# Ecological Aspects of Water Relations of Some Japanese Pines. I. Simulation of Soil Moisture Conditions, Transpiration and Water Deficit Responses in Black pine Seedlings.

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# マツ類の水分バランスに関する生態学的研究 (1) 土壌水分の変動とクロマツ苗の蒸散と水欠差における反応

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## Contents



## 要　　旨

土壌水分を周期的に調節することによって，ポットに植えたクロマツの蒸散と針葉の水欠差を土壌水分の変動と関連させてしらべた。蒸散は土壌が乾くにつれて減少した。そして，針葉の水欠差は土壌がまだ十分湿った状態においてもあらわれた。したがって，砂質壌土では土壌の水ポテンシアルが0付近においても蒸散の低下がおこるであろう。針葉の水欠差は土壌水分の減少に応じて次第に大きくなった。

## Abstract

During April-June 1973, experiments were conducted with three year old Japanese black pine seedlings transplanted into clay pots containing nursery sandy loam soil in a greenhouse. Soil moisture conditions were controlled by three steps of watering regimes to impose three different soil moisture stresses-wet, moist and dry conditions. The soil moisture stress in terms of soil water potential, was obtained by using the conversion from the relationships between soil moisture content and soil water potential characteristics. Transpiration, and needle water deficit responses to the three different soil moisture conditions were studied periodically during both the watering cycles and the prolongation of soil dryness. Rate of water loss from needles of different physiological ages, as well as the same age were compared by cut-leaf and weighing method. Needle water deficit responses were

also examined at the same time as the water loss measurements by taking needle sample to saturation in test tubes containing a saturated piece of foam and kept in the dark for 24 hours.

The results are as follows :

1. Water loss responses of two year and one year old needles were found to be similar in course of weight loss after cutting from shoots as well as during the daily course of water loss rates. Either the soil was nearly saturated or extremely dry.

2. Soil dryness caused the reduction of water loss rate from needles. In sandy loam soil, soil water potential decreased from -4.62 to -12.63 bars ; rates of water loss were found attributable only to the cuticular transpiration.

3. After 12 hours of watering performances, the rates of weight loss recovered at different magnitudes due to the experience of seedlings in the level of soil dryness. The seedlings which experienced the long day water stress could not recover to the rates found in seedlings of least stress. This may be due to the needles still being partly closed owing to inadequate water from soil.

4. Needle water content of seedlings grown in different soil moisture conditions was not too different, except for a slightly higher percentage in dry soils after watering.

5. Needle water deficit occurred even when seedlings obtained a relatively high water potential. During a short time span, needle water deficit was only an approximate indicator of soil water status. The actual effect of needle water deficit on the rate of water loss could not be precisely predicted as they were each determined separately.

6. Needle water deficit could be correlated with soil moisture content in this form :

$$\log_{10}NWD = 0.4716 + 3.7029\ SMC^{-1},$$

where NWD is needle water deficit (% of saturated weight of needles), SMC is soil moisture content (% of soil dry weight). The correlation coefficient (r) is 0.8463.

## Introduction

Ecological distribution and productivity of tree species are usually characterized by the diversity of environmental conditions. One of the most important environmental facors frequently referred to is water availability. Japanese black pine (Pinus thunbergii Parl.) is a typical coniferous tree species growing in a comparatively dry area and predominating in the local soil of the sandy type and in the area which is exposed to the prevailing strong sea breeze.[16] From an ecophysiological point of view, the mentioned conditions imply an environmental stress[11] which causes not only damage to plants, but also limit the availability of soil moisture. In mountainous areas, the soil moisture availability may be limitted by the topographical structure. In this case, the availability of water is of fundamental importance.

This paper deals with the responses to the soil moisture conditions of black pine seedlings grown in pots. Soil moisture conditions are expressed in terms of soil moisture stress[22] which refers to the water potential status of soil and based on the unit of bar. The responses were measured in terms of transpiration and needle water deficit of seedlings which were subjected to the various soil water potentials. The simulation purpose is considered here as a resemblance of the soil moisture conditions in the field and the responses are the results of the water balance in seedlings.

## Materials and Methods

For the purpose of experiments, it was decided to grow the seedlings in a pot or container in order to maintain uniform root distribution, eliminate competition among seedlings and control differences in soil moisture conditions. Three year old nursery-grown seedlings were transplanted into clay pots containing a nursery sandy loam soil mixed with organic composts for satisfactory aeration of the roots. The soil used was sieved to eliminate large particles and debris. The soil in pots was approximately 1.8 kg of dry soil per pot. In order to measure soil moisture conditions in terms of soil water potential, the soil moisture characteristic was studied. The total soil moisture stress expressed in unit of bar of soil water potential measured by the method explained here is the total water potential in which both pure free water and possibly some osmotic solution combined in soil solution were equilibrated with the known vapour pressure of osmotic solution. The method used was adopted from the gravimetric vapour pressure equilibrium method of Slatyer.[18] Following this method, small soil samples, about 3-5 gm of saturated soil were brought to equilibrium with the known vapour pressure of various concentrations of NaCl solution. The method used is similar to that used for measuring the water potential of leaf tissues, and needs a successive constant temperature control and a small desiccator. At the time

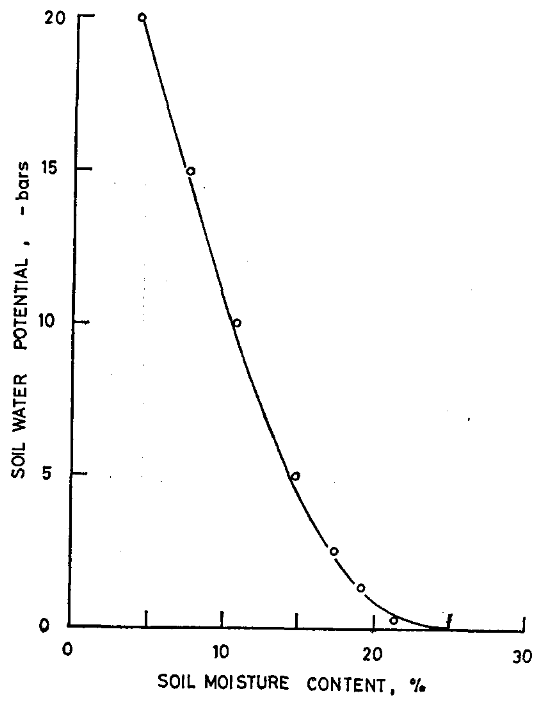



Fig. 1. Soil water characteristics of nursery sandy loam soils. Each point is an average of five samples. Percent soil moisture content is expressed by soil dry weight basis.

of soil water potential measurement, the control water bath was not available for instant use, the micro-desiccators containing soil samples were kept at the control room temperature of 24±1.5°C. The nursery sandy loam soil water potential and soil moisture content relationships is shown in Fig. 1.

