

Drought resistance in seedlings of five important tree species in Tarai region of Uttarakhand

P.B. RAO^{1*}, A. KAUR¹ & A. TEWARI²

¹Department of Biological Sciences, College of Basic Sciences & Humanities, G.B. Pant University of Agriculture & Technology, Pantnagar 263 145, Uttarakhand

²Department of Forestry, Kumaun University, Naini Tal 263 002, Uttarakhand

Abstract: The effect of moisture on seedling growth of *Albizia lebbek* Benth., *Dalbergia sissoo* Roxb., *Leucaena leucocephala* (Lam.) de Wit., *Shorea robusta* Gaertn.f. and *Tectona grandis* L. was evaluated in the Tarai region of Uttarakhand, India during 2002-2004. Seedlings raised in polyethylene bags containing about 4 kg of garden soil were subjected to four watering frequencies by irrigating daily and at 7, 14 and 21 days intervals, respectively designated as no stress, intermediate, high and very high stress. Periodical observations began one month after seedling establishment. Seedling height and dry biomass decreased at very high stress in all species. The reduction (relative to no stress) in height and biomass was maximum in *L. leucocephala* (75.8% and 99.8%) and minimum in *A. lebbek* (53.8% and 81.6%). The average single leaf area also decreased significantly with increasing water stress. The specific leaf area increased with increasing water stress in all species except for *S. robusta*, which showed a reverse pattern. The leaf area ratio increased along with moisture stress (except for *S. robusta*). A reverse pattern was found in relative growth rate and net assimilation rate in all species (except for *S. robusta* and *T. grandis*). Under very high stress, *L. leucocephala* maintained higher ψ and proline content and *A. lebbek* showed lower values indicating, respectively, their drought resistance and susceptibility. The osmotic adjustment in different species under very high stress was in the order: *L. leucocephala* > *T. grandis* > *D. sissoo* > *S. robusta* and > *A. lebbek*. Generally, net photosynthetic rate and transpiration rate decreased and stomatal resistance increased in very high water stress compared to no stress in all species. The percent reduction (relative to maximum) in photosynthesis under severe moisture stress was highest in *A. lebbek* and lowest in *L. leucocephala* and *T. grandis*, whereas transpiration rate was highest in *T. grandis* and lowest in *L. leucocephala* indicating that the latter is more drought resistant.

Resumen: Se evaluó el efecto de la humedad sobre el crecimiento de plántulas de *Albizia lebbek* Benth., *Dalbergia sissoo* Roxb., *Leucaena leucocephala* (Lam.) de Wit., *Shorea robusta* Gaertn.f. y *Tectona grandis* L. en la región Tarai de Uttarakhand, India, durante 2002-2004. Las plántulas, puestas a crecer en bolsas de polietileno que contenían aproximadamente 4 kg de suelo de jardín, fueron sometidas a cuatro frecuencias de riego: diario o a intervalos de 7, 14 y 21 días, respectivamente, tratamientos designadas como sin estrés, estrés intermedio, estrés alto y estrés muy alto. Las observaciones periódicas comenzaron un mes después del establecimiento de las plántulas. La altura y la biomasa seca de las plántulas decrecieron en el tratamiento estrés muy alto en todas las especies. La reducción (en comparación con el tratamiento sin estrés) en altura y biomasa fue máxima en *L. leucocephala* (75.8% y 99.8%) y mínima en *A. lebbek* (53.8% y 81.6%). El área foliar promedio también se redujo

* Corresponding Author; e-mail: bhaskar_20032005@yahoo.co.in

significativamente con el aumento en el estrés hídrico. El área foliar específica aumentó proporcionalmente al incremento en estrés hídrico en todas las especies excepto en *S. robusta*, la cual mostró el patrón opuesto. El cociente de área foliar aumentó con el estrés hídrico (excepto en *S. robusta*). Se encontró un patrón inverso en la tasa relativa de crecimiento y la tasa neta de asimilación en todas las especies (excepto en *S. robusta* y *T. grandis*). Bajo condiciones de estrés muy alto, *L. leucocephala* mantuvo un valor más alto de ψ y de contenido de prolina pero *A. lebbek* mostró valores más bajos, mostrando así, su resistencia y su susceptibilidad a la sequía, respectivamente. El ajuste osmótico en diferentes especies bajo estrés muy fuerte tuvo el siguiente orden: *L. leucocephala* > *T. grandis* > *D. sissoo* > *S. robusta* > *A. lebbek*. En general, la tasa neta fotosintética y la tasa de transpiración decrecieron, y la resistencia estomática aumentó, bajo estrés hídrico muy fuerte en comparación con la ausencia de estrés en todas las especies. La reducción porcentual (en relación con el máximo) en la fotosíntesis bajo un estrés hídrico severo tuvo su máximo en *A. lebbek* y su mínimo en *L. leucocephala* y *T. grandis*, mientras que la tasa de transpiración fue máxima en *T. grandis* y mínima en *L. leucocephala*, lo que indica que esta última es más resistente a la sequía.

Resumo: O efeito da humidade no crescimento das plântulas de *Albizzia lebbek* Benth., *Dalbergia sissoo* Roxb., *Leucaena leucocephala* (Lam.) de Wit., *Shorea robusta* Gaertn.f. e *Tectona grandis* L. foi avaliado na região de Tarai do Uttarakhand, Índia durante 2002-2004. As plântulas, produzidas em sacos de polietileno contendo 4 kg de terra de jardim, foram sujeitas a um frequência de quatro regas diárias e em intervalos de 7, 14 e 21 dias, respectivamente, de acordo com as classe de stress designadas sem, intermédio, elevado e muito elevado. As observações periódicas começaram um mês depois do estabelecimento das plântulas. A altura das plântulas e a biomassa decresceram ao nível de stress muito elevado em todas as espécies. A redução (relativa à ausência de stress) em altura e biomassa atingiu valores máximos na *L. leucocephala* (75.8% and 99.8%) e um mínimo na *A. lebbek* (53.8% e 81.6%). A área foliar média também decresceu significativamente com o aumento do stress hídrico em todas as espécies excepto na *S. robusta*, que mostrou um comportamento inverso. O ratio da área foliar cresceu com o aumento do stress hídrico em paralelo com o stress de humidade (excepto para a *S. robusta*). Em relação à taxa de crescimento relativo, e à taxa de assimilação líquida, encontrou-se um padrão inverso em todas as espécies (excepto para *S. robusta* e *T. grandis*). Sob stress bastante alto, a *L. leucocephala* manteve um elevado ψ e teor de prolina e a *A. lebbek* mostrou os valores mais baixos indicando a sua resistência à secura e susceptibilidade. O ajustamento osmótico em diferentes espécies sob stresses muito elevados situou-se na seguinte ordem: *L. leucocephala* > *T. grandis* > *D. sissoo* > *S. robusta* and > *A. lebbek*. Geralmente, e para todas as espécies, a taxa fotossintética líquida e a taxa de transpiração decresceram e a resistência estomática aumentou sob stress hídrico muito alto quando comparadas com as situações de ausência de stress. A percentagem de redução na fotossíntese (relativa ao máximo) sob stress hídrico severo foi mais elevado na *A. lebbek* e mais baixo em *L. leucocephala* e *T. grandis*, enquanto que a taxa de transpiração foi mais alta na *T. grandis* e mais baixa em *L. leucocephala*, indicando que esta última é mais resistente à seca.

