INTERNODE EXTENSION OF EUCALYPTS REDUCED IN ARTIFICIAL LIGHT*

By K. W. CREMER[†]

In several experiments the author found that eucalypt seedlings grown in artificial light were "dwarfed" compared with those grown in sunlight. The most obvious abnormality in dwarfed seedlings of the species tested was a severe reduction in the elongation of internodes.

This dwarfing effect was first noted in *Eucalyptus regnans* F. Muell. seedlings raised in an LB chamber illuminated for 14 hr daily by fluorescent (Philips TLMF, 3500 W) plus tungsten (600 W) lamps, adjusted to a visual intensity of 3000 f.c. at plant canopy level. The air temperatures were 21 and 16°C during the light and dark periods, respectively, and the total radiation received by the plants was approximately 320 cal cm⁻² per photoperiod.

Subsequently, dwarfing was also noted in *E. obliqua* L'Hérit. seedlings grown in a Zankel chamber illuminated for 12 hr daily at 2500 f.c. by mercury vapour (5600 W) plus tungsten (780 W) lamps. The total radiation during the 12 hr was approximately 290 cal cm⁻². Additional lighting by the tungsten lamps alone was supplied for 2 hr before and after the 12-hr periods of intense lighting.

The aim of the two experiments recorded below was to further characterize the dwarfing effect and to overcome it by modifying the light.

Methods

Light intensities were determined by an EEL selenium barrier cell photometer. Total radiant energy was assessed with a standard Kipp and Zonen solarimeter. Spectral analyses were made with a Beckman spectrophotometer adapted to read relative intensities of irradiation in bandwidths of 2–4 nm. Air temperatures were checked with a thermistor, and leaf temperatures with a tiny thermocouple pressed to the underside of horizontal leaves exposed to radiation from above, but well shielded from the sides. Three environments were provided in experiment 1:

- C1 Zankel chamber No. 1 illuminated by mercury vapour lamps (5600 W) plus tungsten lamps (600 W) at 3000 f.c. intensity at plant level for 16 hr daily. The radiant energy was 420 cal cm⁻² per day. Air temperatures were 21°C during the light and 16°C during the dark.
- C2 Zankel chamber No. 2, as above but with half the light intensity, after removal of 7 of the 14 mercury vapour lamps.
- G Glasshouse without shading or whitewash. Air temperatures controlled at approximately 24°C during the day and 18°C during the night. The photoperiod was about 16 hr. The radiant energy was variable but was estimated to average 440 cal cm⁻² per day.
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E. regnans seedlings were raised in a glasshouse at Canberra to an average height of 4 cm. Two lots of 54 and one lot of 108 plants were chosen at random on 17 December 1969 and exposed in environments C1, C2, and G, respectively, till 12 January 1970. On this date some plants from each of the three environments were transferred to the other two environments, till the final harvest on 24 February 1970. The resulting seven treatments were: C1–C1; C1–G; C2–C2; C2–G; G–G; G–C1; and G–C2. All other factors were kept uniform in all treatments. The plants were grown singly in 13-cm diameter pots filled with equal amounts of perlite and vermiculite. Every morning the pots were watered till they dripped. Every afternoon 50 ml of Hoagland's No. 2 nutrient solution with halved phosphorus content was given to each pot.

Experiment 2 was broadly similar to experiment 1, but three species were used and additional tungsten light was given in one treatment.



Fig. 1.—E. regnans. Plant C grown in glasshouse; plants A and B were established in a glasshouse and then kept for 21 days in a Zankel chamber illuminated for 16 hr daily at 3000 f.c. by mercury vapour plus tungsten lamps. All plants of same age and similar dry weights.

Results

There was no substantial difference in experiment 1 between the plants grown in the two growth chambers, even though the light intensity in one was twice as high as that in the other chamber. Hence the results from the two chambers are combined, except where the contrary is stated.

Although all plants seemed healthy, those grown in the chambers were grossly abnormal in form, while those grown in the glasshouse resembled plants grown in their natural environment (Fig. 1). The effect of the two types of environment on height growth (Fig. 2) was very different, immediate, and reversible; it lasted throughout the period of exposure. In the artificial light height growth was less than half that experienced in the sunlight.

The "normal" pattern of internode lengths is illustrated by G–G in Figure 3. The lengths of mature pairs of internodes* increased to about the sixth pair from the base of the plant. The topmost three pairs (8, 9, 10) were immature and therefore

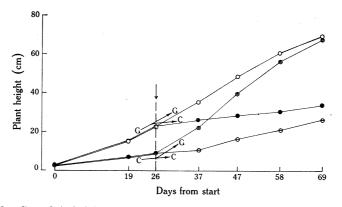


Fig. 2.—Growth in height of *E. regnans* under natural and artificial lighting and the effect of reciprocal transfers. Experiment 1: means of 36 plants per treatment. Vertical arrow indicates day of transfer. G, glasshouse; C, growth chamber.

decreased in length acropetally. The trend was similar in the plants grown in the chambers (C-C), but the lengths of these internodes were less than half of those in the normal plants (G-G).

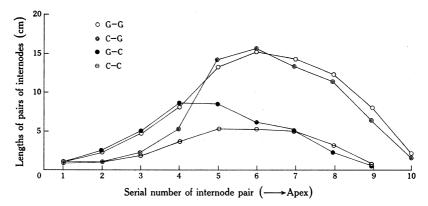


Fig. 3.—Effect of natural (G) and artificial (C) light on the length of stem internodes of *E. regnans* seedlings. The 4th, 5th, and 6th pairs of internodes had emerged but not matured at the time of the reciprocal transfers. Experiment 1; data from three representative seedlings per treatment.

