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Vulnerability to stem xylem cavitation in three *Eucalyptus* spp. clones of 14 months old at two water regimes

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ABSTRACT

The response of three Eucalyptus spp. clones (GC550, GU210 and TAG14) to soil moisture condition was assessed by means of plant water status, leaf gas exchange and stem xylem vulnerability. Data for 14 months old grown in 25 l pots clones were collected on the diurnal variation in leaf water potential (ψ_l), stomatal conductance (g_s) and net CO_2 assimilation rate (A). Main stem xylem vulnerability was assessed using ultrasonic acoustic emissions (UAE). Vulnerability of the main stem was assessed as the leaf water potential corresponding to the maximum rate of acoustic emissions (ψ_l, EPH_{max}), and as the critical water potential triggering cavitation events, calculated as the mean of the water potentials of data points lying between 5 and 10% of the total accumulated emissions (cUAE,%). Early stomatal closure was apparent, maintaining $_l$ constant during the middle of the day in all clones. Stem xylem vulnerability, assessed as both ψ_l,EPH_{max} and ψ_{CAV},cUAE,% showed that the main stem of GC550 was more vulnerable than other two clones, and that low watered plants were more resistant to xylem cavitation than those receiving high water. Midday ψ_l fell below the vulnerability values assessed by both measures across treatments and clones, suggesting lack of stomatal control preventing stem xylem cavitation.

Keywords: *Eucalyptus* spp clones, Stem xylem cavitation, Stomatal limitation, Water supply,

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1. Introduction

The movement of water through the soil-plant-atmosphere continuum, driven by transpiration, supplies water and nutrients to various parts of the plant. The high tensions in the xylem causes dissolved gases to come out of solution into the vapour phase. As the water is under tension, this micro-void will expand explosively to fill the conduit, a process known as cavitation. The cavitated conduit is at a pressure close to a vacuum, and air will come out of neighbouring

wet tissue (and diffuse from the outside of the stem) to fill the conduit with air at atmospheric pressure, forming an embolism. An embolized conduit will not conduct water until ψ_p returns to near-atmospheric pressure and refills the conduit cavitation [1, 2, 3]. There are reports that cavitation predominantly induced in the xylem as a result of drought [4, 5] and freezing [6, 7], temporarily reduces xylem water transport. A reduced water potential can cause reduction in cell expansion, wall synthesis, protein synthesis, stomatal conductance and photosynthesis and an increased xylem dysfunction by cavitation events [8]. Stomatal closure reduces both loss of water and uptake of carbon dioxide so that carbon assimilation by leaves decreases in the water stressed plants [9]. Formation of embolism may be a common occurrence and plays an important role in the inhibition of shoot growth at moderate water deficits [10].

Cavitation events in the tissues can be monitored microscopically [1], hydraulically [11], anatomically [12], and acoustically [13]. Ultrasound acoustic emissions associated with cavitation events [14, 1, 15] are presumably produced by the vibrating walls of cavitating xylem conduits [16]. Both field [17] and *in situ* measurements have been demonstrated, using an UAE on plant material excised from gymnosperms [13] and from angiosperms [18]. Detected UAE data are available for various plant organs [12, 19, 20, 21]. Comparative studies made by [22, 23, 24] demonstrated that cavitation quantified by acoustic emission, hydraulic measurements on air-dehydrated tissue and air pressure injected tissue gave similar results. However, the acoustic emissions technique is nondestructive and allows continuous monitoring [22, 25, 20].

