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Willow water uptake and shoot extension growth in response to nutrient and moisture on a clay landfill cap soil

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Abstract

Extension growth of willow (*Salix viminalis* L.) and changes in soil water were measured in lysimeters containing clay and sandy loam soils with different amendment and watering treatments. No water uptake was found below 0.3 m in the nutritionally poor unamended clay; amendment with organic matter to 0.4 m depth resulted in water extraction down to 0.5 m depth whereas in the sandy loam, there was greater extraction from all depths down to 0.6 m. With water stress, wilting of plants occurred when the volumetric soil water content at 0.1 m was about 31% in the clay and 22% in the sandy loam. Compared with shoots on plants in the amended clay, those in the unamended treatment showed reduced extension growth, little increase in stem basal area (SBA) and a small shoot leaf area, resulting from a reduced number of leaves shoot⁻¹ and a small average area leaf⁻¹. Water stress also reduced shoot extension growth, SBA gain and the leaf area on extension growth. Shoot growth rates were significantly correlated with air temperature and base temperatures between 2.0 and 7.6 °C were indicated for the different treatments. These studies have helped to explain some of the large treatment effects described previously on biomass production and plant leaf area.

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Keywords: Lysimeters; *Salix viminalis*; Soil water; Shoot growth; Short-rotation coppice

1. Introduction

Under the Kyoto Protocol, the UK has a target for reducing its greenhouse gas emissions by 12.5% below 1990 levels by 2012. It also has a domestic goal of generating 10% of electricity from renewable resources by 2010. To meet these targets, a range of measures are being adopted, including a major expansion in the planting of biomass crops to provide renewable fuel for generating power and heat (DEFRA, 2004). In the UK, willow (*Salix* spp.) grown as short-rotation coppice (SRC) is one of the most widely grown of these crops. In view of the relatively low value of biomass, the importance of reducing input costs and adding value by using willow for additional purposes, like

land restoration and remediation, has frequently been stressed (Paulson et al., 2003; Rosenqvist and Dawson, 2005). Post-closure, landfill sites are often under-utilised and SRC offers a potentially attractive option for the subsequent management of these sites (Nixon et al., 2001), particularly if combined with a landfill leachate remediation system (Martin and Stephens, 2006b; WRc, 2002).

In spite of the potential attractions of growing SRC on such sites, many are located on impermeable clay soils, like Oxford clay (Batchelder et al., 1998), which drain poorly and are low in nutrients and organic matter. Moreover, they have restricted reserves of soil water because of the limited depth of the restoration cap which is also often heavily compacted during construction (Bending et al., 1999; Dobson and Moffat, 1993). Oxford clay occurs in one of the driest parts of the UK and SRC established on such sites is likely to yield poorly because of both poor soil conditions and water stress. Compared with the

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amount of data available for willow growing under more favourable conditions, there is little quantitative data on biomass production, dry matter partitioning and water use by willow growing on heavy soils like Oxford clay and on how this is affected by water stress (Nixon et al., 2001). Obtaining such data is a crucial first stage in indicating the potential of SRC systems in such locations and it was to fill this knowledge gap that the research described in two previous papers (Martin and Stephens, 2006a,b) was undertaken.

In this paper, we describe the effects of the different soil and watering treatments on soil water, shoot growth and leaf development. The objectives of this research were to provide soil water measurements to characterise the watering treatments and to investigate some of the seasonal treatment effects described in the two previous papers at the shoot level over shorter time periods.

The economically important component of willow grown for biomass is the stem which is normally harvested in the winter after leaf-fall. Stem dry mass is closely related to both stem length and diameter and regressions of the product of length and the square of diameter account for about 99% of stem dry mass in willow (Hytönen et al., 1987). Shoot growth is not only important for accumulating biomass but also because shoot extension is accompanied by leaf emergence and, therefore, canopy development. Although several studies have reported changes in stem height or diameter over entire growing seasons or rotations (Cogliastro et al., 2001; Hofmann-Schielle et al., 1999; Labrecque and Teodorescu, 2001; Rytter, 2001), we know of no published studies of factors affecting short-term willow shoot growth, in spite of the obvious importance of this for stem biomass production and growth-modelling (Ceulemans et al., 1996). The most important factors affecting shoot growth are likely to be temperature, radiation and daylength (Ceulemans et al., 1996; Kirby, 1995; Jame et al., 1998), water availability (Kozłowski, 1982) and nutrition (Cannell, 1988).

In Sweden, the start and end of the willow growing season has been defined, respectively, as four consecutive days above and below 5 °C (Perttu, 1983). This temperature was also adopted as the base for calculating thermal time by Cannell et al. (1987) who found that leaf area development in willow was a function of thermal time. Their growth model also showed that a rapid development of leaf area early in the season is especially important for maximising radiation interception and biomass production. Porter et al. (1993) showed a positive and significant correlation between the rate of leaf production in willow and temperature, but only up to 14 °C. We have analysed our own shoot growth data in relation to thermal time and present data demonstrating a significant correlation between temperature and shoot growth, even in the middle of the growing season.

2. Methods

Details of the experiment were given in Martin and Stephens (2006a,b). A summary is presented below together

with additional information relating to the soil water and shoot growth studies.

2.1. Site and treatments

Single willow plants (*Salix viminalis* “Jorr”) were planted as cuttings in April 1999 in lysimeters (0.54 m in diameter and 0.9 m deep) at Cranfield University in Bedfordshire, UK (52°N, 0.3°W, at 60 m altitude). Plants were cut back in November 1999 and all the investigations reported here were undertaken in 2001 when plants were in their third year of growth and stems in their second year.

The experiment investigated three Oxford clay soil treatments, simulating different landfill cap conditions: (i) compacted soil (1480 kg m⁻³), S1; (ii) soil cultivated to reduce its bulk density (1270 kg m⁻³), S2 and (iii) cultivated soil (1200 kg m⁻³) improved by the addition of organic matter and fertiliser, S3. For comparison with better growing conditions, a sandy loam soil (Cottenham series) treatment (S4) was included using the same amendments and bulk densities as S3. Biogran (Swiss Combi Technology) was used as the soil amendment and was mixed into the top 0.1–0.4 m of soil of the S3 and S4 treatments at a rate equivalent to 200 t ha⁻¹. This product contains about 50% organic matter, 3.3% total nitrogen, 4.4% total phosphorous (as P₂O₅) and 0.2% potassium (as K₂O). There was a 0.1 m depth of gravel at the bottom of each lysimeter, on top of which a 0.7 m depth of experimental soil was placed. In 1999 and 2000, single applications of nitrogen were made to treatments S3 and S4 at a rate of 200 kg N ha⁻¹. In 2001, N, P and K fertilisers at 300, 150 and 90 kg ha⁻¹, respectively, were applied to treatments S2, S3 and S4 to improve the nutritional status of these soils. At this stage, it was apparent that the lower bulk density of the S2 treatment had resulted in only a small, non-significant improvement in plant growth compared with the S1 treatment and so a fertiliser application was made to this treatment to see if this would improve growth.

