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# Invasion by *Pittosporum undulatum* of the Forests of Central Victoria. III* Effects of Temperature and Light on Growth and Drought Resistance

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*Abstract*

The clumping of invading seedlings of *Pittosporum undulatum* Vent. around the butts of established trees is due partly to the site-dependent survival of seedlings, particularly during summer. *P. undulatum* seedlings were very drought-tolerant when grown at moderately low temperatures (21·4°C day/17·8°C night compared with 27·4°C day/23·9°C night) and in deep shade. Plants droughted at 5°C higher temperatures and higher photon flux densities stopped transpiring and wilted 10–13 days earlier than those droughted under cooler, densely shaded conditions. Well watered seedlings had higher relative growth rates and net assimilation rates when grown under higher temperatures and photon flux densities. Control seedlings were more leafy when grown under low light, as reflected by the specific leaf area, leaf area ratio and root/shoot ratios. The adverse effects of higher photon flux densities and temperatures on the drought tolerance of *P. undulatum* seedlings support the hypothesis that survival of invading seedlings in their first year is dependent on the microclimate.

## Introduction

The distribution of invading *Pittosporum undulatum* is patchy and seedlings tend to be clumped around the butts of established trees (Gleadow and Ashton 1981). Although such colonization patterns could be due to uneven dispersal of seed by vectors (Gleadow 1982), they may involve factors affecting survival. Seedlings planted into a forest of *Eucalyptus cephalocarpa–E. radiata* at Langwarrin (50 km SE. Melbourne) survived only when sheltered by established *P. undulatum* and, to a lesser extent, *Eucalyptus* trees (Gleadow 1982). Possibly the young seedlings can survive the summer only when sheltered from high temperatures, high photon flux densities or both.

In preliminary experiments in a glasshouse, plants droughted in full sunlight died more quickly than shaded plants; however, the effects of temperature and photon flux density on the drought resistance of *P. undulatum* could not be distinguished. The experiment described below was conducted in a controlled environment in an attempt to separate the effects of temperature and photon flux density on *P. undulatum* growth and drought resistance.

## Methods

### *Germination and Growth*

From 30 to 50 seeds were germinated on moistened Whatman No. 30 paper in plastic petri dishes at 20°C in the dark. After 30 days, when germination had begun,

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dishes were transferred to diffuse fluorescent light (4310 lx) for about 10 days. Seedlings, with roots up to 3 cm long, were transplanted into experimental pots and grown in the glasshouse from February until May (16 weeks). Initially the glasshouse was shaded to 40% sunlight, but was in full sunlight for the final 11 weeks (March–May). Temperatures in the glasshouse ranged from 10° minimum to 38°C maximum. Plants were hardened outside (temperature range between 7·5 and 18·5°C) for 2 weeks prior to the experiment. Plants were matched for height and leaf number and organized into nine groups; one group was harvested to measure initial leaf area and total dry weight, the remaining eight groups were assigned to growth cabinets.

### *Experimental Conditions*

The experiment was of a $10 \times 2 \times 2 \times 2$ factorial design: 10 replicates, 2 temperatures, 2 photon flux densities and 2 watering regimes. The temperature regimes were maintained in each of two growth cabinets. The high temperature cabinet was maintained at $27 \cdot 4 \pm 0 \cdot 4$°C day/$23 \cdot 9 \pm 0 \cdot 5$°C night and the low temperature cabinet at $21 \cdot 4 \pm 0 \cdot 5$°C day/$17 \cdot 8 \pm 0 \cdot 4$°C night. Cabinets were lit by fluorescent tubes with a 12 h photoperiod. The quantum flux density of photosynthetically active radiation was $110 \cdot 5 \pm 8 \cdot 3$ $\mu E\, m^{-2}\, s^{-1}$ in the low temperature cabinet and $128 \cdot 5 \pm 8 \cdot 1$ $\mu E\, m^{-2}\, s^{-1}$ in the high temperature cabinet; this is approx. 5% full sunlight. This was reduced by 60% over half the plants with Sarlon shade cloth, which is well above the light compensation point of sun-grown *P. undulatum* seedlings of 1·6% sunlight (Gleadow 1980). Plants were rotated around the cabinets, within their treatment, to reduce edge effects and temperature and photon flux density gradients.

Plants were watered daily and allowed to adjust to the experimental conditions. After 10 days the water content of the soil was raised to near field capacity and the pots were sealed to prevent water loss directly from the pots. Plants in each treatment were divided into two groups. Water was withheld from one group (droughted plants) and the remaining pots were watered up to their field capacity daily (control plants). When 50% of the leaves in any one treatment appeared dead, all plants in that treatment were rewatered.

