

WATER RELATIONS OF THREE PLANTING STOCK TYPES OF *PINUS CARIBAEA* FOLLOWING TRANSPLANTING

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ABSTRACT

The response of *Pinus caribaea* to water stress following transplanting was investigated in a series of experiments in a plant house with three types of planting stock, (a) bare-rooted and wrenched monthly, (b) bare-rooted and wrenched at fortnightly intervals, and (c) potted.

Seedling response, as reflected in relative leaf water content, leaf elongation, and whole plant transpiration was monitored during a drying regime in an environment with a high evaporative demand maintained during daylight hours. Soil water potential and potential evapotranspiration were monitored in conjunction with plant response. Root density and the total length of root per plant were measured at the beginning and end of the drying regime.

The results indicated large differences in the response of bare-rooted and potted planting stock to a regime of drying soil moisture following transplanting. Data for both leaf elongation and transpiration as a function of relative leaf water content indicated that these physiological properties of the three stocks were similar. Modification of the root systems did not greatly alter root density although it did produce large differences in the total length of root per seedling. As differences in the response of planting stock could not be accounted for by differences in root density and the volume of the root zone, it is implied that the seedlings' initial response to water stress was dominated in these studies by the relative water content of the leaf following transplanting.

Interpretation of results in terms of current theory for transfer of water to the root system implies that the effect of root density and the volume of the root zone on the plants' response to water stress requires further study.

INTRODUCTION

The development of a satisfactory planting stock for the establishment of *Pinus caribaea* in Fiji (Rennie, 1974) has involved field and nursery experiments designed to examine the overall performance of bare-rooted and potted stock. To date there have been no physiological studies with *Pinus caribaea* on the comparative response of planting stock to applied water stress.

There are, however, a number of studies (Rook, 1969, 1971, 1973; Van Dorsser & Rook, 1972) on *Pinus radiata* which have considered the physiological consequences

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of undercutting/wrenching as practised in New Zealand or restricted watering as carried out in parts of Australia and South Africa. Both these conditioning practices are designed to improve the seedlings' response to water stress conditions during and immediately following transplanting operations. Rook (1969) and Van Dorsser and Rook (1972) attribute the improved water balance of seedling stock conditioned by undercutting/wrenching to the efficient root system which is developed by the practice. Rook (1973) provides evidence that seedling stock conditioned by restricted watering has an improved water balance by virtue of an efficient stomatal regulation of water loss and enhanced root growth capacity immediately following transplanting.

The conditioning or "design" of a pine seedling to respond favourably to water stress following transplanting, and to subsequently establish rapid and continued growth, can be considered in the first instance in terms of a model based on that of Gardner (1960). Williams (1974) developed an expression in which the leaf water potential ψ_1 is given by

$$\psi_1 = r_r - \frac{Q}{2\pi r_1 L} R_p \quad \text{-----} \quad (1)$$

$$\text{given that } \tau_r = \tau_b - \frac{Q}{4\pi k L} \ln \frac{r_2}{r_1} \quad \text{-----} \quad (2)$$

where τ_r and τ_b is the matric potential (cm) at the root and in bulk soil respectively, Q is the water extraction rate for the root system ($\text{cm}^3/\text{cm}^3/\text{day}$) defined as $Q = v/V$ where v is rate of water loss and V is root zone volume, r_1 is the root radius (cm), L is root density (cm/cm^3) and R_p is the resistance in the plant (day), k is the hydraulic conductivity of the soil (cm/day) and r_2 is half the distance between adjacent roots, defined as $(1/\pi L)^{1/2}$.

The leaf water potential determines, through the leaf moisture characteristic (Jarvis & Jarvis, 1963b), the leaf water content which subsequently determines stomatal aperture, closure and the response of the plant to the water stress condition.

If it can be assumed that the leaf moisture characteristic is beyond manipulation in the nursery, then the seedling characteristics open to manipulation are, the root density (L), the root length per seedling, and thus the root zone volume (V), the relationship between leaf water content and stomatal aperture, and presumably the resistance (R_p) to water movement in the plant itself (Passioura, 1972).

Clearly conditioning by undercutting/wrenching attempts to increase the root density; and to decrease the water extraction rate via the length of root per seedling. For a given evaporative demand the drop in leaf water potential will therefore be minimised and thus will extend the period before the transpiration falls following stomatal closure.

Conditioning by restricted watering is an attempt to increase the resistance in the plant (R_p) by producing a thick cuticle and small stomatal aperture (Rook, 1973) in addition to changing the relationship between leaf water content and stomatal aperture for the seedling so that stomatal aperture and closure responds rapidly to changes in leaf water content. The water extraction rate and the subsequent drop in leaf water potential is therefore minimised for a given evaporative demand. The early stomatal closure ensures conservation of water and the plant will survive as long as leaf water potential remains in excess of the water potential associated with permanent wilting.

It is obvious from equation (1) that in order to survive a period of water stress following transplanting a seedling should have initially a high leaf water potential (or leaf water content).

These concepts provide a theoretical base on which to consider the process by which nursery practice determines the response of planting stock to water stress. The response of *Pinus caribaea* to water stress following transplanting was investigated in a series of experiments with three types of planting stock: (a) bare-rooted and wrenched monthly; (b) bare-rooted and wrenched at fortnightly intervals, and (c) potted.

EXPERIMENTAL METHOD

I. *The Plant System*

Six-month-old potted and bare-rooted *P. caribaea* Mor. var. *hondurensis* Barr. and Golf. stock supplied by the Fiji Department of Forestry were used in this study.

(a) The bare-rooted stock

These seedlings had received one of the following treatments in the nursery beginning at four months:—

- (i) Undercut at a depth of 5-10 cm and wrenched twice with a month between treatments, designated Wrenched Monthly (W/M).
- (ii) Undercut as above, then two weeks later wrenched, and wrenched again at three fortnightly intervals, designated Wrenched Fortnightly (W/F).

These seedlings were carefully removed from the nursery beds, the root systems immediately packed in a puddled clay, and transported to the laboratory, avoiding exposure to direct sunlight. Within three hours of their removal from the nursery beds the seedlings were transplanted to cylindrical plastic pots (18 cm in diameter and 20 cm deep) containing a humic latosol soil which had been prepared to a water content equivalent to a matric potential of approximately -0.3 bars.

(b) The potted stock

These seedlings, grown in a soil mixture (*see* Table 6) contained in a polythene cylindrical pot (approximately 3 cm in diameter and 13 cm deep), were supplied from the same nursery. The potted seedlings were watered to a matric potential of approximately -0.3 bars. The polythene pot was cut away and the seedlings transplanted, following a procedure identical to that for the bare-rooted stock, to cylindrical plastic pots containing the same humic latosol soil maintained at approximately -0.3 bars. These seedlings were designated Potted (P).

Every attempt was made to reproduce the field planting procedure (Rennie, 1974) for both the bare-rooted and potted stock. The resulting root densities (*see* Table 1) and geometries were assumed to represent the field systems. To date, however, there have been no quantitative field estimates of root density or root zone volume following transplanting.

