Oecologia (Berl) (1981) 51:343–350

Oecologia

Root Growth and Water Relations of Oak and Birch Seedlings

O. Osonubi* and W.J. Davies

Department of Biological Sciences, University of Lancaster, Bailrigg, Lancs., U.K.

Summary. First year seedlings of English oak (*Quercus robur*) and silver birch (*Betula pendula*) were subjected to pressure-volume analysis to investigate the water potential components and cell wall properties of single leaves. It was hoped that this rapid-drying technique would differentiate between reductions in plant solute potential resulting from dehydration and the effects of solute accumulation.

Comparison of results from these experiments with those of slow drying treatments (over a number of days) with plants growing in tubes of soil, indicated that some solute accumulation may have occurred in drying oak leaves. High leaf turgor and leaf conductance were maintained for a significant period of the drying cycle. Roots of well-watered oak plants extended deep into the soil profile, and possibly as a result of solute regulation and therefore turgor maintenance, root growth of unwatered plants was greater than that of their well-watered counterparts. This was particularly the case deep in the profile. As a result of deep root penetration, water deep in the soil core was used by oak plants to maintain plant turgor, and quite low soil water potentials were recorded in the lower soil segments.

Root growth of well-watered birch seedlings was prolific but roots of both well-watered and unwatered plants were restricted to the upper part of the profile. Root growth of unwatered plants was reduced despite the existence of high soil water potentials deep in the profile. Shallow rooting birch seedlings were unable to use this water.

Pressure-volume analysis indicated that significant reductions of water potential, which are required for water uptake from drying soil, would occur in oak with only a small reduction in plant water content compared to the situation in birch. This was a result of the low solute potential in oak leaves combined with a high modulus of elasticity of cell walls. Deep rooting of oak seedlings, combined with these characteristics, which will be particularly important when soil deep in the profile begins to dry, mean that this species may be comparatively successful when growing on dry sites.

Introduction

The movement of liquid water from the soil into the root can conveniently be viewed in terms of an Ohm's law-type equation. According to this convention, the rate of water movement is directly proportional to the magnitude of the force driving the flux, which is the water potential gradient between the soil and the root xylem. Flux rate is inversely proportional to a resistance to the movement of water, where resistance is defined as a function of flux and driving force. For water moving from the bulk soil into the root, this resistance comprises at least three major components linked in series. These are the resistance to water movement through the pores between the soil particles (Gardner 1965; Cowan 1965), the resistance to movement across the interface between the soil and the root (Herkelrath et al. 1977a and b) and the resistance to movement of water across the 'root membrane' (Fiscus 1976; Weatherley 1976) into the root xylem. When the soil dries, the large soil pores will empty of water and a vapour gap may form between the root and the surrounding soil. The result of soil drying will therefore be a significant increase in resistance to water movement through the soil and across the soil:root interface. Unless an increase in the driving force for water movement can compensate for such an increase in resistance, the rate of water movement into the root will inevitably decline. For this reason, the growth of roots away from dry soil into wet soil will be important if a high rate of water uptake is to be maintained.

An increase in the driving force for water uptake is brought about by a reduction in the water potential inside the root membrane. This can occur either as a result of a decrease in cell turgor or as a result of a decrease in root solute potential. Sharp and Davies (1979) have noted that an accumulation of solutes in roots will lower root water potential and therefore increase the driving force for water uptake, but also maintain root turgor, the driving force for cell growth. It seems likely that one of the effects of mild water stress is to reduce leaf growth rate, diverting current photosynthate to the roots where it provides a substrate for root growth as well as acting to maintain the driving force for growth (Hsiao and Acevedo 1974). *Quercus robur* and *Betula pendula* are two woody plants commonly found in association in Great Britain. In an earlier report, Osonubi and Davies (1978) suggested that oak seedlings compete efficiently for water because of high root: shoot ratios and low solute potentials. Birch seedlings showed an inability to shift solute potentials to a sufficiently low level for maintenance of turgor and for effective moisture competition on dry sites. In this paper we report on the turgor relations of oak and birch seedlings, the distribution of roots through the soil profile and water uptake rates resulting from the respective root distributions.

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* Present address: Department of Botany, University of Ibadan, Nigeria

Send offprint requests to: W.J. Davies

0029-8549/81/0051/0343/$01.60

Methods

a) The Turgor Relations of Woody Shoots

Pressure-volume analysis was applied to first year seedlings of English oak (*Quercus robur* L.) and silver birch (*Betula pendula* Roth.). This analysis, the theory of which is described by Tyree (1976) and Roberts and Knoerr (1977), is a means of investigating the effects of dehydration on the turgor and solute relations of leaves. Plant material can be dried rapidly, presumably before significant osmoregulation can occur. Therefore the solute relations of leaves dried by this technique can be compared with those of intact plants dried more slowly. It was hoped that this technique would therefore differentiate between the simple effects of dehydration and those of osmoregulation, as well as elucidate other aspects of the water relations of single leaves.