Key words: Drought resistance, growth parameters, photosynthesis, proline, stomatal resistance, transpiration, tree seedlings, water potential.

Introduction

The pressure on existing forest resources has been constantly increasing with the bargeoning

human and cattle population (Singh & Singh 1987). The situation has reached alarming proportion, and massive efforts are required not only to rehabilitate the degraded forest but also to

bring more area under forest. The growing emphasis on forestry and agroforestry programmes in India has resulted in an increasing demand of various multipurpose tree seedlings, and standardization of nursery conditions are necessary to produce healthy seedlings (Rao & Singh 1985). The information on the physiological response of seedlings to environmental stress should be helpful for better understanding of seedling establishment in plantation to avoid large scale failures in different forestry programmes (Rao 1988, 2005). In the present study, seedling growth of five important tree species in Tarai region were examined under a drought stress for a period of one year to compare drought resistance strategy and to find out relationship between different physiological parameters.

Materials and methods

Seedlings of *Albizia lebbek* Benth., *Dalbergia sissoo* Roxb., *Leucaena leucocephala* (Lam.) de Wit., *Shorea robusta* Gaertn.f. and *Tectona grandis* L. were raised by sowing seeds in polyethylene bags containing about 4 kg of garden soil. The established seedlings of all species were subjected to four watering frequencies by irrigating them daily and at 7, 14 and 21 days intervals, respectively designated as no stress, intermediate, high and very high stress. For each species and treatment, 20 bags with one seedling each were maintained.

Observations began after one month of seedling establishment. Height was measured at monthly intervals. Biomass (dried at 60 ± 2 °C) of leaf, stem and roots was recorded by harvesting three seedlings from each treatment at two month intervals. The leaves were clipped from each seedling and outline of each leaf was drawn on graph paper for the determination of average leaf area and total leaf area per seedling in all species (except *L. leucocephala*). Leaf weight ratio (LWR, g g^{-1}), specific leaf area (SLA, $\text{cm}^2 \text{g}^{-1}$), leaf area ratio (LAR, $\text{cm}^2 \text{g}^{-1}$), relative growth rate (RGR, $\text{g g}^{-1} \text{d}^{-1}$) and net assimilation rate (NAR, $\text{g g}^{-1} \text{d}^{-1}$) were determined following Evans (1972).

Photosynthetic rate (P , $\mu \text{mol m}^{-2} \text{S}^{-1}$), transpiration rate (E , $\text{milli mol m}^{-2} \text{S}^{-1}$) and stomatal resistance (R , $\text{M}^2 \text{s mol}^{-1}$) were estimated during winter, autumn and summer seasons by using an open system, portable Infra Red Gas

Analyzer (IRGA, CID 301, P.S., U.S.A.) in the forenoon (10.00 to 12.00). Proline content ($\mu \text{mol g}^{-1}$ f. wt.) in the leaves was estimated according to the procedure of Bates *et al.* (1973) on fresh weight basis. The shoot water status of seedlings was assessed as water potential (ψ) using a Pressure Chamber (PMA) (Kramer 1995). The pre-dawn (ψ , pd) (12.00 noon) and mid-day (ψ , md) (2.00 pm) water potential (MPa) was measured in three different seasons of a year. ANOVA, correlation and 't' test were performed according to Snedecor & Cochran (1969).

Results and discussion

The seedling growth (cm) was maximum under no stress level (control) in all tree species except *S. robusta*, in which it was maximum in intermediate stress (Fig. 1). The reduction in height after one year was $>50\%$ under very high stress in all species as compared to no stress. The relative performance of height growth (relative to control) in low moisture level (very high stress) was minimum in *T. grandis* (0.22) and maximum in *A. lebbek* (0.46). There was significant difference (ANOVA, $P < 0.01$) in growth performance between species. Muthechelien *et al.* (1997) concluded that the water stress significantly reduced shoot length in *Erythrina variegata*. The dry biomass (g) of seedlings also decreased by $>80\%$ under very high stress in all species (Fig. 2). Reduction in biomass

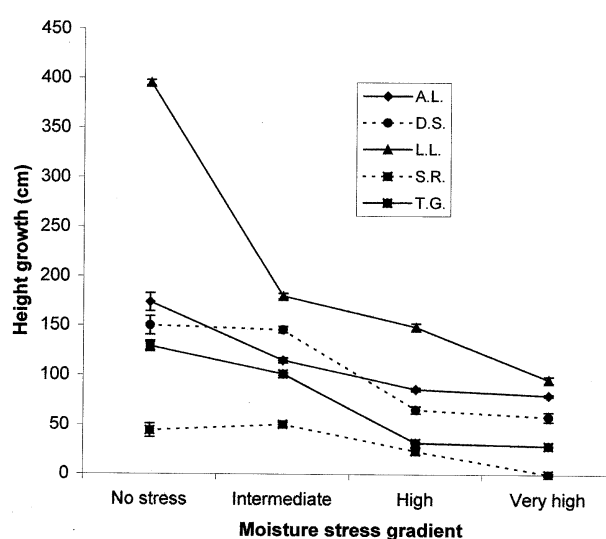


Fig 1. Seedling height at the end of experiment in different tree species under a moisture stress gradient.

