

## ROOT AND SHOOT WATER POTENTIALS IN STRESSED PINE SEEDLINGS\*

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### ABSTRACT

Water potential differences were measured between the soil, roots and shoots of *Pinus radiata* D. Don and *P. brutia* Ten. seedlings grown under controlled climatic conditions. Root growth under stress was strongly affected by climatic treatment, particularly temperature. In both species, water potentials in the cool climates were always less negative than in the warm climates. The relations between shoot ( $\psi_x$ ) and root ( $\psi_r$ ) water potentials were analysed; regression of  $\psi_x$  over  $\psi_r$  with increasing water stress was linear in *Pinus radiata* and curvilinear in *P. brutia*. The implications of the findings are discussed.

### INTRODUCTION

Response of water potentials in pine seedlings to increased soil moisture stress has been studied previously (Heth, 1974; Heth and Kramer, 1975). Tolerance of water stress of *Pinus taeda* L., *P. echinata* Mill., and *P. radiata* D. Don, was evaluated under four combinations of temperature and humidity in controlled environment chambers of the phytotron of Duke University, North Carolina, U.S.A. (Heth and Kramer, 1975). A close relationship was found between temperature and air humidity, and the ability of seedlings to survive after the cessation of watering. It appeared that *P. radiata* was more drought-tolerant than the other two species (as measured by soil water potential at seedling death) in dry-warm, dry-cool and moist-cool environments, but in a moist-warm environment there was little difference between species.

The ability of forest trees to withstand soil moisture stress was later studied in the same phytotron with *P. radiata* from California, *P. taeda* from the southeastern U.S.A., and *P. brutia* Ten. from the eastern Mediterranean region (Heth, 1974). As recommended by Boyer (1967) and Kaufman (1968), plant water stress was expressed by estimating needle water potentials ( $\psi_n$ ) from calibration curves relating xylem water potential ( $\psi_x$ ) to  $\psi_n$ ; the former was measured by the easier, though less accurate, pressure chamber and the latter — by the more precise, but also more involved, thermocouple psychrometer (Richards and Ogata, 1958) improved by Barrs (1969). Since root water potentials measured at the time are reported here for the first time, the present paper completes previous investigations by analysing differences between shoot and root water potentials and the response of root water potential of *P. radiata* and *P. brutia* to increasing moisture stress. Comparisons between species were made on the basis of dry weight and soil moisture potential.

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## MATERIALS AND METHODS

Eight-month-old seedlings of *P. radiata* and *P. brutia* grown in the phytotron of Duke University (Heth and Kramer, 1975) were exposed to four different climatic conditions for about two months (Table 1).

Illumination at a plane of reference 60 cm below the lamps (about 20 cm above the top of the seedlings) with 3000 ft-candles (approximately 32000 lux) for 16 hr per day, was supplied by a combination of incandescent and fluorescent lamps. The lamps were watered regularly until one month after the start of the treatments. The pots were then enclosed in polyethylene bags, sealed around the base of the stem, and kept without watering. Xylem pressure potentials (Kaufman, 1968) of the shoots ( $\psi_x$ ) and roots ( $\psi_r$ ) of three seedlings of each species and treatment were measured after 3-6, 17-20, and 28-31 days in a pressure chamber (Scholander *et al.*, 1965; Slavik, 1974) improved by Waring and Cleary (1967); oven-dry weights were obtained after drying the roots and shoots at a temperature of 70°C for 24 hr. A calibration curve of soil water potential over soil water content was used to evaluate the soil water potential in each pot from its moisture content.

TABLE 1—Temperature and relative humidity treatments

Treatment	Light period (0800-2400 hr)		Dark period (2400-0800 hr)	
	Temperature (°C)	Relative humidity (%)	Temperature (°C)	Relative humidity (%)
Dry warm	30 ± 0.6	65 ± 3	24 ± 0.6	74 ± 8
Moist warm	30 ± 0.2	83 ± 4	24 ± 0.3	81 ± 10
Dry cool	20 ± 0.2	55 ± 4	15 ± 0.3	63 ± 5
Moist cool	20 ± 0.4	70 ± 6	15 ± 0.3	82 ± 16

