ASSESSMENT OF WATER STATUS IN TREES FROM MEASUREMENTS OF STOMATAL CONDUCTANCE AND WATER POTENTIAL

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ABSTRACT

The use of a porometer to measure stomatal conductance is described and the technique briefly reviewed. The relationship between stomatal conductance, g_s and water potential, ψ on cut branches of Scots pine (**Pinus sylvestris** L.) is presented from measurements on two occasions. The changes in ψ on branches with their cut ends in water were small compared with the rapid decreases in ψ on the branches allowed to dry out. Stomatal conductance remained constant as ψ fell from -0.4 to -1.6 MPa but at lower ψ values g_s fell rapidly. The likelihood that decreases in g_s reduce growth rates and the use of the techniques to assess this at different stages of tree growth are discussed.

INTRODUCTION

Several studies have shown that growth of conifer trees (Kramer and Kozlowski, 1960; Lotan and Zahner, 1963) and seedlings (Rutter and Sands, 1958; Jarvis and Jarvis, 1963; Lister *et al.,* 1967; Kaufmann, 1968) is reduced by water stress. Jarvis and Jarvis (1963) and Havranek and Benecke (1978) commented that the reduction in photosynthesis in response to water stress was possibly due to a decrease in stomatal conductance which reduced the rate of influx of carbon dioxide into the leaves. Brix (1962) showed that photosynthesis and transpiration were reduced in proportion when *Pinus taeda* L. seedlings were water stressed, suggesting that the rates were regulated by the stomata but Beadle and Jarvis (1977) calculated that 50% of the reduction in photosynthesis rate in water stressed *Picea sitchensis* (Bong.) Carr seedlings was accounted for by decreasing mesophyll conductance before stomatal regulation became important.

Differences in stomatal response to water stress have been found between species (Jarvis and Jarvis, 1963; Havranek and Benecke, 1978), provenances (Cannell and Last, 1976) and clones within a species (Hellkvist, 1970; Bennett and Rook, 1978) and these results can be used to assess the drought resistance of an individual plant. Diurnal and seasonal variations in stomatal conductance in conifers have been widely studied (see review by Hinckley *et al.,* 1978) and in field conditions changes in stomatal conductance have been related to environmental variables such as light, temperature, and air saturation deficit (e.g., Watts, 1977).

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The measurement of water potential, conveniently made using a pressure chamber with shoots (Scholander *et al.,* 1965) or individual conifer fascicles (Roberts and Fourt, 1977) has been used to assess the water status of conifers (Waring and Cleary, 1967; Ritchie and Hinckley, 1975), and critical limits, beyond which irreversible damage occurs and survival is uncertain have been identified for different species growing in different conditions (Ruetz, 1976; Cleary and Zaerr, 1979). The response of stomatal conductance to water stress varies between species and conditions (Ritchie and Hinckley, 1975) but for conifers it has been demonstrated that a critical value exists, above which stomatal conductance is constant and below which it falls rapidly (Running, 1976; Rook *et al.,* 1978; Beadle *et al.,* 1978).

In this paper the technique of porometry for measuring stomatal conductance will be briefly reviewed and the relationship between stomatal conductance and water potential in cut branches of *Pinus sylvestris* L. presented. The results will be interpreted in a discussion of the assessment of plant water status.

METHODS

Stomatal conductance

Transpiration is the evaporation of water from sites within the leaf and the subsequent diffusion of water vapour to the leaf surface via the stomatal pores or cuticle and into the air beyond. If E is the transpiration rate from the leaf, $\mathrm{g\,mm^{-2}\,s^{-1}}$ and $(\theta_a - \theta_o)$ the water vapour concentration difference between the site of evaporation and the ambient air, $\mathrm{g\,mm^{-3}}$ then a leaf conductance, $\Sigma\, g_l$, $\mathrm{mm\,s^{-1}}$ is defined in equation 1 (Gaastra, 1959).

$$\Sigma\, g_l = \frac{E}{(\theta_a - \theta_o)} \tag{1}$$

$\Sigma\, g_l$ is usually split into three components in parallel referred to as the boundary layer conductance, stomatal conductance, g_s, and the mesophyll conductance together with a cuticular conductance in series with g_s (Gaastra, 1959). Since the mesophyll conductance under normal conditions is very large compared to g_s (Hsiao, 1973) and the cuticular conductance is usually very small compared to g_s, often only 5% of the g_s value (Landsberg *et al.,* 1975), these two components are usually negligible and ignored in the calculations.

