

## **STUDY ON GROWTH AND STOMATAL RESPONSE OF YOUNG POPLAR PLANTS SUBJECTED TO PARTIAL SOIL DRYING**

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**MOHIUDDIN, M., JARVIS, P.G. & RUSSELL, G. 1997. Study on growth and stomatal response of young poplar plants subjected to partial soil drying.** Growth and stomatal response of young poplar plants, grown with part of the roots in drying soil, were studied in the greenhouse of Edinburgh University, United Kingdom as a method of species selection for dry areas. Water relations of leaves and abscisic acid (ABA) content of both leaves and roots were investigated while the roots in moist soil profile were being able to maintain shoot water supply. Leaf and stem growth in association with leaf stomatal conductance were reduced in plants subjected to partial soil drying despite the maintenance of leaf turgor potential. The simultaneous presence of higher ABA content both in roots and leaves over the period of soil drying indicates the influence of signals from roots of drying soil in these reductions. These earlier responses of shoot to soil drying could maintain sustained productivity of plants through sustained utilisation of water in water shortage areas.

Key words: Young poplar - soil drying - growth - stomatal conductance - abscisic acid

**MOHIUDDIN, M., JARVIS, P.G. & RUSSELL, G. 1997. Kajian mengenai pertumbuhan dan tindak balas stomata tumbuhan poplar muda yang terdedah kepada sebahagian pengeringan tanah.** Kajian pertumbuhan dan tindak balas stomata tumbuhan poplar muda yang ditanam dengan sebahagian daripada akarnya dalam tanah kering dijalankan di rumah hijau Universiti Edinburgh, United Kingdom bagi kaedah pemilihan spesies di kawasan kering. Kaitan air dan kandungan asid absisik (ABA) daun dan akar dikaji manakala akar di profil tanah lembab boleh mengekalkan bekalan air kepada pucuk. Pertumbuhan daun dan batang dengan kehadiran konduktans stomata daun berkurangan dalam tumbuhan yang terdedah kepada sebahagian pengeringan tanah walaupun potensi segah daun dikekalkan. Kehadiran serentak kandungan ABA yang lebih tinggi dalam akar dan daun di sepanjang tempoh pengeringan tanah menunjukkan bahawa pengurangan ini dipengaruhi oleh isyarat akar dari tanah yang dikeringkan. Tindak balas awal pucuk terhadap pengeringan tanah ini dapat mengekalkan pengeluaran tumbuhan melalui penggunaan air yang berterusan di kawasan yang mengalami kekurangan air.

## Introduction

Limitation of soil water is one of the most important plant stress variables in many parts of the world because of the uncertainty and periodic variation of precipitation. The characterisation of the growth and stomatal behaviour of plant species in response to limited soil water is necessary for the selection of appropriate species for dry areas. The attributes of a species identified in a short term experiment, particularly in a relatively controlled environment may be used to predict the performance of that species in the field under similar conditions.

As soil dries, the soil water potential is reduced and the frictional resistance to flow increases resulting in decline in the shoot water potential. The effect of low shoot water potential on growth and stomatal conductance has been attributed to the reduction of turgor potential (Turner 1974, Sharp & Davies 1979). Reduction of stomatal conductance and leaf growth has often been found to be associated with turgor decline in water stressed plants (Kelliher *et al.* 1980, Kramer 1983). However, there are several reports of growth and stomatal conductance being affected by soil drying, even though turgor potential was maintained (e.g. Michelena & Boyer 1982, Gollan *et al.* 1986). In recent years attention has focussed on the role of roots in drying soil in the regulation of shoot response through the involvement of a non-hydraulic signal (Gowing *et al.* 1990). This signal is ABA, presumably produced in dehydrating roots and then transported to the leaves in the transpiration stream resulting in stomatal closure (Davies & Zhang 1991) and inhibition of growth (Zhang & Davies 1990).

Therefore, the present study was conducted to investigate the growth and stomatal responses of young poplar plants grown in partially drying soil column with horizontally divided root systems. The roots present in the upper soil column were subjected to soil drying while the roots present in the bottom soil column were being able to maintain continuous shoot water supply.