## RESULTS

Table 2 shows that in both species and in all treatments, soil water potentials ( $\psi$  soil) were higher (less negative) than root water potentials ( $\psi_r$ ) and the latter were higher than the shoot water potentials ( $\psi_x$ ). This suggests a decreasing gradient of water potential from the soil to the roots, and from the roots to the shoot. Regressions of  $\psi_x$  over  $\psi_r$  are given in Figures 1 and 2 for *P. radiata* and *P. brutia*, respectively. The distribution of the data in relation to the line of equal potentials indicates the difference of potentials, i.e., the ability for water to be transferred from the roots to the shoot. It shows that in both species  $\psi_x$  is always lower than  $\psi_r$ , thus confirming the above-suggested water gradient from the roots to the shoot. However, while in *P. radiata* this difference is quite uniform with increasing moisture stress, it seems to be irregular in *P. brutia* (about 0.5 MPa near field capacity, but becomes very small at about -1.5 MPa  $\psi_r$  and again large with increasing moisture stress). A stepwise regression was applied to the data in both species to test the significance of the scatter of the data. The highest significance was obtained in *P. radiata* for a linear regression of  $\psi_x$  over  $\psi_r$ , and in *P. brutia* for a curvilinear regression (Figs. 1 & 2).

TABLE 2—Water potentials (MPa) of soil ( $\psi_{\text{soil}}$ ), roots ( $\psi_{\text{r}}$ ) and shoot ( $\psi_{\text{x}}$ ) of *Pinus radiata* and *Pinus brutia* in four climates

Water potential	Treatment	Moist-cool		Dry-cool		Moist-warm		Dry-warm	
	Days from last watering	6	31	5	30	4	29	3	28
	Species								
$\psi_{\text{soil}}$	<b>P. radiata</b>	-0.03±0.001	-1.65±0.340	-0.02±0.003	-1.06±0.408	-0.03±0.004	-2.14±0.172	-0.06±0.004	-2.30±0.283
	<b>P. brutia</b>	-0.01±0.000	-0.69±0.307	-0.02±0.003	-0.88±0.414	-0.02±0.001	-1.90±0.409	-0.03±0.011	-1.98±0.422
$\psi_{\text{r}}$	<b>P. radiata</b>	-0.37±0.02	-1.68±0.46	-0.36±0.04	-1.52±0.84	-0.57±0.11	-2.43±0.23	-0.73±0.06	-2.60±0.30
	<b>P. brutia</b>	-0.33±0.02	-1.43±0.67	-0.37±0.07	-1.82±0.84	-0.55±0.12	-2.71±0.83	-0.63±0.16	-3.22±0.62
$\psi_{\text{x}}$	<b>P. radiata</b>	-0.60±0.08	-2.02±0.67	-0.58±0.07	-1.68±0.98	-0.85±0.08	-2.71±0.16	-0.91±0.06	-3.05±0.23
	<b>P. brutia</b>	-0.78±0.08	-1.45±0.68	-0.72±0.16	-2.06±0.95	-1.10±0.14	-3.76±1.86	-1.15±0.17	-4.14±1.49

TABLE 3—Shoot and root weights and shoot/root ratios of *Pinus radiata* and *Pinus brutia* in four climates

	Treatment	Moist-cool		Dry-cool		Moist-warm		Dry-warm	
	Days from last watering	6	31	5	30	4	29	3	28
	Species								
Shoot (g)	<b>P. radiata</b>	0.60±0.12	0.96±0.51	0.37±0.08	0.65±0.37	0.41±0.08	0.54±0.08	0.37±0.06	0.54±0.14
	<b>P. brutia</b>	0.30±0.04	0.53±0.05	0.44±0.15	0.53±0.18	0.34±0.03	0.46±0.05	0.31±0.17	0.41±0.16
Root (g)	<b>P. radiata</b>	0.34±0.04	0.74±0.38	0.30±0.05	0.42±0.13	0.31±0.11	0.43±0.11	0.27±0.05	0.34±0.04
	<b>P. brutia</b>	0.34±0.10	0.56±0.11	0.48±0.04	0.63±0.19	0.44±0.22	0.54±0.12	0.39±0.01	0.53±0.28
Shoot/root ratio	<b>P. radiata</b>	1.77±0.53	1.30±0.04	1.24±0.04	1.46±0.38	1.40±0.34	1.30±0.35	1.36±0.14	1.61±0.44
	<b>P. brutia</b>	0.94±0.21	0.96±0.11	0.91±0.26	0.84±0.14	0.88±0.34	0.87±0.17	0.80±0.40	0.85±0.28