Seeds were germinated in moist sand and young seedlings were transplanted into 13 x 20 cm pots containing John Innes No. 1 compost. Matched seedlings were selected for the experiment when they were 12–14 weeks old. Half of the plants were watered well during the evening prior to use and placed for approximately 15 h in a dark growth chamber lined with black polythene sheeting to exclude light. A temperature of 22° C ± 1° C was maintained throughout the dark period. The remaining plants were subjected to a soil drying treatment in the greenhouse until a predawn leaf water potential of -0.5 MPa was recorded. The plants were rewatered and left overnight in the conditions described above. The following morning, turgid shoots of unstressed or prestressed seedlings were severed from the roots, weighed and sealed in a pressure bomb, the inside surface of which was lined with wetted filter paper to minimise water loss from the leaves. Water expressed from the cut end of the shoot was absorbed into a pre-weighed 5 cm long polyethylene tube filled with dry tissue paper. This tube had an inside diameter which was slightly larger than the exposed end of the shoot (Cheung et al. 1975). The shoot was brought to balance pressure and then pressure was increased in steps of about 0.3 MPa over the previous balance pressure. After 10 min at each increased pressure the bomb pressure was reduced until water flow had ceased. The tube and the expressed water were weighed to 0.1 mg on a Mettler balance and converted to volume expressed, Ve, assuming the density of water to be 1 g cm^{-3}. A time lag of about 10 min was allowed and the new balance pressure for the shoot was determined as in an ordinary determination of water potential with a pressure bomb. Balance pressures up to 4.0 MPa in the case of oak shoots and 2.5 MPa in the case of birch shoots were applied. Birch shoots began to yield unusually low amounts of sap at bomb pressures higher than 2.5 MPa. This condition is considered to precede shoot death (Tyree et al. 1973). Six replicates were taken for each treatment. The total volume of sap expressed from the shoot and collected from the cut end of the petiole compared well with the reduction in fresh weight of the leaf over the experimental period (Wilson et al. 1979).

The data obtained were used to plot the relationship between the inverse balance pressure and the cumulative volume of expressed sap (*Ve*) (Cheung et al. 1975) (Fig. 1). The linear part of the graph was obtained by regression analysis where the intercepts and slope were used for further calculations as discussed below. Extrapolation of the linear part of the relationship to $Ve=0$ and $1/P=0$, gave estimates of the inverse of the initial solute potential (ψ_{so}) and the osmotic water content (*Vo*) respectively. The point on the pressure volume curve at which the declining water potential equals the calculated solute potential is regarded as the volume (V_p) at which incipient plasmolysis occurs and also the corresponding solute potential (ψ_{sp}) which can be graphically determined (Fig. 1).

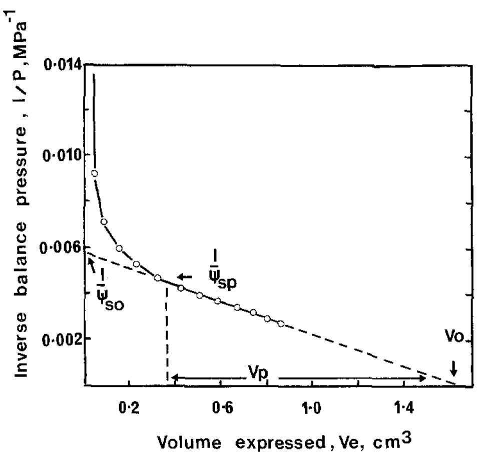

Fig. 1. A plot of the inverse balance pressure ($1/P$) of an oak shoot versus the volume of expressed water. $1/\psi_{so}$ is the inverse of the initial bulk solute potential, $1/\psi_{sp}$ is the inverse of the bulk solute potential at zero turgor, V_p is the osmotic water volume remaining in the shoot at zero turgor and V_o is the original volume of osmotic water in the shoot

On completion of the pressure bomb measurements, leaves and stems were separately weighed and then dried at about 80° C for 48 h before reweighing. The osmotic water fraction (*F*) was obtained by dividing the osmotic water volume by shoot turgid water content:

$$F = Vo/(\text{shoot turgid weight} - \text{shoot dry weight})$$

The non-turgor component (ψ_x) of the water potential was calculated by first normalising the pressure volume curves to total leaf water deficit $WD = Ve$(Shoot turgid weight − shoot dry weight). Then ψ_x was obtained by:

$$\frac{1}{\psi_x} = A + B \cdot WD$$

where *A* and *B* are the intercept and slope of the regression line respectively. ψ_x includes solute and matric potentials because the leaf water deficit is usually considered in relation to total water content instead of osmotic water content of the tissue. Apart from the osmotic water content, the total water content includes water in the cell walls, water of hydration of proteins and other constituents of the tissue in which the forces acting on them are collectively termed matric potential (ψ_m) (Hellkvist et al. 1974).

Turgor potential (ψ_p) was obtained as the difference between total water potential determined with the pressure bomb, and calculated non-turgor component. Solute potential (ψ_s) which is a component part of non-turgor component (ψ_x) was obtained using:

$$\psi_s = \psi_x - \psi_{so} \left[\frac{F}{(F - WD)} - \frac{1}{(1 - WD)} \right]$$

(Hellkvist et al. 1974; Roberts and Knoerr 1977) where the parameters are as previously defined. Matric potential was obtained as the difference between the non-turgor component and solute potential (Hellkvist et al. 1974).

The bulk modulus of elasticity of the tissue (E_t) was calculated using:

$E_t = d\psi_p/dF^*$

where F^* is the fraction of symplasmic water when turgor is greater than zero.

$F^* = (Vo - Vp(Ve)/Vp$ (Cheung et al. 1976).

