

THE INFLUENCE OF SOIL MOISTURE ON WATER POTENTIAL, TRANSPIRATION AND PHOTOSYNTHESIS OF CONIFER SEEDLINGS

by W. M. HAVRANEK* and U. BENECKE*

Aussenstelle für subalpine Waldforschung, Forstliche
Bundesversuchsanstalt, Innsbruck

SUMMARY

The influence of soil moisture content and soil water potential on plant water potential, transpiration and net-photosynthesis of potted larch (*Larix decidua*), spruce (*Picea abies*) and pine (*Pinus cembra*) was studied under constant and close to optimum conditions in a laboratory.

The 'equilibrium' plant water potential measured under 'non-transpiring' conditions came close to soil water potential, but in moist soil the equilibrium potential was slightly lower, particularly in larch where transpiration was not fully arrested. In very dry soil, plants had higher water potential than soil, presumably due to roots exploiting the wettest points within the soil.

Pine, spruce and larch utilised a large part of soil moisture (down to 25wt. % soil water content or -1.5 bars potential) while maintaining plant water potential near -8 , -9.5 and -12.5 bars respectively. A similar pattern occurred in dry soil. The differences between species are explained by differing stomatal sensitivity to water potential.

Pine began a gradual reduction in gas-exchange below a soil water potential of -0.4 bars. Larch showed no marked reduction until the soil potential fell to -3.5 bars but below this the shut-down in gas-exchange was rapid. Spruce lay in between.

In spite of the early and sensitive gas-exchange reduction with decreasing soil moisture, pine maintained the highest net photosynthesis/transpiration ratio and thus used limited soil water more slowly and economically than the other species.

Seedlings maintained a higher rate of gas-exchange in strong light than in weak light, especially at low soil water potentials.

INTRODUCTION

A close correlation has been demonstrated between forest productivity and available soil moisture determined indirectly from preci-

* Present address: Forest Research Institute, University of Canterbury, Box 31011, Christchurch, New Zealand

piration and evapotranspiration budgets^{2 14 20 33}. With tree seedlings in growth chambers one can go further and determine directly the influence of soil water potential on transpiration and photosynthesis. Difficulties are, however, experienced in maintaining uniform soil water potential in the whole root zone since soils dry unevenly, resulting in moisture gradients¹³. To overcome such gradients in the soil or between soil and root surfaces, osmotic solutions have been used either directly or via semi-permeable membranes to maintain a constant and definable water potential in the root zone^{1 11 35}. Here too problems have been encountered, such as solute toxicity to the plants and difficulty in maintaining contact between the membrane and the soil.

With the pressure-chamber technique⁷ it has become possible to measure rapidly with adequate accuracy, plant water potential during active transpiration as well as when in equilibrium with the soil. The question arises to what extent does the equilibrium plant water potential agree with the soil water potential and what are the possible errors.

Soil moisture is often a critical factor for establishment of tree seedlings, even in temperate mountain climates which generally lack long drought periods. Reforestation programmes near the timberline in Austria, where edaphically dry sites and moisture deficits in the topsoil are common, require a better understanding of the influence decreasing soil moisture has on water relations and productivity in seedlings of the main subalpine species.

MATERIALS AND METHODS

Plants consisted of two-year old larch (*Larix decidua* Mill.), three-year old spruce (*Picea abies* (L) Karst.) and four-year old pine (*Pinus cembra* L.), all of high altitude provenances. In late summer 1970, seedlings were transplanted into 850 ml pots using a humose sandy loam taken through a 2 mm sieve. This uniform potmix was known to be suitable for healthy growth of all three species (24% > 0.2 mm, 35% 0.2–0.02 mm, 29% < 0.02 mm mineral soil and 12% organic matter. Water content in per cent dry weight was 46.5% at –0.1 bar and 12.5% at –15 bars, ('available' water = 34%).

Potted plants grew outside in a tree nursery until the start of trials in August 1971. By this time height growth of spruce and pine had ceased, but larch were still actively extending shoots. All seedlings had well developed fine root systems and root:shoot ratios for spruce and pine were 0.9 and 0.7 respectively.

