

Invasion by *Pittosporum undulatum* of the Forests of Central Victoria. IV* Shade Tolerance

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Abstract

Seedlings of *Pittosporum undulatum* were grown under shade screens for 16 days at four flux densities: 97.8, 18.2, 3.4 and 0.4% full daylight, i.e. c. 420, 78, 14 and 2 W m⁻². Seedlings showed moderate tolerance of shade: the growth compensation point for light was 1.6% daylight, the leaf area ratio in full daylight was low (48.96 cm² g⁻¹) and when plants grown at 0.4% were compared with those grown at 97.8% full daylight and there was a fourfold increase in chlorophyll concentration. Leaves were thinner at the lowest flux density because the cells were deflated and there appeared to be only one row of palisade mesophyll cells. On the other hand, there was no large increase in leaf area ratio with shading, no alteration in the chlorophyll *a/b* ratio and no depression of net assimilation rate in full daylight. *P. undulatum* can endure shade but has a higher growth rate when grown at higher photon flux densities. *P. undulatum* is found predominantly in shade owing to the uneven dispersal of seed and the site-dependent survival of seedlings and not because shade is required for maximum growth.

Introduction

Initially, invading *Pittosporum undulatum* Vent. is found predominantly at the butts of established trees and shrubs where the irradiance is frequently between 4-8% full daylight and may be as low as 2% (Gleadow and Ashton 1981). This is due partly to the patchy distribution of seed by birds (Gleadow 1982) and partly to increased drought tolerance of seedlings in sheltered positions (Gleadow and Rowan 1982). However, the level of shade tolerance and whether or not seedlings have a higher growth rate in partial shade compared with full daylight are unknown. This experiment was to determine the shade tolerance of seedlings of *P. undulatum* by using the following criteria.

Sun and shade plants are usually distinguished by the level of light radiation under which they normally grow (Went 1957). Many workers consider that a low compensation point for light at a given time ('instantaneous') or over a period of weeks ('growth' compensation point) indicates whether that species is a sun or a shade plant (Bielecki 1959; Boardman 1977; Huber 1978; Ashton and Turner 1979). Mahmoud and Grime (1974) criticized use of the light compensation point as an estimate of shade tolerance, preferring to measure the negative relative growth rate below the compensation point. Nevertheless, species accepted as shade-tolerant usually have a light compensation point of less than 2% full sunlight (Jarvis 1964). Other properties considered characteristic of shade plants are: high chlorophyll concentration per unit leaf area (Loach 1967; Nobel 1976; Bunce *et al.* 1977), expanded leaf area (Packham and Willis 1977), reduced development of the palisade mesophyll (Jackson 1967; Bjorkman *et al.* 1972; Nobel *et al.* 1975) and increased leaf area ratio in shade compared with full sunlight (Evans and Hughes 1961; Hiroi and

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Monsi 1963). A low photon flux density required to saturate photosynthesis and a low rate of photosynthesis at saturating light are also common (Loach 1967; Bjorkman *et al.* 1972).

Methods

Plant Material

Seedlings of *Pittosporum undulatum*, germinated as described by Gleadow and Rowan (1982), were planted into seed boxes filled with krasnozem top soil and grown in a glasshouse. After 2 weeks, 100 seedlings were transplanted into pots (5 cm in diam.) containing *c.* 260 g soil and returned to the glasshouse for 1 month. Seedlings were then transferred to the open, and full sunlight, for 4 months (July–November). *P. undulatum* grows slowly as a young seedling, until the formation of a terminal closed bud; it then grows in flushes several times a year (Gleadow 1982). Seedlings used in this experiment were just entering the dormant bud phase of growth. Plants were watered with a complete fertilizer three times in the 2 weeks prior to the experiment.

The experiment was conducted in an open area unshaded by buildings or trees. Plants were divided into five groups of 15 replicates. The members of each group were selected to match in height, leaf number and size of the dormant bud. One group of 15 was harvested immediately for initial measurements of dry weight and leaf area. The other four groups were grown at different photon flux densities, achieved by using screens made of one or more layers of Sarlon shade cloth of *c.* 20% transmission. The cloth was suspended on a metal frame and reached to within 20 cm of the ground. Scattered light from the sides was reduced by raising the pots 20 cm off the ground. The ground was also covered with cloth to reduce reflections from the surrounding concrete. The plants, randomly arranged on trays, were watered every second day.

