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Responses of Norway Spruce (*Picea abies* [L.] Karst.) to Water Deficiency

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Summary

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The aim of the investigations was to comprehensively characterise the tree water regime of spruce trees in locations of higher elevation in Eastern Ore Mountains and its modification resulting from water deficiency and decline.

By means of an experimental simulation of water deficiency, concerning three 40-year-old spruce trees, physiological changes which occurred under long-term and extreme drought stress could be observed. Since the beginning of this experiment in spring of 1996 a continuously decreasing water supply has been detected by diminishing values of the pre-dawn water potential. This fact causes higher values of diurnal water potential diminution (from pre-dawn until noon) in 1996 in comparison to the reference trees. During the subsequent growing season these values decreased, while drought stress continued to occur. The decreasing sap flow rate and changing values of pre-dawn water potential, osmotic potential and turgor during the whole period from 1996 indicated different degrees of stress.

The continued physiological activity and the obvious recovery of the experimental trees in spite of long-term drought conditions with extinct water supply from the soil suggest absorption of dew by needles as explanation. This hypothesis is supported by a respective laboratory experiment. These results emphasize the importance of dew, mist and short showers during drought periods for the water balance of trees.

Introduction

Over the past few decades severe stand damages with calamitous consequences occurred as a result of permanently high SO_2 air pollution in locations of mountain ridges and higher altitudes in the Eastern Ore Mountains

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('Erzgebirge') in Germany (NEBE & al. 1995). While there was total loss of the main tree species, Norway spruce, on the mountain ridges, typical crown thinning with partly conspicuous needle loss can be observed in the crown top of trees stocking in the adjacent high altitudes (SCHMIDT-VOGT 1989). This pattern particularly occurs along stand margins suggesting that due to the high acid inputs, among others, disturbances of the tree water balance have to be taken into consideration as causes (LALK & al. 1992).

A number of investigations concerned with the responses of trees to drought stress with subsequent periods of recovery show (CERMAK & al. 1980, GROTE & DOHRENBUSCH 1993, LU & al. 1995) that the data obtained for one area of investigation cannot be simply transferred to another region (ALSHEIMER 1997).

The special situation in the Ore Mountains which is characterised by high SO_2 impact and extreme climate conditions necessitates the conduction of in situ investigations of the water budget and the resistance to drought stress of spruce which is the forest-forming tree species there by nature. The results of these investigations will also serve as a decision-making tool regarding the value of spruce cultivation for the forest reconstruction which has been planned or already begun within the upper Ore Mountains.

Material and Methods

Material

The selected trees are situated on an experimental plot which is located near Altenberg in the Eastern Ore Mountains at an altitude of 750m. The mean annual precipitation accounts for 900 mm.

Three 40-year-old trees of 15m height were selected for the interdisciplinary activities focussing on the water regime under increasing drought stress: trees A1, A2, and A3. Two trees were selected as reference trees on the same plot for the intended investigations, one without any damage symptoms (tree no. 77) and one heavily damaged (tree no. 70). The needle loss of the vigorous tree 77 accounts for an estimated maximum of 5% and that of the damaged tree 70 for an estimated 50%. Although they are almost of the same height today, retrospective measurements of the annual height increment have shown that tree 70 which is damaged today was up to 2.5 m higher than the undamaged tree from 1970 to 1988. The different degrees of damage of these two reference trees permit comparative statements of the water regime of the selected trees.

Experimental simulation of drought stress

To prevent a lateral moistening as well as a lateral below-ground water supply to the roots a ditch of 1.6 m in depth was dug around the drought experiment trees. The ditch sole extended to the heavily compacted zone of the soil basal sequence, thus being an impediment to the farther advance of roots. The root depth was determined in August 1998 by excavating, showing that no root had grown in the basal sequence. The above-ground moistening of the soil was prevented by a roof construction set up at a height of 2.5 m above the ground which limits the root space of the trees.

To obtain physiological measurements, among others, constant heating sap flow measurements according to GRANIER 1985 were carried out in the stem base, in the crown base and in the crown centre, with four measuring points at each stem height. The sapwood area was determined by computer tomography. The xylem water potential was determined by using a pressure chamber according to SCHOLANDER & al. 1965. For this purpose the current year's shoots were used. The osmotic potential was exclusively determined on needles of the shoots also used for measurement of the water potential.