## Materials and methods

Pre-rooted cuttings of poplar (*Populus trichocarpa* × *P. deltoides*) of eight weeks age were grown in specially designed pots (one pot above the other with a number of large holes at the bottom of the upper pot so that the roots of the plants could pass through easily) containing *c.* 3500 cm<sup>3</sup> of soil compost (50% loam soil + 25% sand + 25% peat) column in each. When the roots had occupied a large volume of the lower soil column, half the plants were watered every evening from above (control) and the other half received no water from above (treatment) for a period of 17 days. But in both cases the lower soil column was kept moist so as to maintain a sustained supply of water to the shoot of treated plants. In order to prevent the capillary movement of water from the lower soil column to the one above, a layer of *c.* 4 cm thick small gravels was retained in between the two soil columns. During the 17-day drying cycle, the ranges of mean daily and maximum photosynthetic photon flux density (PPFD) and temperature in the greenhouse were 11-33 and 15-84 mol m<sup>-2</sup> day<sup>-1</sup>, 13 - 20 and 15 - 26 °C respectively.

The soil water contents of the upper soil columns of both control and treatment were measured gravimetrically. Measurements of abaxial stomatal conductance of recently fully expanded leaves were made using a steady-state nulbalance porometer (Li 1600, Li-Cor Inc. Lincoln, Nebraska, USA) after 5-6 hours of photoperiod. The water potential of these leaves was measured using a pressure chamber (Scholander *et al.* 1965). Osmotic potential of 10 mm<sup>3</sup> sap extract of leaves (used for water potential measurement) was also measured using a vapour pressure osmometer (VPO, Wescor model 5100 C, Wescor Inc., England). The turgor potential was calculated by the difference between leaf water potential and osmotic potential. Abscisic acid concentrations of leaf lamina and roots of those plants were determined using radioimmunoassay (RIA) protocol described by Quarrie *et al.* (1988).

The length and width of growing leaves of similar size ( $15.27 \pm 1.46$  cm<sup>2</sup> and  $15.20 \pm 1.32$  cm<sup>2</sup> of control and treatment plants respectively) were measured and later converted into areas using regression equation  $Y = -4.7671 + 0.6314X$ ,  $r^2 = 0.998$ , developed by plotting actual leaf area (measured by a leaf area meter, LI 3100, Li Cor., Lincoln, USA) against the product of length and width of 20 leaves. The length of growing stem of those plants was recorded and later increase in stem length was calculated by subtracting the initial length from the length increased subsequently. The specific leaf area was also derived as leaf area/leaf dry weight using leaf lamina portions (*c.* 2 cm<sup>2</sup>) of both old, fully expanded and expanding leaves of the same plants.

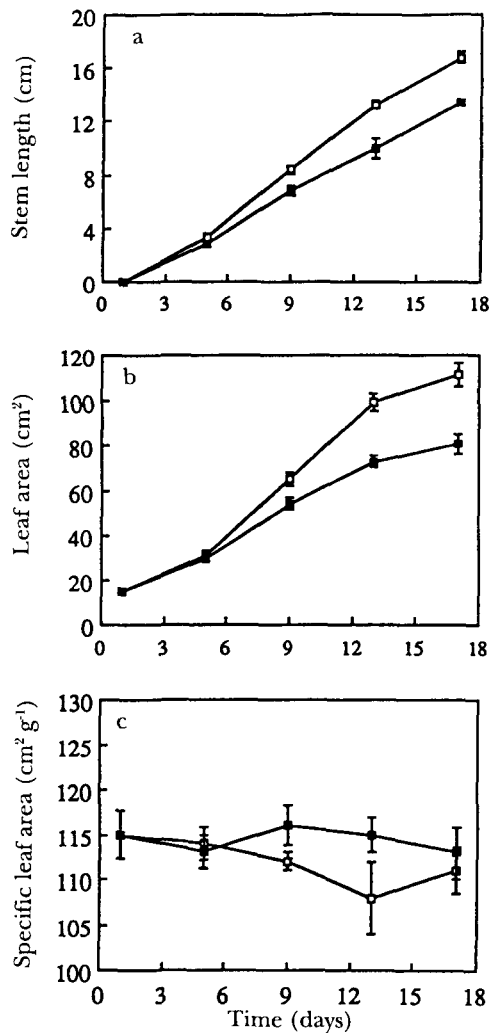
The above measurements were carried out on days 1, 5, 9, 13 and 17 (no root ABA on days 5 and 13) of the experimental period from both the control and treatment plants in six replications of each. Because of the limitation of samples and their processes, the measurements of soil water content and ABA concentration in leaves and roots were in four replications. Means and standard errors of means of each variable were calculated and the paired data were tested by student's *t*-test using STATVIEW package.

