RESPONSE OF SELECTED FORESTRY AND AGROFORESTRY TREE SEEDLINGS TO WATER STRESS
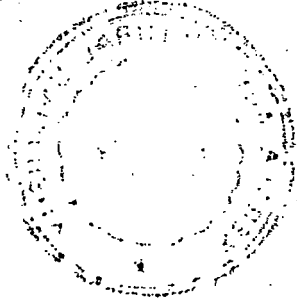
BY

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THESIS

Submitted in partial fulfilment of the
requirements for the degree of

Master of Science in Forestry

Kerala Agricultural University

Department of Tree Physiology and Breeding
COLLEGE OF FORESTRY
Vellanikkara, Thrissur

1996

DECLARATION

I hereby declare that this thesis entitled *Response of selected forestry and agroforestry tree seedlings to water stress* is a bonafide record of research work done by me during the course of research and that this thesis has not previously formed the basis for the award to me of any degree, diploma, associateship, fellowship or other similar title of any other University or Society.

Place : Vellanikkara

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CERTIFICATE

Certified that this thesis entitled *Response of selected forestry and agroforestry tree seedlings to water stress* is a record of research work done by Sri. RAJESH, N. under my guidance and supervision and that it has not previously formed the basis for the award of any degree, fellowship or associateship to him.

Place : Vellanikkara   Dʀ. P.K. ASHOKAN
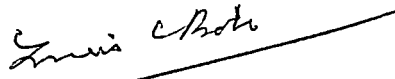Date : 27-02-1996   Chairman
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We, the undersigned members of the Advisory Committee of Sri. RAJESH, N. a candidate for the Degree of Master of Science in Forestry, agree that this thesis entitled *Response of selected forestry and agroforestry tree seedlings to water stress* may be submitted by Sri. RAJESH, N. in partial fulfilment of the requirement for the Degree.

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EXTERNAL EXAMINER

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I shall be failing in my duty if I forget to place on record the facilities offered by my *alma mater*, College of Forestry, Vellanikkara. The uninhibited and timely help by the office and library staff of College of Forestry is warmly acknowledged.

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My parents, brother and other family members was always with me with their uninhibited moral support and boundless affection. I behold to them forever for all I am today and hope to be in future.

Finally I bow my head before THE ALMIGHTY.

RAJESH, N.

To my beloved Grandma

With love......

CONTENTS

SYMBOLS AND ABBREVIATIONS

DAP -   Days after planting

DAS -   Days after the beginning of water stress

NR   -   Not recorded as the plants dried off due to
          severe water stress

SLA -   Specific leaf area

RGR -   Relative growth rate

NAR -   Net assimilation rate

LDR -   Leaf diffusive resistance

ψ -   Leaf water potential

RWC -   Relative water content

~   -   Approximately

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

Introduction

INTRODUCTION

India with its large human and livestock population, is facing a large gap in the present production and projected demands of timber, fuel wood and fodder. A variety of tree species are commonly managed under forestry and agroforestry programmes to meet the increasing demands of industrial timber and fuel wood. Planting of trees, especially in farmlands gained wide popularity in the recent years providing additional benefit to the farmers. A clamour for planting trees like *Tectona grandis* L.F. (teak) and *Acacia mangium* Willd. (mangium) in farmlands has been observed in the recent years especially among the farmers of Kerala. Tree species like *Swietenia macrophylla* King (mahogany) and *Ailanthus triphysa* (Dennst.) Alston. (matti) are also being planted in the homesteads of Kerala.

Water is considered as the most important limiting factor for establishment and growth of trees in dry areas which form about 75 per cent of the total cultivated area in India. The utilization of water by plants varies from species to species and even between types within a species. Regions with abundant, well distributed rainfall develop luxuriant forests whereas regions with consistently severe seasonal drought tend to be grasslands or desert scrub (Kozlowski *et al.*, 1991). Correlation between water supply and growth exist because water scarcity affects most of the physiological processes involved in plant growth. Water deficits can have a

major impact on the establishment success of the seedlings (Stoneman *et al.*, 1994). Water deficit or water stress refers to situations in which plant water potential and turgor are reduced enough to interfere with normal physiological functioning and growth of the plants. The exact cell water potential at which this occurs depends on the kind of plant, the stage of development and the process under consideration (Kramer, 1983). Water deficits can vary in intensity from small decreases in water potential, detectable only by instrumental measurements, through transient midday wilting, to permanent wilting and death by dehydration.

A variety of tree species are widely planted under rainfed situation in various agroclimatological zones of Kerala. These areas are prone to water stress due to the seasonality of rains which result in six to seven months of dry periods. The information about the response of these trees to water stress is of great importance in selecting tree species for different agroclimatic zones.

The response of the trees will vary from species to species and depending on the growth stages also. Young plants are considered to be more susceptible to water stress. Information regarding the response to water stress of tropical tree seedlings are sparse, whereas considerable amount of literature is available on temperate species (Zahner, 1988; Kaufmann, 1968; Cannel *et al.*, 1978; Seiler, 1985; Kozlowski, 1982;

Kozlowski *et al.,* 1991 etc.). Hence it is a felt need to gather scientific information on the response of common tree seedlings to water stress in order to identify suitable tree species for planting in different agroclimatic zones for viable forestry and agroforestry programmes in our state. Hence, an experiment was undertaken to study the response of important forestry and agroforestry tree seedlings to water stress with an objective of investigating morphological, physiological, biochemical or anatomical response of the tree species to water stress. The study also aimed at elucidating the mechanisms if any, involved in the stress tolerance of the selected tree seedlings and ultimately to identify the tree species tolerant to water stress.

REVIEW OF LITERATURE

Water is an important input which limits the distribution and growth of plants. Water deficits influence all phases of tree growth and are probably responsible for more growth loss than all other causes combined (Kramer, 1980). The primary effects of water deficits include a decrease in water content and cell turgor of plant tissue and a decrease in the free energy status or potential of the remaining water. Tree growth is reduced both directly, through the effects on cell turgor and indirectly through the intermediation of seed germination, photosynthesis, respiration, mineral nutrition, enzymatic activity, hormone relations, nitrogen metabolism etc.

There has been a lot of studies on the response of agricultural and horticultural crops to water stress (Giles *et al.*, 1974; Alberte *et al.*, 1977; Evans, 1983; Kramer, 1983; Turner *et al.*, 1986; Momen *et al.*, 1992). However, such studies are limited in forestry species, especially in tropical forestry. The reported findings pertinent to the present investigation are reviewed here.

2.1 Influence of water stress on growth parameters

The most obvious general effect of water stress is the reduction in overall plant size (Kramer, 1983). Water deficit inhibit both leaf growth and internode expansion. Because cell enlargement depends on cell turgor, the

elongation of cells is very sensitive to desiccation. Water stress directly and physically reduces growth by lowering cell turgor, because cell enlargement in response to change in water balance occur too rapidly to be mediated by metabolism (Kozlowski, 1982).

2.1.1 Height growth

After the seedling stage, the effect of water deficits on shoot growth become more complex, and depend in part on growth habitat. A summer drought may or may not influence current year height growth depending on when the water stress occur and on the inherent pattern of shoot elongation of the species affected (Kozlowski, 1982). At the community level, tree height is often reduced by the availability of water and trees usually grow taller in valleys than in shallower dry soils of the adjacent uplands. Waring and Schlensinger (1985) suggested that decreasing predawn water potential is well correlated with a decreased tree height at maturity.

Water stress was observed to severely depress first year loblolly pine seedling growth and high correlations between growth and soil moisture was only found when soil moisture was limiting (Cannell et al, 1978). Driessche (1991) observed a drastic reduction in height growth and dry weight of Pseudotsuga menzeisii, Pinus contorta and Picea glauca seedlings in response to drought stress. Drought caused a significant decline in height growth and new

shoot dry weight in two year old seedlings of *Picea rubens,* but old shoot dry weight, root dry weight and root/shoot ratio were not appreciably affected (Roberts and Cannon, 1992). A similar trend of decreasing height growth was observed in water stressed *Lirodendron tulupifera* seedlings (Cannon *et al.,* 1993.

2.1.2 Leaf growth

One of the damaging effects of water stress is the reduction in leaf area, which reduces the water loss but reduces the surface that carry on photosynthesis. Most of the reduction in leaf area as a result of drought appears to result from slowing of cell expansion. Water stress not only reduce leaf size but often increases the ratio of mesophyll to external leaf surface. Whereas normal diurnal changes in leaf dehydration do not greatly affect final leaf size, desiccation for long period results in smaller leaves (Boyer, 1976). Water deficits also reduces leaf area by leaf senescence and inducing early abscission (Ludlow and Muchow, 1990).

Loblolly and white pine needle growth decreased as mean soil water potential decreased (Kaufmann, 1968). In *Alnus glutinosa* seedlings, water stress treatment reduced leaf size and increased the epicuticular wax content (Seiler, 1985). Restricted water supply caused a five fold reduction in number of leaves per plant and a reduction of up to 20 per cent in average size in *Eucalyptus maculata* and *E. brockwayi* seedlings (Myers and Landsberg, 1989).

Prolonged periodic water shortage reduced the amount of foliage by 90 per cent in *Fagus sylvatica* (Cermak *et al.*, 1993).

In *Pinus contorta*, specific leaf area increased in response to nursery drought treatment (Driessche, 1991). Rhizopoulou and Davies (1993) observed in *Eucalyptus globulus* that although leaf area of unwatered seedlings were less, the corresponding leaf dry weight was quite similar to that of well watered seedlings. Soon after rewatering, leaf area of plants experiencing water shortage was comparable to that of well watered plants. Green house experiments in *Eucalyptus marginata* seedlings by Stoneman and Dell (1993) indicated that rate of leaf growth was very sensitive to water deficits. Stoneman *et al* (1994) again in *E. marginata* seedlings in a soil drying and rewatering experiment reported that the rate of leaf growth declined linearly with predawn leaf water potential to reach zero at -1.5 MPa. There was no recovery of leaf growth rate within the first three days after rewatering.

2.1.3 Root growth

The shoot water deficits that develop on hot sunny days are eventually transmitted to the roots through the sap stream. Water deficits in roots reduce the rate of root elongation, root branching and cambial growth. In a study by Pessin (1939) on long leaf and slash pine seedlings, it was evident that root growth is less affected than shoot growth by varying moisture levels. Although

growth of both root and shoot decreases under drought, the root-shoot ratio generally increases (Kramer and Kozlowski, 1979).

Kaufmann (1968) reported that root growth of loblolly and scot pine seedlings in a slowly drying soil was reduced to about 25 per cent of the rate at field capacity by a soil water potential of -0.6 MPa or -0.7 MPa. Root regeneration of white pine seedlings decreased considerably with increasing soil moisture tension (Day and Mac Gillivray, 1975). Northern red oak (*Quercus rubra*) root regeneration and increasing root length were inhibited at -4 bars and then stopped completely at -6 bars (Larson and Whitmore,1970). Waring and Schlesinger (1985) cited several experiments suggesting that tree roots do not grow much at soil water potential below -7 bars. However, roots resume growth within one or two days after rewatered.

In addition to reduction in root growth, there will be suberisation of roots when water stressed (Kramer, 1969). Eventhough it is said that water absorption is reduced by suberisation, Chung and Kramer (1975) showed that considerable absorption occurs through suberised roots.

In *Alnus glutinosa* seedlings Seiler and Johnson (1984) observed that the root/shoot ratio significantly increased eventhough water stress greatly reduced shoot, root, nodule and total plant dry weight. However, in loblolly pine

seedlings Seiler and Johnson (1988) reported a decreasing trend in the root/shoot ratio in response to water stress. In *Acacia albida* and *A. seyal*, root growth was found to be reduced on soils at or below a water potential of -0.7 MPa (Awodola, 1991). A 385% increase in root:shoot mass ratio for droughted *Asimina triloba* plants was observed by Nash and Graves (1993). Moderate moisture stress applied hastened root dry weight gain but did not affect other morphological characters in *Thuja plicata* (Krasowski and Owens, 1991). When subjected to restricted watering regimes, ten week old seedlings of *Acacia mangium* showed an increase in root growth capacity and root/shoot ratio (Awang and De Chavez, 1993). However, in *Picea rubens,* Robert and Cannon (1992) observed that drought did not affect the root dry weight or root/shoot ratio.

Drought stimulated the growth of fine roots in the surface and upper soils layers in *Fagus sylvatica* (Cermak *et al.,* 1993). Root growth of unwatered *Eucalyptus globulus* seedlings was gradually increased in deeper soil layers, where thick root apices and high soil water depletion per unit length was recorded. As a result, root absorbing surface area was as large in unwatered plants as in well watered plants (Rhizopoulou and Davies, 1993).

2.1.4 Total dry matter production

Water deficits generally have a negative effect on the dry matter accumulation in plants as it impairs with many of the physiological processes which determines growth like photosynthesis, respiration, enzyme activity etc. Dry matter production was significantly affected in four *Acacia* species when controlled watering was employed (Kireger and Blake, 1994).

In a comparative study of *Eucalyptus maculata* and *E. brockwayi* under different levels of water supply, Myers and Landsberg (1989) found that total dry matter production was higher in *E. maculata* but net assimilation rate was higher in *E. brockwayi* seedlings. Water stress reduced dry matter accumulation in *Pseudotsuga menzeisil, Pinus contorta* and *Picea glauca* seedlings grown in containerised nursery (Driessche, 1991). In *Acacia auriculiformis,* Phillips and Riha (1993) reported that above ground biomass accumulation decreased by 21% below that of well watered controls in the moderately drought stressed and by 47% below in severely drought stressed seedlings. Dry matter production was positively correlated with transpirational water use in *Eucalyptus globulus* under water stressed condition (Osorio and Pereira, 1993). However, differences in total plant dry weight under waterstress were less obvious in an experiment conducted with two *Populus* clones and four hybrid progenies (Tshaplinski and Tuskan, 1994).

2.2 Influence of water stress on physiological parameters

Water loss from plant tissues alter a number of physiological processes. It causes a loss of turgor inside the cells, followed by closure of stomata, alteration of cellular membrane relations, reduction of leaf water potential etc. All these together causes metabolic disruption in plants.

2.2.1 Relative water content

Relative turgidity of the leaves can be employed as a measure of water deficit in plants (Weatherley, 1950). Sinclair and Ludlow (1985) proposed that relative water content (RWC) as an alternative measure of plant water status which tells upon the metabolic processes in tissues and lethal leaf water status. They reported that photosynthesis, protein synthesis, NO_3 reduction and leaf senescence are better correlated with changes in cell volume and RWC than with water potential in certain plants.

Coffee leaves maintained a high relative water content under dehydrating conditions, and this has been attributed to an efficient stomatal control (Bierhuizen *et al.*, 1969, Josis *et al.*, 1983). Using detatched loblolly and white pine needles in a Warburg respirometer, Miller and Allen (1971) observed that there is a positive correlation between relative needle water content and stomatal aperture. In *Eucalyptus marginata* seedlings drought

stressed plants maintained a higher relative water content for a given leaf water potential at values below ‾1.5 MPa (Stoneman *et al.*, 1994).

2.2.2 Leaf temperature

Leaf temperature status is an indirect measure of plant water stress (Idso *et al.*, 1978a). When plants were well supplied with water, transpiration would be at the potential rate and the leaves will be relatively cool (Idso *et al.*, 1978b). They also observed a declining trend in transpiration during moisture deficient situation and the concomitant increase in leaf temperature. Such situations will lead to the reduction in photosynthesis resulting in the decline of total biomass production. Decreasing soil moisture resulted in reduced plant water status and stomatal conductance leading to elevated leaf temperature (Mtui *et al.*, 1981).

2.2.3 Stomatal Responses

Stomata begin to close when the turgor of guard cells decreases. Stomata usually close during relatively early stages of leaf water deficit, often long before leaves wilt (Kozlowski, 1976). The reduction of epidermal turgor in plants surrounded by dry air can result in stomatal closure, eventhough bulk leaf water potential is high. Stomatal diffusive resistance was found unaffected by leaf water potential (Culter *et al.*, 1977) in certain plants. The critical leaf water potential for stomatal closure reported for different species should not

be taken too seriously because the value varies for different clones and cultivars (Palardy and Kozlowski, 1979) and because the response of stomata to leaf water deficits is modified significantly by factors like internal CO_2 concentration, air humidity, wind, age of leaf, osmotic adjustments etc. (Davies *et al.,* 1974; Kozlowski and Pallardy, 1979).