During the growing seasons, soil water was measured on most days in the lysimeters with a Diviner capacitance probe (see Section 2.4). During 1999 all lysimeters were well-watered but, starting from 2000, one plant per replicate in each soil treatment was subjected to cycles of water stress while the other continued to be well-watered. In the unstressed treatment, threshold soil water contents corresponding to a soil water potential of -0.05 MPa at 0.2 m depth were used for watering. These were identified from soil water release curves as corresponding to a volumetric soil water content (θ_v) of 47% for the clay and 27% for the sandy loam. Lysimeters in the unstressed treatment were watered on the days that these thresholds were reached at 0.2 m.

Moisture stress was imposed on the stress treatment by allowing the soil water to drop to wilting point before re-watering. Wilting point was determined visually as the point when the majority of leaves on a plant started to droop. In 2001, plants were normally watered on the third

day of wilting, except over one drying cycle in mid- to late-July during which stressed plants in the S2, S3 and S4 treatments were maintained at low values of θ_v for longer periods (6–9 days) to allow shoot growth measurements to be made under more protracted water stress conditions. During this period, catastrophic wilting and defoliation of S3 and S4 plants was prevented by adding small quantities of water (up to 4 l day^{-1}) to these lysimeters at the ends of days when plants appeared particularly stressed. On the completion of each drying cycle, water was added to each lysimeter to return the soil to saturation and the soil was maintained at a high soil water content for several days before starting a new cycle of stress. Since rainwater could not be prevented from entering the lysimeters, the moisture stress treatment could only be imposed during rain-free periods. During 2001, six cycles of soil drying were imposed on the S3 and S4 treatments but only three could be imposed on plants in the S1 and S2 treatments because they used water more slowly and drying cycles were more often interrupted by rain. In figures and tables the two watering treatments are referred to as NS (no stress) and S (stress).

The experiment used a randomised complete block design with three replicates. In each replicate, there were 8 lysimeters, one for each of the 8 treatments ($4 \text{ soils} \times 2 \text{ watering regimes}$).

2.2. Soil characteristics

Soil particle size analysis showed that the unamended Oxford clay contained 5% sand, 43% silt and 52% clay compared with 75% sand, 13% silt and 12% clay in the unamended sandy loam. Soil water release curves for the four soil treatments were determined from soil samples collected in density rings (20 mm deep by 54 mm in diameter) at 0.03 m depth. Curves were determined by a combination of sand table (for water potentials of -0.002 , -0.004 , -0.006 and -0.008 MPa) and pressure membrane techniques (for water potentials of -0.1 , -0.2 , -0.4 , -0.8 and -1.5 MPa) (Smith and Thomasson, 1982). At each water potential, the volumetric soil water content (θ_v) was determined on 3 soil samples. θ_v is defined as the volume of water per unit bulk volume of soil:

$$\theta_v = \text{Volume of water (m}^3\text{)}/\text{volume of dry soil (m}^3\text{)} \quad (1)$$

In this paper θ_v has then been converted to a percentage. Fig. 1 shows soil water release curves for soil from the S3 and S4 treatments. From these, the available water capacities (from -0.005 to -1.5 MPa) were 245 mm m^{-1} for the Oxford clay and 202 mm m^{-1} for the sandy loam. Water release curves for soil from the S1 and S2 treatments were very similar to those of the S3 treatment.

2.3. Shoot growth measurements

During the 2001 growing season, stems on plants in the S1, S2, S3 and S4 treatments had maximum lengths of 2.5,

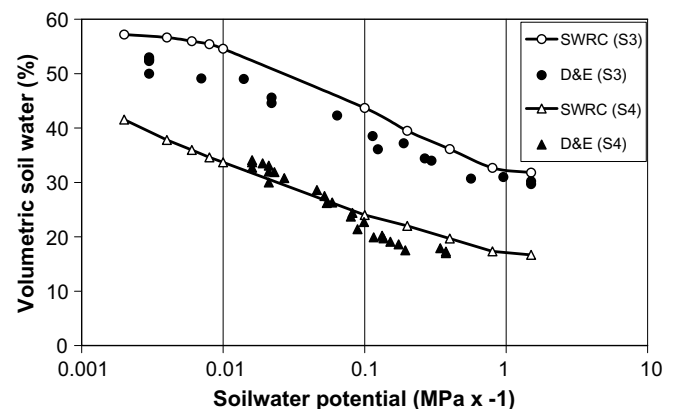


Fig. 1. Laboratory soil water release curves for Oxford clay (SWRC (S3)) and Cottenham series sandy loam (SWRC (S4)) soils compared with lysimeter-derived data (D&E (S3) and D&E (S4)) for θ_v and ψ measured with a Diviner and Equitensimeters, respectively.

3.0, 3.6 and 3.8 m, respectively, and the detailed measurements in these studies required the use of either a ladder or mobile scaffolding as the soil surface in the lysimeters was an additional 1.0 m above ground level. Shoot growth studies were performed on two groups of stems. Group 1 stems were two randomly selected stems from the tallest ten on each plant and were used for short-term growth measurements between 5 June and 25 July 2001.

On each stem, the length of that season's extension growth was measured on the leading shoot. This was defined as the distance from the end of the previous season's growth to the tip of newly expanding leaves at the end of the shoot and was measured at 3–4-day intervals. On the same day, the diameter of each stem was measured 0.1 m from the base using digital callipers (Camlab, Cambridge). To reduce errors, the location of measurement was marked on the stem with indelible ink and the callipers were held at right angles to the longitudinal axis of the stem during measurements. Shoot extension growth and diameter measurements were all made between 09:00 and 11:00 h.

For analysis, diameters were converted to stem basal areas (SBAs), assuming that each stem had a circular cross section. For stems in the S3 and S4 treatments, rates of change in SBA were investigated over three phases of the cycle of water stress: (i) pre water stress – when θ_v at 0.1 m was similar in stressed and unstressed lysimeters (5–19 June); (ii) water stress – when θ_v at 0.1 m was considerably lower in stressed than unstressed lysimeters (20 June to 1 July); and (iii) post re-watering – when θ_v at 0.1 m was similar in stressed and unstressed lysimeters (2–12 July).