Prior to the start of experiments, pots were watered to field capacity and then allowed to dry in a large wind tunnel at Patscherkofel³⁰ under constant conditions of $20.5 \pm 0.5^\circ\text{C}$, 10.5 ± 1 mb v.p.d., 2.5 m sec⁻¹ wind, 18 klx Xenon light and 300 ppm CO₂. To prevent the pots from drying too quickly, they were periodically sealed for 10–20 hours in plastic bags. During these periods, the rate of seedling transpiration was determined gravimetrically. The total drying period from saturation to a soil water potential (Ψ_{ws}) of -15 bars was 10 ± 3 days and to -25 bars it was 15 ± 4 days.

The plant water potential (Ψ_{w}) was measured with a Scholander pressure apparatus on small lateral shoots or needle fascicles. On approaching the balancing point, pressure was applied at a rate of 5–10 sec per bar similar to the method of Richter *et al.*²⁶. Needle fascicles were 0.5 to 0.8 bars higher in water potential than shoots.

At various stages of drying, individual pots were removed from the wind tunnel and placed in darkness in a plastic bag for 12 hours to allow plant and soil water potential to equilibrate under non-transpiring conditions. Individual seedlings were then placed in a smaller climatized wind-tunnel for gas-exchange measurement (net-photosynthesis by infrared gas-analysis, transpiration gravimetrically) during a 5–7 hour period at 30 klx Xenon light. Other parameters were identical to those pertaining during the drying procedure. After reaching stability, photosynthesis and transpiration were maintained at a constant rate for at least 2 hours. On terminating each gas-exchange measurement, the water potential was obtained for lateral shoots (spruce and larch) or needle fascicles (pine). After this, the potted plants were enclosed in a plastic bag for 24 hours to allow plant and soil water to come to equilibrium in darkness. The equilibrium water potential (Ψ_{we}) was then obtained for the shoot as well as for 2–3 mm diameter roots and a soil sample was taken from the wettest part of the root ball for determination of the moisture content by standard gravimetric procedure. Shoot Ψ_{we} values were similar before and after exposure in the wind tunnel indicating that Ψ_{ws} had not changed appreciably during this exposure period.

The relationship between water content and water potential of the soil (Ψ_{ws}) was determined with a ceramic plate extractor at pressures between 0.2 and 16 bars after 2–4 days at each pressure. The osmotic potential of the soil water was found to be small enough to be ignored (< 0.3 bars).

RESULTS

The influence of declining soil moisture on water potentials

The heavy curve in Fig. 1 presents the soil water potential (Ψ_{ws}) as a function of soil water content. From soil saturation down to 28 per cent water content, Ψ_{ws} remained above -1 bar. Thereafter, Ψ_{ws} decreased rapidly with a further decline in water content.

The equilibrium plant water potential (Ψ_{we}) of spruce and pine shown in Fig. 1 deviated from Ψ_{ws} in moist soil by only -0.5 to

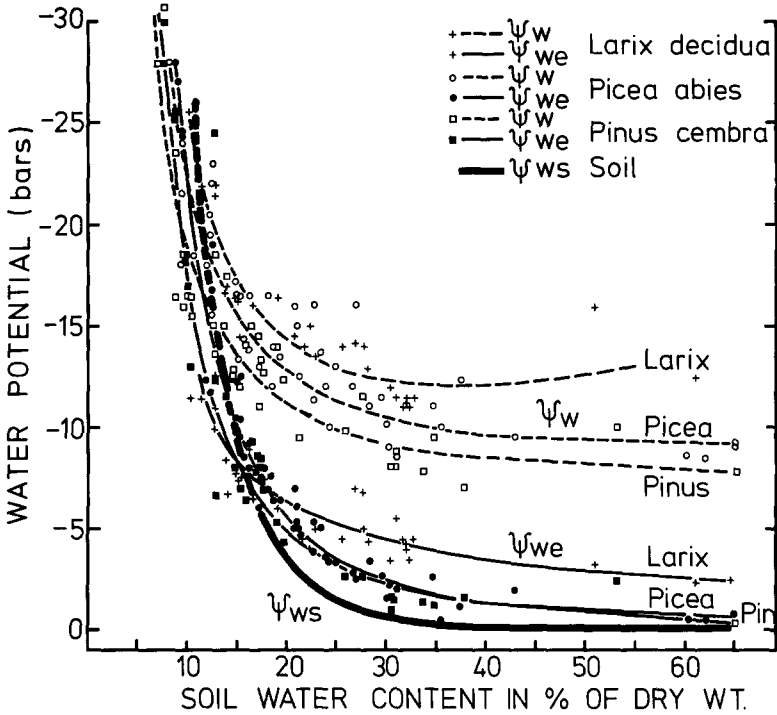


Fig. 1. Water potential in relation to soil moisture content. Ψ_{ws} = soil water potential as determined with a ceramic plate extractor. Ψ_{we} = water potential of seedlings in equilibrium with the soil under non-transpiring conditions of a dark chamber. Ψ_w = seedling water potential in a wind tunnel at $20.5 \pm 0.5^\circ\text{C}$, 10.5 ± 1 mb v.p.d., 30 klx, 2.5 m sec^{-1} , 20°C soil.

