



Water potential and gas exchange did not reflect performance of *Pinus radiata* D. Don in an agroforestry system under conditions of soil-water deficit in a temperate environment

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Abstract

In order to understand how radiata pines respond to declining supply of soil-water in agroforestry systems, we monitored water potential in xylem (ψ_x), osmotic potential (π) and relative water content (q) for fascicles at pre-dawn and at mid-day for 3-year-old trees that were raised from either seedlings (Seedling) or from tissue culture (TC3 and TC4), and grown either alone (Control) or over lucerne (*Medicago sativa*) pasture (Lucerne). Water relations at dawn were mostly similar for all the pines, except late in the season when π was lower, bulk turgor pressure (P), deduced as the difference between ψ_x and π , was higher, for TC3 than for the other two pines. At mid-day, Seedling often had higher ψ_x and π , but because of its poor osmotic adjustment (OA) had lower P , than either TC3 or TC4. The cell walls were more elastic in Seedling with modulus of elasticity (e) of 6.5 MPa compared with 8.1 MPa for both TC3 and TC4, while loss of turgor was estimated to occur at ψ_x of -1.45 MPa for Seedling, -1.38 MPa for TC3 and -1.35 MPa for TC4. All trees irrespective of their origin had higher ψ_x , P , CO_2 assimilation (A), and stomatal conductance (g_s), but lower π , in Control than in Lucerne in which the soil profile was consistently drier. The trends in ψ_x , π , q and A did not reflect the known differences in dry weight of trees, P was in the order TC3 > TC4 > Seedling, consistent with previously reported tree weights. Both TC3 and TC4 had higher P , due to their larger OA , than Seedling, although the latter had higher A . Thus ψ_x and A that are routinely measured may not always adequately explain differences in growth amongst pines; it is advisable that π be determined to allow deductions of P be made when using water relations to analyse plant growth.

Introduction

Availability of soil-water is the key determinant of plant productivity in dry environments, more so in mixed communities where plants compete for the scarce resource. Reductions in transpira-

tion, CO_2 assimilation (A) (Watt et al., 2003) and water potential (Bandara et al., 1999; Sands and Nambiar, 1983) have been reported for pines subjected to reduced supply of soil-water due to inter-specific competition. Many terrestrial species maintain photosynthesis and other physiological functions during soil-water deficits by manipulating the various components of

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their tissue-water status as given by Turner (1981):

$$\psi = P + \pi \quad (1)$$

where ψ is water potential of the tissue (symplast and apoplast), P bulk turgor pressure (a measure of the sum of pressure exerted on cell walls) and π osmotic potential (a measure of solute accumulation). However, ψ is commonly estimated from the pressure needed to balance the force with which the water is held in the xylem (ψ_x) (Turner, 1981). High growth rates in pines have often been associated with high ψ_x (Attiwill and Cromer, 1982; Watt et al., 2003) and needle extension was reported to cease once ψ_x fell to -1.5 MPa (Sands and Correll, 1976). It is understood, however, that maintaining high P is more critical to plant growth since it is directly associated with stomatal function and hence photosynthesis (Hsiao et al., 1976; Morgan, 1984). When plants are subjected to declining supply of soil-water, they may actively accumulate solutes in their cells to lower π thereby ensuring continued flow of water into the cells to maintain high P at a given ψ_x . This process is termed *osmotic adjustment* (OA) because it involves active accumulation of solutes in response to low water potential (Zhang et al., 1999). This then ensures maintenance of physiological processes, especially photosynthesis (Hsiao et al., 1976; Morgan, 1984; Zhang et al., 1999).

Pines differ in their ability to withstand soil-water deficits, i.e., when water available in soil is below what is required by the plant to meet evaporative demand. For example, Rahman et al. (2003a, b) found that under water-limited conditions in Texas, USA, pine trees raised from seedlings maintained favourable water relations, by shutting their stomata, but achieved greater growth, than those trees developed from micro-propagation. While in the Canterbury region of New Zealand, where seasonal soil-water deficit is also common during the growing season, pines established from clonal tissue-culture produced up to 12% more total (shoot plus root) dry-matter than those raised from seedlings when grown with or without pastures (Bandara et al., 1999; Gautam et al., 2002, 2003; Peri et al., 2002). There was, however, no detailed characterisation of water relations in the latter study, but it was likely that differences in the growth of these pines

were associated with their ability for osmotic adjustment and, hence, maintenance of turgor, rather than with just high ψ_x alone. These trees were used in our current study with two objectives: (1) to characterise water relations and gas exchange for pines from three origins in response to groundcover treatments, and (2) to assess whether the known differences in growth of these pines could be explained by their water relations and gas exchange.

