pammenter and Vander Willigen 1998). The shapes of these curves agree well with the observed drought tolerance of the clones (B. Verbizier, personal communication). Clone GG, which is predicted to lose conductivity over a narrow range at high water potentials, suffered considerable (90%) aboveground die-back at the xeric site during the 1992 drought. The GC clones are relatively drought tolerant, and their vulnerability to cavitation indicates a gradual loss of conductivity over a wide range of water potentials. Similarly, Neufeld et al. (1992) reported that, in clonal material of sugar cane, differences in drought susceptibility predicted from vulnerability curves closely match the observed differences in drought tolerance. However, the close correlation between observed drought sensitivity and that predicted from vulnerability curves could also be associated with the degree of drought sensitivity of a species. Compared with other plants, both sugar cane and the *Eucalyptus* clones could be classified along with *Ochroma pyramidale* (Cav.) Urb., *Shefflera morotoni* (Aublet) McGuire, Steyermark, Frodin and *Ceratonia siliqua* L. as drought-evaders, exhibiting high  $k_1$  and thus low xylem pressure potentials and high vulnerability to conductivity loss (Salleo and Lo Gullo 1989, Zotz et al. 1994).

The importance of vulnerability to cavitation must, however, be considered in relation to the ability of the plant to conduct water. Because trees grown at the mesic sites had high conductivities, the degree of cavitation experienced by these trees at midday (corresponding to a water potential of around  $-1.25$  MPa) may not adversely affect the supply of water to their leaves (Figure 5). Trees on the xeric site did not show this excess conducting capacity and thus were more susceptible to water stress, not only because reduced soil water availability is likely to generate lower xylem water potentials, but also because conductivity loss is likely to have a greater impact on these trees relative to trees at the mesic sites. To prevent catastrophic embolism cycles (Tyree and Sperry 1988), trees at the xeric site would have had to reduce transpiration, by decreasing stomatal conductance, at higher water potentials than trees at the mesic sites, which in turn could lead to reduced carbon assimilation.

Leaf specific conductivity is related to transpiration rate ( $E$ ) by  $k_1 = E/(dP/dx)$ , where  $dP/dx$  is the hydrostatic pressure gradient in the xylem (Tyree and Ewers 1991). Because water potentials and branch heights were similar across sites, the

Table 3. Predawn and midday xylem water potentials measured in winter and summer of four *Eucalyptus* clones growing on mesic and xeric sites.

Clone	Site	Winter		Summer	
		Predawn $\Psi$ (MPa)	Midday $\Psi$ (MPa)	Predawn $\Psi$ (MPa)	Midday $\Psi$ (MPa)
GC1	Mesic	$-0.21 \pm 0.11$	$-1.16 \pm 0.16$	$-0.24 \pm 0.07$	$-1.35 \pm 0.21$
	Xeric	$-0.19 \pm 0.09$	$-1.23 \pm 0.18$	$-0.22 \pm 0.11$	$-1.21 \pm 0.17$
GC2	Mesic	$-0.26 \pm 0.13$	$-1.22 \pm 0.15$	$-0.25 \pm 0.13$	$-1.14 \pm 0.17$
	Xeric	$-0.23 \pm 0.10$	$-1.42 \pm 0.20$	$-0.26 \pm 0.10$	$-1.30 \pm 0.22$
GG	Mesic	$-0.18 \pm 0.11$	$-1.33 \pm 0.17$	$-0.24 \pm 0.12$	$-1.25 \pm 0.14$
	Xeric	$-0.22 \pm 0.11$	$-1.10 \pm 0.14$	$-0.28 \pm 0.08$	$-1.23 \pm 0.23$
GU	Mesic	$-0.26 \pm 0.08$	$-1.12 \pm 0.21$	$-0.25 \pm 0.12$	$-1.26 \pm 0.19$

higher  $k_1$  of branches of trees at mesic sites implies higher transpiration rates at the mesic sites than at the xeric sites. The positive correlation between  $k_1$  and growth efficiency (Figure 3) may be a result of efficient water supply to the leaves at the mesic sites permitting high stomatal conductances and hence high rates of carbon assimilation relative to leaves at the xeric site. Although no data on gas exchange rates are available to support this suggestion, it is conceptually similar to the hydraulic limitation hypothesis relating change in growth rate with tree age and the maximum height that is attained (Ryan and Yoder 1997). This hypothesis suggests that the increased hydraulic resistance associated with increased path length or wood age leads to a reduction in stomatal conductance early in the day, thus preventing the development of xylem pressure gradients steep enough to cause significant cavitations. Sperry et al. (1993) and Sperry and Pockman (1993) have demonstrated that experimental reduction of  $k_1$  by stem notching or injection of air into the xylem could bring about a reduction in stomatal conductance and transpiration without decreasing xylem water potential.

In conclusion, these studies with closely related clones of *Eucalyptus* species have demonstrated that xylem hydraulic characteristics such as xylem specific conductivity and leaf specific conductivity are more closely related to water availability than to genetic makeup. Vulnerability of xylem to cavitation differed among clones, rather than with water availability, and the most vulnerable clone was the most drought sensitive. There was a positive correlation between xylem specific conductivity and growth efficiency, but the nature of this relationship remains to be elucidated.

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