

## DAILY TRANSPIRATION RATES OF RADIATA PINE

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### ABSTRACT

The factors affecting daily transpiration rates of individual trees are briefly reviewed, together with models of their relationship. Using experimental data for ramets of seven radiata pine clones growing in volcanic sandy loam, the following equation is constructed:

$$t/E = 25.036 - 33.93 \exp(0.07(5 - S)) + 1.311/E - 0.0074(S - 5)^2$$

for which  $t$  is daily transpiration per tree in ml per g o.d. wt of foliage;  $E$  is open-tank evaporation in cm/day; and  $S$  is soil moisture content expressed as percentage of soil o.d. wt. This equation accounts for 53% of the overall variation. The residual variation may be reduced by a further 11% if coefficients are fitted to the individual clones. Differences of transpiration rates between clones are highly significant.

Comparative data for soil water potential and needle pressure potential are also presented.

### INTRODUCTION

Although earlier writers (MacDougal, 1921; Millett, 1947) have reported on the transpiration of radiata pine (*Pinus radiata* D. Don) there are few published data apart from those of Rook (1969) and Oppenheimer (1968), both dealing with seedlings. Nor do these lend themselves to a formal statement of quantitative relationships between the rate of transpiration and the effective environmental variables. In certain hydrological investigations and field experiments requiring a budgetary control of water consumption, it is frequently impracticable to measure changes in soil moisture storage accurately or frequently enough, and it is then useful to be able to estimate the actual transpiration rates of larger trees. The intervals of time involved usually exceed 24 hours, so that the very extensive literature on diurnal patterns and instantaneous rates of transpiration is not directly relevant.

This paper reports a direct empirical test of such relationships between relative transpiration and soil moisture, with the objective of developing a predictive equation for individual radiata pine trees growing in soil derived from volcanic ash.

The primary factor determining transpiration is the amount of solar energy available at the crown surface of a tree. This controls the "overall evaporative demand" ( $E$ ) (Denmead and Shaw, 1962), which is however also dependent upon wind velocity and the ambient vapour pressure deficit. The maximum rate of transpiration ( $T_m$ ) for any individual tree will be determined by this evaporative demand, but the actual rate of transpiration is further governed by resistances to flow within the plant

and at the root/soil interface. In the context of the "soil-plant-atmosphere continuum" (Gardner, 1965), the mechanism of water transport through a plant is dependent upon maintenance of a sufficient water potential gradient between the root surface and the mesophyll cells of the leaf. If this gradient becomes inadequate, because of an excessive decline in the soil water potential, the guard cells of the stomata will not be able to maintain their turgidity, and they will close off the main route for escape of water vapour. However, since the soil is the source of water transpired by a tree, actual transpiration ( $T$ ) is ultimately determined by the amount of soil moisture currently available to the root system. When the evaporative demand is high, conductivity of water through the soil to the root surface becomes a limiting factor, even at a relatively high soil water potential. Conversely, under conditions of very low evaporative demand, relative transpiration ( $T/E$ ) will be maintained at its corresponding near-maximum value even down to a relatively low soil moisture content, because the rate of supply of soil moisture to the root system is sufficient to meet the (low) rate of transpirational loss.

Baier (1969) has recently reviewed the various postulated relationships between soil moisture supply and actual transpiration, including theories of equal availability throughout the range from field capacity to the permanent wilting point, the assumption of a linear relationship between relative transpiration and available soil moisture, and recent more complex expressions. He tested these alternative relationships in a budgetary calculation of soil moisture depletion, compared with measured soil storage, and concluded that the linear relationship gave the best fit between estimated and measured depletion. However, Gardner and Ehlig (1963) provide a convincing synthesis of evidence for the exponential reduction of relative transpiration from an asymptotic value at about soil field capacity. Necessary conditions for the validity of this model are a uniform root-distribution in a uniform soil-mass, and one of the reasons for the conflict with Baier's conclusions may be that the latter are based on water-depletion down a normal inhomogeneous soil-profile.