Stomatal conductance has been reported varying with leaf water potential by several experiments. In *Alnus glutinosa* seedlings, water stressed individuals showed a much lower initial leaf conductance after which it was gradually dropped as leaf water potential decreased (Seiler, 1985). In the meantime Vance and Running (1985) observed that in *Larix occidentalis* seedlings also, minimum stomatal conductance declined with decreasing leaf water potential. Leaf conductance declined exponentially with decreasing predawn water status in *Ulmus americana* seedlings (Walters and Reich, 1989). Ellsworth and Reich (1992) correlated leaf conductance with predawn leaf water potential in *Acer saccharum* seedlings.

Stomatal closure during the middle of the day has been reported for many species of forest trees (Kramer and Kozlowski, 1979; Kozlowski, 1982). Although mid day stomatal closure has been attributed to several causes, an important factor in the lag of absorption behind transpiration, which induces leaf dehydration and reduction in leaf water potential to a critical level

associated with stomatal closure. For example in days when water deficits in shoots of mature *Acer saccharum* and *Betula papyrifera* trees were not severe, stomatal opening was rather stable throughout the day. During drought, however stomata closed in the afternoon and reopened late in the evening (Pereira and Kozlowski, 1978). Mid day stomatal closure on both leaf surfaces occurred in *Populus* clones when VPD was high (Pallardy and Kozlowski, 1981). Granier *et al.* (1992) observed midday stomatal closure and resultant reduced sap flow in *Goupia glabra,* a rainforest tree species.

Driessche (1991) observed a reverse trend of increasing stomatal conductance in lodge pole pine seedlings when severe nursery drought was imposed.

2.2.4 Transpiration rate

The rate of transpiration is directly dependent to the gradient of water vapour between intercellular spaces of the leaf and ambient air. Although high transpiration rate often causes injury, transpiration is unavoidable because a leaf structure favourable for the entrance of CO_2 also is favourable for the loss of water vapour (Kozlowski *et al.,* 1991). Stomatal closure was found to be an adaptation mechanism for reduced transpiration rate at water deficit condition (Turner *et al.,* 1986). Under certain situations a decrease in stomatal conductance will reduce transpiration relatively more than photosynthesis.

Transpiration rates were often reduced significantly in certain *Acacia* sp. in drier soils (Lange *et al.*, 1987). Rate of transpiration was positively correlated with leaf water potential (Schulze and Hall, 1982). Isolde (1989) observed a morning peak conductance and subsequent decrease for certain Acacias which was more pronounced under water stress, indicating a decisive stomatal regulation of transpiration. In a comparative study of water stress response of *Eucalyptus maculata* and *E. brockwayi* seedlings, Myers and Landsberg (1989) observed that transpiration rates were higher in *E. brockwayii*. Out of the fifteen species of Acacias studied by Srinivasan *et al.* (1989), *A. auriculiforms* had the lowest transpiration rates and stomatal conductance. A study conducted in two rain forest tree species (*Simarouba amara* and *Goupia glabra*) in a plantation revealed that transpiration may be limited by stomatal closure despite a high annual rainfall (Granier *et al.*, 1992).

2.2.5 Leaf water potential (ψ)

Comprehensive reviews on the subject of plant water potential and its relevance to water stress assessment are available (Slatyer, 1967; Slavik, 1974; Turner and Kramer, 1980). A pressure chamber measurement of plant moisture stress provides an estimate of plant water potential. The water potential of leaves can vary over a considerable range (above a critical value) without a marked effect on stomatal aperture (Jarvis, 1980). When a critical

water potential is reached stomata begins to close. Different species respond differently to water stress.

In many species stomatal resistance to air humidity can be correlated with leaf water potential. A study conducted by Guehl *et al.* (1991) on the leaf gas exchange in response to drought found that stomata closed very rapidly in *Abies bornmulleriana* when water supply is withheld even prior to there being any important decrease in leaf predawn water potential. In *Helianthus annuus* and *H. petiolaris*, water stress induced a gradual and similar decrease in leaf conductance from 1.6 to 0.3 cm s^{-1} as water potential decreased from 0.5 to 2.0 MPa (Sobrado and Turner, 1983).

During a summer drought foliar predawn water potential and minimum water potential fell to -4.8 MPa and -5.5 MPa respectively in *Fraxinus excelsior* (Cartier *et al.*, 1992). In *Quercus petreae,* imposed drought caused predawn leaf water potential to reach values as low as -2.0 MPa with a progressive decrease in hydraulic conductance (Breda *et al.,* 1993). Batten *et al.* (1994) observed a predawn leaf water potential of -0.3 MPa in irrigated trees whereas it progressively declined to -0.9 MPa in unirrigated trees. Minimum day time leaf water potential in the unirrigated trees decrease from -1.0 to -1.1 MPa at the beginning of drought period to -2.2 to -2.4 MPa after 3 months.

2.2.6 Photosynthesis

Any serious interference with photosynthesis by water deficits is likely to significantly reduce growth. As leaves become progressively dehydrated the rate of photosynthesis decreases and eventually the process may stop altogether (Brix, 1972, 1979). The initial effect of water stress on photosynthesis appears to be one of lowering stomatal conductance in response to low atmospheric humidity (Schulze, 1986). Although several investigators have shown that increasing water deficits are accompanied by decrease in rate of photosynthesis (Kozlowski, 1949; Brix, 1979; Kriedemann, 1971 etc), there has been a controversy about the critical soil moisture at which photosynthesis is first reduced. The reduction in photosynthesis is generally believed to be brought about by both stomatal and non stomatal inhibition of the process (Teskey *et al.*, 1986).

In two year old loblolly pine seedlings CO_2 uptake decreased with increasing Diffusion Pressure Deficit (DPD) on the needles and photosynthesis was found to be correlated with transpiration rates (Brix, 1962). A linear relationship was found between soil moisture content and photosynthesis of *Pinus sylvestris* seedlings (Schultz and Gautherum, 1971). Decrease in photosynthesis of *Pseudotsuga menzeisii* began when shoot water potential dropped to near -1.0 MPa and at -3.5 MPa the rate was negligible (Brix, 1972).

Rates of net photosynthesis declined drastically in *Ulmus americana* seedlings with decreasing predawn leafwater status (Walter and Reich, 1989).

Xeric seedlings of *Quercus rubra* showed higher photosynthetic rates and stomatal conductance to water vapour than mesic seedlings during well watered conditions. During a drought cycle, xeric seedlings maintained positive net photosynthesis at significantly lower predawn leaf water potential and relative water content (Kubiske and Abrams, 1992). Dickmann *et al.* (1992) observed that drought produced both stomatal and mesophyll limitations in photosynthesis of two clones in poplar and the photosynthesis were significantly reduced during drought. In leaves of young *Quercus petrae* saplings, calculated internal CO_2 were involved in the drought induced reduction of net photosynthesis (Epron and Dreyer, 1993).

Net photosynthesis was reduced by 70 per cent in one year old containerized *Liriodendron tulupifera* seedlings when water supply was with held (Cannon *et al.,* 1993). Stoneman *et al.* (1994) observed a decline of 40% in mid day photosynthetic rates of those of well watered seedlings in *Eucalyptus marginata* at a predawn leaf water potential of -1.0 MPa and reached zero at -2.2 MPa. Photosynthetic rates recovered rapidly following rewatering.

2.3 Influence of water stress on biochemical aspects

There is an increasing evidence that the concentrating effects of dehydration (Potter and Boyer, 1973) and certain cellular solutes (Rao *et al.*, 1987) cause some metabolic alterations during water deficiency. Many of the plant species accumulate substances which are normal cell constituents, particularly free amino acids, during a period of water deficit. The overall observations made in plants under stress conditions indicated that synthesis of chlorophyll, soluble protein and nitrate reductase enzyme reduced and proline accumulation increased with water deficit. Hanson and Hitz (1982) reported that osmotic adjustment occurs by synthesis of organic anions, soluble carbohydrates, amino acids etc. These osmotic agents including proline, betaine, sucrose etc., lowers solute water potential and promote water uptake by tissues while protecting proteins, membranes or other cellular components from dehydration (Fox and Geiger, 1986).

2.3.1 Chlorophyll content

In general, chlorophyll content of leaves reduces with increasing water deficits. Mesophyll cells were more sensitive to water stress and in about 75% of mesophyll cells, the chloroplast become swollen under water stress condition (Giles *et al.*, 1974). In cotton chloroplast membrane integrity was lost under water deficit situation (Vieira de Silva *et al.*, 1974). Chlorophyll content was decreased to almost 60% of control, eight days after irrigation in maize leaves

(Alberte *et al.*, 1977). Makhmuda (1983) reported that moisture stress inhibited biosynthesis of the precursor of chlorophyll in wheat leaves which ultimately reduced the chlorophyll content. In *Grevellia robusta*, the total chlorophyll, chlorophyll 'a' and 'b' contents decreased with increasing water stress. Synthesis/accumulation of chlorophyll 'b' was found to be more sensitive to water stress when compared to chlorophyll 'a' (Nautiyal *et al.*, 1993).

2.3.2 Proline

Proline was first noted to accumulate in wilted plant tissue by Kemble and Mac Pherson (1954) in experiments with excised perennial rye grass. In 1966 three laboratories reported on the phenomenon of proline accumulation during drought stress (Stewart, 1981). Proline accumulates during water stress because water deficit stimulates its synthesis from glutamate by loss of feed back inhibition, decreases the rate of proline oxidation and decrease its incorporation into protein (Kramer, 1983). It has been postulated by Schwab and Gaff, (1986) that protection of membranes is accomplished by the accumulation of proline when cells become dehydrated.

Proline accumulates in all organs of the intact plant during water deficit, although accumulation is most rapid and extensive in leaves (Singh *et al.*, 1973). In a number of plants, osmotic regulation occurs largely by increased foliar synthesis of proline from glutamine (Hanson and Hitz, 1982) by both increasing

activation of regulatory enzymes and enzyme synthesis. High proline accumulation was advocated as a drought resistance mechanism. Hui-Juan and Bin (1993) reported a greater amount of proline accumulation in drought resistant *Robinia pseudoacacia* seedlings.

2.3.3 Soluble proteins

Water stress changes the pattern of protein synthesis in plant tissue. Hulbert *et al* (1988) reported that plants adapt to and tolerate drought stress through response mechanisms including changes in protein. Many such stress related proteins have been reported which are characterized by the type of stress. Those enzymes associated with solute accumulation during osmotic adjustment would be classified as drought stress proteins (Newton *et al.*, 1991).

It is generally thought that total protein accumulation is decreased by drought. Dissociation of polysomes and an accumulation of monosomes occur in cells, when tissue is exposed to water stress (Genkel *et al.*, 1967). Evans (1983) reported that nearly 30 to 50% of the leaf soluble protein was contributed by ribulose 1, 5 bi-5-phosphate carboxylase which was considered to be an important enzyme involved in the reduction of CO_2 in the photosynthetic process. The activity of the above major enzyme was very much reduced under water deficit condition in cotton (Jones, 1973). In wheat leaves

also lesser soluble protein content was reported due to reduced ribulose bi-phosphate activity in response to drought (Mayoral *et al.,* 1981).

Vance and Zaerr (1988) reported qualitative and quantitative changes in the synthesis of proteins in drought stressed *Pinus* seedlings. The accumulation of several low molecular mass membrane and soluble proteins increased during drought conditioning of eight-week-old *Pinus banksiana* seedlings (Mayne *et al.,* 1994). *In vitro* translation studies showed a general increase in the abundance of protein products encoded by MRNA's from drought conditioned seedlings. Thakur(1991) reported an increase in the total aminoacid pool of *Grewia optiva* seedlings in response to water stress.

In short, water stress is having a detrimental effect on overall plant growth and survival due to the altered morphological, physiological and biochemical processes of plant. As a general rule, eventhough the leaf area, shoot growth and root growth are reduced by waterstress, root/shoot ratio has been found to increase in certain cases. Most of the plants respond to low water status by cutting off their transpiration by an active stomatal control and thereby maintaing the water potential. The uptake of water is maintained through the maintenance of osmoticum by the production of various biochemical agents like proline, betaine etc. Several acclimation to waterstress appear to be mediated responses and may be needed to aid survival or even restore near normal functioning of the plants.

MATERIALS AND METHODS

An investigation was carried out, at the College of Forestry, Kerala Agricultural University, Vellanikkara, Thrissur on the response of the seedlings of selected tree species to water stress. The experiment was conducted during the months from December 1994 to May 1995.

3.1 Climate and weather conditions

Geographically, the area is located 40 m above mean sea level at 10° 32'N latitude and 76° 26'E longitude. The area experiences warm and humid climate with distinct summer and rainy seasons. The climatic data for the experimental period are given in Appendix I and II.

The experiment was conducted to study the water stress response of the following species.

a. *Acacia mangium* Willd. (Mangium)

b. *Ailanthus triphysa* (Dennst.) Alston. (Matti)

c. *Pterocarpus marsupium* Roxb. (Bijasal)

d. *Swietenia macrophylla* King (Mahogany)

e. *Tectona grandis* L.F. (Teak)

3.2 Methodology

Seedlings were grown in the nursery beds for about one year. One year old seedlings, showing apparently uniform growth characters, of all the first four species and stumps from one year old seedlings in the case of teak were transplanted in black polythene bags of size 30 x 12 cm, containing 5 kg of 1:1:1 mixture of soil, sand and farm yard manure. All the bags were irrigated well daily till the seedlings established. After that, they were grown with irrigation on alternate days.

The following water stress levels were imposed:

S_0 - Control (watering daily)

S_1 - Water stress for three days (watering once in three days)

S_2 - Water stress for six days (watering once in six days)

S_3 - Water stress for nine days (watering once in nine days)

Depending upon the levels of water stress to be imposed, irrigation was withheld in selected bags for three days, six days and nine days. The moisture content was determined in frequent intervals to keep the plants in the expected levels of soil moisture tension. The cycle continued till the end of the experiment. Whenever there was a break in the stress cycle by rains, a fresh cycle was started by bringing all the bags to saturated soil moisture conditions.

The soil moisture characterisation curve of the potting mixture (Fig.1) was prepared by using a pressure plate - pressure membrane apparatus. The soil water potential (soil moisture tension) corresponding to the moisture content of the bags for different stages of drying was found out from the curve. The soil moisture content for different days of drying and the corresponding soil moisture tension is given below.

Irrigation interval (days)	Soil moisture content (%)	SMT (bars) (approx.)
1 (S_0)	19.08	<0.03
3 (S_1)	9.50	1.0
6 (S_2)	7.40	5.0
9 (S_3)	5.90	10.0

Every time irrigation was done slowly and carefully so that the soil in the bag is just saturated and water just starts seeping out through the drainage hole provided.

The experiment was laid out separately for each species.

