Annales
Geophysicae

The dependence of water potential in shoots of *Picea abies* on air and soil water status

A. Sellin

Department of Botany and Ecology, University of Tartu, Lai 40, EE 2400 Tartu, Estonia, E-mail: arne@zbi.ee

Abstract. Where there is sufficient water storage in the soil the water potential (Ψ_x) in shoots of Norway spruce [*Picea abies* (L.) Karst.] is strongly governed by the vapour pressure deficit of the atmosphere, while the mean minimum values of Ψ_x usually do not drop below -1.5 MPa under meteorological conditions in Estonia. If the base water potential (Ψ_b) is above -0.62 MPa, the principal factor causing water deficiency in shoots of *P. abies* may be either limited soil water reserves or atmospheric evaporative demand depending on the current level of the vapour pressure deficit. As the soil dries the stomatal control becomes more efficient in preventing water losses from the foliage, and the leaf water status, in turn, less sensitive to atmospheric demand. Under drought conditions, if Ψ_b falls below -0.62 MPa, the trees' water stress is mainly caused by low soil water availability. Further declines in the shoot water potential (below -1.5 MPa) can be attributed primarily to further decreases in the soil water, i.e. to the static water stress.

Key words. Hydrology (evapotranspiration · plant ecology · soil moisture).

1 Introduction

By far the largest fraction of terrestrial evaporative water loss passes through the stomatal pores of plant leaves. It is estimated that this pathway accounts for 70% of the evaporative vapour loss in Europe (Maniak, 1988; cited by Körner, 1994), and similar values may apply to other regions. The transfer of water in the soil-plant-atmosphere continuum is considered a catenary process driven by water potential gradient in the system. The pathway of water movement through this continuum represents a hydraulic system containing several resistances to the flow of water (Passioura, 1982; Boyer,

1985; Nobel, 1991). The flow of water along a series of resistances requires a difference in water potentials and this difference is largest when the flow is largest and where the resistance is highest. Plants act as an interface bridging the steep water potential difference between soil and atmosphere.

Soil water potential is a relatively stable characteristic in comparison with that of the atmosphere, which can vary both diurnally and seasonally within a wide range (Kramer and Boyer, 1995; Larcher, 1995). Thus, the rate of water transfer through the soil-plant-atmosphere continuum is mainly determined by atmospheric evaporative demand. However, plants do not represent merely a passive link between the soil and the atmosphere; vegetation, their control of evapotranspiration through stomatal regulation, feeds back on the climate and soil moisture regime. Thereby, the plant water potential depends on the ratio of the water loss from the foliage to its absorption by roots.

The water balance of a plant becomes negative as soon as the uptake of water is insufficient to meet the requirements of transpiration, causing the plant water potential to decline. The plant water stress can be divided into static stress caused by low water availability in the soil, and dynamic stress resulting from the resistance to water flow through the plant due to transpirational water loss from foliage (Tyree and Ewers, 1991). The dynamics of the leaf water potential (Ψ_x) is sometimes treated as a sum of two components (Hinckley and Ritchie, 1973; Lassoie *et al.*, 1983; Pothier *et al.*, 1989). These are base level water potential (base potential, Ψ_b) and diurnal depression from the base level (depression potential, Ψ_d):

$$\Psi_x = \Psi_b + \Psi_d \ . \tag{1}$$

Ψ_b, measured just before dawn, when the water content of leaves and soil is presumed to be in equilibrium, should express the static water stress; Ψ_d indicates the level of the dynamic water stress.

We examined the dynamics of the water potential in shoots (hereafter shoot water potential) of Norway spruce [*Picea abies* (L.) Karst.], one of the main tree

species in northern Europe, to investigate its dependence on the air and soil water status. In Estonia, pure spruce stands and mixed forests with spruce dominance make up 20% of the total area of woodlands, and 26% of the total forest yield (Valk and Eilart, 1974). The annual amount of precipitation in Estonia is sufficient for plant growth, however, in some years both field crops and forest trees may suffer from water deficit due to uneven distribution of precipitation throughout the growing period. The growth and productivity of trees is largely dependent on their water relations (Badot *et al.*, 1990; Alavi, 1996; Bréda and Granier, 1996), as water stress may cause a marked reduction in growth and development. In Estonia, precipitation and air temperature together determine up to 40% of the total variation in the radial increment of spruce trees (Kask, 1992).

The objective of the present study is to elucidate the role of soil drought versus atmospheric evaporative demand in the development of trees' water stress.

2 Materials and methods

2.1 Study site

Experimental work was done at Vooremaa Ecology Station $(58°44'N, 26°45'E)$, Estonia, from June to August in 1994–1996. The annual precipitation in the Vooremaa area ranges from 600 to 630 mm, 400 to 410 mm of this amount falling during the growing season, i.e. during the period when the mean diurnal air temperature is above $+5 °C$. The mean monthly air temperature ranges between $-6.6°$ and $+17.3 °C$. The annual total radiation budget averages $1273 \, MJ \, m^{-2}$ (Russak, 1990).