Light Conditions

The radiant flux density (W m^{-2}) of short-wave radiation (400–1200 nm) experienced under each shade screen was measured relative to full daylight on three cloudy and two sunny days at intervals throughout the day by pyranometers. As the pyranometer was placed in the centre of the screen at the height of the plants, the relative radiant flux density was below 100% even with the full light treatment. The radiant flux densities for each treatment were calculated as a percentage of the mean flux density of full daylight recorded for Melbourne at Highett (Anon. 1978) and are shown in the following tabulation:

	Radiant flux density	
	Relative (% daylight)	Calculated (W m^{-2})
	97.4 ± 1.78	419.58
	18.2 ± 1.39	78.48
	3.4 ± 1.15	14.43
	0.4 ± 0.20	1.77

Temperatures

Maximum–minimum thermometers, sheltered from direct sunlight by ceramic pipes (35 cm long, 9.5 cm in diam.), were placed in each shaded area and the temperatures recorded every second day. Respiration and photosynthesis would not have varied between treatments through differences in temperature because differences between treatments were not significant, as shown in the following tabulation:

	Relative flux density (%)			
	97.4	18.2	3.4	0.4
Maximum (°C)	28.8 ± 1.84	27.6 ± 1.96	27.0 ± 2.01	27.7 ± 2.05
Minimum (°C)	12.4 ± 1.10	12.4 ± 1.08	13.1 ± 1.16	13.8 ± 1.05

In comparison, mean maximum and minimum temperatures recorded for Melbourne by the Bureau of Meteorology for the same period (20 November–5 December 1978) were 23.5 ± 1.28 and $13.7 \pm 0.82^\circ\text{C}$.

Morphology and Growth Parameters

Sixteen days after the initial harvest, leaf area and dry weight were measured. This period was long enough to include adaptation to the new light treatments and short enough to avoid problems with ontogenetic development of the plants (Evans 1972). This interval tested the adaptation of existing leaves to the treatments, since flushes of growth did not occur during the 2 weeks. The measured parameters were used to calculate relative growth rate (R_w), net assimilation rate (E_A) and leaf area ratio (F_A), as described by Gleadow and Rowan (1982). The results were analysed by analysis of variance, the data being transformed to logarithms or inverse sines when necessary.

Pigment Analysis

In a preliminary experiment, plants were grown for 2 months under the same flux densities described above and used for pigment analyses. Ten discs (1 cm in diam.) weighing between 0.5 and 1.0 g were cut with a paper punch from the top five mature leaves on three plants per treatment. The samples were blended twice in 10 ml 80% (v/v) acetone with a Sorval Omnimixer at *c.* 140 V. The solution was filtered through Whatman No. 50 paper and the volume adjusted to 25 ml. The extinction of the solution at 664, 647 and 450 nm was measured with a Pye-Unicam SP6-400 u.v. spectrophotometer. Chlorophyll *a* and *b* concentrations were calculated by use of the revised formulae of Jeffrey *et al.* (1974). The carotenoid concentration was estimated using the formula derived by Jaspers (1965) based on the extinction coefficient of β -carotene at 450 nm. Total chlorophyll per unit area, chlorophyll *a/b* and carotenoid/chlorophyll ratios were calculated and analysed by analysis of variance on arcsine transformed data.

Leaf Anatomy

Leaves from extra plants adapted to the experimental treatments were used to examine the effect of different photon flux densities on leaf anatomy. Pieces of the fourth mature leaf from the apex were cut from near the mid-vein and fixed in Karnovsky's fixative (Karnovsky 1967). After dehydration through ethanol, the pieces were embedded, using JB-4 embedding medium (Polysciences Inc., Warrington, Pa, U.S.A.). Transverse sections, 2.5 μm thick, were cut with a microtome (Cambridge Instruments). The fluorescent stains Calcofluor M2R (0.1%) and Auramine 0 (0.1%) were used to observe cuticle thickness and cell wall arrangement respectively. General anatomy was observed on sections stained with 1.0% toluidine blue. The thickness of the leaves was measured under the microscope and analysed by an analysis of variance.

Results

Growth Measurements and Light Compensation Point

Total dry weight decreased with decreasing photon flux densities (Table 1). No new leaves were produced so there was no significant change in leaf area; however, in a preliminary experiment in which seedlings were grown under shade screen for 2 months, the leaf area was significantly greater in the deepest shade. E_A and R_w , calculated using matched pairs, were approximately proportional to the relative flux density above the compensation point and were negative at 0.4% full daylight (Fig. 1 and Table 1). F_A decreased exponentially with increasing flux density (Fig. 2), although this must have been due mainly to depletion of reserves throughout the plant. When F_A is plotted against the

logarithm of the relative flux density (Fig. 2) the slope is $15.3 \text{ cm}^2 \text{ g}^{-1}$ per unit log (relative flux density). This indicates low shade tolerance (Jarvis 1964).