Present study

The *Eucalyptus* trees produce most of the hardwood in the world, mainly used for mining timber, chip production and pulpwood industries. Drought caused severe mortality of some clones, whereas other clones survived drought [26]. Such losses have raised concern and call for improving silvicultural practices by selecting water use efficient clones that would not only survive but also continue to be productive under restricted water conditions [27]. Such clones need to be assessed physiologically under different conditions or treatments to see if they meet expectations. To our knowledge, few studies have been undertaken into the xylem cavitation of fast and tall growing *Eucalyptus* species or hybrid clones (family Myrtaceae). Studies like those of [28, 26] measured xylem vulnerability in stems and branches only, using the xylem air-permeability method and the low pressure flow conductivity apparatus, respectively. The specific objectives of the present study were: (a) to measure the impact of high and low watering treatments on stem xylem cavitation of potted plants of three selected *Eucalyptus* spp. clones and relate these to leaf physiological properties such as water potential, stomatal conductance and gas exchange characteristics, (b) to assess the effects of treatment and clone on stem vulnerability to cavitation. This involved non-destructive detection of cavitation events using an ultrasonic acoustic emission detector and, (c) to determine if high vulnerability to cavitation leads directly to reduced gas exchange or not.

2. Materials and Methods

2.1. Plant materials and samples

Three *Eucalyptus* spp. clones were selected on the basis of their drought susceptibilities, as assessed from the experiences of field foresters. The clones chosen were GC550, a *Eucalyptus grandis x camaldulensis* hybrid, GU210, an *Eucalyptus grandis x urophylla* hybrid, and TAG14, a pure *Eucalyptus grandis* clone. TAG14 is considered to be drought susceptible, GC550 relatively drought tolerant, whilst the drought response of GU210 which is a recently developed hybrid, is not known. Planting material (rooted macro cuttings) was obtained from Mondi Forests, Tree Improvement Research Unit, Hilton, South Africa. Twelve established cuttings of each of the three *Eucalyptus* spp. clones (GC550, GU210 and TAG14) were planted in 25 l pots, and half were subjected to the 'high' watering treatment and the other half to 'low' water. Planting date was the 24th of February 2000. The 36 pots were arranged in 4 rows (three rows of 12 pots). Within a row pots were 0.1m apart and rows were 0.3m apart. This spacing, which was considerably less than the commercial practice in the field (2 m x 3 m). The potting medium was a mixture of four parts sand, four parts loam and three parts of compost (4:4:3). Plants were grown outdoors in the greenhouse complex, School of Life and Environmental Sciences, University of Natal, Durban, South Africa, fully exposed to natural solar radiation. The 'high water' treatment was designed to mimic the annual rainfall (1280-mm) in the region (16 y of data at KwaMbonambi, Tree Improvement Research, Zululand Division, Mondi Forests, KwaMbonambi, South Africa) where the selected clones were grown, and the low water treatment was at a level of 70% of high water treatment. The surface area (width and height) of the pot was calculated, and the volume of a column of water of this area and 1280 mm of high rainfall data gave the total water to be added to the high water treatment over a year. Macronutrient and fungicides were applied after from six months of planting.

2.2. Diurnal measurement of leaf physiology and xylem cavitations

In this study, diurnal measurements of leaf physiology were taken over the period from December 17th 2000 to March 31st 2001. Measurements were taken from two or three leaves per plant, from upper to mid canopy, at hourly intervals from 06.00 to 12.00, and then every two hours until 18.00. Water potentials were measured non-destructively on potted plants using L-51 leaf hygrometer chambers and an HR-33T Dew Point Microvoltmeter (Wescor Inc., Logan, Utah, U.S.A) in the dew point mode. The leaf hygrometer chambers were attached to the leaves a day prior to the measurements, to ensure equilibration for more than 12 hrs. Measurements of net CO_2 assimilation rate (A), transpiration (E) and stomatal conductance (g_s), were recorded with a portable infrared gas analyzer (model LI-6400, Li-Cor Inc., Lincoln, NE, U.S.A), on leaves adjacent or opposite to the leaves concurrently being measured for leaf water potential.