The study area was situated in a natural uneven-aged *Picea abies* stand with single trees of *Betula pendula* Roth, *Ouercus robur* L. and *Populus tremula* L. The soil was a rich well-drained brown forest soil (Calcaric Cambisol according to FAO classification) formed on red-brown calcareous moraine. Earlier studies conducted in Vooremaa region (Lykhmus *et al.*, 1986) indicated that the forest litter layer and the upper 10 cm of the mineral soil comprised 49%, and the layer at 10–20 cm depth 23% of the absorbing roots; the deeper layer had significantly less of the total mass of absorbing roots in brown forest soil. The pH_{H_2O} of the rooted zone was 5.2. A detailed description of the climate, soil and vegetation of the study area has been previously published (Frey, 1977).

2.2 Pressure chamber measurements

Measurements were carried out on 30- to 40-year-old relatively freely growing trees, with crowns exposed to the east and the south. The height of the sample trees was 11.5 to 12.7 m. The bulk water potential (Ψ_x) was measured by the balancing pressure technique using a Scholander-type pressure chamber (Boyer, 1995). Ψ_x was determined on current-year shoots cut from the middle third of the crown's shaded side in order to minimize the variation in Ψ_x caused by direct radiation. Earlier measurements have revealed that there may be differences in Ψ_x amounting up to 0.35 MPa between shaded and exposed shoots of *P. abies* on sunny summer days (unpublished data). On each day of observation, six shoots were sampled just before sunrise (i.e. 0330 to 0430 h), and after that at two-hourly intervals from 0600 to 2200 h, East European standard time. If current-year shoots were too small for the chamber, samples consisting of both current- and previous-year shoots were used.

As the trees differed in height, sample shoots were situated at various heights above the ground. To eliminate a variation in Ψ_x due to height, the gravitational component of water potential was subtracted from the values obtained with the pressure chamber. The gravitational potential was calculated from the height of the sampled shoots above the ground surface. No correction was made for the solute potential of the xylem sap, as it was considered negligible (Hellkvist *et al.*, 1974).

2.3 Soil and atmospheric characteristics

Three replicate soil cores were collected daily with a manual soil borer at depths of 0–10, 10–20, 20–30 and 30–40 cm. The total soil water content (θ) was determined gravimetrically by drying soil samples at $102 °C$ and was expressed as a percentage of soil dry weight. Available soil water storage (W_{tr}), defined as the one available for transpiration and expressed in mm per 10 cm soil layer, appeared to be a soil water characteristic most relevant to base water potential in *P. abies* (Sellin, 1996). It was calculated as follows:

$$W_{tr} = \rho_s \cdot (\theta - 1.5 W_{mh}) \ , \tag{2}$$

where ρ_s is the soil bulk density (g cm^{-3} and W_{mh}, the maximum soil hygroscopicity (%), both determined separately for each depth. W_{mh} was determined according to the Nikolayev method (Kitse and Rooma, 1984): air-dry soil samples were allowed to saturate in a desiccator above a saturated solution of K_2SO_4, oven-drying weighing procedure followed.

Relative humidity and temperature of the air were recorded simultaneously with the pressure chamber measurements using an aspirated Assmann psychrometer.

2.4 Analysis of results

A daily maximum level of Ψ_x, measured early in the morning and presumed to correspond to the condition of equilibrium between soil and plant water potentials, was always defined as the base potential (Ψ_b) despite the time of observation (Sellin, 1996). Depression potential (Ψ_d) was expressed as a difference between the current level of Ψ_x and Ψ_b. Relative humidity and temperature data were used to calculate vapour pressure deficit of the

atmosphere (VPD) as a measure of the atmospheric evaporative demand. Relationships between the components of shoot water potential and environmental variables were evaluated using non-linear regression procedure based on the least squares method. To approximate the relationships of non-linear character, functions giving the best fit in terms of coefficient of determination (R^2) and standard error of estimate (*SEE*) were chosen. To evaluate the role of soil drought versus atmospheric evaporative demand in the development of trees' water stress, an empirical model predicting the daily evolution of Ψ_x from the current vapour pressure deficit and Ψ_b (taken as an index of the soil water availability) was developed.

3 Results

The base water potential in the shoots of *Picea abies* correlated well with W_{tr} at the depth of 30–40 cm, which explained 77% of the variation in Ψ_b. The best fit resulted from the application of the following hyperbolic function:

$$\Psi_b = -0.119 - \frac{12.0}{W_{tr}^{1.72}}, \ R^2 = 0.768, \ SEE = 0.062 \ , \quad (3)$$

where Ψ_b is the base water potential (MPa) and W_{tr}, the available soil water storage (mm). The relationship between Ψ_b and the soil water availability for Norway spruce, at least in the summer period, was of asymptotic nature: Ψ_b was independent of the soil water storage if W_{tr} was over 15 mm and decreased hyperbolically if W_{tr} dropped below this value (Fig. 1). The relationships between Ψ_b and W_{tr}, measured at other depths, were remarkably weaker (Table 1). Thus, below a certain level of available water in the soil, Ψ_b may be used as an index of soil water status.

