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Water deficit and changes in water relations of sun and shade leaves of *Quercus petraea* (Matt.) Liebl. and *Nothofagus procera* (Poepp. et Endl.) Oerst seedlings

A. B. I. Igboanugo[1]

Department of Pure and Applied Biology, Imperial College of Science and Technology, Silwood Park, Sunninghill, Ascot, Berks., SL5, 7PY England

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Abstract. Seedlings of *Quercus petraea* and *Nothofagus procera* were grown out of doors in pots under two levels of artificial shading and in full light. Using the pressure chamber technique, water potential (Ψ_W) characteristics of mature leaves were compared between treatments. Shading increased solute potential (Ψ_S) and the amount of water sequestered per unit leaf area between full (Ψ_P^{100}) and zero (Ψ_P^0) turgor, but lowered pressure potential (Ψ_P) at Ψ_P^{100}. However, as water was being extracted from leaves, the reductions in Ψ_P in leaves of higher light intensities were progressively much greater (due to their higher bulk modulus of elasticity) than those of dense shade. Consequently, at higher relative symplastic water content (RSWC), Ψ_P in leaves of higher light intensities progressively fell below those of dense shade, remaining lower till their points of zero turgor. Leaves of higher light intensities attained their Ψ_P^0 at higher RSWCs. These findings show that Ψ_W of sun and shade leaves can behave like those of leaves from drought affected and well watered plants respectively and that as plants transpire, sun leaves are better adapted to draw water up plants than shade leaves.

Key words: *Nothofagus procera*; *Quercus petraea*; Water deficits; Water potential; Water relations.

Introduction

In a given deciduous tree species with dense foliage, sun and shade leaves of different grades can be identified. Information on the contributions of sun and shade leaves to the water relations of plant species is scarce. So far, related studies were concerned with the variations in Ψ_W with height in the crown (Hellkvist *et al.*, 1974; Olsson and Milthorpe, 1983), without reference to the degree of shading received by individual experimental leaves or twigs within the crown. Hence, in such studies, it is difficult to seperate the effects due to shading from those due to height. Besides, leaves or twigs of the same age were not used, and age difference can introduce its own error. Also, they did not compare the changes in the different components of Ψ_W following changes in tissue water contents. Using the pressure-volume method, this study quantitatively assesses these changes in exposed and systematically shaded leaves of the same

[1] Present address: Forestry Research Institute of Nigeria, Savanna Station, P.M.B. 1039, Samaru, Zaria, Nigeria.

age from deciduous tree species, *Quercus petraea* and *Nothofagus procera*. Some structural variations between these leaves were also compared. This information is required for a better understanding of how these leaves contribute to the Ψ_w of tree species.

The two species chosen are of contrasting backgrounds, but widely distributed. *Q. petraea* is native to the British Isles and parts of Europe (temperate climate), while *N. procera* is native to Chile (mediterranean climate). It is therefore possible that the Ψ_w of their sun and shade leaves may differ and therefore provide a wider knowledge of the behaviour of sun and shade leaves of deciduous tree species.

Materials and Methods

Plant Materials and Experimental Layout

Three year old seedlings of *Q. petraea* (1+1 seed reference 76 (4331) R, altitude 500 m Spessart Forest Bavanei) obtained from the U. K. Forestry Commission and *N. procera* obtained from a plantation in Windsor Great Park, Windsor, Berkshire, England were grown in 23 cm diameter × 42 cm deep whale hide pots filled with top soil. The experiment was laid out on a flat open area at Silwood Park, Sunninghill, Berkshire. Five plants were used in each light treatment. At the initial Spring flush, leaves borne at the upper portion of the plant, which opened the same day in all treatment were labelled with tags.

Light Treatments and Fertilization

The treatments were full daylight (H), 49% of full daylight (M, produced by shading the plants with two layers of plastic garden netting) and 6.8% of full daylight (L, produced by shading with a sheet of pegboard). The shading was supported by wooden frames 180 cm × 90 cm with legs 120 cm high. The two layers of the plastic garden netting were allowed to extend vertically about 90 cm on all sides of the frames. Similarly, strips of pegboard about 60 cm wide by 180 cm or 90 cm long were attached vertically along the top edges of the lengths and breadths of the frames respectively. The shading intensities were measured by a Licor model 185 light sensor. The seedlings were watered daily. Once a month, 2 g of I. C. I. "Garden plus" (organic based fertiliser) was added.

