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Adaptations to changes in illumination of chloroplast structure, chlorophyll content and light transmission of mature leaves of some deciduous tree seedlings

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Abstract. Four-year-old seedlings of *Quercus petraea* (Matt.) Liebl. and *Nothofagus procera* (Poepp. et Endl.) Oest. were grown out of doors in pots while subjected to three levels of light intensities and to changes in these levels of illumination. Histological and physiological studies of leaves, showed that shading intensity generally increased grana density, chloroplast diameter and chlorophyll content, but decreased leaf light transmission, number of chloroplasts per leaf cell, starch grains and plastoglobuli number per chloroplast. The study has shown that mature leaves of tree seedlings are capable of adapting anatomically and physiologically when faced with drastic changes in light intensity, irrespective of their adaptations during development and that leaf light transmission can serve as a non-destructive means of measuring chlorophyll content.

Key words: Changes in illumination; Chloroplast; Chlorophyll; Deciduous trees; Leaves; Light transmission.

Introduction

Part of the incident light passing through a leaf is scattered (detour effect) and reflected within the leaf (Gates *et al.*, 1965). Thus, light absorption within the leaf is maximized. The amount of light scattered or reflected within the leaf is a function of the leaf water content and the amount and manner of distribution of tissues within the leaf (Gates *et al.*, 1965; Gausman *et al.*, 1970; Sinclair *et al.*, 1973). The amount of light transmitted by the leaf is a major function of the amount absorbed (Terashima and Saeki, 1983).

Chlorophylls are the primary light trapping plant pigments (Katz *et al.*, 1979; Terashima and Saeki, 1983). Their amounts would be expected to affect the amounts of light absorbed or transmitted by leaves. Chlorophyll contents of sun and shade leaves have been shown to vary (Friend, 1960; Bjorkman and Holmgren, 1963; Jarvis, 1964; Smith, 1973). Grana density can also increase with shading (Goodchild *et al.*, 1972; Mache *et al.*, 1973; Skene, 1974). It has also been shown that grana density increased with the transfer of plants from high to low light, but did not change on transfer from low to high light (Skene, 1974). However, the lowest shading employed by Skene (1974) was 33.33% of full daylight. Besides, he sampled the leaves only after one week of transfer. But plants transferred to new conditions can take more than a week to complete their adaptation (Hughes, 1965).

Information on light absorption or transmission of mature leaves as affected by changes in chlorophyll contents is scarce. Also, there is no further published

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data on changes in chloroplast structure of mature leaves following a change of the incident light from low to high light. This study documents evidence of the above named changes, to show how sun and shade leaves contribute to the light use of plants. Such information may also be of value in studies aiming to predict the photosynthetic capabilities of plant canopies.

Materials and Methods

Plant Materials and Experimental Layout

Four-year-old seedlings of *N. procera* (Northern beech) and *Q. petraea* (Sessile oak) were used as experimental materials. *N. procera* is shade intolerant (Veblen *et al.*, 1980), whilst *Q. petraea* is shade tolerant (Jarvis, 1964). Hence, their photosynthetic apparatus may respond differently to changes in light intensity and therefore provide a wider knowledge of how sun and shade leaves can behave in such conditions.

The seedlings were transplanted into 23 cm diameter and 42 cm deep whale-hide pots filled with top soil. The experiment was laid out on the 6th of April 1983, on a flat open area at Silwood Park, Sunninghill, Berkshire (U.K.). Fifteen plants of each species were used in each light treatment. 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 by 90 cm, with legs 120 cm high. The two layers of the plastic garden netting were allowed to extend downwards to 90 cm on all sides of the frames. Similarly, strips of pegboard 60 cm deep by 180 cm or 90 cm long were attached vertically along the lengths and breadths of the upper portions 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 an organically based fertilizer-"Garden plus" (Imperial Chemical Industries) was added. Leaves that opened on the 4th of May in each treatment were selected from the upper parts of the foliage and tagged. On the 1st of August, the plants in each light treatment were labelled and 5 of them were transferred to each of the other two light treatments as follows:

full light to medium light=H-M
full light to low light=H-L
medium light to full light=M-H
medium light to low light=M-L
low light to full light=L-H
low light to medium light=L-M

Hence, it becomes possible to distinguish adaptations to light condition during leaf growth and development from adaptations that occur after the leaf had matured. Measurements were started on the 12th of August in each light treatment, when the leaves were fully mature (about 3 months old) and adaptations to the new light conditions had advanced.

