Modeling tree water deficit from microclimate: an approach to quantifying drought stress

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Summary   Tree water deficit estimated by measuring water-related changes in stem radius (ΔW) was compared with tree water deficit estimated from the output of a simple, physiologically reasonable model (ΔW_E), with soil water potential (Ψ_{soil}) and atmospheric vapor pressure deficit (VPD) as inputs. Values of ΔW were determined by monitoring stem radius changes with dendrometers and detrending the results for growth. We followed changes in ΔW and ΔW_E in *Pinus sylvestris* L. and *Quercus pubescens* Willd. over 2 years at a dry site (2001–2002; Salgesch, Wallis) and in *Picea abies* (L.) Karst. for 1 year at a wet site (1998; Davos, Graubuenden) in the Swiss Alps.

The seasonal courses of ΔW in deciduous species and in conifers at the same site were similar and could be largely explained by variation in ΔW_E. This finding strongly suggests that ΔW, despite the known species-specific differences in stomatal response to microclimate, is mainly explained by a combination of atmospheric and soil conditions. Consequently, we concluded that trees are unable to maintain any particular ΔW. Either Ψ_{soil} or VPD alone provided poorer estimates of ΔW than a model incorporating both factors. As a first approximation of ΔW_E, Ψ_{soil} can be weighted so that the negative mean Ψ_{soil} reaches 65 to 75% of the positive mean daytime VPD over a season (*Q. pubescens*: ~65%, *P. abies*: ~70%, *P. sylvestris*: ~75%). The differences in ΔW among species can be partially explained by a different weighting of Ψ_{soil} against VPD. The ΔW of *P. sylvestris* was more dependent on Ψ_{soil} than that of *Q. pubescens*, but less than that of *P. abies,* and was less dependent on VPD than that of *P. abies* and *Q. pubescens*. The model worked well for *P. abies* at the wet site and for *Q. pubescens* and *P. sylvestris* at the dry site, and may be useful for estimating water deficit in other tree species.

Keywords: Picea abies, Pinus sylvestris, Quercus pubescens, soil water potential, vapor pressure deficit, stem radius changes, tree water relations.

Introduction

Drought stress or water stress are terms widely used to describe the impact of dry climatic conditions on plants (Hinckley et al. 1983, Colombo and Teng 1992, Edwards and Dixon 1995, Borghetti et al. 1998, Sperry et al. 2002, Larcher 2003). Indicators such as soil water content, soil water potential, soil water deficit or precipitation have been used to quantify drought stess (e.g., Rigling et al. 2001, Rieger 2003). Soil water status has been taken as a measure of drought stress in plants on the assumption that soil water status is proportional to plant water status. This is a simplification of complex physiological phenomena (Bond and Kavanagh 1999, Oren and Pataki 2001, Zweifel et al. 2001, 2002, Gao et al. 2002), but when considering stands of trees during a drought, it is easier to measure soil water potential than tree water status. It is of interest, therefore, to know how closely soil water potential is linked to a physiological measure of tree water status?

Plant water status is determined mainly by the physical conditions of the air and soil. Plants have several mechanisms of internal regulation that are partially uncoupled with external conditions, and these are related to the morphological and physiological characteristics of the species (Zweifel et al. 2002). It is the combination of external and internal conditions that determines a plant's response to environment, and it is this response that is the object of interest when investigating drought stress.

Dry soil and air may lead, at first, to adaptive responses in plants but, if prolonged, may cause tissue damage. The difference between the two effects is not always easily discerned. Here, the term "drought stress" refers to either effect.

Tree water status can be investigated by measuring leaf water potential (Ψ_l), but the method is labor-intensive. A less labor-intensive method is to monitor diurnal changes in stem radius with an automated dendrometer (Liu et al. 1995, Zweifel et al. 2000). Diurnal changes in stem diameter are related mainly to changes in bark water deficit and to whole-tree water status (Molz and Klepper 1973, Herzog et al. 1995, Zweifel et al. 2001). Ninety percent or more of the fluctuations occur in the phloem, the rest occurring in the xylem (Irvine and Grace 1997, Zweifel et al. 2000). During the day, water withdrawn from the bark contributes to transpiration causing stem shrinkage. At night the bark is rehydrated and the stem expands (Zweifel 1999). Analysis of dendrometer data allows recognition of not only the diurnal rhythm of depletion and replenishment, but also the dry and wet phases lasting from a

few days to several weeks (Zweifel and Häsler 2001).

In this work, stem radius changes were detrended for growth and used as a direct measure of drought stress in trees. We investigated whether this measure of plant water deficit was predicted by a simple model based on the air-to-soil water potential gradient. The study was conducted with three tree species, *Quercus pubescens* Willd., *P. sylvestris sylvestris* (L.) Karst. and *Picea abies* L., at two climatically different sites (Salgesch and Davos) in the Swiss Alps.

Materials and methods

Study sites and tree species

Data were gathered in a wet subalpine Norway spruce forest located at the foot of Mt. Seehorn (1640 m a.s.l.) near Davos, Switzerland (46°48′59″ N, 9°51′25″ E) and a dry open oak–pine woodland (975 m a.s.l) near Salgesch on the south-facing slope of the main valley of Wallis, Switzerland (46°19′27″ N, 7°34′40″ E).

At Davos, water relations and carbon assimilation of Norway spruce trees (*P. abies*) have been investigated since 1985 (Häsler 1992, Herzog 1995, Zweifel 1999, Zweifel et al. 2002). In this study, a data set for six mature Norway spruce trees (150–250 years old) and their local microclimate from April to September 1998 were analyzed. The trees were part of a group of 46 trees covering an area of 1600 m^2. A detailed map of the stand with locations of the trees investigated is given in Zweifel (1999). Details of stem diameter and tree height are given in Table 1. The soil was classified as a ferric humic podsol (Häsler et al. 1991) with a depth between 0.3 and 1.0 m. Annual precipitation in 1998 was 1012 mm. Mean precipitation for the years 1980–2000 was 1111 mm (Meteo-Swiss, Davos).