Water deficit at zero turgor (WD_p) and leaf dry weight/turgid weight ratio (LDW/LTW) were also calculated.

b) Root Distribution and Water Uptake

Seed was germinated in moist sand and as soon as leaves were visible, seedlings were potted into 7.5 cm pots containing John Innes No. 1 compost. After four weeks in these pots, seedlings with six to ten leaves ranging between 7.5 and 12.0 cm (oak) or 9.0 to 12.0 cm (birch) in height were selected and transplanted into 6.0 cm × 6.0 cm × 33.0 cm plastic tubes lined with black polythene (for easy retrieval of soil columns). The tubes were packed to 30 cm with John Innes No. 1 soil mixture (690 g) to give a bulk density of 0.64 g cm^{-3}. The soil mixture had previously been sifted through a 2 mm sieve. The plants were grown in the tubes for two weeks before the start of the investigation. A preliminary experiment had established that in two weeks, roots would not grow beyond the upper 10 cm of soil. Experimental measurements on oak seedlings were commenced just as a resting bud was breaking and a flush of leaves was starting. Investigations were conducted on a green-house bench under natural light supplemented with 80 Wm^{-2} fluorescent light to provide a sixteen hour day. Greenhouse temperature was 23±1° C and the humidity was uncontrolled.

Thirty five tubes of each species, designated as control plants, were watered every day. An equal number of plants were watered on day one of the experiment and were then left unwatered throughout the two week period of the experiment. These plants are designated as water-stressed plants. Every 2 days, between 12.00 and 14.00 h, measurements of leaf water and solute potentials were made on five control and treatment plants of each species. Leaf diffusive conductance measurements were made on leaves of ten plants of each species. After these measurements were complete, five plants from each treatment were destructively harvested to provide measurements of root density. Soil moisture content was also measured and soil water potential was calculated.

Measurements of leaf diffusive conductance were taken on abaxial surfaces of exposed mature leaves using a Lambda diffusion porometer (Lambda Instruments Co.). The porometer was calibrated under the same conditions as the experimental plants, each time measurements were taken. Leaf water potentials were determined with a thermocouple hygrometer (Sharp and Davies 1979) attached to an HR-33T dew point microvoltmeter (Wescor Inc.). Leaf solute potentials were determined by freezing the leaf tissue enclosed in micro-centrifuge tubes in liquid nitrogen. A 6 mm disc was excised from the leaf and enclosed in a thermocouple hygrometer chamber. The hygrometers had previously been individually calibrated by vapour phase equilibration with NaCl solutions of known water potential. Turgor pressure was estimated as the difference between leaf water and solute potentials assuming matric potential to be zero.

Soil columns were retrieved with the aid of the polythene sheets used in lining the tubes and were sectioned into 10 cm lengths. Soil samples were taken from each section, dried in the oven for 24 h at 80° C, and soil moisture content as a percentage of oven dry weight was calculated. Soil water potential was then determined from a curve of soil moisture percentage versus soil water potential, constructed using a pressure plate apparatus. Soil water potential above −0.1 MPa was determined with soil tensiometers. Soil moisture content in cm^3 of water per cm^3 of soil was obtained by multiplying the fraction of soil moisture content and oven dry weight of soil by the bulk density of the soil (0.64 g cm^{-3}) assuming that the density of water is 1 g cm^{-3}.

The previously sectioned 10 cm soil lengths were soaked in 1% sodium pyrophosphate solution for 24 h to disperse the soil particles. Large roots were recovered by washing out the loose soil over a fine sieve and small roots were floated off the remaining soil and collected by pouring the water over the fine sieve. The root lengths were determined using the intercept technique of Newman (1966) on a perspex plate etched with a 1 cm square grid (Tennant 1975). The value obtained was multiplied by a length conversion factor of 0.7857 (Tennant 1975) to give the actual root length.

Soil water depletion was estimated as the average change in soil water content over time. The average change in soil water content per unit soil volume from one day to the next was divided by 32 h, which represents the daylight hours for two days assuming that there was little root extraction or vertical flux of water at night (Herkelrath et al. 1977a).

Results

a) Solute potentials of both well-watered and previously water-stressed oak seedlings were significantly lower than those of birch seedlings (Table 1). Rapid drying reduced solute potentials of oak seedlings by around 0.2 MPa while solute potentials of birch were reduced by less than 0.1 MPa by this technique. A slower drying treatment prior to pressure:volume analysis reduced solute potentials of both birch and oak by 0.2 MPa, suggesting that both species has the capacity to accumulate solutes in leaves (Table 1). The result of this accumulation and the effects of dehydration were solute potentials of nearly −2.1 MPa in oak leaves but only −1.3 MPa in birch leaves. One consequence of the low initial solute potentials in oak is that oak seedlings may tolerate water potentials as low as −2.1 MPa but still exhibit positive turgor levels, whereas birch seedlings would exhibit zero turgor at water potentials of only −1.3 MPa.

The modulus of elasticity of cell walls of oak leaves was significantly higher than that of birch leaves (Table 1). The result of this is that water potential declines more rapidly in oak seedlings than in birch seedlings subjected to a comparable water deficit (Fig. 2). The combination of high modulus of elasticity and low solute potential in oak leaves means that a water deficit of around 10% will result in a water potential of around −2.0 MPa while a comparable water deficit in birch will generate a water potential of only −1.3 MPa (Table 1, Fig. 2). Prestressing of plant material stiffened the walls of both species (Table 1).