### *Leaf Temperatures*

The temperatures of the top and fourth leaves were measured on six droughted and six control seedlings in each treatment after 15 days of drought by a constan-copper thermocouple, with internal compensation for the reference junction. Temperatures of control and droughted plants were similar (Table 1).

### *Transpiration*

The sealed pots were weighed daily and the reduction in weight was assumed to be water lost through transpiration (Franco and Magalhaes 1965). Two extra pots per treatment, containing soil but no plants, were also sealed. Water was withheld from these pots and they were weighed daily to estimate the amount of water lost directly from the pot as the drought progressed. All values presented have been corrected for the water lost from these pots, between 0·2 and 1·0 g per day. Results are expressed as grams $H_2O$ lost per gram final leaf weight per 24 h to standardize measures between different-sized plants (Evans 1972).

*Water Potential and Relative Water Content*

Twelve extra plants per treatment (eight droughted and four controls) were used for assessing the water status of the plants after 4, 8, 14 and 21 days of drought using three droughted and one control plant each time. Relative water content (RWC) was measured on leaf discs (10 mm in diam.) by the method of Barrs and Weatherley (1962). Leaf water potential ($\psi$) was measured on leaf discs from the same plants by a Wescor HR-33 dewpoint psychrometer with a C-53 sample chamber (Campbell *et al.* 1973; Neumann *et al.* 1974). Large discs were used (10 mm in diam.) to reduce the ratio of cut edge to volume (Nelsen *et al.* 1978). Discs were punched from the fourth top leaf, placed in the chamber with the adaxial surface uppermost and readings taken after 20 min equilibration.

**Table 1. Leaf temperatures of droughted and control seedlings of *P. undulatum* grown under two light levels at two temperatures**

Values given are means ± s.e.

| Conditions | Leaf temperature (°C) | |
|---|---|---|
| | Control plants | Droughted plants |
| Full light (110 $\mu$E m$^{-2}$ s$^{-1}$) | | |
| High temp. (27/24°C) | 23·5±0·86 | 23·3±0·81 |
| Low temp. (21/18°C) | 21·2±0·51 | 21·6±0·37 |
| Shade (70 $\mu$E m$^{-2}$ s$^{-1}$) | | |
| High temp. (27/24°C) | 24·2±0·66 | 23·7±0·87 |
| Low temp. (21/18°C) | 21·7±0·84 | 22·0±0·72 |

*Growth Parameters and Indices*

After 45 days in the cabinets the control plants were harvested and their height, leaf area and leaf, stem, root and total dry weight measured. Growth indices were calculated from these data according to the formulae recommended by Radford (1967) for this type of experiment. The terminology is after Neales and Nicholls (1978), where $R_W$ is mean relative growth rate, $E_A$ is mean net assimilation rate, $F_A$ is leaf area ratio, $S_A$ is specific leaf area and $L_W$ is the leaf weight ratio. The droughted plants were harvested 1 week after rewatering, i.e. after 20, 24, 31 and 35 days for the high temperature–full light, high temperature–shade, low temperature–full light and low temperature–shade treatments respectively, and the primary data treated as for the controls.

## Results

*Transpiration*

The rates of transpiration in all light and temperature conditions were dominated by the watering regimes (Table 2, Fig. 1): control plants transpired at a constant rate throughout the experiment while transpiration rates in droughted plants steadily declined from a rate that was initially higher than the controls in plants grown in the full light, but about equal to controls grown in the shaded treatments (l.s.d. $P < 0 \cdot 05 = 3 \cdot 58$ at day 2). The rate of the decline depended on the environment (Figs 1 and 2). Droughted plants in high temperature–full light ceased transpiring by day 10 and all plants had wilted by day 12, whereas plants in low temperature–shade did not start to wilt until after 15 days of drought and transpiration did not stop until day 23. The two other treatments, high temperature–shade and low temperature–full light, correlated with stresses intermediate to those above (Fig. 2).