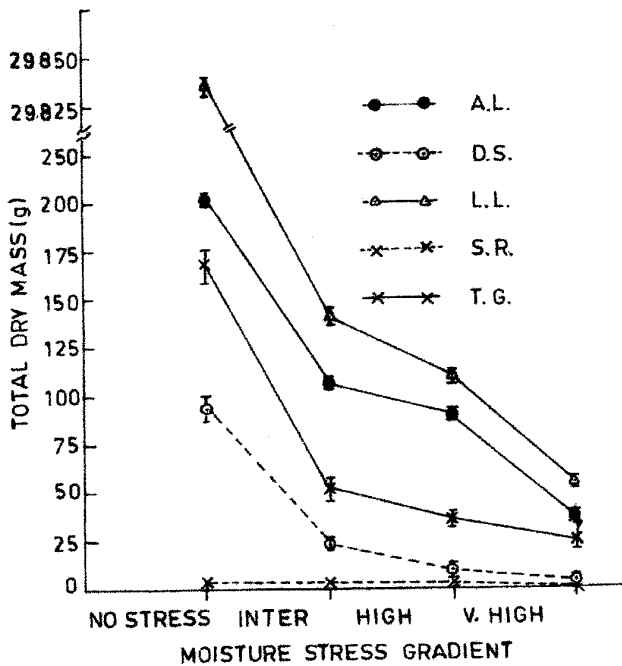


Fig 2. Seedling biomass of different species at the end of experiment under a moisture stress gradient.

was maximum in *L. leucocephala* (99.8%) and minimum in *A. lebbek* (81.6%) under very high stress (Fig. 2). Reduction in total seedling dry matter yield under water stress conditions has also been reported by Rao (1988) in *Quercus floribunda* and *Cupressus torulosa* (13 – 30%); Rao & Singh (1985) in *Quercus leucotrichophora* and *Pinus roxburghii* (22 – 38%) and Thomas (2000) in four different species. In the present study, the values of reduction were very high indicating that these species are more sensitive to water stress. The response of seedlings to different moisture levels was evaluated in terms of height : weight ratio of stem and the values for different species ranged from 1.44 to 5.22 in *A. lebbek*; 1.33 to 53.70 in *D. sissoo*; 0.02 to 2.97 in *L. leucocephala*; 22.89 to 45.83 in *S. robusta* and 2.33 to 5.85 in *T. grandis*. ANOVA indicated that the differences between species, treatments and species x treatments were significant at $P < 0.01$. The decrease may be due to decline in net assimilation, brought about by decreased leaf water potential (De Puit & Caldwell 1975). The effect of water stress on yield may be accentuated, since the rate of decline in photosynthesis may be more than that of respiration under water stress (Levitt 1972).

The average leaf area decreased with increasing stress in all the species (Fig. 3). In very high stress, the decrease was maximum (52.9%) in *L. leucocephala* and minimum (25.5%) in *D. sissoo*. ANOVA indicated that the differences between species, treatments and species x treatments were significant at $P < 0.01$. Since water stress reduced leaf number, total leaf area was also reduced. Adverse effect of water stress on leaf expansion has also been reported by Virgin (1965) for different species. Rao & Singh (1985) suggested that leaf structure goes through ontogenic progression, which at the same time is sensitive to environmental changes, leading to large changes in SLA. SLA increased with increasing water stress in all species except *S. robusta*, where the pattern was reversed (Fig. 4). Low SLA was obtained in *L. leucocephala* compared to other species, whereas comparatively high values were found in very high stress in all species. However, the differences between species and treatments were not-significant (ANOVA). Increased SLA must imply important anatomical changes in mesophyll and palisade layers (Hiesey *et al.* 1971).

The LAR increased along with moisture stress in all species except *S. robusta*, in which it decreased (Fig. 4). ANOVA showed no significant differences for both species and treatments. A reverse trend was observed in RGR and the RGR differences between species and treatments were significant (ANOVA, $P < 0.01$). A similar trend was also found with NAR in all species except in *S. robusta* and *T. grandis* showing higher values at intermediate stress in the former and upto no stress in the latter species (Table 1). Root growth depends on shoot growth, and root : shoot ratio changes with environmental treatment (Davidson

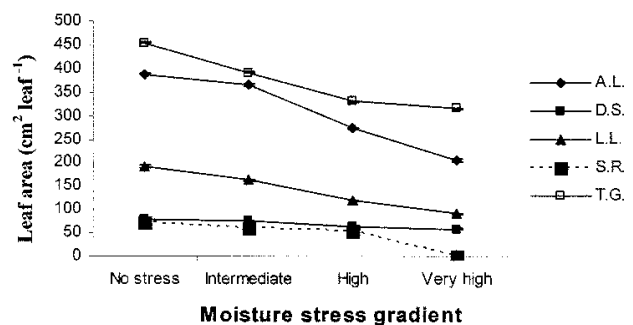


Fig 3. Average leaf area in seedlings of different tree species at the end of experiment under a moisture stress gradient.