The slope of the line showing the relationship between the inverse of leaf solute potential and the volume of water expressed from the leaf (see methods) is an indication of the sensitivity of leaf solute potential to the effects of dehydration. Interestingly, the solute potential of well-watered birch leaves decreases more significantly with increasing water deficit than the solute potential of oak leaves (Table 1). Prestressing greatly increases the sensitivity of solute potential of oak leaves to increasing water deficit. Conversely, the solute potential of birch leaves became less sensitive to water deficit following a prestressing treatment. These changes in slope, coupled with comparatively small changes in solute potential with prestressing mean that this treatment may significantly alter the osmotic water volume. With

Table 1. Summary of the tissue water relations of shoots from two woody seedlings. WW = unstressed, WS = prestressed, ψ_{so} = bulk initial solute potential at zero or near zero water deficit, ψ_{sp} = bulk solute potential at incipient plasmolysis, WD_p = water deficit at incipient plasmolysis, F = osmotic water percentage, E = bulk modulus of elasticity, LDW/LTW = ratio of leaf dry weight to leaf turgid weight

	Slope MPa^{-1}	ψ_{so} (MPa)	ψ_{sp} (MPa)	WD_p (%)	F (%)	E (MPa)	LDW/LTW
WW *Quercus robur*	−0.0048 (±0.001)	−1.64 (±0.1)	−1.80 (±0.13)	12.0 (±1.0)	85.0 (±1.0)	7.54 (±0.52)	0.34 (±0.02)
WS *Quercus robur*	−0.0074 (±0.001)	−1.84 (±0.07)	−2.09 (±0.09)	13.0 (±1.0)	81.0 (±2.0)	8.28 (±0.3)	0.37 (±0.01)
% increase (+)/decrease (−)	(−) 52.38	(−) 12.09	(−) 16.09	(+) 8.33	(−) 4.71	(+) 9.83	(+) 8.82
WW *Betula pendula*	−0.0063 (±0.001)	−1.04 (±0.03)	−1.10 (±0.04)	7.0 (±1.0)	60.0 (±3.0)	5.50 (±0.2)	0.22 (±0.01)
WS *Betula pendula*	−0.0045 (±0.001)	−1.25 (±0.03)	−1.32 (±0.06)	9.0 (±1.0)	82.0 (±9.0)	6.38 (±0.15)	0.28 (±0)
% increase (+)/decrease (−)	(+) 27.98	(−) 19.64	(−) 18.68	(+) 28.57	(+) 36.67	(+) 15.91	(+) 27.27

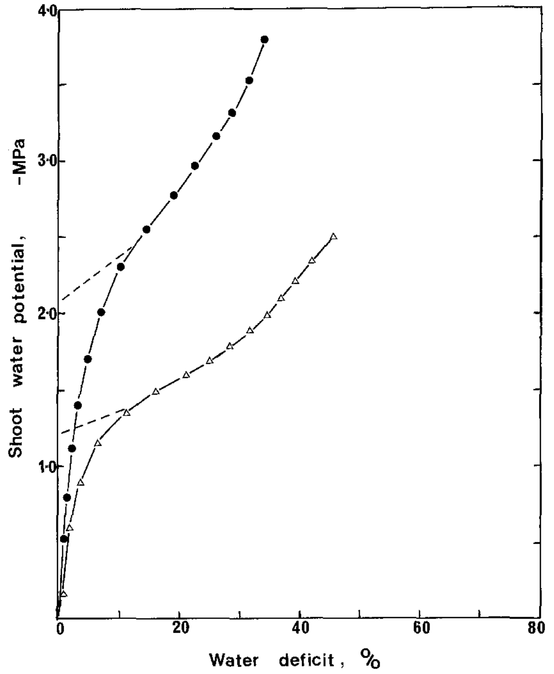

Fig. 2. Shoot water potential as a function of water deficit (Ve/(shoot turgid weight – shoot dry weight) for prestressed seedlings of Quercus *robur* (○) and Betula pendula (△). Dotted line shows variation in leaf solute potential

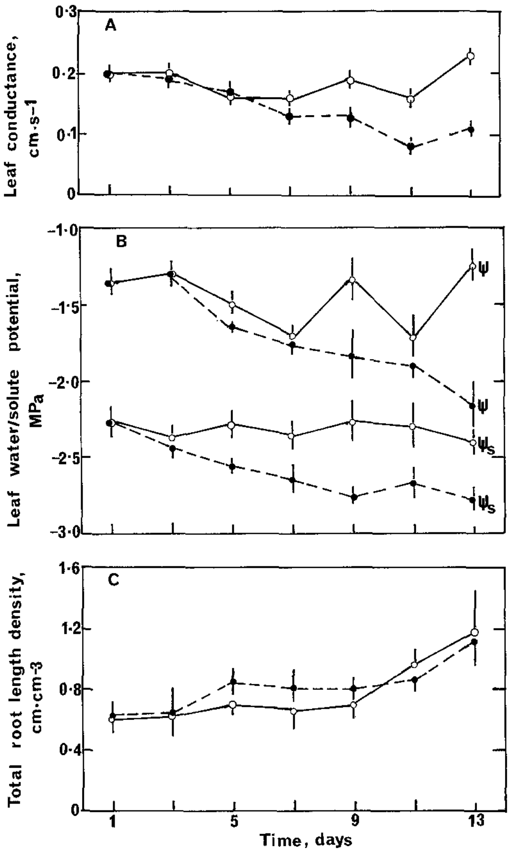

Fig. 3. The influence of developing water stress on **A)** leaf conductance, **B)** leaf water and solute potential, and **C)** total root length density of *Quercus* seedlings. ○——○ well-watered seedlings. ●——● water-stressed seedlings. Water was withheld from water-stressed seedlings on day 1 and all measurements were taken during the hours in the middle of the light period. All points are means with standard error indicated

prestressing, oak seedlings exhibited only a small decrease in osmotic water percentage while birch seedlings showed a significant increase in osmotic water percentage (Table 1).