Pressure-Volume Technique

Where water losses from leaves are controlled, the pressure chamber method provides accurate measurements of Ψ_w (Hellkvist *et al.*, 1974; Ritchie and Hinckley, 1975; Powell and Blanchard, 1976; Ishihara and Hirasawa, 1978; Turner and Long, 1980).

Measurements were made after one year of shading treatment. Five of the mature leaves of same age were sampled per treatment. Water losses from these leaves were controlled by cutting petioles of each of the three experimental leaves (one from each light treatment) under water. The leaves were then allowed to stand in distilled water to equilibrate for twenty-four hours in closed opaque plastic containers lined with tissue paper.

Measurements from these leaves were made simultaneously soon after removal from the containers using three seperate pressure bombs (Scholander *et al.*, 1965). Equilibrium was reached at each occasion before balancing pressure was measured, by reducing the pressure by 0.1 MPa and waiting for five minutes before checking the balancing pressure to agree within 0.007 MPa (Tyree *at al.*, 1978). In the measurements, each experimental leaf was subjected to a repeated sequence of operations which involved:

(a) weighing vials containing filter paper discs for sap collection.

(b) determining leaf turgid weight (TW),

(c) Sap removal by increased pressure at increment of 0.14 MPa,

(d) determining balance pressure (water potential, Ψ_w),

(e) releasing of pressure,

(f) reweighing vial with filter paper to obtain extracted symplastic water (ESW),

(g) reweighing leaf after determining the final balance pressure and final extracted symplastic water (LW),

(h) determining leaf area (LA), and

(i) leaf dry weight (DW) after drying to a constant weight at 80°C.

Operations "a-f" were repeated fourteen times in each leaf, before finishing with "g" and "h". Symplastic water left in the leaf after obtaining the final balance pressure (SLW) was calculated as LW-DW. Total leaf water content (V_t) was calculated as TW-DW. Relative symplastic water content (RSWC, %) at each balancing pressure was calculated from

$$RSWC=\frac{V_t-ESW}{V_t}\times 100\ (\%) \qquad (1)$$

where V_t=total leaf water content and ESW= extracted symplastic water at each RSWC.

A pressure-volume curve was then derived from each leaf by plotting $\frac{1}{\Psi_W}$ against RSWC (Scholander *et al.*, 1965; Hellkvist *et al.*, 1974). Ψ_W, Ψ_S and Ψ_P were determined from the curves at each RSWC (Tyree and Hammel, 1972; Hellkvist *et al., loc. cit.*). The means of values of Ψ_W, Ψ_S and Ψ_P at each RSWC interval were obtained per treatment. Höfler diagrams were constructed for each species with these means (Höfler, 1920):

Volumetric Bulk Modulus of Elasticity (ε)

ε between Ψ_P^{100} and Ψ_P^0 was calculated according to Kaplan and Gale (1974) where

$$\varepsilon=\frac{D_P}{DRSWC}\times 100\ (\%) \qquad (2)$$

where D_P=change in pressure and DRSWC= change in relative symplastic water content.

Bound Water Content (B)

B was determined as

$$B=\frac{V_t-V_0}{V_t} \qquad (3)$$

where V_t=total leaf water content and V_0= maximum possible volume of extractible symplastic water.

Specific Leaf Weight (SLW)

SLW was determined with the equation

$$SLW=\frac{DW}{LA}(g\ cm^{-2}) \qquad (4)$$

where DW=leaf dry weight and LA=leaf area.

Quantity of Water Lost Between Ψ^{100} and Ψ^0 per Unit Leaf Area (W^0/LA)

W^0/LA was determined with the equation

$$W^0/LA=\frac{V_0^{100}}{LA}(g\ cm^{-2}) \qquad (5)$$

where V_0^{100}=total extracted symplastic water between full and zero turgor and LA= leaf area.

Leaf Anatomical Properties

Transverse sections 25 μ thick were prepared from five other tagged experimental leaves in each treatment by means of a Cambridge rocker microtome fitted with a freezing stage. Temporary slides were prepared with the sections mounted in glycerol jelly. Measurements were then made of leaf thickness, the dimensions and distributions of the palisade and spongy mesophyll cells.

Statistical Analysis

Treatment differences were compared, using "Student's" *t*-test (Zar, 1974).