Table 1. Growth measurements and parameters of seedlings grown under four photon flux densities

The F ratios from the analysis of variance and their significance are given. Initial harvest values (I) are given where applicable. D , total dry weight; A , total leaf area; L_N , total leaf numbers; R_W , mean relative growth rate; F_A , leaf area ratio. Means in the same row with the same letter are not significantly different at $P < 0.05$ using Duncan's multirange test. *** $P < 0.001$

	Relative flux density (%)				F ratio	I
	97.4	18.2	3.4	0.4		
D (g)	2.31 ^a	2.06 ^{ab}	1.98 ^b	1.47 ^c	10.42***	1.84
A (cm ²)	111.84 ^a	110.02 ^a	109.06 ^a	101.29 ^a	0.45	103.20
L_N	14.2 ^a	14.5 ^a	15.5 ^a	14.7 ^a	0.72	12.9
R_W (cm ² g ⁻¹ day ⁻¹)	0.030 ^a	0.009 ^{ab}	0.005 ^b	-0.015 ^c	14.44***	
F_A (cm ² g ⁻¹)	48.96 ^a	54.11 ^{ab}	57.43 ^b	71.41 ^c	17.76***	

The flux density at which E_A is zero is the light compensation point. From Fig. 1, this is estimated to be 1.6% full daylight, i.e. 6.9 W m^{-2} short-wave radiation (Table 1) or 3.5 W m^{-2} photosynthetically active radiation (PAR) (Monteith 1973). The sharp decline in dry weight near the light compensation point and the corresponding 75% drop in E_A make it difficult to determine exactly where the plot of E_A crosses the horizontal axis; however, the error is reduced because only interpolation is required (Hughes 1966).

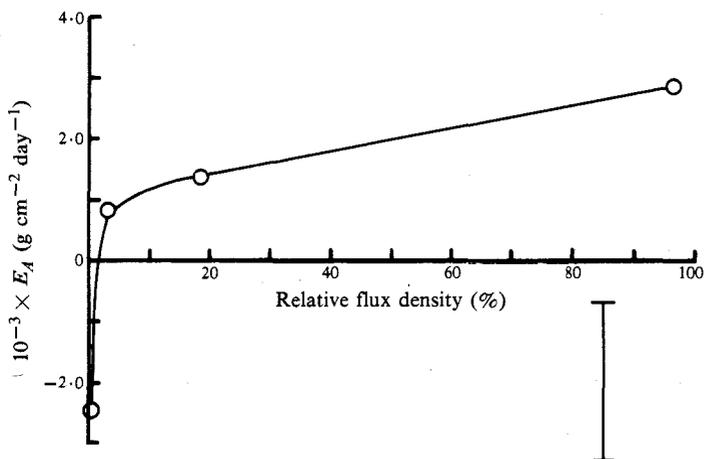


Fig. 1. Net assimilation rate of *P. undulatum* seedlings grown at four levels of shade for 16 days. The light compensation point is estimated from this diagram to be 1.6% full daylight.

Pigment Analysis

The total amount of chlorophyll increased with increasing shade on a leaf area basis; however, chlorophyll a/b ratios did not differ significantly (Table 2). The carotenoid concentration increased significantly in plants grown under the lowest flux density but the carotenoid/chlorophyll ratio was significantly lower in all three shade treatments.

Leaf Anatomy

The leaves adapted to full daylight had three rows of palisade mesophyll cells while leaves adapted to the 0.4% light treatment appeared to have fewer rows (Fig. 3). This suggests that there was some degree of adaptation of existing leaves to the new light treatments and implies that the leaves used for the anatomical study were not fully mature.