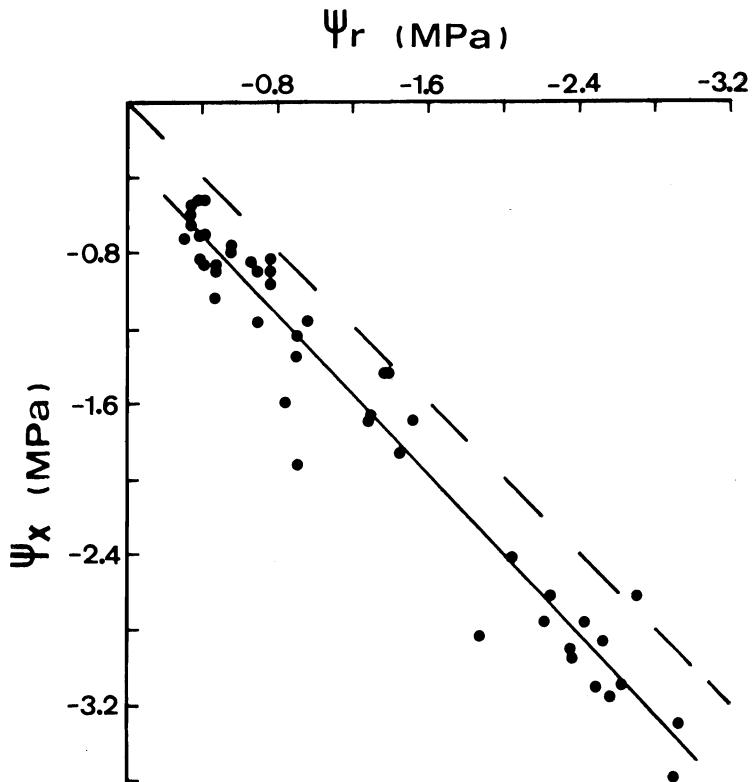


FIG. 1—Linear regression of xylem water potential of shoot ( $\psi_x$ ) over roots ( $\psi_r$ ) in *P. radiata*.

$$\psi_x = -0.2875 - 0.1068 \psi_r$$

( $N = 46$ ;  $R^2 = 0.948$ )  
 --- line of equal potentials

At the end of the experiment  $\psi$  soil,  $\psi_x$  and  $\psi_r$  of the two species were always lower in the warm climates than in the cool ones (Table 2).

Table 3 shows the mean dry weights of shoots and roots, and the shoot/root ratios of the seedlings. Shoot weights of *P. radiata* at the end of the experiment were heavier than those of *P. brutia* in all climates, while root weights of the latter exceeded those of *P. radiata* in all climates except for the moist-cool treatment. Shoot/root ratios in *P. radiata* were always larger than in *P. brutia*.

#### DISCUSSION

In a previous investigation, the drought tolerance of *P. radiata* was found to be highest under moist-cool conditions (Heth and Kramer, 1975). This fact may be related to its moist active root growth as recorded in this study (Table 3). In effect, only in this treatment was root growth so strong that, in spite of marked shoot growth, the shoot/root ratio decreased within 25 days from 1.8 to 1.3 (Table 3). This intensive root and shoot growth might also explain the soil water depletion expressed by the relatively low  $\psi$  soil on the 31st day in the moist-cool climate, as compared with much