Results

$RSWC^0$

Between Ψ_P^{100} and Ψ_P^0, $RSWC^0$ increased

Table 1. *Ψ_P at full (Ψ_P^{100}) and zero (Ψ_P^0) turgor, Ψ_S at full (Ψ_S^{100}) and zero (Ψ_S^0) turgor, RSWC at zero turgor ($RSWC^0$) and quantity of water lost between Ψ_P^{100} and Ψ_P^0 per unit leaf area (W^0/LA) in leaves of* ***Q. petraea*** *and* ***N. procera*** *grown at different light intensities ($\pm S.E._{xt;\ p=0.05}$)*

Species	Light intensity[1]	Ψ_P^{100} (MPa)	Ψ_P^0 (MPa)	Ψ_S^{100} (-MPa)	Ψ_S^0 (-MPa)	$RSWC^0$	W^0/LA (gm^{-2}; 10^{-3})
Q. petraea	H	9.51±0.32*	0.25a±0.03*	9.52±0.13*	10.87±0.71*	91.08±1.74*	0.70 ±0.10*
	M	7.07±0.26*	0.33a±0.04*	7.07±0.35*	7.48±0.23*	86.91±1.30*	8.12b±1.70*
	L	4.50±0.54*	1.06 ±0.03*	4.50±0.63*	4.75±0.62*	74.01±0.95*	9.91b±0.43*
N. procera	H	11.52±0.47*	0.34 ±0.05*	11.52±0.55*	12.39±0.71*	91.87±1.15*	5.38 ±1.0*
	M	9.49±0.28*	0.51 ±0.06*	9.49±0.38*	10.77±0.82*	84.69±1.75*	8.64 ±0.81*
	L	5.17±0.34*	0.77 ±0.08*	5.17±0.26*	5.89±0.45*	76.04±0.93*	14.09±1.55*

[1] H=full day light; M=49% of full day light; L=6.8% of full day light.
* Significant at 5% level. In each species, between light treatment and within each property, means followed by the same letter are not significantly different at 5% level.

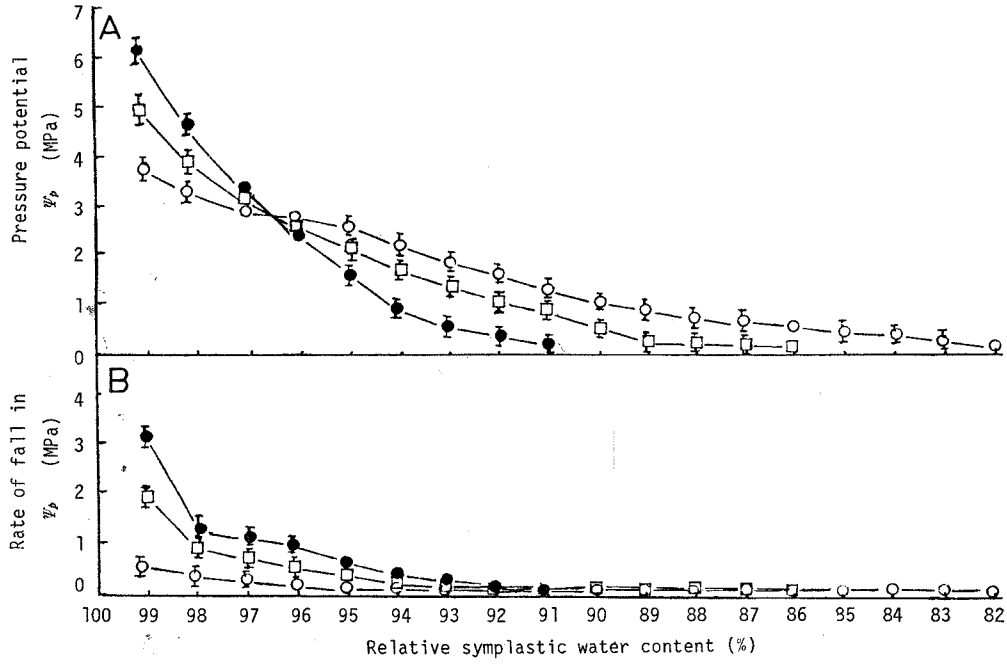

Fig. 1. Changes in (A) pressure potential (Ψ_P) and (B) rate of fall in Ψ_P with changes in relative symplasmic water content in leaves of *Q. petraea* grown at full light (●), medium light (□), and dense shade (○). Vertical bars show $\pm S.E._{xt;\ p=0.05}$ on two sides of the mean.