Measurement of Light Transmission

The light source was of the mecury vapour lamp, provided with a meter to read off lamp illuminance. The amounts of full and monochromatic lights (different bands) transmitted by the experimental leaves were monitored with time, with the plants transported from the field into the laboratory during each measurements.

Light transmitted through the experimental leaves was measured with a Lambda LI 1905 quantum sensor connected to a Licor model LI 185 quantum meter amplifier. Measurements were made weekly from mid August to early October, using the following series of "CINEMOID" colour filters (Strand Electric, U.K.): clear (No. 30), blue (No. 20), green (No. 23), yellow (Nos. 33 and 38), red (No. 14). The light meter used is not sensitive to far red light and therefore no measurements were made in this band. Also, no attempt was made to distinguish direct and diffuse transmission or to measure reflection.

Five leaves from each of the five plants were used in each light treatment. Firstly, light transmitted through the filters at the same level to each experimental leaf was noted. With each leaf interposed between each filter and the photocell (avoiding the mid-rib and the major veins), light transmitted through the leaf was measured and calculated as the mean of six readings taken at various parts of the leaf. Light transmission was calculated as the ratio of light transmitted through each leaf to that transmitted through the particular filter as above without the leaf interposed (Gates *et al.*, 1965).

Determination of Chlorophyll Content

Chlorophyll contents of the above mentioned experimental leaves were determined in mid-October soon after the last light transmission measurements.

Six leaf discs each 1 cm in diameter were punched out of these leaves (3 from each side of the mid-rib). Chlorophylls were determined in 80% acetone, as described by Vernon (1960), whereby the different water contents of the experimental leaves were taken into account in determining the acetone dilutions. Absorbances were determined with a Beckman Spectrophotometer at 645 and 663 nanometers.

Histological Measurements

Transverse sections 25 μ thick were prepared from the middle part of the remaining experimental leaves by means of Cambridge rocker microtome fitted with a freezing stage. Temporary slides were prepared with the sections mounted in glycerol jelly. Chloroplast diameters and number per cell in both the palisade and spongy mesophyll cells were then measured.

Leaf tissues for electron microscopy were also obtained from the middle portions of the remaining experimental leaves. Specimens sectioned were limited to those from the highest and lowest light intensities. Small squares (1-2 mm) of the leaf tissues were cut from leaf discs under the fixative-glutaraldehyde (2%) in 0.1M sodium cacodylate buffer (pH 7) to which caffeine (0.5% v/v) was added to eliminate problems of excess tannin in the material (Lawton *et al.*, 1979). The cut squares were left in the fixative at room temperature overnight, rinsed for one hour in the 0.1M sodium cacodylate/caffeine buffer. The samples were further post fixed for two hours in 1% osmium tetroxide in 0.1M sodium cacodylate buffer. They were then progressively dehydrated through a series of graded acetone. Embedding was carried out in 100% spurr resin. Blocks were sectioned with 45° glass knives and sections mounted on uncoated 3 mm diameter 300 mesh grids. The tissues were post stained sequentially in 1% uranyl acetate in alcohol and 1% lead citrate. Chloroplasts in the sections were then viewed with the Philips 300 Electron microscope and their photomicrographs taken.

Grana density, number of plastoglobuli and starch grains per chloroplast were measured as counts at regular intervals across chloroplasts in five photomicrographs printed at the same final magnification in all treatments, using the multipurpose test system (Weibel and Scherle, 1966). Percentage of stroma per chloroplast sample was similarly calculated (Weibel and Scherle, 1966).

Correlations

In each species, mean full light transmission of five other leaves of the same age as the experimental leaves above, were measured per treatment and chlorophyll contents of these leaves were immediately determined as previously described. Light transmission was then correlated with chlorophyll contents.

Statistical Analysis

Treatment means were compared using the Student-Neuman-Keul multiple range test (Zar, 1974).

Results and Discussion

The prime function of leaves is to carry out photosynthesis. It would obviously be advantageous if all leaves on a plant are able to adapt so as to exploit the light environment in which they exist in the most efficient way. The species used in this study were shown to produce leaves with the light transmission, structure and composition of the photosynthetic apparatus much affected by the ambient light conditions.