## Results and discussion

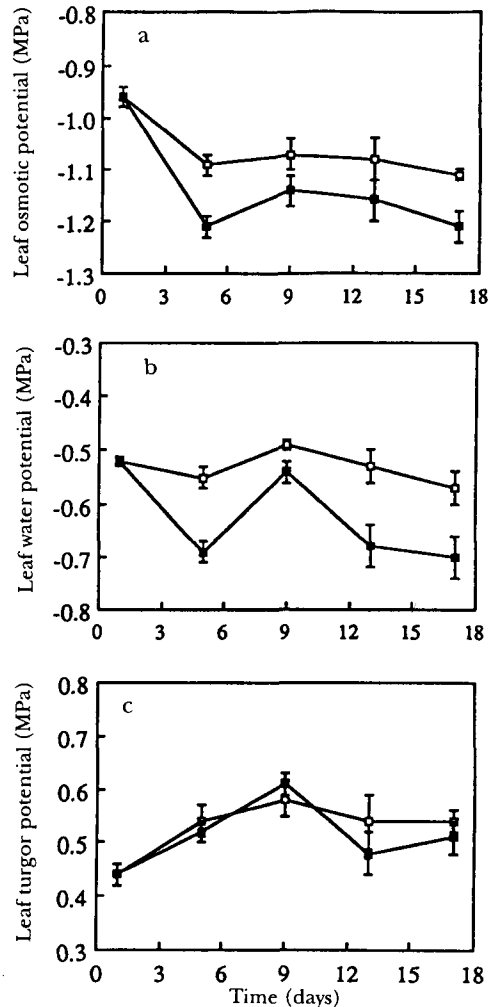
With the gradual decline of soil water content the growth and stomatal conductance of treated poplar plants were reduced to a level lower than that of well-watered ones (Table 1 & Figure 1) in the absence of any detectable change in leaf turgor potential (Figure 2c). This is in agreement with the influence of non-hydraulic signals from the roots of drying soil in the regulation of shoot behaviour (Gollan *et al.* 1986). The observation of stronger linear relationship between stomatal conductance and soil water content rather than with bulk leaf water potential (Figure 3) supports the argument.

However, just after the onset of soil drying (on day 5), the bulk leaf water potential of treated plants was significantly lower than that of controlled plants (Figure 2b). Possibly, sudden onset of soil drying could immediately induce hydraulic tension in the xylem, resulting in the reduction in water potential gradient (Boyer & Nonami 1990) and eventually the decline in leaf water potential.

Because of such reduction in the water potential gradient, the supply of water to the growing cells is reduced and consequently growth is affected with the decline in turgor pressure (Turner *et al.* 1985). Thus the hydraulic influence of drying soil on shoot growth cannot be ruled out. But in this experiment the leaf expansion and stem elongation were affected (Figure 1) despite the maintenance of leaf turgor potential at low leaf water potential (Figure 2) as reported by Westgate and Boyer (1985) in maize and Gowing *et al.* (1990) in apple clones. Moreover, there was no change in the specific leaf area of treated plants over the period of drying cycle although the leaf expansion was affected (Figure 1). The existence of continuous shoot water supply by the roots available in moist soil profile of the lower pot may limit the carbohydrate accumulation in cell contents of leaf.



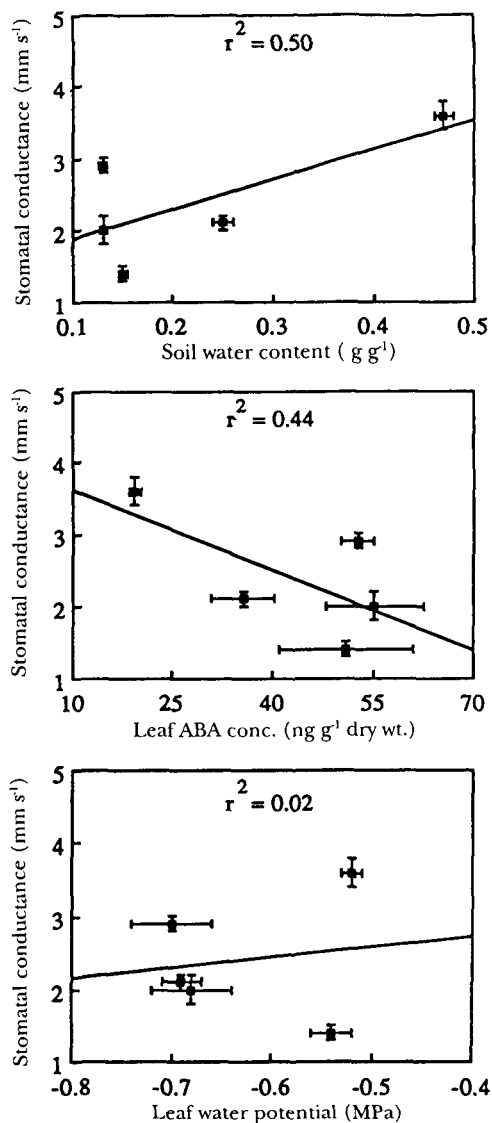
**Figure 1.** Increase in stem length (a) and leaf area (b), and change in specific leaf area (c) of poplar plants over the period of soil drying. □ well watered and ■ unwatered. Points are means of six measurements  $\pm$  one standard error of the mean.