II. *Plant response*

(a) Leaf length

Between two and four mature leaves 1 to 3 cm in length were tagged for each plant. Length was measured using a pair of vernier calipers at intervals of 7-10 days during the hours 1500 to 1800 local time. Error in the estimate was ± 0.05 cm.

(b) Leaf mass

At the conclusion of the study leaves were classified according to age and length.

TABLE 1—Seedling characteristics of the three planting stocks of *P. caribaea* immediately following transplanting to experimental plots

Characteristic	Stock		
	Potted (P)	Wrenched fortnightly (W/F)	Wrenched monthly (W/M)
Seedling height* (cm)	40.3(+3.3)	21.4(+3.6)	25.4(+4.2)
Root length† (cm)	410 (+50)	105 (+61)	216 (+56)
Root density† (cm/cm ³)			
at 0- 5 cm	2.1 (+0.3)	1.5 (+0.4)	2.8 (+0.3)
5-10 cm	1.3 (+0.2)	0.7 (+0.3)	1.1 (+0.4)
5-15 cm	1.0 (+0.4)	0.2 (+0.3)	0.5 (+0.3)
Root/shoot ratio*	0.22(+0.10)	0.16(+0.05)	0.25(+0.12)

* Standard deviation for 15 observations

† Standard deviation for 5 observations

The relationship of the area to oven-dry mass was estimated (Whiteman & Koller, 1964). Parallel studies on plant height, leaf length, and leaf mass were used to estimate leaf mass as a function of time for each of the treatments.

(c) Relative leaf water content

At appropriate periods throughout the study any two mature leaves from each plant were sampled, bulked for each treatment and the relative leaf water content estimated (Clausen & Kozłowski, 1965). From preliminary studies in which a standard error of $\pm 2\%$ was determined, it was decided to sample at 1500 hours local time. This time generally coincided with the minimum relative water content of the leaves in their daily cycle.

(d) Root length and density

At the conclusion of the study half of the replicates from each treatment were randomly sampled for total root length whilst the other half were sampled for root density. The whole root systems were washed carefully onto a nylon sieve. The roots were separated by flotation and graded into sizes of diameter > 1.0 and < 1.0 mm. These roots were lain on graph paper and the length estimated. For each of the six treatments at least four root systems were measured directly. The remaining root lengths were estimated from the mass/length factor calculated for each planting stock.

Soil cores (4 cm in diameter by 5 cm in length) were taken at a depth of 5 and 10 cm immediately beneath the seedling. Roots contained in these cores were washed onto a sieve and length estimates made directly on at least four samples for each of the treatments. Root density (length per unit volume of soil) was estimated from the mass/length factors calculated for each treatment and the dimension of the core.

(e) Transpiration

Evaporation from the soil surface was reduced to between 2-4% of the average daily water loss, by a layer of polyurethane beads and a polyethylene pot cover.

A piece of sacking over the cover maintained the soil temperature within reasonable limits (27-38°C) during daylight hours. Transpiration was measured by weight change to an accuracy of ± 0.5 g. Measurements were made at approximately 800 and 1600 hours each day.

III. The Soil System

The soil used was humic latosol clay soil (see Table 6). It was passed through a 4-mm sieve for the experiments and for the moisture characteristic studies. The moisture characteristic was determined in a pressure membrane over the range -0.3 to -15.0 bars. Bulk density in both the experimental pots and in the moisture characteristic studies was approximately 1.00 g/cm^3 .

The bulk soil water content was estimated from the mass changes in the soil plant system, corrections being made for mass change of seedling. Preliminary studies on plant mass, leaf length and plant height provided the basis for this correction. The estimates of water content were checked by mini-core sampling and by an osmotic tensiometer (Peck & Rabbidge, 1968). From the water content and the soil moisture characteristic an estimate of soil matric potential was made. The error estimate lies in the range ± 0.4 to ± 1.0 bars.

IV. The Environment

The study was conducted in a plant house with a "plexiglass" roof. An estimate of potential evapotranspiration based on a black Bellani plate atmometer ranged from 0.7 to 7.8 mm/day with an overall mean for the study period of 4.7 ± 1.4 mm/day.

The temperature and relative humidity followed a regular daily pattern whereby temperature increased from 600 hours to a maximum between 1200 and 1400 hours and subsequently declined until approximately 1800 hours, when it stabilised at a level which was maintained during the night. This was accompanied by a corresponding fall in relative humidity from 600 to 1200 hours, followed by a slow rise to levels which were maintained during the night. The mean daytime (600-1800 hours) temperature and relative humidity based on 2 hour samples was $26.5 \pm 3.0^\circ\text{C}$ and $74 \pm 11\%$ respectively. The mean night time (1800-600 hours) temperature and relative humidity was $22.6 \pm 2.0^\circ\text{C}$ and $86 \pm 8\%$ respectively for the 50 day period of study.

The average short wave radiation was $6.6 \pm 2.9 \times 10^6 \text{ J/m}^2/\text{day}$.

V. The Experiments

All seedlings after transplanting to pots were maintained at approximately -0.3 bars in an environment in which Bellani plate evaporation was 1 mm/day for a period of 72 hours. For each of the three (W/M; W/F and P) planting stocks there was:

- (i) a control water regime in which the bulk water content was maintained by watering daily to a water content equivalent to a matric potential of approximately -0.3 bars. From mini-cores (1.0×5.0 cm) a direct estimate of water content provided good evidence that variation in bulk soil matric potential was small, bearing in mind the hysteresis in the moisture characteristic at these water contents. These treatments were designated W/M/C, W/F/C and P/C respectively.

(ii) a soil water stress regime in which the pots were allowed to dry by transpiration.

These treatments were designated W/M/S, W/F/S, P/S respectively.

Twelve apparently uniform, healthy plants were selected for each of the above six treatments.

RESULTS

(a) Water status of the seedling

Relative leaf water content for both treatments of each of the three stocks is presented as a function of time after transplanting in Fig. 1. Clearly the bare-rooted stock is very different from the potted stock in terms of initial water status. Both bare-rooted stocks, maintained at "field capacity", show declining water status for approximately 7 days before beginning a recovery which is incomplete under these conditions until day 30. Both bare-rooted stocks, subjected to the drying regime, failed to improve on their initial water status which progressively declined with time.