The daily course of xylem cavitation events was followed by detection of ultrasonic acoustic emissions (UAE) using a model I15I, ultrasonic sensor and preamplifier model 4615, Physical Acoustic Corp., Princeton, NJ, USA from the main stems of the plants being studied for water relations and gas exchange. An UAE sensor was mounted on the main stem 0.2 m above the soil surface at 18.00 h the day prior to the day that measurements, of the stem over-bark diameter were made. A software package written for use with a personal computer was used to download the record of cumulated events (CE) and events per hour (EPH) during the measured time intervals. EPH were plotted in relation to time, and as concurrent leaf water potentials were measured, EPH could be plotted as a function of leaf water potential concurrently with stomatal conductance. Also, cumulated UAE were expressed as a percentage of the first plateau maximum corresponding to the cumulative number of UAE recorded at the time, as described by [20]. The percentage of cumulated UAE (cUAE, %) was also plotted against water potential recorded concurrently.

3. Results

3.1. Diurnal patterns of physiological parameters

Changes in leaf water potential from 06.00 h to 18.00 h were measured. Leaf water potential decreased in all three clones from morning to midday, and then recovered slightly in the afternoon, although this was less marked in TAG14. Leaf water potential was marginally higher in high watered than low watered plants of GU210 and TAG14, but no difference was apparent between watering treatments in GC550. However, pooled values of midday xylem water potentials (Table 1) revealed that neither watering treatment ($n=6$; $F=0.41$, $P=0.524$) nor clone ($F=0.25$, $P=0.781$) had any significant effect.

3.2. Stem xylem cavitation

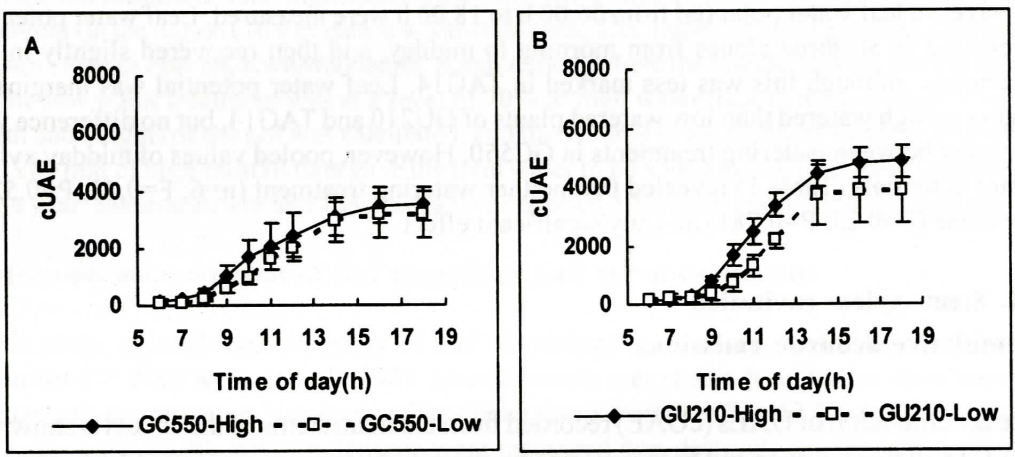
Cumulative acoustic emissions

The accumulation of UAEs (cUAE) recorded from the main stems of the shoots is shown in Fig.1. In all three clones and both watering treatments there was a rise in UAEs from early morning, levelling off around midday or shortly thereafter. The accumulation of events corresponded with the decrease in leaf water potential. High watered plants tended to show more total events of cUAE than those subjected to low water; there was a significant difference in total cUAE at 09.00 h ($F=5.02$, $P=0.033$) and calculated EPH at 08.00 h and 09.00 h ($P<0.014$), where high watered clones produced a higher number of cUAE events than low watered clones. This difference could be a result of differences in stem thickness. The high-watered plants had greater over-bark diameter at the site of mounting of the detector ($F=40.77$, $P=0.011$) (see Table 1). Thus in the high-watered plants the detector was in

contact with a greater area of stem, hence detected more events. However, there were no significant differences in the total cUAE (for 12 hours) between watering treatments (F=1.94, P=0.172).