Denmead and Shaw (1962) present empirical evidence (from experiments with maize) that confirm these syntheses, but they further show that both the asymptotic value and the lower limit of available soil moisture depend upon the level of the evaporative demand.

## METHODS

The experimental material comprised ramets of seven clones of radiata pine (FRI Nos. 448, 450, 451, 454, 456, 457 and 460) that are being used extensively for investigating environmental effects on growth. The trees had been rooted as cuttings and grown for two years in the nursery prior to their transfer to plastic buckets of 8.9 litres capacity in June, 1970. The buckets were filled to within 25 mm of the top with potting soil comprising equal parts of loam and volcanic sand, packed to a bulk density ranging between 0.67 and 0.84. The soil surface was covered with wood wool and then sealed over with a polythene cover, tied around the base of the tree, in order to reduce surface evaporation. The base of the bucket was perforated to permit drainage of excess water and aeration of the soil.

The trees were then grown under conditions of minimal moisture stress, in order to promote maximum foliage development, until ready for initiation of the transpiration

measurements at the end of January, 1971. From three individuals matched for crown size within each clone, one individual was allocated at random to each of three replications. Each unit was then stood in an outer bucket inserted in an open-air bed of lump pumice tuff, to prevent insolation of the containers, and watered periodically to reduce fluctuations of soil temperatures. The layout was fully randomised around four Jessep atmometers and other units containing soil thermometers, and tensiometers.

From the end of January, each replicate of seven trees was taken through a succession of cycles of soil moisture depletion, the cycles being staggered in time, in order that transpiration rates could be measured concurrently at high, medium and low levels of soil moisture availability. Each replication, in turn, was brought up to saturation and then subjected to cumulative depletion, without further watering, until the daily transpiration rate approached the limits of measurement. Daily transpiration rates were determined by weighing each unit at 0815 each day, the difference from the previous weight in grams being recorded as an equivalent volume of water transpired during the preceding 24 hr. Weights were determined to the nearest gram, using an Ohaus balance. (During previous trials, two units without trees, but identical in all other respects, had been weighed daily to determine the amount of water lost by evaporation alone. It was exceptional for this to exceed 10 ml in any 24-hr period, and in no case did such loss exceed 20 ml. This compared with an average daily transpirational loss of 160 ml.) When containers were rewatered at the beginning of each cycle they were checked for any flow of water from the basal holes. If this occurred the data for the ensuing 24 hours were discarded. No measurements were taken during periods of rain, or when the foliage was still wet from previous rain or heavy dew.

The Jessep atmometers were read daily at the same time as units were weighed. The resulting data on atmometer loss provided an estimate of daily open tank evaporation, according to the methods detailed by Haggart (1969). Converted to metric units, her equation becomes:

$$E = 0.0243 + 0.00653 L \dots \dots \dots (1)$$

wherein L is the daily mean loss per atmometer, in ml, and E is expressed in cm of open tank evaporation per day.

On completion of the experiment, the trees were destructively sampled and the total fresh and oven-dry (o.d.) weights of foliage, branches, stem and root system determined for each individual. Oven-dry weight of foliage for each unit is shown in Table 1.

Analysis of variance indicated that neither the sum of squares for differences between replications (F ratio = 0.52, with 2 and 12 d.f.) nor that for differences between clones (F ratio = 1.81, with 6 and 12 d.f.) was significant. Crown growth was completed

TABLE 1—Final oven-dry weights of foliage for each clone in g, by replications

Rep.	Clone						
	448	450	451	454	456	457	460
I	39.1	35.0	48.4	34.4	49.5	28.0	45.4
II	26.9	48.6	52.3	39.5	30.8	37.8	48.2
III	39.9	37.7	49.7	50.1	53.9	34.4	40.7

prior to initiation of the experiment, and it is assumed that the o.d. weight of foliage was constant throughout.