Chloroplast number per palisade and spongy mesophyll cells increased with the increase in light intensity (Table 1). Chloroplast diameter was found to be lar-

Table 1. *Changes in mean chloroplast diameter and number per palisade and mesophyll cells of* ***Q. petraea*** *and* ***N. procera*** *leaves given different light intensity treatments*

Cell type	Light*	*Q. petraea*		*N. procera*	
		Number of chloroplasts	Chloroplast diameter (μm)	Number of chloroplasts	Chloroplast diameter (μm)
Palisade	H	23.1±0.3	2.7±0.2 b**	20.4±0.7	2.8±0.2
	M	16.8±0.4	3.3±0.3 ab	15.5±0.4	3.5±0.1 e
	L	10.2±0.2 h	4.3±0.2 c	6.2±0.3	4.6±0.1 fg
Spongy	H	10.7±0.2 h	3.3±0.1 a	12.5±0.5	3.6±0.1 e
	M	9.1±0.2 d	3.9±0.2 b	7.9±0.6	4.2±0.2 f
	L	8.6±0.3 d	4.5±0.03 c	4.0±0.2	5.2±0.3 g

* H, M, and L represent full, medium and low light, respectively.

** In each species, between palisade and spongy mesophyll cells and light treatments, means±S.E.$_{xt;\ p=0.05}$ followed by the same letter are not significantly different at the 5% level.

ger where leaves received lower light intensities and increased from the palisade to the mesophyll cells (Table 1). This is generally consistent with the findings of Priestly (1925b), Rabinowitch (1945) and Kirk *et al.* (1967). Grana density was also found to decrease with the increase in irradiance (Table 2; Figs. 1 and 2). This is similar to those reported elsewhere in other species of plants (Goodchild *et al.*, 1972; Mache *et al.*, 1973; Skene, 1974). According to Björkman *et al.* (1972) and Boardman *et al.* (1975), such decreases in grana density in high light, may be associated with increased quantities of the electron transport components. Thicker chloroplasts in relation to light path (adaxial-abaxial direction) and denser grana with decreasing light intensity treatments are adaptations to maximize the absorption of light quanta at lower light intensities (Boardman *et al.*, *loc. cit.*). On transfer however, L-H resulted in scanty grana, but large stroma (Table 2; Fig. 2). Conversely, grana density increased in H-L as the stroma size decreased (Table 2; Fig. 2). Except for L-H plants in the two species, the results obtained here with the transferred

Table 2. *Changes in grana and plastoglobuli densities and percentage of stroma in chloroplasts of* ***Q. petraea*** *and* ***N. procera*** *leaves given different light intensities* ($\pm S.E._{xt;\ p=0.05}$)

Species	Light*	Density (μm^{-2})		Percentage of stroma per chloroplast sample
		Grana (10^{-3})	Plastoglobuli (10^{-4})	
Q. petraea	H	0.12±0.002	0.47±0.01 a**	80.3±3.5
	L	0.61±0.01	0.29±0.002	24.1±0.8 e
	L-H	0.16±0.003	0.49±0.03 a	76.0±1.7 b
	H-L	1.08±0.03	0.36±0.001	21.8±0.5 ce
N. procera	H	0.14±0.001	0.71±0.003	72.4±2.8 bd
	L	0.77±0.03	0.03±0.001 b	20.1±0.9 c
	L-H	0.18±0.01	0.07±0.001	68.4±2.1 d
	H-L	0.63±0.01	0.03±0.001 b	19.7±0.8 c

* H and L represent full and medium lights, while L-H and H-L represent plants transferred from low to full and high to low lights, respectively.