At Salgesch, pubescent oak (*Q. pubescens*) and Scots pine (*P. sylvestris*) are the most abundant tree species. Some *Q. pubescens* trees are up to 110 years old, although most are less than 70 years old. Most dominant *P. sylvestris* trees are between 100 and 150 years old (A. Rigling, WSL, Birmensdorf, Switzerland, personal communication). Continuous measurements of the local climate and vegetation began in April 2001. Data from April 1 to September 30 in 2001 and 2002 were analyzed. The seven trees investigated (five *Q. pubescens*, two *P. sylvestris*) stood in a typical patch (32 m^2) consisting of 17 *Q. pubescens*, four *P. sylvestris* and two *Viburnum lantana* L. trees (> 2 cm in stem diameter), surrounded by grass and bare rock. The trees investigated represented the largest individuals in the patch. Tree heights and diameters are given in Table 1. The soil on this steep south-facing slope (about 25°) is shal-

low, with a maximum depth of 0.1–0.2 m at the measurement site. It is classified as a rendzic leptosol on solid rock limestone, according to the FAO classification system (Rigling et al. 2002). This type of soil generally has a low water-holding capacity. Annual precipitation was 650 mm in 2001 and 690 mm in 2002 (MeteoSwiss, Sion, 20 km west-southwest of the site). Mean annual precipitation over the last two decades (1983–2002) was 623 mm (MeteoSwiss, Sion).

Microclimate measurements

At Davos, air and dew point temperatures (VTP6, Meteolabor AG, Wetzikon, Switzerland) were measured on a tower at 2, 10 and 20 m above ground (Zweifel 1999) and were used to calculate the vapor pressure deficit of the air (VPD). Soil water potential (Ψ_{soil}) was measured at depths of 0.2, 0.4 and 0.7 m with 16 automated tensiometers with pressure transducers (Marthaler et al. 1983).

At Salgesch, four combined air temperature and relative humidity sensors (HygroClip S, Rotronic, Bassersdorf, Switzerland) were placed just inside the periphery of the crowns and two were placed inside the crown about 1 m above the ground. Soil water potential was measured with four electronic equitensiometers at 0.05 to 0.10 m depths (ML2, Delta-T Devices, Cambridge, U.K.).

Measurements were recorded at 10-s intervals and averaged every 15 min at Davos and every 10 min at Salgesch. For further analyses, the mean values of VPD and Ψ_{soil} for each site were used.

Stem radius changes

Stem radius changes were measured with point dendrometers (Davos: POD, Agricultural Electronics Corporation, Tucson, AZ; Salgesch: constructed by the Institute of Plant Sciences, University of Bern). The six *P. abies* trees investigated at Davos were each equipped with a dendrometer at breast height on the uphill (western) side of the stem. At Salgesch, the dendrometers on the seven trees monitored (*Q. pubescens* and *P. sylvestris*) were mounted at about 0.5 m above ground on the uphill (northern) side of the stem. Dendrometers operated on the basis of a linear variable differential transformer placed in an enamel housing (at Davos) or a carbon fiber frame (at Salgesch). Dendrometers were installed by implanting three stainless steel threaded rods into the heartwood and the rods were connected by mounting struts to the tree. The sensing rod was pressed lightly against the tree stem with a weight (Davos) or a spring (Salgesch). The contact point of the dendrometer head was positioned 1 to 6 mm below the bark surface, but within the outermost dead layer of the bark. Dendrometer

Table 1. Characteristics of the tree species studied and the number of trees sampled at the two sites.

Species	Site	No. of trees	Range of tree heights (m)	Range of stem diameters (cm)
Picea abies	Davos	6	15.0–25.0	16.2–50.0
Quercus pubescens	Salgesch	5	3.5–4.0	7.2–9.5
Pinus sylvestris	Salgesch	2	3.5–5.0	11.9–23.2

measurements at Davos were corrected for temperature sensitivity (Zweifel and Häsler 2000). At Salgesch, the sensitivity of the dendrometers to temperature was negligible owing to the use of a temperature-insensitive carbon fiber frame and an improved electronic transformer (Weggeber potentiometer LP-10F, Pewatron AG, Wallisellen, Switzerland). The electronic resolution of the dendrometers was 3.7 µm at Davos and 0.4 µm at Salgesch.

Tree water status

Changes in stem radius are determined by: (1) stem growth through newly built layers of woody cells; and (2) water-related swelling and shrinking of elastic tissues located mainly in the bark (Zweifel et al. 2000). Thus, an increase in radius (neglecting small fluctuations in stem radius (estimated to be < 10%) due to changes in the sapwood (Irvine and Grace 1997)) may be caused by growth, higher water content in the bark or both. A decrease in radius is most likely caused by depletion of water in the bark. However, to distinguish changes in stem radius due to changes in tissue water content from changes due to growth, dendrometer data were detrended for growth (see Figure 1) as follows:

(i) Set $x = 1$.

(ii) Find the maximum value in the dendrometer data (P_x) and draw a horizontal line to the end of the data set (to the right).

(iii) Starting in the horizontal position, increase the slope of the line past (left) P_x until it touches the next maximum point, P_{x+1}.

(iv) Set $x = x + 1$.

(v) Repeat steps (iii) and (iv) until the earliest data point is reached.

The differences between the constant 'growth line' and the dendrometer data were interpreted as measures of bark water deficit, and were taken to be equal to tree water deficits (ΔW).

Model for tree water deficit

Tree water potential is linked to conditions of both air and soil. An elementary approach to integrating both sets of conditions to the water potential of a tree is to calculate the difference between VPD and Ψ_{soil}. Adopting this approach, tree water deficit (ΔW_E) was estimated as:

$$\Delta W_E = \left(VPD - \frac{\Psi_{soil}}{k_1} \right) k_2 \tag{1}$$

where parameter k_1 (dimensionless) weights the effect of Ψ_{soil} on ΔW_E in relation to the impact of VPD, and parameter k_2 (mm kPa^{-1}) relates the change in stem radius (mm) to the change in water potential (kPa). Values of Ψ_{soil} were always negative, and those of VPD were always positive. Thus, as VPD increased and Ψ_{soil} decreased (i.e., became more negative), ΔW_E became more positive, i.e., the gradient between soil and air steepened.
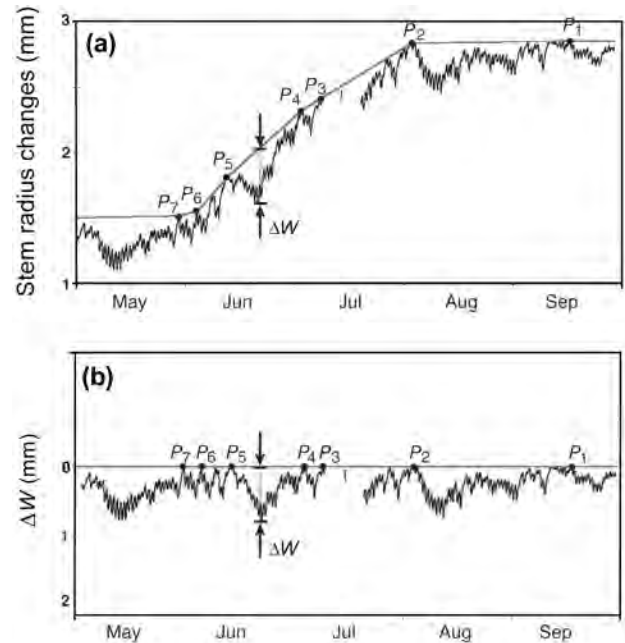

Figure 1. Detrending the dendrometer data for growth of a *Picea abies* tree at Davos, May–September 1998: (a) continuous measurements of stem radius; and (b) tree water deficit (ΔW), as the difference between the "growth line" and measurements. Symbols P_1 to P_7 indicate the dates when ΔW was 0.

