Plant responses to water stress: changes in growth, dry matter production, stomatal frequency and leaf anatomy

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Abstract

The responses of seedlings of three fast growing tree species, *Eucalyptus* hybrid (*E. camaldulensis* × *E. teriticornis*), *Casuarina equisetifolia* and *Melia azedarach*, to different levels of soil moisture in controlled glasshouse conditions were compared. The survival percentage, height of plants, number of leaves per plant, number of branches, fresh mass and dry mass of roots, stems, branches and leaves decreased in the three species with increasing water stress. Stomatal frequency and length of stomata in *Eucalyptus* and *Melia* also decreased with increasing water stress. However, no significant difference was obtained in the width of stomata and the ratio of number of open stomata to total number of stomata per unit area. The leaf thickness decreased, but the thickness of palisade parenchyma increased with increasing water stress in *Eucalyptus* hybrid and *Casuarina*. Leaf thickness of *Melia* did not show any significant variation due to water stress.

Introduction

Plants may adjust to a limited water supply through minimizing water loss, by increased extraction of water from soil, and by increased ability to tolerate low tissue water potential without injury. Decrease in water loss may be achieved by the closure of stomata and through morphological changes minimizing the radiation absorbed by the leaves. Each of these means of adaptation to drought has important limitations and each results in a reduction of carbon gain.

Initial growth is an important factor in the subsequent survival and development of individual tree species. The faster growing seedlings have an initial competitive advantage but they react differently to varying soil moisture. In the field, it is not only the absolute value of water deficiency that can be tolerated, but also the

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response to continuously changing soil moisture that is important for survival (Mazzoleni and Dickman 1988).

The aim of this paper is to compare the response of three tree species to water stress and this screening was done in controlled laboratory conditions.

Materials and methods

One year old seedlings of *Melia azedarach, Eucalyptus* hybrid (*E. camaldulensis* × *E. teriticornis*) and *Casuarina equisetifolia* were transplanted from polybags to earthenware pots filled with garden soil, sand and farm yard manure in 2:1:1 ratio in April 1991. After 15-d acclimatization of seedlings in the pots (one seedling per pot), these were moved to a glasshouse and divided into 5 lots of 10 pots in each, and kept under different water stress conditions created by watering (500 cm^3 of water per pot) daily (control) or at intervals of 4, 10 and 15 d.

Growth parameters were recorded for three months at 15-d intervals. After 60 d, leaves of the seedlings (only those which were developed subsequent to transfer under stress conditions) were used for measurements of stomatal conductance and leaf anatomical features. At 10.00 h a thin layer of collodion was applied with a brush to the lower surface of leaves, allowed to dry, peeled off and observed under a microscope. Stomatal counts, number of stomata open, length and width of stomatal pore were recorded on 5 leaves of each species from each treatment and in 10 randomly chosen microscopic fields (area 0.0855 mm^2) of each leaf peeling. Therefore, each figure in the text is based on counts of 50 microscopic fields.

The leaves taken from similar nodes (6th leaf from the top) of each species from each treatment were fixed in formalin-acetic acid-alcohol for anatomical studies. Hand cut transverse sections of the leaves were obtained from the middle part of the leaf. The anatomical characteristics were recorded from 10 cross sections in each variant. Soil moisture content was measured gravimetrically (samples were dried at 75 °C for 4 d).

Data were statistically analysed for standard errors (SE) and correlation coefficients.

Results and discussion

The soil moisture percentage ranged from 25 % to 0.6 % under different water stress conditions, the maximum temperature was 38.7 °C in May and the minimum 15 °C in April. The relative humidity was 89 to 94 % at 07.00 and 42 to 71 % at 14.00.

The survival percentage under mild stress was highest in *Casuarina*, *i.e.* 100 % survival up to 7-d watering interval. At 15-d interval, 80 % of *Melia* and 70 % of *Casuarina* and *Eucalyptus* seedlings died. There was sharp decrease in plant height of *Eucalyptus* and *Casuarina* with increasing water stress, except that, the maximum plant height and total growth of *Melia* was observed at watering with 4-d interval. The number of leaves per plant, number of branches, fresh and dry mass of root, stem, branch and leaves and the total biomass were significantly decreased with increasing water stress in the three species (Fig. 1, 2 ,3).