Events per hour (EPH)

The rate of accumulation of acoustic events, together with the corresponding stomatal conductances are shown in Fig.2. Maximum events per hour (EPH_{max}) tended to be slightly higher in high watered plants than those receiving low water, except for GC550. EPH_{max} occurred later in the morning than maximum stomatal conductance, indicating that the partial stomatal closure that occurred was inadequate to prevent further cavitation events (transpiration continued to increase in response to increasing VPD, data not shown). EPH_{max} occurred slightly earlier in high watered plants (09.00 h to 10.00 h) than in the low watered plants (10.00 h to 11.00 h). Leaf water potentials at EPH_{max} are shown in Table 1. Leaf water potential corresponding to EPH_{max} were lower in low watered plants in GU210 and TAG14, but a two-way ANOVA showed that neither watering treatment (F=2.01, P=0.165) or clone (F=0.19, P=0.823) had any significant effect on ψ_L at EPH_{max}.



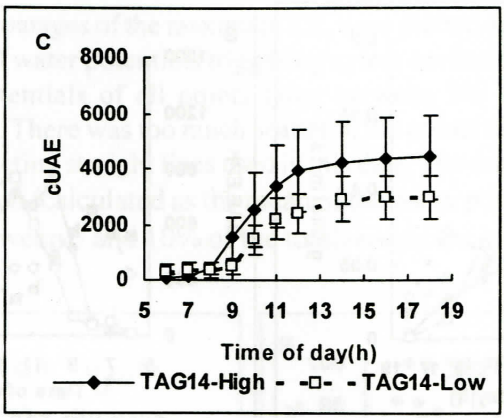


Figure 1: Accumulation of ultrasonic acoustic emissions (cUAE), indicating xylem cavitation events in the main stem of three *Eucalyptus* spp. clones grown for 14 months in 25 l pots, and subjected to high or low watering regimes. Error bars represent the ± SEM of the mean (n=6).

Table 1: Mean midday leaf water potential, mean leaf water potential measured at the time of EPH_{max}, mean threshold leaf water potential triggering xylem cavitation assessed from acoustic emission data (ψ_{CAV}cUAE,%) (see text for details) with the stem over-bark diameter where UAE sensor was mounted, of three *Eucalyptus* spp. clones grown for 14 months in 25 l pots, and subjected to high or low watering treatment. Means ±SEM (n=6). Letters represent (under each parameter) the means separation by Scheffe's multiple range tests, showing comparison within the high (upper case lettering) and low (lower case lettering) watering treatments separately ($P<0.05$).

Clones	Treatments	ψ Midday (MPa)	ψ_L,EPH_{max} (MPa)	ψ_{CAV},cUAE,% (MPa)	Stem OBD (mm)
GC550	High	-2.17 ± 0.44^{A}	-1.77 ± 0.18^{A}	-0.96 ± 0.21^{A}	14.70 ± 0.61^{AB}
GC550	Low	-2.04 ± 0.59^{a}	-1.67 ± 0.53^{a}	-0.73 ± 0.19^{a}	11.83 ± 0.44^{a}
GU210	High	-2.10 ± 0.57^{A}	-1.59 ± 0.55^{A}	-1.02 ± 0.16^{A}	16.03 ± 0.56^{A}
GU210	Low	-2.41 ± 0.65^{a}	-2.30 ± 0.58^{a}	-1.44 ± 0.16^{ab}	12.19 ± 0.65^{a}
TAG14	High	-2.17 ± 0.67^{A}	-1.40 ± 0.33^{A}	-0.81 ± 0.22^{A}	13.13 ± 1.30^{B}
TAG14	Low	-2.80 ± 0.55^{a}	-2.15 ± 0.41^{a}	-2.31 ± 0.43^{b}	11.57 ± 0.49^{a}