The containers were fully occupied by the trees' root systems. Total oven-dry weight of the soil in each unit was determined by sub-sampling. The quantity of water in any bucket at 0815 each day was calculated as the difference between its total weight and the aggregate of soil o.d. weight, tree fresh weight, and the weight of bucket, wood wool and polythene. Soil moisture percent (S) was then calculated as an average of the initial 0815 value and that 24 hours later, for each day, expressed as a percentage of soil o.d. weight.

Moisture characteristics of the soil were determined by pressure membrane apparatus (between -1 and -15 bars) and by tensiometer (down to -0.7 bars). The latter were installed in buckets of the same soil sown with blue lupins and watered from below until their root-systems fully occupied the soil. Successive cycles of depletion from field capacity were then run, and the units weighed at each increment of soil moisture tension. Corresponding values of soil moisture as a percentage of soil o.d. weight were calculated. Combining these tensiometer and pressure membrane determinations of soil water potential (SWP), a linear regression was calculated for their logarithmic values against ln (S):

$$\ln (-\text{SWP}) = 9.5509 - 3.00055 \ln (S) \dots \dots \dots (2)$$

with  $r^2 = 0.993$ , and wherein SWP is soil water potential, in bars.

Values calculated from this equation are plotted as a moisture characteristic curve in Fig. 1.

### ANALYSIS OF RESULTS

Denoting replication, clone and day by subscripts *i*, *j* and *k* respectively, the daily transpiration rate ( $T_{ijk}$ ) for each tree was divided by o.d. wt of foliage in the crown ( $f_{ij}$ ) to convert to a uniform basis of comparison ( $t_{ijk}$ ), in ml per g o.d. wt of needles: If the daily mean value of the estimated tank evaporation is represented by  $E_k$  then the relative transpiration, as previously defined, is given by  $t_{ijk}/E_k$ . When these values were plotted against corresponding values of soil moisture percentage ( $S_{ijk}$ ) it became apparent that the data should be approximated by a curve derived from the negative exponential of  $S_{ijk}$ , intersecting the abscissa at between 5 and 10 percent and approaching an asymptotic value at field capacity (ie., about 35-40% of soil o.d. wt). Thus a first step in fitting a model to the data would be:

$$t_{ijk}/E_k = a + b_1 \exp (-c(S_{ijk} - 5)) \dots \dots \dots (3)$$

wherein *a*,  $b_1$  and *c* are constants, whose value is to be determined. As the minimum calculated value of  $S_{ijk}$  was 5.15, the intercept on the abscissa was arbitrarily set at 5 percent, in order to avoid changes of sign in the bracketed term. The inclusion of a constant term, *a*, in the equation eliminates the consequent constraint on the fitted curve to pass through the point  $S_{ijk} = 5$ .

This model should conform, in part, with the theoretical syntheses mentioned earlier. However, it is also necessary to allow for the effect of evaporative demand (*E*) on the level of soil moisture at which rate of unsaturated flow becomes limiting. This may be tested by including an additional term incorporating the reciprocal of *E*, i.e., a third term  $b_2(1/E_k)$ .