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

Table 3. *Changes in mean chlorophyll contents of* ***Q. petraea*** *and* ***N. procera*** *leaves given different light intensity treatments* ($\pm S.E._{xt;\ p=0.05}$)

Light treatment*	*Q. petraea*				*N. procera*			
	Chlorophyll (mg cm^{-2})				Chlorophyll (mg cm^{-2})			
	a	*b*	Total	*a*/*b* ratio	*a*	*b*	Total	*a*/*b* ratio
H	0.41±0.02 a*	0.57±0.01	0.98±0.04 g	0.73±0.02 j	0.64±0.04 m	0.31±0.03 rs	0.95±0.07 a	2.06±0.14 z
M	0.58±0.02	0.81±0.02 c	1.39±0.03 i	0.72±0.03 j	1.49±0.06 p	0.87±0.03 t	2.36±0.05 v	1.72±0.10 z
L	0.76±0.04 b	1.15±0.03	1.91±0.04 h	0.66±0.03 j	0.80±0.05 q	0.62±0.08	1.42±0.11 w	1.30±0.14 xy
H-M	1.74±0.13 b	1.44±0.05	3.18±0.12	1.21±0.11 k	1.81±0.06	1.65±0.08	3.46±0.13	1.10±0.09 v
H-L	1.22±0.11	0.86±0.09 c	2.08±0.19 h	1.43±0.05 l	0.92±0.04 q	0.65±0.05	1.57±0.04 w	1.42±0.04 x
M-H	0.44±0.03 a	0.48±0.03 e	0.92±0.04 g	0.92±0.13 d	0.69±0.03 mn	0.37±0.03 r	1.06±0.05 u	1.86±0.04 z
M-L	1.84±0.02 b	1.86±0.18 f	3.71±0.03	0.99±0.01 k	1.38±0.07 p	0.84±0.04 t	2.05±0.05	1.65±0.05
L-H	0.40±0.12 a	0.43±0.09 e	0.83±0.19 g	0.94±0.16 d	0.50±0.05 n	0.26±0.03 s	0.76±0.06	1.90±0.07 z
L-M	2.59±0.04	1.78±0.06 f	4.38±0.09	1.46±0.05 l	1.64±0.05	0.88±0.03 t	2.53±0.06 v	1.85±0.09 z

* H, M and L treatments represent full, medium and can lights respectively, while H-M, H-L, M-H, M-L, L-H and L-M represent plants transferred from full to medium, full to low medium to full, medium to low, low to full and low to medium lights, nespectively.

** In each chlorophyll property, between light intensity treatments, means followed by the same letter are not significantly different at the 5% level.