Porometers

During the last 15 years the measurement of stomatal conductance has been facilitated by the design of portable porometers which consist of a chamber enclosing a leaf and a humidity sensor which records the change in humidity as the leaf transpires. There are two types of porometer in general use at the present. In the first type (e.g., Van Bavel *et al.,* 1965; Monteith and Bull, 1970; Byrne *et al.,* 1970) the chamber is firstly flushed with dry air and the time taken for an increase in humidity between two fixed points is then recorded. Calibration of this type of porometer is achieved by using artificial leaves made from wet filter paper and plates with small holes drilled into them. The second is a continuous flow type (e.g., Parkinson and Legg, 1972; Day, 1977) where a stream of dry gas is passed into the chamber at a constant rate and the humidity of the gas leaving the chamber is measured. Another version of this type is the null balance design (Beardsell *et al.,* 1972) where the humidity is kept constant, usually at the ambient air level by controlling the flow rate of dry gas into the chamber. The incorporation of a fan in the chambers of the second type of porometers ensures thorough mixing of the air and also increases the boundary layer conductance. Calculations of stomatal conductance are made from the humidity, the flow rate of dry gas into the chamber, and the foliage area incorporated. Beardsell *et al.* (1972) designed their chamber so that leaves of complex shapes, such as conifer shoots could be included for the measurement. The relative merits and errors involved in the individual systems are discussed in the articles referred to above.

There have been some studies where comparisons of stomatal conductance using different porometers have been made (e.g., Landsberg *et al.,* 1975) and it has been strongly emphasised by Landsberg *et al.* (1975) and Watts (1977) that it is important to frequently check and cross-check the calibrations of the instruments using an independent method such as the loss in weight of potted plants growing in controlled environments. Day (1977) checked the calibration on his porometer using a "mock leaf" constructed from a microporous polypropylene film, the "stomatal" conductance of which was independently measured by weighing. Several types of porometers are now commercially available.

With complex leaf shapes such as conifer shoots the surface area has to be measured. Consistent with the practice of expressing stomatal conductance on a single surface area basis when using flat leaves with stomata on one surface only, many reports with complex leaf shapes continue to express results using projected area (e.g., Watts, 1977) whereas other authors (e.g., Running, 1976; Bennett and Rook, 1978) use total surface area as a basis for expressing their data.

Measurements

On two occasions, 5 June and 12 August 1977 two branches were cut from 30-year-old Scots pine (*Pinus sylvestris* L.) trees growing in north-eastern Scotland. Both days were warm and sunny. The control branch was immediately re-cut under water while the other branch was allowed to dry out. At frequent intervals after cutting measurements of stomatal conductance on five shoots on each branch were made using a null balance diffusion porometer (Beardsell *et al.,* 1972) and, simultaneously, water potential measurements were made on three fascicles from each branch using a pressure chamber (Roberts and Fourt, 1977). At the end of each experiment the shoots used in the porometer chamber were removed and their projected foliage areas measured using an optical planimeter (model LI 3000, Lambda Instruments Corp.). Stomatal conductances were expressed on a projected foliage area basis and to convert them to a total surface area basis they should be divided by 2.6. This is the ratio of total surface area to projected surface area for a cross section of a *Pinus sylvestris* fascicle.

RESULTS

The mean shoot stomatal conductances, g_S and mean needle water potentials, ψ during the course of the two experiments are shown in Figs. 1a and 1b. On 12 August mean stomatal conductances were higher than those on 5 June and this would be expected from seasonal variations in g_S which have been recorded by Watts (1977).