Soil moisture conditions were controlled by the regulation of watering regimes, performed in the evening, and soil moisture content obtained by weighing pots and by periodical extraction of soil samples from pots to determine the soil moisture content directly. The increase in weight of seedlings was found negligible and was not large enough to cause serious error in determining the soil moisture content by this method. Before the commencement of the soil moisture stress or drought treatments, each pot was covered by a vinyl bag with a hole at the bottom to facilitate drainage, and the pots were sealed with a rubber band at the base of the seedlings. The band was removed during watering. The water loss from soil is attributable only to loss through seedlings. The treatments were : daily watering to keep the soil water potential approach to zero, watering every two days, and watering every four days to impose drought or stress around the root zone of the seedlings. The three treatments were designated as wet, moist, and dry. The treatments started after transplantation for one month and seedlings obtained regular watering till the roots were assumed to be firmly and well established. The number of days that soil water stress could be successfully imposed were determined from the curve of daily change in soil water potential. This curve was constructed from the conversion of soil moisture content - soil water potential relationships. An example of soil water potential development during the successive drying out and waterings is shown in Fig. 2.

The average soil water potentials during the experiments were calculated from the primary data and a graph similar to Fig. 2. The total soil water potential-days were added and then divided by the number of day of experiments. It was assumed that the small fluctuation of soil water potential within the day was small and negligible. Actually, there

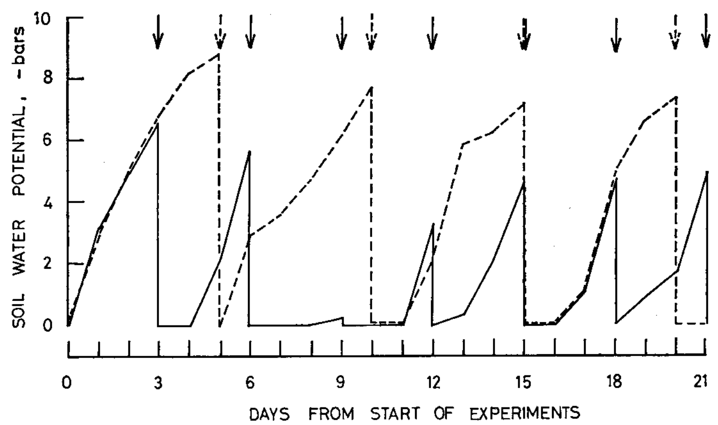



Fig. 2. An example of water potential curves during the experiments. The figure shows only the two stress experiments of moist and dry treatments for wet treatment the water potontial was kept at zero. —— ; moist treatment, ······ ; dry treatment. Arrows Show waterings.

were large changes in soil moisture content (% of soil dry weight), especially in the conditions that allowed seedlings to transpire mostly in wet and moist soils as well as during the recoveries of transpiration after watering in dry soils. But such differences become very small when soil moisture content was converted to soil water potential form.

Transpiration measurements were conducted twice under green-house conditions. The first measurement was done on May 24, at the time when the dry treatment was extreme (the last day of the drying out cycle), the moist treatment was also at the end of a 2 days drying out cycle. The second measurement was done during one watering cycle of 5 days began from June 8 - June 12. The method used was cut-leaf and weighing by a torsion balance of 1 gm capacity and 0.5 mg sensitivity. To counter the objections on physical grounds to the cut-leaf method of transpiration measurement, the fact that it provides a rapid and useful relative measure of transpiration led to its adoption for this study. The method was adopted from that of Hygen[7] which was found capable of detecting the differences of water loss response as affected by the variations of both atmospheric and soil moisture conditions and especially of assessing the various phases of water loss in a semi-quantitative way. The needle samples used were one and two year old needles, and the responses were determined separately.

Needle water deficit is a component of relative water content (RWC), or relative turgidity in Weatherley's terminology.[23] The principle and method used will be briefly described as follows :

The randomly selected needle pairs were cut off at the base from shoots, immediately weighed to obtain the field fresh weight (FW) and the cut-ends of needles were kept in contact with saturated foam with distilled water in standard laboratory test tubes (15 cm long). The saturated foam facilitated keeping only the cut-ends attached to a thin film of water and reduced the time for surface drying of the superficial water that remained on the soaking surfaces. The tubes containing the needle samples were kept airtight and placed in a dark cabinet at room temperature (about 20°C). It was found that the time needed to bring the whole needles to saturation was more than 24 hours. This time was taken into account in the case of needles which were slightly or severely dry. After keeping the samples until they became saturated in the given time interval, they were then brought out, the soaking surfaces dried with absorbing papers and the saturated weight (SW) obtained by weighing. The samples were dried to the constant dry weight (DW) in an oven at 85°C. The relative water content was determined as ;

$$RWC=\frac{FW-DW}{SW-DW}\times 100 = \text{relative turgidity of Weatherley},$$ [23]

the needle water deficit (NWD) which defined the deficiency of needles to attain a saturation state was then calculated as ;

$$NWD=100-RWC \; ; \; \%$$

The measurements of needle water deficit were conducted during the soil moisture stress treatments imposed in the greenhouse. The regular sampling time was in the early morning just before starting the transpiration measurement, because the fluctuations in water deficit during the day always caused by the lag of absorption to substitute the water loss by transpiration[10] as well as by other causes which prevent reliable results. The early morning water deficit in needles is an estimate of water status both in soil and plant body, and is considered as an indicator of water balance in the present study.