To allow for differences in size between the stems, the relative rate of increase in SBA (RSBA) over each period was calculated for each stem by expressing the increase in SBA per unit of its SBA at the start of the period:

$$\text{RSBA} = ((\text{SBA}_2 - \text{SBA}_1)/(\text{SBA}_1)) \times (1/(t)) \text{ mm}^2 \text{ mm}^{-2} \text{ d}^{-1} \quad (2)$$

where SBA_1 and SBA_2 are for the start and end of each period, respectively and t is the number of days in each period.

A separate group of 6 stems treatment⁻¹ was measured at monthly intervals to provide data on stem leaf area (Martin and Stephens, 2006a) and data from the 2001 extension growth of these stems (group 2 stems) were used to complement those from group 1 stems. These data were length of 2001 extension growth, number of emerged leaves and average area leaf⁻¹. A leaf was considered to have emerged when it was free from other leaves around the growing point. Average area leaf⁻¹ was calculated from leaf area measurements determined for every tenth leaf along the extension growth or, where this would have been fewer than 5 leaves, from a minimum of 5 leaves shoot⁻¹ selected at regular intervals along the extension growth. Area was calculated by measuring leaf length (from the tip to the base of the lamina) and width (at the widest point) and using the linear regression of Martin and Stephens (2006a):

$$A = 0.729(LW) \quad (3)$$

Where A is area (cm²), L is length (cm) and W is width (cm).

To relate shoot and leaf growth to temperature, thermal time (°Cd) was calculated as the sum of average daily temperatures above a 5 °C base temperature. A start date of April 1 was used which was when shoot growth started at the trial. Meteorological data came from the Cranfield University Silsoe meteorological site, about 200 m from the lysimeters.

2.4. Soil water measurements

In March 2001, a single Diviner access tube was installed in every lysimeter, halfway between the willow stump and the wall of the lysimeter, leaving a minimum of 0.1 m of soil between the edge of the access tube and the edge of the lysimeter. This would have been adequate for accurate soil water measurements because 99% of the Diviner's response is within 0.1 m of the wall of the access tube (Paltineanu and Starr, 1997). Access tubes were driven into a hole augured slightly smaller than the diameter of the tube. Readings were taken every 0.1 m from 0.1 to 0.6 m depth, between 07:30 and 09:00 h. Data for θ_v are either presented for individual depths which are specified, or as the average over all measurement depths in the lysimeters ($L\theta_v$). Values of θ_v obtained at each depth were assumed to reflect the value of θ_v in the 0.1 m layer of soil above that depth.

The Diviner manufacturer's calibration equation was used to calculate θ_v :

$$SF = a(\theta_v^b) + c \quad (4)$$

Where a is 0.2746, b is 0.3314, c is 0 ($r^2 = 0.998$) and SF is scaled frequency:

$$SF = (Fa - Fs)/(Fa - Fw) \quad (5)$$

Where F_s is the sensor reading in soil and F_a and F_w are the sensor readings in an access tube located in air and water, respectively.

For some investigations, Diviner values of θ_v were used to calculate the volume of water in the 0.1 m layer of soil above the depth of the measurement:

$$V_w = \theta_v V_s \quad (6)$$

Where V_w is the volume of water (cm³) and V_s is the volume of soil (cm³). For all depths at which θ_v was measured, V_s was calculated as a cylinder with height 10 cm and diameter equal to the diameter of the lysimeter soil core (54 cm).

To compare Diviner θ_v readings with soil water potential (Ψ , MPa), one Equitensiometer (Type EQ1, Delta-T devices, Cambridge, UK) was installed between 20 July and 20 August 2001 at 0.1 m depth in each of one S3 and S4 lysimeter and Ψ recorded daily immediately after taking the Diviner readings.

2.5. Data analysis

Data were analysed using Genstat 5 – Release 4.1 (NAG Ltd, Oxford). For extension shoot length and SBA from group 1 shoots, a mean value was determined for the two stems measured plant⁻¹ and plant means were analysed by a two-way ANOVA in randomised blocks. Data from group 2 shoots were analysed by a two-way ANOVA using a randomised block design but it was not possible to use the underlying experimental design of the lysimeters because not all lysimeters had shoots which were accessible from the mobile scaffolding. For these stems, blocking was based upon a ranking of stem length at the end of the 2000 growing season – this ensured that stems of the same relative vigour were compared with each other. Where data are presented for repeated measurements made over a period of time, separate ANOVAs were performed on the data from each measurement occasion. In ANOVAs, the statistical significance of the effect of soil, watering regime and their interaction was determined from F ratios while that between treatment pairs was tested with the Student t-test using the appropriate standard error of the difference between means. A 5% significance level was adopted for identifying significant treatment effects.

3. Results

3.1. Soil water

To compare Diviner θ_v measurements with the water release characteristics of the experimental soils, θ_v values recorded at 0.1 m depth for S3 and S4 soils in July and August 2001 were plotted against the corresponding values of Ψ measured with Equitensiometers and are shown in Fig. 1 with the soil water release curves for these soils. For the values of Ψ recorded with the Equitensiometers,

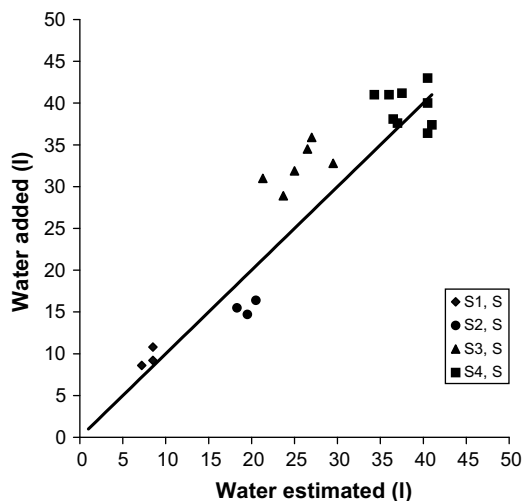


Fig. 2. Comparison of the amount of water added to lysimeters in the stressed soil treatments on re-watering and the amount estimated from soil water measurements with the Diviner. Points are for individual lysimeters and the line shown is the 1:1 line. Data are only presented for drying cycles which were not affected by rain.

all the Diviner θ_v values in the clay and those below a Ψ of about -0.1 MPa in the sandy loam were lower than expected from the soil water release curves by about 8–10%. At large negative matric potentials this may have resulted, in part, from the rate of change in θ_v being faster than the response time of the equitensiometers, particularly in the sandy loam.