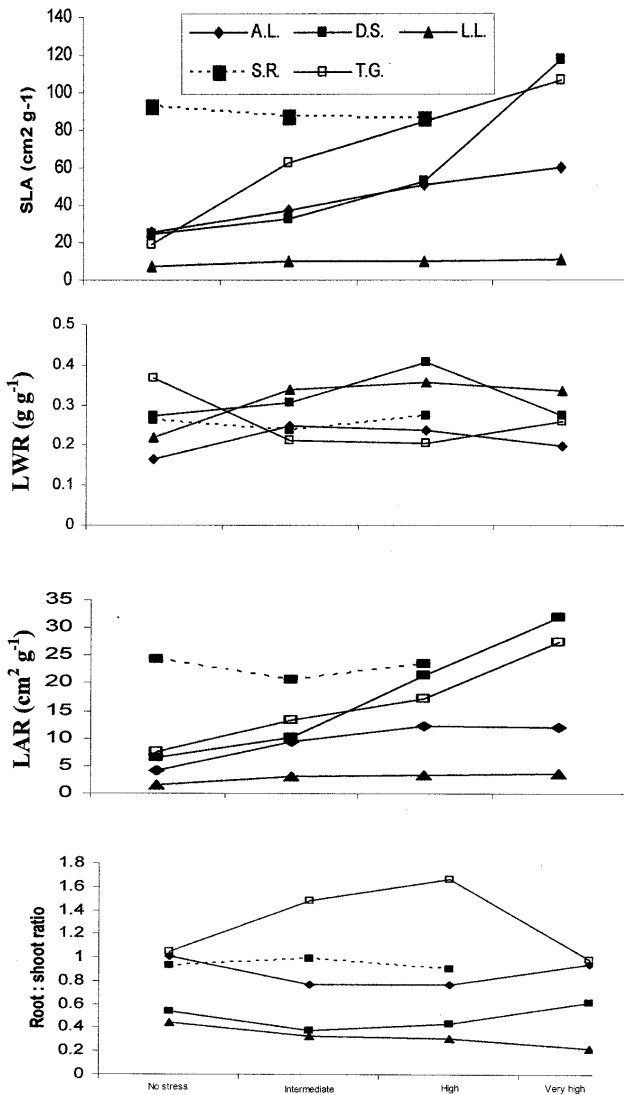


Fig 4. Average (across all six samples) SLA, LWR, LAR and root : shoot ratio in seedlings of different tree species in a moisture stress gradient.

1969). According to Loomis *et al.* (1971), the water stress slows shoot growth more and sooner than it does root growth. In the present study, the root : shoot ratio did not show any definite trend. It increased either upto intermediate stress in *S. robusta* or high stress in *T. grandis*. In the rest of the species, it decreased with increased stress from no stress to intermediate stress in *D. sissoo*; high stress in *A. lebbek*; and very high stress in *L. leucocephala* (Fig. 4). Thus, the root : shoot ratio decreased under very high stress compared to no stress in all species except *D. sissoo*, in which it increased indicating its high tolerance stress

compared to others. The t test indicated significant differences between no stress and very high stress ($P < 0.01$) in all species (except *T. grandis*, non-significant).

Measurement of water potential is the most meaningful property to understand plant water relationship, particularly under drought. The pre-dawn (pd) and mid-day (md) water potential in the present study indicated that it varied significantly across the seasons and species (Figs. 5 & 6). Williams *et al.* (1997) also reported seasonal variations in ψ of oak species. In all species, ψ md was always lower than ψ pd (Figs. 5 & 6).

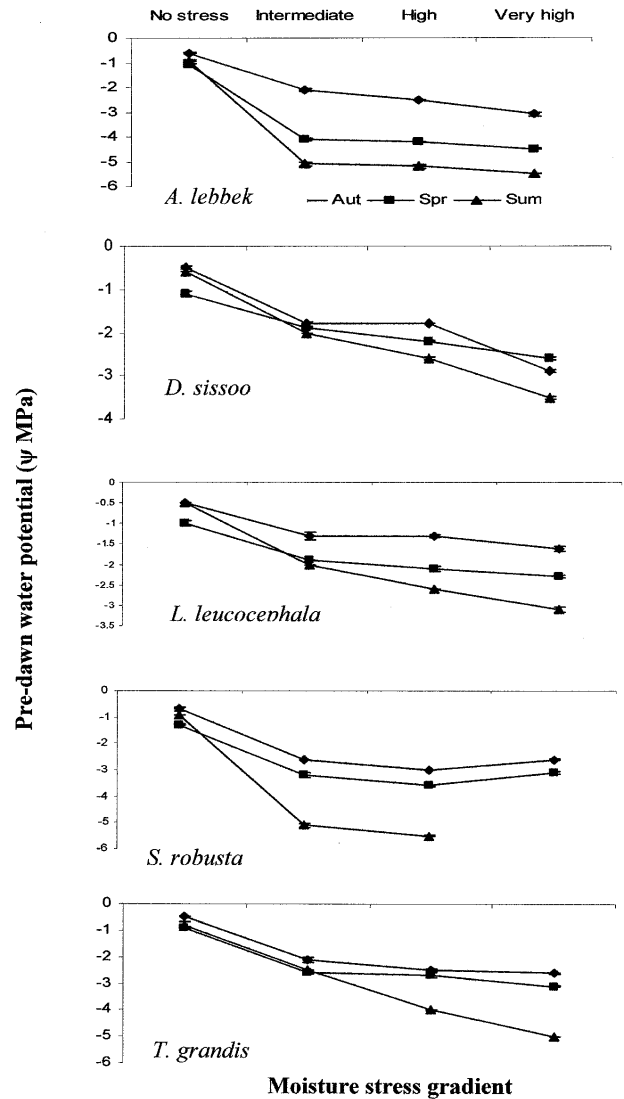


Fig 5. Seasonal variation in pre-dawn water potential (ψ , MPa) in seedlings of different tree species growth in a moisture stress gradient.

Table 1. Average (across all six samples) relative growth rate (RGR, g g⁻¹ d⁻¹) and net assimilation rate (NAR, g g⁻¹ d⁻¹) in different tree species under a moisture gradient during one year period.

Species/Parameter	No stress	Intermediate	High	Very high
Relative growth rate (RGR, g g ⁻¹ d ⁻¹)				
<i>A. lebbek</i>	0.6612	0.3512	0.2456	0.1143
<i>D. sissoo</i>	0.3144	0.0741	0.0318	0.0176
<i>L. leucocephala</i>	0.4077	0.4395	0.3450	0.0906
<i>S. robusta</i>	0.0172	0.0134	0.0074	*
<i>T. grandis</i>	0.5629	0.1678	0.1196	0.0890
Net assimilation rate (NAR, g g ⁻¹ d ⁻¹)				
<i>A. lebbek</i>	0.1469	0.0790	0.0648	0.0587
<i>D. sissoo</i>	0.1458	0.0554	0.0388	0.0667
<i>L. leucocephala</i>	2.7134	0.0367	0.0375	0.0269
<i>S. robusta</i>	0.0439	0.0459	0.0318	*
<i>T. grandis</i>	0.0793	0.1066	0.1083	0.1047

* Seedlings could not survive till the end of experiment.

Table 2. Free proline content (μ mol g⁻¹ f. wt.) in the leaves of different tree species seedlings under a moisture gradient at the end of the experiment (Mean \pm S.E.).