The latter part of these experiments, in addition to the experiments explained above, aimed at the assessment of the relationships between needle water deficit and soil moisture condition, so it was proposed to follow the development of needle water deficit during the prolongation of soil moisture stress. Six potgrown seedlings of the same experiment were used. The whole soil mass in pots were brought to saturation at a very low soil moisture stress (zero bar ; soil water potential) at the outset of the experiment and watering was practically stopped. The whole pots were covered with vinyl bags to prevent water loss through the soil surface. Changes in soil water potential and needle water deficit were followed periodically until the soil become very dry. The method of soil water potential and needle water deffcit measurements were practically the same as has been described earlier.

Table 1. Soil moisture content (% dry weight), soil water potential (—bars) and atmospheric conditions during the transpiration and needle water deficit measurements in each period.

| Periods | Treatments | Soil moisture conditions | | Atmospheric conditions | | | |
|---|---|---|---|---|---|---|---|
| | | SMC % | SWP —bars | T ; °C max | T ; °C min | RH % | SD mmHg |
| I, 24/5/1973 | wet | 35.13 | 0.00 | 25.8 | 13.0 | 49.25 | 10.03 |
| | moist | 15.30 | 4.62 | | | | |
| | dry | 12.60 | 7.11 | | | | |
| II, 8/6/1973 | wet | 39.09 | 0.00 | 24.8 | 16.6 | 69.73 | 5.88 |
| | moist | 34.11 | 0.00 | | | | |
| | dry | 8.04 | 12.83 | | | | |
| 9/6/1973 | wet | 37.81 | 0.00 | 27.4 | 19.1 | 24.5 | 9.55 |
| | moist | 38.17 | 0.00 | | | | |
| | dry | 34.23 | 0.00 | | | | |
| 10/6/1973 | wet | 38.34 | 0.00 | 27.6 | 20.0 | 64.44 | 8.75 |
| | moist | 31.15 | 0.00 | | | | |
| | dry | 29.20 | 0.00 | | | | |
| 11/6/1973 | wet | 36.78 | 0.00 | 29.4 | 20.2 | 66.62 | 8.52 |
| | moist | 23.21 | 0.00 | | | | |
| | dry | 22.95 | 0.00 | | | | |
| 12/6/1973 | wet | 36.34 | 0.00 | 31.2 | 20.4 | 63.85 | 10.82 |
| | moist | 33.17 | 0.00 | | | | |
| | dry | 17.19 | 3.15 | | | | |

SMC =Soil moisture content, average of 10 samples (%)
SWP =Soil water potential, (—bars)
T =Air temperature, (C°)
RH =Relative humidity, (%)
SD =Saturation vapour pressure deficit of atmosphere, (mmHg)

The needles used were those grown during the previous season.

The atmospheric conditions were allowed to vary as they might under natural conditions because the greenhouse was only equipped to keep the seedlings away from natural rain. During the transpiration measurements, they were recorded by using a whirling Asman psychrometer at frequent intervals. The soil moisture and atmospheric conditions during the transpiration and needle water deficit measurements are summarized in Table 1. The greenhouse conditions during the entire period of soil moisture stress treatments averaged 20.08°C ; air temperature, 72.84 % ; relative humidity and 3.46 mm per day ; evaporation of distilled water filled up the predetermined levels of the laboratory petri dishes. The petri dishes were randomly placed outside and among the rows of pot-grown seedling on the greenhouse bench. All experiments were conducted in the Kyoto University greenhouse between April 4 - June 12, 1973.

## Results and Discussion

1. Rate of water loss from needles of different physiological ages : The transpiration expressed here will be considered as the water transfer through the transpiring surfaces. In Fig. 3 ; weight loss of needles was followed after randomly detaching the needle pairs from shoots and the weight changes were recorded at frequent intervals. The reduction of weight follows the specific curve exactly. According to Hygen[7], the type of curves could be divided into three phases, namely : the rapid reduction of weight from the beginning till the curve departs from linearity which is a stomatal transpiring phase, the concave part is a stomata closing phase, and the last part of the curve, which shows a rather constant linear trend, is a cuticular transpiring phase. Therefore, the weight loss of both one and two year old needles during dry treatment may be attributable to cuticular transpiration, for the curve continues censtantly from the beginning. Almost the same trend occurred even when the weight changes were followed up to about six hours after detachment. Among the needles from the later two conditions, the wet and moist treatments, the weight loss was rapid during the first phase, became concave sometime later and then became constant. These then are considered stomatal transpiration.

Extending the experiments throughout the day at hourly intervals, a curve similar to those in Fig. 3 could be obtained. The first phase of weight loss in wet and moist treatments, as well as the whole phase of dry treatment were converted to water loss rate (mg/g f wt. min). The diurnal trend of water loss rates is shown in Fig. 4. The water loss rate of needles during dry treatment was found to remain constant throughout the day both for one and two year old needles ; (Fig. 4 ; c), but the other two conditions showed relatively high rates and fluctuations. There were slightly different water loss rates for one and two year old needles in wet treatment (Fig. 4 ; a) which showed early high rates, drops around midday and relatively low rates occurring from the late afternoon through the evening. This is in contast to the moist treatment (Fig. 4 ; b). The undetectable different rate of water loss of the two needle ages, is presumably because the two had reached a quite similar stage. The two year old needles referred to in this experiment were those grown about two years ago and the one year old needles were those developed during the previous season. This is in contrast to Parker[12], who reported that older leaves of ponderosa pine lost water more rapidly than younger leaves. He suggested that this might result from decreased activity of the guard cells and increased permeability of the cuticle in older leaves.

The soil water potentials during that period obtained an average of -7.11 bars in dry treatment, -4.62 bars in moist treatment, while the wet treatment was maintained at a high water potential (Table 1). Examining the soil moisture characteristic curve in Fig. 1, the water loss from needles was reduced as the soil moisture condition diminished or stress occurred during the soil drying out. Due to the reduction of soil water potential, the diminishing of a small soil water potential caused great changes in responses of apparent water loss. The ranges of water potential found in moist and dry treatments are still within the available ranges of sandy loam soil, but the rate of water loss changes abruptly, The sandy loam soil is naturally very permeable, the conductivity of water in soil may be very good if soil is in saturation[19]. The large reduction of water loss may be caused by a poorly developed root system which could not sustain a long day and high rate of transpiration[3]. However, if the reduction of water loss in this case is compared to other experimental results, it is found that black pine seedlings give different results. Rutter and