Materials and methods

Site

The study was undertaken at Lincoln University in the Canterbury region of New Zealand ($43^{\circ}38'$ S, $172^{\circ}26'$ E, 20 m altitude) between July 1993 and January 1994 in an agroforestry experiment involving a selection of pasture species and *Pinus radiata* on a free-draining silt loam soil. The experiment was established in 1990 using pine trees of five different origins, which were planted into four understorey pasture species and a control of bare ground. The trees were of the same genetic origin; the seedlings planted were either cloned through tissue culture or raised from seeds collected from open pollinated trees as described by Mead et al. (1993) who also presented further details of the genetics of trees and the treatments used here. The trees were transplanted into pre-sown pastures in 7 m rows with 1.4 m intra-row spacing producing a stand density of 1000 stems ha^{-1} , but were thinned progressively to 800 stems in 1992, and then to 600 stems in 1993. The same experiment was used in earlier studies (Bandara et al., 1999, 2004; Gautam et al., 2002, 2003; Peri et al., 2002; Yunusa et al., 1995a, b) that have given detail descriptions of soil and climate at the site. Although rainfall is more/less uniformly distributed (average 60 mm per month) throughout the year, hot conditions and high vapour pressure deficit of the air (D) in summer (December–February) cause high evaporative demands that are in excess of precipitation and so plants experience soil-water deficit during this time.

In the current study, we used trees that were raised from seedlings (Seedling) or from plantlets

developed through tissue culture (TC3 and TC4) and were transplanted over two understorey treatments of either bare ground (Control) or lucerne pasture (Lucerne); the former was kept mostly weed-free using herbicides. Both TC3 and TC4 were the same as Clone 3 and Clone 4 used by Gautam et al. (2002), and TC3 was also used by Bandara et al. (1999). Measurements of ψ_x and π were made monthly on three trees for each of the three types of pine. We used one-year-old fascicles chosen from the third uppermost fully expanded whorls on the sunny northern side of the trees. Details of the specific measurements are given below.

Xylem water potential (ψ_x) and relative water content (q) of fascicles

From each tree, 10 fascicles were picked from four whorls at pre-dawn (~0400 h) and at noon (between 11:30 and 12:30 h). The samples were kept in sealable plastic bags, which were placed in ice and transported to the laboratory where measurements were made within two hours of sampling. A pressure chamber (PMS Instruments, Corvallis, USA) was used to measure ψ_x on fascicles as described by Turner (1981). Another set of four fascicles per tree was used to estimate the relative water content (q) from their fresh weight (fw), turgid weight (tw) after floating in distilled water for 24 h, and dry weight (dw) after drying at 60 °C for 48 h:

$$q = \frac{(fw - dw)}{(tw - dw)} \quad (2)$$

Osmotic potential (π)

This was measured with a psychrometer (SC10A, Decagon Devices) on fascicles taken from the same whorls of the trees as used for ψ_x samples. A set of two fascicles were taken per tree, quickly placed in sealable plastic bags and kept in ice, and later transferred into a deep-freezer set at -105 °C for 18 h. The bags were placed under warm running tap for about 2 min to thaw the samples, which were then cut into pieces with a pair of sterile scissors and then placed in a disposable syringe to express the sap into sample cups of the

psychrometer. The cups were loaded into the psychrometer chamber and left to equilibrate for 1 h before measurement were made following the procedures described in the SC10A manual. We considered the dilution of the symplast by apoplastic water to be negligible and so it was not included in our analysis of π (e.g., Angadi and Entz, 2002; Clifford et al., 1998), because this dilution generally accounts for less than 6% of the symplast (D. Eamus, personal communication). We obtained P as the difference between π and ψ_x (Eq. 1); ψ_x at turgor loss was estimated from regression of P on ψ_x by subtending the points where the regression lines intercepted the 1:1 line (i.e., when $\pi = \psi_x$ and so $P = 0$ (Eq. 1) to y -axis as proposed by Morgan (1995). The modulus of elasticity (e) was taken as the slope of regression of P on q , i.e., $\Delta P / \Delta q$, following Melkonian et al. (1982).

Water relations at full turgor

Fascicles were collected from each tree as described above on 22 July 1993 and 4 January 1994. These were fully hydrated in a dark cold room (~5 °C) by standing the fascicles in distilled (reagent grade) water contained in Petri-dishes for at least 36 h. Two fascicles from each sample were frozen at -105 °C for 24 h before measurements to obtain osmotic potential at full turgor (π_{100}). OA was taken as the change in π_{100} between the two periods, i.e., situations of vastly different levels of supply of water, as used in other studies (Angadi and Entz, 2002; Augé et al., 2003; Jiang and Huang, 2001; Meier et al., 1992).