Parameterization of ΔW_E

To parameterize ΔW_E, the data sets for *P. abies*, *Q. pubescens* and *P. sylvestris* were divided into 10 classes of Ψ_{soil} values. Within each class, best-fit estimates of k_1 and k_2 were found with a least-squares procedure (Excel Solver, Frontline Systems, Incline Village, NV), minimizing the sum of residuals between ΔW_E and ΔW. This was to give a reasonably even representation of values over the whole range of Ψ_{soil} and to cater to the strong positive, non-normalizable skew in its frequency distribution. Each class contained the same number of values and, as a consequence, the classes had increasingly large widths with increasing Ψ_{soil}. The estimates of k_1 and k_2 over the 10 classes were formulated as nonlinear functions of Ψ_{soil} (Equations 2 to 4). These equations were used to run the model over whole seasons with a wide range of Ψ_{soil} values.

In the Davos data set, where values for a variable were missing, all values for that data point in time were omitted across all variables. The same approach was used for Salgesch; but also, where points in time were missing for any one year, the corresponding points were omitted for the other year. Thus, the 2001 and 2002 data sets were weighted equally in the analysis. The resulting numbers of points for Davos and Salgesch were 14,688 and 40,530 respectively.

Statistical test of goodness of fit

To determine whether ΔW_E estimated drought stress better than either VPD or Ψ_{soil} alone, the goodness of fit of ΔW_E, VPD and Ψ_{soil} to ΔW was investigated with the bootstrap procedure. There were two principal considerations. (a) The data

sets showed obvious strong temporal autocorrelation (i.e., series of consecutively increasing and decreasing values), and therefore most points were not statistically independent of one another. (b) A model relating ΔW to Ψ_{soil} or VPD should have data points spread evenly across the whole range of Ψ_{soil}, i.e., the fitting should not be biased by the considerably more frequent low Ψ_{soil} values. To achieve this, two time points were selected from each of the Ψ_{soil} classes, using random numbers drawn (with replacement) from a uniform probability density function. The data were ln-transformed (to cater for remaining non-normality within classes), and Pearson's coefficient of correlation found between the pairs of variables (ΔW with each of ΔW_E, Ψ_{soil} and VPD; $n = 20$). The procedure was repeated 1000 times. Confidence limits (95%) were estimated as the mean $\pm$ 2 SE of the coefficients. A significantly better fit of ΔW_E to ΔW in comparison to Ψ_{soil} and VPD was inferred when the limits did not overlap.

Results

Tree water deficits

Dendrometer data from Davos and Salgesch were transformed to ΔW by the algorithm described (Figure 1b). The mean standard deviation of ΔW between trees was 0.045 mm for *Q. pubescens*, 0.052 mm for *P. sylvestris* and 0.054 mm for *P. abies*. Variations in stem diameter over a period of 2 months in 2002 are shown for *Q. pubescens* and *P. sylvestris* at Salgesch in Figure 2. The variation was usually most noticeable during dry periods and approached zero after heavy precipitation. The general course of ΔW over a season was similar among individual trees within a species. Therefore, in further analyses, the mean values for each species were used.

Seasonal fluctuations in tree water deficit

Both diurnal and seasonal amplitudes of ΔW were of the same order of magnitude for all trees despite the differences between the sites (Figures 3c, 4c, 4e, 5c and 5e). Diurnal amplitude of ΔW reached 0.25 mm, and maximum values of ΔW over a growing season were 0.4 to 0.5 mm for all trees.

The two species at Salgesch grew within the same plot and had the same microclimatic conditions. The course of ΔW within seasons in *Q. pubescens* was similar to that in *P. sylvestris*, despite the one being deciduous and the other being a conifer (Figures 4c, 4e, 5c and 5e).

Rainfall and VPDs were lower at Salgesch than at Davos (Figures 3–5). Salgesch also has a lower soil water storage capacity than Davos. The Ψ_{soil} at Salgesch dropped to as low as –0.3 MPa (Figures 4b and 5b), whereas at Davos, Ψ_{soil} reached minimal values of –0.02 MPa (Figure 3b). A combination of low Ψ_{soil} and a moderate VPD (e.g., June 24–27, 2002; Figure 2) or moderate Ψ_{soil} and a high VPD (e.g., June 12–13, 2002; Figure 2) led to less extreme values of ΔW.

Model of tree water deficit

The model of tree water deficit (Equation 1), parameterized with constant (species-specific) k_1 and k_2 for the entire sets of

data (one to two seasons), showed a satisfactory long-term course but overestimated the diurnal amplitude of ΔW. The bias was reduced by optimizing k_1 and k_2 for distinct ranges of Ψ_{soil} and the estimates of k_1 and k_2 over 10 Ψ_{soil} classes were formulated as nonlinear functions of Ψ_{soil} (Figure 6):

$$k_{1\,Quercus} = 5.71 + 0.34\text{abs}(\Psi_{soil}) + 0.0012(\text{abs}(\Psi_{soil}))^2 \quad (2a)$$
$$(r^2 = 0.88)$$

$$\frac{k_{2\,Quercus}}{k_{1\,Quercus}} = 15.0\text{abs}(\Psi_{soil})^{-0.55} \quad (r^2 = 0.97) \quad (2b)$$

$$k_{1\,Pinus} = 3.86 + 0.08\text{abs}(\Psi_{soil}) + 0.0018(\text{abs}(\Psi_{soil}))^2 \quad (3a)$$
$$(r^2 = 0.81)$$

$$\frac{k_{2\,Pinus}}{k_{1\,Pinus}} = 20.1\text{abs}(\Psi_{soil})^{-0.57} \quad (r^2 = 0.92) \quad (3b)$$

$$k_{1\,Pinus} = 1.04\text{abs}(\Psi_{soil}) + 0.0027(\text{abs}(\Psi_{soil}))^2 \quad (4a)$$
$$(r^2 = 0.40)$$

$$\frac{k_{2\,Picea}}{k_{1\,Picea}} = 28.4\text{abs}(\Psi_{soil})^{-0.36} \quad (r^2 = 0.56) \quad (4b)$$

where abs(Ψ_{soil}) is the absolute value of Ψ_{soil}. The model was run with Equations 1 to 4 over entire seasons during which Ψ_{soil} varied widely.