The cells in leaves grown in 0.4% daylight appeared deflated, and overall the leaves were thinner (Table 3), suggesting that all the available reserves were used in respiration. The stomata were level with the epidermis and their position did not vary markedly between

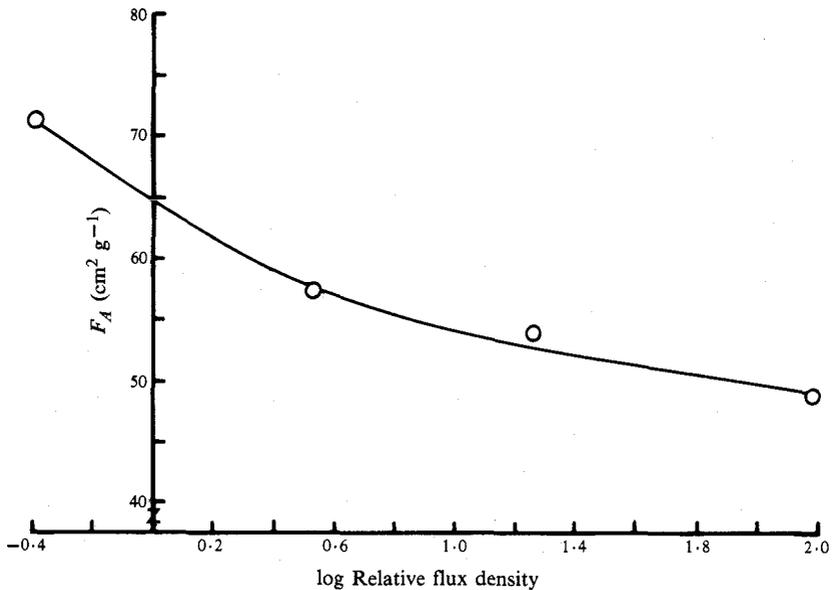


Fig. 2. Relationship between leaf area ratio of seedlings grown at four levels of shade and the logarithm of the relative flux density. The gentle slope of this line indicates that *P. undulatum* is not a shade plant.

treatments. In leaves from the full daylight treatment, the epidermis was occasionally double. The thicknesses of the leaves from the three highest radiant flux densities were not significantly different from each other (Table 3). The thickness of the cuticle was much the same in plants from all treatments ($3.3\text{--}3.8 \mu\text{m}$).

Table 2. Chlorophyll and carotenoid concentrations ($\text{mg l}^{-1} \text{cm}^{-2}$) and their ratios, of seedlings grown under four photon flux densities

The *F* ratios from the analysis of variance are given. Means in each row with the same letter are not significantly different at $P < 0.05$ using Duncan's multirange test. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

	Relative flux density (%)				<i>F</i> ratio
	97.4	18.2	3.4	0.4	
Total chlorophyll	3.961 ^a	7.516 ^b	12.666 ^c	16.218 ^d	33.79***
Chlorophyll <i>a/b</i>	2.538	2.437	2.444	2.235	0.22
Carotenoids	1.525 ^a	1.787 ^a	2.406 ^a	4.635 ^b	6.29**
Carotenoid/chlorophyll	0.418 ^a	0.238 ^a	0.191 ^b	0.280 ^b	4.66*

Discussion

The response of seedlings of *Pittosporum undulatum* to shade can be considered characteristic of both sun and shade plants. The results are difficult to interpret because the rates of growth of leaves and stems of *P. undulatum* vary with the time of bursting of the apical bud. By selecting uniform plants, no buds burst during the 16 days of this experiment, ensuring that plants from all treatments were at the same ontogenetic stage at the end of the experimental period. This explains why there was no increased leaf area of the seedlings grown in deep shade (Table 1; Packham and Willis 1977); however, there