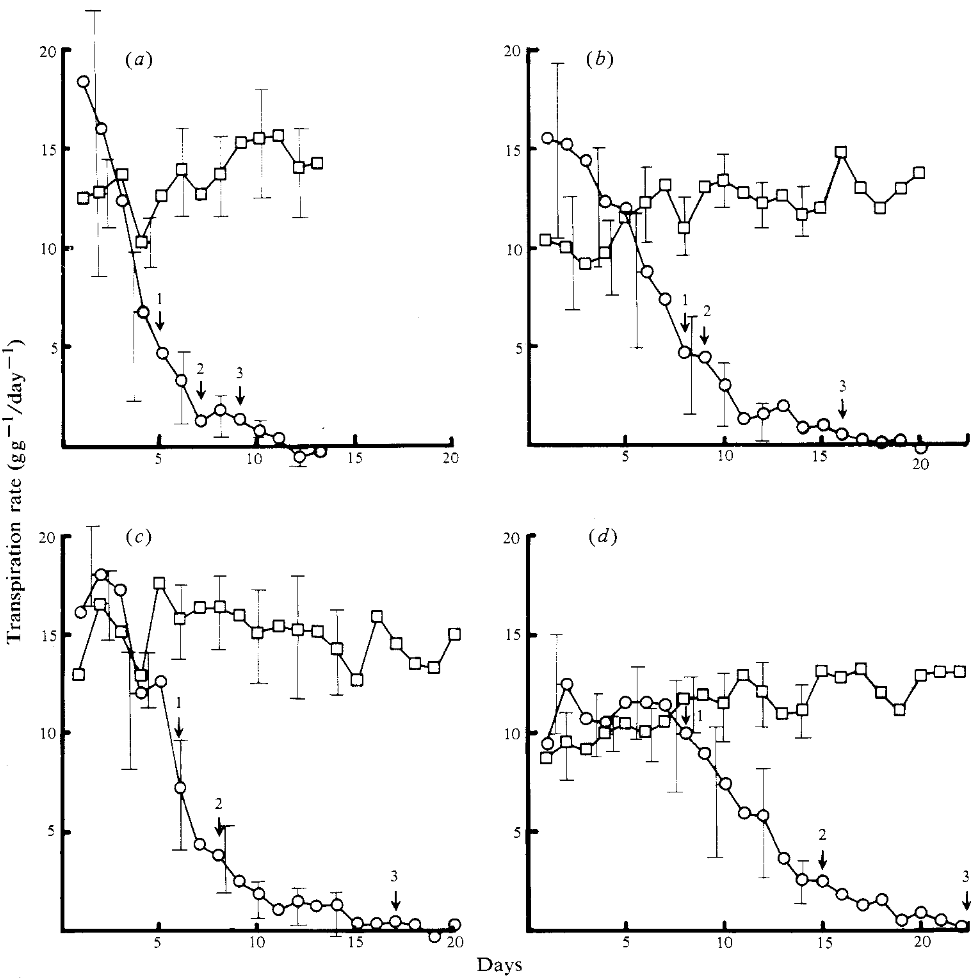


**Fig. 1.** Transpiration rate of control (□) and droughted (○) seedlings of *P. undulatum* grown under (*a*) high temperature–full light, (*b*) low temperature–full light, (*c*) high temperature–shade and (*d*) low temperature–shade. Arrow 1 indicates at least one plant in that treatment was wilted, arrow 2 half the plants were wilted and arrow 3 all seedlings were wilted. Bars indicate ±s.d. of the mean.

*Leaf Water Potential and Water Content*

The RWC and $\psi$ of the leaves were highest in the low temperature–shade environment (Table 3, Fig. 3). The two other treatments showed stresses intermediate to these. All values decreased in droughted plants with time from an initial, control water potential of $-13\cdot8 \pm 0\cdot47$ bars and a RWC of $89\cdot8\% \pm 0\cdot53$, but the rate of the decline depended on the environment (Fig. 3). Leaf RWC and $\psi$ were compared with the changing transpiration rates by pooling the data from all treatments (Fig. 4): leaf RWC and $\psi$ were maintained near control values in all plants with transpiration rates between 17 and 5 g g$^{-1}$ day$^{-1}$. With continued droughting, transpiration decreased to below 5 g $g^{-1}$ $day^{-1}$, and the $\psi$ and RWC declined proportionally (Fig. 4). The seedlings began to wilt at the beginning of this phase, i.e. when the RWC fell below 80% and the $\psi$ dropped to −25 bars (Fig. 3).