The daily values of Ψ_d decreased with increasing VPD, while the relationship can be approximated as follows (Fig. 2):

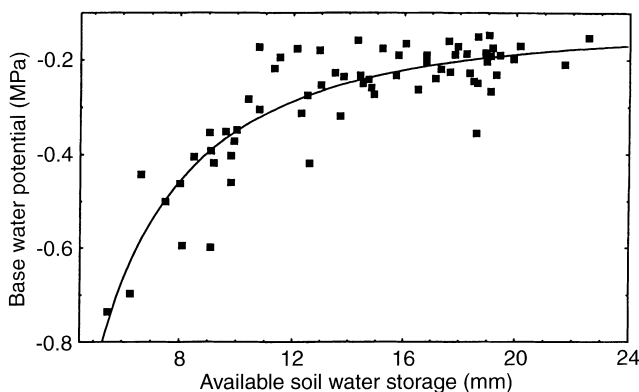$$\Psi_d = -0.509(1 - e^{-5.08 \cdot VPD^{1.52}}),$$
$$R^2 = 0.464, \ SEE = 0.177 \ , \quad (4)$$

Fig. 1. The base water potential (Ψ_b) of shoots versus available soil water storage (W_{tr}) at the depth of 30–40 cm

Table 1. Coefficients of determination (R^2) and standard errors of estimate (*SEE*) for the regressions of base water potential from available soil water storage ($\Psi_b = a + b/(W_{tr}^c)$)

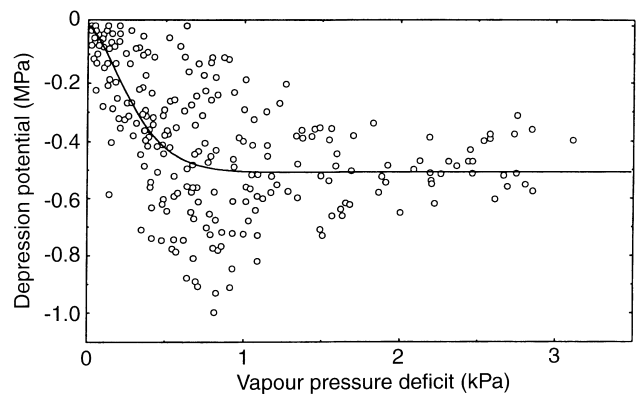| Soil depth layer, cm	Number of observations	Coefficient of determination	Standard error of estimate
0–10	50	0.469	0.101
10–20	71	0.693	0.072
20–30	50	0.752	0.069
30–40	71	0.768	0.062

Fig. 2. The depression potential (Ψ_d) of shoots versus current vapour pressure deficit of the atmosphere (VPD)

where VPD is the current vapour pressure deficit of the atmosphere (kPa). VPD alone explained only 46% of the variability in Ψ_d, while the daily values of the bulk water potential (Ψ_x) were more closely ($R^2 = 0.643$) related to vapour pressure deficit of the atmosphere. Studying the influence of the soil water availability on the parameters of Eq. (4) indicated that the second parameter (equal to -5.08 in the regression equation) was most sensitive to soil humidity. As there was a strong correlation between Ψ_b and W_{tr}, the second parameter was replaced with a function of Ψ_b and all parameters were re-estimated:

$$\Psi_d = -0.616(1 - e^{\frac{0.291 VPD^{1.15}}{\Psi_b + 0.0933}}), \ R^2 = 0.593, \ SEE = 0.154 \ . \quad (5)$$

The application of Ψ_b as an additional independent variable improved significantly the approximation of Ψ_d from VPD (Eq. 5). The variation in depression potential depending on the base water potential and vapour pressure deficit of the atmosphere is illustrated in Fig. 3.

The addition of Ψ_b and Ψ_d (Eq. 1) resulted in an empirical model explaining the combined effect of soil water availability and atmospheric evaporative demand on shoot water potential (Fig. 4):

$$\Psi_x = \Psi_b - 0.616(1 - e^{\frac{0.291 VPD^{1.15}}{\Psi_b + 0.0933}}),$$
$$R^2 = 0.708, \ SEE = 0.154 \ . \quad (6)$$

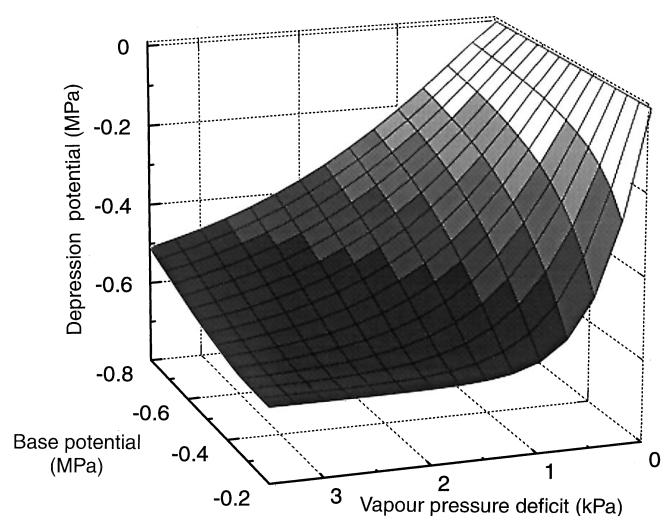The current vapour pressure deficit and base water potential combined accounted for 71% of the total vari-

Fig. 3. Variation in depression potential (Ψ_d) depending on the base water potential (Ψ_b) and vapour pressure deficit of the atmosphere (VPD). The means for the intervals of Ψ_d indicated by consecutive tones from *white* to *dark grey*: $-0.11, -0.21, -0.31, -0.41,$ and -0.51 MPa

ability of the shoot water potential in the studied Norway spruce trees. The first coefficient (-0.616) in the expression of the depression potential in Eq. (5) and (6) indicates the value of the asymptote, i.e. a theoretical minimum value of Ψ_d. Thus, if Ψ_b is below -0.62 MPa (corresponds to $W_{tr} < 6.4$ mm at the depth of 30–40 cm), the primary reason of trees' water stress is always the soil water deficiency.