Experimental design : CRD

Treatments : 4

Replications : 5

(Each replication had four seedlings)
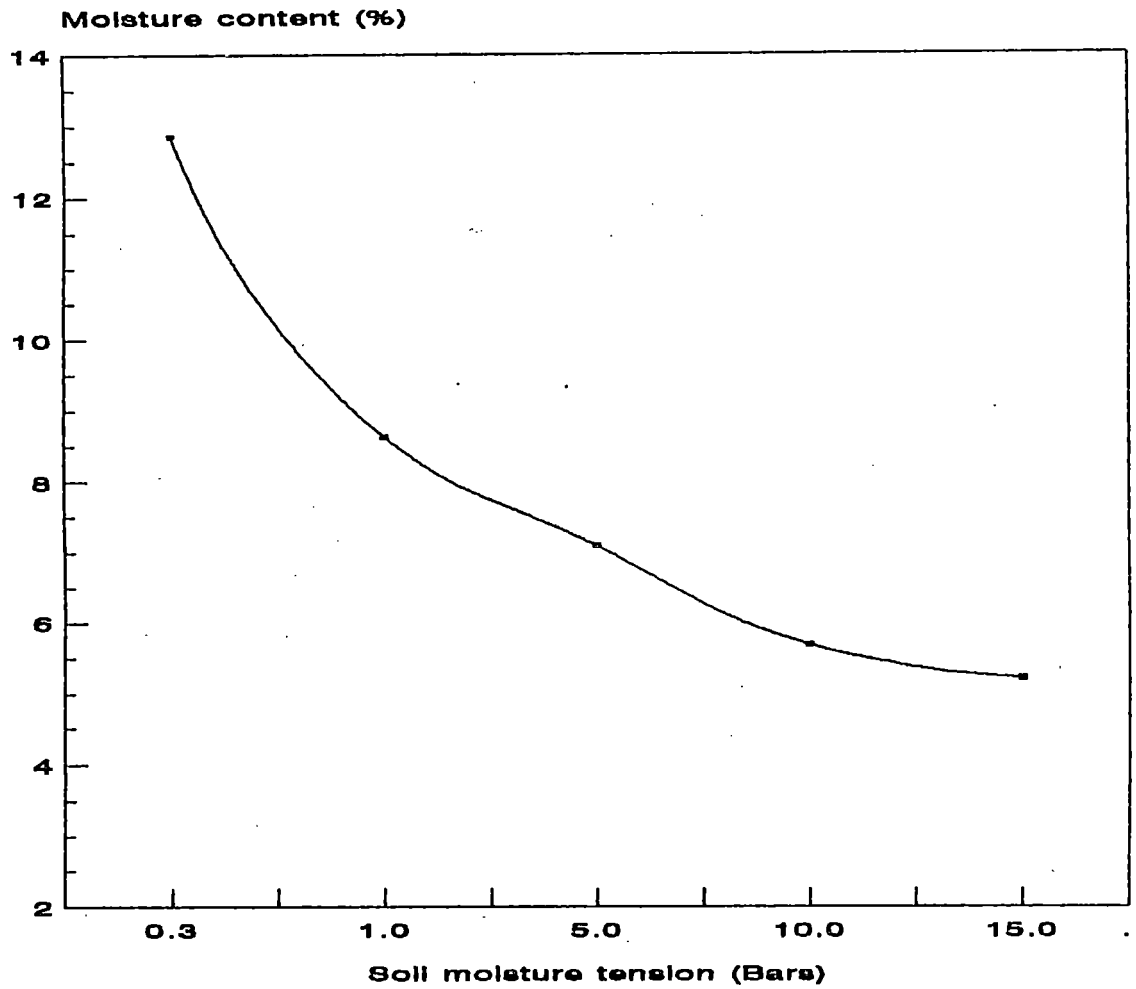
Fig.1. Soil moisture characterisation curve of the potting media

3.3 Observations recorded

3.3.1 Growth parameters

Destructive sampling at the rate of three plants per treatment was done at an interval of 30 days for 120 days. After measuring height, rooting depth, collar diameter and number of leaves, the leaves, stem and roots were separated and the dry weight of each recorded separately. The following observations were recorded.

3.3.1.1 Plant height

Plant height was taken from the collar to the tip of the growing point using a metre scale.

3.3.1.2 Rooting depth

Root depth was measured from the collar to the tip of the longest root and the mean was expressed in cm.

3.3.1.3 Collar diameter

The collar diameter was measured with the help of a vernier callipers and expressed in mm.

3.3.1.4 Number of leaves

At the time of each destructive sampling, the number of leaves of the seedlings was counted.

3.3.1.5 Leaf area

The leaf area of individual plants were measured with an Area meter (Model L1-3100, L1-Cor, Nebraska, USA) and was expressed in cm^2.

3.3.1.6 Stem weight

The destructively sampled seedlings of each species under different water stress levels were removed of leaf and the root portion from the collar and dried in an oven at 60-80 °C for 48 hours after initial drying for few days in shade. Average dry weight (g) of the stem for seedlings was calculated.

3.3.1.7 Leaf weight

After shade drying, the leaves used were taken from the shoots earlier used for stem weight estimation were dried in a hot air oven at 60-80 °C for 48 hours. The dry weight was recorded and the average leaf dry weight per seedling was expressed in g.

3.3.1.8 Root weight

The roots separated at the collar region of the same seedlings was used to record stem weight. The samples were dried in an oven at 60 to 80 °C for 48 hours after shade drying. The average root weight (g) per seedling was estimated.

3.3.1.9 Shoot weight

Shoot dry weight was calculated by summing the average weight of the leaf and stem of each plant.

3.3.1.10 Root-shoot ratio

Root-shoot ratio was calculated by dividing the average of the root weight by shoot weight of each plant.

3.3.1.11 Total dry matter production

Total dry matter production was obtained by the summing of shoot weight and root weight and expressed as g plant^{-1}.

3.3.1.12 Specific leaf area

Specific leaf area was calculated by dividing the leaf area by leaf weight per plant and the average value expressed as m^{2}g^{-1}.

3.3.1.13 Relative growth rate

Relative growth rate (RGR) was calculated from the following formula given by Blackman (1919).

RGR	=	$(\log_e w_2 - \log_e w_1)/t_2-t_1$
W_2	=	Dry weight estimate at time t_2
W_1	=	Dry weight estimate at time t_1

3.3.1.14 Net assimilation rate

Net assimilation rate (NAR) is an index of the productive efficiency of plants calculated in relation to total leaf area. NAR is calculated from the formula given below.

$$\text{NAR} = (w_2-w_1)/(t_2-t_1) \times (\log_e LA_2 - \log_e LA_1)/LA_2 - LA_1$$

W_1	=	Dry weight at time t_1
W_2	=	Dry weight at time t_2
LA_1	=	Leaf area at time t_1
LA_2	=	Leaf area at time t_2

3.3.2 Physiological parameters

3.3.2.1 Relative water content

Relative water content (RWC) of the leaf was worked out using the following formula suggested by Barrs and Weatherley (1962). Physiologically mature leaf was fixed by visual observation. It was third to fourth leaf in *Acacia mangium, Ailanthus triphysa, Swietenia macrophylla* and *Pterocarpus marsupium* and second to third leaf in the case of *Tectona grandis*. Leaf punches were taken from physiologically mature leaves by using a steel puncher with diameter of 1.5 cm. Three samples were taken from each plant at 0800 hrs and 1400 hrs IST and used for estimation.

$$\text{RWC (\%)} = \frac{\text{Fresh weight - Dry weight}}{\text{Turgid weight - Dry weight}} \times 100$$

3.3.2.2 Leaf water potential (ψ)

A Scholander type pressure chamber (Soil Moisture Equipment Corporation, Ohio, USA) was used for finding out the leaf water potential (ψ). Measurements were made on mature leaves and five plants per treatment were sampled. The leaves were enclosed in a polybag before being detached (Turner, 1988). The balancing pressure was taken as the water potential (Milburn, 1979). Measurements were taken from 0600 hrs to 1800 hrs IST at 2 hours interval in each treatment.

3.3.2.3 Leaf diffusive resistance

A steady state porometer (Model LI-1600, LI-Cor, Nebraska, USA) was used to measure the leaf diffusive resistance (LDR) of the leaves. Physio-logically mature leaves well exposed to solar radiation were selected for measurements. Measurements were taken on the abaxial surface and five plants were selected from each treatment in all the species and the mean was expressed in m mol m^{-2} s^{-1}.

Observations were recorded during every day after the beginning of water stress cycle (DAS) at 0800 hrs and 1400 hrs IST till the end of the cycle to know the pattern of development of stress which lasted for six days in teak and nine days in rest of the species.

Diurnal variations in leaf diffusive resistance was also measured from 0600 to 1800 hrs IST. Measurement were made from five plants per treatments in all the species.

3.3.2.4 Transpiration rate

Transpiration rate were recorded by a steady state porometer. Measurements were done on well exposed mature leaves (same as of diffusive resistance) at 0800 hrs and 1400 hrs IST. Observations were made on five plants per treatment and the mean expressed in $\mu g\ cm^{-2}s^{-1}$.

3.3.2.5 Leaf temperature

Steady state porometer was also used for recording leaf temperature of the seedlings. Leaf temperature from five plants per treatment was taken from the same leaf as of diffusive resistance measurement at 0800 hrs and 1200 hrs IST. Apart from this, diurnal variation in leaf temperature was also observed from 0600 to 1800 hrs IST in each of the treatments in different species.

3.3.2.6 Net photosynthesis

Net photosynthesis was measured with a portable infrared gas analyzer (IRGA) (Model L1 6200, Li - Cor, Nebraska, USA) using a one litre leaf chamber. The leaf chamber has sensors for measuring photosynthetically active radiation (PAR), relative humidity, leaf and chamber

temperatures. The measurements were recorded on the data logger supplied with the instrument. The Pn was calculated in the data loggers itself using the software provided with it by the manufacturers. The data were later transferred to a computer and processed further. The measurements were recorded at 2 hrs interval from 0800 hrs to 1600 hrs IST.

3.3.3 Biochemical parameters

Biochemical estimations were conducted using fully expanded leaf (mostly second or third leaf from the top) which were sampled during predawn hours (0700 to 0800 hrs IST) at the end of the growth period (120 DAP). Three replicates were used from each treatment for the estimation. In teak, none of the parameters could be estimated due to the interference of phenols in the leaf.

3.3.3.1 Chlorophyll content

Chlorophyll content of the leaf was estimated following the method of Starner and Hardley (1967). Samples were collected from the selected plants, cut into pieces and mixed well; 0.1 g of the sample was weighed into a mortar and ground with a pestle to extract the chlorophyll using 80 per cent acetone. The extract was filtered using Whattman No.1 filter paper and made up to 25 ml using 80 per cent acetone. The absorbance were read at 663 nm and 645 nm wave length in a spectrophotometer. The

chlorophyll 'a', chlorophyll 'b' and total chlorophyll of each samples were calculated using the following formulae.

Chlorophyll 'a' (mg g^{-1} of tissue)

$$= 12.7 \ (\text{OD at 663 nm}) - \frac{2.69 \ (\text{OD at 645 nm}) \ x \ V}{1000 \ x \ w}$$

Chlorophyll 'b'(mg g^{-1} of tissue)

$$= 22.9 \ (\text{OD at 645 nm}) - \frac{4.68 \ (\text{OD at 663 nm}) \ x \ v}{1000 \ x \ w}$$

Total chlorophyll (mg g^{-1} of tissue)

$$= 20.2 \ (\text{OD at 645 nm} + \frac{8.02 \ (\text{OD at 663 nm}) \ x \ v}{1000 \ x \ w}$$

OD = Optical density

V = Final volume of 80 per cent acetone extract

W = Fresh weight of tissue in gram

3.3.3.2 Proline content

Fresh leaf samples were collected from selected plants, cut into pieces and mixed well. A known amount of the leaf material (500 mg) is homogenised with 10 ml of 3 per cent aqueous sulphosalicilic acid, centrifuged at 3000 r for ten minutes. Two ml of the supernatant liquid was

taken and the following reagents were added: 2 ml of glacial acetic acid, 2 ml of acid ninhydrin mixture, 2 ml of 6 N orthophosphoric acid. The contents were allowed to react at 100 °C for 1 hour and the reaction was terminated by keeping it in an ice bath for ten minutes. The reaction mixture was mixed vigorously with 4 ml of toluene using a mixer for 10 - 20 seconds. The upper coloured chromophore containing toluene was aspirated from the aqueous phase and warmed at room temperature and the OD was read at 520 nm in a spectrophotometer. The proline content was determined from a standard curve of pure proline as per Bates *et al.* (1973) and expressed in μg g^{-1} fresh weight.

3.3.3.3 Soluble protein

The procedure given by Lowry *et al.* (1951) was followed for the estimation of soluble protein content. Foliar samples were collected fresh from selected plants in each treatment, cut into pieces and mixed well. Five hundred mg of the leaf material was extracted with 10 ml of 80% ethanol. From the aliquot 0.1 ml was pipetted into a test tube, made up to 2 ml with distilled water and 5 ml of alkaline copper reagent was added. After 5 minutes, 0.5 ml of Folin phenol reagent was added to the above solution. The OD was measured at 620 nm using a spectrophotometer. The amount of protein is estimated after referring to a standard curve with bovine serum and was expressed in mg g^{-1} of sample.

Alkaline copper reagent

> Reagent A : 2% Sodium carbonate in 0.1 N NaoH

> Reagent B : 0.5% Copper sulphate (CuSo$_4$ - 5 H$_2$O) in 1% potassium
>
> sodium tartarate

50 ml of Reagent A and 1 ml of Reagent B were mixed prior to use.

3.4 Anatomical studies

Physiologically mature leaves well exposed to sun were selected for anatomical studies. Hand sections of the leaves were taken and stained in saphranine and examined under the low power and high power of light microscope. Photographs of the section were taken, examined and their anatomical details as influenced by different levels of water stress was observed.

3.5 Statistical analysis

The data were subjected to Analysis of Variance for Completely Randomised Design (Panse and Sukhatme, 1989). Correlation analysis of various plant characters was done with PC using MSTAT-C package.

Results

RESULTS

Responses of *Ailanthus triphysa* (Dennst.) Alston., *Acacia mangium* Willd., *Swietenia macrophylla* King, *Pterocarpus marsupium* Roxb. and *Tectona grandis* L.F. to water stress with respect to their morphological, physiological, biochemical and anatomical parameters were recorded, analysed statistically and presented in this chapter.

4.1 *Ailanthus triphysa* (Matti)

4.1.1 Growth attributes

4.1.1.1 Plant height

The plant height of *A. triphysa* at 30, 60, 90 and 120 days after planting (DAP) are given in Table 1. There was a reduction in plant height when the seedlings were subjected to water stress. The reduction in plant height was significant at 30 and 90 DAP. In the initial stages, the reduction in plant height due to water stress was prominent. However, there was no significant difference in the plant height recorded at 120 DAP.

4.1.1.2 Rooting depth

The rooting depth measured for *A. triphysa* at 30, 60, 90 and 120 DAP are presented in Table 1. There was no significant differences in the rooting depth of *Ailanthus* at various stages due to the effect of water stress levels, except at 30 DAP. At 30 DAP, the rooting depth of the seedlings

Table 1   Plant height, rooting depth and collar diameter of *A. triphysa* seedlings as affected by different levels of water stress

Stress levels	Plant height (cm)				Rooting depth (cm)				Collar diameter (mm)			
	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP
S_0	36.5	34.0	34.0	41.5	40.0	36.8	33.5	47.5	13.3	11.0	15.9	16.8
S_1	30.0	33.3	33.5	44.3	33.0	38.3	34.0	36.2	12.3	11.5	13.2	16.0
S_2	28.0	26.0	42.3	45.0	36.3	34.5	39.0	37.0	11.4	10.8	14.9	13.8
S_3	26.8	33.3	29.3	41.8	33.5	38.3	40.3	46.8	10.0	10.8	11.7	11.9
F	*	NS	*	NS	*	NS	NS	NS	*	NS	NS	*
LSD (0.05)	7.9	-	12.4	21.5	5.7	-	18.7	-	2.1	-	-	3.4
SEM±	2.0	9.0	3.16	5.5	1.4	3.6	4.8	3.9	0.53	1.3	1.0	0.9

* Significant at 5% level   ** Significant at 1% level   NS - Not significant

Plate 1   One year old *A. triphysa* seedlings grown under
            different levels of water stress for 90 days

Plate 2   One year old *S. macrophylla* seedlings grown under
            different levels of water stress for 90 days

significantly decreased due to the influence of water stress. However, there was no significant differences between water stress levels of S_1, S_2 and S_3.

4.1.1.3 Collar diameter

The collar diameter recorded at various stress stages for *A. triphysa* are presented in Table 1. At all the different stages of growth, collar diameter showed a decrease due to the effect of water stress. At 60 and 90 DAP, though the values showed a decrease, they were not significantly different. At 120 DAP, the collar diameter of unstressed (S_0) and severely stressed (S_3) plants were significantly different.