The validity of the model (Equation 1) proposing that the difference VPD – Ψ_{soil} was the driving factor behind changes in ΔW was tested by linear regression. Tree water deficit was regressed on Ψ_{soil} and VPD singly and in combination. The signs of the coefficients, which relate algebraically to k_1 and k_2, supported the physical model as being the best-fitting alternative. With $n = 1000$ runs, the percentages of cases in which the regression coefficients had signs in the expected direction (VPD positive, Ψ_{soil} negative) were 86.1, 90.5 and 99.5 for *P. abies*, *Q. pubescens* and *P. sylvestris*, respectively. The corresponding mean r^2 values were 0.53, 0.49 and 0.64. For a field data set, this strongly supports the physical model proposed in Equation 1.

For the three species, ΔW_E best agreed with ΔW (Table 2). For *P. abies*, the agreement was marginally (but significantly) better than with VPD alone, whereas for *Q. pubescens* and *P. sylvestris*, the improvement over VPD or Ψ_{soil} alone was substantial. Significant differences among species were achieved after 200 runs. The trends in ΔW were well reproduced by ΔW_E (Figures 3–5), except for a few short periods.

Large residuals between ΔW_E and ΔW occurred more often during long dry periods when small rainfall events had no effect on the Ψ_{soil} measurements. In these cases, e.g., from late August to early September 2001, ΔW was underestimated by ΔW_E (Figure 4). On days with low Ψ_{soil}, there was a tendency toward larger residuals during the daytime; ΔW was then overestimated by ΔW_E.
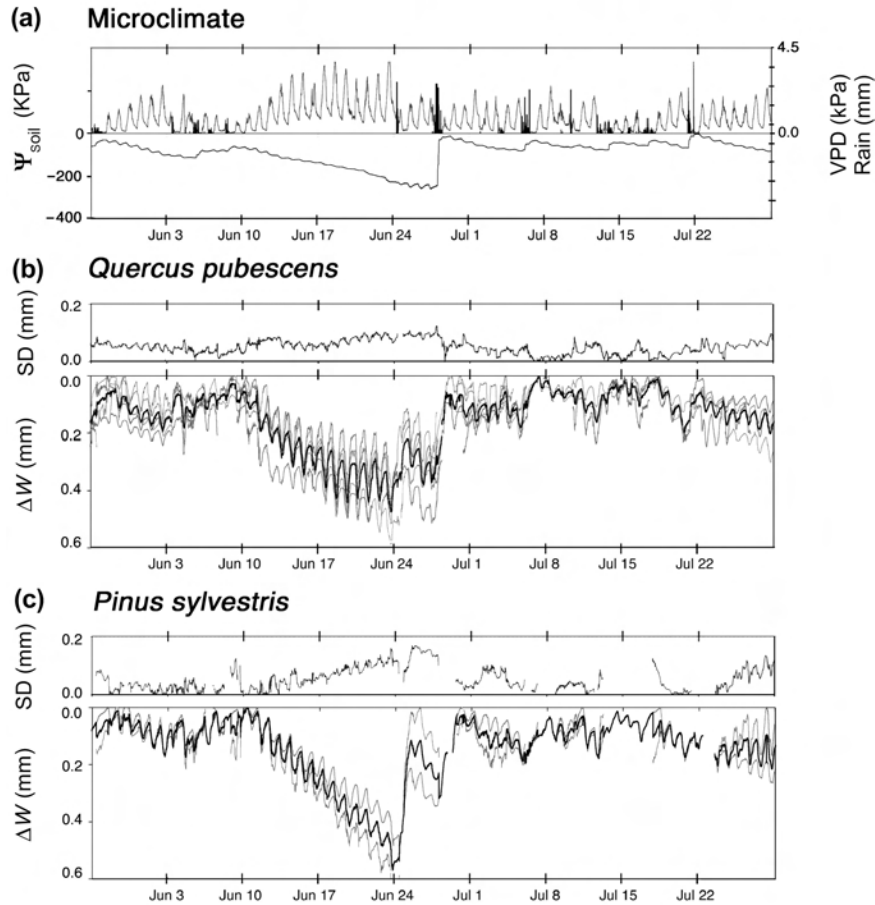
Figure 2. (a) Soil water potential (Ψ_{soil}), vapor pressure deficit (VPD) and rain at Salgesch, May–September 2002. Variability of tree water deficit (ΔW) with time for different trees of (b) *Quercus pubescens* and (c) *Pinus sylvestris*. The responses of individuals are shown by gray lines and the means by black lines (SD = standard deviation).

Relationships between ΔW, VPD and Ψ_{soil}

The relationships between ΔW and the dryness of the air (VPD) and soil (Ψ_{soil}) is shown by an example of 4 days at Salgesch (Figure 7). Because both VPD and Ψ_{soil} fluctuated with time, and the response of ΔW to a certain change in VPD (or Ψ_{soil}) was not constant, a typical hysteresis pattern occurred when ΔW was plotted against either variable (Figure 7).
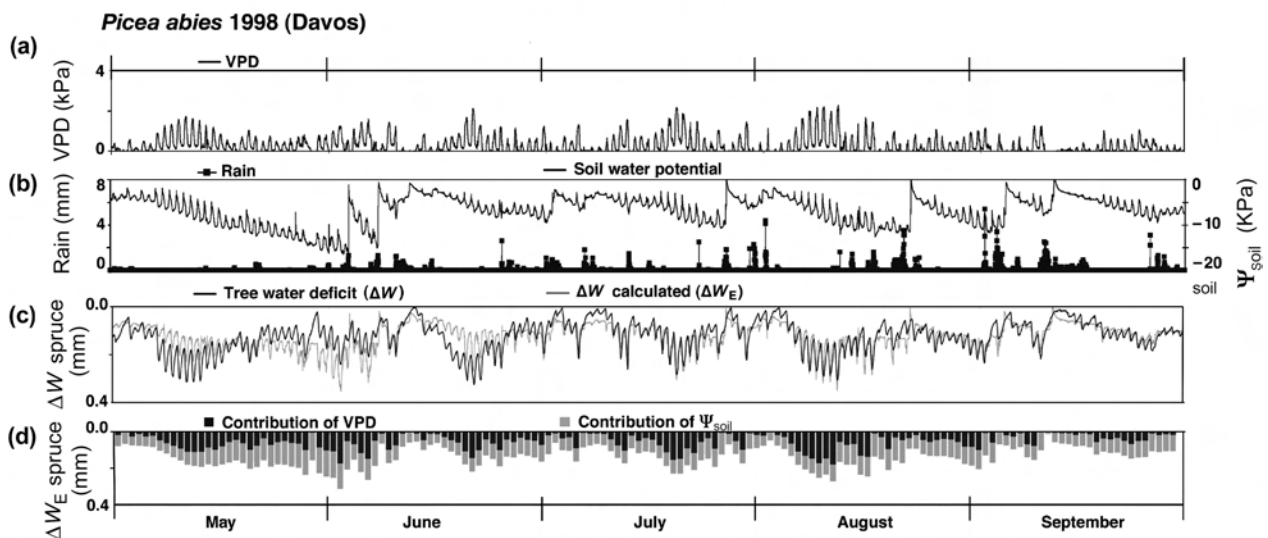

