WATER RELATIONS AND LEAF GROWTH

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Summary

Cell expansion may be described in physical terms by a model in which growth and turgor are linearly related above a threshold value for turgor. Tissue extensibility, an indication of the capacity of cell walls to loosen, is the gradient of this line.

The growth of leaves and leaf cell turgor have been directly correlated, but much of the information on the physical characteristics of growth has been obtained from simpler tissue types. For leaves of bean, variation in cell wall extensibility (WEX) may often be the factor controlling growth, maturation, and the response to a decreased water supply (Van Volkenburgh and Cleland, 1980; Davies and Van Volkenburgh, 1983).

Diurnal patterns of leaf growth in woody plants cannot always be explained in terms of daily fluctuations in turgor and for birch leaves WEX and growth are correlated.

1. Introduction

The growth of young expanding leaves depends upon cell division being followed by irreversible cell expansion. The expansive growth of plant cells results from cell wall loosening and extension being accompanied by an influx of water and, for growth to continue, turgor must be maintained above the point at which the yield stress becomes limiting. The process is illustrated in equation 1 which is simplified after Lockhart (1965).

$$\text{Growth} = M\,(P - Y) \qquad 1$$

Where M is the cell wall extensibility (WEX) and is the slope of the curve relating growth to turgor. P the turgor pressure and Y the yield threshold, which is the minimum turgor required for growth, given by the intercept of the P axis when growth and turgor are plotted.

Growth has often been directly correlated with turgor (Boyer, 1968; Bunce, 1977) but expansion growth is also related to the biochemical processes which alter cell wall properties. Cell expansion is one of the most sensitive processes affected by water deficit (Hsiao, 1973), resulting in decreased leaf extension and growth and, although the effects of water deficit on dry matter production and extension growth are well documented for certain species (e.g. cotton, Cutler and Rains, 1977), it is only recently that the other factors affecting the growth of leaves at the cellular level have been considered.

2. The assessment of turgor in growing cells

The techniques for assessing the water status of a plant have been reviewed thoroughly (Turner, 1981), and in most instances turgor is estimated as the difference between solute and water potential. For growing leaves, consisting of cells at different stages of growth and differentiation and of distinct tissue types, the problem of turgor assessment is complex.

Water potential has been measured using intact leaves (Boyer, 1968), excised leaves (Squire and Ong, 1983) and leaf pieces (Davies and Van Volkenburgh, 1983) and in many studies measurements from different techniques have been compared, revealing either good agreement between techniques (Campbell and Campbell, 1974) or clear discrepancies (Turner *et al.*, 1984).

Figure 1. - Relationship between water potential measured by *in situ* psychrometers and that measured by pressure chamber for first year seedlings of *Acer* ( ) and *Betula* ( ).

For young expanding leaves of sycamore (Acer pseudoplatanus) and birch (Betula pendula), both in situ psychrometers and a pressure chamber have been used to detect changes in leaf water status, but the relationship was not 1:1 (Figure 1). In both fully hydrated and wilted leaves, the psychrometer underestimated leaf water potential when compared to values given by the pressure chamber. Despite these differences, in situ psychrometers may still be used to follow dynamic changes in leaf water status.

Excised leaf discs placed in psychrometer chambers for several hours may also give inaccurate estimates of water and solute potential. Solute absorption from the apoplast and the continued growth of leaf tissue are two sources of error. Recently Cosgrove et al (1984), working on pea stem segments, have quantified excision effects successfully. They observed that continued growth of cells occurred when tissue was placed into psychrometer chambers and predicted that because the tissue was isolated from its water supply, stress relaxation would occur and growth would cease as the turgor of the cells became limiting. From this, the amount of turgor necessary for growth, (Y), was estimated and compared with the turgor measured directly using a pressure probe. Y was estimated as 0.28 MPa.

In leaf tissue, stress relaxation has not been used to measure Y. Westgate and Boyer (1984) showed that the water potential in the elongating region of maize leaves did not differ when measured on excised and intact tissue, but unfortunately no direct estimate of turgor was made. Leaf discs, taken from expanding leaves of birch and sycamore, and placed in psychrometer chambers at 10°C (to retard growth) or 25°C (to allow stress relaxation) gave similar values for turgor. For these slow growing leaves, therefore, the use of excised leaf discs in psychrometer chambers may provide a reasonable estimate of turgor in the intact plant.

The miniaturized pressure probe has been used to measure turgor directly in only a few higher plant cells. Hopefully, use of the instrument in leaf cells will allow us to determine, with a high degree of accuracy how turgor and growth are related.

3. Growth and cell wall extensibility

The physical model advanced by Lockhart (1965), predicts that in turgid cells, growth will continue if biochemical modifications of the cell wall (cell wall loosening) result in irreversible cell wall extension.

The amount of cell wall loosening has been assessed as 'plasticity', measured using killed plant tissue in which the hydrostatic and turgor forces are removed. Plasticity and growth have been correlated and the importance of WEX has been reviewed by Cleland (1983). The 'Acid growth hypothesis' has been used to explain the expansive growth of Avena coleoptiles (Rayle and Cleland, 1970). Pumping of H^+ from the plasma membrane causes acidification of cell walls, which results in cell wall loosening and growth. Auxin promotes growth by increasing H^+ secretion.