The number of drying cycles during 2001 varied between treatments because of differences in plant leaf area and water use which resulted in shorter, more frequent cycles for the largest plants (S4 and S3 treatments) and fewer but longer cycles for the smallest plants (S2 and especially the S1 treatment). The most accurate measurements of water use by stressed plants were obtained during a small number of drying cycles which were not affected by rain (two for S3 and S4 treatments and one for S1 and S2 treatments). For these, the increase in soil water estimated from the Diviner measurements of θ_v on re-watering was compared with the amount of water added during watering (minus the quantity collected as drainage on the following day; Fig. 2). For calculating the change in soil water in the S2, S3 and S4 treatments which all had roots down to the gravel layer of the lysimeters, it was assumed that θ_v at 0.7 m was the same as at 0.6 m and that, by the end of a drying cycle, all the water had been extracted from the gravel layer (0.7–0.8 m depth, 50% pore space). For the S1 treatment, in which plants had very few roots below 0.3 m, the comparison was based solely on the changes in θ_v between 0 and 0.6 m. Compared with the 1:1 line, the agreement is reasonable and the average estimated values of water added for treatments S1, S2, S3 and S4 were 85%, 125%, 78% and 97%, respectively of the actual values.

On re-watering the water stress treatments during 2001, considerably more water had to be added to lysimeters in

the S4 sandy loam treatment (c. 40 l) than to those in the S3 clay (c. 30 l). Diviner readings showed that this resulted from considerable quantities of soil water being removed from all depths in the sandy loam (Fig. 3d) while in the clay little was removed from the bottom of the profile and most was removed from the top (Fig. 3c). Thus, in the sandy loam, 36% of the water extracted from the top 0.6 m of the profile by 17 September came from 0–0.2 m depth, 35% from 0.2–0.4 m and 29% from 0.4–0.6 m. This compares with figures for the S3 treatment of 50% from 0–0.2 m, 33% from 0.2–0.4 m and 17% from 0.4–0.6 m. The same trend was seen in the other clay treatments with 85% (S1) and 88% (S2) of the water extracted by the end of the stress periods in Fig. 3 coming from 0–0.2 m depth. In all treatments, soil water was extracted first from the upper soil layers and then from the lower ones.

Within a given treatment, stressed plants tended to wilt at a similar θ_v . In treatments S2 and S3 this occurred when θ_v at 0.1 m was about 31% and in treatment S4 this was at about 22%. Re-watering was normally followed by leaf yellowing and some defoliation of the oldest leaves.

3.2. Effects of soils, watering regime and temperature on shoot growth

Table 1 shows the average increase in length of group 1 shoots by soil and watering regime over the period of the shoot studies. The main effect of soil on extension growth was significant and can be attributed to the shorter growth in the S1 than in the S2 and S4 treatments. Similarly, the main effect of watering regime was significant and resulted from shorter extension growth in all the stressed soil treatments but particularly in S2 and S1. Within the soil treatments, water stress reduced extension growth by between 10% (S4) and 33% (S2).

An initial analysis of shoot extension rates of unstressed plants over all the 2–3-day measurement periods during the study showed considerable variation although a significant part of this could be attributed to temperature. Thus, for each soil treatment linear regressions of the average shoot extension rate over each measurement period on the average daily temperature of the period accounted for 52%, 66%, 51% and 47% of the variation in shoot extension rate in treatments S1, S2, S3 and S4, respectively (Table 2). There were significant differences between the slopes and intercepts of the lines, however. The intercept value on the x -axis for the 4 lines varied from 2.0 °C (S2) to 7.6 °C (S1) and had an average of 2.8 °C. Since this was not substantially different to the 5 °C base temperature used in other studies (Cannell et al., 1987; Perttu, 1983), the latter temperature was adopted and shoot extension was therefore corrected for this by dividing by the number of day degrees above a 5 °C base temperature in each measurement period. Averaged over the 15 measurement periods of the study, temperature corrected shoot extension rates for the S1, S2, S3 and S4 treatments were 0.37, 0.62, 0.46 and 0.46 mm (°C > 5 d)⁻¹, respectively.

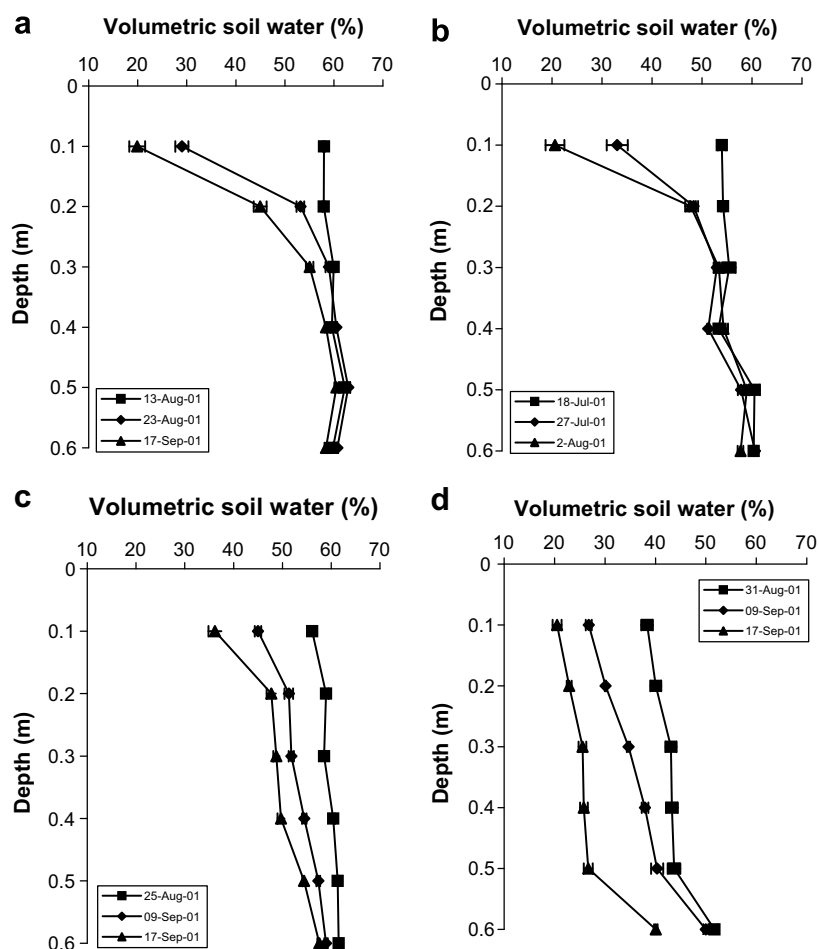


Fig. 3. Variation in θ_v with depth in lysimeters containing plants in the stressed watering regime of soil treatments S1 (a), S2 (b), S3 (c) and S4 (d) at the beginning, middle and end of a drying cycle in August–September 2001 (S1, S3 and S4) and during July–August (S2). Bars indicate the s. e. of the mean ($n = 3$).