Species	No stress	Intermediate	High	Very high
<i>A. lebbek</i>	3.24 \pm 0.01	3.47 \pm 0.01	4.06 \pm 0.03	5.19 \pm 0.02
<i>D. sissoo</i>	5.21 \pm 0.01	16.72 \pm 0.03	24.61 \pm 0.03	33.43 \pm 0.60
<i>L. leucocephala</i>	0.26 \pm 0.01	18.51 \pm 0.03	26.39 \pm 0.17	34.68 \pm 0.01
<i>S. robusta</i>	3.07 \pm 0.18	5.49 \pm 0.01	12.38 \pm 0.08	*
<i>T. grandis</i>	4.99 \pm 0.13	10.07 \pm 0.03	17.42 \pm 0.13	37.90 \pm 0.13

* Seedlings could not survive till the end of experiment.

Interestingly, lower values were found in *S. robusta* under high stress in ψ pd and very high stress in ψ md compared to others indicating high sensitivity to even moderate drought (Figs. 5 & 6). The ψ pd indicates how plant integrates with soil water availability and the level of moisture at which it begins to develop daily water deficits (Molchanov & Molchanova 2000; Pallardy *et al.* 1991). In all three seasons, the ψ declined with increasing moisture stress in all species except *D. sissoo* and *L. leucocephala*, in which it was almost constant during autumn from intermediate to high and then declined under very high stress. High ψ was measured in *L. leucocephala* and low in *A. lebbek* under very high stress across the seasons. Drought tolerant plants of *Cocao* trees maintained a high water potential than drought susceptible plants in dry months (Balasimpha *et al.* 1991). Thus, *L. leucocephala* maintained higher ψ pd (-3.1 MPa) even under severe stress indicating its drought resistance; *T. grandis* (-5.0 MPa) and *A. lebbek* (-5.5 MPa) had low ψ pd, which may be due to their drought sensitive nature; and

intermediate response in the rest of species (Fig. 5).

Severe water stress induces numerous metabolic irregularities in plants. Free proline accumulation upto 100 times of the normal has been used as a single parameter to measure drought (Bates *et al.* 1973). In the present study, free proline accumulation was remarkable in all species in response to drought (Table 2). Increase in free proline content under stress may be due to disturbed metabolism (Fukutoku & Yamada 1981; Sharma *et al.* 1987). Karolewski (1996) and Lansac *et al.* (1994) have reported increase in proline in response to water stress in various tree species. In the present study, *L. leucocephala* exhibited a marked increase in free proline content under very high stress indicating its drought tolerant nature as compared to others (Table 2). It clearly shows that a fast growing species does better than slow growing species with regard to osmotic adjustment. Sivakumar *et al.* (1998) reported that water stress increased the proline content in *Tamarindus indica*, *Albizia lebbek*,

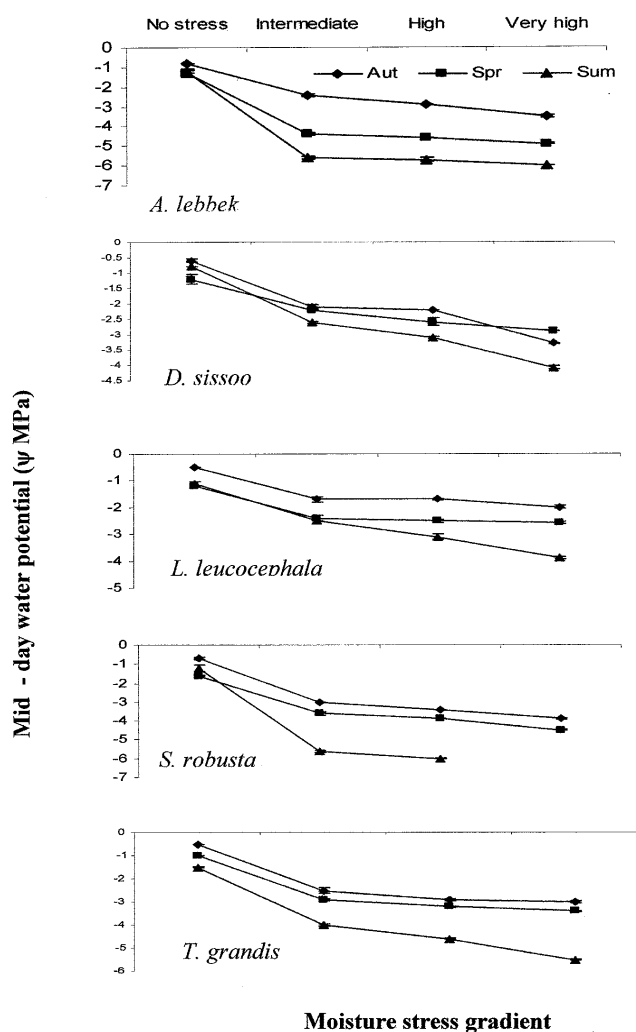


Fig 6. Seasonal variation in mid-day water potential (ψ , MPa) in seedlings of different tree species growth in a moisture stress gradient.

Azadirachta indica and *Eucalyptus tereticornis*. In the present study, ANOVA indicated that the differences were significant between species at $P < 0.05$ and treatments at $P < 0.01$. In addition, under very high stress, the values of ψ were positively correlated with the proline content ($P < 0.01$). Thus, proline accumulation may serve as a promising index for drought tolerance in different plant species.

Osmotic adjustment involves uptake, internal production or transfer of osmotically active substances such as inorganic ions (K, Mg, Cl, Ca, NO_2 , etc.), sugars and amino acids such as proline (Arndt *et al.* 2000). In the present study, the osmotic adjustment of species on the basis of free proline accumulation in the leaves of one year old

seedlings was assessed and all the species showed active osmotic adjustment by accumulating free proline content. *L. leucocephala* had the highest proline content (34.68) and *A. lebbek* the lowest (5.19) (Table 2). Gonzalez *et al.* (1999) studied the physiological response of *Laurus azorica* and *Viburnum rigidum* to drought stress and found that proline content in *L. azorica* leaves increased sharply at -2.6 MPa whereas in *V. rigidum*, it did not change even at -3.5 MPa indicating significant osmotic adjustment of *L. azorica*. Osmotic adjustment of tree species through solute accumulation had also been reported by various authors (Arndt *et al.* 2000; Thomas & Gausling 2000). In the present study, the osmotic adjustment in different species followed the order: *L. leucocephala* > *T. grandis* > *D. sissoo* > *S. robusta* and > *A. lebbek* (Table 2).