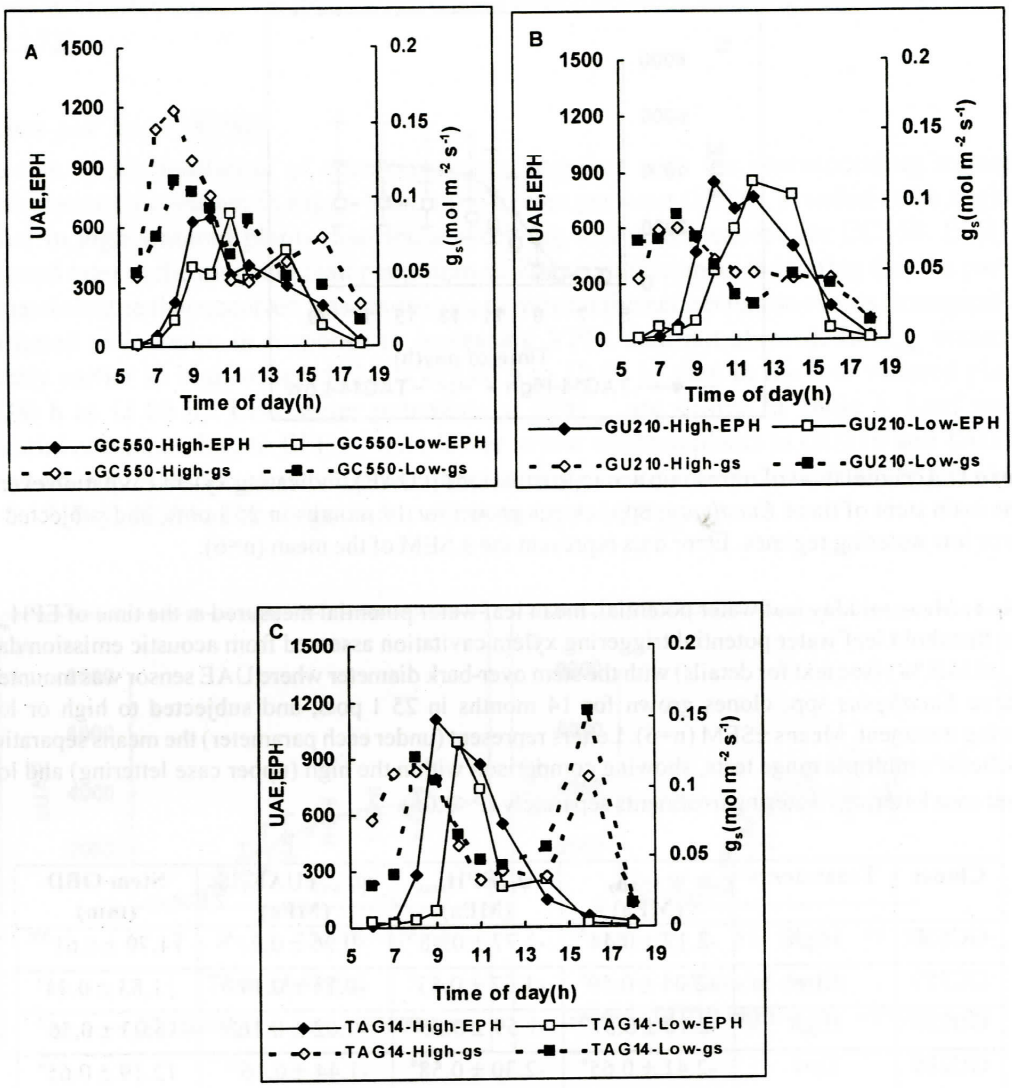


Figure 2: Concurrently measured rates of ultrasonic acoustic emissions (events per hour; UAE, EPH; n=6) and stomatal conductances of three *Eucalyptus* spp. clones grown for 14 months in 25 l pots, and subjected to high or low watering treatment.