Examination of the plotted data for each replication indicated that the simple

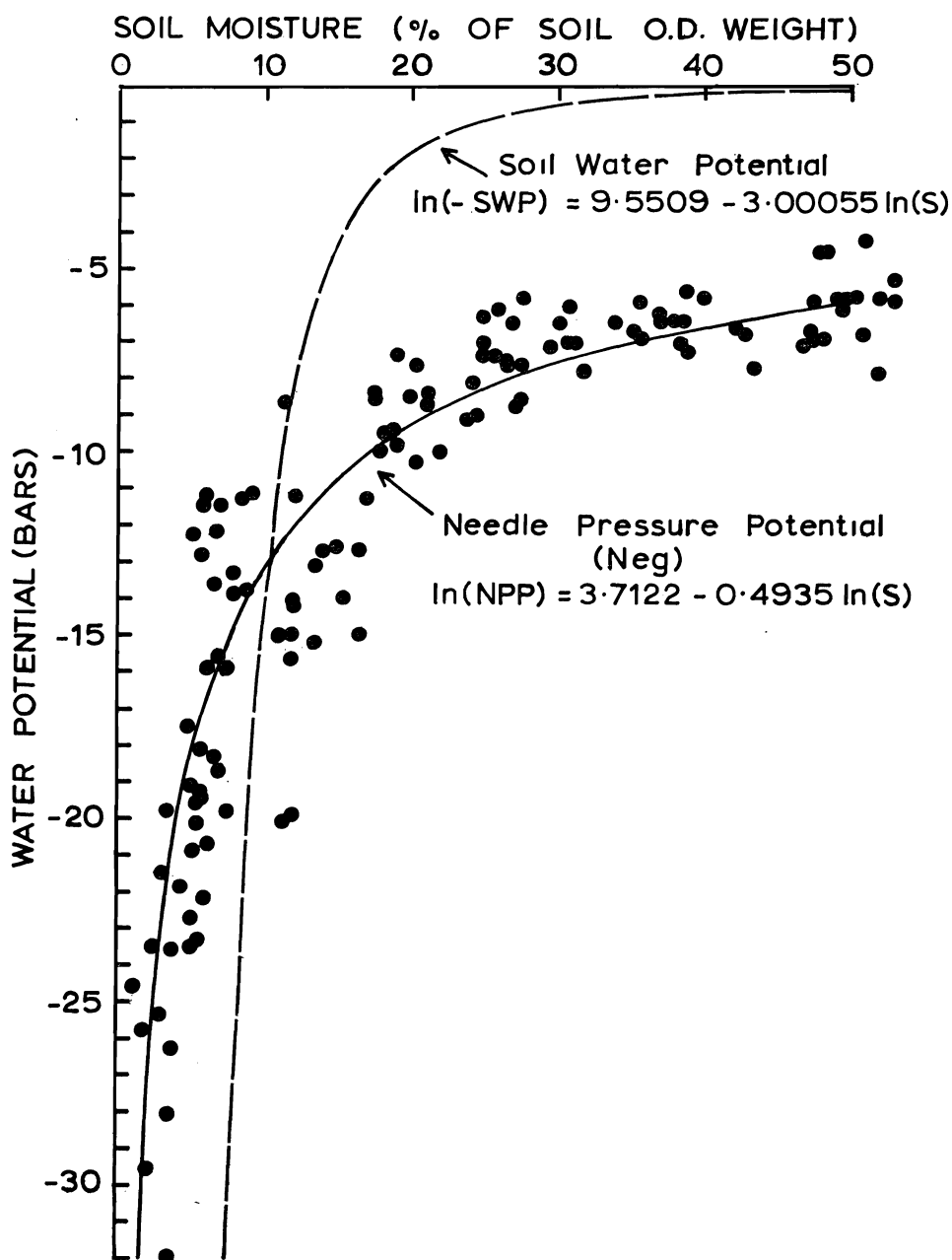


FIG. 1—Curves of soil water potential and needle pressure potential (expressed as negative values corresponding with leaf water potential) calibrated against given levels of soil moisture content.

assumption regarding an asymptotic value of  $t$  must be modified once soil moisture rises above field capacity, because thereafter the transpiration rate of radiata pine quite clearly diminishes again. In order to allow for this contingency, the model should include a further term or terms involving  $S_{ijk}$ . These may be linear, quadratic or of even higher order, and may be expected to have a negative coefficient ( $b$ ). Thus the completed model becomes:

$$t_{ijk}/E_k = a + b_1 \exp(-c(S_{ijk} - 5)) + b_2(1/E_k) + b_3(S_{ijk} - 5) + b_4(S_{ijk} - 5)^2 \dots \dots \dots (4)$$

Representing these terms and coding as follows:

$$Y = t_{ijk}/E_k = T_{ijk}/(f_{ij} \times E_k)$$

$$X_1 = \exp(-c(S_{ijk} - 5))$$

$$X_2 = 1/E_k$$

$$X_3 = (S_{ijk} - 5)/10$$

$$X_4 = (S_{ijk} - 5)^2/100$$

The model may be expressed as a linear equation:

$$Y = a + b_1X_1 + b_2X_2 + b_3X_3 + b_4X_4 \dots \dots \dots (5)$$

in which the  $a$  and  $b$  coefficients are to be estimated from the data by minimising the residual sum of squares about the fitted equation.