Net photosynthetic rate and transpiration rate decreased in very high stress compared to no stress in *A. lebbek*, *D. sissoo* and *L. leucocephala* in all seasons (except autumn in *L. leucocephala*) whereas, it increased in both *S. robusta* and *T. grandis* (Figs. 7 & 8). However, the stomatal resistance increased in very high stress compared to no stress in all species and in all three seasons except *A. lebbek*, in which it decreased in autumn (Fig. 9). Decreased photosynthesis under severe stress was reported in *Tectona grandis* (Rajendrudu & Naidu 1998) and in different woody species (Morinaga & Sykes 2001; Ramanjulu & Sudhakar 1998; Ranney *et al.* 1990). However, the transpiration rate was less affected than photosynthetic rate as suggested by Germana & Chartzoulaski (1997). The reduction (percentage of maximum) in photosynthesis under very high stress varied from species to species (Fig. 7) and it was highest in *A. lebbek* and lowest in *L. leucocephala* and *T. grandis*, whereas the transpiration rate was highest in *T. grandis* and lowest in *L. leucocephala* (Fig. 8). The initial limitation on photosynthesis during water stress is believed to be stomatal restriction of CO_2 availability (Chaves 1991). However, as leaf ψ decreases further, non-stomatal limitations occur (Renou *et al.* 1990). Stomatal control of photosynthesis accounted for less than 50% change in carbon fixation under water stress (Ni & Pallardy 1991). According to He *et al.* (1995), water stress affects the photochemical events largely by reducing electron transport in

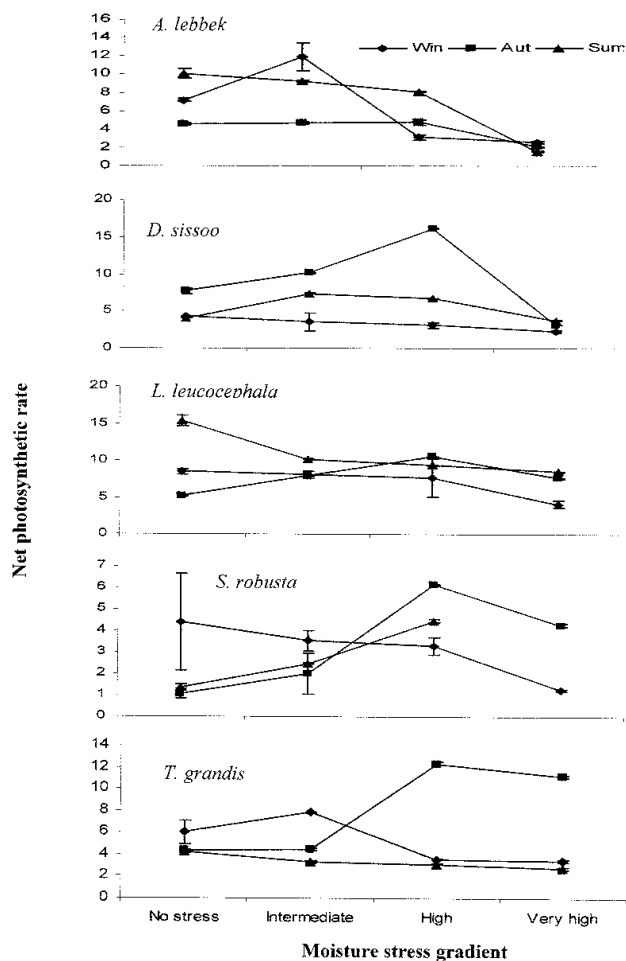


Fig 7. Seasonal variation in net photosynthetic rate (P , $\mu \text{ mol m}^{-2} \text{ S}^{-1}$) in seedlings of different tree species growth in a moisture stress gradient.

photosystem-2 (PS-2). However, some investigations confirm the drought tolerant nature of PS-2 (Fedina & Popova 1996; Kicheva *et al.* 1994). Water stress also reduced the activity of Ribulose-1-5 diphosphate carboxylase that leads to reduced photosynthesis (Raggi 1992). Under severe drought, photosynthesis and chlorophyll content (unpublished data) were positively correlated ($P < 0.05$) during both autumn and summer; whereas the SLA and stomatal resistance were negatively correlated ($P < 0.01$) only during spring; and both photosynthesis and transpiration with water potential (ψ) were positively correlated ($P < 0.05$) during summer.

Drought tolerant species have a capacity to maintain relatively high rate of photosynthesis under drought (Gu *et al.* 1999). Thus, *L. leucocephala* showed its drought tolerance by