Figure 3. Seasonal courses of microclimatic conditions and tree response of *Picea abies* at Davos in 1998 (wet site): (a) vapor pressure deficit (VPD), (b) soil water potential (Ψ_{soil}) and rainfall, (c) measured (ΔW) and estimated (ΔW_E) tree water deficits and (d) the daytime contribution of VPD and Ψ_{soil} to ΔW_E.

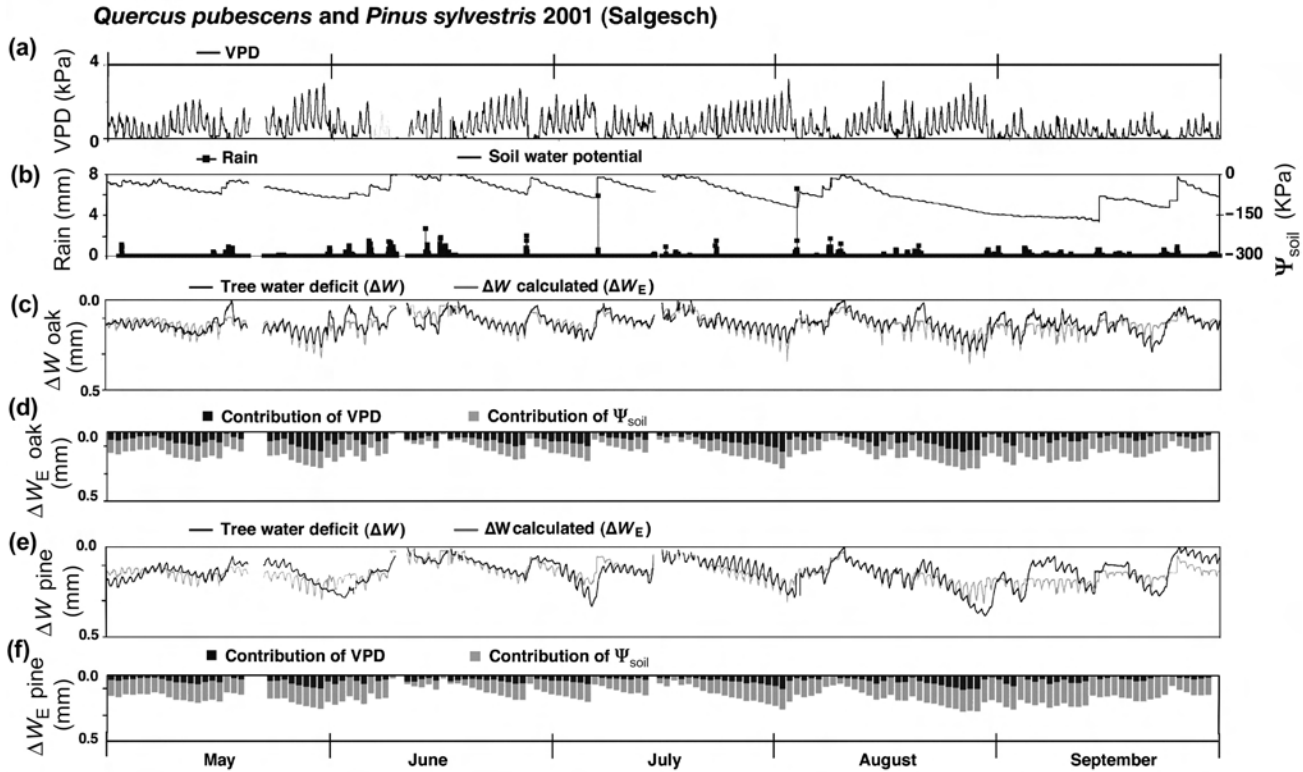**Quercus pubescens and Pinus sylvestris 2001 (Salgesch)**

Figure 4. Seasonal courses of microclimatic conditions and tree response of *Quercus pubescens* and *Pinus sylvestris* at Salgesch in 2001 (dry site): (a) vapor pressure deficit (VPD), (b) soil water potential (Ψ_{soil}) and rainfall, (c) measured (ΔW) and estimated (ΔW_E) tree water deficits, and (d) the daytime contribution of VPD and Ψ_{soil} to ΔW_E.