—2.0 bars, whereas for larch the difference was often more than —4 bars. With decreasing soil moisture, Ψ_{we} progressively approached Ψ_{ws} in all three species until in dry soil below —8 bars, Ψ_{we} values were higher than Ψ_{ws} .

The equilibrium water potential (Ψ_{we}) of spruce and pine shoots was found on average to be identical with that of roots. Only for larch in moist soil ($\Psi_{ws} > -6$ bars) were root values always higher than the corresponding shoot values in spite of determinations being completed within 2 minutes of excision. A deliberate exposure of 3–4 minutes to the laboratory air prior to pressure-chamber determination, decreased the Ψ_{we} value further to —7 bars, suggesting that in larch, transpiration was not fully arrested during the mea-

surement procedure and consequently the true Ψ_w was never attained.

Under the constant conditions of the wind-tunnel, Fig. 1 shows that all three species utilised a large part of soil water while maintaining Ψ_w near -8 bars in pine, -9.5 bars in spruce and -12.5 bars in larch.

With further soil water depletion below 25 per cent (Ψ_{ws} , -1.5 bars), Ψ_w decreased more slowly than Ψ_{ws} until the difference between Ψ_w and Ψ_{ws} reached zero and thereafter crossed-over so that Ψ_w was higher than the expected Ψ_{ws} value.

Regression analyses of the different water potentials against soil water content are presented in Table 1.

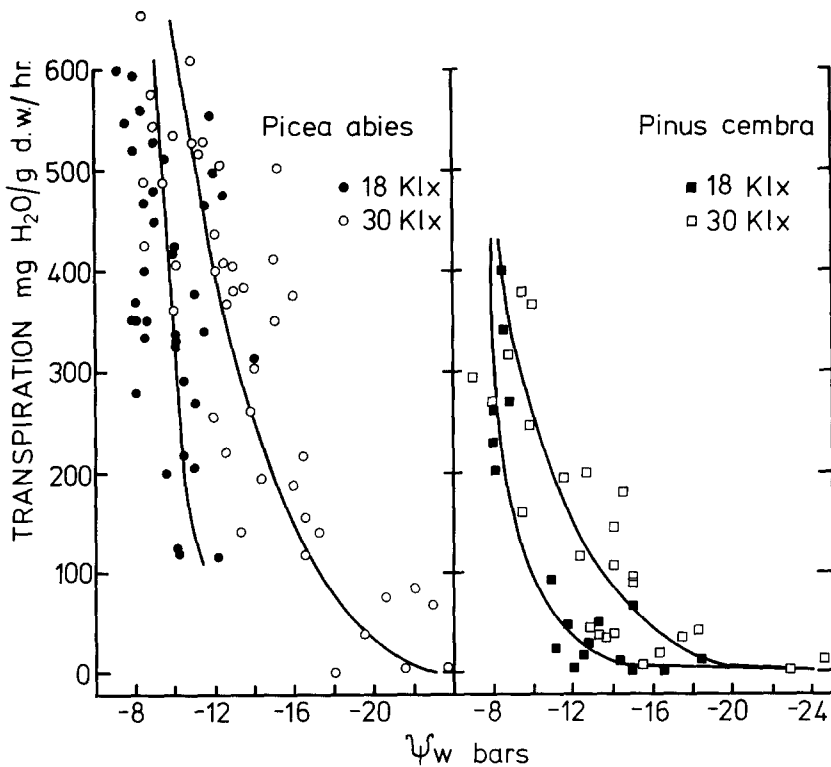


Fig. 2. Transpiration of spruce and pine needles in relation to xylem water potential (Ψ_w) measured over a range of soil moisture levels. Ψ_w was determined after transpiration was measured in a wind tunnel at 18 klx or 30 klx under otherwise identical conditions.