In Fig. 4 it can be seen that increasing VPD had a stronger effect on the water status of the trees in the case of wet soil, causing a steeper decline in Ψ_x as compared to drought conditions. Certain theoretical minimum
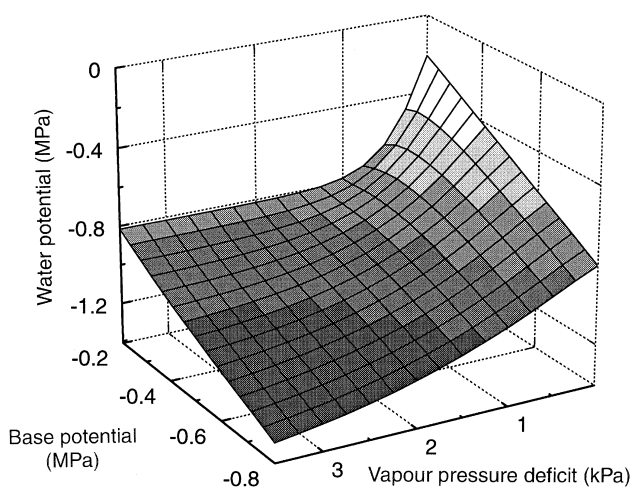

Fig. 4. The shoot water potential (Ψ_x) as a function of the base water potential (Ψ_b) and vapour pressure deficit (VPD). The means for the intervals of Ψ_x indicated with the consecutive tones from *white* to *dark grey*: $-0.40, -0.58, -0.76, -0.94,$ and -1.12 MPa

values of Ψ_x correspond to different levels of the soil water availability: the drier the soil, the lower the base water potential and the more negative values of Ψ_x will be observed. Proceeding from the empirical data and using the model derived, one can predict the level of atmospheric evaporative demand causing Ψ_x to approach the minimum (Table 2).

Ψ_b occurs in both terms of Eq. (6), while its influence (i.e. impact of the soil water availability) on shoot water status is of dual nature. On the one hand (the first term), the lower the Ψ_b, the smaller (more negative) the Ψ_x. On the other hand (the second term), the lower the Ψ_b, the smaller the absolute value of the diurnal depression (Fig. 3) and the larger (less negative) the Ψ_x.

Depending on the combination of air and soil humidities, different patterns in the daily dynamics of the shoot water potential were observed and are illustrated in Fig. 5.

1. Under high soil water availability ($W_{tr} > 15$ mm at the reference depth) and low atmospheric evaporative demand (VPD<0.9 kPa) the dynamics of Ψ_x was controlled by VPD: Ψ_x followed closely the current level of VPD throughout the day (Fig. 5A).

2. Under high soil water availability and high atmospheric evaporative demand (VPD>0.9 kPa) Ψ_x decreased with increasing VPD up to a certain level about midday, while a further increase in VPD after midday was accompanied by an increase in Ψ_x. In the afternoon Ψ_x matched the changes in VPD as well, but demonstrated a marked hysteresis (Fig. 5B).

3. When the soil condition reached drought ($W_{tr} <$ 10 mm), accompanied usually by very dry air in the daytime (VPD>2 kPa), Ψ_x was coupled with the evolution of VPD only in the morning. After midday Ψ_x did not match VPD and no noticeable recovery of Ψ_x could be observed before night fall (Fig. 5C).

Thus, the impact of atmospheric evaporative demand on shoot water supply weakened significantly with increasing water deficiency in the soil, and this may be attributed to more efficient stomatal control on transpirational water loss from foliage. The threshold values of the shoot water potential, inducing a stomatal closure (judged by the onset of Ψ_x recovery at continuing increase in VPD) at midday, decreased with decreasing soil water level (Fig. 6).

Table 2. Theoretical minimum values of the shoot water potential Ψ_{min} and the corresponding atmospheric evaporative demands (VPD) causing water potential to approach the minimum value predicted from the model for different levels of the soil water status (Ψ_b)