Table 1
The effect of soil and watering regimes on the increase in length shoot⁻¹ (mm) and stem basal area shoot⁻¹ (SBA; mm²) of main shoots on stressed and unstressed plants between 5 June and 28 July 2001

Treatment ^a	Increase in length (mm) ^a		Increase in SBA (mm ²) ^a	
	NS	S	NS	S
S1	199	138	5.2	2.2
S2	295	199	109.2	60.3
S3	203	167	87.9	33.9
S4	221	199	109.2	49.7
SED ^b	17.8		10.3	

Probability levels of *F* ratios for treatment main effects and interactions

Soil	0.004	<0.001
Watering regime	<0.001	<0.001
Soil × watering regime	0.29	0.06

The top part of the table shows treatment means and the bottom part shows the significance of treatment main effects and interactions.

^a Soil treatments are indicated by S1, S2, S3 and S4. NS and S indicate the non-stressed and stressed watering regimes, respectively.

^b Standard error of the difference between treatment means with 14 degrees of freedom.

Table 2
Linear regression equations for the average rate of shoot growth (mm d⁻¹) on average air temperature (°C d⁻¹) for unstressed plants in different soil treatments over 2–3-day periods ($n = 15$) between 5 June and 28 July, 2001

Treatment	Equation	SE slope	SE intercept	<i>r</i> ²	df
S1	$y = 0.45x - 3.15$	0.12	2.01	0.52	13
S2	$y = 0.48x - 0.98$	0.10	1.61	0.66	13
S3	$y = 0.39x - 1.29$	0.10	1.67	0.51	13
S4	$y = 0.29x + 0.32$	0.09	1.43	0.47	13

For each measurement period, temperature corrected shoot extension rates, S_t , were then compared with average θ_v measured with the Diviner. For stressed plants in the three clay treatments, S_t was more highly correlated with θ_v averaged over 0.1 and 0.2 m than with θ_v at any single depth or combination of depths. For these plants, simple linear regressions of S_t on the average θ_v over these depths accounted for 35% (S1) and 67% (S2 and S3) of the variation in S_t . The equations are given in Table 3 together with that for the S4 treatment, for comparison. In the latter,

Table 3

Linear regression equations for temperature corrected rates of shoot growth ($\text{mm } (^\circ\text{C} > 5 \text{ d})^{-1}$) on θ_v averaged over 0.1 and 0.2 m for stressed plants in different soil treatments over 2–3-day periods ($n = 15$) between 5 June and 28 July 2001

Treatment	Equation	SE slope	SE intercept	r^2	df
S1	$y = 0.01x - 0.20$	0.01	0.18	0.35	13
S2	$y = 0.04x - 1.25$	0.01	0.33	0.67	13
S3	$y = 0.04x - 1.63$	0.01	0.38	0.67	13
S4	$y = 0.04x - 0.91$	0.01	0.22	0.72	13

however, S_t was most highly correlated with θ_v averaged over all six depths and the equation for this line was $y = 0.04x - 1.08$ ($r^2 = 0.81$; s.e. of the slope, 0.01; s.e. of the intercept, 0.20; df 13).

Fig. 4a and b show changes in S_t and θ_v at 0.1 m for plants in the S2 and S4 soil treatments, respectively, during a drying cycle in June and July. For each soil, separate ANOVAs were performed for each measurement period on the data from the 6 shoots in each water stress treatment. In the S4 treatment, when θ_v of both stressed and unstressed plants was high at the start (13–20 June) and end (1–8 July) of the cycle, there were no significant differences in S_t but between 20 June and 1 July, when θ_v

dropped to about 25% in the stressed treatment, S_t was significantly lower in this treatment. Similarly for the S2 treatment, with high θ_v at the start (10–20 June) and end (12–25 July) of the drying cycle, there were no significant differences in S_t but between 20 June and 12 July, when θ_v was below about 30%, S_t was significantly lower in stressed plants. After watering, S_t of stressed plants recovered quickly to similar levels as that of unstressed plants and, in fact, it was often higher than that of unstressed plants in the 3–6 days after removing stress.

There was a very significant main effect of soil and watering regime on SBA (Table 1). The increase in SBA in the S1 treatment was significantly less than in the other treatments and in the S3 treatment was significantly less than in the S2 and S4 treatments. Water stress significantly reduced the gain in SBA of stressed plants in the S2, S3 and S4 soil treatments. Changes in SBA over 3–4-day periods were small, however, and could not reliably be analysed in the same way as the stem length data.

Using time course plots of soil water as a guide, three periods were identified for the S3 and S4 treatments corresponding to (i) pre water stress (5–20 June); (ii) water stress (20 June to 1 July); and (iii) post re-watering (1–12 July). There were no differences between treatments in RSBA