TABLE 1

Regression functions of water potentials in bars on soil water content (W) as a percentage dry weight. r = correlation coefficient. Ψ_w = transpiration water potential. Ψ_{we} = equilibrium water potential under non-transpiring conditions. Ψ_{ws} = soil water potential

Soil	$\log -\Psi_{ws} = 2.915 + 0.000 \log W - 1.408 \log^2 W$	($r = 0.99$)
Larch	$\log -\Psi_{we} = 1.929 - 0.863 \log W$	($r = 0.91$)
	$\log -\Psi_w = 3.569 - 3.180 \log W + 1.019 \log^2 W$	($r = 0.89$)
Spruce	$\log -\Psi_{we} = 3.334 - 1.991 \log W$	($r = 0.97$)
	$\log -\Psi_w = 2.920 - 2.194 \log W + 0.616 \log^2 W$	($r = 0.86$)
Pine	$\log -\Psi_{we} = 3.102 - 1.856 \log W$	($r = 0.94$)
	$\log -\Psi_w = 2.775 - 2.077 \log W + 0.578 \log^2 W$	($r = 0.93$)

Water potential and transpiration were measured during soil desiccation at two levels of light, 18 and 30 klx, but otherwise under the standard conditions described previously. Fig. 2 shows that at 18 klx, transpiration of spruce and pine declined to $\frac{1}{3}$ or less of maximum rates without any marked change in plant water potential. At

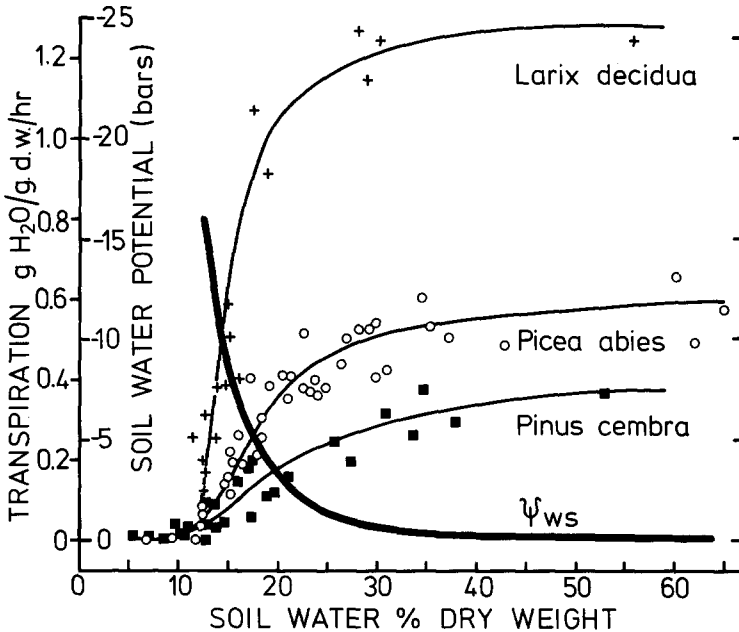


Fig. 3. Transpiration in a wind tunnel of larch, spruce and pine needles in relation to soil moisture content and soil water potential. Experiment at $20.5 \pm 0.5^\circ\text{C}$, 10.5 ± 1 mb v.p.d., 30 klx, 2.5 m sec $^{-1}$. Each value represents a single plant.

the higher light level of 30 klx, both species allowed Ψ_w to decrease ca. 4 bars lower than at 18 klx before restricting transpiration to the same extent.

Thus at the low light level stomatal closure occurred at higher water potentials (*i.e.*, low moisture stress) and more abruptly than at the higher light level.

Transpiration and net-photosynthesis in relation to soil moisture

Broadly, under the experimental conditions used, transpiration (Fig. 3) and net-photosynthesis (Fig. 4) showed the first slight decline at ca. 35 per cent soil moisture ($\Psi_{ws} -0.4$ bars) and a marked decline at ca. 25 per cent ($\Psi_{ws} -1.5$ bars). At a soil water content of 10-12 per cent ($\Psi_{ws} < -16$ bars), CO_2 - compensation point was reached and cuticular transpiration prevailed.