UAE as a percentage of maximum cumulated cavitation events

UAEs, expressed as percentages of the maximum CE, were plotted against leaf water potential (Fig. 3). The critical leaf water potentials triggering xylem cavitations were estimated as the means of the water potentials of all points lying between 5% and 10% of total cUAE (ψ_{CAV},cUAE,%) [20, 21]. There was too much scatter in the points to undertake the analytical procedure of two intersecting straight lines used in this data. The critical leaf water potentials triggering xylem cavitation (calculated as the mean of the water potentials corresponding to acoustic emissions between 5 and 10% of the total) are shown in Table 1.

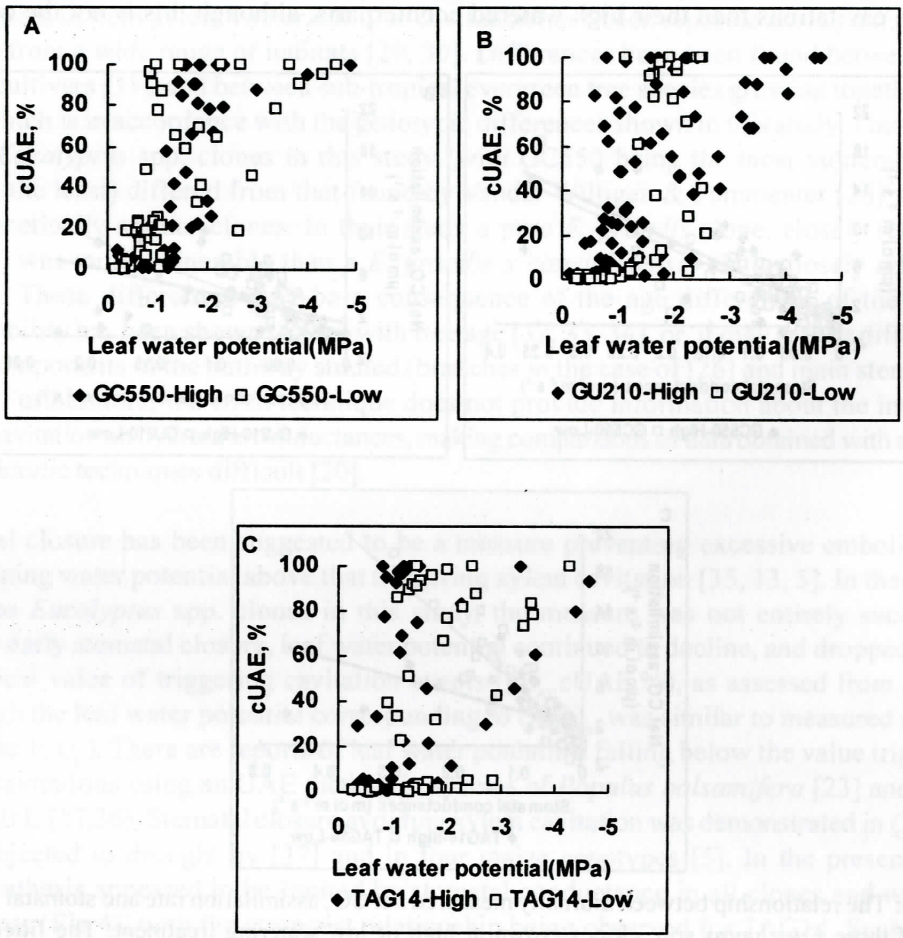


Figure 3: Cumulated UAE (cUAE) from the main stem, expressed as percentage of the maximum, plotted against leaf water potential for three *Eucalyptus* spp. clones grown at high or low watering treatment.