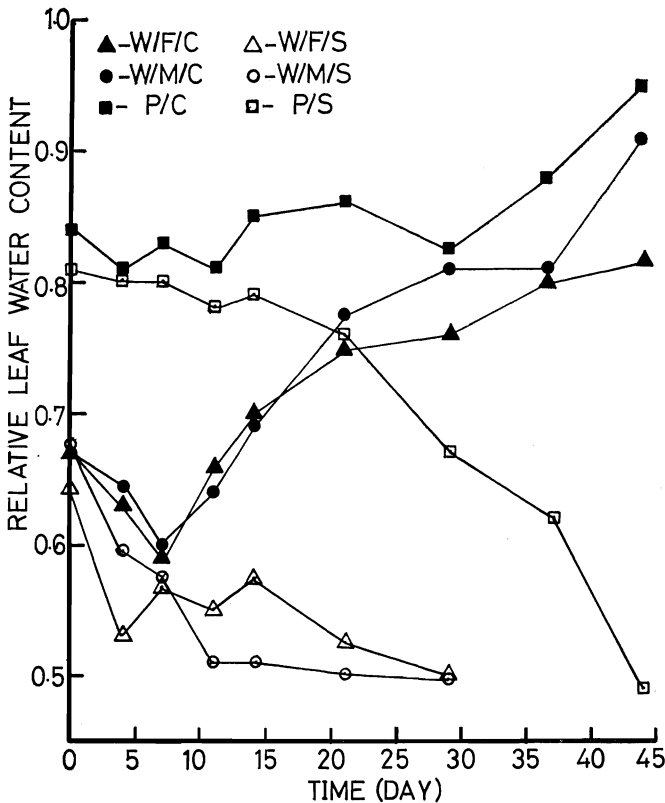


FIG. 1.—Relative leaf water content with time following transplanting for three *P. caribaea* planting stocks subjected to (a) a drying soil water regime (W/F/S, W/M/S, P/S) and (b) a soil water regime in which the matric potential was maintained at approximately -0.3 bars (W/F/C, W/M/C, P/C). Standard error at $P = 0.05$ was ± 0.02 .

This is in strong contrast to the potted stock which maintained a relative leaf water content which could not be distinguished from that of the control for a period of approximately 10 days. Thereafter the decline in its relative leaf water content was still relatively slow in that it was not until day 25 that it fell below 0.70. (In preliminary work it was shown that the relative leaf water content associated with a permanently wilted condition was approximately 0.54.)

Fig. 2 illustrates the relative leaf water content relative to the control as function of bulk soil matric potential for the three drying regimes. The response to bulk soil matric potential following transplanting is clearly different between the bare-rooted and the potted stock.

Under the evaporative demand experienced in this study the potted seedlings appear to be able to maintain their water status over a range of matric potential from -0.3 to -2.0 bars before a significant decrease, whereas the relative leaf water content for the bare-rooted stock fell immediately at -0.3 bars. At -3.0 bars the

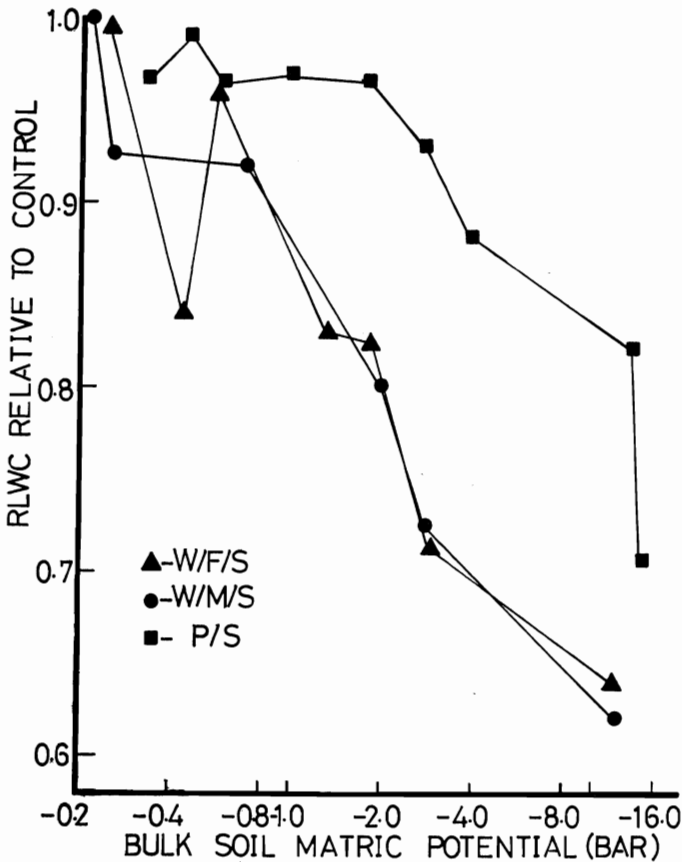


FIG. 2—Relationship between relative leaf water content (RLWC) relative to control and bulk soil matric potential for three planting stocks of *P. caribaea* during a drying regime following transplanting.

potted stock is 0.92 that of control whilst the bare-rooted stocks are approximately 0.72 of the control. The responses of the two bare-rooted stocks are indistinguishable from each other but very different from that of the potted stock.

(b) Elongation of the leaf

Some indication of the growth of the seedling following transplanting is provided by the rate of leaf elongation as presented as a function of time in Fig. 3. The