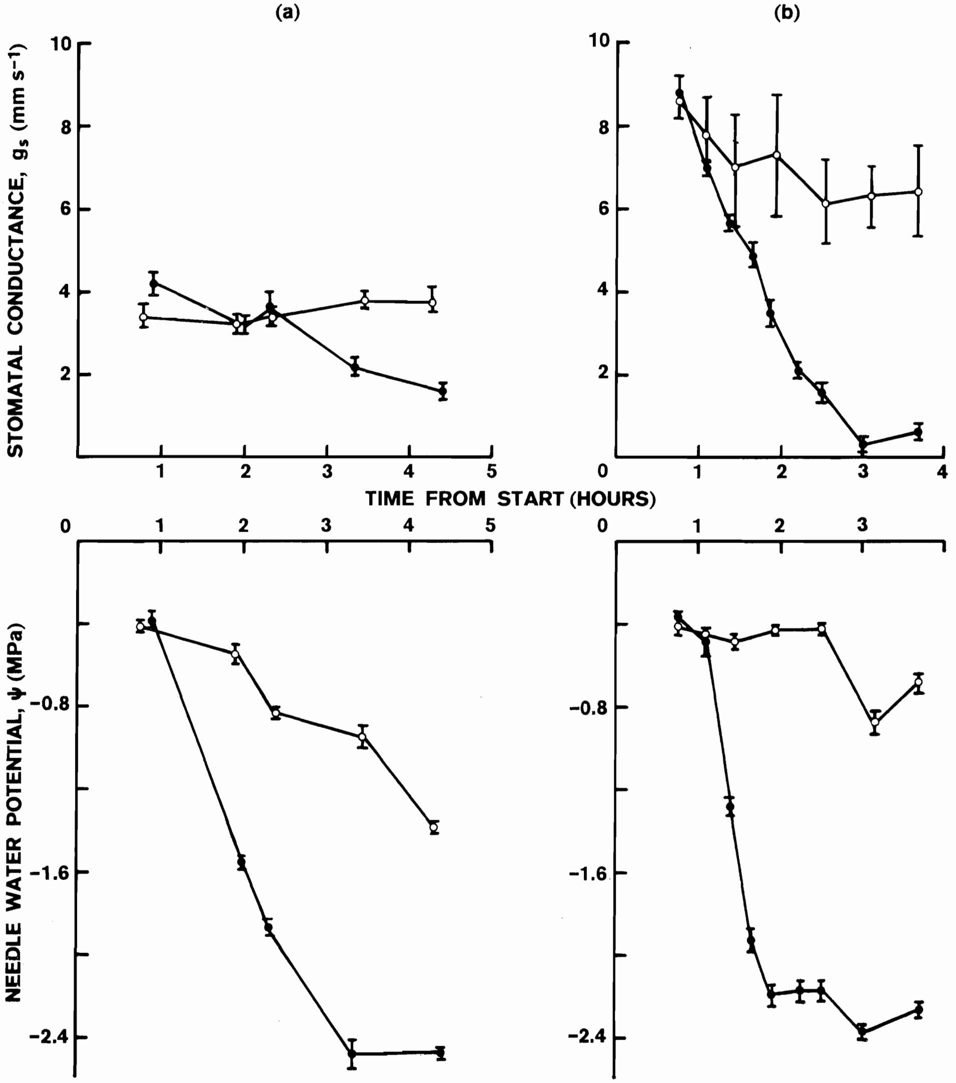

FIG. 1—Measurements of stomatal conductance and water potential for the control (open circles) and drying (filled circles) branches on (a) 5 June and (b) 12 August 1977. Stomatal conductances and water potential measurements are means of 5 and 3 replicates, respectively and the vertical bars indicate standard errors.

On 5 June g_S on the control branch remained constant whereas on 12 August it fell by about 30%. This decrease in g_S was probably due to increasing air saturation deficit during the course of the measurement period (Watts, 1977). On both occasions g_S on the drying branches fell dramatically. Water potential on the control branches fell slightly from —0.4 to —1.2 and —0.9 MPa on 5 June and 12 August, respectively, but the fall in ψ on the drying branches was much steeper and reached minima of —2.4 MPa.

In Fig. 2 relative stomatal conductances for each branch are plotted against needle water potential. Relative stomatal conductances were calculated by normalising the results on the maximum conductance values. Relative stomatal conductance remained constant at a maximum level as ψ decreased from —0.4 to about —1.6 MPa but, as ψ decreased further, relative stomatal conductance fell steeply.