There were, however, distinct specific differences in the sequence of gas-exchange reduction. *Pinus cembra* began at a soil water con-

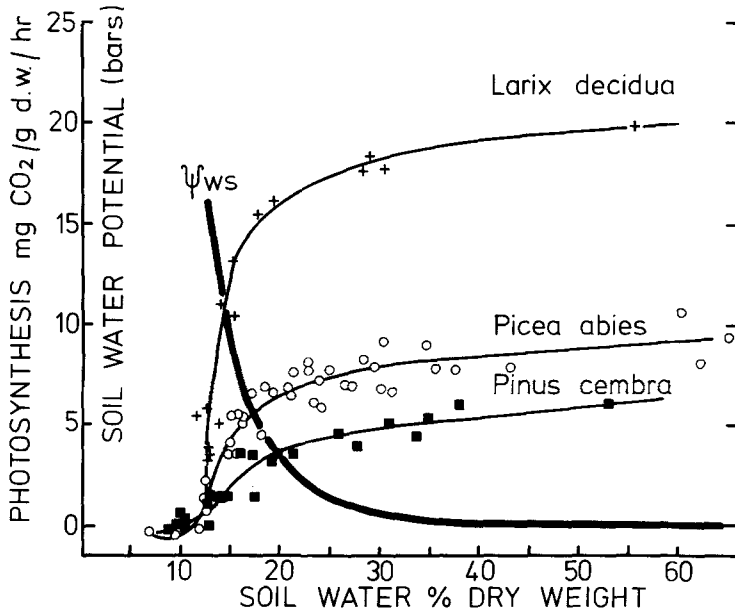


Fig. 4. Net-photosynthesis under constant conditions in a wind tunnel of larch, spruce and pine needles in relation to soil moisture content and soil water potential. Experiment at $20.5 \pm 0.5^\circ C$, 10.5 ± 1 mb v.p.d., 30 klx, 2.5 m sec⁻¹. Each value represents a single plant.

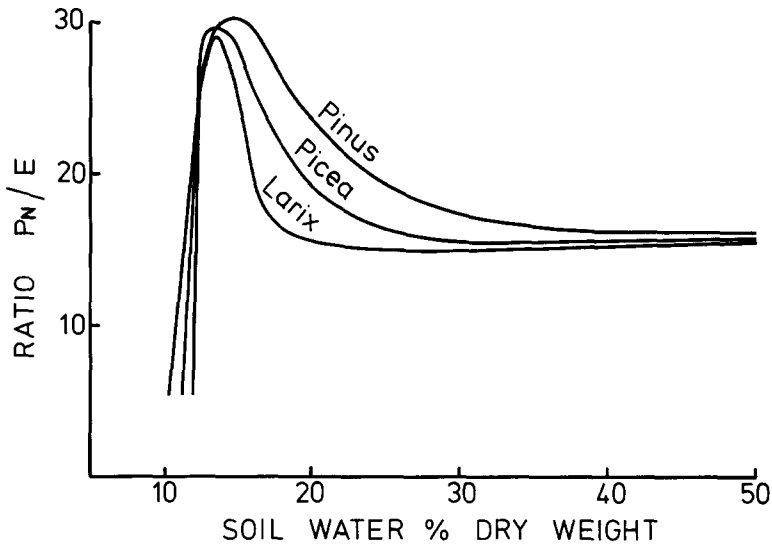


Fig. 5. Change in the ratio, net photosynthesis:transpiration ($P_n/E \times 10^{-3}$) with soil moisture content for larch, pine and spruce.

tent of 35 per cent (-0.4 bars) to gradually decrease gas-exchange with further reduction in soil moisture. Larch, at the other end of the scale, showed no marked reduction until soil moisture dropped to 20 per cent (-3.5 bars), but below this gas-exchange was rapidly reduced. When comparing the species at a soil water potential of -3.5 bars for example, pine had reduced transpiration to 47 per cent and photosynthesis to 58 per cent of maximum values while for spruce, the figures were 60 per cent and 70 per cent, and for larch 80 per cent and 80 per cent respectively. Generally, transpiration dropped faster than photosynthesis, transpiration reaching 50 per cent of its maximum rate at a soil water potential (Ψ_{ws}) of *ca* -3.0 bars in pine, -4.5 in spruce, -8.5 in larch and photosynthesis reaching 50 per cent of maximum rates at Ψ_{ws} -5.0 bars, -8.0 bars and -11.0 bars, respectively.