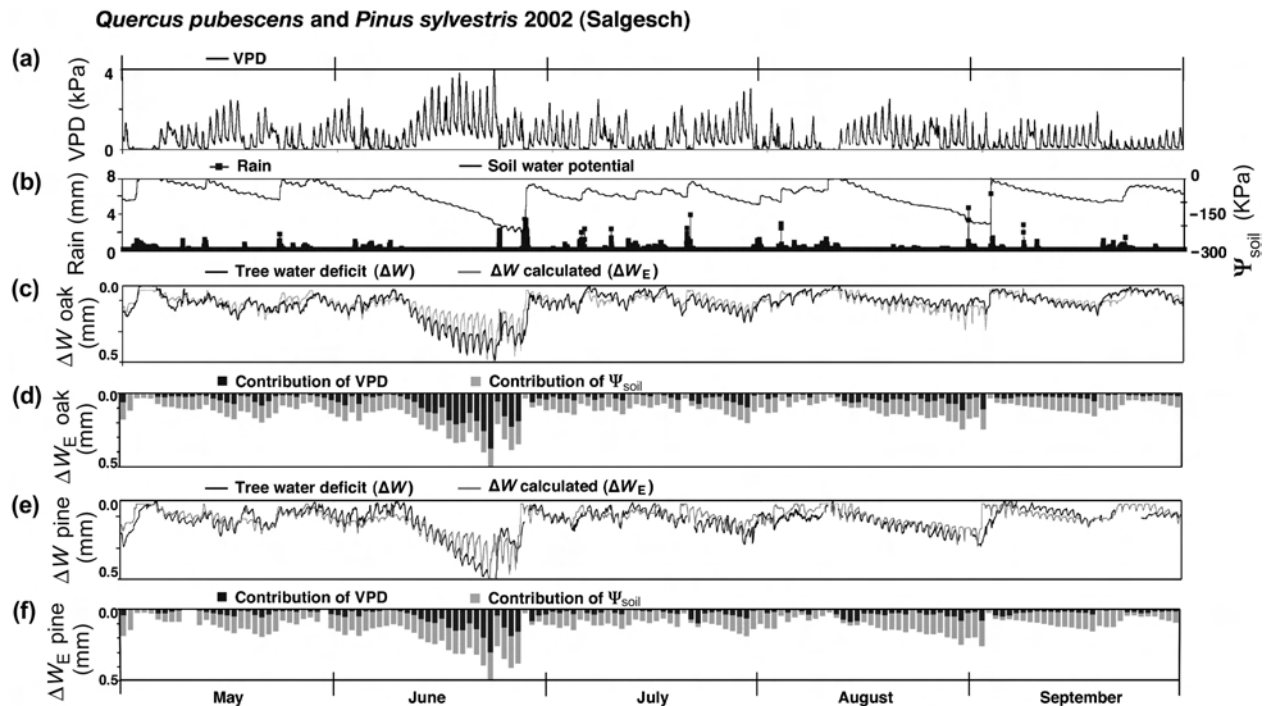**Quercus pubescens and Pinus sylvestris 2002 (Salgesch)**

Figure 5. Seasonal courses of microclimatic conditions and tree response of *Quercus pubescens* and *Pinus sylvestris* at Salgesch, in 2002 (dry site): (a) vapor pressure deficit (VPD), (b) soil water potential (Ψ_{soil}) and rainfall, (c) measured (ΔW) and estimated (ΔW_E) tree water deficits, and (d) the daytime contribution of VPD and Ψ_{soil} to ΔW_E.

Within the observed 2-year period, *Q. pubescens* and *P. sylvestris* differed slightly in their ΔW responses to dry climatic conditions. The largest differences were observed during the dry periods. The ΔW reached higher values in *P. sylvestris* than in *Q. pubescens* and seemed to be determined less by low Ψ_{soil} in *Q. pubescens* than in *P. sylvestris* (Figures 3–5).

A mathematical analysis of the proposed model ΔW_E (Equations 1 to 4) gave insight into the dependence of ΔW_E to VPD and Ψ_{soil} (Figure 8). At any given value for Ψ_{soil}, the sensitivity of ΔW_E on VPD was highest for *P. abies*, followed by *Q. pubescens* and *P. sylvestris*. Soil water potentials less than –50 kPa resulted in unrealistic high values of ΔW for *P. abies* (not shown in Figure 8a). This result corresponds to the naturally occurring range of Ψ_{soil} at Davos which was never less than –20 kPa. At any given VPD, ΔW_E of *Q. pubescens* increased less than ΔW_E of *P. sylvestris*, when Ψ_{soil} decreased, even though these response curves had different shapes at different VPDs. The response curves of *P. abies* were much steeper than those of the other species (Figure 8b).

The contribution of VPD and Ψ_{soil} to ΔW_E varied strongly with time of day. Vapor pressure deficit contributed less to ΔW_E at night than during the day because of the strong diurnal character of VPD (VPD returned to close to zero overnight). The relevance of the contribution of VPD to ΔW_E became obvious when small amounts of precipitation failed to moisten the soil significantly but induced rehydration of the tree, presumably through an effect on VPD (e.g., Figures 3a–c: July 20–25, 1998; Figures 5a–c: June 24–28, 2002).

The relative contribution of VPD to ΔW_E, in comparison to the contribution of Ψ_{soil} weighted by the coefficient k_1 to ΔW_E (Equation 1), varied between 22 and 37% (Table 3). *Pinus sylvestris* had the lowest percentages of VPD contribution and was more strongly affected by dry soil than *Q. pubescens* at Salgesch. *Quercus pubescens* responded more strongly to VPD than *P. sylvestris*. These findings match the response curves in Figure 8b. The percentage contribution of VPD to ΔW_E for *P. abies* was between the percentages for the two species at Salgesch, but may not be directly compared with them because *P. abies* experienced a different microclimate (air and soil) at a different site and in a different year.

Discussion

Detection and simulation of tree water deficits

The initial goal of this work was to find a method to quantify drought stress of trees and to estimate this measure with a simple but physiologically reasonable model with Ψ_{soil} and VPD as inputs. Dendrometer data detrended for growth led to ΔW values that were interpreted as a direct physiological measure of drought stress (Figure 1).

A simple, physically based model (ΔW_E) using a weighted difference between Ψ_{soil} and VPD estimated ΔW without including further climatic factors or requiring detailed knowledge of tree water relations, such as species-specific water storage properties or the impact of species-specific stomatal regulation on plant water deficit (Figure 2). Quantitative comparison of model output with measured data provided strong evidence that the chosen approach explained the course of ΔW well, leading to the conclusion that ΔW is largely determined by air and soil conditions. The tree physiological responses to drought (e.g., stomatal regulation) seemed to have little influence on ΔW; the differences between *Q. pubescens* and *P. sylvestris* were small, with no qualitative difference between the species. The general course of ΔW over two seasons was similar between the deciduous and conifer species at the same site.

The seasonal course of tree water deficit could be explained largely by changes in ΔW_E (Equation 1). Depending on the sensitivity of a tree species to air or soil dryness, or both, the weighting factors in Equation 1 changed (Figure 6), but VPD
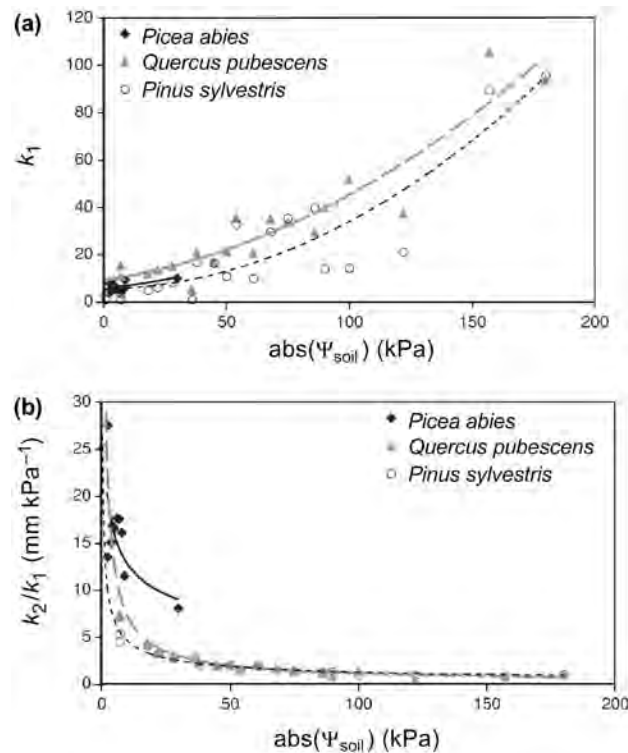

Figure 6. Parameters (a) k_1 and (b) k_2/k_1 of Equation 1 as Ψ_{soil}-dependent functions for *Picea abies*, *Quercus pubescens* and *Pinus sylvestris*. Abbreviation: abs(Ψ_{soil}) = absolute value of soil water potential.