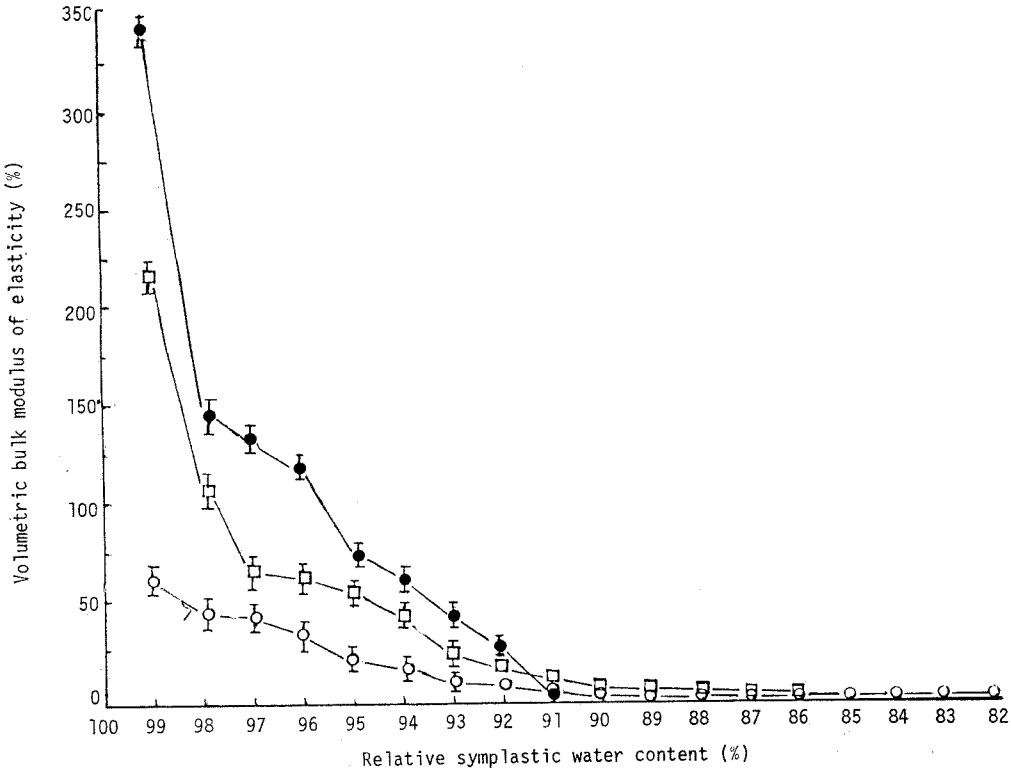

Fig. 2. Changes in volumetric bulk modulus of elasticity with changes in relative symblasmic water content in *Q. petraea* leaves grown at full light (●), medium light (□), and dense shade (○). Vertical bars show $\pm S.E._{xt:\,p=0.05}$ on two sides of the mean.

Table 2. *B, TW/DW and SLW* ($\pm S.E._{xt:\,p=0.05}$) *of* ***Q. petraea*** *and* ***N. procera*** *leaves grown in different light intensity treatments*

Species	Light intensity	Bound water (B) (g)	TW/DW ($g\ g^{-1}$)	SLW (gm^{-2})
Q. petraea	H	0.29a±0.11	1.05±0.13*	0.76±0.15*
	M	0.35a±0.13	1.46±0.11*	0.43±0.07*
	L	0.30a±0.10	2.13±0.09*	0.34±0.05*
N. procera	H	0.41b±0.24	1.10±0.05*	0.60±0.05*
	M	0.32b±0.10	1.55±0.15*	0.37±0.05*
	L	0.30b±0.13	2.41±0.20*	0.31±0.03*

* Significant at 5% level. In each species, between light treatments and within each property, means followed by the same letter are not significantly different.