Two-way ANOVA showed that both watering treatment (F=11.00, P=0.004) and clone (F=6.21, P=0.009) had significant effects. In GU210 and TAG14 the water potential triggering cavitation events was lower in low watered than high watered plants, whereas in GC550 the opposite was observed. The two-way ANOVA showed a significant interaction between watering treatment and clone interaction (F=8.61, P=0.002) on the measured initiation leaf water potentials triggering xylem cavitations. Also, the critical water potential was higher in GC550 than in the other clones. These patterns were similar to those of water potentials corresponding to EPH_{max} (Table 1), even though the treatment differences in EPH_{max} were not significantly different. The data suggest that low watered plants of GU210 and TAG14 were less vulnerable to xylem cavitations than their high watered counterparts, although this is not the case for GC550.

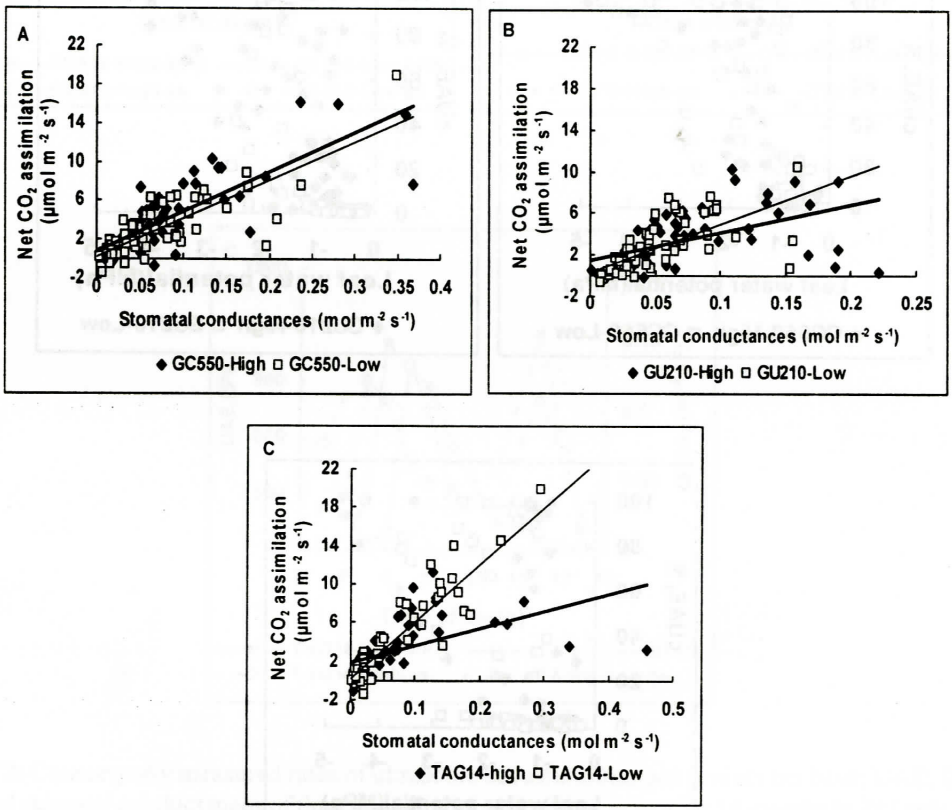


Figure 4: The relationship between diurnally measured net CO_2 assimilation rate and stomatal conductances of three *Eucalyptus* spp. clones grown at high or low watering treatment. The fitted linear regression lines are for high (bold) and low (thin) watered, respectively.