b) Under the experimental conditions, well-watered oak seedlings exhibited leaf water potentials of around −1.4 MPa and solute potentials of around −2.3 MPa during the middle part of the light period (Fig. 3). The soil drying treatment resulted in a reduction of leaf water potential but solute potential also declined so that leaf turgor remained relatively constant until day 9 of the drying cycle (Fig. 3). On this day, leaf conductance was also reduced below the conductance exhibited by well-watered leaves. Total root length density of unwatered plants may have exceeded that of well-watered plants until moderate stress developed (day 9) and despite further stressing was not significantly reduced below that of well-watered plants (Fig. 3).

During the hours in the middle of the light period, well-watered birch leaves exhibited a turgor of only around 0.4 MPa,

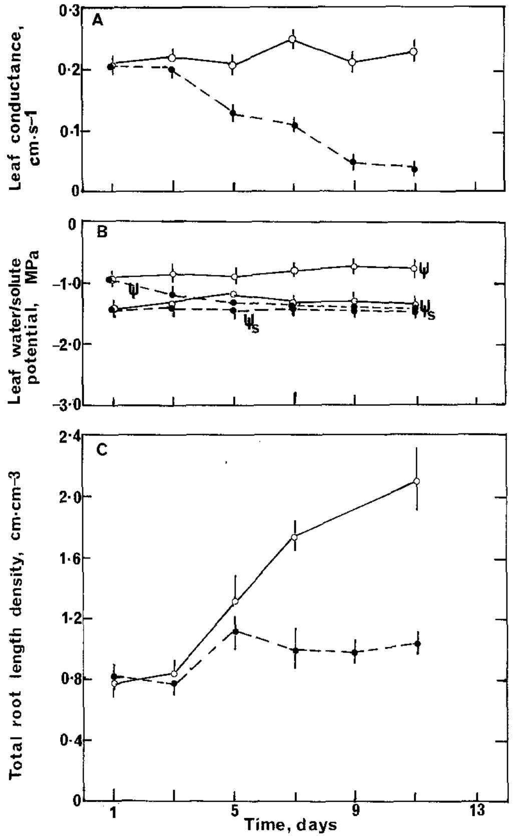

Fig. 4. The influence of developing water stress on *A)* leaf conductance, *B)* leaf water and solute potential, and *C)* total root length density of *Betula* seedlings. o——o well watered seedlings. ●——● water-stressed seedlings. Water was withheld from water-stressed seedlings on day 1 and all measurements were taken during the hours in the middle of the light period. All points are means with standard error indicated

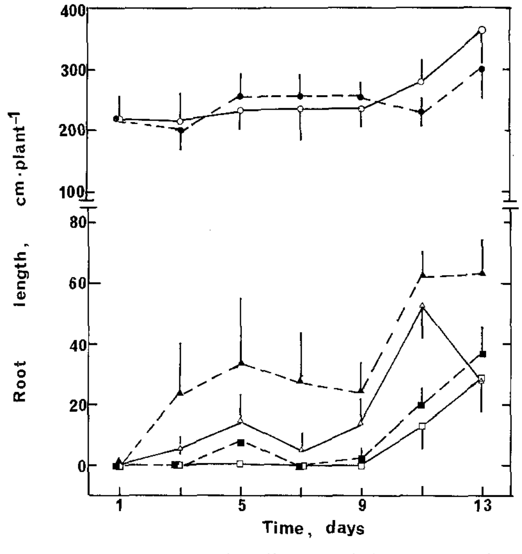

Fig. 5. Root growth of well-watered (*open symbols with solid lines*) and water-stressed (*closed symbols with broken lines*) *Quercus* seedlings as a function of time in different soil segments, 0–10 cm (*circles*), 10–20 cm (*triangles*), 20–30 cm (*squares*). Water witheld from water-stressed seedlings on day 1 and all measurements taken during the hours in the middle of the light period. All points are means with standard error indicated