The reciprocal transfers caused marked reversals in these trends. Not only those internodes which emerged from the buds after the transfers, but also those which

^{*} The leaves of eucalypts are initiated in opposite and decussate pairs. Except in juvenile shoots, an internode develops between the two members of a pair of leaves. This internode and the one above the pair of leaves are here termed a "pair of internodes".

had not matured before the transfers (pairs 4, 5, 6) were affected. For instance, the fifth pair of internodes would have been expected to grow to 5 cm if it had remained in the chambers, but on transfer to the glasshouse the initial influence of the chambers was lost and the pair grew to 14 cm.

Although the graphs for increases in internode numbers resembled those for height growth, the differences between treatments were comparatively negligible. The average number of pairs of stem internodes was $9 \cdot 9$ in the glasshouse-grown plants and $8 \cdot 9$ in the chamber-grown plants at the end of the experiment.

Compared with the variations in height, the differences in dry weight between the seven treatments were also minor. Combining the treatments which produced normal and dwarfed plants, respectively, the following final mean dry weights per plant were recorded:

	Normal plants	Dwarfed plants
Weight of leaves (g)	$6 \cdot 6$	7.7**
Weight of stems (g)	$3 \cdot 8$	$2 \cdot 6^{***}$
Weight of roots (g)	$4 \cdot 9$	3·9 (n.s.)
Totals (g)	$15 \cdot 3$	14·2 (n.s.)
** $P < 0.01$.	*** $P < 0.001$.	n.s., not significant.

Although the top and total dry weights of normal and dwarfed plants did not differ significantly, the distribution of the dry weight amongst leaves and stems did. The dwarfed plants were more leafy.

In experiment 2 it was found that all three species tested, *E. regnans*, *E. viminalis* Labill., and *E. pauciflora* Sieb. ex Spreng. were dwarfed in the Zankel chamber (Z1) illuminated for 8 hr daily with mercury vapour (5600 W) and tungsten (600 W) lamps at 2700 f.c. intensity (total radiation for the 8 hr was approximately 190 cal cm⁻²). However, in the second Zankel chamber (Z2), where the above illumination was followed by an additional treatment for 6 hr with tungsten light (600 W), but only at 60 f.c. intensity, the form and growth of all three species were greatly improved, though not quite to the standards obtained concurrently in the glasshouse (G). Experiment 2 also provided a marked example of the influence of light quality or photoperiod or both on the development of *Funaria hygrometrica* Hedw. and *Ceratodon purpureus* (Hedw.) Brid. The gametophores of these mosses covered 1%, 50%, and 75% of the soil surface in Z1, Z2, and G, respectively.

In contrast to sunlight and tungsten lamps, about 80% of the visible light emitted by the mercury vapour lamps was in six narrow (2–10 nm widths) spectral bands, and two of these (namely 660–664 nm, and 434–438 nm) are particularly important in morphogenesis. The energy in the far-red band (around 730 nm) was extremely weak by comparison with the red band (around 660 nm). Since the tungsten lamps accounted for only 2–3% of the total visual light intensity in the chambers, their contribution towards rectifying the imbalance of the light appeared to be negligible while the mercury vapour lamps were on.

Discussion

The dwarfing experienced in artificial light was evidently not due to differences in genetic constitution, nutrient or water supply, total light energy, temperature, or photoperiod. The first three factors were essentially similar in dwarfed and normal plants. The dwarfing was similar in C1 and C2 where light intensities were 1500 f.c. and 3000 f.c., respectively. Temperatures above 30°C have been found by the author to reduce internode lengths and apical dominance in *E. regnans*; critically high temperatures were, however, not reached in the present experiments. Severe dwarfing has been observed with photoperiods of 8, 14, and 16 hr.

The dwarfing effect obtained in the present experiments is ascribed to the imbalanced composition (especially with respect to the red and far-red bands) of the artificial light and its influence on the phytochrome system. Stem elongation is one of the several growth responses known to be influenced by phytochrome action (e.g. Downs, Hendricks, and Borthwick 1957; Hendricks and Borthwick 1963; Nakata and Lockhart 1966; Salisbury and Ross 1969). However, the details of the mechanism of this response are largely unknown, and the responses vary with the spectral composition, intensity, duration, and sequences of irradiation.

The above experiments appear to be the first to indicate a phytochrome response in eucalypts, apart possibly from quantitative photoperiodic responses in total growth. In experiment 2 and those reported by Scurfield (1961) and Green (1967) the eucalypts' growth was accelerated when day lengths were increased with tungsten light at intensities close to the compensation point. The possible implication of phytochrome in both of these responses needs to be checked by tests in which the dark period is interrupted.

In view of the finding (Mohr 1969) that irradiation for only a few minutes is required to establish photostationary states in the phytochrome system, it is remarkable that irradiation for 2 hr with tungsten light at the end of the day was not noticeably successful in relieving the dwarfing effect in *E. obliqua* and that irradiation for 6 hr in experiment 2 was largely, but not entirely, effective. However, complete relief from the dwarfing effect of mercury vapour plus tungsten lights by extension of the day with purely tungsten light can hardly be expected since a major part of the daily shoot extension of *E. regnans* occurs during daylight hours. Cremer (1962) found that in 10 saplings in the field 78% of the height growth occurred during daylight.

Another approach to improved artificial lighting could be through the use of aged mercury vapour lamps. After burning for 11,000 hr, the lamps in the Zankel chambers had almost lost their peak of emission at 660–664 nm. Bean plants appear to be dwarfed under new mercury vapour lamps, but not under old ones (D. J. Carr, personal communication). Other promising approaches are through modifications to the coatings of fluorescent tubes (Thomas and Dunn 1967; Helson 1969).

The above results show the critical importance of light composition on the development of some eucalypts in growth chambers, and re-emphasize the need to devise properly balanced lighting systems for experimentation with plants in controlled environments.

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