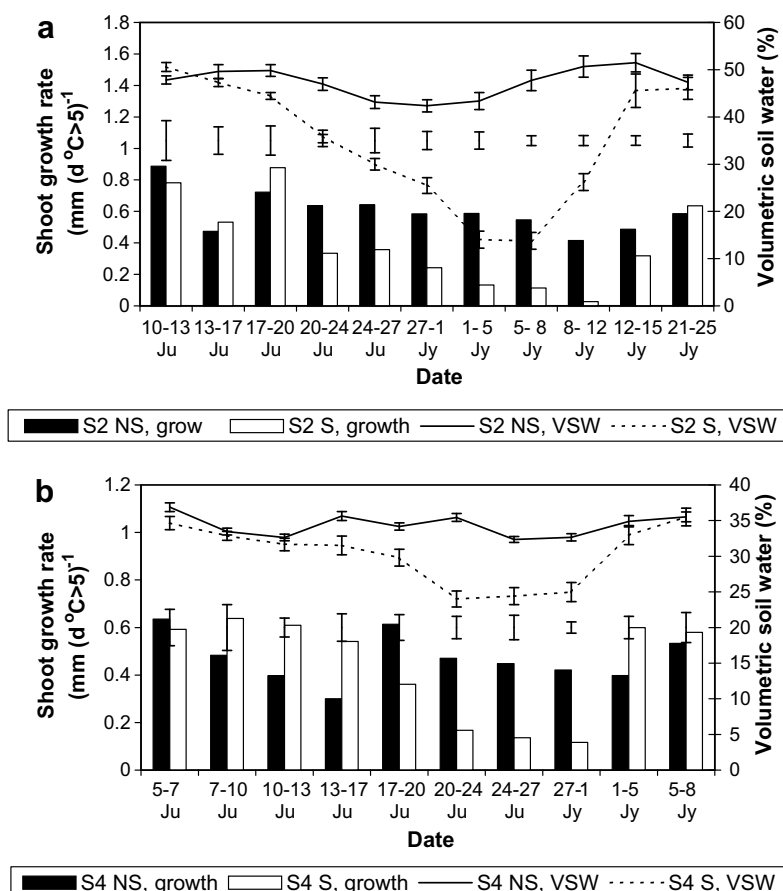


Fig. 4. S_t and θ_v at 0.1 m for stressed and unstressed plants growing in Oxford clay (S2 treatment) from 10 June to 25 July (a) and a sandy loam (S4 treatment) from 5 June to 8 July (b). Bars for θ_v indicate the standard error of each average ($n = 3$). The lowest line of bars represent the SED between S_t values in each measurement period (8 df).

Table 4

Average relative rates of increase in SBA (RSBA; $\text{mm}^2 \text{mm}^{-2} \text{d}^{-1}$) for unstressed (NS) and stressed (S) plants in the soil treatments S3 and S4 during 3 phases of the stress cycle: (i) prior to water stress (5–20 June); (ii) during water stress (20 June to 1 July) and (iii) after water stress (1–12 July)

Soil treatment	5–20 June		20 June to 1 July		1–12 July	
	NS	S	NS	S	NS	S
S3	0.67	0.56	0.64	0.03	0.53	0.61
S4	0.65	0.82	0.89	0.07	0.66	0.58
df	6		6		6	
SED	0.22		0.14		0.14	
<i>Probability levels of F ratios for treatment main effects and interactions</i>						
Soil	0.46		0.18		0.61	
Watering regime	0.83		<0.001		0.97	
Soil × watering regime	0.38		0.31		0.44	

The top part of the table shows treatment means and the bottom part shows the significance of treatment main effects and interactions.

before or after the water stress period but there was a very significant reduction in the RSBA of stressed plants during the water stress period (Table 4). During this period, the θ_v at 0.1 m averaged 32% and 24% in stressed lysimeters of the S3 and S4 treatments, respectively, compared with 52% and 33% in unstressed lysimeters of the same treatments. A similar trend was found with the S2 treatment but this could not be included in the analysis with the S3 and S4 treatments because it was at a different stage in its drying cycle. The very small increase in SBA in the S1 treatment prevented similar analysis for this treatment.

3.3. Effects of soil and watering regime on extension growth leaf development

The effects of treatments on number of leaves shoot^{-1} , average area leaf^{-1} and leaf area shoot^{-1} on the 2001 extension growth of group 2 shoots are shown in Table 5. There was a significant main effect of soil on all variables while watering regime affected number of leaves and leaf area shoot^{-1} . Number of leaves shoot^{-1} was significantly lower in the S1 treatment and higher in the S4 treatment than in the other soil treatments and was reduced in all soil treatments by stress. Average area leaf^{-1} was significantly smaller in the S1 treatment and larger in the S2 and S4 treatments than in the other treatments. Apart from in the S3 soil treatment, average area leaf^{-1} was less in all stress treatments although this was only significant in the S4 treatment. Leaf area shoot^{-1} was significantly higher in the S4 and S2 than in the other soil treatments. In all soil treatments, except the S3, it was reduced by stress.

At the end of July, when leaf number was at about its maximum and extension growth had almost ceased, there were highly significant linear correlations between the number of leaves on the extension growth and the length of this growth so that length accounted for 67%, 65%, 83% and 81% of the variation in leaf number in treatments S1, S2, S3 and S4, respectively. These relationships were signifi-

Table 5

Number of leaves shoot^{-1} , average area per leaf and leaf area shoot^{-1} on 2001 main shoot extension growth of unstressed (NS) and stressed (S) plants in different soil treatments (S1, S2, S3 and S4) at the end of July 2001

Soil treatment	Number of leaves shoot^{-1}		Average area leaf^{-1} (cm^2)		Leaf area shoot^{-1} (cm^2)	
	NS	S	NS	S	NS	S
S1	26.8	23.8	5.9	5.1	156.0	122.2
S2	34.0	27.3	11.1	9.5	379.4	264.6
S3	33.3	30.8	7.2	8.1	250.7	266.2
S4	43.5	34.5	11.4	8.3	503.5	292.7
df	35		35		35	
SED	2.1		0.7		40.3	

Probability levels of F ratios for treatment main effects and interactions

Soil	<0.001	<0.001	<0.001
Watering regime	0.01	0.08	0.04
Soil × watering regime	0.58	0.31	0.22

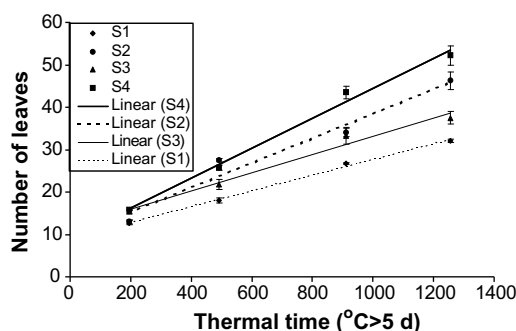


Fig. 5. The number of leaves on main shoot extension growth of leading shoots of unstressed willow plants in relation to thermal time from April 1 2001. Equations for the lines were: S1 ($y = 0.02x + 9.18$); S2 ($y = 0.03x + 9.41$); S3 ($y = 0.02x + 11.60$); S4 ($y = 0.04x + 9.04$). Bars indicate the standard error of means.

cantly affected by soil treatments but there was no interaction with stress.

There was a linear increase in leaf number with thermal time (Fig. 5) calculated from April 1 using a base temperature of 5 °C. This shows clearly the low rate of leaf emergence for the S1 treatment.

4. Discussion

Changes in θ_v with soil depth (Fig. 3) during water stress reflected the distribution of root dry mass at harvest in November 2001 (Martin and Stephens, 2006a). Nutritionally deprived plants on Oxford clay (S1) had few roots below 0.3 m and the measurements of θ_v showed them to be largely dependent on water above this depth. Plants in the S2 treatment showed a very similar pattern of water extraction, even though the top-dressing of fertiliser in 2001 resulted in a 4-fold increase in root dry mass and about a 2-fold increase in water use (Martin and Stephens, 2006b) over S1 plants. Although the effect of applying a top-dressing of fertiliser to the S2 treatment was only

monitored over a single growing season, the data suggest that it did not substantially improve the ability of S2 plants to extract water at depth.