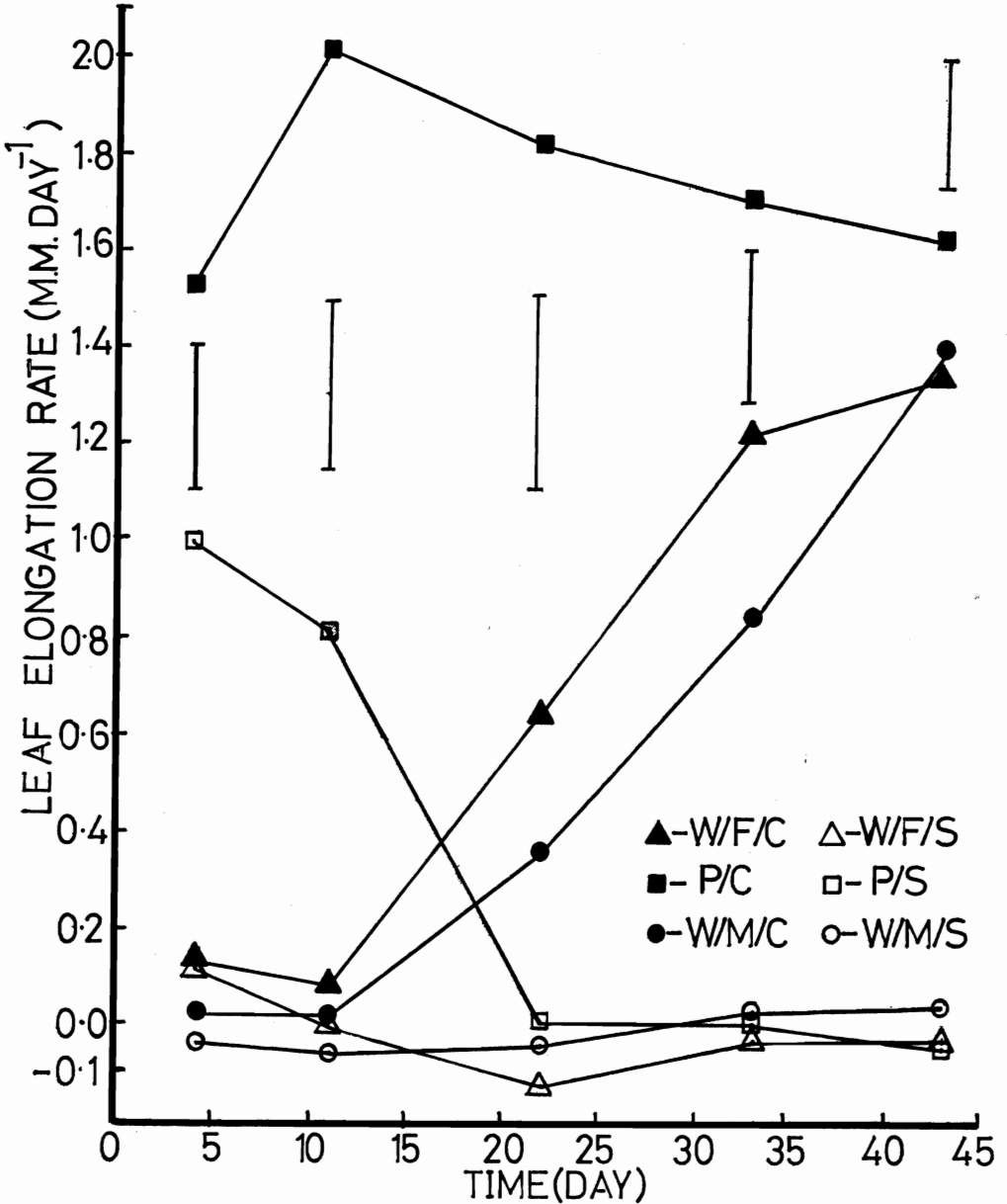


FIG. 3—Leaf elongation rate as function of time following transplanting for three planting stocks of *P. caribaea* subjected to two soil moisture regimes. Vertical bars represent the Duncan Multiple Range at $P = 0.05$.

bare-rooted stocks subjected to the drying regime showed no growth following transplanting. Again this is in contrast to the potted stock which was able to maintain a reasonable leaf elongation rate (> 0.5 mm/day) for approximately 14 days under the environmental conditions studied. It is interesting to note that nearly two weeks is required before the bare-rooted control plants begin to show a significant growth rate. Some 40 days after transplanting the bare-rooted stock and the potted stock appeared to have similar leaf elongation rates under the control moisture regime. Although the estimation of leaf elongation does not permit the estimation of growth rates over short periods, the data do suggest that leaf elongation of the control potted seedlings was retarded for less than three days following transplanting.

The behaviour of the bare-rooted seedlings in the control treatments (W/M/C and W/F/C) and the potted seedlings under water stress (P/S) provided an opportunity to study the relationship between water status of the plant and leaf elongation.

The relationship between leaf elongation rate (LER) and relative leaf water content (RLWC) for all three stocks can be described by

$$\text{LER} + 10 = 663.9591 - 23.8612(\text{RLWC}) + 0.213459(\text{RLWC})^2$$

$(r^2 = 0.89)$

where LER is expressed in $\text{m} \times 10^{-5}$ per day and RLWC is a percentage. Fig. 4 suggests that the water status/growth physiology all three seedling stocks are in fact similar. Clearly for this species the elongation of the leaf is negligible for relative leaf water contents less than 0.65.

The relationship between elongation of the leaf (LER) and bulk soil matric potential is provided for the potted seedlings by $\ln(\text{LER}) = 4.1579 - 0.8269 \ln |\tau_b|$ ($r^2 = 0.81$) where LER is expressed in $\text{m} \times 10^{-5}$ per day and τ_b is expressed in bars. No such relationship could be provided for the two bare-rooted stocks as their rate of elongation was nearly zero. Although the growth rates were estimated over a period of 3 to 7 days (and as a consequence soil matric potential was decreasing over the period) a useful relationship between the mean bulk matric potential and the average growth rate for individual plants is apparent. These data clearly indicate that the rate of leaf elongation decreases very rapidly as the soil matric potential decreases. The rate of elongation decreased by a factor of two as the matric potential decreased from -0.3 to -2.0 bars. The mean leaf elongation rate for all potted seedlings in the drying regime was 0.90 ± 0.38 mm/day, at -0.3 ± 0.2 bars and this decreased to 0.48 ± 0.28 mm/day at -2.2 ± 0.6 bars.

(c) Transpiration

Daily transpiration for the three seedling stocks subjected to a drying regime is presented as a function of time in Fig. 5 (a). The rate of transpiration for the potted seedling was significantly greater than that of the bare-rooted stock for a period of approximately 10-12 days—thereafter all three rates were indistinguishable. There was a sixfold decrease in transpiration with time for the potted stock in contrast to a twofold decrease for both bare-rooted stocks.

Fig. 5 (b) illustrates the daily rates of transpiration for the control treatments for the three seedling stocks. The transpiration rates for the potted stock were twice to three times that of the bare-rooted material for the first 40 days, but these differences disappeared thereafter. The rate of transpiration of the potted seedlings increased