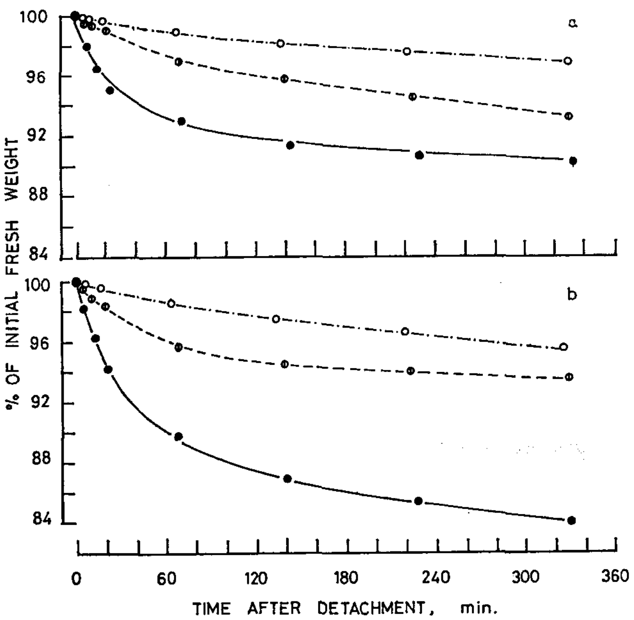



Fig. 3. Examples of weight loss-time curve, a comparison of needles of different physiological ages. Samples are reproduced from the greenhouse experiments. a) one year old needles, b) two year old needles. ●-● ; needles from wet treatment, ⦶- -⦶ ; needles from moist treatment, ○ -•-○ ; needles from dry treatment. For explanation see text.

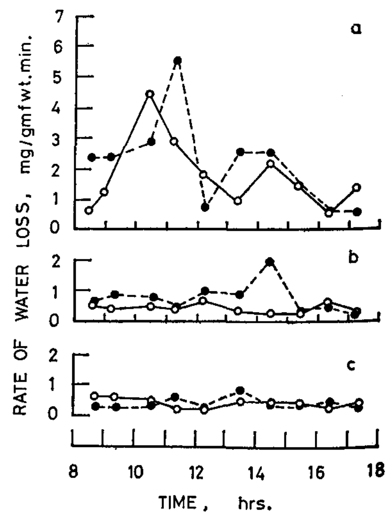
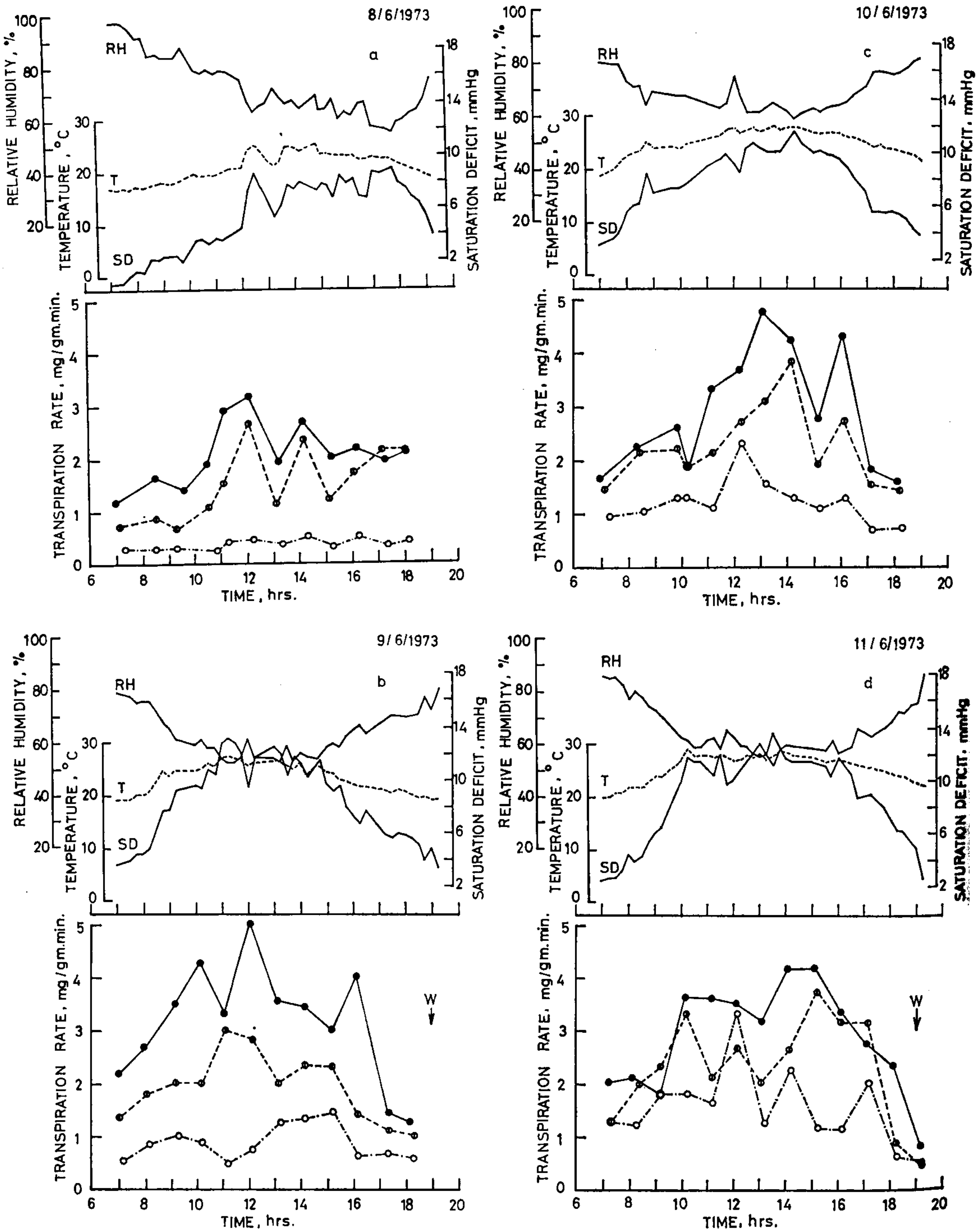



Fig. 4. Rates of weight loss from needles of different physiological ages at different time of a day while the seedlings were exposed to the total soil moisture stress. a) wet treatment, b) moist treatment, c) dry treatment. ○—○ ; one year old needles, ●- -● ; two year old needles.