CO₂ assimilation and stomatal conductance

These were measured on fascicles in the whorls used for ψ_x with a portable infrared gas analyser (LiCor 6200, LI-COR Instruments, Lincoln, NE) between 0900 and 1200 h on clear days. The fascicles were inserted into the analyser chamber and the point of insertion marked to allow estimate of the surface area later. The surface areas of the fascicle inserted were obtained from the average diameter and length of their needles, assuming that the fascicle consisting of three needles formed a cylinder. The data for A and stomatal conductance in this paper are presented on this basis.

Soil water

We used a neutron-probe (Troxler 4300), which was calibrated for the site in an earlier study, to monitor soil-water over 1.0 m depth along two pre-installed aluminium access tubes located around the Seedling trees. The top 0.1 m of the profile was monitored with a Time Domain Reflectometry (TDR). Details of these measurements have been described previously (Yunusa et al., 1995a).

Data analysis

Analysis of variance was performed on all data using the univariate option in the General Linear Model within SPSS software package Version 10.0.5 (SPSS Incorp 1999). Means were compared using LSD at 5% significance level, unless stated otherwise. No significant interactions of groundcover and tree-type were observed on majority of the variables measured. Therefore, unless stated otherwise, the means presented here for groundcover treatments were pooled across tree-types and *vice versa* for groundcovers.

Results

Weather

The weather conditions (Figure 1) during the study period were typical of the region in that the winter (up to day 60) was colder, more humid and less windy than the following days that became increasingly windy, hotter, sunnier and drier. The study period was a particularly dry season in that even in the winter months (July and August) rainfall was much lower than evaporation with ratio of precipitation-to-evaporation of 0.35; this ratio fell progressively to 0.32 by October and to 0.26 by the end of the study. Thus the pines experienced water deficit for much of the growing season.

Groundcover influences on water relations

Water relations were largely similar for both groundcovers at dawn (Figure 2a–d). The ψ_x at pre-dawn differed between the two treatments only on day 84 (22 September), when it was lower for Lucerne than for Control. At mid-day

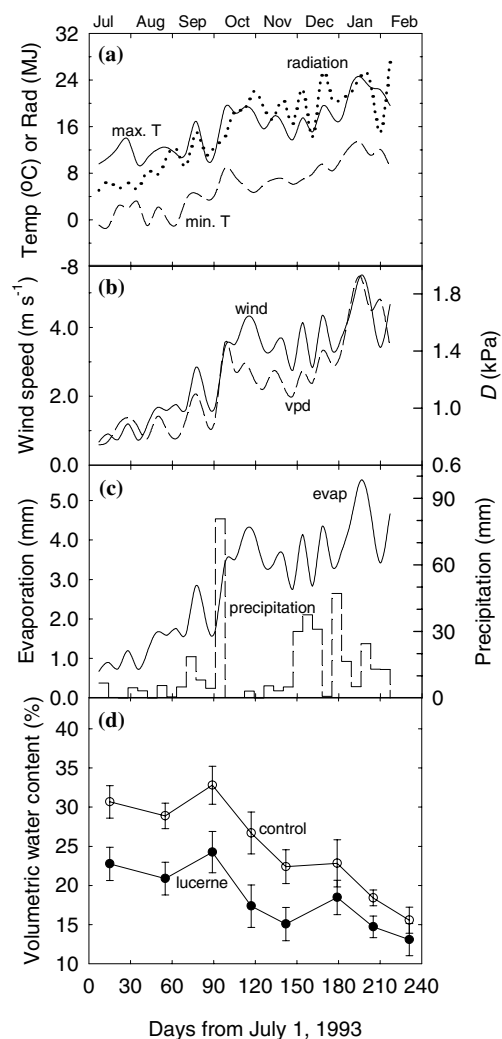


Figure 1. Weather conditions for Lincoln, New Zealand, in 1993/1994: (a) Minimum and maximum temperatures and radiation, (b) Wind speed and vapour pressure deficit (D), (c) Potential evaporation and totals for weekly precipitation, and (d) Volumetric water content (\pm standard errors of means) of the top 1.0 m of the soil around radiata pines grown either without (Control) or with lucerne groundcover.