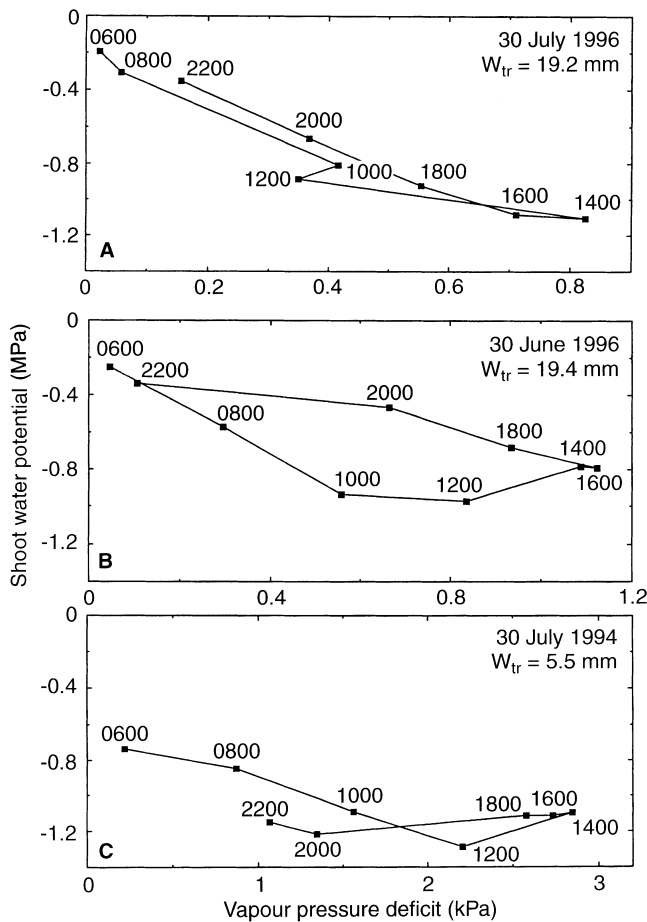| Ψ_b, MPa	Ψ_{min}, MPa	VPD, kPa
-0.1	-0.72	0.10
-0.2	-0.82	1.09
-0.4	-1.02	2.72
-0.6	-1.22	4.21
-0.8	-1.42	5.62

Fig. 5A–C. Daily patterns of the shoot water potential depending on the combination of air and soil conditions. **A** high soil water availability and low atmospheric evaporative demand; **B** high soil water availability and high atmospheric evaporative demand; **C** low soil water availability and high atmospheric evaporative demand. Note, the *horizontal axes* for **A**, **B** and **C** are *different*
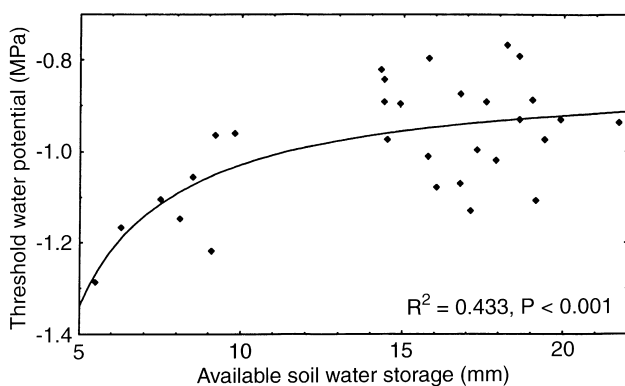

Fig. 6. The threshold values of the shoot water potential inducing a stomatal closure at midday versus available soil water storage at the depth of 30–40 cm

4 Discussion and conclusions

There was a good correlation between Ψ_b and the available soil water storage at the depth of 30–40 cm, which explained 77% of the variation in Ψ_b in the shoots

of *Picea abies*. The relationship between soil water storage and Ψ_b for Norway spruce was of asymptotic nature (Fig. 1): Ψ_b was independent of the soil water level if W_{tr} was over 15 mm and decreased hyperbolically if W_{tr} dropped below this value. A similar pattern of variation in Ψ_b, depending on the soil water content, has been described for other conifers (Hinckley and Ritchie, 1973; Aussenac *et al.*, 1984) as well as broad-leaved tree species (Thompson and Hinckley, 1977; Garnier and Berger, 1987; Bréda *et al.*, 1995). Thus, Ψ_b can be used as an index of soil water status, but it becomes more responsive under dry soil conditions.

The fact that Ψ_b was most closely related to W_{tr} at the depth of 30–40 cm (Table 1) was to some extent unexpected, because most of the active root system in Norway spruce trees growing in brown forest soil is superficial (Lykhmus *et al.*, 1986). Bishop and Dambrine (1995) demonstrated that the main water uptake by spruce trees in a podsolized forest soil comes from the zone ranging from the mor layer to 5 cm below the mor-mineral soil contact. This apparent discord can be explained by the following facts. Firstly, there is a high spatial and temporal variability in water content of the upper soil layers, while deeper layers are more homogeneous in this respect. Secondly, lowered water absorption by superficial roots due to drying of upper soil horizons can be compensated by deeper roots, the contribution of which to the total water uptake increases during a soil drying cycle. The Ψ_b is determined by the water status of the wettest rooted zone rather than that of the main localization of the absorbing roots (Bréda *et al.*, 1995; Hinckley *et al.*, 1978; Sala *et al.*, 1981).