Sands[13] followed the transpiration of P. sylvestris seedlings during the day at four different ranges of soil moisture tension (matric potential), using the same method as in the present study. They found lower and earlier maximum daily rates up to soil moisture tensions of 1-2 atm. At soil moisture tensions of more than 5 atm stomatal transpiration was not appreciable. Satoo and Namura[15] found the sudden decrease of transpiration of red pine seedlings begun when the water retaining power of soil reached 8-9 atm, and a constant rate was attained when the water retaining power became nearly equivalent to the permanent wilting percentage. Jarvis and Jarvis also[8] found that pine seedlings (P. sylvestris) were more sensitive to the decreasing of soil water potential than those of aspen, birch or spruce.

2. Rate of water loss during one watering cycle : The experiments were begun at the last period of the drying out cycle of moist and dry treatments on June 8, and on other days began after 12 hours of watering and after drying out so that the moist treatment seedlings were subjected to two waterings on the evening of June 8 and June 11 while dry treatment obtained one watering only on the evening of June 8. From the early morning to the evening, at hourly intervals, measurements were carried out practically the same as in experiment 1. Fig. 5 ; shows the rates of water loss of one year old needles(presumably grown during the last season). As depicted in Fig. 5, the course of water loss during the day could be observed due to the soil moisture and the atmospheric conditions changes The diurnal course of water loss in needles of wet and moist soils followed atmospheric changes and corresponded almost exactly, but in dry treatment it showed an independence of atmospheric conditions especially in the first period (Fig. 5 ; a). Water loss from plant caused by the surrounding atmosphere is common. The interraction of atmospheric condition and soil moisture conditions can be explained by physical processes. First, considering the rate of water transfer from the needle surface to the atmosphere, and second the rate of water transport from soil through plant and to the atmosphere. In the first case, as a generalization, needles from wet and moist treatment attained high potential ; on the other hand, the physiological performance of absorption to make up for the loss of water during the previous night is resumed after watering. The needles may reach a saturation state in both treatments. The evidence is partly supported here - the needles of both mentioned treatments maintained relatively high rate of water loss which is attributable to stomatal transpiration, while the dry treatment showed a rather low rate. The rate of water evaporation from the needle surfaces to the vicinity of the atmosphere around the needles is caused by a gradient of vapour concentration or vapour pressure between the needles and the surrounding air.[9,10,17,18] Kramer and Kozlowski[9] conclude that plants transpire when the vapour pressure in their leaves exceeds that in the surrounding air and anything that increases the steepness of this gradient increases the rate of transpiration. Therefore, the different rates found in needles of different soil moisture conditions must result from this phenomenon. Since the whole system consists of not only needles and the surrounding air but is continuous from soil to plant to atmosphere, then the potentials of the whole systems must be considered. According to Gardner[5] and Cowan,[3] the transport of water from soil to plant to atmosphere is analogous to Dacy's law, that is the movement of water from soil through plant to make up for the demand of the atmosphere results from the poten-




tial difference between the plant and the soil and the rate of movement is impeded by a combination of plant and soil resistances. In the saturated soil and plant surface, the resistances may be negligible, in which case the rate of water movement is caused by the difference of water potential in the two systems. Considering the results of the present

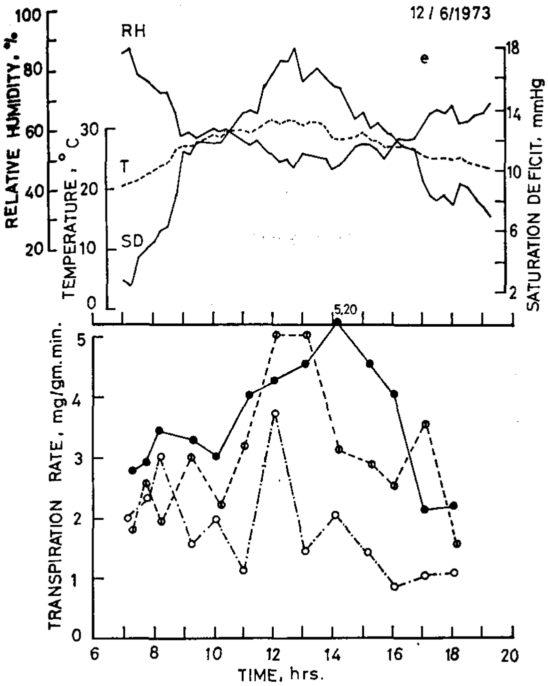



Fig. 5. Rates of water loss (mg / gmf wt. min) of black pine needles during the succesive drying out of soils in pots and the atmospheric conditons. ●—● ; wet treatment ⦶—⦶ ; moist treatment, ○—○ ; dry treatment. a) every day watering in wet treatment ; 2 days drying in moist treatment ; and 4 days drying in dry treatment. Average soil water potentials were zero in wet and moist treatments throughout the periods indicated in a, b, c, d and e, and -12.83 and -3.15 bars in dry treatments in period a and e respectively W ; in b indicates the first waterings in moist and dry treatments, in d the second watering in moist treatment only. The waterings indicated in the figures ware performed during the last 12 hours prior to the water loss measurements.