**Table 2. *F* ratios calculated from analysis of variance of transpiration rates of droughted and control seedlings (D) of *P. undulatum* grown at two temperatures (T) and two light levels (L) for every second day up to 14 days of drought**

Growing conditions are given in Table 1. Degrees of freedom for each source of variation (treatment) are given

| Source | d.f. | Days of drought | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | 2 | 4 | 6 | 8 | 10 | 12 | 14 |
| Reps | 9 | 1·6 | 1·8 | 1·7 | 0·9 | 0·9 | 1·5 | 5·9 |
| T | 1 | 22·2*** | 0·1 | 0·7 | 0·4 | 0·5 | 0·4 | 3·4 |
| L | 1 | 0·7 | 5·4* | 5·6* | 16·4*** | 1·3 | 9·8** | 2·0 |
| T × L | 1 | 6·2* | 10·8** | 3·8 | 0·3 | 0·4 | 0·2 | 0·0 |
| D | 1 | 14·4** | 0·1 | 63·0*** | 155·4*** | 261·7*** | 368·1*** | 601·3*** |
| T × D | 1 | 0·7 | 6·9* | 42·0*** | 39·6*** | 27·3*** | 23·1*** | 17·4*** |
| L × D | 1 | 0·9 | 0·0 | 7·3** | 2·6 | 9·4** | 5·5* | 4·3* |
| T × L × D | 1 | 0·0 | 2·7 | 1·1 | 3·9 | 3·3 | 2·0 | 0·3 |

*$P < 0·05$. **$P < 0·01$. ***$P < 0·001$.

## *Growth Parameters and Indices*

The total dry weight of control plants was approx. 50% greater than that of droughted plants in the full light treatments and 15% greater than that of those droughted in the shaded treatments (Table 4, Fig. 5). Although droughted plants were harvested earlier than the controls, this should not have altered the results because water stress limits most of the essential physiological processes necessary for growth (Slatyer 1967; Hsiao 1973). In control plants the $R_W$ was 75% and the $E_A$ 80% greater in the full light treatments, and seedlings grown under the higher temperatures were

**Table 3. Analysis of variance, including mean square of the error (MSQ) and *F* ratios, of water potential ($\psi$) and relative water content (RWC) of droughted and control seedlings of *P. undulatum* grown at two levels of light (L) and two temperatures (T) over 3 weeks (t)**

Growing conditions are given in Table 1. Data are shown in Fig. 3

| Source | d.f. | $\psi$ | | RWC | |
|---|---|---|---|---|---|
| | | MSQ | *F* ratio | MSQ | *F* ratio |
| T | 1 | 1024 | 11·4** | 0·181 | 59·3*** |
| L | 1 | 1261 | 14·0** | 0·061 | 20·0*** |
| T × L | 1 | 10 | 0·1 | 0·001 | 0·4 |
| t | 2 | 2885 | 32·1*** | 0·333 | 109·3*** |
| T × t | 2 | 721 | 8·0** | 0·119 | 39·0*** |
| L × t | 2 | 349 | 3·9* | 0·019 | 6·4** |
| T × L × t | 2 | 19 | 0·2 | 0·001 | 0·4 |
| Error | 24 | 90 | | 0·003 | |
| Total | 35 | 354 | | 0·036 | |

*$P < 0·05$. **$P < 0·01$. ***$P < 0·001$.