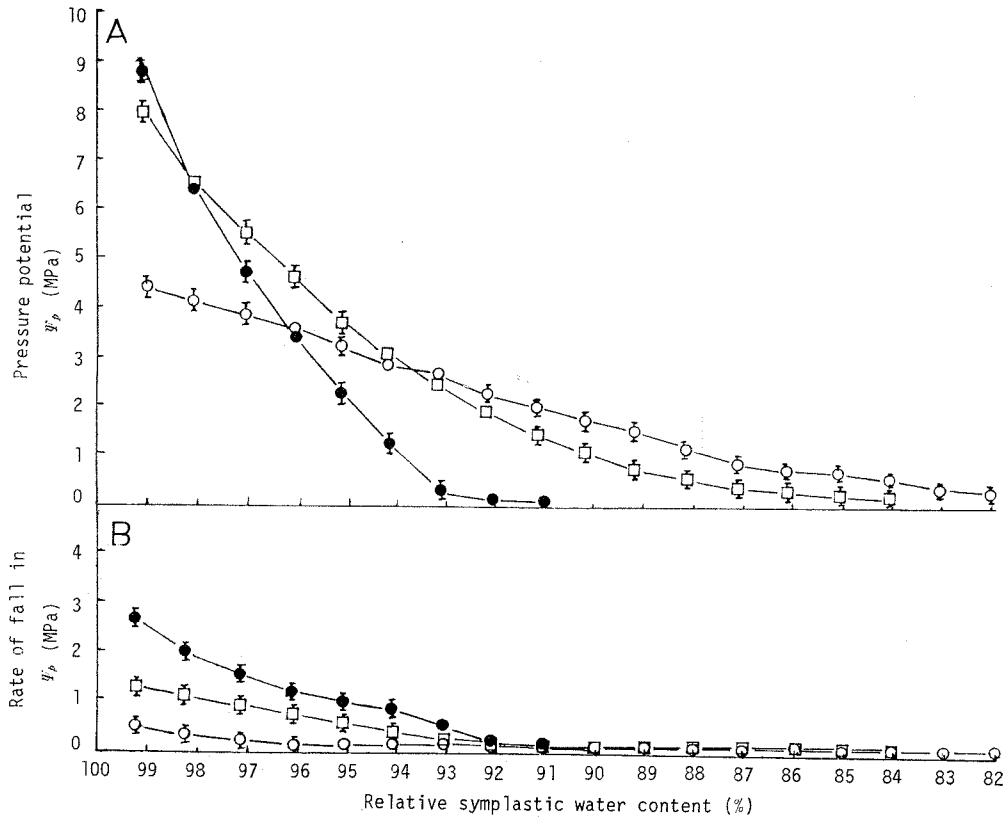

Fig. 3. Changes in (A) pressure potential (Ψ_P) and (B) rate of fall in Ψ_P with changes in relative symplasmic water content in leaves of *N. procera* grown at full light (●), medium light (□), and dense shade (○). Vertical bars±S. $E._{xi:\ p=0.05}$ on two sides of the mean.

Table 3. *Mean leaf anatomical properties of* ***Q. petraea*** *and* ***N. procera*** *leaves grown at different light intensities* (± $S.E._{xi:\ p=0.05}$)

Species	Light intensity	Leaf thickness (μm)	Number of palisade cells (10^3 cells mm^{-2})		Palisade cell length (μm)		Palisade cell breadth (μm)		Spongy cell length (μm)	Spongy cell breadth (μm)	Number of spongy cells (10^3 cells mm^{-2})
			upper	lower	upper	lower	upper	lower			
Q. petraea	H	173.4±1.0*	15±1*	13±1	60.91±2.31*	26.95±1.70	7.57 ±0.42*	11.0±0.7	18.75±0.38*	12.30±0.47*	13±0.5*
	M	149.7±1.6*	12a±1*	—	46.75±0.80*	—	9.53 ±0.31*	—	15.58±0.64*	14.87±0.43*	11±0.4*
	L	115.4±2.1*	12a±1*	—	34.39±0.54*	—	10.80 ±0.33*	—	13.88±0.33*	19.99±0.32*	8±0.1*
N. procera	H	167.9±2.6*	21 ±1*	10±1	57.82±1.3*	38.9 ±0.7	7.13 ±0.22*	11.5±0.2	18.34±0.39*	13.56±0.61*	12±0.3*
	M	114.7±1.4*	9 ±0.4*	—	42.55±1.37*	—	12.09c±0.35*	—	15.91±0.65*	18.31±0.36*	9±0.8*
	L	66.8±1.5*	8b±3*	—	27.40±0.91*	—	12.79c±0.58*	—	12.04±0.25*	20.33±0.62*	6±0.7*

* Significant at 5% level. In each species, between light treatments and within each property, means followed by the same letter are not significantly different.

with the decrease in solar radiation intensity treatment (P=0.05; Table 1). In the two species, $RSWC^0$ was higher with the increase in solar radiation intensity treatmnet (P=0.05; Figs. 1 to 4).