4.1.1.4 Number of leaves

The number of leaves per plant were reduced drastically due to the influence of water stress (Table 2). Significant difference in number of leaves were observed at all the stages of growth. At 30 DAP variation was from 10.5 to 6.0 whereas at 120 DAP, the reduction became more steeper with values ranging from 14.0 to 5.0 for water stress levels S_0 and S_3 respectively.

4.1.1.5 Leaf Area

The leaf area per plant (Table 2) showed a decrease in all the water stressed plants over the control. At 30 DAP, though the leaf area showed an increase over the unstressed control, the difference was not significant. The

Table 2   Number of leaves. leaf area, leaf weight and specific leaf area of *A. triphysa* seedling as affected by   different levels of water stress

Stress levels	Number of leaves (no plant[-1])				Leaf area (cm²)				Leaf weight (g)				Specific leaf area			
	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	1 D
S_0	10.5	11.0	12.5	14.0	604	1162	978	1610	10.5	15.9	11.0	14.2	0.58	0.73	0.89	
S_1	8.0	9.0	10.5	10.5	711	849	643	1246	8.5	10.3	7.1	12.1	0.84	0.83	0.90	
S_2	7.5	6.5	11.5	9.5	709	785	547	1006	8.2	9.0	6.3	9.5	0.87	0.87	0.87	
S_3	6.0	5.5	5.5	5.5	653	306	396	696	6.8	4.6	3.7	4.1	0.97	0.66	0.09	
F	*	*	**	**	NS	*	**	**	*	**	**	**	*	NS	*	
LSD (0.05)	4.2	3.1	1.9	2.6	-	434	35	208	3.5	1.4	1.1	1.9	0.32	-	0.50	
SEM±	1.1	0.79	0.50	0.66	71	110	9	53	0.89	0.36	0.28	0.48	0.25	0.22	0.36	

* Significant at 5% level   ** Significant at 1% level   NS - Not significant

4.1.1.8 Shoot weight

The shoot dry weight of *A. triphysa* seedlings (Table 3) decreased significantly due to water stress. Shoot weights were reduced to 13.80 g in S_3 plants compared to 32.5 g in control at 120 DAP. However, the difference in shoot weight, between levels S_0 and S_1 were not significant.

4.1.1.9 Root weight

The root dry weight showed a decreasing trend as the water stress levels were increased (Table 3). At 30 and 60 DAP, the root weight recorded for S_2 and S_3 were significantly different from that of S_0 and S_1. But at 90 and 120 DAP, the reduction was more prominent, with all the treatments showing significant differences at 90 DAP.

4.1.1.10 Root - shoot ratio

The effects of water stress on the root-shoot, weight ratios of *A. triphysa* (Table 3) were not pronounced. At 30 DAP, the values for S_1 and S_2 were significantly higher compared to unstressed control. The root/shoot ratios were not significantly different at other stages of growth.

4.1.1.11 Total dry matter production

Total dry matter production was reduced due to the effect of water stress (Table 3). At 30 DAP, the water stress reduced dry matter production in all the water stress levels (S_1, S_2 and S_3) with pronounced reduction in S_3

Table 3　Shoot weight, root weight, root/shoot ratio and total dry matter production in *A. triphysa* seedlings as affected by different levels of water stress

Stress levels	Shoot weight (g)				Root weight (g)				Root/shoot ratio				Total dry matter production (g)			
	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP
S_0	24.0	33.6	25.1	35.5	9.0	12.8	15.0	14.9	0.37	0.34	0.65	0.43	33.0	45.0	39.0	50.4
S_1	16.1	27.0	20.8	37.3	9.0	11.4	7.5	10.2	0.56	0.48	0.33	0.27	25.2	40.0	31.2	47.4
S_2	15.0	18.4	23.0	24.4	8.7	6.4	10.4	8.0	0.58	0.35	0.43	0.33	23.6	24.8	34.9	32.4
S_3	12.6	9.3	9.4	13.8	5.4	3.2	9.5	6.2	0.43	0.34	0.89	0.45	18.0	12.5	20.4	20.0
F	*	**	*	**	*	**	**	**	*	NS	NS	NS	*	**	*	**
LSD (0.05)	7.2	5.1	9.0	8.4	3.5	3.7	2.4	1.9	0.1	-	-	-	10.6	8.4	9.3	7.2
SEM±	1.9	1.3	2.3	2.1	0.89	1.0	0.62	0.49	0.03	0.03	0.50	0.08	2.7	2.1	2.4	1.8

* Significant at 5% level　　** Significant at 1% level　　NS - Not significant

42

Table 4   Relative growth rate, net assimilation rate and relative water content of leaves of *A. triphysa* seedlings as affected by different levels of water stress

Stress levels	Relative Growth Rate (mg g^{-1} wk^{-1})			Net Assimilation Rate (mg cm^{-2} wk^{-1})			Relative Water Content (%)	
	30-60 DAP	60-90 DAP	90-120 DAP	30-60 DAP	60-90 DAP	90-120 DAP	0800 (hrs)	1400 (hrs)
S_0	1.8	2.5	2.4	0.10	0.10	0.07	61.61	65.41
S_1	2.01	2.6	2.5	0.11	0.09	0.11	67.24	70.57
S_2	0.85	2.0	2.2	0.06	0.06	0.07	74.28	74.52
S_3	0.81	0.98	0.90	0.03	0.04	0.02	64.16	68.57
F	**	**	**	**	**	*	NS	NS
LSD (0.05)	0.19	0.58	0.41	0.03	0.3	0.06	-	-
SEM±	0.05	0.14	0.11	0.01	0.01	0.02	3.28	2.67

* Significant at 5% level   ** Significant at 1% level   NS Not significant

plants. At 60 and 120 DAP, severe reduction in dry matter production was observed in S_2 and S_3, with S_3 recording the least values.

4.1.1.12 Relative Growth Rate (RGR)

The mean relative growth rate (RGR) of *A. triphysa* seedlings in response to different levels of water stress are given in Table 4. Between 30 to 60 DAP, mild water stress did not affect the RGR, but moderate and severe water stress reduced RGR significantly. During the next two stages (ie. 60-90 DAP and 90-120 DAP), only severe water stress reduced the RGR significantly.

4.1.1.13 Net Assimilation Rate (NAR)

The mean values of NAR for *A. triphysa* seedlings are given in Table 4. Moderate and severe water stress reduced the NAR significantly, whereas mild water stress did not show significant variation due to water stress.

4.1.2 Physiological parameters

4.1.2.1 Leaf diffusive resistance (LDR)

The data on leaf diffusive resistance recorded over a nine day water stress cycle are presented in Table 5. Leaf diffusive resistance increased both at 0800 hrs and 1400 hrs due to water stress. In the case of S_0, the values recorded at predawn and midday showed consistency over the nine day

Table 5　Leaf diffusive resistance (m mol m^{-2} s^{-1}) in *A. triphysa* seedlings as affected by different　levels of　water stress through a nine day cycle

Stress levels	1 DAS		2 DAS		3 DAS		4 DAS		5 DAS	
	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)
S_0	4.71	3.93	4.62	4.15	5.13	4.08	5.67	4.04	5.77	4.13
S_1	5.17	10.23	4.95	7.44	8.09	8.82	9.65	10.25	6.03	7.02
S_2	7.31	5.83	7.93	7.46	8.49	10.42	6.52	18.92	14.07	47.27
S_3	8.83	6.00	8.07	8.56	8.55	12.08	10.39	17.15	9.47	25.61
F	**	**	**	**	**	**	**	**	**	**
LSD (0.05)	2.1	1.10	0.95	0.87	0.79	1.0	1.20	1.2	1.20	5.30
SEM±	0.69	0.38	0.32	0.29	0.26	0.34	0.41	0.41	0.38	1.76

Stress levels	6 DAS		7 DAS		8 DAS		9 DAS	
	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)
S_0	5.33	4.09	5.55	4.15	4.34	4.26	5.78	4.12
S_1	8.76	9.76	8.69	10.29	6.20	7.87	8.57	9.95
S_2	24.59	75.79	8.57	6.29	7.79	8.35	8.07	11.03
S_3	12.72	32.43	16.74	42.39	18.03	72.23	19.61	102.43
F	**	**	**	**	**	**	**	**
LSD (0.05)	1.16	3.59	0.93	2.86	1.70	2.15	0.93	2.95
SEM±	0.39	1.20	0.31	0.95	0.57	0.72	0.31	0.98

* Significant at 5% level　　** Significant at 1% level　　DAS Days after the beginning of stress

cycle. For S_1, at 1 DAS, the predawn values did not differ significantly, but the midday values were significantly higher. At 3 DAS, both predawn and midday values were above that of control. Water deficits induced higher LDR values at 6 DAS in S_2 (water stress for six days) when compared to S_0 and S_1. Both the predawn and midday values at the beginning (1 DAS) and end (6 DAS) of the cycle were significantly above that of control and S_1. The increase in diffusive resistance through the six day cycle was gradual. In the case of S_3 (nine day cycle), the LDR values at 0800 and 1400 hrs varied significantly from the control.

The diurnal variations in the leaf diffusive resistance of *A. triphysa* seedlings at different levels of water stress is given in Fig.2 and Appendix III. Values of LDR for S_0 (control) declined from 0600 hrs to 1200 hrs with a sharp decline from 0600 hrs to 0800 hrs. From 1200 hrs onwards resistance values increased gradually. In the case of S_1 also, the pattern was similar but for a slight increase in the LDR during the mid hours. In general, there was an increase in the LDR recorded for S_2 (six days stress) and S_3 (nine days stress). The values for S_2 showed a sharp rise upto 1400 hrs after a slight decline from 0600 to 0800 hrs. After 1400 hrs again there was a decline towards late evening. A decline was observed for S_0, S_1 and S_2 during predawn hours which was absent in severely stressed (S_3) plants. The peak resistance was at 1200 hrs which declined towards evening.

4.1.2.2 Transpiration rate

The rate of transpiration in *A. triphysa* seedlings recorded at 0800 hrs and 1400 hrs over a nine day water stress cycle are presented in Table 6. The transpiration from control plants did not show much variation through the cycle. In plants stressed for three days (S_1), transpiration reduced significantly from the control both at 0800 hrs and 1400 hrs. The trend continued throughout the stress period. Water stress significantly reduced the transpiration rates in S_2 (six days stressed plants) at both predawn and midday measurements. Plants stressed for nine days (S_3) exhibited further reduction in the transpiration rates. However, the transpiration rates were recouped following rewatering in all the stressed treatments.

4.1.2.3 Leaf temperature

The leaf temperature of *A. triphysa* seedlings exposed to different levels of water stress are given in Table 7. At the start of the stress cycle (1 DAS), though the midday measurements varied significantly between treatments, predawn values did not vary. At 3 DAS, the plants experiencing water stress for 3 days (S_1) showed significant difference from control during both the measurements. Leaf temperature at 1400 hrs increased significantly for S_2 at 6 DAS. However at 9 DAS, S_3 plants did not show significant variation in leaf temperature at 1400 hrs, whereas values at 0800 hrs showed significant variation.

Table 6 Transpiration rate (μg H_2O cm^{-2} s^{-1}) in *A. triphysa* seedlings as affected by different levels of water stress through a nine day cycle

Stress levels	1 DAS 0800 (hrs)	1400 (hrs)	2 DAS 0800 (hrs)	1400 (hrs)	3 DAS 0800 (hrs)	1400 (hrs)	4 DAS 0800 (hrs)	1400 (hrs)	5 DAS 0800 (hrs)	1400 (hrs)
S_0	2.71	5.35	2.93	5.49	2.07	5.04	2.45	5.63	2.28	5.09
S_1	2.42	2.12	2.72	3.27	1.44	2.81	1.47	2.64	2.37	3.37
S_2	2.97	3.75	1.69	3.27	1.46	1.06	2.12	1.55	1.24	0.78
S_3	2.95	3.72	1.66	2.78	1.49	1.02	1.28	1.27	1.42	0.99
F	**	**	**	**	**	**	**	**	**	**
LSD (0.05)	0.21	0.67	0.44	0.68	0.24	0.37	0.28	0.36	0.29	0.35
SEM±	0.07	0.22	0.15	0.23	0.08	0.12	0.09	0.12	0.09	0.12

Stress levels	6 DAS 0800 (hrs)	1400 (hrs)	7 DAS 0800 (hrs)	1400 (hrs)	8 DAS 0800 (hrs)	1400 (hrs)	9 DAS 0800 (hrs)	1400 (hrs)
S_0	2.47	5.46	2.49	5.27	2.93	5.68	2.46	5.41
S_1	1.61	1.44	1.46	2.48	3.25	3.09	1.76	1.49
S_2	0.47	0.35	2.83	3.83	1.76	1.53	1.58	1.25
S_3	0.94	0.68	0.85	0.96	0.74	0.41	0.72	0.29
F	**	**	**	**	**	**	**	**
LSD (0.05)	0.30	0.29	0.21	0.36	0.33	0.34	0.33	0.35
SEM±	0.10	0.10	0.07	0.12	0.11	0.11	0.11	0.12

* Significant at 5% level   ** Significant at 1% level   DAS Days after the beginning of stress

Table 7 Leaf temperature (°C) in *A. triphysa* seedlings as affected by different levels of water stress through a nine day cycle

Stress levels	1 DAS		2 DAS		3 DAS		4 DAS		5 DAS	
	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)
S_0	27.82	33.90	27.44	32.54	25.60	33.66	26.54	33.56	26.96	33.70
S_1	27.10	34.06	27.40	32.88	25.98	34.34	26.58	34.30	27.02	32.28
S_2	27.18	34.12	27.34	32.94	26.20	34.80	26.24	34.78	25.74	35.70
S_3	27.52	34.30	28.10	34.00	26.94	34.94	27.84	34.36	27.26	33.54
F	**	NS	*	**	**	**	**	*	**	**
LSD (0.05)	0.36	-	0.62	0.59	0.48	0.46	0.55	0.95	0.43	0.40
SEM±	0.12	0.17	0.21	0.20	0.16	0.15	0.18	0.32	0.14	0.13

Stress levels	6 DAS		7 DAS		8 DAS		9 DAS	
	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)
S_0	28.98	33.44	26.80	33.84	24.60	35.12	26.92	35.18
S_1	27.12	34.04	27.30	34.04	25.12	35.54	27.16	35.16
S_2	27.10	36.86	27.16	34.00	25.20	35.60	27.04	35.08
S_3	26.18	34.94	26.58	35.64	24.70	35.52	27.58	35.28
F	NS	**	**	**	**	NS	**	NS
LSD (0.05)	-	0.46	0.34	0.27	0.21	-	0.30	-
SEM±	0.98	0.15	0.11	0.09	0.07	0.21	0.10	0.11