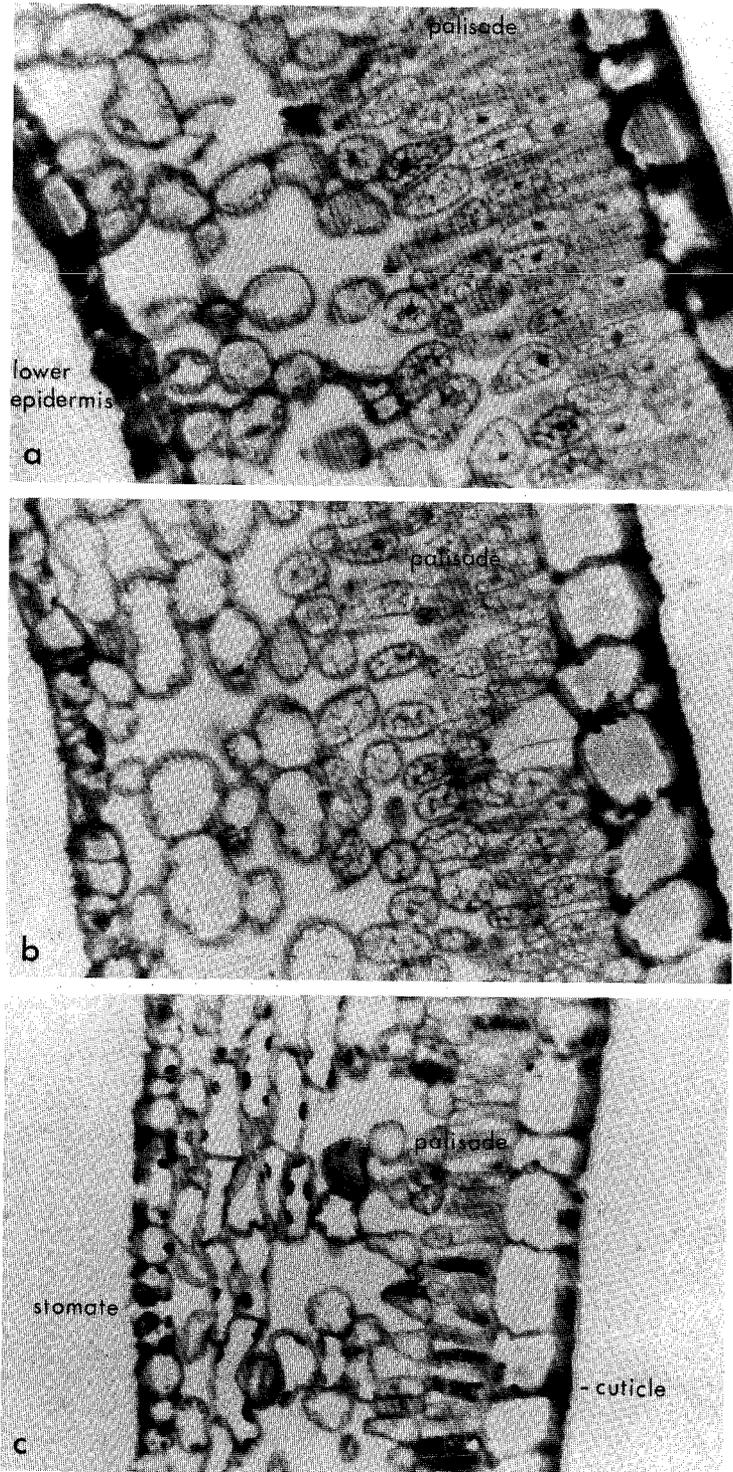


Fig. 3. Transverse sections of leaves of *P. undulatum* seedlings grown in (a) full daylight, (b) 18% daylight and (c) 0.4% daylight. The palisade mesophyll was thinner in leaves grown in deep shade but the cuticle thickness remained constant.

was some adaptation of existing leaves to the new light climates (Fig. 3 and Table 2). F_A increased significantly with increasing shade (Table 1 and Fig. 2), presumably because the existing leaves became thinner through deflation of cells and by reducing the number of layers of palisade mesophyll cells (Table 3 and Fig. 3), as is common at low radiant flux densities (Packham and Willis 1977). On the other hand, the slope of the plot of F_A against the logarithm of relative flux density (Fig. 2) was only $15.3 \text{ cm}^2 \text{ g}^{-1}$ per unit log (relative flux density). Although this is an underestimate, owing to the design of the experiment, it is less than half the value calculated for the shade-tolerant *Quercus petraea* (43) and only 8% of the value for *Impatiens parviflora* (190; Jarvis 1964). On the other hand, this parameter does not always correlate with shade tolerance (Loach 1970) and may be correlated with total daily radiation rather than relative flux density (Bormann 1956).

Table 3. Leaf and cuticle thicknesses of leaves from seedlings grown under four flux densities

Means in same row with the same letter are not significantly different at $P < 0.05$ using Duncan's multirange test. Cuticle thicknesses were not significantly different

	Relative flux density (%)			
	97.4	18.2	3.4	0.4
Leaf thickness (mm)	0.25 ^a	0.24 ^a	0.25 ^a	0.16 ^b
Cuticle thickness (μm)	3.3	3.8	3.8	3.5

Light interception by a plant depends on the chlorophyll concentration and the angle between the leaf lamina and the light source. *P. undulatum* has the broad, horizontal mesic leaves (Gleadow and Ashton 1981) characteristic of shade plants (Donald 1961); this may cause the leaf scorching in full sunlight observed on hot days. In the field trials (Gleadow 1982), the lower leaves of seedlings of *P. undulatum* senesced soon after new leaves had been produced, thus maximizing light utilization, a characteristic common to many shade-tolerant species (Went 1957). Ashton and Frankenberg (1976) reported similar behaviour in *Acmena smithii*.