Ψ_P and ε

In the two species, Ψ_P^{100} increased with increase in light intensity treatment (P=0.05; Table 1). However, as water was extracted from leaf cells and Ψ_P began to fall, leaves of higher light intensities progressively experienced greater fall in Ψ_P with each unit fall in RSWC (P=0.05; Figs. 1 and 3). Hence, at lower RSWCs the trend reversed and Ψ_P became higher with increase in the degree of shading down to the points of Ψ_P^0 (P=0.05; Figs. 1 and 3).

ε increased with light intensity treatment in the two species (Figs. 2 and 4).

W^0/LA

Between Ψ_P^{100} and Ψ_P^0, the quantity of water lost per unit leaf area increased with the shading intensity (P=0.05; Table 1).

SLW and TW/DW

SLW increased, but TW/DW ratio decreased with increase in the radiation intensity treatment in both species (P=0.05; Table 2).

Bound Water Conten (B)

There were no significant differences between treatments in B in the two species (Table 2).

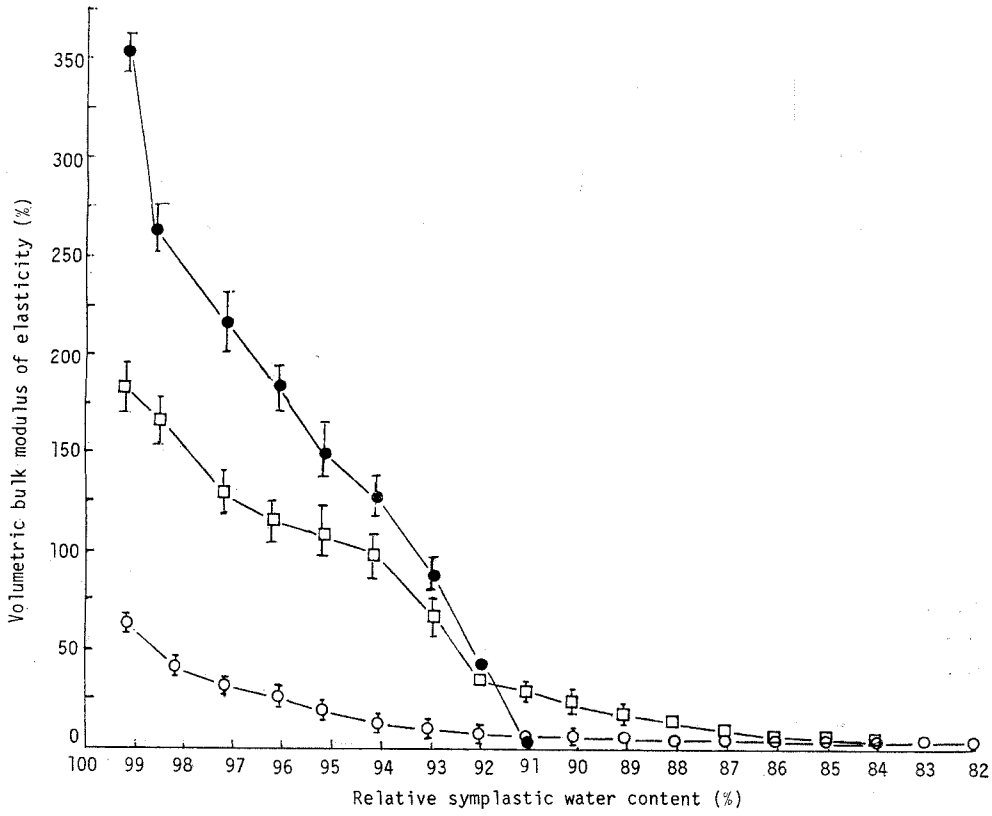

Fig. 4. Changes in bulk modulus of elasticity with changes in relative symplastic water content in *N. procera* leaves grown at full light (●), medium light (□), and dense shade (○). Vertical bars show ± S. E.$_{xt;\ p=0.05}$ on two sides of the mean.