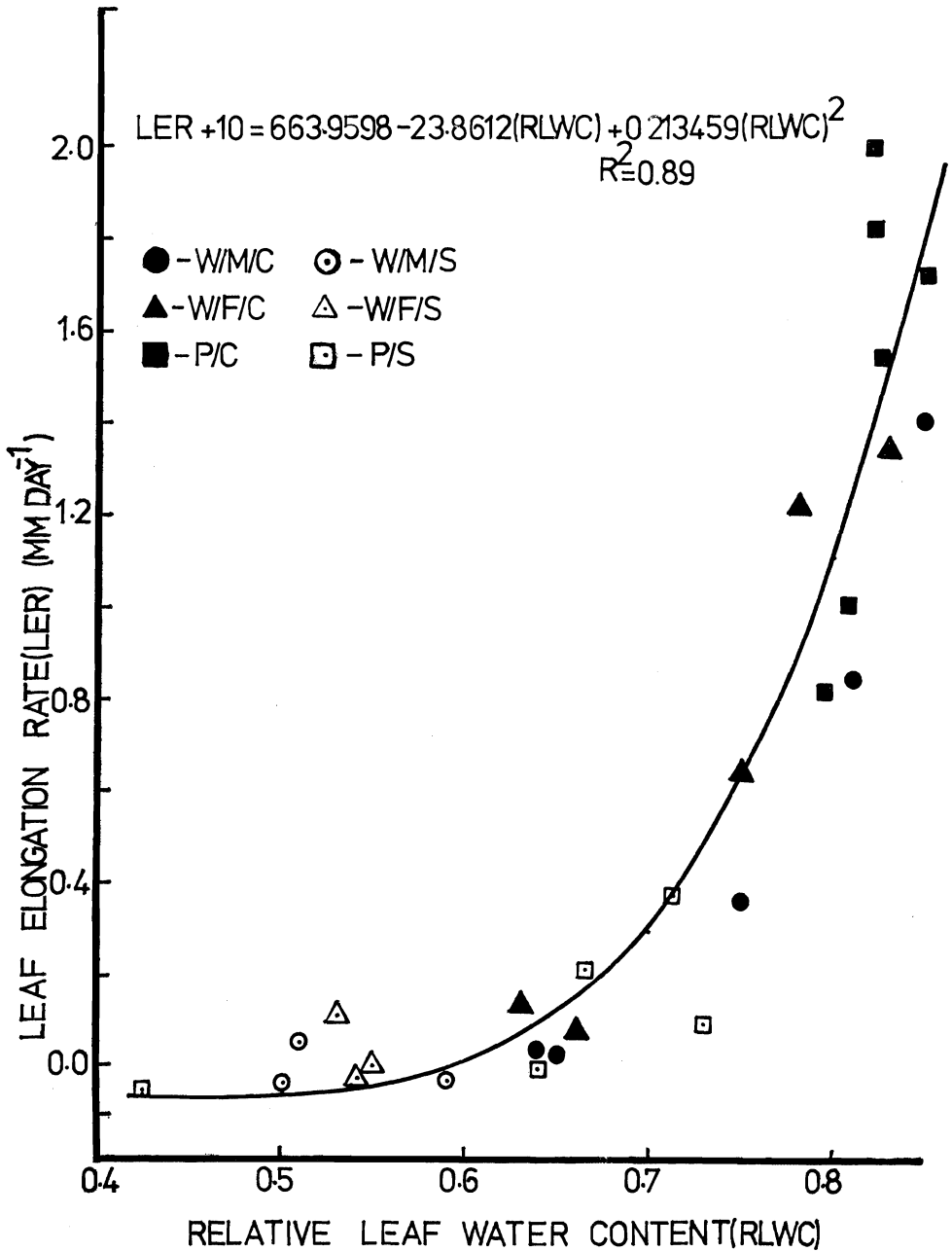


FIG. 4—Relation between leaf elongation rate and relative leaf water content for three planting stocks of *P. caribaea* subjected to two soil moisture regimes following transplanting.

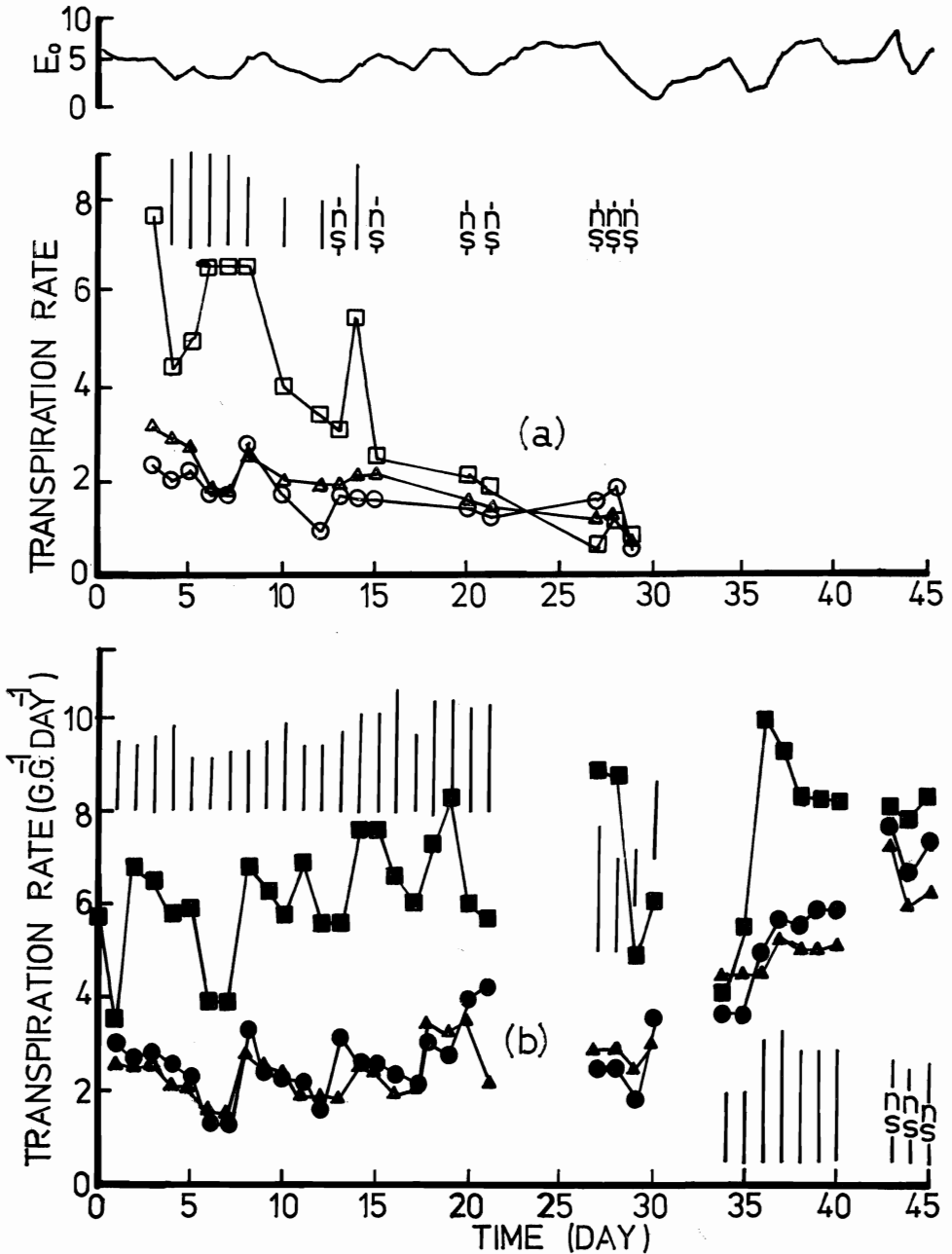


FIG. 5—Transpiration rate (g/g od leaf/day) of three planting stocks of *P. caribaea* following transplanting to
 (a) a drying soil moisture regime (P/S, W/F/S, W/M/S) and
 (b) a soil moisture regime in which matric potential was maintained at approximately -0.3 bars (P/C, W/F/C, W/M/C). Vertical bars represent the Duncan Multiple Range at $P = 0.05$. E_0 is the potential evapotranspiration (mm/day) as estimated from Bellani plate.

Note: □ - P/S; ■ - P/C; △ - W/F/S; ▲ - W/F/C; ○ - W/M/S; ● - W/M/C.

very little following transplanting, but that of the bare-rooted stock showed a progressive increase for approximately 30 days. These data illustrate once again that under this favourable moisture regime and environment the bare-rooted seedlings took at least 20 to 30 days to establish rapid growth and active transpiration.