(Figure 2e–h), ψ_x was generally more negative for Lucerne than for Control, with the difference being significant from September onwards and was due to a drier soil profile in Lucerne (Figure 1D). Fluctuations in ψ_x at midday for either groundcover was generally narrow (between -1.06 and -1.51 MPa), except for a steep decline on day 116 (26 October) associated with the preceding extended dry period. Both pre-dawn and mid-day values for ψ_x did not

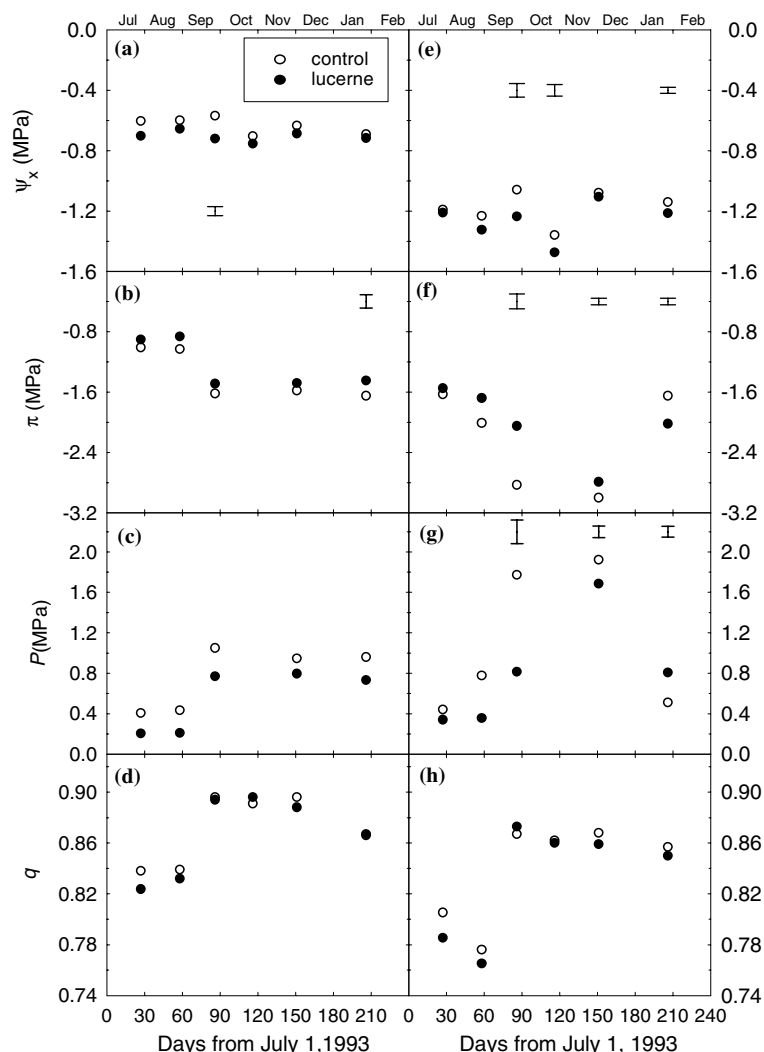


Figure 2. Components of needle-water status for radiata pine grown either without (Control) or with lucerne groundcover at Lincoln, New Zealand, in 1993/1994: (a & e) water potential (ψ_x), (b & f) osmotic potential (π), (c & g) turgor pressure (P), (d & h) relative water content (q). Measurements were made before dawn (a–d) or around mid-day (e–h). Bars represent LSD ($P < 0.05$).

strictly reflect the decline in soil-water, so that the 50% fall in the latter induced less than a 20% reduction in pre-dawn ψ_x from -0.60 to -0.75 MPa at the conclusion of the study.

At dawn π was similar for the two groundcovers, but at mid-day (Figure 2f) it was lower for Control than for Lucerne after day 90 (from October). The response by P to groundcover treatment was inverse that of π , during most of the season. While groundcover had no significant effect on P at dawn, P at noon was consistently lower in Lucerne than in Control. Daytime P (Figure 2g) attained peak values of 1.8 MPa in

Control and 1.65 MPa in Lucerne around day 150 (late November). There was no significant influence of groundcover on q either at dawn or at mid-day.