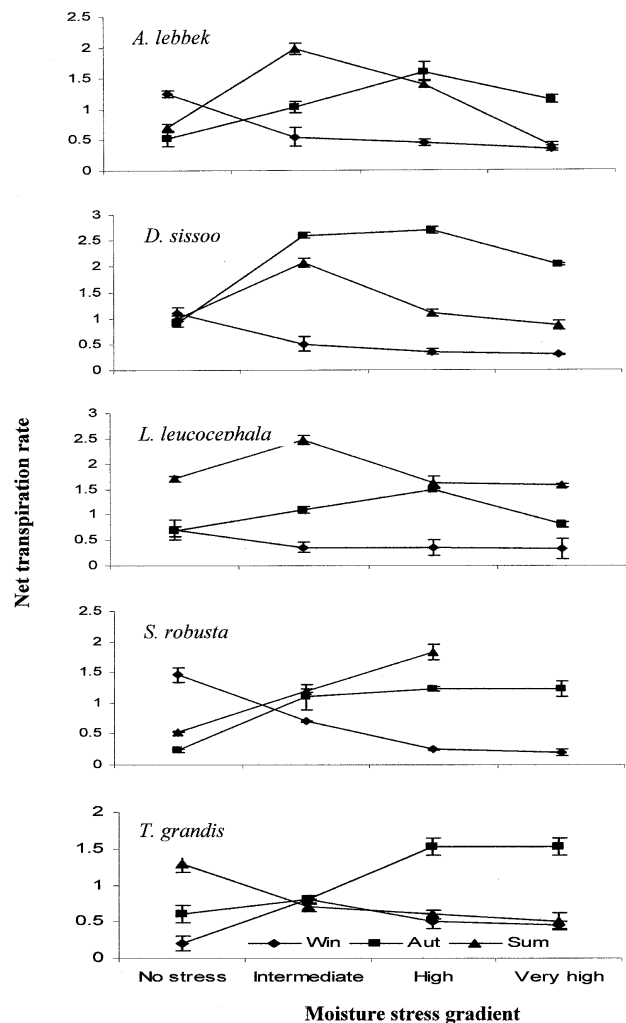


Fig 8. Seasonal variation in net transpiration rate (E , $\text{milli m}^{-2} \text{ S}^{-1}$) in seedlings of different tree species growth in a moisture stress gradient.

maintaining relatively high photosynthesis and low transpiration even under very high stress. Reduction in water loss by stomatal behaviour is one of the adaptive responses of maintaining high water use efficiency during drought (Raggi 1992). Nautiyal *et al.* (1996) reported that high water stress induces reduction in chlorophyll synthesis, which may ultimately lead to low photosynthetic activity and less dry matter production.

Acknowledgements

We are thankful to Professor S.P. Singh, FNA, Department of Botany, Kumaun University, Naini Tal and Professor R.C. Pant, Department of Plant Physiology, CBSH, G.B. Pant University of

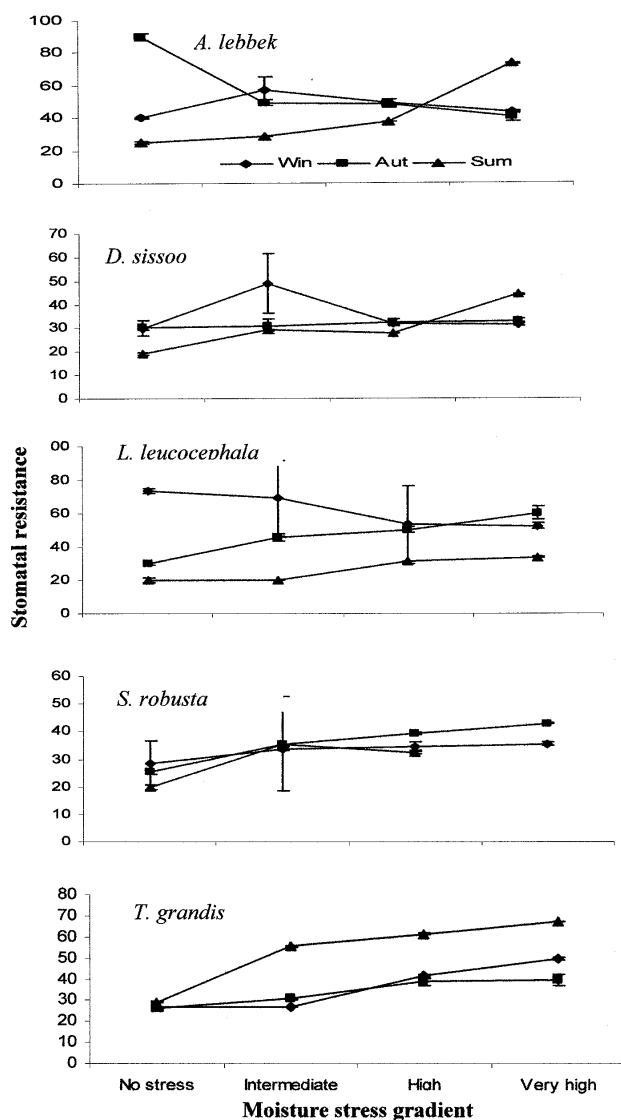


Fig 9. Seasonal variation in stomatal resistance ($R, M^2 s mol^{-1}$) in seedlings of different tree species growth in a moisture stress gradient.

Agriculture & Technology, Pantnagar, for providing facilities and critical suggestions during the experimental period. We are indebted to the unknown reviewer(s) for their critical and constructive comments on the ms. The senior author is also thankful to the Govt. of U.P. for providing partial finance in the form of a research project.

References

Arndt, S.K., W. Wanek, S.C. Clifford & M. Popp. 2000. Contrasting adaptations to drought in field grown

Ziziphus mauritiana and *Prunus persica* trees : water relations, osmotic adjustment and carbon isotope composition. *Australian Journal of Plant Physiology* **27** : 985-996.

Balasingh, D., E.V. Daniel & P.G. Bhat. 1991. Influence of environmental factors on photosynthesis in *Cocoa* trees. *Agricultural and Forest Meteorology* **55** : 15-21.

Bates, L.S., R.P. Waldren & I.B. Teare. 1973. Rapid determination of free proline for water stressed studies. *Plant and Soil* **39** : 205-207.

Chaves, M.M. 1991. Effects of water deficits on carbon assimilation. *Journal of Experimental Botany* **42** : 1-16.

Davidson, R.L. 1969. Effect of root/shoot ratios in some pasture grasses and clover. *Annals of Botany* **53** : 561-569.

De Puit, J.E. & M.M. Caldwell. 1975. Gas exchange of three cool semi-desert species in relation to temperature and water stress. *Journal of Ecology* **63** : 835-836.

Evans, G.C. 1972. *The Quantitative Analysis of Plant Growth*. Blackwell Scientific Publications. Oxford.

Fedina, I.S. & A.V. Popova. 1996. Photosynthesis, photorespiration and proline accumulation in water stressed pea leaves. *Photosynthetica* **32** : 213-220.

Fukutoku, Y. & Y. Yamada. 1981. Sources of proline nitrogen in water stressed soybean (*Glycine max* L.). I. Protein metabolism and proline accumulation. *Plant and Cell Physiology* **22** : 1397-1404.

Germana, C. & K.S. Chartzoulaski. 1997. Experiences on the response of almond plants (*Amygdalus communis* L.) to water stress. *Acta Horticulture* **449**: 497-503.