An iterative routine was incorporated in the computer programme, to ascertain what value of the constant  $c$  (over the range from  $-0.03$  to  $-0.15$ ) would maximise the sum of squares attributable to the equation. A preliminary comparison of the variation of  $Y$  associated with each of the four independent variables showed that much the greatest sum of squares was due to the exponential term,  $X_1$ . Moreover this was maximised when  $c = -0.14$ . See Table 2.

TABLE 2

Term	Sum of Squares
$X_1$	16513.58
$X_2$	75.05
$X_3$	9121.90
$X_4$	5273.16
Total variation	37609.25

A stepwise regression procedure was used to determine the order in which successive variables produced the greatest reduction of the residual sum of squares. This resulted in promotion of  $X_4$  ahead of  $X_2$  and  $X_3$ . Moreover, it was found that the overall sum of squares attributable to the regression on  $X_1$ ,  $X_4$  and  $X_2$  was maximised when  $c = -0.07$ .  $X_{3.142}$  was then not significant. See Table 3.

TABLE 3

Term	Sum of Squares	F ratio
$X_1$	14750.94	605.6
$X_{4.1}$	3186.21	130.8
$X_{2.14}$	2037.35	83.6
Residual	17634.76	E.M.S. = 24.36
TOTAL:	37609.25	on 727 d.f.

The regression coefficients and their standard errors for the equation on  $X_1$ ,  $X_4$  and  $X_2$  were calculated as:

	S.E.
$a = +25.0359$	$\pm 0.795$
$b_1 = -33.9809$	$\pm 1.383$
$b_4 = -0.7373$	$\pm 0.053$
$b_2 = +1.3114$	$\pm 0.143$

The final equation may thus be written:

$$t/E = 25.04 - 33.98 \exp(-0.07(S - 5)) - 0.0074(S - 5)^2 + 1.31/E \quad (6)$$

Parameters of this equation for relative transpiration rate ( $t/E$ ) are plotted in Fig. 2 against soil moisture and values of open-tank evaporation (E) selected to cover the normal range in the Rotorua region.