Influence of plant source on water relations

There were generally no significant differences amongst the pines in their ψ_x , π and P measured at dawn (Figure 3a–d) for most of the growing season, except for a significant increase in P for TC4 that was associated with a decrease in π at the end of the monitoring period. Measurements

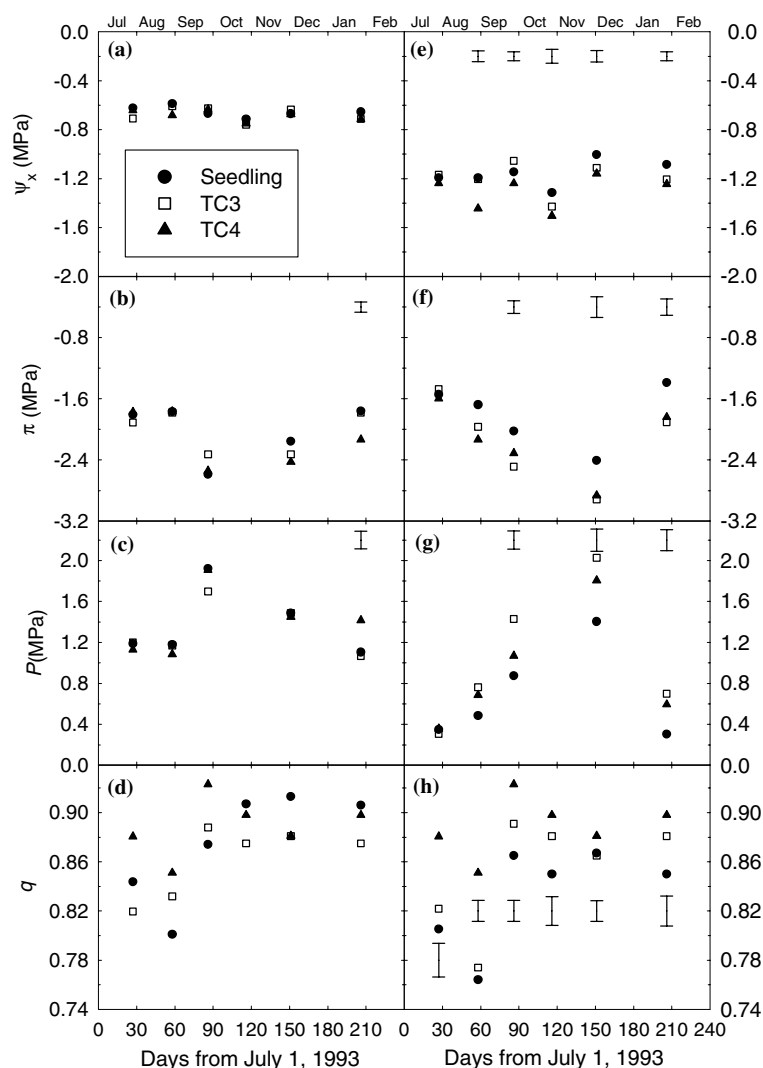


Figure 3. Components of needle-water status for radiata pines established from seeds (Seedling) or from cloned plantlets (TC3 & TC4) grown in an agroforestry system at Lincoln, New Zealand, in 1993/1994: (a & e) water potential (ψ_x), (b & f) osmotic potential (π), (c & g) turgor pressure (P), (d & h) relative water content (q). Measurements were made before dawn (a–d) or around midday (e–h). Bars represent LSD ($P < 0.05$).

around mid-day (Figure 3e–h), however, showed that the source of planting material had significant influence on water status of the needles. Seedling often had the highest ψ_x and π , which were, respectively, significantly higher than those for either TC4 or TC3. Seedling, however, had the lowest P of the three pine-types, and the trend in this variable was $TC3 > TC4 > Seedling$ in which the difference between TC3 and Seedling was significant. Although there was no well defined trend in q amongst pine-types at

dawn, TC4 consistently had significantly higher q than Seedling at mid-day.

To further characterise water relations in these pines in response to competition in an agroforestry system, π was determined at full turgor (π_{100}) to estimate OA on two dates that differed in their soil-water content. In July when soil-water content was high, the π_{100} was similar for both groundcovers, even though both TC3 and TC4 had lower values in Lucerne than in Control (Table 1). Control had higher π_{100} than

Table 1. Osmotic potential for pine fascicles at full turgor (π_{100}) measured at noon and the associated osmotic adjustment (OA) at Lincoln, New Zealand

Pine source	π_{100} (MPa) 22 July 1993			π_{100} (MPa) 4 January 1994			OA (MPa)		
	Control	Lucerne	Mean	Control	Lucerne	Mean	Control	Lucerne	Mean
Seedling	-0.96b	-0.66a	-0.85A	-2.11a	-2.23b	-2.17A	-1.15a	-1.57b	-1.36A
TC3	-0.74a	-1.54c	-1.14A	-2.31b	-3.18c	-2.75B	-1.57b	-1.64b	-1.61B
TC4	-0.68a	-1.08b	-0.96A	-2.08a	-3.04c	-2.56B	-1.40ab	-1.96c	-1.68B
Mean	-0.79A	-1.10A		-2.17A	-2.82B		-1.37A	-1.72B	

Means followed by different letter(s) are significantly different at $P < 0.05$: lowercase letters are for interaction effects and upper-case letters compare overall effects of groundcover (column) or Pine Source (row).