The turgor as a reasonable value for describing the water status of needles, in this investigation was computed from the difference of water potential and osmotic potential (LARCHER 1994).

Investigations of water absorption via the needle surface

For the experiment of water absorption single needles were removed from a selected shoot of a tree subject to moderate drought stress to test the hypothesis of possible water uptake via the needle surface. In order to avoid loss of water via the needle bases, the spots of needle separation were carefully sealed with varnish. Subsequently, eight collective samples (each consisting of 20 needles) were compiled, and the weights of the freshly removed needles were immediately determined. Six of these collective samples were then wettened by permanent sprinkling with water. During the whole experimental period of eight hours the samples were dried on their surfaces half-hourly and weighed. The weight increase observed was interpreted as water uptake. These experiments were run simultaniously, parallel in two variants of light radiation (600µE m^{-2} s^{-1} and 10µE m^{-2} s^{-1}) each with three needle samples. The two needle samples left (without sprinkling) were also weighed regularly as control. The loss in weight by transpiration was recorded.

Weather during the trial

During the time of experiment there were three periods of water deficiency. The first one occured in April 1996 after three months of very cold temperatures (down to -20°C), when abruptly a mild period set in with temperatures up to 20°C and still frozen ground beneath a snow cover. The second drought period began in August 1997 and went on until mid September. The spring of 1998 began warm and dry, from mid May until mid June there was only little precipitation.

Results

As a result of the relatively moist and cool summer of 1996 the water potential of the trees of the drought experiment started to decrease only since August 1996 (Fig.1). After the water potential had assumed a level in spring 1997 again similar to that of the 1996 growing season, a distinct decrease of the pre-dawn water potential until August 1997 was obvious. This minimum value coincides with the maximum of the mean day temperature in 1997. The further course of the pre-dawn water potential is characterised by strong fluctuations which again have a rising tendency from September until November.

Fig. 2 shows the diurnal course of parameters of the water status on June 3rd 1998 after a four-week drought period. A rain shower (6.4 mm) occurred in the early morning at 5:00 a.m., during which the needles of the tree crowns were wetted. During this event the water potential of the drought experiment trees A1 and A2 increased a great deal, while that of reference tree 77 increased slightly. This was followed by a decrease until 4:00 p.m., and finally by another increase of the water potential until 8:00 p.m. The course of the turgor, deduced from this course and that of the osmotic potential, in reference tree 77 indicates a relatively balanced run of the turgor in the diurnal course. The minimum value is reached at 2:00 p.m. after a gradual decrease of the turgor during the morning hours. The

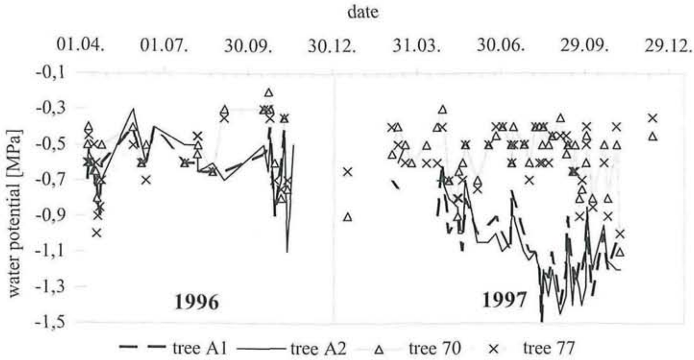

Fig. 1. Course of pre-dawn water potential in the upper crown of sample trees A1 and A2 submitted to conditions of prevention water supply, reference tree 70 (heaviliy damaged) and healthy reference tree 77, during 1996 and 1997.

values increase until the evening; the starting value from the morning is even exceeded at about 8:00 p.m. As for the drought experiment trees A1 and A2 higher diurnal fluctuations in turgor corresponding to the course of radiation were ascertained for that day. However, both experimental trees have in common that, subsequent to the rainfall event in the morning, a higher turgor value could be determined than that before sunrise (prior to the rain shower).