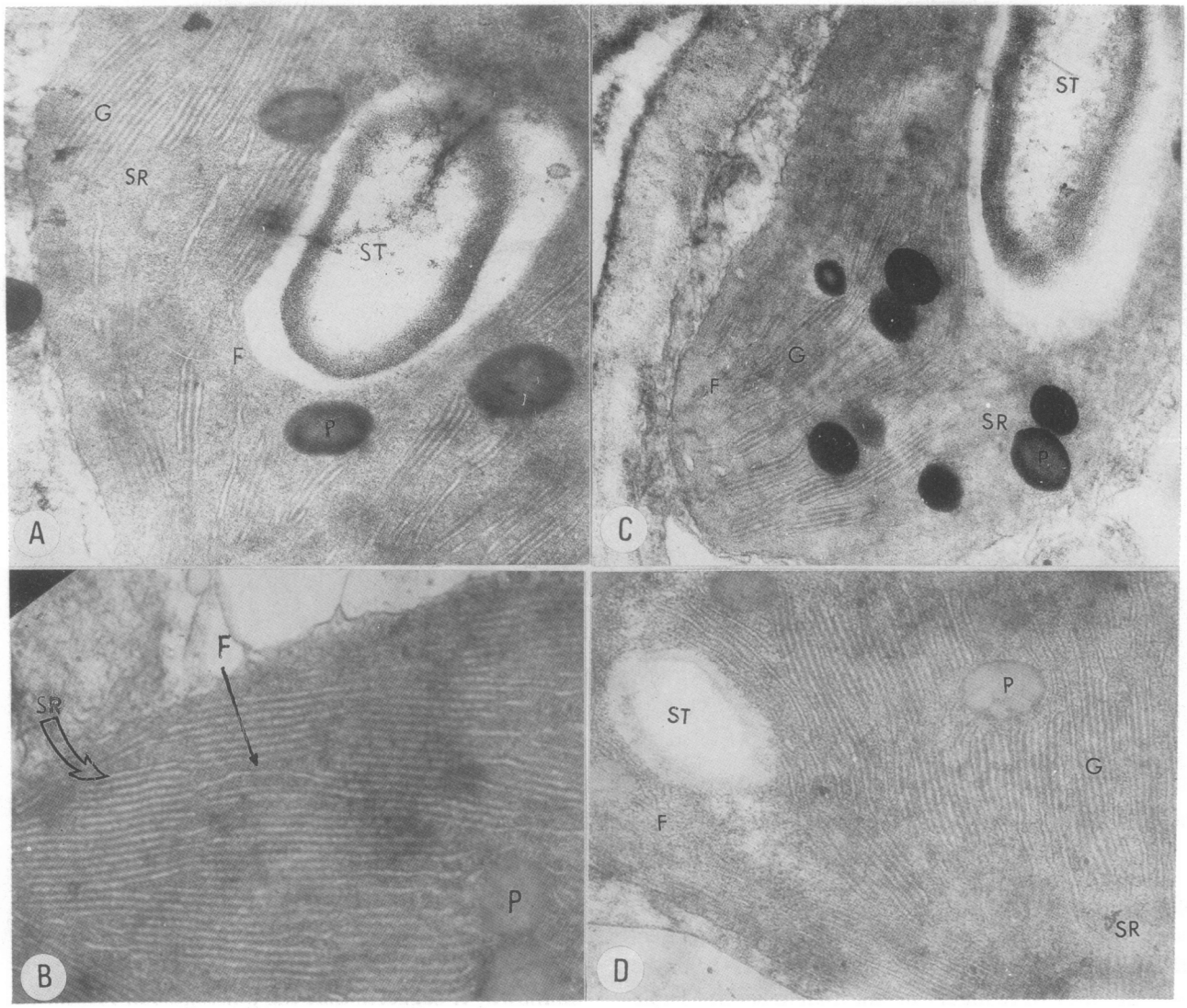

Fig. 1. Chloroplasts of leaves of *Q. petraea* (A, B) and *N. procera* (C, D) grown in (A, C) full daylight and (B, D) dense shade (×19400), G=grana; SR=Stroma; F=fret; P=plastoglobulus; ST=starch grain.

plants are similar to that of Skene (1974) in apple. However, he did not observe any change in grana thickness with the transfer from low to high light. The seven day time lag between his transfer and sampling dates may have been inadequate for his shade grown plants to complete their biochemical and ultrastructural adaptations to full light. However, plants transferred to new environments can take more than a week to complete their adaptations (Hughes, 1965). Denne (1976) also found that *Picea sitchensis* transferred to more adverse light and temperature conditions took longer time to adapt anatomically than those transferred to less adverse ones. In terms of chloroplast transformations, the transfer from low to high light is a movement from a benign to an adverse condition. The plants used in this study were however left for more than six weeks in their new light environments before samples were collected for electron microscopy. Also, while Skene (1974) applied 33.3% of full light, the shading employed in this study was 6.8% of full day-