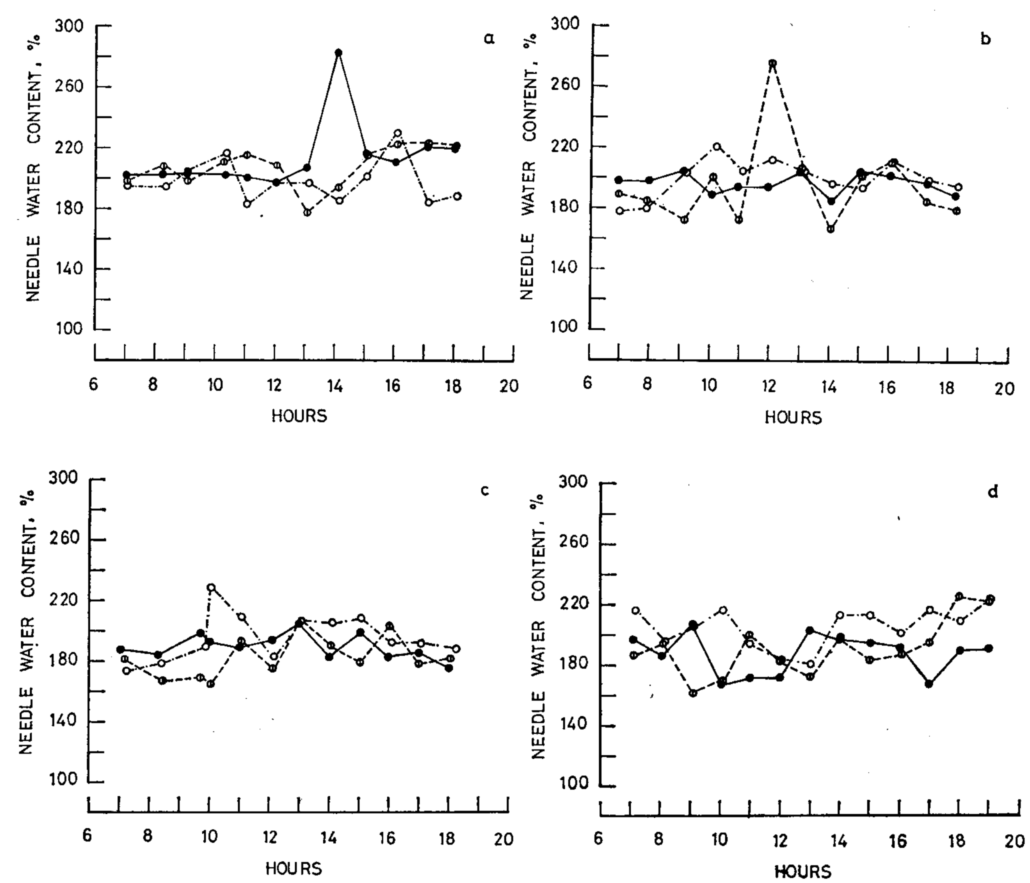
experiments, as shown in Fig. 5 ; a, the average soil water potentials were particularly high (approaching zero bar) in wet and moist treatments, and averaged -12.83 bars in dry treatment (see also Table 1), thus large differences were found in wet and moist treatments compared with dry treatment. It should be taken into consideration that there were large differences in water potentials between needles and soils in the different treatments too. Denmead and Shaw[4] reported that transpiration rates from corn plants grown in containers in the field depended on the potential evapotranspiration and the soil suction. They found that for the moderate potential transpiration rates (3-4 mm per day), the actual transpiration rate fell below the potential rate when the average soil suction in the root zone was about 2 bars, and when the potential transpiration rates were as high as 6-7 mm per day, this decline in relative transpiration rate occurred at about 0.3 bar. When the potential transpiration rate was only 1.4 mm per day, the relative transpiration did not decline until about 12 bars.

In the present study, during other periods (Fig. 5 ; b, c and d), the rates of weight loss recovered, especially those of moist and dry treatments. The recoveries followed after the seedlings were watered. The average water potential did not largely depart from zero (high water potential), but the rates were still different in all treatments. On the last day of the soil drying out cycle in dry treatment (Fig. 5 ; e), the average soil water potential was -3.15 bars, the water loss was largely diminished, but still attained rather high rates. It may be stated then, that once plants are subjected to drought or soil moisture stress and subsequently obtain water even up to considerably high water potential, the plants do not recover abruptly and this causes cyclic variations in the activities of plants particularly in the activities of water exchange between plant leaves and the atmosphere. The earlier high rates were accompanied by high soil water potential that caused the stomata to remain open, and the latter diminishing rates probably caused the stomata to be partly closed due to the reducing soil water potential. Other activities may be caused by soil moisture stress. Brix[1] reported the recovery of photosynthesis after water stress in loblolly pine seedlings. He considered this to be greatly influenced by the root system, that is a decrease in water absorbing or water conducting capacity of root system during wilting (plant water stress) results in a slow rate of decrease of water stress in the leaves, following re-watering of the soil. Our present study does not go into those aspects yet, but as the results show here we may consider that these phenomena may occur in black pine seedlings too.

3. Needle water content during one watering cycle : The needle samples from the experiments on water loss in section 2 were dried in an oven to their constant dry weight at 85°C. The daily changes of needle water content is shown in Fig. 6, and the average of the whole samples are summarized in Table 2. The needle water content seems not to follow any exact trend. This probably is due to the nature of needles and the fact that the course of water absorption from the root to substitute the water loss did not occur at the same time.[10] In wet and moist treatments, the fact that the seedlings were allowed to transpire most of the water might have caused this effect. Weatherley[24] found a relatively constant leaf water content in cotton plants during the day even though the transpiration was very high. He attributed this to absorption and transpiration being at nearly equal rates. In this experiment, considering the entire period of one watering cycle, the needle water content may be considered as nearly constant rather than any large changes occurring, because the period of soil water diminishing was not long enough and permanent dryness of soil did not develop. Satoo and Namura[15] noted that the water content of red pine seedlings did not decrease until the water retaining power of the soils exceeded 15 atm. In the present study, the dry treatment found the decrease in water content to be -12.83 bars in period a of the dry treatment only 16 % lower than that found in wet treatment. But on the subsequent day (periods b, c and d), the needle water content changes were slightly higher. The differences were not statistically significant.

The meaning of needle water content in this case seems to be more an indicator of harmful effects to the seedlings than as an indicator of activities. Tazaki[21] and Satoo[14] found the lethal evel of seedlings by using the water content as an indicator. Black pine yearlings of sand dune community and red pine seedlings were reported to be killed if the water content decreased to the level of about 100% (dry weight basis). Stranaky and Wilson[20] reported that if the water content of loblolly and longleaf pines was reduced to 105 %, the young growth wilted. In the present study, the seedlings decreased their rates of water loss remarkably in response to small changes of soil moisture content, but they were still alive, as could be observed from the recovery of seedling activities in form of transpiration when needle water content became as high as usual, so that harmful effects might not occur.