*Significant at 5% level   ** Significant at 1% level   NS - Not significant
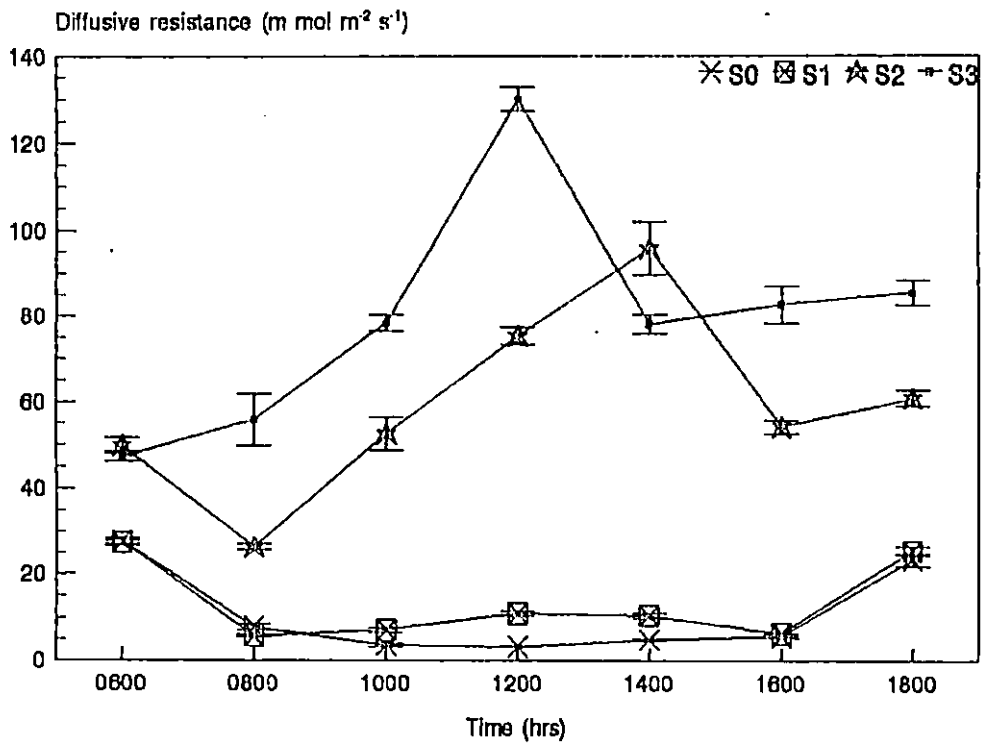
Fig.2. Diurnal variations in the leaf diffusive resistance of *A. triphysa* seedlings as affected by different levels of water stress
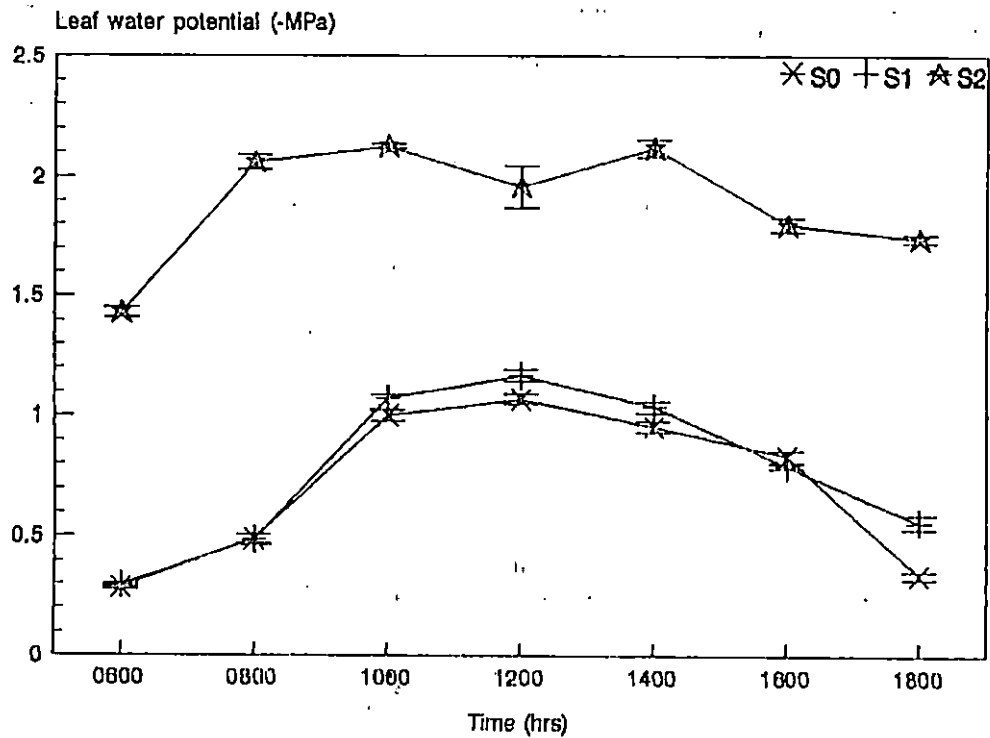
Fig.3. Diurnal variations in the leaf water potential of *A. triphysa* seedlings as affected by different levels of water stress

4.1.2.4 Leaf water potential

The diurnal variations in the leaf water potential (ψ) of *A. triphysa* seedlings exposed to different levels of water stress are given in Fig.3 and Appendix III. Control (S_0) and moderately (S_1) stressed plants showed similar variation with minimum values recorded at 1200 hrs. The ψ recorded by moderately stressed plants (S_2) were much lower than the values obtained for S_0 and S_1 (Fig. 4). Leaf water potential decreased (ψ) in all the plants with the progress of the day but increased towards the evening. However, the decline in water potential from 0600 hrs to 0800 hrs was sharp in S2 plants.

4.1.2.5 Relative water content (RWC)

The relative water content of the leaves as influenced by different levels of stress are presented in Table 4. At 0800 and 1400 hrs, no significant difference was observed among treatments except for S_2 where a slightly higher value was recorded.

4.1.2.6 Net photosynthesis

The diurnal variations in the net photosynthesis of *A. triphysa* seedlings as affected by different levels of water stress are shown in Fig.4. In general, unstressed (S_0) and mildly stressed (S_1) plants showed more net photosynthesis than moderately (S_2) and severely stressed (S_3) plants. There was a rise in net photosynthesis at 1000 hrs for S_1 and S_2. In the case of S_3, the net photosynthesis declined sharply with time, upto 1200 noon. A decline at 1200 hrs has been noticed in all the treatments which was more

Net photosynthesis (μ mol m^{-2} s^{-1})
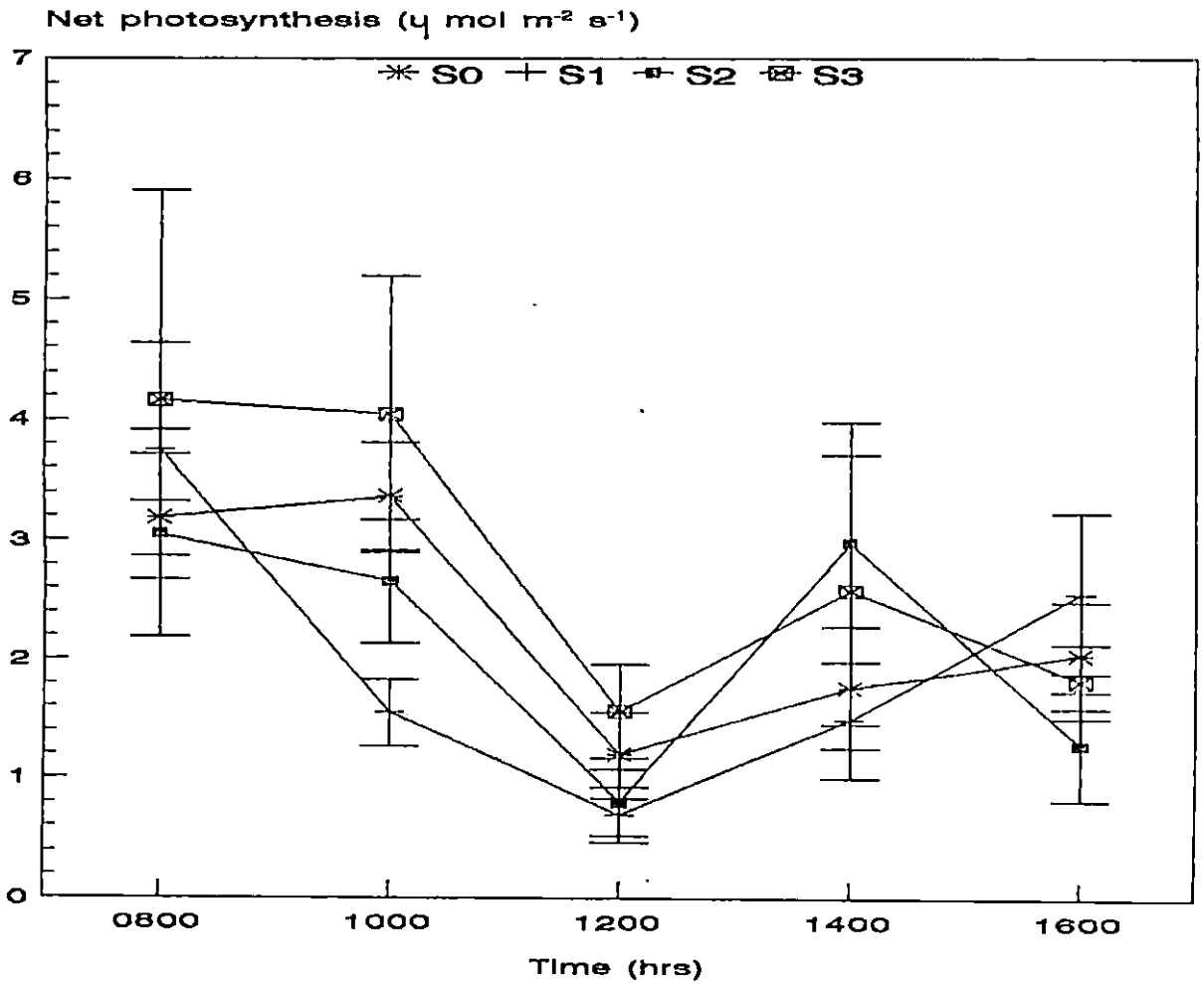
Fig.4. Diurnal variations in the net photosynthesis of *A. triphysa* seedlings as affected by different levels of water stress

pronounced in unstressed plants. From 14.00 to 16.00 hrs also the net photosynthesis was highest for S_0 and it followed in the order $S_1 > S_2 > S_3$.

4.1.3 Biochemical attributes

4.1.3.1 Chlorophyll content

The chlorophyll 'a', chlorophyll 'b' and total chlorophyll contents of *A. triphysa* seedlings experiencing water stress at different levels are given in Table 8. Chlorophyll 'a' contents were lower for stressed plants. The values for S_1 and S_3 decreased significantly from control. Water stress reduced the chlorophyll 'b' content in all the stressed treatments. The value observed for control differed significantly from S_1, S_2 and S_3. S_1 and S_2 were on par but S_3 was significantly below the other water stress levels. The total chlorophyll content was also reduced due to the water stress. However, the values for S_2 did not show significant difference from the control.

4.1.3.2 Proline content

Proline content increased in the leaves of *A. triphysa* as the intensity of stress increased (Table 8). The values recorded for control (S_0) and water stressed plants (S_1, S_2 and S_3) differed significantly from each other. The lowest contents of proline was observed in unstressed plants and the highest in severely stressed plants.

Table 8 Biochemical attributes of *A. triphysa* seedlings as affected by different levels of water stress at the end of growth period

Stress levels	Chlorophyll 'a' (mg g^{-1})	Chlorophyll 'b' (mg g^{-1})	Total Chlorophyll (mg g^{-1})	Proline (μg g^{-1})	Soluble protein (mg g^{-1})
S_0	0.95	0.16	1.11	5.90	4.58
S_1	0.68	0.13	1.07	6.35	7.27
S_2	0.92	0.15	0.81	6.71	12.02
S_3	0.60	0.08	0.62	7.49	14.77
F	**	*	**	**	**
LSD (0.05)	0.13	0.07	0.12	0.26	0.66
SEM±	0.04	0.02	0.04	0.08	0.25

* Significant at 5% level   ** Significant at 1% level

Table 9   Inter-correlation matrix of total dry matter production and other plant characters in *Ailanthus triphysa*

Character	LA	LW	CD	SW	RW	RSR	SLA	TDMP
LN	0.627**	0.763**	0.667**	0.784**	0.236	-0.126	-0.004	0.640**
LA		0.797**	0.401**	0.757**	0.563**	0.183	-0.069	0.823**
LW			0.351	0.859**	0.286	-0.127	0.266	0.717**
CD				0.608**	0.123	-0.084	-0.325	0.459*
SW					0.292	-0.178	-0.119	0.810**
RW						0.735**	-0.536*	0.798**
RSR							-0.513*	0.339
SLA								-0.404

* Significant at 1% level   ** Significant at 0.1% level   LA   - Leaf area
RW   - Root weight   LW   - Leaf weight   RSR   - Root shoot ratio
SW   - Shoot weight   CD   - Collar diameter   TDMP - Total drymatter production
SLA   - Specific leaf area

Table 10   Inter-correlation matrix of net photosynthesis and other physiological parameters in *A. triphysa*

Characters	LT	CON	TRN	CIN	NP
QNT	0.732**	0.308	0.456*	0.446*	0.061
LT		0.008	0.208	0.423*	-0.235
CON			0.796**	0.254	0.611**
TRN				0.299	0.624**
CIN					-0.094

* Significant at 1% level   ** Significant at 0.1% level   LT - Leaf temperature   CON - Conductance
CIN - Internal CO$_2$ QNT - Quantum influx   NP - Net photosynthesis   TRN - Transpiration

4.1.3.3 Soluble protein

Soluble protein content (Table 8) in the fresh leaves of *A. triphysa* seedlings were found to increase with increase in water stress levels and the variations were significantly different.

4.2 *Acacia mangium* (Mangium)

4.2.1 Growth attributes

4.2.1.1 Plant height

The height of *Acacia mangium* seedlings at 30, 60, 90 and 120 DAP are given in Table 11. Plant height was not affected significantly by water stress upto 60 DAP. At 90 DAP, the reduction in plant height was significant for plants under six days (S_2) and nine days (S_3) water stress cycle. However, mildly stressed (S_1) plants did not differ from the control significantly. Similar trend was observed at 120 DAP also.

4.2.1.2 Rooting depth

The rooting depth of *A. mangium* seedlings (Table 11) did not show significant differences due to the water stress treatments, except at 90 DAP, where the rooting depth was slightly higher for moderately stressed (S_2) plants, but were on par with control and severely water stressed (S_3) plants.

Table 11   Plant height, rooting depth and collar diameter of *A. mangium* seedlings as affected by different levels of water stress

Stress levels	Plant height (cm)				Rooting depth (cm)				Collar diameter (mm)			
	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP
S_0	112.0	112.5	135.8	138.5	49.8	46.5	51.5	57.3	10.1	9.9	13.1	12.9
S_1	93.0	111.0	132.8	117.9	41.5	45.3	47.8	41.0	10.0	9.6	10.3	11.1
S_2	115.0	97.8	99.5	108.9	47.3	48.0	53.5	41.3	11.3	9.7	9.5	10.0
S_3	101.0	97.8	98.0	75.4	57.8	49.1	57.5	60.0	9.8	8.5	10.7	9.6
F	NS	NS	*	*	NS	NS	NS	NS	NS	NS	*	*
LSD (0.05)	-	-	29.5	34.1	-	-	-	-	-	-	3.3	3.3
SEM±	9.2	9.8	7.5	8.7	3.0	2.5	1.2	6.7	1.1	0.80	0.83	0.83

* Significant at 5% level   NS - Not significant

Plate 3   One year old *A. mangium* seedlings grown under
            different levels of water stress for 90 days

Plate 4   An *A. mangium* seedling which dried up completely
            when subjected to S_3 level of water stress

4.2.1.3 Collar diameter

The collar diameter of *A. mangium* at 30, 60, 90 and 120 DAP are given in Table 11. No significant differences were observed at 30 or 60 DAP. However, at 90 DAP and 120 DAP the collar diameters were reduced significantly for all the water stressed seedlings when compared to that of control. A decreasing trend was observed in collar diameter at 120 DAP as the stress levels intensified.

4.2.1.4 Number of leaves

The number of leaves per plant observed at different growth stages as affected by different levels of water stress are given in Table 12. Water stress significantly affected the number of leaves at all the stages of growth. At 90 and 120 DAP, a more severe reduction in the leaf number was observed due to the effect of water stress. However, there were no significant differences between the severely stressed and moderately stressed plants at both the growth stages.