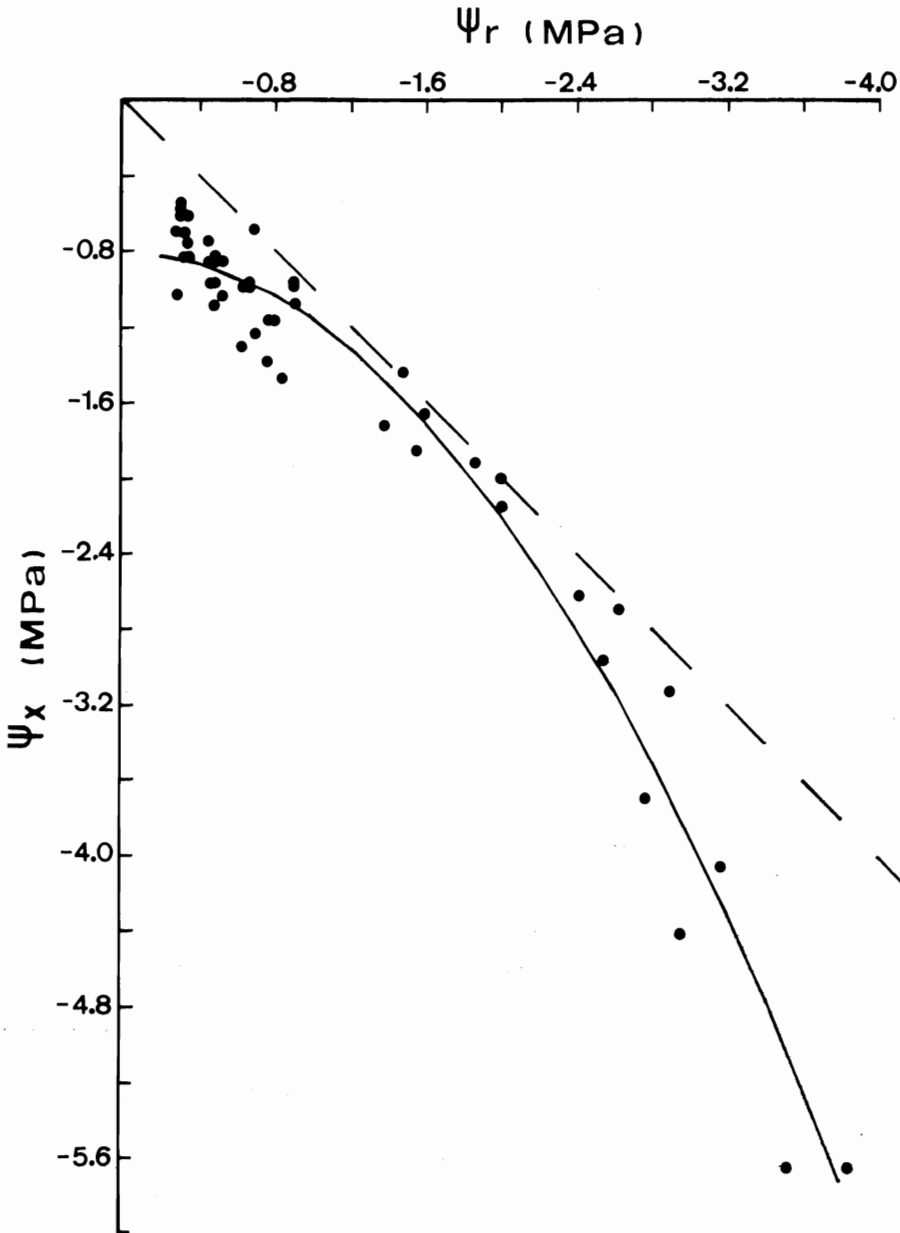


FIG. 2—Curvilinear regression of xylem water potentials of shoot ( $\psi_x$ ) over roots ( $\psi_r$ ) in *P. brutia*.

$$\psi_x = -0.78363 - 0.00595 \psi_r - 0.00326 \psi_r^2$$

(N = 49;  $R^2 = 0.963$ )

--- line of equal potentials

less intensive soil moisture extraction in the dry-cool climate (Table 2). Air humidity seems to have some effect on growth of *P. radiata* but appears less important than the temperature; it seems to affect the roots more than the shoots (Table 3).

In *P. brutia*, however, it seems that air moisture has very little, if any, effect on root and shoot growth (Table 3). Root growth of this species is apparently more intensive than shoot growth in all treatments; the shoot-root ratio was always less than one (Table 3). This seems to be a genetic characteristic which enables the species to overcome soil drying during the long Mediterranean summer. In both species, values of  $\psi$  soil in different treatments showed marked differences according to temperature, but were little affected by air humidity; similar relations were found with regard to  $\psi_r$  and  $\psi_x$ , but plants in dry-air chambers apparently had somewhat lower values of root and shoot water potentials as compared with plants in humid chambers (Table 2).

As shown earlier (Heth, 1974), needle water potentials of *P. brutia* near field capacity were lower than those of the more mesophytic North American *P. radiata* and *P. taeda*. The present study shows that near field capacity,  $\psi_x$  is lower in *P. brutia* than in *P. radiata* when  $\psi_r$  is similar (Figs. 1 & 2). For  $\psi_r$  of  $-1.2$  to  $-1.8$  MPa,  $\psi_x$  of *P. brutia* nearly equals  $\psi_r$ , but with increasing moisture stress  $\psi_x$  becomes much lower than  $\psi_r$ , possibly because of a greater resistance to water transfer. According to Y. Zohar (pers. comm.) water potential in drought-tolerant eucalypts was lower than in non-tolerant species; this may be due to the stronger linkage, in the matrix (matrix potential).

This could explain the curvilinear shape of the regression in *P. brutia* (Fig. 2) in contrast to the linear shape found in *P. radiata* (Fig. 1). Regressions of  $\psi_x$  over  $\psi_r$  were also found to be linear in the relatively mesophytic *P. taeda* and *P. echinata*, while a curvilinear shape was found in the west-Mediterranean *P. halepensis* (Heth, unpubl.). This seems to suggest that there might be a relation between drought tolerance and the pattern of the regression of  $\psi_x$  over  $\psi_r$ , a curvilinear shape indicating a higher rate of tolerance than a linear one. If, indeed, the curvilinear regression of  $\psi_x$  over  $\psi_r$  is related to higher drought tolerance, studies of the relation between water potentials of shoots and roots could provide important information for evaluating the adaptation to arid conditions of various species and seed sources.

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