Gonzalez-Rodriguez, A.M., M.S. Jimenez, D. Morales, G. Aschan & R. Losch. 1999. Physiological responses of *Laurus azorica* and *Viburnum rigidum* to drought stress : Osmotic adjustment and tissue elasticity. *Phyton-Horn* **39** : 251-263.

Gu, Z., J.J. Hu, J.L. Wen & S.Q. Wang. 1999. A study on adaptability of maple to drought stress. *Journal of Northwest Forestry College* **14** : 1-6.

He, J.X., J. Wang & H.G. Liang. 1995. Effects of water stress on photochemical function and protein metabolism of photosystem-II in wheat leaves. *Physiologia Plantarum* **93** : 771-779.

Hiesey, W.M., M.A. Nobs & O. Bjorkman. 1971. *Experimental Studies on the Nature of Species. V. Biosystematics, Genetics and Physiological Ecology of the Erythrina*. The Section of Mimulus Publ. Carnegie Inst. No. 628, Washington D.C.

Karolewski, P. 1996. Role of proline in higher plants under conditions of abiotic stress. *Wiadomosci Botaniczne* **40** : 67-81.

- Kicheva, M.I., T.D. Isonov & L.P. Popova. 1994. Stomatal and non stomatal limitations to photosynthesis in two wheat cultivars subjected to water stress. *Photosynthetica* **30** : 107-116.
- Kramer, P.J. 1995. *Water Relations of Plants*. Academic Press, New York.
- Lansac, A.R., J.P. Zaballos & A. Martin. 1994. Seasonal water potential changes and proline accumulation in mediterranean shrub land species. *Vegetatio* **113** : 141-154.
- Levitt, J. 1972. *Responses of Plants to Environmental Stresses*. Academic Press, New York.
- Loomis, R.S., W.A. Williams & M.G. Hall. 1971. Agricultural Productivity. *Annual Review of Plant Physiology* **22** : 431-468.
- Molchanov, A.G. & T.G. Molchanova. 2000. Pre-dawn water potential of oak leaves as an indicator of plant water supply. *Lesovedenie* **2** : 72-74.
- Morinaga, K. & S.R. Sykes. 2001. Effect of salt and water stress on fruit quality, physiological responses, macro and micro element contents in leaves of *Satsuma mandarin* trees under green house conditions. *JARQ* **35** : 53-58.
- Muthuchelian, K., C. Murugan, N. Nedunchezian & G. Kukandaivelu. 1997. Photosynthesis and growth of *Erythrina variegata* as affected by water stress and triacontanol. *Photosynthetica* **33** : 241-248.
- Nautiyal, S., D.S. Negi & Shiv Kumar. 1996. Effect of water stress and antitranspirants on the chlorophyll contents of leaves of *Pongamia pinnata* (L.) Piere. *Indian Forester* **122** : 1018-1022.
- Ni, B.R. & S.G. Pallardy. 1991. Stomatal and nonstomatal limitations to net photosynthesis in seedlings of woody angiosperms. *Plant Physiology* **99** : 1502-1508.
- Pallardy, S.D., J.S. Pereira & W.C. Parker. 1991. Measuring the state of water in tree systems. pp. 27-76. In: J.P. Lassoic & J.M. Hinckley (eds.) *Techniques and Approaches in Forest Tree Ecology*. CRC Press, Boca Ratom F.L.
- Raggi, V. 1992. Changes in water relations and in some physiological functions of bean under very light osmotic shock induced by polyethylene glycol. *Physiologia Plantarum* **84** : 537-548.
- Rajendrudu, G. & C.V. Naidu. 1998. Effect of water stress on leaf growth and photosynthetic and transpiration rates of *Tectona grandis*. *Biologia Plantarum* **40** : 229-234.
- Ramanjulu, S. & C. Sudhakar. 1998. Photosynthetic characteristics in mulberry during water stress and rewatering. *Photosynthetica* **35** : 259-263.
- Ranney, T.G., T.H. Whitlow & N.L. Bassuk. 1990. Response of five temperate deciduous tree species to water stress. *Tree Physiology* **5** : 439-448.
- Rao, P.B. 1988. Effect of environmental factors on germination and seedling growth in *Quercus floribunda* and *Cupressus torulosa* tree species of central Himalaya. *Annals of Botany* **61** : 531-540.
- Rao, P.B. 2005. Effect of shade on seedling growth of five important tree species in Tarai region of Uttaranchal. *Bulletin of the National Institute of Ecology* **15** : 161-170.
- Rao, P.B. & S.P. Singh. 1985. Response breadths on environmental gradients on germination and seedling growth in two dominant tree species of central Himalaya. *Annals of Botany* **56** : 783-794.
- Renou, J.L., A. Gerbaud, D. Just & M. Andre. 1990. Differing substomatal and chloroplastic CO₂ concentration in water stressed wheat. *Planta* **182** : 415-419.
- Sharma, B.B., K.J.A. Mageed & P.N. Wattal. 1987. Studies on water stress in kinnow as influenced by irrigation schedules and nitrogen applications. *Indian Journal of Horticulture* **44** : 52-56.
- Shivkumar, V., K. Ramachandran, V. Ravichandran & V. Mallika. 1998. Effect of drought hardening on proline content of tree seedlings. *Annals of Plant Physiology* **12** : 82-84.
- Snedecor, G.W. & W.G. Cochran. 1969. *Statistical Methods*. 6th edn. Oxford & IBH Publishing Co., India.
- Singh, J.S. & S.P. Singh. 1987. Forest vegetation of the Himalaya. *Botanical Review* **53**: 80-192.
- Thomas, F.M. 2000. Growth and water relations of four deciduous tree species occurring at Central European tree line sites on shallow calcareous soils : Physiological reactions of seedlings of severe drought. *Flora Jena* **195** : 104-115.
- Thomas, F.M. & T. Gausling. 2000. Morphological and physiological responses of oak seedlings. *Annals of Forest Science* **57** : 325-333.
- Virgin, H.L. 1965. Chlorophyll formation and water deficit. *Plant Physiology* **18** : 994-1000.
- Williams, R.J., B.A. Myers, W.J. Muller, G.A. Duff & D. Eamus. 1997. Leaf phenology of woody species in north Australian Tropical Savannah. *Ecology* **78**: 2542-2558.