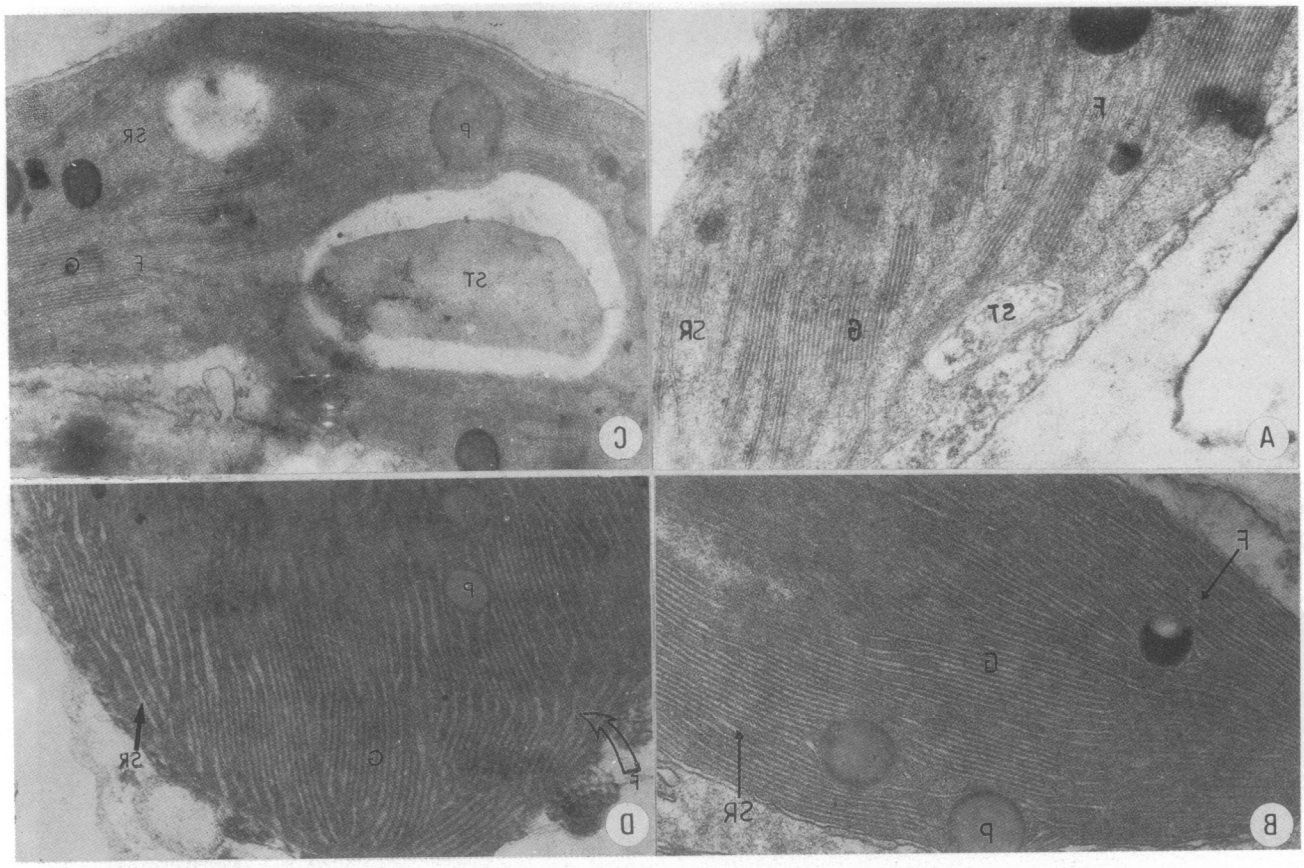

Fig. 2. Chloroplasts of mature leaves of *Q. petraea* (*A*, *B*) and *N. procera* plants transferred from (A, C) low to full light and (B, D) full to low light (×26291). G = grana; SR = stroma; F = fret; P = plastoglobulus; ST = starch grain.

light. These differences may account for the differences in results. In full, low or L-H light, grana densities were similar in the two species. In H-L leaves however, they were higher in oak than in beech (Table 2; Fig. 2). Although the reason for this behaviour is unknown, it shows that chloroplasts from mature leaves in the two species can adapt differently when faced with changes in light intensity.

Starch grians were prevalent in H and L-H chloroplasts studied (Table 2; Fig. 2). This suggests that under full light, carbohydrates are synthesized in excess of rate of translocation out of the leaves, hence, some starch was stored. It was possible that the starch grains found in H-L chloroplast in beech was remainder from H (Table 2; Fig. 4). Unlike starch grians, plastoglobuli were observed in all samples (Tabel 2; Figs. 1 and 2). They have been suggested to be stored lipids (Robards, 1970). Plastoglobuli density observed in L-H leaves in beech, were much lower than in H. Although, the reason for this behaviour is unknown, it suggests that the plastoglobuli formation in L-H leaves could not adapt to the H light regime within the period of transfer in this study.

In oak, chlorophyll contents per unit area increased with the decrease in light intensity (Table 3). In the transferred plants however, although chlorophyll contents adapted to the new light levels, they were generally doubled when transferred to M and L (Table 3). The reason for this response is unknown. These results generally agree with those of Priestley (1925b) and Jarvis (1964). However, in beech, chlorophyll content was highest in M, but lowest in H (Table 3). Veblen *et al*. (1980) classed *Nothofagus* as shade-intolerant genus. It was possible that L (6.8% light)

Table 4. *Changes in the monthly light transmission of mature leaves of* ***Q. petraea*** *and* ***N. procera*** *leaves given different light intensity treatments*

In each species and light type, between light intensity treatments, means followed by same letter are not significantly differnet at 5% level. H, M and L treatments represent full, medium and low lights respectively, while H-M, H-L, M-H, M-L, L-H and L-M represent plants transferred from full, to medium, full to low, medium to full medium to low, low to full and low to medium lights respectively.