4. Needle water deficit in pot grown seedlings : The needle water deficit measurements were conducted at the same time as in periods of water loss measurement in section 1 and 2, but the samples used were taken only in the early morning at about 6.30-7.30 am. The



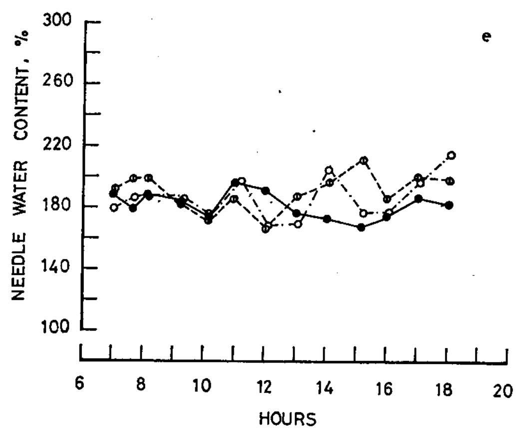




Fig. 6. Needle water content of potted black pine seedlings during the successive drying out of soils. ● ; needles from wet treatment, ⦶ ; needles from moist treatment, ○ ; needles from dry treatment. The conditions are as indicated in Fig. 5.

Table 2. Average needle water content (% dry weight) of seedlings during the successive drying out and after waterings. Periods and conditions are as indicated in Fig. 5.

| Periods | Treatments | Average needle watercontent,* % |
|---|---|---|
| a | wet<br>moist<br>dry | 214.33<br>208.25<br>198.42 |
| b | wet<br>moist<br>dry | 197.19<br>195.53<br>201.90 |
| c | wet<br>moist<br>dry | 189.91<br>184.51<br>197.11 |
| d | wet<br>moist<br>dry | 187.00<br>187.81<br>204.01 |
| e | wet<br>moist<br>dry | 182.14<br>190.50<br>185.40 |

* Average of 12 samples for each treatment, and there is no significant difference in all periods and treatments at P 0.5—1 %.

results shown in Fig. 7 as a comparison between rates of water loss and needle water deficit were the results of the experiments that were performed almost consecutively between the two measurements. During the successive days of soil drying out, the needle water deficit developed very greatly in the dry treatment as compared to the wet and moist treatments. They were found inconsistent even in the relatively saturated soils. Water deficit in needles occurred very greatly in wet and moist treatments probably due to the rapid loss of water during the previous days. Rutter and Sands[13] stated that another cause may be the lack of aeration around the roots. Direct correlation between the water loss and needle water deficit could not be obtained here because the two responses were each determined separately, but as is shown in Fig. 7, the needle water deficit and rates of water loss followed similar trends during the successive soil drying out and after watering.

On the first period, needle water deficit in dry treatment occurred about 9 % while the moist and wet were 5 and 3.6 % respectively. The reduction of transpiration resulting from needle water deficit are clearly observed. After seedlings were obtained watered, needle water deficit decreased and was followed by transpiration increase, but the decreasing of needle water deficit was found to be different among the treatments. On the subsequent day to the watering, needle water deficit in dry treatment was slightly reduced while the other two treatments still developed greatly and the transpiration rates increased in all treatments. When needle water deficit in all treatments became nearly coincident on the

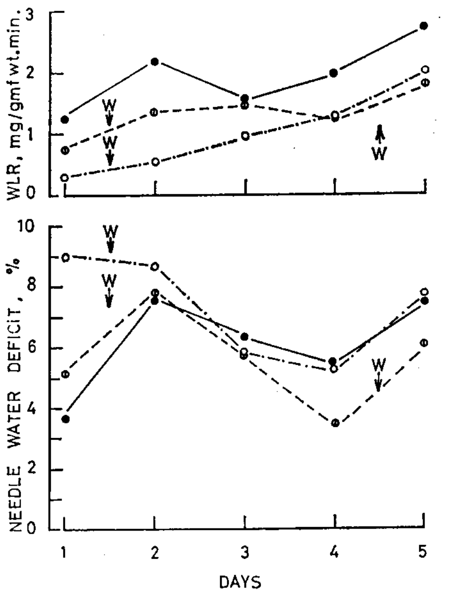



Fig. 7. Needle water deficit (%) and rates of water loss (mg / gmfwt. min) during the successive drying out of soil. ●—● wet treatment, ⓘ—ⓘ ; moist treatment, ○—·—○ ; dry treatment, W ; indicates the waterings, One point is an average of three samples. WLR is water loss rate.

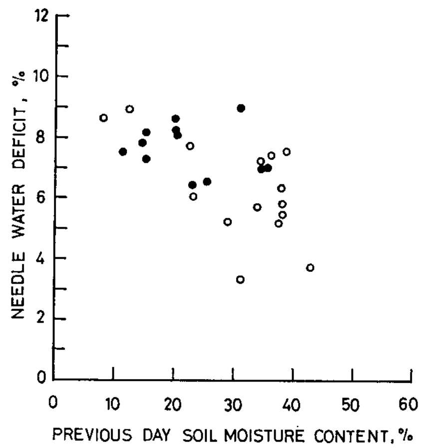



Fig. 8. Needle water deficit (% of saturated weight) and soil moisture content during a short periods in pot grown black pine seedlings. ● ; data from the experiments at the same period as in 1, ○ ; data from experiments at the same period as in 2.

second day following the watering (day 3), transpiration rates of wet and moist treatments were nearly equal, but the dry treatment was still lower. In the later two periods, needle water deficit in wet and dry treatments were almost at the same level, but the moist treatment was reduced to nearly the minimum. During these later periods there were no clear effects of needle water deficit on transpiration rate, but it may be considered that needle water deficit might develop eventhough the seedlings obtained much or little water. In case of seedlings obtaining much water as in wet treatment, transpiration occurred greatly but in dry treatment transpiration was rather low due to the soil water becoming less. In both cases, the absorption of water might dominate the effects on needle water deficit, that is in wet treatment the needle water deficit developed owing to the lag of absorption to make up for the high water loss while in dry treatment needle water deficit might be caused by both the lag and the small amount of water in soil. The result of needle water deficit found in the periods just prior to the transpirations observations were likely to depend on the previous day soil moisture conditions.