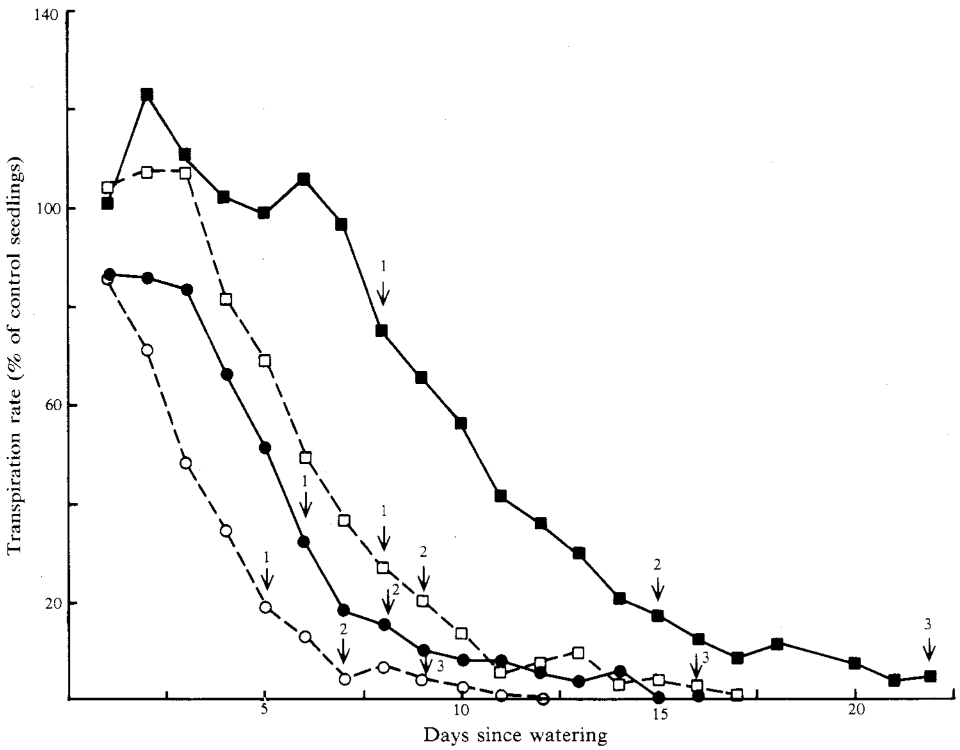


**Fig. 2.** Transpiration rate of droughted *P. undulatum* seedlings expressed as a percentage of the transpiration rate of control seedlings in four different light/temperature environments. ○ High temperature–full light; □ low temperature–full light; ● high temperature–shade; ■ low temperature–shade. Arrow 1 indicates at least one plant in that treatment was wilted, arrow 2 half the plants were wilted and arrow 3 all seedlings were wilted.

**Table 4. *F* ratios calculated from analysis of variance of growth parameters of well watered and droughted seedlings (D) of *P. undulatum* grown at two light levels (L) and two temperatures (T)**

Growing conditions are given in Table 1. R/S, root/shoot ratio; W, total dry weight; $L_W$, leaf weight ratio; $R_W$, mean relative growth rate

| Source | d.f. | R/S | W | $L_W$ | $R_W$ |
|---|---|---|---|---|---|
| Reps | 9 | 1·4 | 11·1*** | 1·1 | 8·7** |
| T | 1 | 10·0** | 3·5 | 3·3 | 1·4 |
| L | 1 | 21·8*** | 100·6*** | 13·7*** | 90·5*** |
| T × L | 1 | 1·1 | 1·5 | 0·4 | 2·7 |
| D | 1 | 9·2** | 124·9*** | 17·2** | 93·9*** |
| T × D | 1 | 0·0 | 4·7* | 1·4 | 4·0* |
| L × D | 1 | 12·1*** | 44·3*** | 23·2*** | 25·0*** |
| T × L × D | 1 | 0·0 | 2·6 | 4·0* | 4·7* |
| Error | 63 | | | | |

$^*P < 0{\cdot}05$. $^{**}P < 0{\cdot}01$. $^{***}P < 0{\cdot}001$.

1·6 cm taller than those grown under the same photon flux density but at lower temperatures (Tables 4–6, Fig. 5). There was no interaction between temperature and photon flux density; however, both significantly interacted with the watering regime,