The rate of transpiration relative to that of the control (TRC) for the three seedling stocks subject to the drying regime is expressed as a function of the bulk soil matric potential by $TRC = 0.8250 - 0.2326 \ln |\tau_b|$ ($r^2 = 0.90$) where TRC is expressed as a ratio and τ_b is expressed in bars. This ratio provides a comparative indication of the influence of matric potential on water transport in the three seedling stocks. It has been well established by Denmead & Shaw (1967) and others that a unique transpiration-soil matric potential relationship exists for a given level of potential evapotranspiration. It follows that if the potential evapotranspiration varied greatly for a given matric potential large variations in this ratio would result. Increases in potential evapotranspiration will cause the ratio to fall at a given matric potential and vice versa. For example the ratio for the potted seedlings ranged from 0.33 for a matric potential of -3.20 bars at a potential evaporation of 6.1 mm/day to 0.72 for a matric potential of -2.90 at a potential evaporation of 4.8 mm/day. Bearing this in mind there was little evidence in these data to suggest that the three stock differed in transpiration response to decreasing matric potential and all data were adequately described by the above regression.

Transpiration rate (TR) as a function of relative leaf water content (RLWC) for all seedling stocks can be described by

$$\ln (TR) = -2.5755 + 0.05192 (RLWC) \quad (r^2 = 0.71)$$

where transpiration rate is expressed in g/g/day and RLWC is a percentage. Transpiration increased rapidly when the water content of the leaf exceeds approximately 0.80 as illustrated in Fig. 6. This suggests that stomatal closure occurred when the water content of the leaf was approximately 0.80. Jarvis & Jarvis (1963) showed that stomatal closure for *P. sylvestris* occurred at relative water contents below 0.78. The similarity of the relationships in Figs. 4 and 6 and the suggestion that stomatal closure is associated with a relative leaf water content of approximately 0.80 serve to demonstrate the well established relationships that exist between stomatal closure, growth and transpiration for a plant under water stress. It would appear that the three planting stocks are similar in their growth and water transport responses to soil water stress.

(d) The root system

The total length of the root system per plant and the length of root per unit volume of soil (root density) for the three planting stocks at the conclusion of the study appear on Tables 2 and 3. A comparison of Tables 1 and 3 shows that for all three stocks there is a twofold or threefold increase of the root length during the first 45 days following transplanting to soil in the absence of soil moisture stress. The largest increase in root length occurred in the W/M bare-rooted stock. Potted seedlings subjected to a drying regime following transplanting showed a small amount of growth while both bare-rooted stocks showed little change.

The root densities which were estimated at 0-5, 5-10 and 10-15 cm directly beneath the axis of the seedling range from 0.1 to 3.0 cm/cm³. The root densities (see Table 2) were similar for each of the three stocks at each depth; however there is a trend

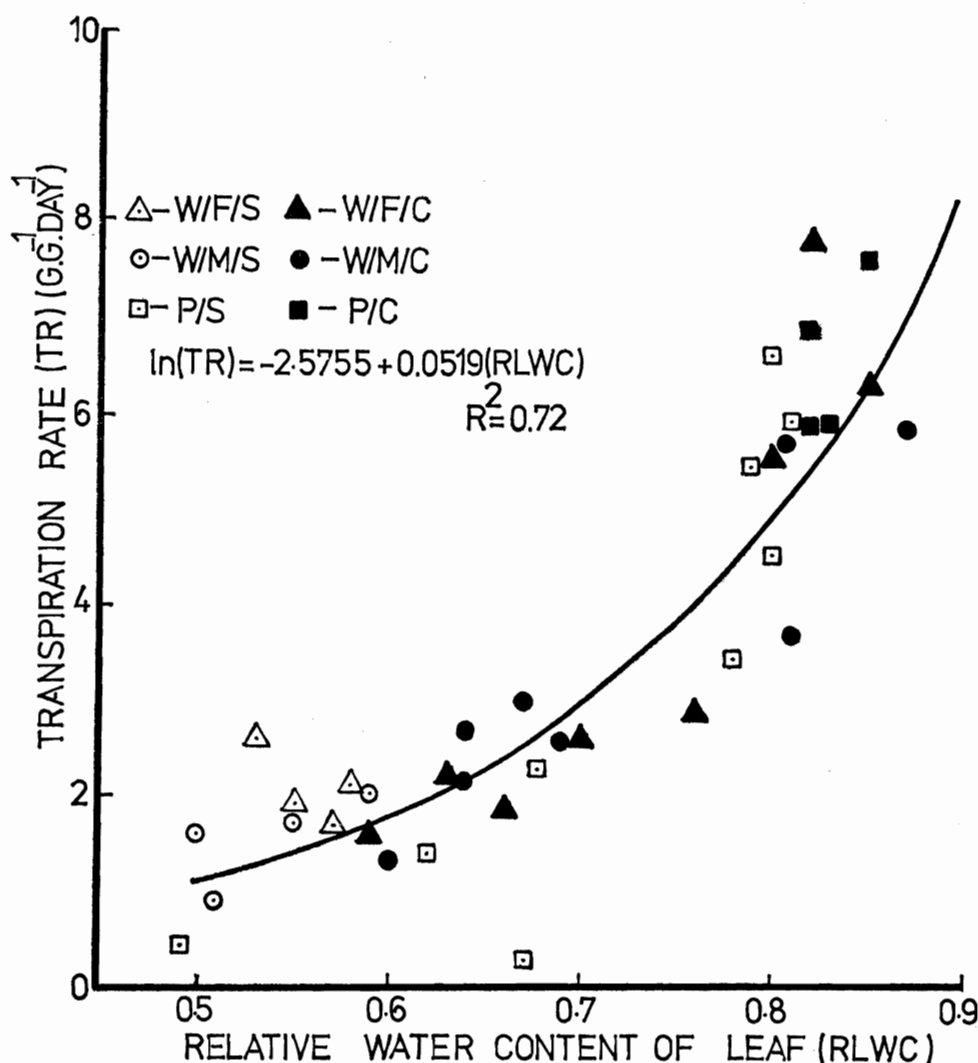


FIG. 6—Transpiration rate (g/g od leaf/day) expressed as function of relative leaf water content for three planting stocks of *P. caribaea* subjected to two soil water regimes.