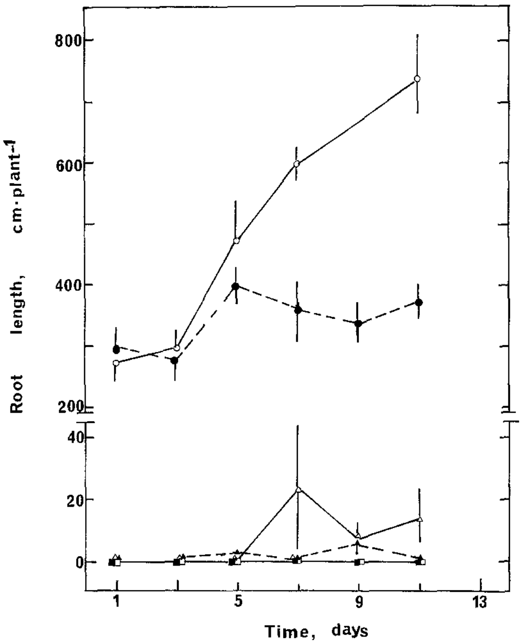

Fig. 6. Root growth of well-watered (*open symbols with solid lines*) and water-stressed (*closed symbols with broken lines*) *Betula* seedlings as a function of time in different soil segments, 0–10 cm (*circles*), 10–20 cm (*triangles*), 20–30 cm (*squares*). Water witheld from water-stressed seedlings on day 1 and all measurements taken during the hours in the middle of the light period. All points are means with standard error indicated

a water potential of −1.0 MPa and a solute potential of around −1.4 MPa (Fig 4). The soil drying treatment resulted in a rapid reduction in leaf water potential but leaf solute potential did not decline so that a negligible leaf turgor was recorded by day 5 of the drying cycle. Stomatal conductance of water stressed plants was significantly reduced on this day (Fig. 4). During the two week experimental period, total root length density of well-watered plants increased very significantly from around 0.8 cm cm^3 to around 2.0 cm cm^3 but no significant growth by roots of water stressed plants was detected beyond day 5 of the drying cycle and root length density of these plants did not increase beyond 1.2 cm cm^{-3} (Fig. 4).

Further analysis of root growth by the two species shows a significant increase in the length of oak roots in the upper 10 cm of the soil cores which were well-watered for the 13 day experimental period (Fig. 5). After 9 days, well-watered plants extended roots into the 10–20 cm and the 20–30 cm segments of the core. The result of witholding water for only 3 days was increased root extension into the 10–20 cm soil segment and root extension into the 20–30 cm segment may also have occurred more rapidly as a result of the water stress treatment (Fig. 5).

Neither well-watered or water-stressed birch seedlings exhibited significant root extension below 10 cm during the course of the experiment (Fig. 6). Nevertheless, well-watered seedlings did produce a lot of roots in the upper 10 cm of soil while root growth of water stressed plants was severely limited after day 5 of the drying treatment (Fig. 6).

By the end of the experimental period, transpiring oak seedlings reduced the water content and water potential of unwatered soil in the upper 10 cm of the profile to 0.10 cm^3 cm^3 and −0.7 MPa respectively (Fig. 7). For the first five days of the experiment, soil water did not decline, but during the next 8 days water potential was reduced to −0.1 MPa, reflecting a marked

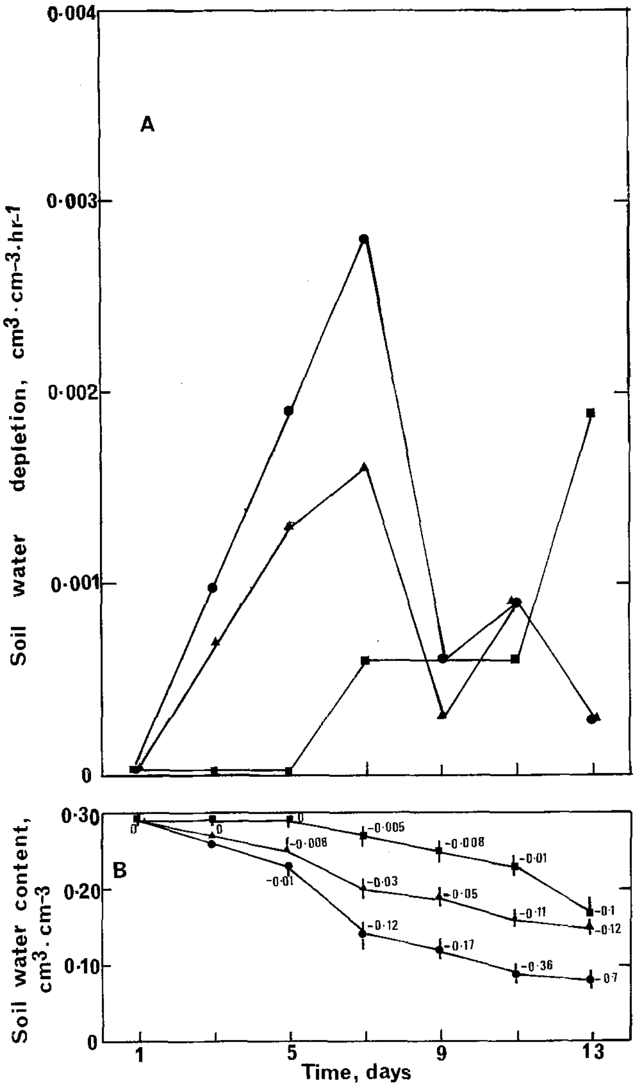

Fig. 7A, B. Soil water depletion rate (**A**) and soil water content and potential (**B**) as a result of water loss by unwatered *Quercus* seedlings. Variation in 0–10 cm (●), 10–20 cm (▲) and 20–30 cm (■) soil segments is shown. Numbers indicate soil water potential in MPa. Points are means with standard errors indicated