3. Discussion

Vulnerability to xylem cavitation of the main stem, detected from the critical leaf water potential triggering xylem cavitation (ψ_{CAV}cUAE,%) differed significantly between treatment and among clones, with a positive interaction between the two factors. This is in contrast to a study by Vander Willigen & Pammenter [26], who showed that the xylem vulnerability (quantified by an hydraulic method) of branches of *Eucalyptus* spp. clones was influenced by genotype but not by water availability (mesic or xeric sites). The ψ_L,EPH_{max} was slightly lower than ψ_{CAV}cUAE,%, and vulnerability assessed this way showed no significant differences between treatments and clones. However, ψ_L,EPH_{max} showed similar patterns to ψ_{CAV}cUAE,% Differences in stem xylem vulnerability to cavitation have been reported among a number of species from a wide range of habitats [29, 30]. Differences have been found between three coffee cultivars [31], and between sub-tropical evergreen tree species growing together [18], all of which is in accordance with the genotypic differences shown in this study. The ranking of the *Eucalyptus* spp. clones in this study (with GC550 being the most vulnerable, and TAG14 the least) differed from that found by Vander Willigen & Pammenter [26] working with genetically similar clones. In their study a pure *E. grandis* clone, closely related to TAG14, was more vulnerable than a *E. grandis x camaldulensis* clone closely related to GC550. These differences may be a consequence of the age differences of the plants. Vulnerability has been shown to vary with tree age [32, 33, 34], or, it may reflect differences in the components of the pathway studied (branches in the case of [26] and main stem in this study). Furthermore, the UAE technique does not provide information about the impact of xylem cavitation on hydraulic conductances, making comparisons of data obtained with acoustic and hydraulic techniques difficult [20].

Stomatal closure has been suggested to be a measure preventing excessive embolisms by maintaining water potential above that triggering xylem cavitation [35, 13, 5]. In the case of the three *Eucalyptus* spp. clones in this study, the measure was not entirely successful. Despite early stomatal closure, leaf water potential continued to decline, and dropped below the critical value of triggering cavitation events (ψ_{CAV}cUAE,%), as assessed from cUAEs (although the leaf water potential corresponding to EPH_{max} was similar to measured midday ψ_L, Table 1; ψ_L). There are reports of leaf water potentials falling below the value triggering xylem cavitations using an UAE method in species of *Populus balsamifera* [23] and *Pinus sylvestris* L.[17,36]. Stomatal closure avoiding xylem cavitation was demonstrated in *Quercus* spp. subjected to drought by [37] and in four maize genotypes [5]. In the present study photosynthesis appeared to be limited by stomatal conductance in all clones and watering treatments (Fig 4), with the strongest relationship being observed for TAG14. Such strong stomatal limitation of photosynthesis, possibly preventing the development of excess xylem tension avoiding a runaway embolism cycle during period of severe water stress, is associated with the cost of decreased productivity. A model describing runaway embolism cycles by [38] has shown that xylem cavitation can be controlled by either stomatal closure or a reduction in

leaf area. When data for A and g_s were pooled across watering treatments, GC550 showed stronger relationship between these variables (r^2=0.65) than other two clones (r^2 <0.48). Furthermore, the total leaf area was significantly lower than that of the other two clones (Data not shown). These data are in accord with the higher vulnerability of GC550, although the lower leaf area did not prevent cavitations occurring. The question of whether vulnerability to cavitation is determined by genotype or whether growth conditions have an effect has been raised by [18]. There are reports that stem xylem vulnerability to cavitation, measured by hydraulic and UAE methods, was the same in a wet and dry site [39, 36, 26]. On the other hand, in this present study two of the clones were less susceptible to xylem cavitation under low than high watering conditions, and there are other reports of differences in xylem vulnerability between mesic and xeric sites consistent with this. [28] reported that seedlings of *E. camaldulensis* collected from a xeric environment showed lower xylem vulnerability than those collected from a mesic site. Similarly, a Douglas fir population from a mesic environment was more vulnerable to cavitation in both stems and roots than two dry site populations [40]. Furthermore, [41] found interpopulation variation in resistance to drought-induced xylem cavitation in *Populus trichocarpa* Torr. & A., with populations from moist environments showing less resistance to drought-induced xylem cavitation than those from dry environments. Also, [39] found that root xylem vulnerability of *Acer grandidentatum* was higher in the riparian (wet) than slope (dry) site. The differences between clones and the effect of watering treatment on the three *Eucalyptus* spp. clones in this study suggest that xylem vulnerability can be driven by the effect of soil water as well as genotype.

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