Amendment of Oxford clay with biogran (S3) improved root growth down to the depth of the amendment (0.4 m) and below this in the stressed treatment, but there was less root growth and water uptake below this depth than occurred in the similarly amended sandy loam soil (S4) in which larger amounts of water were extracted from all depths. In other crops, it has been shown that improved nutrition has resulted in greater water uptake and allowed the extraction of water from a greater depth in the profile (Pandey et al., 2000; Eghball and Maranville, 1993). The suggestion from these results is that without amendment of Oxford clay with organic matter (and probably also fertiliser), willow will have shallow root systems which will limit growth and make it susceptible to water stress. While soil amendment with organic matter and fertiliser can dramatically improve growth, the data suggest that beneficial effects in terms of increasing water availability are likely to be restricted, at least in the short-term, to about the depth of the amendment. Although needing confirmation, the data indicated that top-dressing Oxford clay without incorporating organic matter may not be as effective at improving rooting depth as using both practices.

In the S2 and S3 treatments, wilting occurred when θ_v at 0.1 m was about 31% whereas in the sandy loam it occurred at about 22%. From the soil water release curves and the Equitensimeter readings, these points correspond to soil water potentials of about -1.5 MPa in the clay and -0.2 MPa in the sandy loam. It was not possible to define these points accurately, however, as variations occurred within the water release curves and at the dry end of the curve, small differences in soil moisture equate to large changes in soil water potential. It is likely that wilting occurred at a higher (less negative) water potential at 0.1 m in the sandy loam than in the clay because water was rapidly depleted throughout the whole profile in this treatment and rates of evapotranspiration (ET) were high ($13.61 \text{ day}^{-1} \text{ plant}^{-1}$ in mid-July). In contrast, all the clay treatments had access to water at considerably higher water potentials at the bottom of the rooting zone and lower rates of ET – 1.2, 3.0 and $7.31 \text{ day}^{-1} \text{ plant}^{-1}$ in mid-July for the S1, S2 and S3 treatments, respectively. The combination of a water reserve at the bottom of the rooting zone and a particularly low demand for water ($0.91 \text{ day}^{-1} \text{ plant}^{-1}$ by mid-September) may explain the lack of wilting by plants in the S1 treatment in mid-September, even though θ_v at 0.1 m was below the level at which wilting occurred in the other clay treatments (Fig. 3a).

It was previously suggested (Martin and Stephens, 2006a) that the poor growth of plants in the S1 treatment resulted from inadequate nutrition, as no fertiliser was added to this treatment and soil analyses showed that Oxford clay had particularly low levels of N and P. The effects of this at the shoot level can be seen by comparing the S1 and S2 treatments, as the growth of plants in these

treatments was very similar up to April 2001, when the S2 treatment received a first application of N, P and K. Poor nutrition (S1) was characterised by reduced extension growth, little increase in SBA (Table 1) and a small shoot leaf area (Table 5), resulting from a low number of leaves shoot^{-1} and a very small average area leaf^{-1} . All of these variables were significantly larger in the S2 treatment, resulting in large visual differences between the two treatments which had not been apparent in 1999 and 2000 and which were not indicated by any of the growth measurements made in those years. The effect of improved nutrition (usually including nitrogen) on increasing plant leaf area and/or leaf area index is well-documented for trees as well as other plants (Cannell, 1988; Eck, 1984; Fircks et al., 2001; Pandey et al., 2000) and others have also related this to increases in leaf number (Liu and Dickmann, 1992) and/or leaf size (Heilman and Xie, 1994; McDonald, 1989). Over the growing season, improved nutrition can also increase radiation interception by plant canopies by promoting early-season leaf growth and/or prolonging leaf growth at the end of the season (Cannell, 1988; Ericsson et al., 1996; Fircks et al., 2001).

Martin and Stephens (2006a) suggested that the growth of unstressed plants in the S3 treatments may have been constrained by waterlogging, resulting from over-watering. There is further evidence for a constraint on growth in this treatment from the present study in which increase in shoot length and SBA (Table 1), number of leaves shoot^{-1} , average area leaf^{-1} and leaf area shoot^{-1} (Table 5) were all low in the unstressed S3 treatment compared with the S2 and S4 treatments which received similar amounts of mineral fertiliser in May 2001. In poplar, Liu and Dickmann (1992) found that waterlogging had a similarly adverse effect on leaf area development as drought under both high and low nitrogen regimes and adverse effects on growth have been described for a wide range of forest trees (Kozłowski, 1986). This suggests that use of a leachate irrigation system with willow on Oxford clay would require careful monitoring of soil water to prevent soil waterlogging adversely affecting growth and water uptake.

Water stress was shown to significantly reduce willow shoot extension growth (Table 1). Stress also reduced the leaf area on extension growth, principally because leaf number was highly correlated with shoot length but also because area leaf^{-1} was often reduced (Table 6). Water stress has frequently been reported to reduce plant leaf area or leaf area index (Braatne et al., 1992; Cannell, 1988; Gholz et al., 1990; Ogbonnaya et al., 1998; Souch and Stephens, 1998) and reductions in both leaf number (Liu and Dickmann, 1992) and leaf size (Chartzoulakis et al., 2002) have been demonstrated. With severe stress, premature leaf senescence and abscission occurs (Kozłowski, 1982). It is not clear from the present study whether defoliation or a slower rate of leaf emergence was the more important factor in contributing to the lower number of leaves on the extension growth of stressed plants. In studies combining nutritional and water stress treatments, improved nutrition

has usually resulted in larger increases in leaf area development and growth in the absence of water stress than with it. This can also be seen in the present study by comparing stressed and unstressed plants in the nutritionally poor S1 treatment and the nutritionally improved S2 treatment (Table 5). Here, in the absence of water stress, improved nutrition (S2) caused a 26% increase in leaf number shoot⁻¹, an 88% increase in area leaf⁻¹ and a 143% increase in leaf area shoot⁻¹ compared with the unstressed S1 treatment. With water stress, improved nutrition caused smaller increases (15% for leaf number shoot⁻¹, 86% for area leaf⁻¹ and 117% for leaf area shoot⁻¹).

The effect of water stress on reducing shoot extension appeared to be restricted to periods when θ_v in the root zone was low and when this constraint was removed, normal growth was resumed, although higher growth rates were often measured after stressed plants were re-watered. This probably reflects “stored growth” caused by the expansion of cells which were prevented from doing so during the stress period (Acevedo et al., 1971). Analysis of SBA data indicated that this, too, was similarly affected by stress and that significant reductions in the rate of increase in RSBA only occurred in stressed plants when θ_v in the root zone was low.