The rates of net-photosynthesis per unit of transpired water (P_n/E) also showed distinct differences between species (Fig. 5). This P_n/E ratio increased more strongly with declining soil moisture for pine than spruce or larch. Thus at low levels of soil moisture primary productivity relative to water use was greatest in pine, least in larch with spruce intermediate. Quantitatively this is most

significant between 30 and 20 per cent soil moisture (Ψ_{ws} -0.5 bars to -3.5 bars) where gas-exchange is still more than 50 per cent of maximum rates.

DISCUSSION

The pre-dawn plant water potential has been used as an estimate of soil water potential on the assumption that Ψ_{we} is at or close to equilibrium with Ψ_{ws} ^{9 15 32}. However, the prerequisite that transpiration is totally arrested for a sufficient time to allow plant/soil equilibrium to be reached is in reality more easily achieved in the laboratory than in the field.

Although our measurements of Ψ_{we} came close to the expected equilibrium with Ψ_{ws} , in moist soil Ψ_{we} was always slightly lower than Ψ_{ws} while in very dry soil plants had a higher potential than that obtained for the soil. Similar results were obtained for *Nicotiana*⁵, *Pinus mugo* and *Alnus viridis*³.

One reason for the lower Ψ_{we} values compared with Ψ_{ws} could be that a small excess pressure is required to bring Xylem water back to the cut surface²⁶. However, more probably, transpiration at the actual moment of measurement may not have been completely arrested, especially in larch. Hinkley⁹ reported that *Abies* seedlings had a high dark transpiration in moist soil but closed stomata more tightly in drying soil until dark transpiration was near zero at Ψ_{ws} -7.5 bars. Assuming a similar stomatal behaviour in our species, the decreasing discrepancy between Ψ_{ws} and Ψ_{we} down to Ψ_{ws} -8 bars would then be related very closely to increasing stomatal closure.

The higher Ψ_{we} values in very dry soil (< -8 bars) we assume were primarily caused by roots utilising the wettest points within the soil^{25 28}. Soil moisture determinations always give a mean value, whereas for the plant the wettest sites where it has roots are most significant to Ψ_{we} . Soil type also can be expected to influence the extent of these apparent Ψ_{we}/Ψ_{ws} differences³. However, they may in part also have been due to errors in determining the Ψ_{ws} /moisture content curve with the ceramic plate extractor, since in very dry soil, contact between the ceramic plate and the soil could have been lost. In spite of this, we conclude that in dry soil, Ψ_{we} determined with the pressure chamber technique offers for many soils a much

more useful measure of soil moisture available to plants than direct determinations of soil moisture or Ψ_{ws} (*cf*¹⁰). In moist soil, *i.e.*, when soil moisture was not a 'limiting factor'⁷, each species developed a different level of leaf water potential (*cf*¹⁸). We assume that under identical environmental conditions, the balance between opening and closing is maintained at a higher Ψ_w in pine than in spruce or larch by the stomatal control mechanism. This different sensitivity of stomata to a decreasing Ψ_w also occurs in dry soils and seems to be the main reason for specific differences in the decline of Ψ_w , transpiration and photosynthesis. However, Ψ_w measurements under two different light levels but otherwise similar conditions, showed that this 'species-determined' relationship between Ψ_w and stomatal aperture, and hence transpiration, can be altered considerably by light intensity (Fig. 2). We conclude from these results that seedlings are able to maintain a higher gas-exchange rate in strong light than in weak light, especially when Ψ_{ws} and thus Ψ_w are low. Similar results were obtained for cotton in field experiments²³.

With decreasing Ψ_{ws} , *P. cembra* reacted very sensitively, showing a quick decline in transpiration comparable to that of *P. ponderosa* and *P. contorta* under similar experimental conditions¹⁹. Our spruce seedlings responded almost exactly like *Picea engelmanni*, whereas transpiration in larch seems to have been far less efficiently controlled by stomata than in *Pseudotsuga menziesii* or in *Abies grandis*¹⁹. In fact, transpiration of larch appeared to be dependent on Ψ_{ws} , giving a linear decline with Ψ_{ws} , until at ca -17 bars wilting point of young tips was reached and older needles were cast. Cuticular transpiration is certainly also important and in larch contributes more to the total transpiration than in spruce or pine, but it was not quantitatively assessed.