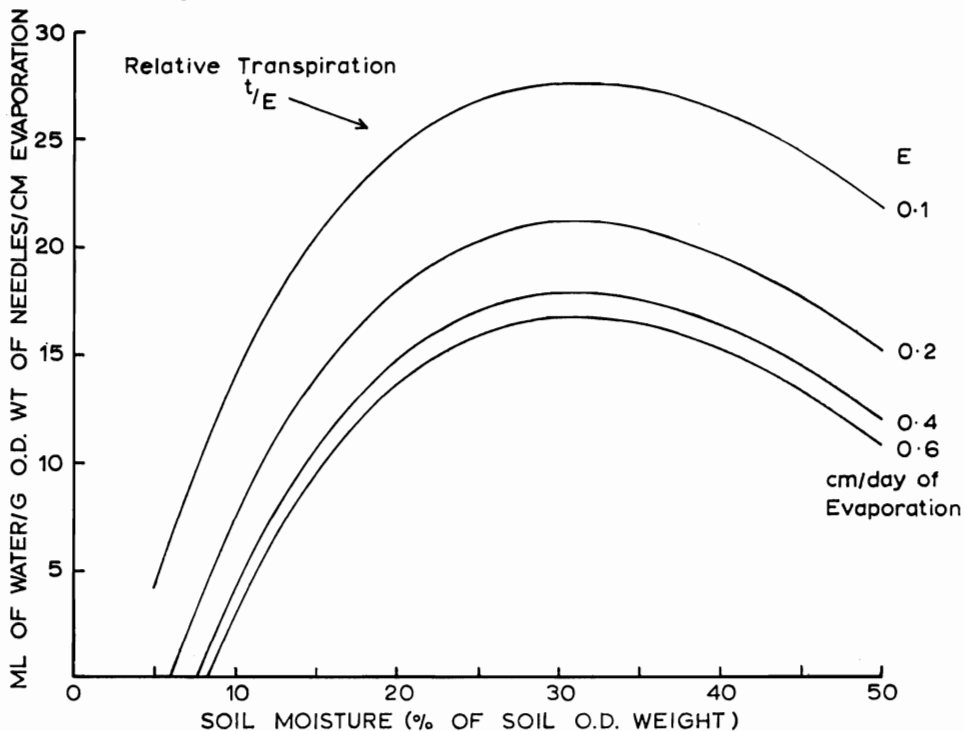


FIG. 2—Relative transpiration, as a mean over all seven clones, against soil moisture content, under four different rates of daily evaporation.

The predicted daily transpiration rates obtained by multiplying through the whole equation by specified values of E, are presented in Table 4.

TABLE 4—Transpiration rates in ml per go.d wt of foliage per day at specified rates of tank evaporation

Tank Evap. cm/day	Soil Moisture as % of Soil o.d. Weight											
	5	7	9	11	15	20	25	30	35	40	45	50
0.1	0.42	0.86	1.23	1.56	2.05	2.46	2.68	2.76	2.74	2.62	2.43	2.18
0.2	—	0.40	1.15	1.80	2.80	3.60	4.06	4.22	4.16	3.92	3.54	3.04
0.3	—	—	1.08	2.04	3.54	4.77	5.43	5.67	5.58	5.22	4.75	3.90
0.4	—	—	1.00	2.29	4.28	5.92	6.80	7.12	7.00	6.52	5.80	4.76
0.5	—	—	0.93	2.53	5.00	7.05	8.15	8.55	8.45	7.85	6.90	5.65
0.6	—	—	0.85	2.78	5.77	8.29	9.54	10.0	9.84	9.18	8.04	6.48
0.7	—	—	0.78	3.02	6.51	9.38	10.9	11.5	11.3	10.6	9.10	7.35

In order to obtain corresponding estimates of daily transpiration by an individual tree it is necessary to multiply these unit values by the estimated o.d. weight of foliage. A more appropriate but difficult measure of crown size would be the area of transpiring surface. Estimates of needle surface area for trees used in this investigation ranged between 150 and 200 sq cm per g.o.d. weight of foliage.

#### *Clonal Differences*

The amount of variation accounted for by the predictive equation is 53%. This can be improved further if differences between the clones are also taken into account. Thus, if the relationships are calculated independently for each clone, the residual variation not accounted for is reduced from 17634.76 to 13556.20 — i.e., by a further 11%. The difference between these residuals, on 24 d.f., is highly significant.

Individual coefficients for each clone are given in Table 5.

TABLE 5—Regression coefficients for transpiration rates of individual clones

Clone:	448	450	451	454	456	457	460
a	+ 23.82	+ 25.68	+ 30.71	+ 31.25	+ 22.14	+ 29.09	+ 21.31
b <sub>1</sub>	— 33.86	— 34.26	— 41.56	— 44.57	— 30.91	— 39.59	— 31.49
b <sub>4</sub>	— 0.883	— 0.814	— 1.338	— 1.039	— 0.776	— 0.853	— 0.337
b <sub>2</sub>	+ 2.002	+ 1.329	+ 1.506	+ 1.513	+ 1.256	+ 1.834	+ 0.717



Parameters of relative transpiration ( $t/E$ ) for each clone, at an assumed rate of evaporative demand ( $E$ ) of 0.4 cm/day, are presented in Fig. 3.