All the chlorophyll *b* in the chloroplasts of higher plants is in the light-harvesting chlorophyll-protein complexes (Thornber *et al.* 1979) located on the thylakoid membranes of the grana (Andersson and Anderson 1980). The low chlorophyll *a/b* ratio often associated with shade plants (Withers 1979) is therefore consistent with the large granal stacks found in shade plants (Boardman 1977). However, in *P. undulatum* the decrease in chlorophyll *a/b* in plants grown at 0.4% full daylight for 2 months was not significant at the 5% level (Table 2), although the chlorophyll per unit area increased fourfold. Thus, seedlings adapted to shade must have increased granal (*b*) and stromal (*a*) chlorophylls, without a significant change in ratio, consistent with the intermediate status of this species as a shade plant.

The growth compensation point of *Pittosporum undulatum* seedlings was estimated to be 1.6% full daylight (mean temperature 20°C) or $c. 3.5 \text{ W m}^{-2}$ PAR (Fig. 1); this is below the 2% which Jarvis (1964) considers indicative of a shade-tolerant species. The plants were grown in full daylight prior to the imposition of light treatments, thus the growth compensation point of plants adapted to shade can be expected to be very much less than the 1.6% measured. For comparison, the growth compensation point was 5.5% in *Lathyrus maritum* (Blackman and Black 1959), 3% in *Pseudotsuga taxifolia* (Bates and Rosen 1928, cited in Bielecki 1959) but only 1.15% in *Nothofagus cunninghamii* (Howard 1973) and 0.9% in *Agathis australis* (Bielecki 1959). K. Monk (unpublished data) measured the instantaneous light compensation point of *P. undulatum* leaves using a gas exchange method under a tungsten light source (Leith and Ashton 1961); the compensation point was 300 lx (0.3% daylight) in sun leaves and 140 lx (0.14% daylight) in shade leaves (mean temperature 18°C). The instantaneous compensation point is lower than the growth compensation point we measured because it reflects the minimum amount of light needed

for photosynthesis, whereas we measured the minimum amount of light needed for growth. It is comparable with species found in the understorey of a *Eucalyptus regnans* forest, measured with similar equipment (100–300 lx; Ashton and Turner 1979). Seedlings of *P. undulatum* in our experiment did not produce flushes of leaf growth during the experimental period: further long-term experiments are needed to determine the effect of growth flushes on the assessment of the light compensation point.

Often the shade tolerance of a species, determined by some of the criteria described earlier, does not correlate with the behaviour of the plant in the field. For example, young seedlings of *Eucalyptus regnans* have a growth compensation point for light of 1.5–1.7%, yet seedlings are unable to regenerate under an *E. regnans* canopy (Ashton and Turner 1979). Although the measured compensation point for *P. undulatum* is similar (1.6%), the compensation point in the field may be different as it is influenced by fungal and insect attack (Vaataja 1962; Jarvis 1964; Grime 1966): *P. undulatum* contains various resins, saponins and essential oils (Power and Tutin 1906; Cornforth and Earl 1938) that may arrest the growth of some fungi (Shcherbonovskii and Nilov 1967). It is likely that these resins and saponins confer disease resistance on seedlings and thus enable them to survive extreme shade. *P. undulatum* may be able to survive dense shade, losing only a small amount of dry matter in resisting fungal and insect attack, and with a small negative R_w , but maintain the ability to grow quickly when a gap forms in the canopy. This is similar to the pattern of regeneration seen in many tropical rainforest trees (Richards 1969).

In conclusion, *Pittosporum undulatum* is not highly shade-tolerant and seedlings do not require some shade for maximum growth, as does the New Zealand tree *Agathis australis* (Bieleski 1959). *P. undulatum* can exploit high photon flux densities, yet has the capacity to endure shade. Some of the characteristics discussed in this paper explain how it can grow and remain vigorous in dense shade, but reasons why seedlings of *P. undulatum* are predominantly found in shaded sites must be related to (1) the uneven distribution of seed (Gleadow 1982); (2) the higher drought tolerance of seedlings in shade (Gleadow and Rowan 1982); and (3) the competitive ability of the seedlings (Gleadow 1980).

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