4.2.1.5 Leaf Area

The leaf area of *A. mangium* seedlings at different growth stages (30, 60, 90 and 120 DAP) are presented in Table 12. At 30 DAP, though the leaf area was significantly affected by water stress a consistent pattern was not observed. Moderate and severe water stress reduced the leaf area of the

Table 12   Number of leaves, leaf area, leaf weight and specific leaf area of *A. mangium* seedling as affected by different levels of water stress

Stress levels	Number of leaves (no plant^{-1})				Leaf area (cm^2 plant^{-1})				Leaf weight (g)				Specific leaf area (m^2 g^{-1})			
	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP
S$_0$	35.0	28.5	53.5	55.0	2089	1900	3084	2587	26.4	19.1	35.1	21.3	0.78	0.99	0.87	1.2
S$_1$	24.5	33.0	30.5	39.0	1813	2028	1691	1936	19.3	15.1	19.7	20.8	0.94	1.3	0.86	0.95
S$_2$	26.0	29.0	22.0	28.5	3125	986	998	856	31.3	12.0	13.9	10.6	0.99	0.82	0.72	0.82
S$_3$	16.5	19.5	16.0	24.0	2658	590	607	582	25.9	8.4	6.4	5.8	1.0	0.70	1.0	1.0
F	**	*	**	**	*	*	**	**	*	*	**	*	*	NS	NS	NS
LSD (0.05)	5.4	11.0	11.7	13.5	786	991	630	372	6.5	4.7	6.8	10.5	0.16	-	-	-
SEM±	1.4	2.8	3.0	3.4	200	253	161	95	1.7	1.2	1.7	2.7	0.12	0.39	0.37	0.44

* Significant at 5% level   ** Significant at 1% level   NS - Not significant

seedlings at 60 DAP. At 90 and 120 DAP, leaf area was reduced in all the water stressed plants compared to that of control.

4.2.1.6 Leaf weight

The mean values on dry weight of leaves are presented in Table 12. The leaf weight was reduced due to the effect of water stress at all the different growth stages with minimum effect in the initial stages (30 DAP). Water stress reduced the leaf weight from 60 DAP onwards. A severe reduction in leaf weight, as compared to the control was observed at 90 and 120 DAP due to water stress.

4.2.1.7 Specific leaf area

The specific leaf area of A. mangium seedlings are given in Table 12. Specific leaf area was increased significantly for severely stressed (S_3) plants at 30 DAP when compared to other plants. From 60 DAP onwards, specific leaf area did not show significant variation.

4.2.1.8 Shoot weight

The dry weight of shoot of A. mangium at 30, 60, 90 and 120 DAP are presented in Table 13. The influence of water stress on dry weight of shoot was significant from 30 DAP onwards. Shoot weights were significantly reduced for moderately and severely stressed plants at 60 DAP. A more severe reduction in the shoot weights could be observed both at 90 and 120

DAP due to the effect of water stress. At 120 DAP, the dry weight of shoot of severely stressed plants (S_3) were significantly lower than that of all other water stress levels.

4.2.1.9 Root weight

The dry weight of roots of the seedlings as influenced by the water stress levels are presented in Table 13. The root weight observed in *A. mangium* seedlings did not show any significant differences between water stress treatments at 30 and 60 DAP. However, the dry weight of roots observed for the water stressed plants at 90 and 120 DAP were significantly below that of the control. A severe reduction in the root dry weight with increasing water stress was observed at 120 DAP.

4.2.1.10 Root - Shoot ratio

The mean values on root - shoot ratio are given in Table 13. Water stress had no significant influence on the root - shoot weight ratios of *A. mangium* seedlings except at 60 DAP. At 60 DAP, moderately stressed (S_2) and severely stressed (S_3) plants showed significantly higher values when compared to that of control.

4.2.1.11 Total dry matter production

The mean values on total dry matter production in *A. mangium* seedlings are presented in Table 13. The influence of water stress on total

Table 13 Shoot weight, root weight, root/shoot ratio and total dry matter production in *A. mangium* seedlings as affected by different levels of water stress

Stress levels	Shoot weight (g)				Root weight (g)				Root/shoot ratio				Total dry matter production (g)			
	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP
S_0	49.5	40.8	84.6	65.4	17.8	17.3	27.0	17.6	0.36	0.78	0.56	0.41	67.3	58.1	111.6	83.1
S_1	39.2	36.6	84.6	52.9	21.5	18.8	19.7	12.9	0.54	0.87	0.56	0.41	60.8	55.3	74.3	65.8
S_2	60.1	26.0	38.4	31.9	26.0	18.6	11.4	7.5	0.44	1.3	0.49	0.34	86.1	44.6	49.8	39.4
S_3	45.2	19.2	25.3	23.4	15.5	14.5	14.5	6.2	0.33	1.3	0.76	0.37	60.7	33.7	39.8	29.6
F	*	*	*	*	NS	NS	*	*	NS	*	NS	NS	NS	NS	*	*
LSD (0.05)	14.9	15.6	37.6	35.5	-	-	14.2	10.7	-	0.43	-	-	-	-	50.3	45.4
SEM±	3.8	4.0	9.6	9.1	3.6	3.9	3.6	2.7	0.06	0.11	0.11	0.07	6.6	7.8	12.8	11.6

* Significant at 5% level   NS - Not significant

Table 14   Relative growth rate, net assimilation rate and relative water content of leaves of *A. mangium* seedlings as affected by different levels of water stress

Stress levels	Relative Growth Rate $(mg\ g^{-1} wk^{-1})$			Net Assimilation Rate $(mg\ cm^{-2} wk^{-1})$			Relative Water Content (%)	
	30-60 DAP	60-90 DAP	90-120 DAP	30-60 DAP	60-90 DAP	90-120 DAP	0800 (hrs)	1400 (hrs)
S_0	2.2	2.0	2.3	0.06	0.22	0.12	87.75	88.52
S_1	2.1	0.91	0.85	0.07	0.10	0.06	81.41	82.98
S_2	2.9	0.99	0.99	0.06	0.05	0.04	80.81	74.42
S_3	3.0	1.4	0.73	0.02	0.02	0.02	82.75	61.49
F	**	**	**	*	**	**	NS	*
LSD (0.05)	0.34	0.26	0.34	0.03	0.03	0.03	-	22.28
SEM±	0.09	0.07	0.39	0.01	0.01	0.01	2.92	7.01

* Significant at 5% level   ** Significant at 1% level   NS Not significant

dry matter production was evident from 90 DAP onwards. Water stress significantly reduced the dry matter production recorded both at 90 and 120 DAP. At 120 DAP, the dry weight of severely stressed (S_3) plants was significantly lower than that of all the other water stress levels.

4.2.1.12 Relative Growth Rate (RGR)

The relative growth rate of *A. mangium* seedlings in response to different levels of water stress are given in Table 14. RGR was reduced significantly during 60-90 and 90-120 DAP due to water stress. Significant reductions was observed at all the levels of water stress with severe reductions during 90-120 DAP.

4.2.1.13 Net Assimilation Rate (NAR)

The net assimilation rates of *A. mangium* seedlings are given in Table 14. During the 30-60 DAP only severe water stress significantly reduced the NAR, whereas at 60-90 DAP and 90-120 DAP, water stress at all levels significantly reduced the NAR as compared to control.

4.2.2 Physiological parameters

4.2.2.1 Leaf Diffusive Resistance (LDR)

The values on leaf diffusive resistance recorded in *A. mangium* seedlings as influenced by water stress are presented in Table 15. The LDR recorded were lowest for the control and increased with the increasing levels

Table 15 Leaf diffusive resistance (m mol m^{-2} s^{-1}) in *A. mangium* seedlings as affected by different levels of water stress through a nine day cycle

Stress levels	1 DAS		2 DAS		3 DAS		4 DAS		5 DAS	
	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)
S_0	6.08	7.27	5.88	7.65	4.54	7.78	6.51	8.10	6.22	8.99
S_1	10.13	10.62	8.79	13.37	15.09	27.71	15.00	11.33	18.83	13.29
S_2	12.05	12.93	11.53	17.73	17.79	25.59	18.77	42.62	18.48	74.87
S_3	11.05	12.49	13.17	17.76	21.31	30.35	33.03	56.75	36.95	92.31
F	**	**	**	**	**	**	**	**	**	**
LSD (0.05)	2.14	2.84	1.85	2.62	3.60	3.14	3.38	2.59	2.86	7.09
SEM±	0.71	0.95	0.62	0.87	1.20	1.04	1.12	0.86	0.95	2.36

Stress levels	6 DAS		7 DAS		8 DAS		9 DAS	
	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)
S_0	6.83	7.57	7.61	7.17	5.44	8.36	6.13	10.56
S_1	16.04	29.75	18.40	12.17	9.76	15.30	9.85	29.31
S_2	34.23	123.15	20.85	14.75	14.63	18.25	11.89	29.39
S_3	42.95	162.83	44.80	93.07	40.55	141.75	49.67	187.11
F	**	**	**	**	**	**	**	**
LSD (0.05)	2.42	11.55	4.45	6.56	3.31	4.69	2.55	3.97
SEM±	0.81	3.85	1.48	2.19	1.10	1.56	0.85	1.32

* Significant at 5% level   ** Significant at 1% level   DAS Days after the beginning of stress

of water stress. At 1 DAS , all the water stressed plants were having significantly higher LDR above the control both at 0800 and 1400 hrs. At the end of the three day cycle, S_1 (water stressed for 3 days) plants were having significantly higher LDR than the control during the morning as well as the afternoon hours. Plants stressed for six days (S_2) were showing significantly higher LDR values than the control and plants stressed for only three days at 6 DAS for both predawn and midday measurements. A steep rise in the midday values could be observed for S_2 at 6 DAS. Leaf diffusive resistance was significantly above all the other treatments at both the measurements for severely water stressed plants (S_3). Both the predawn and midday LDR showed a steep rise over the control at 9 DAS.

The diurnal variations in the leaf diffusive resistance of *A. mangium* seedlings as influenced by different water stress levels are given in Fig.5 and Appendix IV. Leaf diffusive resistance decreased slightly from 0600 to 0800 hrs in S_0 and was more or less steady afterwards till dusk where it again showed a slight increase. In the case of mildly stressed plants (S_1) a slight peak was observed at 1200 hrs. A midday increase in the LDR was observed in all the water stressed plants. For S_2 and S_3 the LDR values rose gradually with time and two distinct peaks could be seen at 1400 hrs which then declined. A decline in the leaf diffusive resistance with the sunrise (0600 to 0800 hrs) was observed in all the plants irrespective of the difference in water stress levels.
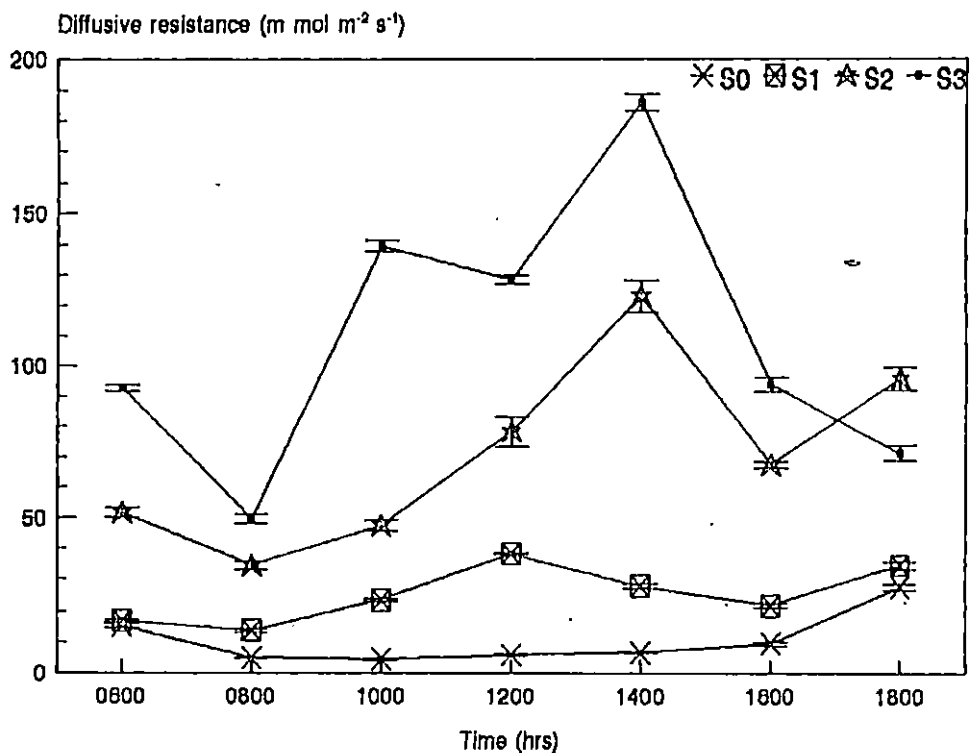
Diffusive resistance (m mol m^{-2} s^{-1})

Fig.5. Diurnal variations in the leaf diffusive resistance of _A. mangium_ seedlings as affected by different levels of water stress

Leaf water potential (-MPa)
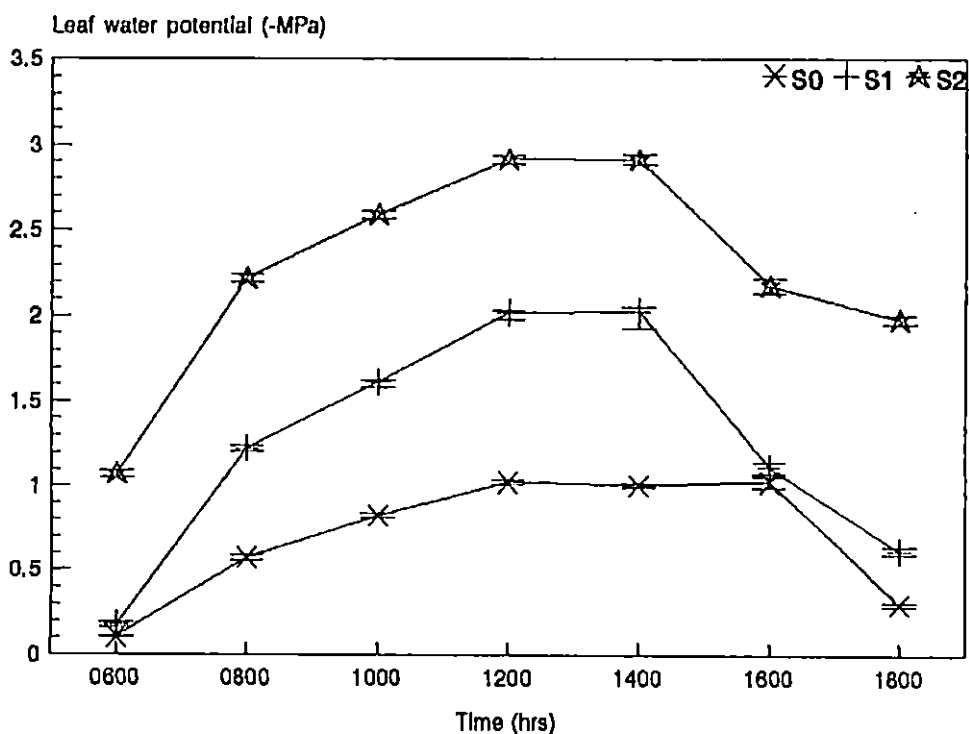
Fig.6. Diurnal variations in the leaf water potential of _A. mangium_ seedlings as affected by different levels of water stress

4.2.2.2 Transpiration rate

The transpiration rate in *A. mangium* seedlings as influenced by different water stress levels are given in Table 16. At the start of the water stress cycle (1 DAS), all the water stressed treatments had their transpiration significantly below the control. For plants experiencing water stress for three days (S_1), the transpiration rates were reduced below control at 3 DAS during both predawn and midday measurements. Water stress reduced the transpiration rates significantly for moderately stressed (S_2) plants at 6 DAS. At 9 DAS also the severely stressed (S_3) plants were showing reduced transpiration rates with respect to the other treatments.

4.2.2.3 Leaf temperature

The leaf temperature of *A. mangium* seedlings as influenced by the different water stress cycles are presented in Table 17. No significant difference in leaf temperature was observed at 1 DAS among the different water stress level. At 3 DAS, mildly stressed plants (S_1) showed significantly higher leaf temperature at 0800 and 1400 hrs. Leaf temperature of moderately stressed plants (S_2) were significantly higher at 6 DAS during both predawn and midday measurements. However, no significant differences were observed at 9 DAS in severely stressed plants (S_3) during either measurements. Eventhen, the leaf temperatures recorded were slightly above than that of the control.