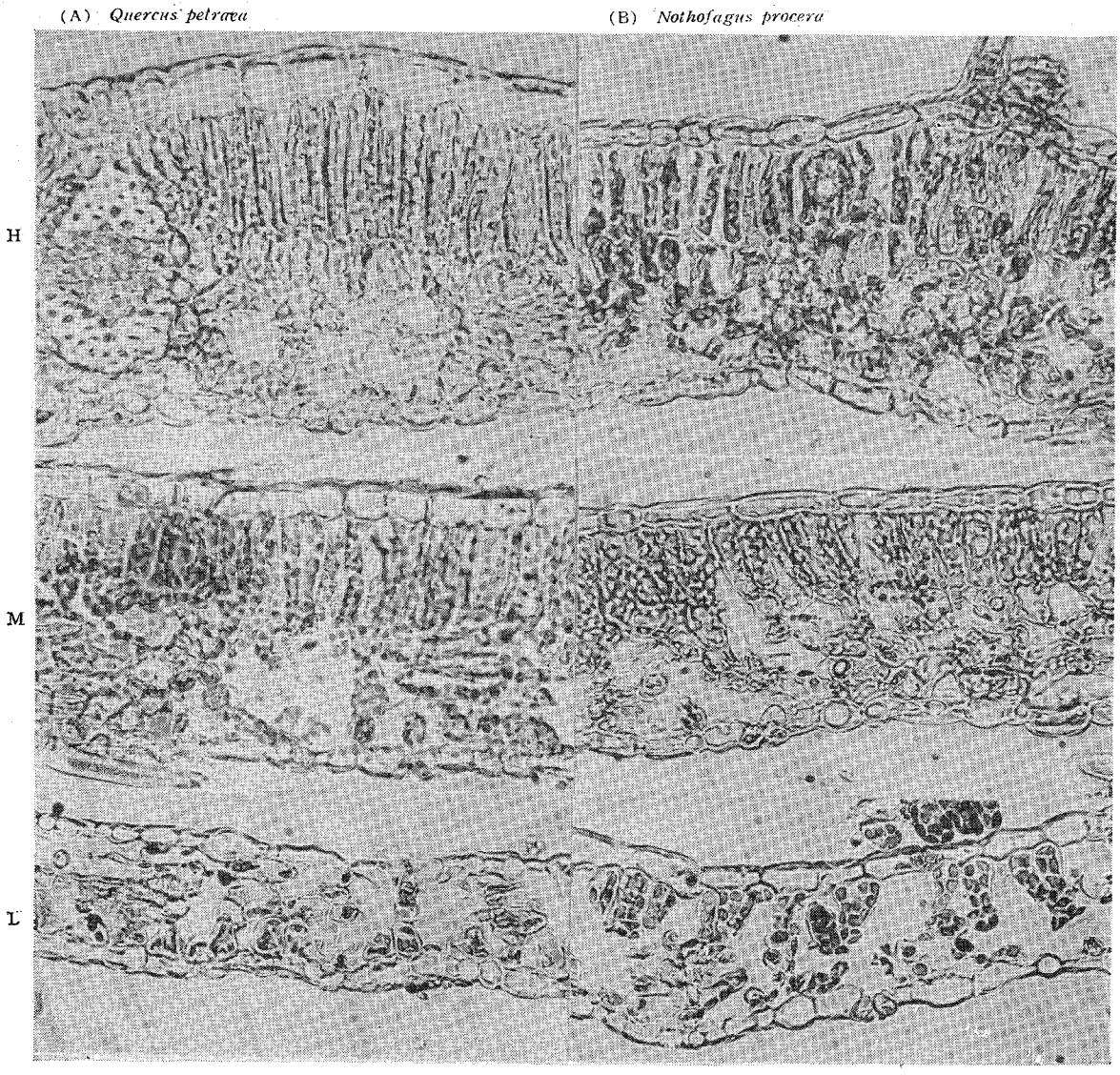

Fig. 5. T.S. of leaves of (A) ***Quercus petraea*** and (B) ***Nothofagus procera*** grown in full light (H), medium light (M) and dense shade (L). ×400

Leaf Anatomy

Leaf thickness, palisade and spongy cell length, and numbers per unit leaf area increased with the solar radiation intensity treatment (P=0.05; Table 3, Fig. 5.) However, shading intensity increased palisade and spongy cell breadths (P=0.05; Table 3, Fig. 5.)

Discussion

Although *Q. petraea* and *N. procera* are of contrasting geographical origins, their sun and shade leaves behaved alike in their responses to water losses. However, there was evidence that water relations of leaves in dense shade, intermediate and full light differed. It is possible that *N. procera* grown in Windsor great Park (England) had become adapted to the environment.