Lucerne in January 1994 when soil-water content was low, and both TC3 and TC4 had lower values than Seedling, especially when associated with the pasture. All the pines showed some degree of osmotic adjustment, with OA being larger in Lucerne than in Control. Although OA for TC3 and TC4 was similar in Control, TC3 had larger OA in Lucerne than in Control. Overall, both TC3 and TC4 had similar OA , with difference between TC4 and Seedling being significant.

There was a significant relationship ($P < 0.05$) between π and ψ_x during the season, the slopes of these regressions were significantly ($P < 0.05$) different, being -2.8 MPa for Seedling, -9.3 MPa for TC3 and -4.3 MPa for TC4. This again demonstrated a smaller change in π per unit change in ψ_x for Seedling compared with the other two. The ψ_x at loss of turgor was estimated to be -1.45 MPa for Seedling, -1.38 MPa for TC3 and -1.35 MPa for TC4. Elastic moduli (e) obtained from the slopes of the regressions of P on q were 6.5 MPa for Seedling and 8.1 MPa for TC3 and TC4, indicating that the cell wall was more elastic in Seedling than in the other two.

Responses in CO_2 assimilation and stomatal conductance

In January, there were reductions of 44% in A and 49% in g_s for pines in Lucerne compared with those in Control (Table 2). There were no differences between the three pines in their A or g_s during the comparatively more humid and cooler period in November, but during the warm and dry period in January (Table 2) A was in the

order Seedling $>$ TC4 $>$ TC3, with the difference between TC4 and TC3 being significant. The differences in g_s between the pines were not significant at both times of measurement. For all pines, A declined curvilinearly with increases in D (Figure 4).

Discussion

Differences in water status and gas exchange of the needles between the groundcovers were associated with those in soil-water content. Reductions in both A and g_s in Lucerne compared with Control (Table 2) indicated the high sensitivity of these processes to soil-water deficit.

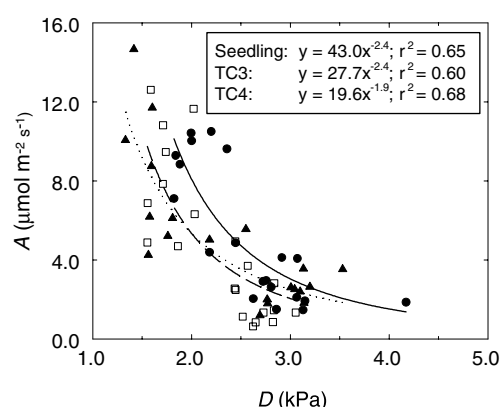


Figure 4. Response of instantaneous CO_2 assimilation (A) to vapour pressure deficit of the air (D) for radiata pines in Seedling (○, ●), TC3 (□, ■) or TC4 (△, ▴) grown in Control (clear symbols) or Lucerne (black symbols) groundcover at Lincoln, New Zealand, in 1993/1994. The lines were fitted into data for Seedling (solid), TC3 (broken) and TC4 (dotted).

Table 2. Instantaneous CO₂ assimilation (A) and stomatal conductance (g_s) for trees of radiata pine originating from Seedling or from plantlets (TC3 and TC4) and grown either without (Control) or with lucerne groundcover (Lucerne) at Lincoln, New Zealand

Plant variables	Treatments	09 Nov 93	22 Jan 94
<i>Groundcover effects</i>			
A ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Control	na	3.12a
	Lucerne	na	1.75b
g_s ($\text{mmol m}^{-2} \text{s}^{-1}$)	Control	na	0.029a
	Lucerne	na	0.015b
<i>Source effects</i>			
A ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Seedling	10.24a	2.96a
	TC3	8.97a	1.78b
	TC4	8.33a	2.55ab
g_s ($\text{mmol m}^{-2} \text{s}^{-1}$)	Seedling	0.215a	0.024a
	TC3	0.222a	0.018a
	TC4	0.183a	0.023a

na, data not measured.

Means followed by different letter(s) are significantly different at $P < 0.05$.