Table 2. Means (± 2 SE) of correlation coefficients (*r*) between ln-transformed change in tree water deficit (ΔW) and the estimated change in tree water deficit (ΔW_E), vapor pressure deficit (VPD) and soil water potential (Ψ_{soil}) for three tree species at Davos and Salgesch, based on 200 runs of random subsamples ($n = 20$). Coefficients in the same column with different small letters differ significantly ($P < 0.05$).

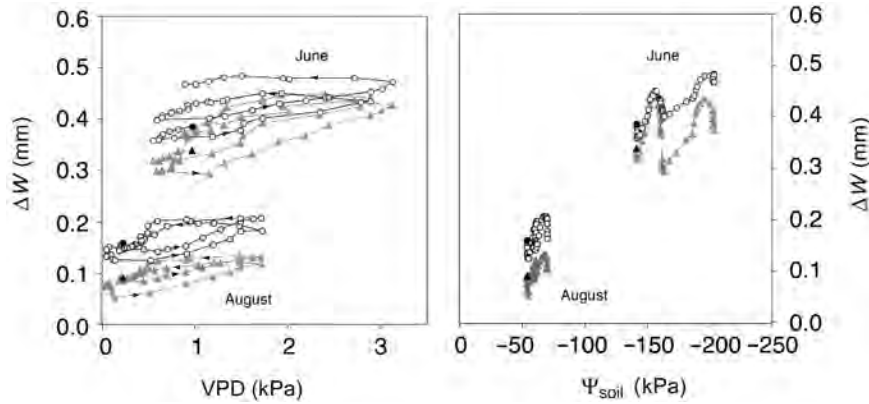|	Picea abies		Quercus pubescens		Pinus sylvestris	
	Mean	2 SE	Mean	2 SE	Mean	2 SE
ΔW_E	0.696 a	0.027	0.813 a	0.016	0.698 a	0.022
VPD	0.645 b	0.021	0.551 c	0.023	0.361 c	0.025
Ψ_{Soil}	0.366 c	0.029	0.640 b	0.024	0.643 b	0.025

Figure 7. Relationships between (a) tree water deficit (ΔW) and vapor pressure deficit (VPD), and (b) ΔW and soil water potential (Ψ_{soil}) for 4 days in 2002: *Quercus pubescens* (grey triangles) and *Pinus sylvestris* (open circles). The black symbols mark the starting hour (June 21, 0000 h and August 21, 0000 h). Arrows indicate the sequence in time (1 h between data points).

and Ψ_{soil} always had strong impacts on tree water status. Interpreting drought stress of trees solely on the basis of Ψ_{soil} can therefore lead to inaccurate estimates of tree water status. This finding is supported by many other studies (e.g., Jarvis 1975, Hinckley et al. 1978, Holbrook 1995, Sellin 1998, Oren and Pataki 2001).

As a first approximation of ΔW, Ψ_{soil} can be weighted in a way such that the negative Ψ_{soil} mean value reaches 65 to 75% of the positive VPD daytime mean value over a season (Table 3, *Q. pubescens* < *P. abies* < *P. sylvestris*). Detailed analyses were based on the model (Equation 1) with k_1 and k_2 as Ψ_{soil}-dependent functions (Equations 2–4). The coefficient k_1 was then positively related to abs(Ψ_{soil}). The increase in k_1 as soil dries can be explained by increased flow resistance between the soil and the tree's water storing tissues in comparison to the flow resistance between internal storage and the transpiration (at any given stomatal aperture). This decouples Ψ_{soil} from ΔW. The transpired water is therefore more strongly withdrawn from internal storage tissues, which means that the impact of a certain change in VPD on ΔW is greater when the soil is dry than when it is wet (Figures 6a and 8a). This finding is supported by the work of Phillips et al. (1996, 1997), in which it was shown that the proportion of water withdrawn from internal storage tissues for transpiration increases with decreasing Ψ_{soil}.

The ratio k_2/k_1 changed most (and attained the highest values) when Ψ_{soil} was between 0 and –30 kPa (Figures 6b). In this wet range, the difference between VPD and Ψ_{soil} must be multiplied by a higher k_2 value to accurately predict the change

in tree radius from the water potential gradient (in kPa). One reason for this may be that, when ΔW is small, a small water potential gradient causes a greater stem radius change than when ΔW is large, i.e., water is easier to withdraw from storage tissues close to saturation than from tissues far from saturation (see desorption curves in Zweifel et al. 2001).

The relationship between ΔW_E and Ψ_{soil} is more complicated and depends on the tree species and the range of VPD values. For *P. abies*, the impact of a given change in Ψ_{soil} on ΔW_E is greater at high VPD than at low VPD. For *P. sylvestris* and *Q. pubescens*, this is true for Ψ_{soil} greater than about –30 kPa. Under wet soil conditions, the impact of a given change in Ψ_{soil} on ΔW_E is greater at low VPD than at high VPD (Figure 8b).

Overall, the simple mechanism worked well for a conifer at a wet site and a deciduous species and a conifer at a dry site. Because water relations of all tree species depend on the difference in Ψ between soil and air, the method proposed may be useful for estimating ΔW of other tree species.