TABLE 2—Root density* (cm/cm³) at three depths for three planting stock of *P. caribaea* subjected to two water regimes

Depth (cm)	Planting stock and water regime					
	P/C	P/S	W/M/C	W/F/S	W/F/C	W/F/S
0- 5	2.6(±0.5)	2.1(±0.4)	3.0(±0.5)	3.0(±0.6)	2.7(±0.5)	1.5(±0.3)
5-10	1.5(±0.3)	1.3(±0.3)	0.3(±0.3)	1.1(±0.5)	0.6(±0.4)	0.7(±0.3)
10-15	0.9(±0.4)	1.1(±0.4)	0.3(±0.4)	0.6(±0.3)	0.1(±0.3)	0.1(±0.2)

* Standard deviation for 6 observations

TABLE 3—Whole plant root length* (cm) for three planting stocks of *P. caribaea* subjected to two water regimes

	Planting stock and water regime					
	P/C	P/S	W/M/C	W/M/S	W/F/C	W/F/S
Root length (cm)	884(+71)*	484(+56)	946(+51)	276(+58)	272(+52)	97(+65)

* Standard deviation of 6 observations

for lower density for the W/F bare-rooted seedlings. Root density in the control treatments were not significantly different from the stressed regimes except at a 0.5 cm depth for the W/F bare-rooted stocks where root density increased in the absence of moisture stress. Generally the length of root in each stock increased following transplanting whilst the root density in the immediate root zone remained relatively constant. It would appear that water stress following transplanting seriously retarded root development in terms of total root length per plant but in general had little effect on root density in the immediate root zone.

The observation that root density was similar for both bare-rooted and potted stock and that differences in the total root length per plant existed illustrate that the volume of soil in the immediate vicinity of the root system (root zone volume) is the characteristic which distinguishes the three seedling stocks.

(e) Flow of water to the root

From the water loss per plant, root length and root density an estimate was made of water flux to the roots under these experimental conditions. The flux to the root (q) expressed as mg per cm of root length per day for the three stocks maintained at a matric potential of approximately -0.30 bars is shown in Table 4.

TABLE 4—Estimated water flux to the root (mg/cm/day for seedlings maintained at a matric potential of approximately -0.30 bars

Day	Seedling stock			Potential evapotranspiration (mm/day)
	P/C	W/M/C	W/F/C	
36	18.9(+4.0)	9.9(+1.8)	35.3(+ 9.1)	2.1
37	18.6(+4.5)	9.8(+1.8)	42.5(+12.1)	5.9
38	17.4(+4.1)	12.5(+1.3)	39.3(+ 6.7)	7.1
43	24.3(+7.5)	17.9(+1.2)	60.8(+18.1)	7.7
44	28.4(+7.7)	15.0(+2.2)	68.2(+18.9)	6.0
45	24.4(+5.9)	17.4(+1.7)	55.9(+18.5)	4.5
46	24.2(+5.7)	15.5(+1.3)	55.6(+15.1)	4.2

Although the roots of potted stock had fluxes which were consistently larger than the W/M bare-rooted stocks, these were significantly smaller than those for the W/F bare-rooted stock. This reflects the root length per plant as shown in Tables 1 and 3. The estimated water flux to the root for the three seedlings during a drying regime is presented as a function of soil matric potential in Table 5. The decrease in flux to the root with decreasing matric potential is clearly apparent in all stocks. The estimated flux of water to the root was of a similar magnitude for the potted and the W/M bare-rooted stock but very much less than that for the W/F bare-rooted stock. The rate at which water was absorbed per unit length of root was apparently different for the two bare-rooted stocks. This of course assumes that absorption takes place over the whole length of the root system. Nevertheless it appears that it is possible to manipulate the root length of seedlings in such a way as to regulate the magnitude of the water flux to the root. There are few estimates for water flux to the root available, however, this range of water fluxes (1.5 to 70 mg/cm/day) is generally larger than that reported by Lawlor (1972) for *Lolium perenne* but smaller than that used by Gardner (1960) and Cowan (1965) in their models for water flow to plant roots.

TABLE 5—ESTIMATED WATER FLUX TO THE ROOT (q) AT VARIOUS BULK SOIL MATRIC POTENTIALS (τ_b) FOR SEEDLINGS DURING A DRYING REGIME

DAY	Seedling Stock						Potential Evapo- transpirations (mm/day) E_0
	τ_b (bars)	P/S (mg/cm/day)	τ_b (bars)	W/M/S (mg/cm/day)	τ_b (bars)	W/F/S (mg/cm/day)	
1	- 0.31	16.5 ± 1.6	- .22	36.2 ± 9.4	- 0.24	44.4 ± 8.8	5.0
4	- 0.57	12.6 ± 1.9	- 0.57	15.2 ± 6.4	- 0.46	35.2 ± 10.8	2.9
5	- 0.60	14.9 ± 2.4	- 0.64	13.0 ± 3.2	- 0.52	36.2 ± 3.6	4.1
8	- 0.82	18.4 ± 3.3	- 0.77	17.4 ± 3.2	- 0.59	38.3 ± 8.9	5.2
12	- 2.60	9.7 ± 1.3	- 2.70	4.7 ± 2.1	- 2.51	26.8 ± 7.1	2.8
13	- 2.70	8.9 ± 2.4	- 2.82	10.10 ± 3.8	- 2.90	32.6 ± 10.1	3.1
15	- 3.20	7.2 ± 2.6	- 3.20	10.8 ± 1.1	- 2.90	32.6 ± 10.1	6.1
27	-13.2	1.6 ± 0.9	-10.2	10.8 ± 2.8	-11.70	7.6 ± 5.6	7.1
29	-13.5	1.5 ± 0.3	-11.8	2.53 ± 1.4	-11.8	7.2 ± 3.8	2.4
30	-14.0	2.1 ± 0.2	-	-	-12.3	7.2 ± 3.3	1.0

DISCUSSION

The response of seedlings as reflected in the relative water content of the leaf, the rate of elongation of the leaf and the transpiration rate clearly show that the potted stock was able to continue functioning for a longer period from the onset of a drying regime than either of the two bare-rooted stocks of *Pinus caribaea* used. This is by no means unexpected although field experiments to date have been conducted with relatively wet conditions following transplanting and the fundamental differences in performance between potted and bare-rooted stock although inferred had not been

demonstrated (Rennie, 1974). It would be unwise to extrapolate further than to conclude that the potted and bare-rooted stock as studied were very different in their response to water stress conditions following transplanting.

The two bare-rooted stocks, although very different in basic root and shoot form (*see* Table 1), were very similar in terms of their response to applied water stress. The length of root per plant and the subsequent water flux into the root were different as was the growth rate of roots following transplanting. If the response of these seedlings to water stress was being determined by the efficiency of the root system one would expect, from our theoretical consideration, that the two bare-rooted stocks should be quite different in their response. The W/M stock with its greater root length could be expected to maintain a higher relative leaf water content than the W/F stock. As this is not reflected in the data one must consider that in this instance the root system is not the factor determining the plant response.

The relative leaf water content immediately following transplanting for the two bare-rooted stocks is similar, but it is significantly lower than that of the potted stock. It is implied therefore that the response of the bare-rooted stock is determined in this instance by the low relative leaf water content immediately following transplanting. They are lower than those reported by Rook (1969) for *P. radiata* bare-rooted stock, but they are similar to *P. caribaea* bare-rooted stock used in other studies (Williams, unpublished data).