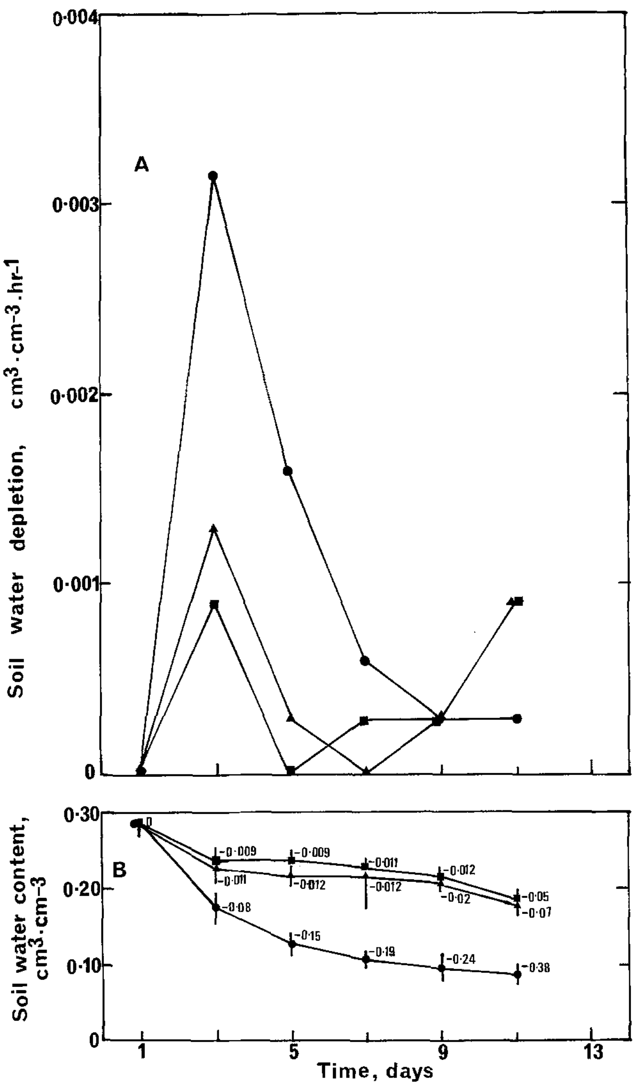

Fig. 8A, B. Soil water depletion rate (**A**) and soil water content and potential (**B**) as a result of water loss by unwatered *Betula* seedlings. Variation in 0–10 cm (●), 10–20 cm (▲) and 20–30 cm (■) soil segments is shown. Numbers indicate soil water potential in MPa. Points are means with standard errors indicated

increase with time in the soil water depletion rate for this layer (Fig. 7). Depletion rate for the upper two layers increased markedly up to 7 days into the experiment, but declined thereafter presumably as a function of soil drying.

During the first 3 days of the experiment, birch seedlings reduced the water content throughout the profile (Fig. 8). The depletion rate was particularly high in the upper 10 cm of soil. Depletion from the soil between 10 and 30 cm in depth was significantly smaller than that exhibited by oak seedlings. Soil in these layers was not dried below −0.07 PMa although the upper layer was dried to −0.38 MPa (Fig. 8).

Discussion

The results of this study confirm the suggestion made by Osonubi and Davies (1978) that oak seedlings may generate low water potentials while maintaining high turgor. Low solute potential combined with high modulus of elasticity means that oak seedlings can, by losing only a small amount of water, generate the low water potentials required to extract water from dry soil. Prestressing acts to increase the sensitivity of solute potential and therefore water potential of oak leaves to decreasing water content, as well as increasing the modulus of elasticity. Both of these changes may therefore be of some advantage to plants growing in areas of limited water availability (Tyree 1976; Roberts and Knoerr 1977).

Jones and Turner (1978) report that when *Sorghum* leaves are subjected to water stress they exhibit a significant increase in modulus of elasticity of cell walls. Interestingly, Elston et al. (1976) have shown an opposite effect of water stress on the leaves of field beans. Wilson et al. (1980) note, however, that a change in modulus of elasticity may not represent a real change in the rigidity of cell walls. These authors argue that small water stress-induced changes in the modulus of elasticity of cell walls of four tropical forage species may not be a function of a change in wall structure but rather a mathematical consequence of a lower solute potential at full turgor and a greater maximum turgor potential. Stress-induced increases in the leaf dry weight/

turgid weight ratio (Table 1) do suggest that water stress may have thickened and therefore stiffened walls of oak and birch leaves. Nevertheless, such an increase in rigidity might have been expected to decrease the water deficit at zero turgor (Wilson et al. 1980) but this was apparently not the case with these leaves (Table 1).

In the experiment where plants were dried over a two week period (Fig. 3) solute potential of oak leaves declined such that leaf turgor was maintained at around 1.0 MPa until after the ninth day of the drying cycle. These results confirmed the results of experiment a) and suggested that net accumulation of solutes must have occurred for turgor to be maintained as leaves dried (Hsiao et al. 1976). Maintenance of leaf turgor was presumably responsible for high leaf conductances exhibited by the unwatered seedlings (Fig. 3). High conductance would allow photosynthesis to continue at a high rate and the resulting photosynthate would be available for continued root growth (Fig. 3). Hsiao and Acevedo (1974) have argued that a slight reduction in leaf turgor may reduce leaf expansion while photosynthesis may continue at a high rate. This combination of events would mean that photosynthate would be available to the roots, both as a substrate for growth and as an osmoregulant, maintaining turgor, the driving force for growth. An increase in root:shoot ratio and a net increase in root growth which are characteristics of water-stressed plants (Sharp and Davies 1979) can both be explained by such a shift in comparative sink strength. At intermediate levels of water stress, oak seedlings may have shown a net increase in the growth of roots (Fig. 3). This was particularly the case deeper in the soil profile (Fig. 5).