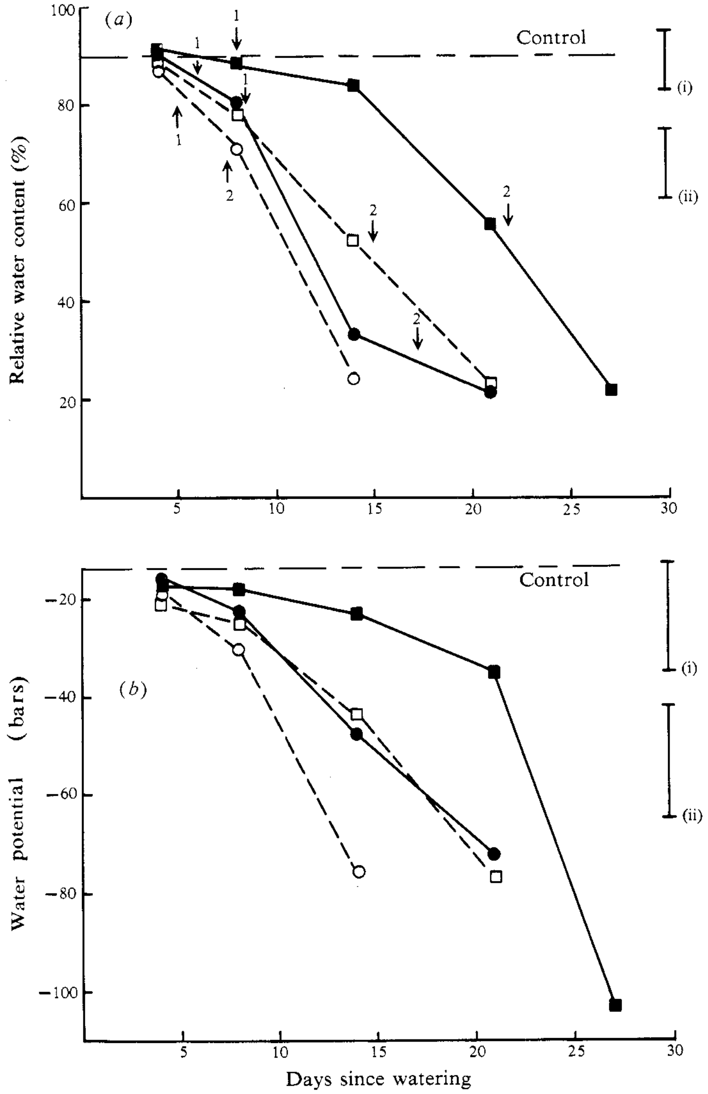


**Fig. 3.** Relationship between (*a*) leaf relative water content and (*b*) leaf water potential and the duration of droughting in seedlings of *P. undulatum*. Error bar (i) is used to compare means of different treatments on any one day; error bar (ii) to compare means on different days within one treatment (Federer 1955). Arrow 1 indicates when wilting started in that treatment and all plants had wilted by arrow 2. Symbols as for Fig. 2.

compounding the total dry weight increase and the higher $R_W$ in well watered plants (Table 4, Fig. 5). The root/shoot ratio was smaller in plants grown in the shaded treatments, higher temperatures and under water stress (Table 4, Fig. 5).

The shaded plants were more leafy than the unshaded plants, although total leaf area did not vary significantly. This is reflected by the greater $F_A$, $L_W$ and $S_A$ in the plants grown in the low light treatments (Table 5). Total leaf area ($A_L$), $F_A$ and $L_W$ were greater in high temperatures and $S_A$ was greater in low light (Tables 5 and 6).

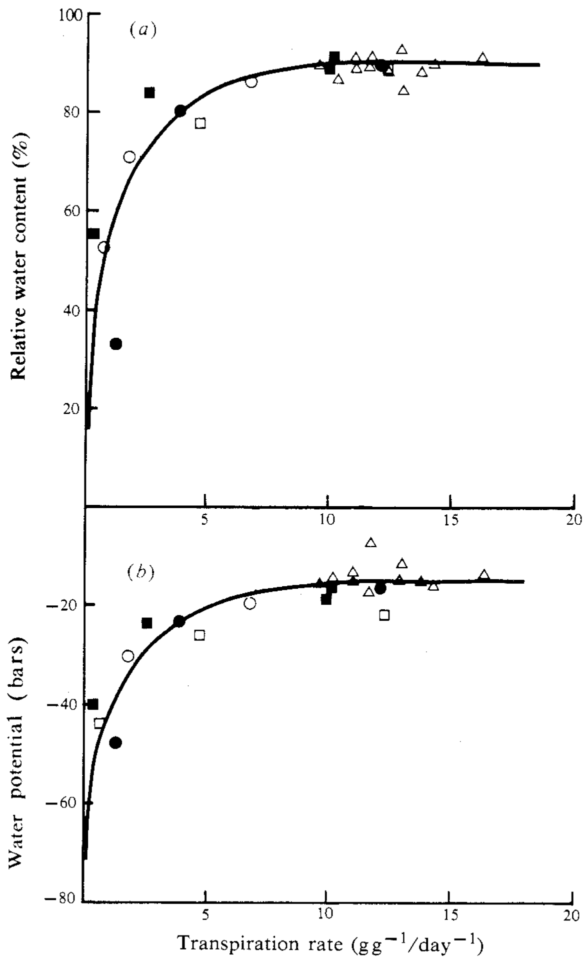


**Fig. 4.** Relationship between (*a*) leaf relative water content and (*b*) leaf water potential and the transpiration rate for all light and temperature treatments. Symbols as for Fig. 2, plus △ watered controls.