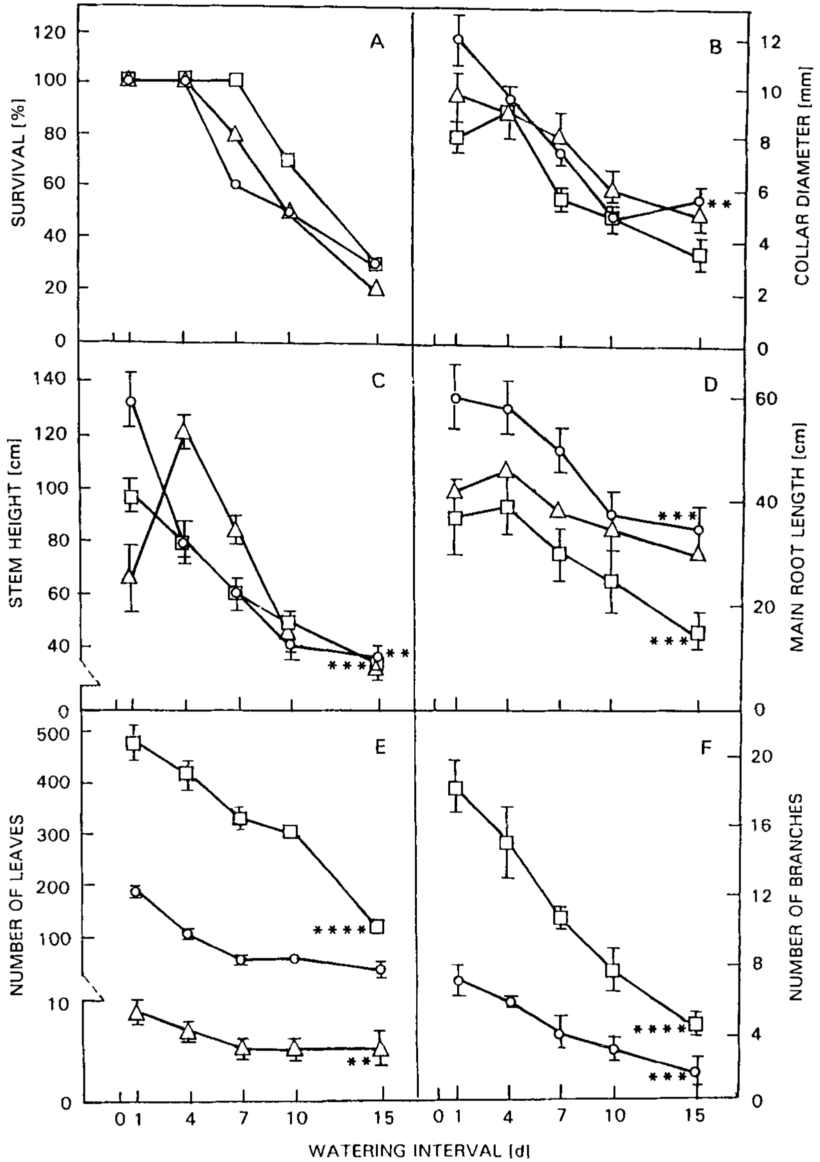

Fig. 1. Survival percentage (A), collar diameter (B), stem height (C), main root length (D), number of leaves (E), and number of branches (F) at different watering intervals. *Eucalyptus - circles, Melia - triangles, Casuarina - squares*; ** - significant at $P < 0.05$, *** - significant at $P < 0.01$, **** - significant at $P < 0.001$.

The stomatal density per unit leaf area, number of open stomata, and the length and width of stomata were significantly decreased with increasing water stress in all the species. The reduction in water loss somewhat balanced the low water availability in the soil, thus the leaf water potential decreased slightly, but not significantly as compared with controls (unpublished results). The thickness of leaf at both mid-rib and laminar portions was increased at the 4-d watering interval, and