The daily values of the shoot water potential in *P. abies* were closely related to vapour pressure deficit of the atmosphere: VPD explained 64% of the diurnal variation in Ψ_x. The daily dynamics of leaf water potential in several other European woody species are also strongly governed by atmospheric evaporative demand (Matejka and Huzulák, 1984; Huzulák and Matejka, 1986; Linnenbrink *et al.*, 1992). Our results indicated that the daily pattern of shoot water potential reflects interaction between changing soil water supplies and atmospheric evaporative demands. If Ψ_b is above −0.62 MPa, the principal factor causing the water deficiency in the shoots of *P. abies* may be either limited soil water reserves or evaporative demand depending on the current level of the vapour pressure deficit. Under drought conditions, if Ψ_b falls below this value, the tree's water stress is primarily caused by low soil water availability. The empirical model (Eq. 6) derived for predicting Ψ_x from the current vapour pressure deficit and base water potential described 71% of the total variability of the shoot water potential in the studied Norway spruce trees.

The amount of variance explained by this model ($R^2 = 0.71$, *SEE* = 0.15 MPa) is comparable with that of similar models proposed for other species. Pothier *et al.* (1989) presented a model for dynamics of Ψ_x in *Picea mariana* (Mill.) BSP depending on potential evapotranspiration as a measure of the atmospheric evaporative demand. The latter explained 79% of the variation in Ψ_x

on separate days, but R^2 was improved to 0.87 if pre-dawn water potential was added to the model. The atmospheric evaporative demand and soil moisture together have been reported to explain 25–53% of the variation in daily minimum water potential in the leaves of *Eucalyptus microtheca* F. Muell. (Tuomela and Kanninen, 1995) and 77% in those of *Quercus* species (Badot *et al.*, 1994). The probable error of the analogical model derived for three shrub species by Huzulák and Matejka (1983) varied within the range of 0.09–0.12 MPa. Thompson and Hinckley (1977) described a model which simulated Ψ_x for *Quercus alba* L., using soil moisture content, VPD and solar radiation (set to be non-limiting) as input variables. The average residual error of Ψ_x ranged from 0.03 to 0.26 MPa for different test days.

The sensitivity of trees' water status to the atmospheric evaporative demand depended on the soil water availability (Fig. 4). Depending on the combination of air and soil humidities different patterns in the daily dynamics of the shoot water potential can be observed. In cases of wet soil, the shoot water potential decreases quickly with increasing VPD, while the daily course of Ψ_x is coupled with the current level of the evaporative demand (Fig. 5A). Under high water availability in the soil, minimum Ψ_x can be reached at low levels of VPD already (Table 2). After Ψ_x has fallen to a certain level (-0.8 to -1.2 MPa), the stomata will significantly narrow and a further rise in VPD after midday will be accompanied by an increase in Ψ_x (Fig. 5B). The decline of leaf water potential below certain threshold values and/or transpiration rate attained to a high level induce fast turgor changes in guard cells (Franks *et al.*, 1997), which cause stomatal closure to avoid further dehydration leading to the xylem dysfunction through run-away embolism. In contrast to that, under drought conditions Ψ_x declines slowly (Fig. 4), giving evidence of weakening of the impact of the evaporative demand on shoot water supply due to more efficient stomatal control on transpirational water loss from the foliage. The correlation between stomatal conductance and Ψ_b in *P. abies* has been confirmed by Cienciala *et al.* (1994) and Lu *et al.* (1995). At low soil water availability Ψ_x is coupled with VPD only in the morning. Reaching a threshold value about midday, Ψ_x causes the onset of stomatal closure, preventing its further decline. After midday Ψ_x does not vary with VPD and no noticeable recovery of Ψ_x can be observed before nightfall (Fig. 5C). The increase of hydraulic resistance in the soil-root interface (Barataud *et al.*, 1995) and probably in the xylem as well (Sellin, 1991) reduces water transport to leaves and makes fast recovery of Ψ_x impossible under severe drought conditions. The threshold value of Ψ_x, inducing a stomatal closure, decreases with decreasing soil water level (Fig. 6).

With increasing VPD, the water supply for leaves lags increasingly behind the transpirational water losses, causing Ψ_x in leaves to decline. Our results revealed a clear pattern: the lower the soil water availability, the smaller the Ψ_d and the less the the daily amplitude of Ψ_x (Fig. 3). The same fact has been stated concerning other conifers (Lassoie *et al.*, 1983) as well as hardwoods (Huzulák and Matejka, 1986; Sasse and Sands, 1996):

although the minimum Ψ_x reached during a day decreased as the soil dried, the differences between minimum Ψ_x and Ψ_b diminished. As soil water decreases, stomata will close more, preventing lethal diurnal depression in leaf water potential. Franco *et al.* (1994) reported for *Larrea tridentata* (D.C.) Cov. that the lower the pre-dawn xylem water potential, the weaker the effect of VPD on stomatal conductance. Soil drying stimulates the production of chemical signals in the roots, which are transferred via transpiration stream to the shoot. Chemical and/or hydraulic signals springing from the root system trigger osmotic adjustment of the leaf cells, modulating thus the opening capacity of the stomatal pores (Jackson *et al.*, 1995; Liang *et al.*, 1996; Tardieu *et al.*, 1996), allowing needles to tolerate increasingly more negative water potentials, stomata remaining open thereby. Of course, other physiological mechanisms may be involved in the trees' acclimation to drought as well. Zine E1 Abidine *et al.* (1994) found that drought preconditioning enabled seedlings of *Picea mariana* (Mill.) BSP to maintain a substantially higher level of stomatal conductance and photosynthesis during a severe water stress as compared to unconditioned seedlings, but this effect was not accompanied by any changes in the concentration of osmotically active solutes.