		Q. petraea									*N. procera*								
Time of measurement	Filter used	Untransferred plants			Transferred plants						Untransferred plants			Transferred plants					
		H	M	L	H-M	H-L	M-H	M-L	L-H	L-M	H	M	L	H-M	H-L	M-H	M-L	L-H	L-M
Mid August	Full-light	0.095	0.068	0.063	0.081	0.077	0.072 d	0.066	0.088	0.072 d	0.193	0.064	0.149	0.125	0.190	0.072	0.066	0.150	0.051
	Blue	0.030	0.018	0.013	0.029	0.025	0.019	0.014	0.045 e	0.041 e	0.040	0.015	0.039 d	0.038 d	0.034 c	0.034 c	0.017	0.042 e	0.040 de
	Green	0.112	0.107	0.089	0.106 f	0.098	0.106 f	0.109 f	0.107 f	0.095	0.205 a	0.117	0.203 a	0.119	0.201 f	0.112 g	0.114 g	0.210	0.200 f
	Yellow	0.138	0.102	0.090	0.124	0.116	0.095	0.105 g	0.125	0.108 g	0.218	0.010	0.214	0.155	0.198	0.084	0.109	0.217	0.095
	Red	0.060	0.044	0.036	0.058 c	0.059 c	0.049	0.077	0.054	0.050	0.095	0.040	0.089	0.088 h	0.086 h	0.078	0.051	0.102	0.044
Mid September	Full-light	0.068	0.052	0.056	0.057 i	0.051 h	0.069	0.050 h	0.071	0.056 i	0.089	0.061	0.074	0.057	0.091	0.095 i	0.077	0.094 i	0.065
	Blue	0.019 s	0.018 s	0.011	0.015 j	0.009	0.020	0.009	0.015 j	0.016 j	0.035	0.010	0.029	0.009	0.034	0.040	0.031 j	0.031 j	0.011
	Green	0.113	0.082	0.055	0.086	0.050	0.115	0.060	0.108	0.079	0.123	0.099	0.112	0.069	0.092	0.127	0.114	0.125	0.102
	Yellow	0.118	0.096	0.073	0.089	0.063	0.117	0.067	0.111	0.099	0.164	0.083	0.108	0.075	0.099	0.168 k	0.110	0.166 k	0.085
	Red	0.049	0.033	0.029	0.035 k	0.032 k	0.046	0.028	0.052	0.038	0.062	0.036	0.046	0.037 l	0.049	0.070	0.051	0.060	0.039 l
Mid October	Full-light	0.059	0.044 a	0.040 a	0.048 m	0.035	0.061 l	0.039	0.063 l	0.047 m	0.082	0.053	0.070	0.055 m	0.065	0.079	0.067	0.094	0.055 m
	blue	0.010	0.009 b	0.008 b	0.007 nm	0.006 nm	0.013	0.005 m	0.012 p	0.011 p	0.024	0.008	0.020	0.007	0.014	0.025 n	0.018	0.025 n	0.010
	Green	0.092	0.075	0.047	0.081	0.045	0.088	0.050	0.105	0.087	0.107	0.075	0.101	0.077 p	0.100	0.098 r	0.078 p	0.109 r	0.081
	Yellow	0.107	0.070	0.061	0.085	0.056	0.097	0.072	0.110	0.073 q	0.121	0.070	0.099	0.065	0.092 t	0.114	0.091 t	0.125	0.064 s
	Red	0.038	0.031	0.026	0.033 r	0.029	0.044	0.034 r	0.040	0.035	0.056	0.032	0.041	0.030 u	0.038	0.060	0.044	0.050	0.029 u

Table 5. *Correlation coefficients (r) for relationship between mean light transmission (LT) and chlorophyll content (CC; mg cm^{-2}) in leaves of* ***Q. petraea*** *and* ***N. procera*** *given different light intensity treatments.*

Species		Light intensity treatment*									r
		H	M	L	H-M	H-L	M-H	M-L	L-H	L-M	
Q. petraea	CC	1.1	1.4	2.4	2.5	2.1	0.9	2.7	0.8	2.9	
											-0.88**
	LT	0.063	0.047	0.013	0.031	0.015	0.061	0.010	0.065	0.028	
N. procera	CC	1.0	2.5	1.6	3.1	1.3	1.9	1.8	1.2	2.7	
											-0.93**
	LT	0.067	0.022	0.045	0.011	0.049	0.030	0.039	0.043	0.019	

* H, M and L treatments represent full, medium and low lights respectively, while H-M, H-L, M-H, M-L, L-H and L-M represent plants transferred from full to medium, full to low, medium to full, medium to low, low to full and low to medium lights respectively.