Increased root penetration by unwatered oak seedlings was apparent early in the soil drying cycle (Fig. 5). This resulted in a high rate of water extraction from the 10–20 cm soil segment during the first 7 days of the drying cycle and an increasing rate of extraction from the 20–30 cm segement for the last 8 days of the experimental period (Fig. 7). Clearly the utilisation of water deep in the soil core is an important factor contributing to the maintenance of turgor, high leaf conductance and continued growth of unwatered oak seedlings. Depletion rates from the upper 20 cm of soil declined after 7 days drying, presumably as a function of decreasing soil water potentials and increasing resistances to movement across the soil and into the root.

Pressure, volume analysis confirmed the results of Osonubi and Davies (1978) and showed that leaves of birch seedlings have comparatively high solute potentials. This combined with a low modulus of elasticity means that relatively large losses of water are required to generate low water potential and therefore leaves must generally exhibit quite low levels of turgor. Psycrometer measurements confirmed that this was the case (Fig. 4) and that a slow drying treatment rapidly reduced leaf turgor to a negligible level. These results strongly suggest that birch seedlings would not grow successfully in soil that is only moderately dry.

Prestressing treatment increased the modulus of elasticity of birch leaves, meaning that greater reductions in water potential result from a given reduction in water content. Birch leaves also showed some solute accumulation following prestressing (Table 1) but the increase in somotic water percentage coupled with the decline in sensitivity of solute potential to change in water content suggests some stress-induced breakdown of macromolecules and therefore an irreversible effect of water stress. Slow drying experiments failed to detect any solute regulation in birch leaves, with the result that turgor declined rapidly when plants were not watered (Fig. 4).

Well-watered birch seedlings exhibited rates of root extension which were significantly larger than those shown by well-watered oak seedlings. Not surprisingly, in view of the rapidly declining turgor in unwatered seedlings, root growth of birch seedlings did not continue beyond day 5 of the stress cycle. This limitation correlated well with a significant reduction in leaf conductance and therefore presumably with a limitation in photosynthesis. Unwatered plants exhibited no significant root extension into the lower root segments (Fig. 6). Clearly therefore, even well-watered oak seedlings and certainly water-stressed oak seedlings are significantly deeper rooted than comparably sized birch seedlings (Toumey 1929; Holch 1931; Hough et al. 1965).

The very significant root development by birch seedlings in the 0–10 cm soil segment results in a very rapid depletion of soil water in this segment (Fig. 8). The rapid decline in depletion rate after day 3 is presumably a function of declining soil water availability and the build up of a significant resistance to water movement across the interfaces between roots and soil. Although roots of the water-stressed plants did not penetrate the 10–20 cm and 20–30 cm soil segments some water was lost from this soil (Fig. 8), presumably as a result of vertical movement through the profile to areas of low water potential. Despite this movement, soil water potential in the lower 20 cm of soil remained comparatively high. Therefore the reduction in leaf turgor and consequently the reduction in growth occurred despite the comparatively high availability of water deep in the profile.

In Britain, oak and birch trees are commonly found in association. Birch is well-known as a fast-growing pioneer species, rapidly colonising land newly available to trees. As such, this species must show some degree of drought tolerance. Osonubi and Davies (1980) have suggested that this tolerance may be related to a capacity to slow the development of stress which is based upon a high stomatal sensitivity to decreases in atmospheric humidity and increases in plant water stress. Osonubi and Davies (1978) noted that the growth and development of birch seedlings was reduced by comparatively mild stress. This study has shown that even well-watered birch seedlings do not utilize water deep in the profile and therefore survival of seedlings depends upon frequent replenishment of soil water.

Even well-watered birch seedlings exhibit low leaf turgors and therefore this species is susceptible to any factor which decreases turgor. Clearly, dehydration is one such influence, (Fig. 4) as are any factors causing an increase in solute potential. Such increases may occur under low light conditions as a result of reductions in photosynthetic rate and therefore in levels of current photosynthate (Sharp et al. 1978). It is well-known that birch seedlings are very intolerant of shade (Nicholson and Clapham 1975). It seems likely that this intolerance may be based upon the low plant turgor.

In Europe, oak seedlings are recognised as relatively drought tolerant. This is clearly based upon a deep rooting pattern, enhanced by water stress, and an effective use of water available in the soil profile. Growth of roots away from drying soil slows the development of high resistances to water movement across the soil:root interface. A high leaf turgor resulting from low solute potential also contributes to drought tolerance. When soil water is depleted, a high modulus of elasticity means that a lower water potential for further water extraction can be generated with little reduction in water content. Pre-stressing increases the capacity of this species to minimize the effects of witholding water. In association with birch, oak seedlings will effectively compete for water, such that turgor is maintained at low soil moisture potentials and also under low light conditions. Under such conditions, oak will eventually dominate and mixed oak and birch stands will eventually become pure stands of oak.

Acknowledgements. O.O. thanks the Forest Research Institute of Nigeria for financial support.

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Received March 18, 1981