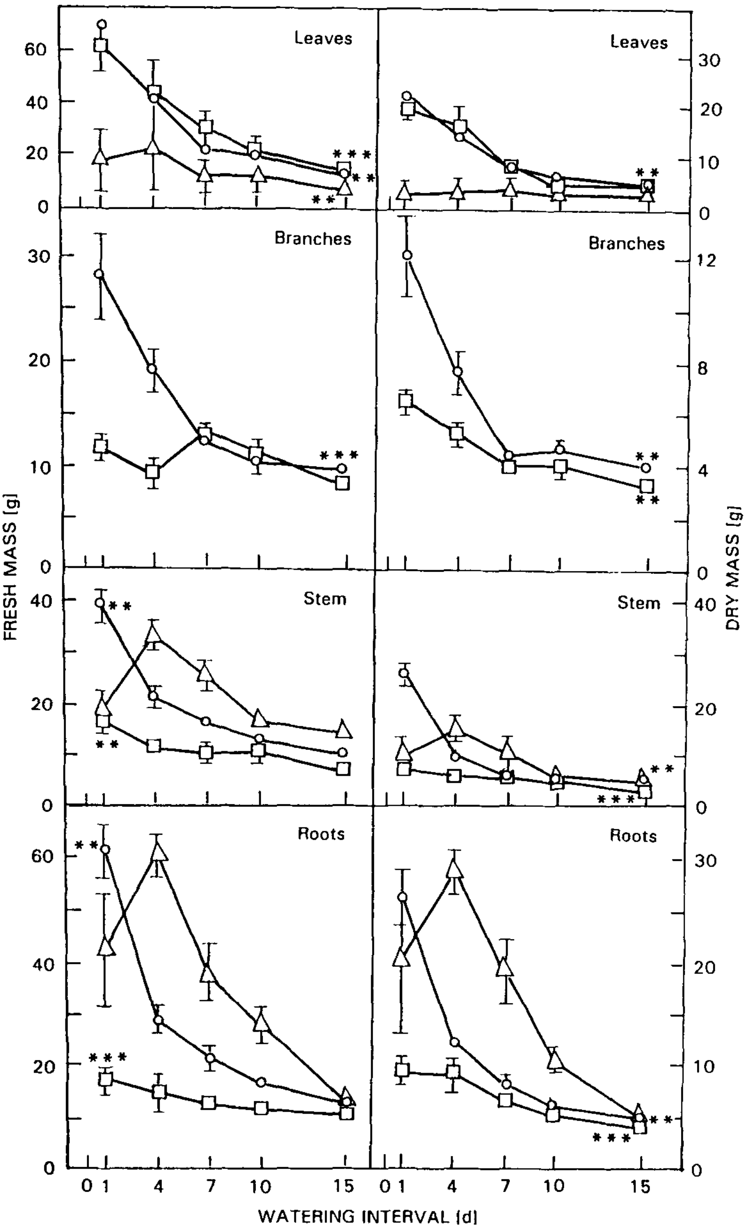

Fig. 2. Fresh and dry mass of roots, stems, branches and leaves under different watering intervals. *Eucalyptus - circles, Melia - triangles, Casuarina - squares*; ** - significant at $P < 0.05$, *** - significant at $P < 0.01$.

then invariably decreased with increasing water stress. The thickness of palisade parenchyma increased significantly with increasing water stress in *Eucalyptus* and *Casuarina* leaves, but not in *Melia* leaves (Fig. 5).

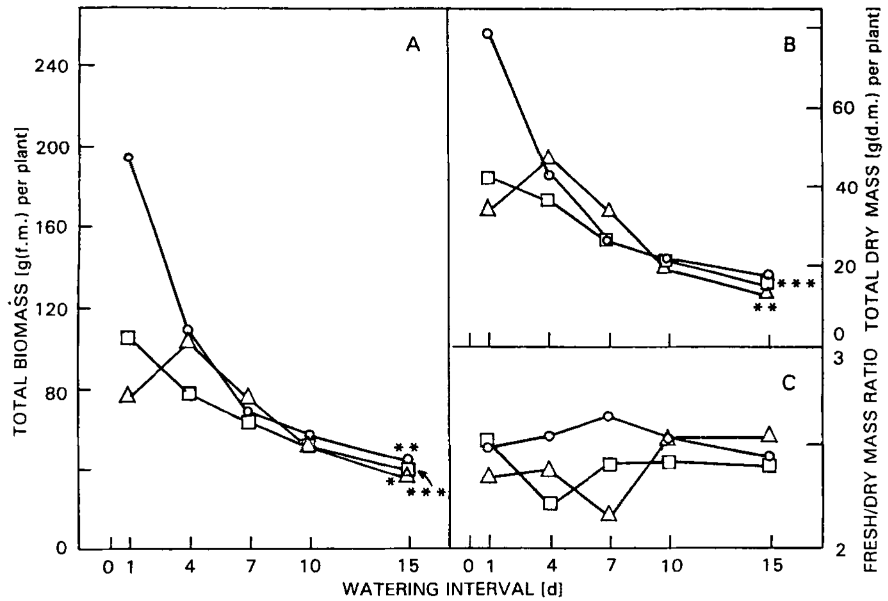

Fig. 3. Total fresh mass (A), total dry mass (B) and fresh mass/dry mass ratio (C) under different watering intervals. *Eucalyptus - circles, Melia - triangles, Casuarina - squares*; * - significant at $P < 0.1$, ** - significant at $P < 0.05$, *** - significant at $P < 0.01$.

The results of this experiment support many other findings that show a reduction of growth before the wilting point is reached (*e.g.* Handson and Hitz 1982, Van Volkenburgh and Boyer 1985, Hennessey *et al.* 1986, Myers and Landsberg 1989, Abrams *et al.* 1990, 1992, Griffin *et al.* 1991, Delgado *et al.* 1992, Goubin and Kemp 1992, Wang *et al.* 1992). It is apparent that the relationship between water stress and growth is very complex, involving many physiological processes. Some investigators claim that the most serious effect of drought is a reduction of photosynthetic surface and of dry matter production. However, the reduction in net photosynthetic rate per unit of surface is also important. The large decrease in photosynthetic rate per unit leaf area which occurs in plants subjected to water stress is usually attributed to stomatal closure. This view is supported by our experiments.