To summarize, where there is sufficient water storage in the soil the shoot water potential of Norway spruce is strongly governed by the vapour pressure deficit of the atmosphere, while the mean minimum values of Ψ_x usually do not drop below -1.5 MPa under meteorological conditions prevailing in Estonia. As the soil dries the stomatal control becomes more efficient in preventing water losses from the foliage, and the leaf water status, in turn, less sensitive to atmospheric evaporative demand. Further decrease in the shoot water potential (below -1.5 MPa) can be attributed primarily to a decrease in soil water, i.e. to the static water stress. Thus, the trees' responsiveness to atmospheric factors is determined by the soil water availability.

Topical Editor J.-P. Duvel thanks P. Viterbo and another referee for their help in evaluating this paper.

References

Alavi, G. Radial stem growth of *Picea abies* in relation to spatial variation in soil moisture conditions, *Scand. J. For. Res.*, **11**, 209–219, 1996.

Aussenac, G., A. Granier, and M. Ibrahim, Influence du dessèchement du sol sur le fonctionnement hydrique et la croissance du douglas (*Pseudotsuga menziesii* (Mirb.) Franco), *Acta Oecol. Oecol. Plant.*, **5**, 241–253, 1984.

Badot, P. M., P. Perrier, and M. J. Badot, Dépérissement, déficit hydrique et variations de croissance radiale chez le *Picea abies*, *Can. J. Bot.*, **68**, 1536–1541, 1990.

Badot, P.-M., É. Lucot, and S. Bruckert, L'humidité du sol en profondeur constitue, en milieu de journée, la principale source de variation du potentiel hydrique foliaire de peuplements de Chêne (*Quercus* sp.), *C.R. Acad, Paris. Sci.*, **317**, 341–345, 1994.

Barataud, F., C. Moyne, N. Bréda, and A. Granier, Soil water dynamics in an oak stand. 2. A model of the soil-root network compared with experimental data, *Plant Soil*, **172**, 29–43, 1995.

Bishop, K., and E. Dambrine, Localization of tree water uptake in Scots pine and Norway spruce with hydrological tracers, *Can. J. For. Res.*, **25**, 286–297, 1995.

Boyer, J. S., Water transport, *Ann. Rev. Plant Physiol.*, **36**, 473–516, 1985.

Boyer, J. S., *Measuring the Water Status of Plants and Soils*, Academic Press, San Diego, 1995.

Bréda, N., and A. Granier, Intra- and interannual variations of transpiration, leaf area index and radial growth of a sessile oak stand (*Quercus petraea*), *Ann. Sci. For.*, **53**, 521–536, 1996.

Bréda, N., A. Granier, F. Barataud, and C. Moyne, Soil water dynamics in an oak stand. 1. Soil moisture, water potentials and water uptake by roots, *Plant Soil*, **172**, 17–27, 1995.

Cienciala, E., A. Lindroth, J. Čermák, J.-E. Hällgren, and J. Kučera, The effects of water availability on transpiration, water potential and growth of *Picea abies* during a growing season, *J. Hydrol.*, **155**, 57–71, 1994.

Franco, A. C., A. G. de Soyza, R. A. Virginia, J. F. Reynolds, and W. G. Whitford, Effects of plant size and water relations on gas exchange and growth of the desert shrub *Larrea tridentata, Oecologia*, **97**, 171–178, 1994.

Franks, P. J., I. R. Cowan, and G. D. Farquhar, The apparent feedforward response of stomata to air vapour pressure deficit: information revealed by different experimental procedures with two rainforest trees, *Plant, Cell Environ.*, **20**, 142–145, 1997.

Frey, T. (Ed), *Spruce Forest Ecosystem Structure and Ecology. 1. Introductory Data on the Estonian Vooremaa Project*, Acad. Sci. ESSR, Tartu, 1977.

Garnier, E., and A. Berger, The influence of drought on stomatal conductance and water potential of peach tress growing in the field, *Sci. Hort.*, **32**, 249–263, 1987.

Hellkvist, J., G. P. Richards, and P. G. Jarvis, Vertical gradients of water potential and tissue water relations in Sitka spruce trees measured with the pressure chamber, *J. Appl. Ecol.*, **11**, 637–668, 1974.

Hinckley, T. M., and G. A. Ritchie, A theoretical model for calculation of xylem sap pressure from climatological data, *Am. Midl. Nat.* **90**, 56–69, 1973.

Hinckley, T. M., J. P. Lassoie, and S. W. Running, Temporal and spatial variations in the water status of forest trees, *For. Sci. Monog.*, **20**, 1–72, 1978.

Huzulák, J., and F. Matejka, A model for the leaf water potential daily dynamics of dominant shrub species in an oak-hornbeam forest, *Biológia* (Bratislava), **38**, 411–418, 1983.

Huzulák, J., and F. Matejka, Determination of soil moisture causing plateau on the curve of leaf water potential daily course, *Biológia* (Bratislava), **41**, 47–55, 1986.

Jackson, G. E., J. Irine, J. Grace, and A. A. M. Khalil, Abscisic acid concentrations and fluxes in droughted conifer saplings, *Plant, Cell Environ.*, **18**, 13–22, 1995.