**Figure 2.** Osmotic potential (a), water potential (b) and turgor potential (c) of fully expanded poplar leaves as a function of time after water was withheld from day 1. □ well watered and ■ unwatered. Points are means of six measurements  $\pm$  one standard error of the mean.

These results of the present study indicate that the reduction in shoot growth is likely influenced by the endogenous growth inhibitor like abscisic acid (ABA). The presence of the increased concentration of leaf ABA in plants subjected to partial soil drying over that of well-watered plants (Table 1) is in agreement with the study of Zhang and Davies (1990). This regulation of shoot growth by endogenous ABA may be attributable to the reduction of cell wall extensibility (Van Volkenburgh & Davies 1983). Similarly, in treated plants, the reduction in stomatal conductance was also associated with the simultaneous presence of increased concentration of ABA, both in leaves and roots (Table 1), suggesting stomatal control by ABA (Zhang *et al.* 1987). Possibly, ABA produced in dehydrating roots

of drying soil and transported by the xylem stream to the stomata may have led to stomatal closure (Davies & Zhang 1991). The complete recovery of stomatal conductance in treated plants ( $9.42 \pm 0.87 \text{ mm s}^{-1}$  compared to that of control plants  $7.57 \pm 0.20 \text{ mm s}^{-1}$ ) within two days of the end (day 17) of the drying cycle is also an indication of the total decline in ABA transport to the shoot due to the lack of xylem stream from the roots of dry soil. This is because of the fact that the soil compost in the top pot was completely dry (Table 1) at that time when sufficient shoot water supply was being maintained by the roots in the bottom pot.



**Figure 3.** Linear relationship between abaxial stomatal conductance and soil water content, leaf ABA concentration and leaf water potential in poplar plants. Points are means  $\pm$  one standard error of the mean. Data were collected over a time course of soil drying and plants were sampled at 5 - 7 h into the photoperiod of each day.

However, in the present study, the linear relationship of stomatal conductance with leaf ABA was not as strong as with soil water content (Figure 3). Therefore, the reduction in stomatal conductance and shoot growth of poplar plants is attributed to the role of signal originating from the root environment. These responses of poplar plants could maintain their sustained productivity in dry areas before any damaging affects of water stress develop.

**Table 1.** Change in soil water content (SWC) of the upper soil column, root abscisic acid (RABA), leaf abscisic acid (LABA) and stomatal conductance (SC) as a function of time after water was withheld from day 1. Values are means  $\pm$  one standard error of the means.

Time (days)	C/T *	Variables			
		SWC (g g <sup>-1</sup> )	RABA (ng g <sup>-1</sup> d.w.)	LABA (ng g <sup>-1</sup> d.w.)	SC (mm s <sup>-1</sup> )
1	C	0.47 $\pm$ 0.01	24.05 $\pm$ 2.06	19.31 $\pm$ 0.86	3.55 $\pm$ 0.16
	T	0.47 $\pm$ 0.01	24.05 $\pm$ 2.06	19.31 $\pm$ 0.86	3.55 $\pm$ 0.16
5	C	0.37 $\pm$ 0.01	-	21.83 $\pm$ 1.79	2.80 $\pm$ 0.20
	T	0.22 $\pm$ 0.01	-	35.60 $\pm$ 4.72	2.22 $\pm$ 0.13
9	C	0.42 $\pm$ 0.01	20.58 $\pm$ 2.53	24.27 $\pm$ 2.37	3.15 $\pm$ 0.33
	T	0.15 $\pm$ 0.004	83.95 $\pm$ 8.85	51.12 $\pm$ 10.03	1.48 $\pm$ 0.14
13	C	0.35 $\pm$ 0.01	-	31.01 $\pm$ 3.16	3.96 $\pm$ 0.18
	T	0.13 $\pm$ 0.003	-	55.25 $\pm$ 7.41	1.62 $\pm$ 0.03
17	C	0.38 $\pm$ 0.01	20.57 $\pm$ 3.25	25.01 $\pm$ 4.17	4.50 $\pm$ 0.20
	T	0.13 $\pm$ 0.004	87.36 $\pm$ 10.07	52.79 $\pm$ 2.46	2.77 $\pm$ 0.09

\*C = control, T = treatment.

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