As one would expect from an increase in the stomatal diffusive resistance, transpiration decreased earlier than photosynthesis^{8 17 33}, thus changing the ratio between Pn and E (Fig. 5). Cembra pine reduced the gas-exchange rates early with decreasing soil moisture, but maintained a higher ratio Pn:E, *i.e.*, it uses the limited soil water more slowly and more economically for primary production than spruce. Larch reacted quite differently and did not conserve water to avoid moisture stress, but maintained high production rates until severe moisture stress forced a rapid shut down and then shed needles when the drought persisted. Minor soil deficits, therefore,

seem to have little effect on transpiration and photosynthesis of larch, whereas, in agreement with other results for conifer seedlings^{11 19 27 29}, cembra pine and spruce restricted their gas-exchange progressively and at $\Psi_{ws} -1$ or -2 bars the reduction was already considerably. As soon as low Ψ_{ws} , or the physiologically similar effect of a recently transplanted root system, makes water uptake difficult pine is shown to be the most competent in avoiding severe plant moisture stress, larch the least.

In the reforestation of dry sunny mountain slopes one can thus expect seedling survival during the early establishment period to be high for cembra pine, moderate for spruce and poor for larch as has been confirmed in field trials³¹ and forestry practice.

ACKNOWLEDGEMENTS

The technical assistance of Mr C. Körner is gratefully acknowledged. Regression functions were computed by Dr J. Bachler. These studies were initiated while one of us (U.B.) held a DSIR research fellowship (New Zealand) and a DAAD bursary (Federal Republic of Germany).

Received 30 November 1976

REFERENCES

- 1 Babalola, O., Boersma, L. and Youngberg, C. T., Photosynthesis and transpiration of Monterey Pine seedlings as a function of soil water suction and soil temperature. *Plant Physiol.* **43**, 515-521 (1968).
- 2 Bassett, J. R., Tree growth as affected by soil moisture availability. *Soil Sci. Soc. Am. Proc.* **28**, 436-438 (1964).
- 3 Benecke, U., Physiologische Untersuchungen zur Eignung verschiedener Baumarten bei der Aufforstung in Hochlagen. *Forschungsber. Forstl. Forschungsanst. München* **5**, pp 87 (1972).
- 4 Boyer, J. S., Leaf water potential measured with a pressure chamber. *Plant Physiol.* **42**, 133-137 (1967).
- 5 De Roo, H. C., Water stress gradients in plants and soil-root systems. *Agron. J.* **61**, 511-515 (1969).
- 6 Duniway, J. M., Comparison of pressure chamber and thermocouple psychrometer determinations of leaf water status in tomato. *Plant Physiol.* **48**, 106-107 (1971).
- 7 Elfving, D. C., Kaufmann, M. R. and Hall, A. E., Interpreting leaf water potential measurements with a model of the soil-plant-atmosphere continuum. *Physiol. Plant.* **27**, 161-168 (1972).
- 8 Gaastra, P., Photosynthesis of crop plants as influenced by light, carbon dioxide, temperature and stomatal diffusive resistance. *Meded. Landbhogesch. Wageningen.* **59**, 1-68 (1959).