Kask, P., Climate-radial increment relationships in Estonian conifer stands, *Proc. Estonian Acad. Sci. Ecol.*, **2**, 22–27, 1992.

Kitse, E., and I. Rooma, Laboratory course of soil science, Eesti Põlluumajanduse Akadeemia, Tartu, 1984. (in Estonian)

Körner, Ch., Leaf diffusive conductances in the major vegetation types of the globe, *Ecophysiology of Photosynthesis*, Springer-Verlag, Berlin Heidelberg New York, 463–490, 1994.

Kramer, P. J., and J. S. Boyer, *Water Relations of Plants and Soils*, Academic Press, San Diego, 1995.

Larcher, W., *Physiological Plant Ecology*, Springer-Verlag, Berlin Heidelbeg New York, 1995.

Lassoie, J. P., P. M. Dougherty, P. B. Reich, T. M. Hinckley, C. M. Metcalf, and S. J. Dina, Ecophysiological investigations of understory eastern redcedar in Central Missouri, *Ecology*, **64**, 1355– 1366, 1983.

Liang, J., J. Zhang, and M. H. Wong, Stomatal conductance in relation to xylem sap abscisic acid concentrations in two tropical trees, *Acacia confusa* and *Litsea glutinosa, Plant, Cell Environ.*, **19**, 93–100, 1996.

Linnenbrink, M., R. Lösch, and L. Kappen, Water relations of hedgerow shrubs in northern Central Europe. I. Bulk water relations, *Flora*, **187**, 121–133, 1992.

Lu, P., P. Biron, N. Bréda, and A. Granier, Water relations of adult Norway spruce (*Picea abies* (L) Karst) under soil drought in the Vosges mountains: water potential, stomatal conductance and transpiration, *Ann. Sci. For.*, **52**, 117–129, 1995.

Lykhmus, K., R. R. Lasn, and T. A. Oja, Growth of the European spruce roots as related to soil conditions, *Pochvovedeniye*, **6**, 89- -97, 1986 (in Russian)

Maniak, U., *Hydrologie und Wasserwirtschaft - Einführung für Ingenieure*, Springer-Verlag, Berlin Heidelberg New York, 1988.

Matejka, F., and J. Huzulák, Dependence of the leaf water potential of forest trees on the atmospheric evaporative demand, *Biológia* (Bratislava), **39**, 25–30, 1984.

Nobel, P S., *Physicochemical and Environmental Plant Physiology*, Academic Press, San Diego, 1991.

Passioura, J. B., Water in the soil-plant-atmosphere continuum, *Encyclopedia of Plant Physiology. New Series*, Springer-Verlag, Berlin Heidelberg New York, **12B**, 5–33, 1982.

Pothier, D., M. Bédard, R. Caissy, and J. Stein, Variations du potentiel hydrique de plants d'épinette noire en pépiniére en fonction de variables météorologiques, *Nat. Can.*, **116**, 61–68, 1989.

Russak, V., Solar radiation, Climate of Tartu and its changes during the recent decades, Eesti TA Astrofüüsika ja Atmosfääri-füüsika Instituut, Tartu, 51–78, 1990 (in Estonian)

Sala, O. E., W. K. Lauenroth, W. J. Parton, and M. J. Trilica, Water status of soil and vegetation in a shortgrass steppe, *Oecologia*, **48**, 327–331, 1981.

Sasse, J., and R. Sands, Comparative responses of cuttings and seedlings of *Eucalyptus globulus* to water stress, *Tree Physiol.*, **16**, 287–294, 1996.

Sellin, A., Hydraulic conductivity of xylem depending on water saturation level in Norway spruce (*Picea abies* (L.) Karst.), *J. Plant Physiol.*, **138**, 466–469, 1991.

Sellin, A., Base water potential of *Picea abies* as a characteristic of the soil water status, *Plant Soil*, **184**, 273– 280, 1996.

Tardieu, F., T. Lafarge, and T. Simonneau, Stomatal control by fed or endogenous xylem ABA in sunflower: interpretation of correlation between leaf water potential and stomatal conductance in anisohydric species, *Plant, Cell Environ.*, **19**, 75–84, 1996.

Thompson, D. R., and T. M. Hinckley, A simulation of water relations of white oak based on soil moisture and atmospheric evaporative demand, *Can. J. For. Res.*, **7**, 400–409, 1977.

Tuomela, K., and M. Kanninen, Effects of vapour pressure deficit and soil water content on leaf water potential between selected provenances of *Eucalyptus microtheca* in an irrigated plantation, Eastern Kenya, *Silva Fenn.* **29**, 217–224, 1995.

Tyree, M. T., and F. W. Ewers, The hydraulic architecture of trees and other woody plants, *New Phytol.*, **119**, 345–360, 1991.

Valk, U., and J. Eilart, Forests of Estonia, Valgus, Tallinn, 1974. (in Estonian)

Zine El Abidine, A., P. Y. Bernier, J. D. Stewart, and A. P. Plamondon, Water stress preconditioning of black spruce seedlings from lowland and upland sites, *Can. J. Bot.*, **72**, 1511–1518, 1994.