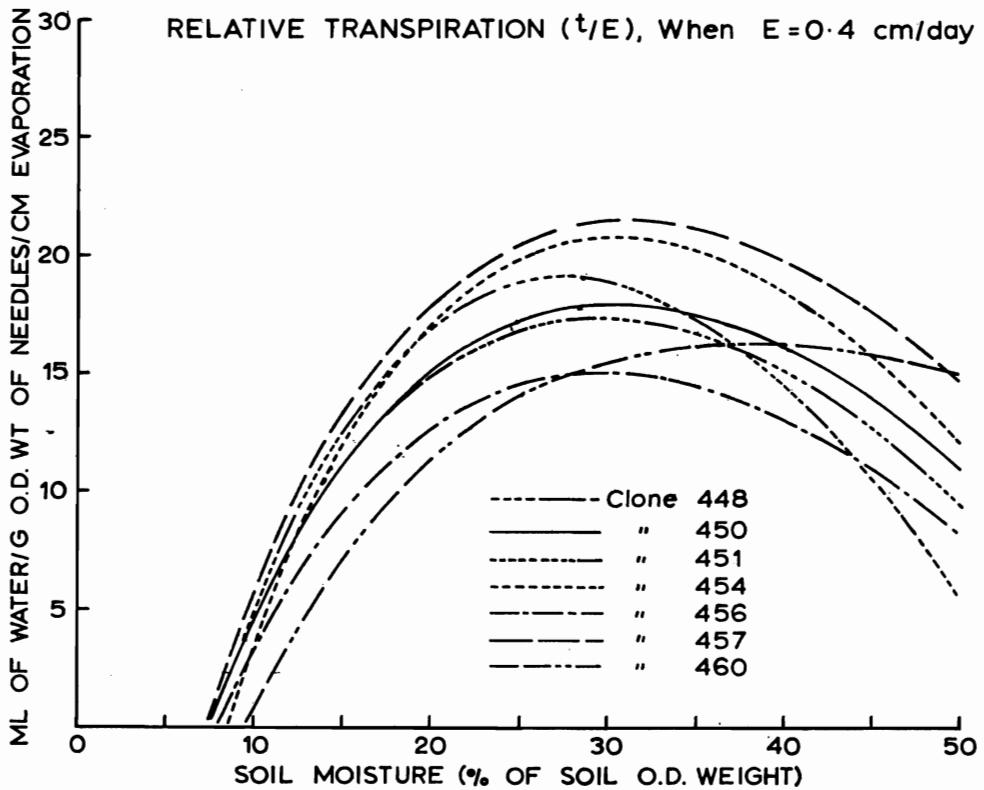


FIG. 3—Relative transpiration, for individual clones, against soil moisture content when daily evaporation rate is 0.4 cm of water from standard open tank.

### DISCUSSION

The empirical test clearly supports a negative exponential model for the daily transpiration rate of individual young radiata pine trees, although the simple exponential relationship is strongly modified by a quadratic term in the final model. Inspection of the plotted curves in Fig. 2 shows that these reach their maximum values at a soil moisture content of about 31% of soil o.d. wt. From equation (6) it may be calculated that, if one accepts the convention that a tension of one-third atmosphere (0.338 bars) approximates field capacity, the equivalent moisture content for the soil used in this experiment is 34.8%. Thus, transpiration rates of radiata pine attain their maximum values at about 90% of field capacity, and progressively diminish either way from this level. At about 18 or 19% s.m. (corresponding swp — 2 to — 2.5 bars) daily transpiration begins to diminish rapidly, and reaches a negligible rate at about 7% s.m. (— 35 bars), when the evaporation rate ( $E$ ) is at its mean value of 0.275 cm/day. Similar

results for tree species have been reported elsewhere: *viz.* Vznuzdaev (1969) found that the transpiration rates of pine, oak and elm saplings were correlated with air temperature and humidity so long as soil moisture tension remained above  $-2.5$  atmospheres ( $-2.53$  bars), but below this level transpiration decreased sharply and soil moisture depletion occurred at a much slower rate. Gulidova and Afanas'eva (1957) similarly noted that the transpiration rate of four tree species declined very rapidly when soil moisture decreased below about 70 to 75 percent of field capacity, and thereafter remained more or less constant. Satoo and Namura (1953) state that the transpiration of *Pinus densiflora* diminished gradually as soil water potential decreased to about  $-8$  or  $-9$  bars, and then dropped suddenly to a minimal rate which remained constant down to a soil water potential of  $-15$  bars. The data presented by Babalola *et al.* (1968) on radiata pine are unfortunately confined to the swp range between  $-0.35$  bars and  $-2.45$  bars. They do however indicate the dominating influence of swp at levels lower than this experimental range.