** Significant at 1% level.

plants may have been very close to the long term compensation point and that a decrease in chlorophyll content was a result of this. In the transferred plants in beech, chlorophyll content also adapted to the new light levels (Table 3). The reductions in chlorophyll contents in L-H in both species (Table 3) could have resulted from traumatic effects of exposure to full light, resulting in chlorophyll denaturation. It was visually observed that the leaves of L-H were bleached. In beech, chlorophyll bleaching affected all leaves in L-H, irrespective of height of attachment, but in Oak the effect was only obvious in the upper leaves.

In oak, chlorophyll *b* contents were generally higher than chlorophyll *a*, but in beech, chlorophyll *b* contents were generally lower than chlorophyll *a* (Table 3). This suggest that there are also species differences in the synthesis of chlorophyll components. Chlorophyll *a* : *b* ratios generally decreased with light intensity in both species (Table 4). This corresponds to the observations of Friend (1960) and Björkman and Holmgren (1963), who showed that high light intensity was associated with lower chlorophyll *b* contents than chlorophyll *a*, thus resulting in higher chlorophyll *a* : *b* ratios.

Light not transmitted through the leaf is either absorbed or reflected. Leaves that had higher chlorophyll contents, showed lower light transmission and vice versa (Tables 3 and 4). Although, lower light transmission suggests higher light absorption (Terashima and Saeki, 1983), higher light absorption in plants of lower light intensity treatments would not be followed by higher photosynthetic rates, for shade leaves generally have lower photosynthetic rates in high light than sun leaves (Böhning and Burnside, 1956), owing to their having lower quantities of several components of the electron transport chain than sun leaves (Björkman, 1972; Boardman *et al.*, 1972). The proportion of the incident radiation absorbed is primarily the function of chlorophyll contents (Gates *et al.*, 1965), although pheophytins, carotenoids and xanthophylls can also absorb some light. Gausman *et al.* (1970) showed that the band range 0.50 μm is dominated by pigment absorption. The lower amounts of blue and red light transmitted (Table 4) are consistent with the known properties of chlorophyll is *a* and *b* whose absorption peaks are in these bands, respectively. This also explains the higher amounts of green, yellow and red lights transmitted (Table 4). Full light transmission correlated negatively with chlorophyll content (Table 5).

Light transmission in both species declined with leaf age (Table 4). On transfer, light transmission of leaves also adapted to the new light environments, the adaptations being more obvious as from mid-September (Table 4). The observation generally agrees with that of Willstatter and Stoll (1913), as quoted by Gausman *et al.* (1970). Undoubtedly, as leaves age, they accumulate materials on the leaf surfaces that increase reflectivity or reduce absorption of light. However,

the lamp illuminance was also known to decrease with time. It was likely that this was partly responsible for the results. The foregoing shows that in mature leaves, the photosynthetic apparatus can adapt to changes in solar radiation intensity and that these adaptations are reflected in the quantities of light transmitted through these leaves. Hence, light transmission of leaves, can serve as a non-destructive means of measuring chlorophyll contents.

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落葉樹幼株成熟葉之葉綠體結構、葉綠素含量及光穿透性對光照變化之適應

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置於室外盆栽之四年生的 *Quercus petraea* (Matt.) Liebl. 及 *Nothofagus procera* (Poepp. et Endl.) Oest. 之幼株施以三種強度之光照處理，並互換此不同之光照。由葉的組織學及生理上的研究顯示，陰暗之光度普偏地提高了葉綠餅密度、葉綠體直徑及葉綠素含量，但降低了葉的光穿透性和細胞中葉綠體、澱粉粒與葉綠體中之球狀體 (plastoglobuli) 的數目。此研究顯示樹木幼株之成熟葉可藉由解剖及生理上的適應來面對劇烈的光照變化，而不會影響其生長發育上的適應，且葉的光穿透性可作爲非破壞性測量葉綠素含量的方法。