Impact of wet and dry air on tree water deficit

Tree water deficit was sensitive to small amounts of rain or slight decreases in VPD even when Ψ_{soil} remained constant. Small rain events affected VPD, even when they only moistened the uppermost layer of soil, and the trees responded with a reduction in ΔW. At Salgesch, the dry soil absorbed small amounts of water in the surface few millimeters. Below this shallow wet layer, the soil remained dry. Because the roots of the trees may have little access to this moist layer, it is inferred that water from light rain events affected the trees
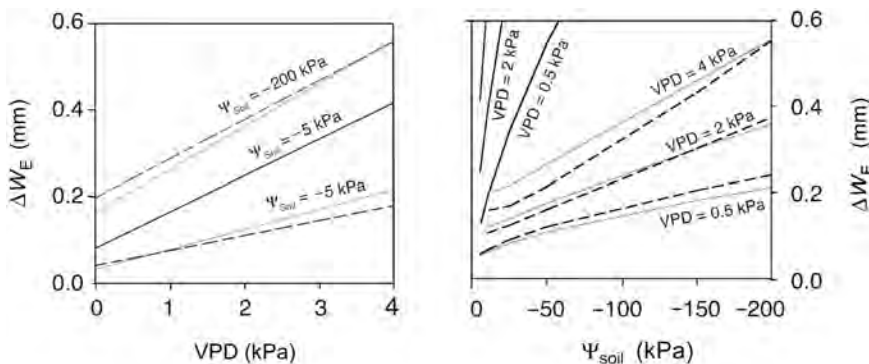

Figure 8. Relationship between (a) modeled tree water deficit (ΔW_E) and vapor pressure deficit (VPD) and (b) ΔW_E and soil water potential (Ψ_{soil}) modeled with Equations 1 to 4 for *Quercus pubescens* (gray line), *Pinus sylvestris* (dashed line) and *Picea abies* (black line).

Table 3. Relative contributions of the mean daytime vapor pressure deficit (VPD) between 0900 and 1500 h, and the mean soil water potential (Ψ_{soil}) weighted by the coefficient k_1 (see Equation 1 in text) to the estimated change in tree water deficit (ΔW_E) for three tree species.

Species	Year	% Contribution	
		VPD	Ψ_{Soil}
Picea abies	1998	31	69
Quercus pubescens	2001	33	67
	2002	37	63
Pinus sylvestris	2001	22	78
	2002	26	74

through its effect on VPD, not soil water content. High sensitivity to VPD was also observed at Davos, where the ΔW of *P. abies* responded to changing VPD despite the wet soil conditions.

According to the model proposed, a reduction in VPD leads to a reduction in ΔW, even if Ψ_{soil} remains low. A release of tree-internal negative pressure (due to the low VPD) seems to result in water flowing back to the bark, causing it to swell. Saturated air within the crown or liquid water drops on the leaves quickly increase Ψ_l. The bark, with the lowest Ψ, can then be viewed as the strongest sink within the flow-and-storage system of a tree; its elastic tissues draw available water from the soil via the roots or from the leaves via the branches causing a detectable increase in stem radius. The amount of water needed to replenish the bark after water depletion was estimated for *P. abies* by Zweifel and Häsler (2001) to be a function of the tree's stem diameter at breast height. Using their equation, the *P. abies* trees investigated here would need about 2 l, *Q. pubescens* about 0.1 l and *P. sylvestris* about 0.5 l of water to replenish bark tissues (assuming that the *P. abies* function applies to *Q. pubescens* and *P. sylvestris*).

Our results agree with the conclusions of others who showed that the physiological response of trees to the atmospheric environment (e.g., VPD) depends on the dryness of the soil (Hinckley et al. 1978, Pataki et al. 1998*a*, Sellin 1998, Oren and Pataki 2001). Depending on the difference between Ψ_{soil} and VPD, coupling between plant Ψ and Ψ_{soil} varies (Zweifel et al. 2002). This may account for the varied conclusions that have been drawn about the relationship between predawn plant Ψ and Ψ_{soil} (Hinckley et al. 1983, Sellin 1996, 1998, Lebourgeois et al. 1998, Pataki et al. 1998*b*, Sturm et al. 1998).

Species-specific sensitivities to VPD and Ψ_{soil}

Sensitivity of ΔW to VPD and Ψ_{soil} appeared to be species-specific. Tree water deficit was more strongly coupled with VPD in *Q. pubescens* than in *P. sylvestris* (Figure 8a) (Figures 4, 5 and 8b).

Although the responses of ΔW_E to VPD and Ψ_{soil} in *P. abies* differed from those of the other species (Figure 8), the contribution of VPD and Ψ_{soil} to ΔW_E was similar to that of the other

species under the relatively wet conditions prevailing at Davos (Table 3). In contrast, Gao et al. (2002) reported a generally greater dependence of water status on air humidity in conifers than in deciduous trees. However, Gao et al. (2002) investigated only VPD-dependent stomatal responses of *P. abies,* not the sensitivity of ΔW to both VPD and Ψ_{soil}. It is reasonable, from a physiological point of view, that the rapid closing of stomata in dry air may lead to stronger dependence of ΔW on Ψ_{soil} than when the stomata remain open.

From what depth do trees draw water?

The question arises whether the measured Ψ_{soil} values were representative of the conditions under which the tree roots were taking up water. At Salgesch, the soil is shallow and heterogeneous, and Ψ_{soil} was measurable only in the uppermost layer (< 15 cm depth) of stones and soil. The calculation of ΔW_E with Equation 1 depends on the quality of the Ψ_{soil} data, but as shown, the model mostly fitted the data well. There were, however, some periods in which the calculated ΔW values fitted the measured values poorly (e.g., late August 2001; Figure 5). For these periods, the trees probably either (1) drew water from greater depths (i.e., from deep cracks in the rocks below the soil layer), and therefore, the Ψ_{soil} measurements were not representative, or (2) the equitensiometers were insufficiently sensitive to detect small changes in Ψ_{soil} under dry soil conditions. An analysis of the residuals between ΔW_E and ΔW supported these suggestions because there was a trend toward larger residuals during long dry periods.

Potential for improvement of the tree water deficit model

Estimation of tree water deficits with ΔW_E (Equation 1) can be improved by incorporating aboveground climatic factors in addition to VPD. The transpiration of trees is dependent not only on VPD (which reflects temperature and relative humidity), but also on wind and radiation (Penman 1948, Monteith 1965, 1995, Zweifel et al. 2002). Further, stomatal regulation strongly determines the water relations of a tree and thus has a distinct impact on ΔW (Bond and Kavanagh 1999, Oren and Pataki 2001, Zweifel et al. 2001, 2002, Gao et al. 2002). A more sophisticated tree water model, going beyond a weighted difference between VPD and Ψ_{soil} (Bond and Kavanagh 1999, Oren and Pataki 2001, Zweifel et al. 2001, 2002, Gao et al. 2002) might yield more accurate predictions. However, the large residuals of ΔW_E during certain dry periods (e.g., late August 2001; Figure 4) may reflect errors in the measurement of Ψ_{soil}, not a flaw in the model.

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