Leaves of higher light intensities had lower quantities of tissue water per unit amount of

dry matter accumulated, higher leaf thickness and SLW and greater number of tissues per unit amount of leaf area (Tables 2 and 3) These indicate higher dry matter production in these leaves (Pearce *et al.*, 1969, Durnhoff and Shibbes, 1970, Anake *et al.*, 1977, Wilson *et al.*, 1980) and greater tissue rigidity (Jones and Turner, 1978). This was evident in the changes observed in ε (Figs. 2 and 4). ε increased linearly with light intensity treatment (Figs. 2 and 4). Higher ε denotes decreased elasticity of leaf cells and this was found to alter the relationship between Ψ_P and tissue water content (Figs. 1 to 4). Thus, although Ψ_P^{100} decreased with shading intensity, as water was extracted from leaf cells and Ψ_P started decreasing in these leaves, Ψ_P decreased at greater rates in leaves of higher light intensities (Figs. 1 and 3), with a result that at about 96% RSWC in *Q. petraea* and between 93-97% RSWC in *N. procera*, the trend reversed as Ψ_P became higher with shading intensity (Figs. 1 and 3). Total loss of turgor represented by Ψ_P^0, occurred at a much lower Ψ_W and higher RSWC in leaves of full light intensity than those of medium and dense shade (Figs. 1 to 4). These findings confirm the hypothesis of Weatherly (1970), who showed that in tissues with decreased elasticity (higher ε), a large fall in Ψ_P follows a small fall in cell volume and that Ψ_P^0 would occur at higher RSWC than in more elastic tissues.

Between Ψ_P^{100} and Ψ_P^0, the trend of treatment differences in Ψ_S did not alter, remaining lower with increase in solar radiation intensity treatment (Table 1). Weatherly (1966), argued that a cell with lower Ψ_S can maintain turgor and turgor mediated processes to lower values of Ψ_W than those with higher Ψ_S. The above findings show that sun leaves can behave like drought affected leaves, while shade leaves behave like those of well watered plants (Grace and Russell, 1977; Cutler *et al.*, 1977; Olsson and Milthorpe, 1983).

The B values were found to vary between 0.29 and 0.41 in all treatments (Table 2). This range corresponds well with that found for other woody species in literature (Kramer, 1975; Warren-Wilson, 1967; Hellkvist *et al.*, 1974). Generally, an increase in B value has been associated with increased volume of cell wall material (Boyer, 1967), but this study does not include data on cell wall components or cell wall thickness, although SLW, leaf thickness and TW/DW ratio were found to vary (Tables 2 and 3). A decrease in TW/DW and an increase in the other properties would operate in the direction of higher water holding capacities of leaf tissue cell walls (Gaff and Carr, 1961). The lack of difference in B (Table 2) is interesting because TW/DW decreased with increase in light intensity treatment (Table 2) and this is generally associated with an increase in B (Hellkvist *et al.*, 1974). The reason for this lack of difference is unknown.

Since the reduction in Ψ_W in plant leaves is the driving force for water uptake from the soil, these findings have shown that as plants transpire, sun leaves are better adapted to draw water up plants than shade leaves.

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缺水與 *Quercus petraea* 及 *Nothofagus procera* 苗之向陽及遮蔭葉之水分關係的變化

A. B. I. Igboanugo

Department of Pure and Applied Biology., Imperial College of Science and Technology, Silwood Park, Sunninghill, Ascot, Berks., SL5, 7PY England UK

Quercus petraea 和 *Nethofagus procera* 的苗以兩種人工遮蔭及自然光照處理種於室外盆栽，應用壓力室技術比較處理間成熟葉片之水勢 (Ψ_W)，遮蔭可增加溶質勢 (Ψ_S) 及在完全膨壓 (Ψ_P^{100}) 及無膨壓 (Ψ_P^0) 之間單位葉面積隱涵的水量，但在 Ψ_P^{100} 壓力勢 (Ψ_P) 會降低。然而，當水開始自葉片粹取出來，高光照强度的葉片 Ψ_P 之降勢比高遮蔭處理爲高（因其有較高的彈性容積係數）。因此，在較高的相對共體質水分含量 (RSWC) 時，高光照强度處理葉片之 Ψ_P 漸漸下降到較密遮蔭處理葉片者爲低，且保持較低的 Ψ_R 至無膨壓爲止。高光照强度葉片在較高的 RSWC 達到 Ψ_P^0。這些現象表示向陽和遮蔭的葉片的 Ψ_W 分別表現與乾旱和水分充足的植株一樣，而當蒸散時，向陽的葉片比遮蔭葉更易將水分吸取上來。