- 9 Hinkley, T. M. and Ritchie, G. A., Reaction of mature *Abies* seedlings to environmental stresses. *Trans. Miss. Acad. Sci.* **6**, 24–36 (1972).
- 10 Hinkley, T. M. and Ritchie, G. A., A theoretical model for calculation of xylem sap pressure from climatological data. *Am. Midl. Nat.* **90**, 56–69 (1973).
- 11 Jarvis, P. G. and Jarvis, M. S., The water relations of tree seedlings. I. Growth and water use in relation to soil water potential. II. Transpiration in relation to soil water potential. *Physiol. Plant.* **16**, 215–235 and 236–253 (1963).
- 12 Kaufmann, M. R., Water relations of pine seedlings in relation to root and shoot growth. *Plant Physiol.* **43**, 281–288 (1968).
- 13 Kausch, W., Saugkraft und Wassernachleitung im Boden als Physiologische Faktoren. Unter besonderer Berücksichtigung des Tensiometers. *Planta* **45**, 217–263 (1955).
- 14 Kramer, P. J. and Kozlowski, T. T., *Physiology of trees*. McGraw-Hill Book Comp. Inc. New York pp 642 (1960).
- 15 Klepp, B., Diurnal pattern of water potential in woody plants. *Plant Physiol.* **43**, 1931–1934 (1958).
- 16 Lange, O. L., Losch, R., Schulze, E. D. and Kappen, L., Responses of stomata to changes in humidity. *Planta* **100**, 76–86 (1971).
- 17 Larcher, W., The influence of water stress on the relationship between CO₂ uptake and transpiration. *In* *Water Stress in Plants*, Ed. Slavik, B., Czech Acad. Sci., Prague, pp 184–263 (1965).
- 18 Lopushinsky, W., Stomatal closure in conifer seedlings in response to leaf moisture stress. *Bot. Gaz.* **130**, 258–263 (1969).
- 19 Lopushinsky, W. and Klock, G. O., Transpiration of conifer seedlings in relation to soil water potential. *For. Sci.* **20**, 181–186 (1974).
- 20 Moehring, D. M. and Ralston, C. W., Diameter growth of Loblolly Pine related to available soil moisture and rate of soil moisture loss. *Soil Sci. Soc. Am. Proc.* **31**, 560–562 (1967).
- 21 Morris, J. Y. and Tranquillini, W., Über den Einfluss des osmotischen Potentials des Wurzelsubstrates auf die Photosynthese von *Pinus contorta* – Sämlingen im Wechsel der Jahreszeiten. *Flora Abt. B.* **158**, 277–287 (1969).
- 22 Müllerstaël, H., Untersuchungen über den Gaswechsel zweijähriger Holzpflanzen bei fortschreitender Bodenaustrocknung. *Beitr. Biol. Pflanz.* **44**, 319–341 (1968).
- 23 Pallas, J. E., Michel, B. E. and Harris, D. G., Photosynthesis, transpiration, leaf temperature, and stomatal activity of cotton plants under varying water potentials. *Plant Physiol.* **42**, 76–88 (1967).
- 24 Raschke, K., Stomatal responses to pressure changes and interruptions in water supply of detached leaves of *Zea mays* L. *Plant Physiol.* **45**, 415–423 (1970).
- 25 Rawlins, S. L., Gardner, W. R. and Dalton, F. N., In situ measurement of soil and plant leaf water potential. *Soil Sci. Soc. Am. Proc.* **32**, 468–470 (1968).
- 26 Richter, H., Halwachs, G. and Holzner, W., Saugspannungsmessungen in der Krone eines Mammutbaumes (*Sequoiadendron giganteum*). *Flora* **161**, 401–420 (1972).
- 27 Rutter, A. J. and Sands, K., The relation of leaf water deficit to soil moisture tension in *Pinus sylvestris* L. I. The effect of soil moisture on diurnal changes in water balance. *New Phytol.* **57**, 50–65 (1958).
- 28 Slavikova, J., Die maximale Wurzelsaugkraft als Ökologischer Faktor. *Preslia* **37**, 419–428 (1965).
- 29 Stransky, J. J. and Wilson, D. R., Terminal elongation of Loblolly and Shortleaf pine seedlings under soil moisture stress. *Soil Sci. Soc. Am. Proc.* **28**, 439–440 (1964).
- 30 Tranquillini, W., Das Klimahaus auf dem Patscherkofel und seine Bedeutung für die Aufforstung der subalpinen Entwaldungszone. *Allgem. Forstztg.* **80**, 72–74 (1969).
- 31 Tranquillini, W. and Rabensteiner, G., Über den Einfluss von Antitranspiran-

- ten und Wurzelfrischhaltemitteln auf den Gaswechsel junger Fichten, Zirben und Lärchen, sowie über die Bedeutung dieser Präparate für Hochlagenaufforstungen. Mitt. Forstl. Bundes Versuchsanst Wien, **96**, 75-102 (1972).
- 32 Waring, R. H. and Cleary, B. D., Plant moisture stress: Evaluation by pressure bomb. *Science* **155**, 1248-1254 (1967).
 - 33 Zaher, R., Water deficits and growth of trees. In *Water deficits and Plant Growth* (ed. T. T. Kozlowski), Vol. II, 191-254. Acad. Press New York and London (1968).
 - 34 Zavitkovski, J. and Ferrell, W. K., Effect of drought upon rates of photosynthesis, respiration, and transpiration of seedlings of two ecotypes of Douglas-fir. *Bot. Gaz.* **129**, 346-350 (1968).
 - 35 Zur, B., Osmotic control of the matric soil-water potential. I. Soil-water system. *Soil Sci.* **102**, 394-398 (1966).