An earlier study found that transpiration in radiata pine declined by up to 60% in response to a relatively small fall in soil-water potential from saturation to -0.4 MPa (Squire et al., 1987). Differences in ψ_x between the groundcovers, although numerically small, could have a long-term cumulative effect on dry matter production. Bandara et al. (1999) calculated cumulative water-stress integral (Myers, 1988) over 1 year and observed that it increased by up to 62% for the pines in Lucerne compared with those in Control. Applying the same scheme we found integral values of 12 MPa-day for pines in Control compared with 24 MPa-day for those in Lucerne over the 6-month period. Poor water relations for pines in Lucerne (Figure 2) are consistent with a reported 64% decrease in the dry-matter of trees in this groundcover (6.1 kg/tree) compared with Control (16.9 kg) in the winter of 1993 (Gautam et al., 2003); a similar trend in tree growth was repeated two seasons later in 1995/1996 season when increments in tree weight were reduced by about 58% in Lucerne relative to Control (Bandara et al., 1999). Inter-specific competition for limited soil-water in this agroforestry system causes an inverse relationship between dry weights of the trees and those of the associated pastures in a given season (Yunusa et al., 1995b).

Water potential in the needles remained largely stable for all the pines during most of the season despite significant reductions in

soil-water, because the trees adjusted their π . Most often, Seedling had the highest ψ_x either at dawn or at mid-day especially from November onwards, but this was achieved through stomatal closure (Table 2), contrary to the experience of Rahman et al. (2003b). High ψ_x and g_s nevertheless, must have enabled Seedling to achieve high rates of A , despite its low P , especially in January. Seedling had highly elastic cell walls in which e was 6.5 MPa compared with 8.1 MPa for the other two pines. High elasticity of cell wall for Seedling ensured P remained mostly above certain critical level not to have caused loss of turgor and cessation of photosynthesis. This critical value could be as low as 0.3 MPa for alga *Chara coralline* (Proseus et al., 2000), our pines attained this value at mid-day only at the end of the monitoring season in January (Figure 3g). Mid-day ψ_x were often above the critical values (-2.0 to -1.5 MPa) (Rahman et al., 2003b; Sands and Correll, 1976) not to have stopped growth processes entirely. They did suggest, however, that photosynthesis in our pines must have been confined mostly to morning hours before mid-day when P and ψ_x could decline below their critical values. Inhibition of growth and other physiological processes during the day in dry environments is often associated with high D (Attiwill et al., 1982; Benecke, 1980; Lu et al., 2003; Thompson and Wheeler, 1992). The trends in A observed in the current study

Table 3. Averages for the mid-day water potential (ψ_x), turgor pressure (P) and relative water content (q) measured between September 1993 and February 1994, and above-ground dry-matter (DM) measured in July 1993 for pines established from seeds (Seedling) or from cloned plantlets (TC3 & TC4)

Pine source	Dawn			Mid-day			DM (kg/tree) ^a
	Ψ_x (MPa)	P (MPa)	q	Ψ_x (MPa)	P (MPa)	q	
Seedling	-0.68a	1.42b	0.89a	-1.14a	0.78b	0.86a	9.0c
TC3	-0.69a	1.69a	0.89a	-1.20a	1.08a	0.86a	12.1a
TC4	-0.71a	1.54b	0.91a	-1.29a	0.73b	0.88a	10.2b

Means in the same column followed by the same letter(s) are not significantly different at $P \leq 0.05$.

^aFrom Gautam et al. (2003).

(Figure 4) are therefore consistent with common experience. Benecke (1980) observed a 23% decline in A with every 1.0 kPa increase in D in Canterbury, where our current study was undertaken; he observed that in early autumn D increased from ~ 0.2 kPa at sunrise to more than 1.6 kPa in the afternoon. The diurnal fluctuations in D and in A would be larger in spring and summer when our current work was undertaken than in autumn. Terrestrial plants generally restrain vapour loss and gas exchange around mid-day in response to rising D , consistent with the finding by Lu et al. (2003) that g_s tends to fall almost linearly with increases in D once the latter exceeded 1.0 kPa.