In an attempt to observe the direct effect of soil moisture conditions on needle water deficit, the relationships between needle water deficit and soil moisture content are shown in Fig. 8. The needle water deficit correlates with the previous day's soil moisture content at least in a short period. The needle water deficit decreases as the soil moisture content increases. During the day a deficit might develop, but the effect of other factors prevents the direct effect of soil moisture.[13] Weatherley[23] showed the correlation between the previous day's evaporation and the water deficit in cotton plants. But evaporation could not be isolated from the effect of soil moisture since the plant was still grown in soil. The rela-

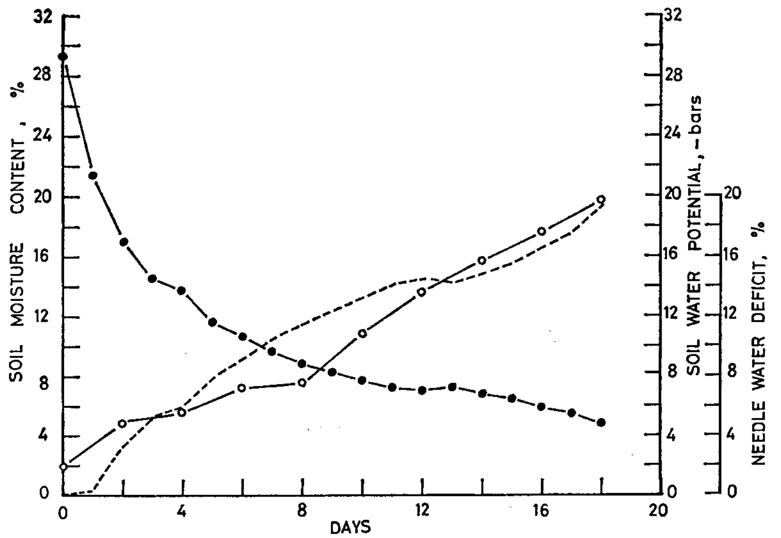



Fig. 9. The course of soil dryness and the progressive needle water deficit development. Soil moisture content was followed at every day intervals, needle water deficit was measured at 2 days intervals. ●—● ; soil moisture content (6 samples average), ○—○ ; needle water deficit (6 samples average),········· ; soil water potential (stress) development converted from the reationships shown in Fig. 1.

tionships of soil moisture content and needle water deficit during the short period gave only a rough estimate of the effects of soil moisture on needle water deficit, but at least it showed that whenever soil moisture conditions change, a water deficit usually occurrs and also causes the reduction of transpiration rate.

5. Needle water deficit during the prolongation of soil drying out : From the beginning of the expriment, the six samples of potgrown seedlings obtained watering to saturation. The soil moisture content detected at 12 hours following the watering showed that the maximum soil moisture content was 35.92 % and the minimum was 23.36 % on the basis of soil dry weight. The average soil moisture content of the total six samples was 29.29 % as shown in Fig. 9.

When soil was progressively dried, the needle water deficit developed rapidly, as depicted in the first part of Fig. 9, then become less rapid about six days later. When soil was dried to about -11.40 bars, the deficit developed to a very high rate. This was probably due to the loss of water from seedlings which occurred at a high rate. As compare with Fig. 5, where the seedlings show a nearly constant rate of transpiration attributed to cffticular transpiration, the soil water potential was about -12.83 bars (see also Table 1) and the needle water deficit was about 9 % (see Fig. 7), which almost coincided with the results of this experiment. After this period, the water deficit developed linearly due to progressive soil moisture stress. It was found that the seedlings did not show any symptoms of wilting even though the soil became very dry. When soil water potential was reduced to about -19.40 bars, the needle water deficit reached its highest level and probably still continued to develop even though the soil moisture content become extremely low. Following the course of needle water deficit at an interval of every two days in the early morning, the relationships between soil moisture content and needle water deficit was found highly correlated as shown in Fig. 10.

The relationships are found wéll correlated in the form :

$$\log_{10} NWD = 0.4716 + 3.7029\, SMC^{-1},$$

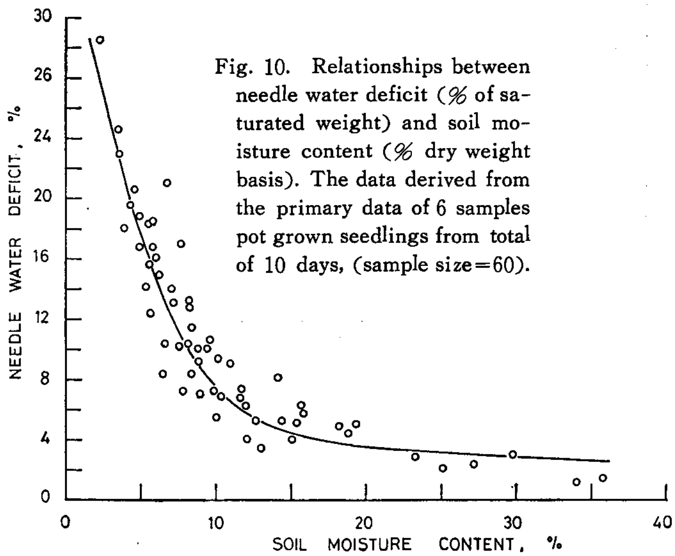



Fig. 10. Relationships between needle water deficit (% of saturated weight) and soil moisture content (% dry weight basis). The data derived from the primary data of 6 samples pot grown seedlings from total of 10 days, (sample size=60).

where NWD stands for the needle water deficit in % of water saturated weight and SMC is soil moisture content in % of soil dry weight. The corresponding correlation coefficient (r) is 0.8463. The relationship resembles that of soil moisture content and soil water potential (Fig. 1). We may consider that when the soil becomes very dry or soil water potential becomes limited, the needle water deficit, especially in black pine, follows almost the same course. Harms[6] found that different species of tree seedlings such as slash pine, longleaf pine, sand pine and turkey oak developed water deficit differently. The differences found between the black pine and those investigated by Harms[6] are due not only to the difference in species but also to the soil used in the experiment. The above mentioned investigator used sandy soils in which soil moisture stress may occur rapidly even though there is only a small change in soil moisture content. The results found in black pine were obtained in sandy loam soils ; in another kind of soil, black pine may act differently. Moreover, the age of seedlings also caused differences, especially due to the difference in physiological ages of leaves, as was well demonstrated by Catsky[2] in other plants.

According to this part of the present study, changes in the water status of soil within a small range affects the activities of Japanese black pine seedlings measured in forms of transpiration and needle water deficit responses. The transpiration decreases when soil water potential decreases. Even with a slight change in water status around the roots, the associated effects in form of water deficit, can be readily observed as the result of that change. An important effect of soil water status is then considered to be one of the factors that control the internal water balance in black pine as in other plants.

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