Table 16 Transpiration rate (μg H_2O cm^{-2} s^{-1}) in *A. mangium* seedlings as affected by different levels of water stress through a nine day cycle

Stress levels	1 DAS		2 DAS		3 DAS		4 DAS		5 DAS	
	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)
S_0	1.94	3.20	1.80	3.24	2.49	3.14	1.39	3.02	1.57	3.30
S_1	1.07	1.72	1.25	1.87	0.79	1.09	0.69	2.25	0.56	1.87
S_2	0.98	2.10	1.03	1.33	0.72	1.06	0.62	0.63	0.68	0.41
S_3	0.95	1.69	0.85	1.49	0.55	0.52	0.35	0.90	0.46	0.37
F	**	**	**	**	**	**	**	**	**	**
LSD (0.05)	0.26	0.70	0.19	0.45	0.19	0.54	0.21	0.53	0.16	0.40
SEM±	0.09	0.23	0.07	0.15	0.07	0.18	0.07	0.18	0.05	0.13

Stress levels	6 DAS		7 DAS		8 DAS		9 DAS	
	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)
S_0	1.51	3.87	1.26	3.45	1.89	3.10	1.82	2.47
S_1	0.61	0.98	0.52	2.29	1.24	1.50	0.95	0.79
S_2	0.38	0.26	1.29	1.75	0.83	1.35	0.97	0.90
S_3	0.30	0.20	0.22	0.31	0.31	0.23	0.24	0.15
F	**	**	NS	**	**	**	**	**
LSD (0.05)	0.12	0.44	-	0.44	0.36	0.44	0.21	0.24
SEM±	0.04	0.15	0.40	0.15	0.12	0.15	0.07	0.08

* Significant at 5% level   ** Significant at 1% level   NS Not significant

Table 17 Leaf temperature (°C) in *A. mangium* seedlings as affected by different levels of water stress through a nine day cycle

Stress levels	1 DAS		2 DAS		3 DAS		4 DAS		5 DAS	
	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)
S_0	24.28	32.96	24.94	33.26	24.50	33.00	22.82	32.96	22.88	33.00
S_1	24.26	32.54	25.04	33.26	24.96	33.52	23.62	33.56	23.68	33.32
S_2	24.04	33.30	25.08	33.22	25.26	33.84	23.82	34.06	24.14	33.56
S_3	24.10	33.34	25.00	33.24	25.18	34.00	23.82	34.18	24.50	33.96
F	NS	NS	NS	NS	*	**	*	**	**	**
LSD (0.05)	-	-	-	-	0.49	0.48	0.93	0.35	0.45	0.32
SEM±	0.12	0.27	0.36	0.35	0.16	0.16	0.31	0.11	0.15	0.11

Stress levels	6 DAS		7 DAS		8 DAS		9 DAS	
	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)
S_0	24.24	33.76	23.72	33.56	26.44	34.04	26.08	36.24
S_1	24.56	33.96	24.48	33.90	26.52	35.44	26.74	36.26
S_2	25.16	35.74	24.44	34.18	26.86	35.04	26.76	35.50
S_3	24.98	35.00	24.66	34.18	27.06	35.20	26.42	36.76
F	**	**	**	*	NS	**	NS	NS
LSD (0.05)	0.48	1.09	0.50	0.49	-	0.48	-	-
SEM±	0.16	0.37	0.17	0.16	0.24	0.16	0.44	0.39

* Significant at 5% level   ** Significant at 1% level   NS - Not significant

67

4.2.2.4 Leaf water potential

The diurnal variations in the leaf water potential (ψ) of *A. mangium* seedlings exposed to different levels of water stress are given in Fig.6 and Appendix IV. Leaf water potential (ψ) decreased with increasing levels of stress with control showing maximum values. The pattern of variation shown by mildly (S_1) and moderately stressed (S_2) plants were similar though moderately stressed (S_2) plants exhibited much lower water potential. The variation from 1200 to 1400 hrs was not significant in any of the treatments.

4.2.2.5 Relative water content (RWC)

The relative water content of the leaves of *A. mangium* seedlings experiencing water stress at different levels are given in Table 14. The RWC did not show significant variation among the treatments at 0800 hrs. However, water stress levels affected the RWC of the leaves at 1400 hrs. The RWC of all the water stressed treatments were significantly below the control. The relative water content in the severely stressed (S_3) plants was reduced significantly below that of all the other plants.

4.2.2.6 Net photosynthesis

In general, the net photosynthesis was lower in all the water stressed plants when compared with the control (Fig. 7). There was a decline in the photosynthesis towards the mid day in all the treatments and thereafter increased towards dusk except for the severely stressed (S_3) plants. The

Net photosynthesis (y mol cm^{-2} s^{-1})
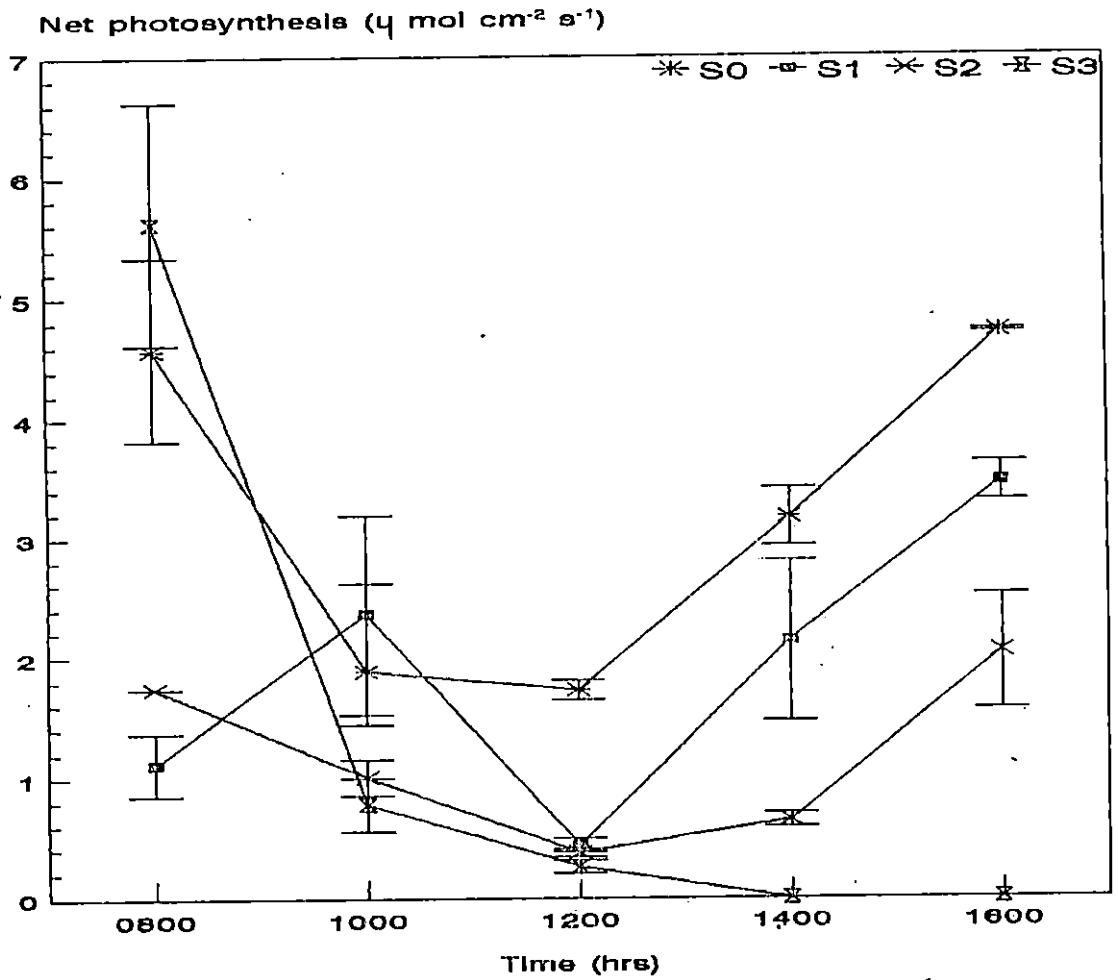
Fig.7. Diurnal variations in the net photosynthesis of *A. mangium*
seedlings as affected by different levels of water stress

decline in net photosynthesis of severely stressed plants (S_3) from 0800 to 1000 hrs was steeper when compared to the other treatments. At 1400 hrs, the net photosynthesis in S_3 plants reached zero after which, no photosynthesis was observed.

4.2.3 Biochemical attributes

4.2.3.1 Chlorophyll content

The chlorophyll 'a', chlorophyll 'b' and total chlorophyll contents in *A. mangium* seedlings experiencing water stress at different levels are given in Table 18. Chlorophyll 'a' content did not differed significantly among treatments except for S_3, where the content was below the unstressed control. Water stress reduced the chlorophyll 'b' content significantly in S_1, S_2 and S_3. However, there was no significant differences among S_1, S_2 and S_3. Total chlorophyll also exhibited a similar trend as that of chlorophyll 'b' with reduced content.in S_1, S_2 and S_3.

4.2.3.2 Proline content

Proline content increased in the leaves of *A. mangium* as the intensity of the water stress increased (Table 18). Eventhough the water stressed plants showed an increased proline level, S_1 and S_2 were on par. Highest proline content was observed in the severely stressed (S_3) plants.

Table 18 Biochemical attributes of *A. mangium* seedlings as affected by different levels of water stress
at the end of growth period

Stress levels	Chlorophyll 'a' (mg g^{-1})	Chlorophyll 'b' (mg g^{-1})	Total Chlorophyll (mg g^{-1})	Proline (μg g^{-1})	Soluble protein (mg g^{-1})
S_0	0.41	0.25	0.43	4.05	8.68
S_1	0.40	0.14	0.40	5.21	10.63
S_2	0.39	0.20	0.39	5.68	11.55
S_3	0.31	0.12	0.32	6.70	13.88
F	**	*	*	**	**
LSD (0.05)	0.06	0.01	0.08	0.83	1.03
SEM±	0.02	0.00	0.02	0.25	0.32

* Significant at 5% level   ** Significant at 1% level

Table 19   Inter-correlation matrix of total dry matter production and other plant characters in *A. mangium*

Character	LA	LW	CD	SW	RW	RSR	SLA	TDMP
LN	0.543*	0.495*	0.713**	0.737**	0.375	-0.190	0.038	0.689**
LA		0.927**	0.596**	0.838**	0.703**	-0.36	0.584**	0.860**
LW			0.544*	0.863**	0.701**	-0.36	0.674	0.880**
CD				0.788**	0.568**	-0.27	-0.093	0.783**
SW					0.665**	-0.423	0.281	0.978**
RW						0.189	0.172	0.807**
RSR							-0.287	-0.281
SLA								0.271

* Significant at 1% level   ** Significant at 0.1% level   LA   - Leaf area
RW   - Root weight   LW   - Leaf weight   RSR   - Root shoot ratio
SW   - Shoot weight   CD   - Collar diameter   TDMP - Total drymatter production
SLA   - Specific leaf area

Table 20   Inter-correlation matrix of net photosynthesis and other physiological parameters in *A. mangium*

Characters	LT	CON	TRN	CIN	NP
QNT	0.917**	-0.389	-0.117	0.247	-0.389
LT		-0.530**	-0.341	0.106	-0.622
CON			0.938**	0.455*	0.854**
TRN				0.526**	0.756**
CIN					0.456*

* Significant at 1% level   ** Significant at 0.1% level   LT - Leaf temperature   CON - Conductance
CIN - Internal CO_2 QNT - Quantum influx   NP - Net photosynthesis   TRN - Transpiration

4.2.3.3 Soluble protein

The mean values on soluble protein is given in Table 18. Water stress increased the soluble protein levels in *A. mangium*. All the water stressed plants (S_1, S_2 and S_3) recorded significantly higher values above control. However, the variation between S_1 and S_2 was not significant.

4.3 *Swietenia macrophylla* (Mahogany)

4.3.1 Growth attributes

4.3.1.1 Plant height

The plant height recorded for *Swietenia macrophylla* seedlings at 30, 60, 90 and 120 DAP are presented in Table 21. At 30 or 60 DAP, there was no significant variation in plant height due to water stress. However, a decreasing trend in plant height was observed from 60 DAP onwards. Water stress significantly reduced the height of the seedlings in S_1, S_2 and S_3 plants when compared to the control at 90 DAP. At 120 DAP only S_2 and S_3 plants showed significant reduction in plant height below control.

4.3.1.2 Rooting depth

The rooting depth of *S. macrophylla* seedlings exposed to different levels of water stress are given in Table 21. No significant variation was observed in rooting depth among the different water stress levels at any of the stages of growth.

Table 21 Plant height, rooting depth and collar diameter of *S. macrophylla* seedlings as affected by different levels of water stress

Stress levels	Plant height (cm)				Rooting depth (cm)				Collar diameter (mm)			
	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP
S_0	82.8	106.3	115.0	128.5	30.8	30.5	34.8	43.0	11.9	14.4	16.7	18.7
S_1	102.0	94.5	94.5	123.6	40.5	31.0	30.5	43.2	14.0	14.4	14.1	14.2
S_2	92.8	88.3	97.8	91.0	35.5	34.0	33.8	37.3	15.1	12.4	14.7	13.0
S_3	94.0	85.8	97.3	81.5	32.0	35.8	34.7	39.6	11.3	12.1	12.7	12.0
F	NS	NS	*	*	NS	NS	NS	NS	NS	NS	NS	*
LSD (0.05)	25.4	46.8	16.4	31.0	14.5	8.6	7.9	9.8	3.3	2.6	5.2	5.0
SEM±	6.5	11.9	4.2	7.9	3.7	2.2	2.0	2.5	0.84	0.66	1.3	1.3

* Significant at 5% level   ** Significant at 1% level   NS - Not significant

4.3.1.3 Collar diameter

The collar diameter of the *S. macrophylla* seedlings at different stages of growth are presented in Table 21. At 30, 60 and 90 DAP, there was no significant variation in collar diameter among different treatments. However, water stress significantly reduced the collar diameter in all the water stressed (S_1, S_2 and S_3) plants below control at 120 DAP.

4.3.1.4 Number of leaves

The number of leaves per plant of *S. macrophylla* seedlings as affected by water stress are presented in Table 22. Water stress significantly reduced the number of leaves at all the growth stages. At 30 DAP, the number of leaves in all the water stressed plants were lower than that of control, with S_3 plants significantly different from all the other treatments. At 60 DAP, S_0 and S_1 were on par. Significant reduction in the number of leaves was also observed at 90 DAP. At 120 DAP, mildly stressed (S_1) plants were on par with control, however, moderate (S_2) and severely stressed (S_3) plants were significantly different from control.

4.3.1.5 Leaf area

The leaf area recorded for *S. macrophylla* seedlings at 30, 60, 90 and 120 DAP are presented in Table 22. During the initial stage (30 DAP), no significant variation was observed in leaf area. From 60 DAP onwards, all the treatments were significantly different among each other.

Table 22   Number of leaves, leaf area, leaf weight and specific leaf area of *S. macrophylla* seedling as affected by different levels of water stress

Stress levels	Number of leaves (no plant $^{-1}$)				Leaf area (cm^2 plant $^{-1}$)				Leaf weight (g)				Specific leaf area (m^2 g^{-1})			
	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP
S$_0$	17.0	17.0	20.5	35.0	1587	3113	3299	4239	15.5	27.3	32.1	42.5	1.0	1.1	1.0	0.99
S$_1$	13.0	13.5	18.5	30.0	2247	2704	1810	3056	19.9	23.0	18.8	19.8	1.1	1.2	0.97	1.5
S$_2$	9.5	11.5	13.5	14.5	2278	891	1181	1901	23.7	9.9	11.5	10.2	0.96	0.91	1.0	1.9
S$_3$	7.0	5.5	10.5	8.5	1839	688	661	942	17.2	2.6	4.2	8.3	1.1	2.7	1.6	1.2
F	**	*	*	**	NS	**	**	**	NS	**	**	**	NS	**	*	*
LSD (0.05)	3.5	6.1	5.9	5.7	-	265	216	455	-	4.2	3.8	3.1	-	0.48	0.33	0.42
SEM±	0.90	1.6	1.5	1.5	589	68	55	116	3.9	1.1	0.96	0.80	0.38	0.34	0.23	0.30

* Significant at 5% level   ** Significant at 1% level   NS - Not significant

4.3.1.6 Leaf weight

The leaf dry weight of *S. macrophylla* seedlings presented in Table 22 did not show any significant differences at 30 DAP. At 60 and 90 DAP, water stress reduced the leaf weight and all the treatments were significantly different from each other. However, towards the end (120 DAP), S_2 and S_3 plants which were on par, showed significantly lower leaf dry weight as compared to S_1 and control plants.