The present study showed that the seedlings could sustain water stress up to 4 or 5 d, but afterwards broad leaved species (*Melia* and *Eucalyptus*) suffered more rapidly than narow leaved species (*Casuarina*). Nevertheless, a good survival of all can be achieved by watering at least at weekly intervals.

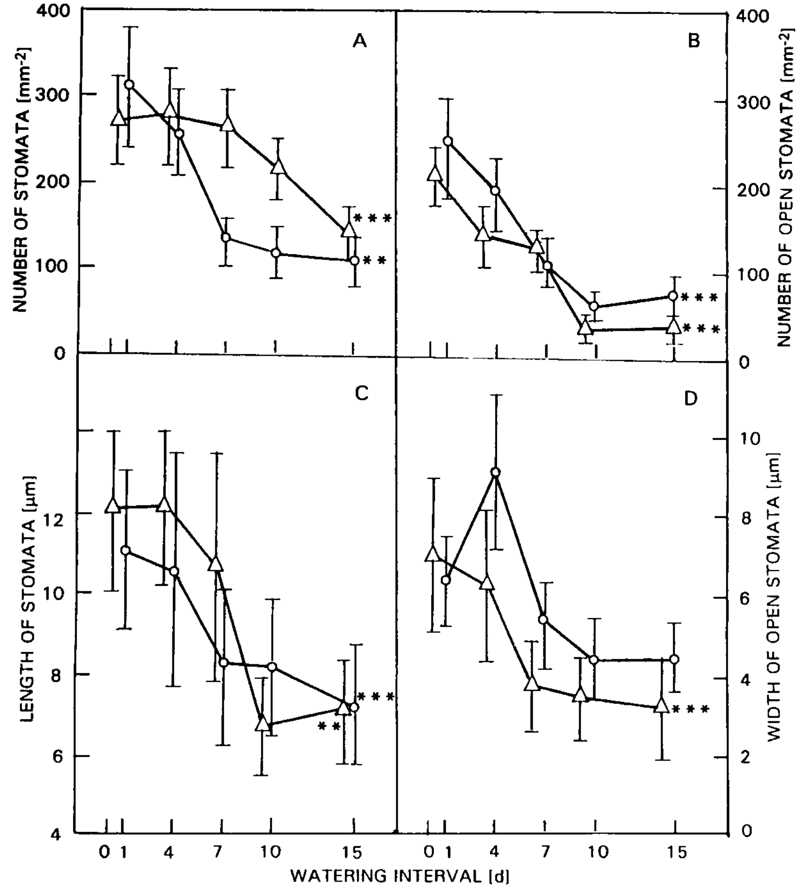

Fig. 4. Number of stomata per unit area (A), number of open stomata (B), length of stomata (C), and width of stomata (D), at different watering intervals. *Eucalyptus - circles, Melia - triangles*; ** - significant at $P < 0.05$, *** - significant at $P < 0.01$.

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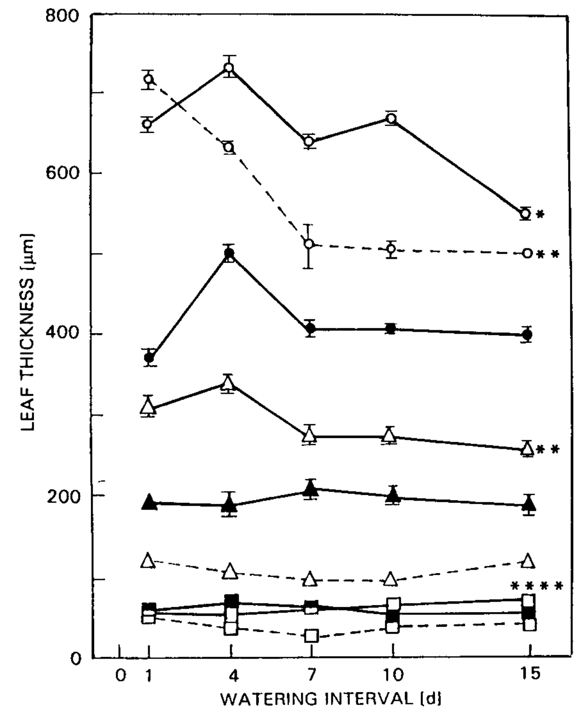

Fig. 5. Leaf thickness at mid-rib position (*circles*), laminar position (*triangles*) and thickness of palisade parenchyma (*squares*) under different watering intervals. *Eucalyptus - open points, full lines; Melia - closed points, full lines; Casuarina - open points, dashed lines*; * - significant at $P < 0.1$, ** - significant at $P < 0.05$, **** - significant at $P < 0.001$.

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