**Table 5. Mean growth indices of well watered seedlings of *P. undulatum* grown at two light levels and high (H) and low (L) temperatures**

$E_A$, net assimilation rate; $F_A$, leaf area ratio; $L_W$, leaf weight ratio; $S_A$, specific leaf area

| | Full light | | Shade | |
|---|---|---|---|---|
| | H | L | H | L |
| $E_A$ ($mg\,cm^{-2}\,day^{-1}$) | 1·62[a] | 1·92[a] | 3·48[b] | 3·53[b] |
| $F_A$ ($cm^2\,g^{-1}$) | 104·00[b] | 77·00[a] | 177·00[d] | 149·00[c] |
| $L_W$ ($g\,g^{-1}$) | 0·58[b] | 0·53[b] | 0·66[a] | 0·64[a] |
| $S_A$ ($cm^2\,g^{-1}$) | 181·00[c] | 148·00[d] | 267·00[a] | 231·00[b] |
| Height (cm) | 6·8[a] | 5·7[ab] | 6·8[a] | 5·4[b] |

Means in rows with same superscript are not significantly different at $P < 0·05$ using Scheffé's test.

## Discussion

Statistical analysis of the results of this experiment in a growth cabinet shows that temperature alone had an insignificant effect on transpiration (Table 1); however, the interaction of temperature and the water regime was highly significant from day 6 onwards, when higher temperatures increased transpiration in control plants but decreased it in droughted plants (Fig. 2, Table 2). Transpiration rate declined more rapidly in seedlings droughted at high compared with low temperatures. As the transpiration rate should be a function of stomatal aperture, we conclude that this is brought about by an effect on stomatal aperture. This is similar to the accelerated closure of stomata seen in cotton at high temperature and low turgidity (Dale 1961). Droughted plants grown in the full light actually transpired faster than control plants for the first few days of droughting (Fig. 1), an effect observed in *Eucalyptus viminalis* by Ladiges (1976).

**Table 6. *F* ratios calculated from analysis of variance of growth parameters of well watered seedlings of *P. undulatum* grown under two light levels (L) and two temperatures (T)**

$A_L$, total leaf area; other abbreviations as for Table 5

| Source | d.f. | $A_L$ | Height[A] | $S_A$ | $F_A$[A] | $E_A$ |
|---|---|---|---|---|---|---|
| Reps | 9 | 4·4** | 3·9** | 3·3* | 2·5 | 3·1* |
| T | 1 | 22·0*** | 20·7*** | 51·8*** | 50·6*** | 2·1 |
| L | 1 | 0·1 | 0·6 | 316·5*** | 317·4*** | 208·7*** |
| T×L | 1 | 0·9 | 0·0 | 0·1 | 3·2 | 2·1 |
| Error | 27 | | | | | |

[A] Data log transformed prior to analysis of variance.
*$P < 0·05$. **$P < 0·01$. ***$P < 0·001$.

At any one temperature, seedlings droughted in high light wilted and ceased transpiring sooner than those in low light; as D. Moore (unpublished data) found that stomata of *P. undulatum* began to close when the photon flux density fell below 150 $\mu$E $m^{-2}$ $s^{-1}$, stomata would be partially closed in the higher of the two light treatments (approx. 115 $\mu$E $m^{-2}$ $s^{-1}$) and presumably substantially closed at lower flux density (approx. 70 $\mu$E $m^{-2}$ $s^{-1}$). Statistical analysis showed significant effects of light alone between day 4 and day 8, when the rate of transpiration at high light was lower than at low light, and interaction between light and water regime after day 4 owing to the lack of effect of photon flux density at low temperatures in control plants.

Transpiration was not reduced markedly in any of the light/temperature treatments until a critical water deficit was reached (RWC = 80%; $\psi = -25$ bars: Figs 3 and 4): the first signs of wilting were detected soon after this. A similar response occurred in *Nothofagus cunninghamii* (Howard 1973) and *Eucalyptus viminalis* (Ladiges 1974). With extended stress, RWC fell to 35% and $\psi$ to $-80$ bars, when the leaves began to dry and crack; beyond this point, leaves no longer recovered with rewatering. The equivalent RWC correlating with leaf death in *N. cunninghamii* was much higher (70%) (Howard 1973), suggesting that *P. undulatum* is drought resistant.

Severely wilted, but not dry, leaves of *P. undulatum* can regain their turgidity with rewatering. Plants 25–100 cm tall beneath dense *Cupressus macrocarpa* canopies at Shoreham can remain wilted for most of the summer (D. H. Ashton, personal communication). One large seedling was kept wilted in the laboratory for 12 days without permanent damage. Recovery from water stress after rewatering shows that

*P. undulatum* is drought tolerant rather than drought avoiding. *P. undulatum* has other characteristics untypical of drought-avoiding plants, such as a thin cuticle 3 μm thick (cf. 9–18 μm for *E. goniocalyx*, Ashton *et al.* 1975), shallow roots (Gleadow and Ashton 1981) and glabrous leaves that do not abscise when stressed. Stomatal closure does not protect the plant from water stress, since wilting begins well before $\psi$ and RWC have fallen very far (Figs 2 and 3), again indicating drought tolerance rather than avoidance.