The inadequacies of a "permanent wilting point" at 15 atmospheres (15.2 bars) tension, conceived as a lower limit to the plant-available soil water, have been fully discussed elsewhere particularly by Slatyer (1957), who pointed out that the limits of soil moisture availability depend upon both soil type and the species of plant concerned. Thus Oppenheimer (1968) stated that Shomer-Ilan had "been able to show that *P. radiata* is greatly inferior in its capacity to use moisture below the conventional wilting percentage than either *P. pinea* or *P. halepensis*. She found osmotic pressures of only 8-15 atm. (8.1-15.2 bars) in roots of *P. radiata* as compared with 12-23 in *P. halepensis* and 18-29 in *P. pinea*." In order to secure data that would indicate the magnitude of the water potential gradients occurring in this investigation, a series of measurements of needle pressure potential (npp) was made on trees of the same clones and age growing under the same conditions as the transpiration units. Npp determinations were made at dawn, in duplicate for each tree, using a pressure chamber (cf. Gifford, 1972) and the soil moisture content of each unit was determined by weighing immediately afterwards. Mean values for each tree are plotted in Fig. 1, together with a curve fitted to the data:

$$\ln(\text{npp}) = 3.71 - 0.494 \ln(S) \quad r^2 = 0.826$$

That this curve crosses the curve of soil water potential, necessarily implies a reversal of the usual positive water potential gradient between soil and root system. There are at least two possible explanations for this: the ability of radiata pine to absorb dew or condensed water vapour through the sheathed base of its needle fascicles (Leyton and Armitage, 1968), and the possibility that pockets of soil within the soil container would be at a swp sufficiently greater than the overall (mean) value to permit local water transfer to roots during the night, when conductivity would be non-limiting. A further possibility is that evaporation of intra-vesicular water from the pumice soil particles would similarly condense on the roots during the night. However, the negative gradient would be eliminated very soon after sunrise, with the onset of transpiration and the ensuing rapid decrease of leaf water potential. As estimated by npp, the minimum value that was measured on these radiata pine saplings during the day was about  $-35$  bars. Normally during the midday period, individual trees appear to oscillate between about  $-13$  and  $-25$  bars; but trees that have been maintained under conditions of extreme soil moisture stress for many months, and have become

adjusted to it, appear to stabilise between  $-23$  and  $-29$  bars, showing a much narrower range of diurnal oscillation than trees with an ample supply of water. These data do not lend themselves to a determination of actual water potential gradients between soil and transpiring surface, since the determinations of soil water were all average values for the whole container, and some internal variability of swp would be inevitable.

Major differences of transpirational response between the seven clones in this study are apparent in Fig. 3. Firstly, the range of differences is such that the highest clone (No. 457) has overall rates of transpiration 50% greater than those of the least clone (No. 456). Similar high transpiration rates for Clone 457 had been found earlier, in 1968/69, when investigating unexpected mortality of ramets in another experiment. Secondly, whereas transpiration rates for six of the clones follow much the same trends, with a maximum at about field capacity and declining to negligible levels at a swp of about  $-28$  bars or less, Clone 460 appears to behave rather differently. Thus, it appears to attain peak transpiration rates at about 8 or 9% above soil field capacity and minimum rates at a swp as high as  $-17$  bars. Surprising as these differences may appear, it should be recorded here that the clones concerned were originally selected at random from open-sown nursery beds of one-year-old seedlings, and to this extent must be regarded as a random, although limited, sample of a normal radiata pine population.

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