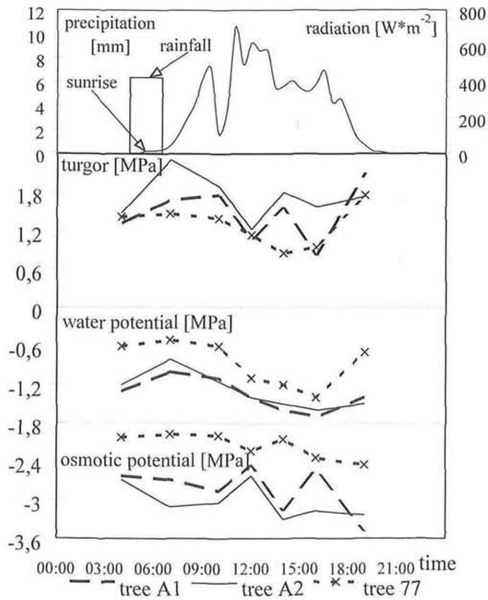

Fig. 2. Diurnal course of the parameters of water status on June 3rd 1998, after a three-week drought: turgor, water potential and osmotic potential, compared to precipitation and radiation (above); arrow: a 6.4 mm rain shower at 04:30 a.m., just before sunrise. For explanation of tree no. see legend in fig.1.

The weighing of the drought-stressed, water-sprinkled needles under laboratory conditions showed a clear increase in weight during progress of the experiment (Fig.3). It is obvious that in the low light variant (10µE m^{-2} s^{-1}) the weight of the needles increased rather uniformly, whereas a weight increase in the light variant (600µE $m^{-2}s^{-1}$) was obviously less pronounced and subject to distinct fluctuations. The conversion of these values can be interpreted as water uptake (in gH_2O gdw^{-1}).

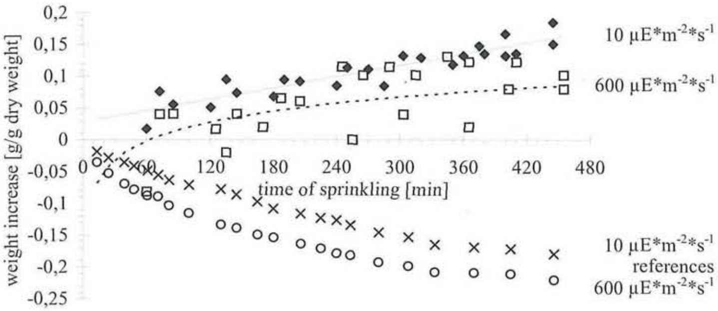

Fig. 3. Course of weight increase of detached permanently sprinkled needles; the low light variant (◆) shows a linear increase, the light variant (□) a moderate increase with high deviation; comparison with the reference without sprinkling: (o) for 600 µE m^{-2} s^{-1} and (x) for 10 µE m^{-2} s^{-1}).

Discussion

The main topic of the investigations are the results obtained regarding the water regime during advanced drought stress. Because of the relatively cool and moist weather during the growing season of 1996 the soil water supply entered the deficiency range only slowly. So the physiological reactions to drought stress became obvious only rather weakly and late in that growing season (in August). The declining values of the early morning pre-dawn water potential on the drought experiment trees allone allow us to conclude a deterioration of the water supply relations in the soil and in the tree stems. The results showed that the correlation between sap flow rate and radiation decreased with the length of the experiment (from 1995 to 1997), until finally in 1997 a distinct dependence of the sap flow on radiation could no longer be ascertained (Fig.4). Regarding the reference trees this observation could not be made.