The leaf areas shoot⁻¹ in Table 5 are useful for considering the development of leaf area at the shoot level but do not reflect the actual plant leaf areas reported previously (Martin and Stephens, 2006a) because of the large differences which occurred between treatments in the number of stems plant⁻¹ and also between stems, in the number with lateral shoots. As a result, the maximum plant leaf area for the S3 treatment was about twice that of the S2, a very different situation to that indicated by the data in Table 5. It should also be noted that, for some treatments, the leaves enumerated on the 2001 extension growth represented only a small proportion of the leaf area on the stems within the study. Thus, for the S1, S2, S3 and S4 treatments, respectively, these leaves averaged 44%, 22%, 12% and 12% of the leaf area of the stems which were in the study. The results described may therefore not necessarily be applicable to the other leaves, which were mostly on one-year-old wood. These figures show that in the S1 treatment there was a much higher proportion of the stem leaf area on the current year's extension growth than in the other treatments. It may be that, with poor nutrition, priority is given to leaf development on the current season's growth – this would be advantageous because this growth would usually be located where light intensity is highest.

Shoot growth rates were shown to be significantly correlated with air temperature (Table 2) and a base temperature between 2.0 °C and 7.6 °C was indicated by extrapolation of regression lines. Variations in the base temperature for shoot growth and development have also been shown to occur in tea as a result of seasonal and nutritional effects (Stephens and Carr, 1993) and in leaf emergence in barley as a result of differences in the sowing date (Kirby et al., 1982). In our study, the highest base temperature occurred

in the nutritionally deficient S1 treatment which also had the lowest rates of shoot extension. The average leaf emergence rate (Fig. 5) of plants in this treatment was also significantly lower than those of the S2 and S4 treatments (0.02 leaves (°C > d)⁻¹ compared with 0.03 and 0.04 leaves (°C > d)⁻¹ for the S2 and S4 treatments, respectively). Under field conditions the slow development of leaf area would put such plants at an additional disadvantage since they would intercept less solar radiation early in the season (Cannell et al., 1987) and this would make them more likely to experience weed competition than well fertilised plants. One possible advantage to these plants of a higher base temperature is that this would help them to avoid or reduce the damage from early-season frosts and hence wasting nutrient reserves, which were probably very limited in this treatment. In Fig. 5, all the lines have an intercept on the x-axis well before a thermal time of zero, suggesting an earlier start date and/or a lower base temperature than has been used. Another possibility is that leaf emergence rates are more rapid early in the season which could be possible since the first leaves are considerably smaller than later leaves.

In a study of leaf demography in willow, Porter et al. (1993) found that leaf production rate was linearly related to temperature for periods when average temperature was below about 14 °C and their data indicated a base temperature for leaf production ranging from 6.0 to 7.0 °C for 3 clones. For periods with mean temperatures above 14 °C, however, there was little correlation. Although our data were for shoot growth rather than leaf emergence, they showed no evidence for such a discontinuity of response. Since Porter et al.'s data were collected from stands of willow, it may be that seasonal changes in stand canopy development, for example mutual shading of shoots, affected the response to temperature. Our own shoots were leading shoots on individual plants which were not affected by the canopy of their neighbours. While the range of our base temperatures for shoot extension growth (2.0–7.6 °C) covers the range found by Porter et al., ours were lower for all treatments except the S1. Base temperatures of between about 0 and 5 °C have been reported for other temperate crops like wheat (Kirby, 1995), barley (Kirby et al., 1982) and rape (Morrison et al., 1989).

Porter et al. (1993) found that the onset of decline in the number of leaves of their 3 willow clones occurred at about 1650 °C d using a 0 °C base temperature. Using an April 1 start date, this corresponds to a date of August 2 for our 2001 data which is just after the date when we recorded maximum leaf area (July 25) and August 8 for 2000, just before the date of the maximum leaf area for most treatments (August 10). This may therefore be a useful way of predicting the time of maximum LAI in willow.

In the plants investigated in the present paper, stem extension growth occurred in 2001 from April to the end of July or early August, when leaf production ceased. Increases in SBA occurred over a slightly longer period, up to about early September. The shoot growth studies

therefore only covered the latter half of the growing season and by the start of the study period the shoot length of unstressed plants was 47% (S1), 45% (S2), 59% (S3) and 62% (S4) of their end-of-season length. Differences are therefore possible between what has been found in the present study and growth in the early part of the season.

In conclusion, results from this study provide some mechanisms for the treatment effects reported in previous papers in this series. Thus, within watering regimes, major differences were reported in stem dry matter production which was highly correlated with leaf area duration (Martin and Stephens, 2006a). Differences in plant leaf area resulted from differences in number of stems plant⁻¹, but results from the present study show that other factors contributed to this, particularly differences in rates of shoot extension (because leaf number shoot⁻¹ was highly correlated with shoot length) and average area leaf⁻¹.

Values for shoot extension growth, area leaf⁻¹ and shoot leaf area were particularly low in the nutrient-poor, unamended S1 treatment. The dramatic effect of improving the nutritional status of the Oxford clay was evident from the higher rates of shoot extension growth and larger area leaf⁻¹ and shoot leaf area of shoots in the S2 treatment reported in this paper. In 2000 and 2001, the water stress treatment caused large reductions in stem biomass production in all soil treatments (Martin and Stephens, 2006a). Stem biomass was determined by relationships between stem dry mass and SBA and results in this paper from measurements of short-term changes in both extension growth and SBA indicate that reduced growth (and hence, probably biomass production) in the water stress treatments was limited to periods when θ_v was low.

It was previously shown that there were large differences in seasonal and short-term rates of evapotranspiration in the different treatments (Martin and Stephens, 2006b) as well as major differences in the distribution of roots down the soil profile (Martin and Stephens, 2006a) and the present study has shown the effect of this on the extraction of soil water by stressed plants. Particularly striking was the limited depth range of water uptake (0–0.3 m) in the S1 and S2 clay treatments which received no amendment with organic matter, compared with the greater depth of uptake (0–0.5 m) in the amended S3 clay and the uptake from the whole profile (0–0.6 m) in the S4 sandy loam.

The implications for using willow SRC as a method for restoring landfill sites capped with nutrient-deficient clay are that, unless nutritional amendments are possible, the restoration process will be extremely slow and liable to failure through the inability of the trees to compete with other vegetation for water, nutrients and, ultimately, light.

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