Maintenance of A in Seedling, despite its low P was surprising. Assimilates produced from A could be used either for growth or respiration, but increments in needle-length for intact Seedling trees in Control were reported to be 17% lower (153 mm) compared with those of TC3 (172 mm) during the following season (Bandara et al., 1999). This suggested that maintenance respiration could be larger in Seedling that had dense canopies, which at age of 3 years had a mean needle-to-stem ratio of 1.7:1.0 compared with 1.5:1.0 for TC3 and TC4 (G. Bandara, unpublished data). Thus, the clumped canopy in Seedling would increase respiratory demand for assimilates by the shaded needles (Lavinge and Ryan, 1997). Bandara et al. (2004) reported that foliage efficiency (annual dry-matter increment per unit foliage mass) at 5 years of age was 25% lower for Seedling than for TC3; whereas removing the bottom branches, which were normally shaded (Whitehead et al., 1990), the difference in needle-length and total (shoot and root) tree dry-matter between Seedling and TC3 were either

reversed or eliminated. They found that needle-length for pruned trees in Control were 169 mm for Seedling compared with 156 mm for TC3, while tree weight increased by 56.8 and 55.4 kg respectively. It was also possible, however, that differences in maintenance respiration was associated with tissue nitrogen as found previously in radiata pines (Ryan et al., 1996) and in other woody species (Eamus et al., 1999), but we did not explore this in the current study.

Although, it is generally difficult to extrapolate from physiological processes at needle scale to whole-plant growth, the similarity amongst these pines in their ψ_x was not consistent with reported differences in their tree weights either in pure stands or when associated with pastures in agroforestry systems (Bandara et al., 1999; Gautam et al., 2002, 2003). A lack of data on tree dry-matter at the time of this study inhibited a comprehensive analysis of the relationship between tree growth and components of water-status of the needles. However, assuming that differences amongst the pines in their dry-matter production in the season of current study (1993/94) were similar to those in the preceding season as measured in winter 1993, the latter could be used to explore relationship between growth and variables of water relations (Eq. (1)) obtained in our current study. The trend in tree dry-matter for the pines in 1993 (Gautam et al., 2003) were consistent with that in the seasonal (September–January 1993/94) averages of P only and not with those of ψ_x or π or even of q (Table 3). Coefficient of correlation between dry-matter was highest (0.99) with P at dawn then followed by with P at noon (0.93), and was less than 0.50 with the other variables. This close relationship between tree dry-matter and P was consistent

with the analysis of several authors (e.g., Hsiao et al., 1976; Morgan, 1984; Turner, 1981) that maintenance of high P , rather than high ψ_x , is more critical to growth.

The magnitudes for components of tissue-water in this study were mostly different from those found for container-grown or younger conifers in other environments. The OA (Table 1) was larger, while ψ_x at loss of turgor (-1.35 to -1.45 MPa) were lower, than those found by Nguyen-Queyrens and Bouchet-Lannat (2003); they reported or cited OA of between 0.15 and 0.60 MPa for *P. pinaster* and other conifers grown in containers. Unlike the container-grown trees, those in the current study had experienced three summers, when supply of soil-water was generally limited (Peri et al., 2002; Yunusa et al., 1995a), that could have conferred resilience on the pines to better withstand soil-water deficit (Meier et al., 1992). The values we presented here are within those reported for olives (*Olea europaea*) in which OA of up to 1.48 MPa and π at loss of turgor of between -3.85 and -2.06 MPa were found (Dichio et al., 2003). Age of trees could also be a factor in their responses to limited soil-water. In a field study in New Zealand, Watt et al. (2003) found that ψ_x declined by up to 3.0 MPa in one-year old pines when associated with broom (*Cytisus scorparius* L.), compared with less than 0.5 MPa in the current study. This was most likely due to the high planting density of 1250 stems ha^{-1} in that study, and, as found earlier by Sands and Nambiar (1983), to restricted root system of the young pines that could explore only limited soil volume. These differences in the magnitudes of responses could simply be due to genetic sources of the trees used in this study and those in the other studies.

Conclusion

Differences in the ψ_x amongst the three pines were numerically small throughout the period of this study, but they differed in their underlying mechanism on how the relative stability in ψ_x was achieved. Those trees developed from tissue culture had a greater capacity for osmotic adjustment than those raised from seeds. Seedling pines maintained favourable ψ_x and q at the expense of high P because of its poor capacity for osmotic

adjustment. Those pines from tissue culture, on the other hand, exhibited high osmotic adjustment that lowered π and ensured high P . Both ψ_x and P were reduced in the lucerne groundcover due to low availability of soil-water, especially during periods of active growth in spring and summer. The higher growth rates reported for TC3 and TC4 in previous studies were, therefore, associated with a greater capacity of clonal trees for osmotic adjustment and to maintain high P than Seedling trees.

In conclusion, when water relations are applied to characterise differences in growth amongst varieties and species of plants, π should be determined in addition to the routinely measured ψ_x to allow deductions of P to be made. Furthermore, instantaneous measurements of water relations variables and gas exchange may not always provide adequate explanation for differences in plant growth.

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