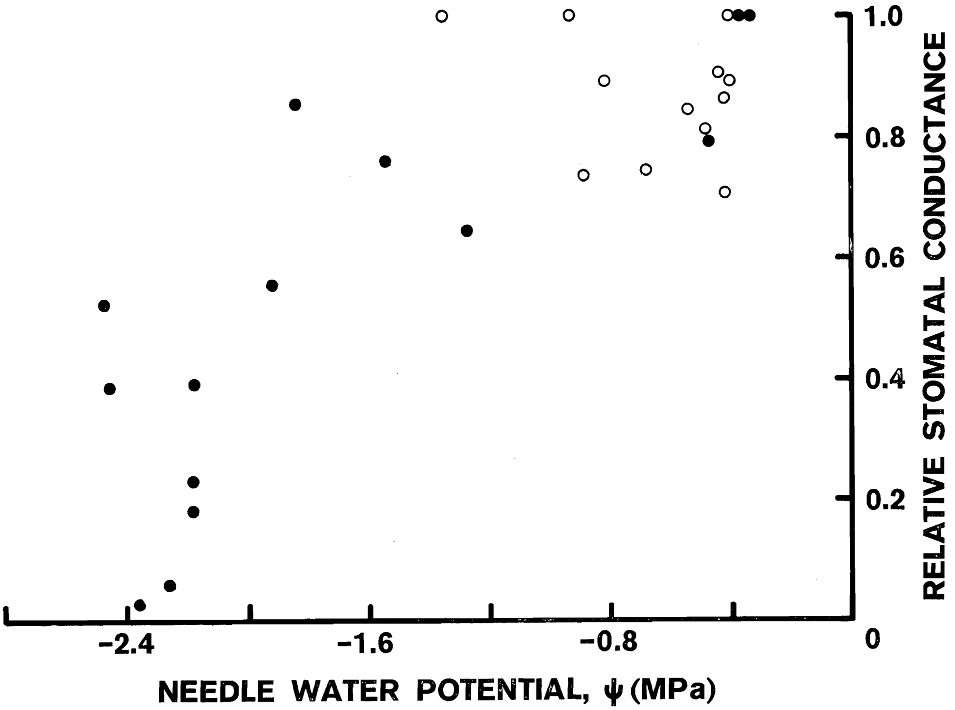

FIG. 2—Scatter diagram of relative stomatal conductance against water potential for all branches. Symbols are the same as in Fig. 1.

DISCUSSION

The effect of other environment variables on g_S was small in comparison with the effect of decreasing water potential. As the cut branches dried out a threshold or critical water potential was reached, below which stomatal conductance decreased. A response of this type has been reported for other conifer species and a critical water potential of —2.0 MPa was found for *Pseudotsuga menziesii* (Mirb.) Franco (Running, 1976), —1.1 MPa for *Pinus radiata* D.Don (Rook *et al.,* 1978), and between —1.6 and —2.7 MPa for *Picea sitchensis* (Bong.) Carr. according to the time of year (Beadle *et al.,* 1978).

Ecologically the consequence of this critical value is that normal daily fluctuations in ψ are not severe enough to reduce g_S and only when the critical range is reached is g_S reduced. This would result from increased evaporative demand on a plant, increased plant resistance, root damage, a reduction in soil water potential, or loss of water supply to the roots.

If ψ is severely reduced then irreversible damage will result and the plant may not survive (Cleary and Zaerr, 1979) but before this occurs it is likely that decreased g_s will affect growth of reductions in transpiration and photosynthesis rates. The porometer and the pressure chamber can be used to make quick and easy measurements on trees in different stages of growth to establish the critical water potential beyond which a decrease in g_s will occur. Once a relationship in Fig. 2 is established for a species in its growing conditions then regular measurements can be used to assess whether action should be taken to change the growing conditions to maintain g_s at its maximum value. With seedlings in the nursery this might involve irrigation or shading and with the transplanting of young trees this might indicate that more care is required to reduce damage to the root systems. With mature trees the techniques can be used in helping to assess the species which are most likely to maintain high growth rates throughout the season at a site with certain climatological conditions. It is important that the relationship in Fig. 2 is determined for different species and growing conditions since it is unlikely that it will be the same through seasonal changes or for seedlngs and more mature trees. There is also a danger that the application of results from cut branches to plants growing in their natural conditions will lead to misleading interpretations.

One important consideration of the techniques employed in this study which should be emphasised is that assessment of plant water status can be made within a few hours without any need to measure soil water potential or requirement to know details of the soil type or structure.

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