The pre-dawn water potential, which increasingly dropped during the second year of the experiment (in 1997), could be explained by the fact that the minimal value of –2.1 MPa (tree A1) or –2.2 (tree no. 70) did not fall below this in the growing season (Fig.1). Moreover, the fact that the noon water potential did not fall below the value of –2.2 MPa strongly emphasises that also after two growing

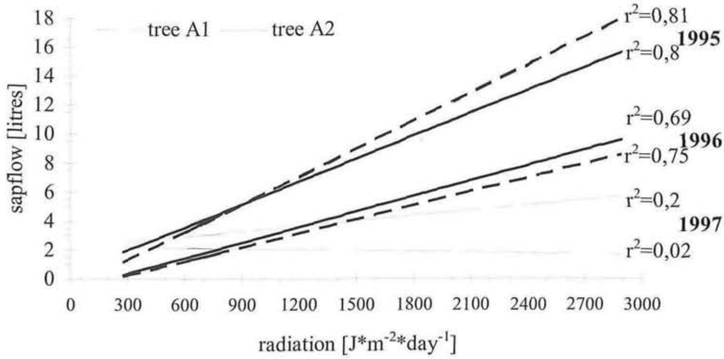

Fig. 4. Dependence on radiation of diurnal sapflow in 0.6m height (sample trees A1 and A2) showing a decreasing correlation in three years subsequent to the start of the drought experiment (1996, 1997 and 1998).

seasons the water balance under increasing drought stress continued to be actively regulated by stomata or compensating mechanisms (CANNY 1998, e.g.). This statement is additionally substantiated with regard to the diurnal course of sap flow in the drought experiment trees A1 and A2 (Fig.5). The abrupt and strong decrease of sap flux density in the crown at 11:00 a.m. already indicated a restriction of transpiration due to the closure of stomata which commenced at this point of time. It is only under weak light conditions in the evening that the xylem flow within the crown started to increase again to 'refill' the stem reservoir that was used up during the day. The gradual and sluggish process of refilling the stem storage was shown by the delay in the diurnal course at the lower measuring points. The continued decrease of the needle water potential starting at noon and the thus occurring decrease of the turgor up to the afternoon or its continued low level can be regarded as evidence of the greatly deteriorated water replenishment during the day.

The observation that the trees of the drought experiment were nevertheless still vigorous and capable of reactions, after two growing seasons with only initial declining symptoms (and, starting from 1997, with almost extinct water supply from the soil) can only be explained by the fact that spruce needles (and shoots) are enabled to take up water to a decisive extent in the form of dew, fog or rain via their surface during advanced drought stress. This hypothesis is supported by the following results:

- Great variations occur in the pre-dawn water potential, which were also observed in the reference trees 70 and 77, mainly during the drought periods (Fig.1), and the maximum values of these variations occur after nights with dew and a very high relative air humidity.
- In the diurnal course of turgor on June 3rd 1998 at first an increase was obvious, resulting from a rain shower in the morning hours subsequent to the pre-dawn measurement, before the expected decrease of turgor values occured during the further course of the day (Fig.2).

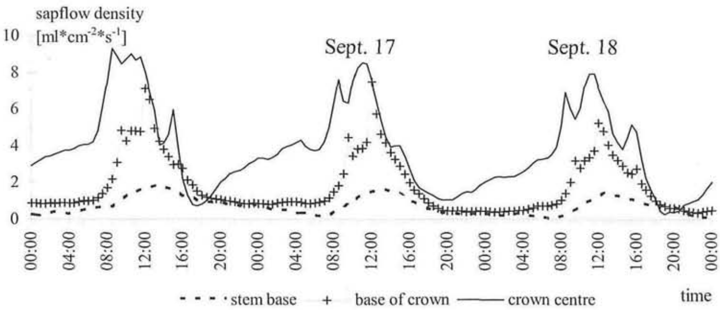

Fig. 5. Diurnal course of sap flow in different stem parts of sample tree A1 during advanced drought stress, Sept. 16th - Sept. 18th 1997.

- The results obtained in the laboratory experiment concerning the increase in weight of the sprinkled needles point to a water uptake via the needle surface (Fig.3). In this regard, the question of if the light relations and thus the gap of the stomata really play a role, still needs to be clarified.

Furthermore, the question of the mechanisms which facilitate a water uptake has to be unravelled. The hypothesis that a water uptake is possible via the needle (and shoot) surface underlines the ecological importance of dew and fog for the water balance and of the freight of substances carried in fog for the stands in higher-altitude sites of the Ore Mountains. So far an absorption ('negative transpiration') has not been taken into account in ecophysiological or meteorological water regime assessments and cannot yet be ascertained by measurement technology.

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