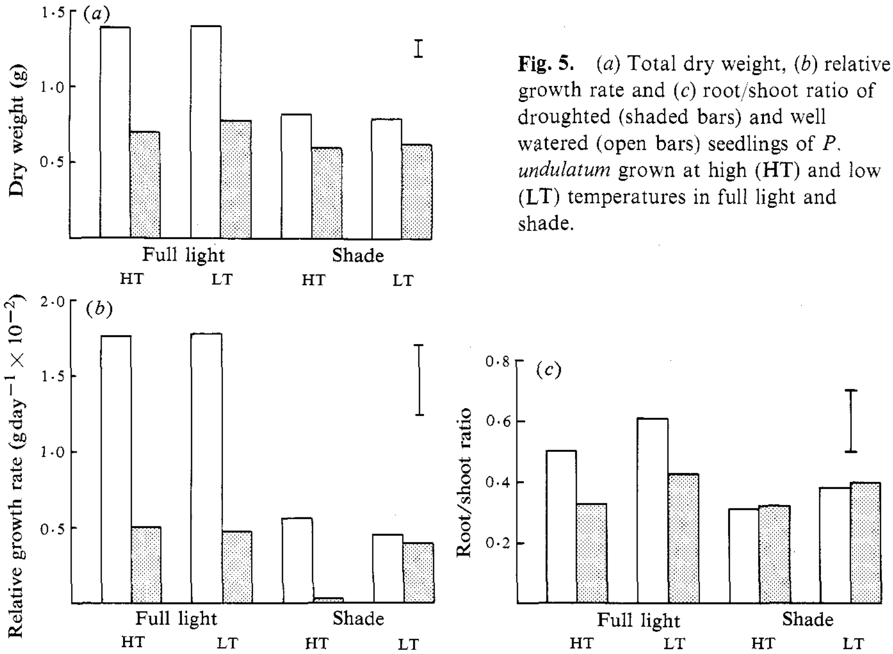


**Fig. 5.** (*a*) Total dry weight, (*b*) relative growth rate and (*c*) root/shoot ratio of droughted (shaded bars) and well watered (open bars) seedlings of *P. undulatum* grown at high (HT) and low (LT) temperatures in full light and shade.

The effects of temperature, photon flux density and duration of treatment on $\psi$ and RWC were highly significant (Table 3) and interactions between duration of treatment and temperature or photon flux density were significant or highly significant (Table 3). As the photon flux density used in the experiments examining the effect of it and temperature on the growth parameters was limited by that available in the growth cabinets (5% full sunlight), the light reactions of photosynthesis with low temperature coefficients would tend to limit the overall rate of the process, and the lack of temperature effects on $R_W$ and $E_A$ observed would not be unexpected. The only significant effect of temperature in Table 4, where the responses of droughted and control plants to temperature and photon flux density were examined, was on the root/shoot ratio, while $L_W$ was not affected. As leaf area of the brittle leaves of droughted plants could not be measured, analyses of parameters including leaf area in their calculation could only be made on undroughted plants (Tables 5 and 6). These calculations show that temperature significantly affected leaf area, height, $S_A$ and $F_A$, but not $E_A$, and interactions between photon flux density and temperature were not significant.

*P. undulatum* seedlings are less drought resistant when grown under less dense shade and moderately high temperatures, but if well watered would grow faster under these conditions (Fig. 5). This implies that under well watered conditions *P. undulatum* would grow more vigorously, in terms of $R_W$ and dry weight, in exposed sites; however, at Langwarrin all seedlings transplanted to open sites and 50% of self-sown seedlings at eucalypt butts died during the summer (Gleadow 1982). *Rhododendron macrophyllum* in Britain behaves similarly: plants growing in the open showed more symptoms of stress but overall yielded a greater woody biomass (Gholz 1978). The success of *P. undulatum* is determined primarily by the survival of the colonizing seedlings and only secondarily by the growth rate of the seedlings; thus the pattern of invasion initially dictated by the distribution of seeds by birds (Gleadow and Ashton 1981; Gleadow 1982) is strongly reinforced by the site-dependent survival of seedlings.

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