Although both bare-rooted and potted stock were transplanted to the same humic latosol the soil in the immediate rooting zone for the potted stock was a potting mixture of 90% ferruginous latosol and 10% coarse river sand. The degree to which this soil difference contributed to the superior response of the potted stock can be gauged to some extent from a comparison of soil hydraulic properties as set out in Table 6. The available water between -0.3 and -15.0 bars is practically identical for the two soils, however the estimated hydraulic conductivity (Millington & Quirk, 1961) of the potting mixture is much smaller than the humic latosol. During the initial stages when the roots of the potted seedling were predominantly in the potting mixture it could be

TABLE 6—Moisture characteristic, estimated hydraulic conductivity and mechanical analysis, for the potting mixture and the humic latosol soil

	Matric potential (bars)						
	-0.3	-1.0	-2.0	-4.0	-6.0	-10.0	-15.0
Volumetric water content:							
Humic latosol*	0.330	0.293	0.281	0.273	0.238	0.216	0.193
Potting mixture †	0.275	0.223	0.208	0.192	0.178	0.165	0.138
Hydraulic conductivity (cm/day):							
Humic latosol*	6×10^{-2}	8×10^{-3}	3×10^{-3}	7×10^{-4}	-	9×10^{-5}	-
Potting mixture †	2×10^{-2}	1×10^{-3}	2×10^{-4}	4×10^{-5}	-	6×10^{-6}	-

* 9.6% coarse sand, 58.1% fine sand, 17.3% silt, 35% clay

† 28.6% coarse sand, 31.4% fine sand, 19.4% silt, 20.6% clay

expected that the bare-rooted stock would be advantaged because of the better water transmission properties of the humic latosol. It would seem unlikely that the superior performance of the potted stock could be attributed to the soil potting mixture in this instance, although this could be very important under different circumstances. This being so, it would appear that the relative leaf water content and the root length per plant immediately following transplanting are the two plant characteristics which appear to contribute to the differences between the bare-rooted and potted stock.

A potted stock is widely used under conditions of high moisture stress (Donald, 1971; Goor & Barney, 1968) and it could be implied that this stock has a high level of survival (Rennie, 1974) by virtue of its high relative leaf water content at transplanting and its considerable length of root per seedling; although the influence of the potting mixture could be important in many situations.

The transpiration of *P. caribaea* seedlings was similar in magnitude to that reported by Jarvis & Jarvis (1963), for *P. sylvestris* seedlings, and by Jackson *et al.* (1973) for *P. radiata*. The values appear to range between 1 and 10 g per g of oven-dry leaf per day for the range of evaporative demand encountered.

A sharp decrease in transpiration and leaf elongation of potted seedlings occurred when matric potential fell below approximately -2.0 bars. This response pattern is similar to that reported by Jarvis & Jarvis (1963, a) for *P. sylvestris*. Transpiration rate and leaf elongation in both pine species appear to be sensitive to small decreases in soil matric potential. Jarvis & Jarvis (1963) for *P. sylvestris* and my data for *P. caribaea* show that the small changes in leaf water content bring large decreases in the transpiration rate and leaf elongation. Jarvis & Jarvis (1963) showed that for *P. sylvestris* the stomata usually close at relative leaf water contents below 0.78. A similar behaviour in *P. caribaea* would explain to a large extent the rapid increase in transpiration and leaf elongation at leaf water contents above 0.8.

The importance of the root zone volume and the root density in the design of a planting stock is clear from the theoretical considerations, unfortunately the present data are inconclusive on the role these two parameters play in determining the response of a planting stock to water stress following transplanting. This is in part due to the dominant influence of the relative leaf water content immediately following transplanting in these studies. Further quantitative experimental and theoretical work, which examines current models for water transfer to the root in light of plant response, is necessary before an attempt can be made to evaluate quantitatively the influence of conditioning in the nursery on the water relations of pine planting stock.

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REFERENCES

- CLAUSEN, J. J. and KOZLOWSKI, T. T. 1965: Use of the relative turgidity technique for measurement of water stresses in gymnosperm leaves. *Canad. J. Bot.* **43**: 306-16.
COWAN, I. R. 1965: Transport of water in soil-plant atmosphere system. *J. appl. Ecol.* **2**: 221-9.

- DENMEAD, O. T. and SHAW, R. T. 1967: Availability of soil water to plants as affected by soil moisture content and meteorological conditions. **Agron. J.** **54**: 385-90.
- DONALD, D. C. M. 1971: Water requirements in the South African forest nursery. **Forestry in South Africa**, **12**: 25-33.
- GARDNER, W. R. 1960: Dynamic aspects of water availability to plants. **Soil Sci.** **89**: 63-73.
- GOOR, A. Y. and BARNEY, C. W. 1968: Forest tree planting in arid zones. Ronald Press, New York.
- JACKSON, D. S., GIFFORD, H. H. and HOBBS, I. W. 1973: Daily transpiration rates of **Pinus radiata**. **N.Z. J. For. Sci.** **3**: 70-81.
- JARVIS, P. G. and JARVIS, M. S. 1963a: The water relations of tree seedlings. I. **Physiologia Pl.** **16**: 215-35.
- 1963b: The water relations of tree seedlings. II. **Physiologia Pl.** **16**: 501-16.
- LAWLOR, D. W. 1972: Growth and water use of **Lolium perenne**. **J. appl. Ecol.** **9**: 79-98.
- MILLINGTON, R. J. and QUIRK, J. P. 1961: Permeability of porous solids. **Trans. Faraday Soc.** **57**: 1200-6.
- PECK, A. J. and RABBIDGE, R. M. 1969: Design and performance of an osmotic tensiometer for measuring capillary potential. **Proc. Soil Sci. Soc. Amer.** **33**: 196-202.
- PASSIOURA, J. B. 1972: The effect of root geometry on the yield of wheat growing on stored water. **Aust. J. agric. Res.** **23**: 745-52.
- RENNIE, I. 1974: The establishment of **Pinus caribaea** var. **hondurensis** in Fiji—site and techniques. **N.Z. J. For.** **19**: 57-66.
- ROOK, D. A. 1969: Water relations of wrenched and unwrenched **P. radiata** seedlings on being transplanted into conditions of water stress. **N.Z. J. For.** **14**: 50-8.
- 1971: Effect of undercutting and wrenching on growth of **Pinus radiata** D. Don seedlings. **J. appl. Ecol.** **8**: 477-90.
- 1973: Conditioning radiata pine seedling to transplanting, by restricted watering. **N.Z. J. For. Sci.** **3**: 54-69.
- VAN DORSSER, J. C. and ROOK, D. A. 1972: Conditioning of radiata pine seedlings by undercutting and wrenching description of methods, equipment and seedling response. **N.Z. J. For.** **17**: 61-73.
- WHITEMAN, P. G. and KELLER, D. 1964: Environmental control of photosynthesis and transpiration in **Pinus halepensis**. **Israel J. Bot.** **13**: 166-76.
- WILLIAMS, J. 1974: Water in the soil-plant system. International Plant Physiology Symposium, Massey Univ. Aug. 1973. **Royal Soc. N.Z. Bull.** **12**: 312-6.