4.3.1.7 Specific leaf area

The specific leaf area of *S. macrophylla* seedlings are presented in Table 22. There was no significant variation at 30 DAP. At 60 DAP, water stress increased the specific leaf area significantly in severely stressed (S_3) plants. The trend was similar during 90 DAP also. At 120 DAP, only moderately stressed plants showed a significant increase in specific leaf area.

4.3.1.8 Shoot weight

The shoot dry weight recorded for *S. macrophylla* seedlings at different growth stages are presented in Table. 23. Shoot weight was reduced significantly by water stress during all the growth stages except at 30 DAP. At 60 DAP, water stress reduced the shoot weight of plants and all the treatments were significantly different. The shoot weight in S_1, S_2 and S_3 plants were lower than the control at 90 DAP. At 120 DAP, though the

shoot weight of water stressed (S_1, S_2 and S_3) plants were lower than that of control, no significant variation was observed among them.

4.3.1.9 Root weight

The dry weight of roots of *S. macrophylla* seedlings are presented in Table 23. There was no significant differences in root weight due to water stress at 30 DAP. However, from 60 DAP onwards, there was significant variation among the treatments. At 60 DAP, the root weight were significantly reduced due to the effect of water stress. Water stress reduced the root weight at 90 and 120 DAP also. At 90 DAP, S_1, S_2 and S_3 plants were on par. Eventhough, at 120 DAP, the moderately (S_2) and severely stressed plants (S_3) recorded a lower shoot weight as compared to unstressed plants, the difference between S_2 and S_3 plants were not significantly different.

4.3.1.10 Root-shoot ratio

The root-shoot weight ratios observed in *S. macrophylla* plants at different growth stages are presented in Table 23. No significant variations in the root-shoot ratio was observed at any of the growth stages except at 60 DAP. Severely stressed (S_3) plants recorded significantly higher root-shoot ratio at 60 DAP when compared to the other treatments. At 90 and 120 DAP, a decreasing trend was observed, but no significant difference was observed.

Table 23   Shoot weight, root weight, root/shoot ratio and total dry matter production in *S. macrophylla* seedlings as affected by different levels of water stress

Stress levels	Shoot weight (g)				Root weight (g)				Root/shoot ratio				Total dry matter production (g)			
	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP
S_0	41.1	68.0	96.3	129.0	12.8	15.1	25.7	29.8	0.31	0.37	0.40	0.36	53.8	83.0	122.0	158.7
S_1	64.1	57.0	61.6	69.5	20.3	13.0	12.3	14.6	0.33	0.38	0.33	0.29	84.4	69.9	73.9	84.1
S_2	73.1	39.8	56.5	42.6	19.2	11.0	16.2	10.9	0.26	0.37	0.36	0.34	92.3	50.8	72.8	53.5
S_3	47.6	23.4	35.4	35.6	13.4	8.7	10.4	7.0	0.28	0.42	0.27	0.26	61.0	32.1	45.8	42.5
F	NS	**	*	*	NS	**	*	**	NS	*	NS	NS	NS	**	*	**
LSD (0.05)	-	7.5	24.7	45.6	-	1.8	12.0	5.8	-	0.05	-	-	-	8.4	36.3	50.9
SEM±	9.8	1.9	6.3	11.6	2.4	0.45	3.0	1.5	0.00	0.01	0.04	0.03	11.8	2.1	9.2	13.0

* Significant at 5% level   ** Significant at 1% level   NS - Not significant

Table 24   Relative growth rate, net assimilation rate and relative water content of leaves of *S. macrophylla* seedlings as affected by different levels of water stress

Stress levels	Relative Growth Rate (mg g^{-1} wk^{-1})			Net Assimilation Rate (mg cm^{-2} wk^{-1})			Relative Water content (%)	
	30-60 DAP	60-90 DAP	90-120 DAP	30-60 DAP	60-90 DAP	90-120 DAP	0800 (hrs)	1400 (hrs)
S_0	4.1	3.2	2.1	0.13	0.09	0.09	58.55	64.23
S_1	3.7	2.8	2.0	0.10	0.11	0.11	57.92	55.89
S_2	2.5	1.9	1.7	0.07	0.04	0.06	57.98	52.70
S_3	1.1	1.0	0.96	0.04	0.05	0.06	58.58	46.26
F	**	**	**	**	**	**	NS	*
LSD (0.05)	0.35	0.88	0.31	0.03	0.03	0.03	-	10.92
SEM±	0.09	0.22	0.08	0.01	0.01	0.01	2.89	3.35

* Significant at 5% level   ** Significant at 1% level   NS - Not significant

4.3.1.11 Total dry matter production

There was no significant variation in the total dry matter production at 30 DAP (Table 23). From 60 DAP onwards, water stress significantly affected the dry matter production. At 60 DAP, total dry matter produced in all the water stressed plants were significantly different and lower than the control. At 90 and 120 DAP, the dry matter production was reduced significantly in all the water stressed plants.

4.3.1.12 Relative Growth Rate (RGR)

The mean values on the RGR of *S. macrophylla* seedlings in response to water stress are given in Table 24. Water stress at all levels significantly reduced the RGR in *S. macrophylla* seedlings at 30-60 DAP. During 60-90 and 90-120 DAP intervals, though RGR was reduced due to water stress, significant reductions were observed only in moderate and severely water stressed plants.

4.3.1.13 Net Assimilation Rate (NAR)

The net assimilation rate (NAR) calculated for *S. macrophylla* seedlings at different stages of growth are given in Table 24. NAR was reduced significantly due to water stress at all the levels during 30-60 DAP. However, during 60-90 and 90-120 DAP intervals, as in the case of RGR only moderate and severely stressed plants showed significant reductions due to water stress.

4.3.2 Physiological parameters

4.3.2.1 Leaf Diffusive Resistance (LDR)

The data on leaf diffusive resistance recorded in *S. macrophylla* seedlings as influenced by different levels of water stress are presented in Table 25. At the beginning of the cycle (1 DAS), there was no significant variation in the predawn leaf diffusive resistance. However, at midday S_2 and S_3 plants showed a significant rise in the leaf diffusive resistance though S_1 was on par with control. At the end of 3 days of water stress, the mildly stressed plants showed a higher predawn leaf diffusive resistance. Water stress induced higher LDR in S_2 plants at 6 DAS. Both the predawn and midday values were significantly above that of control. Severely stressed (S_3) plants, at the end of nine days water stress, increased their LDR, significantly above all the other treatments.

The diurnal variations in the leaf diffusive resistance of *S. macrophylla* seedlings experiencing water stress at different levels is given in and Fig. 8 and Appendix V. There was a steep decline in the diffusive resistance in water stressed treatments from 0600 to 0800 hrs which was not much prominent in control. However, from 0800 hrs onwards, the LDR of water stressed (S_1, S_2 and S_3) plants started increasing while that of control plants still decreased and maintained stability till 1600 hrs which then increased. S_1 and S_2 plants showed a more or less similar pattern in the increase while S_3 plants showed further severe fluctuations. There was a peak

Table 25 Leaf diffusive resistance (m mol m^{-2} s^{-1}) in *S. macrophylla* seedlings as affected by different levels of water stress through a nine day cycle

Stress levels	1 DAS		2 DAS		3 DAS		4 DAS		5 DAS	
	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)
S_0	9.02	8.14	5.08	5.42	5.84	9.05	4.70	8.18	5.56	7.79
S_1	8.93	8.44	6.99	10.23	8.76	8.53	7.15	8.60	5.95	8.95
S_2	8.73	12.20	8.09	14.05	11.61	12.74	10.36	16.13	11.58	30.63
S_3	9.83	17.71	9.34	15.91	15.11	18.87	21.35	30.23	31.42	42.79
F	NS	**	**	**	**	**	**	**	**	**
LSD (0.05)	-	1.64	1.66	2.85	1.27	1.44	2.55	5.31	2.32	2.51
SEM±	0.61	0.55	0.56	0.95	0.42	0.48	0.85	1.77	0.77	0.84

Stress levels	6 DAS		7 DAS		8 DAS		9 DAS	
	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)
S_0	5.19	6.48	5.01	7.65	5.36	7.90	5.40	9.40
S_1	7.49	7.67	7.23	8.27	5.89	8.99	6.75	10.19
S_2	13.44	41.19	11.82	9.84	7.21	8.22	6.81	7.63
S_3	28.91	63.76	18.46	77.31	24.98	99.51	15.89	113.23
F	**	**	**	**	**	**	**	**
LSD (0.05)	4.35	7.91	1.75	2.22	2.73	2.72	0.80	4.55
SEM±	1.45	2.64	0.58	0.74	0.91	0.91	0.27	1.52

*Significant at 5% level **Significant at 1% level DAS Days after the beginning of stress

in the diffusive resistance of S_3 plants at 1400 hrs which then declined behind S_1 and S_2 by 1600 hrs. The variations during 1000 to 1200 hrs were not significant in any of the treatments.

4.3.2.2 Transpiration rate

The transpiration rates of the water stressed seedlings of *S. macrophylla* recorded at 0800 and 1400 hrs are presented in Table 26. At the first day of stress, transpiration rates did not vary significantly at 0800 hrs. At 1400 hrs, water stress reduced the transpiration rates significantly in S_2 and S_3 plants. At the end of 3 days of water stress, predawn transpiration rates were reduced, though midday value showed no significant variation. The transpiration rates were reduced significantly in S_2 plants at sixth day of water stress. Plants stressed for nine days (S_3) exhibited a further reduction in the transpiration rates. However, the transpiration rates were recouped following rewatering in all the water stressed treatments.

4.3.2.3 Leaf temperature

The leaf temperature of *S. macrophylla* seedlings exposed to different levels of water stress are presented in Table 27. At the start of the cycle, midday leaf temperatures were increased significantly due to water stress, though the predawn values showed no variation. Plants experiencing water stress for 3 days (S_1) increased their predawn leaf temperature significantly above that of control. However, midday values were not affected by water

Table 26 Transpiration rate (μg H_2O cm^{-2} s^{-1}) in *S. macrophylla* seedlings as affected by different levels of water stress through a nine day cycle

Stress levels	1 DAS		2 DAS		3 DAS		4 DAS		5 DAS	
	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)
S_0	1.34	3.15	2.19	3.07	2.30	3.07	1.89	2.96	2.55	3.06
S_1	1.44	3.36	1.55	2.65	1.47	2.88	1.26	2.57	2.63	2.49
S_2	1.49	2.17	1.38	1.82	1.51	2.35	0.91	1.73	1.27	0.52
S_3	1.37	1.87	1.18	1.76	0.89	1.57	0.41	0.44	0.61	0.47
F	NS	**	**	**	**	**	**	**	**	**
LSD (0.05)	-	0.29	0.34	0.42	0.19	0.31	0.27	0.30	0.35	0.26
SEM±	0.12	0.10	0.11	0.14	0.06	0.10	0.09	0.10	0.12	0.09

Stress levels	6 DAS		7 DAS		8 DAS		9 DAS	
	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)
S_0	2.73	4.35	1.84	2.56	1.77	3.06	2.53	2.88
S_1	1.76	3.42	1.31	2.78	2.87	2.55	2.40	2.49
S_2	1.13	0.53	0.98	2.48	1.95	2.88	2.70	2.83
S_3	0.55	0.42	0.67	0.37	0.51	0.29	0.79	0.29
F	**	**	**	**	**	**	**	**
LSD (0.05)	0.61	1.00	0.14	0.33	0.20	0.29	0.21	0.25
SEM±	0.20	0.34	0.05	0.11	0.07	0.09	0.07	0.08

* Significant at 5% level   ** Significant at 1% level   NS - Not significant

Table 27   Leaf temperature (°C) in *S. macrophylla* seedlings as affected by different levels of water stress through a nine day cycle

Stress levels	1 DAS		2 DAS		3 DAS		4 DAS		5 DAS	
	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)
S_0	25.44	36.92	25.82	36.90	25.50	38.42	26.70	37.96	26.56	37.32
S_1	25.26	37.00	26.02	36.38	26.10	38.88	26.70	37.96	26.92	37.36
S_2	25.62	37.12	26.52	36.28	26.20	38.88	26.68	38.38	26.86	37.98
S_3	25.50	37.24	25.98	36.92	26.86	38.82	26.92	38.52	26.96	38.12
F	NS	**	*	NS	**	NS	NS	**	**	**
LSD (0.05)	-	0.14	0.50	--	0.56	-	-	0.32	0.23	0.35
SEM±	0.13	0.05	0.17	0.48	0.19	0.15	0.10	0.11	0.08	0.12

Stress levels	6 DAS		7 DAS		8 DAS		9 DAS	
	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)
S_0	30.14	36.38	24.56	37.88	24.44	38.00	25.96	38.08
S_1	29.82	36.26	25.00	38.12	24.84	38.70	26.28	38.48
S_2	30.08	34.72	25.10	38.34	25.12	38.98	26.60	39.02
S_3	30.42	37.08	25.40	38.54	25.34	39.24	26.96	39.32
F	NS	NS	*	**	**	**	**	**
LSD (0.05)	-	-	0.60	0.28	0.42	0.33	0.34	0.29
SEM±	0.21	0.82	0.20	0.09	0.14	0.11	0.11	0.10

* Significant at 5% level   ** Significant at 1% level   NS - Not significant   DAS   Days after the beginning of stress
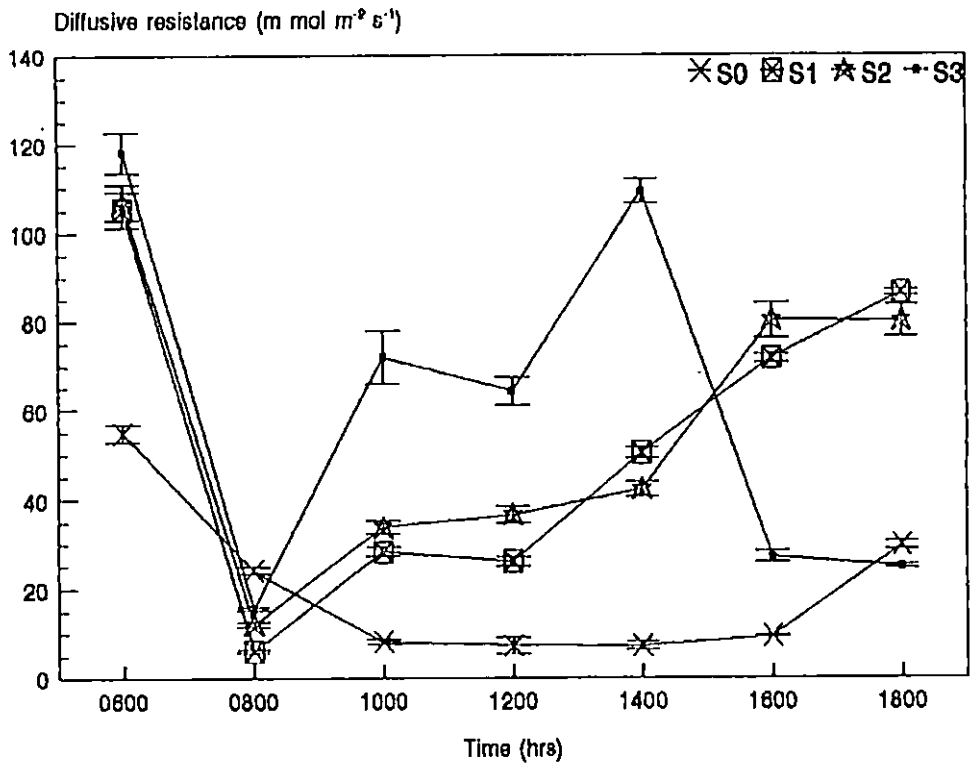
Fig.8. Diurnal variations in the leaf diffusive resistance of *S. macrophylla* seedlings as affected by different levels of water stress
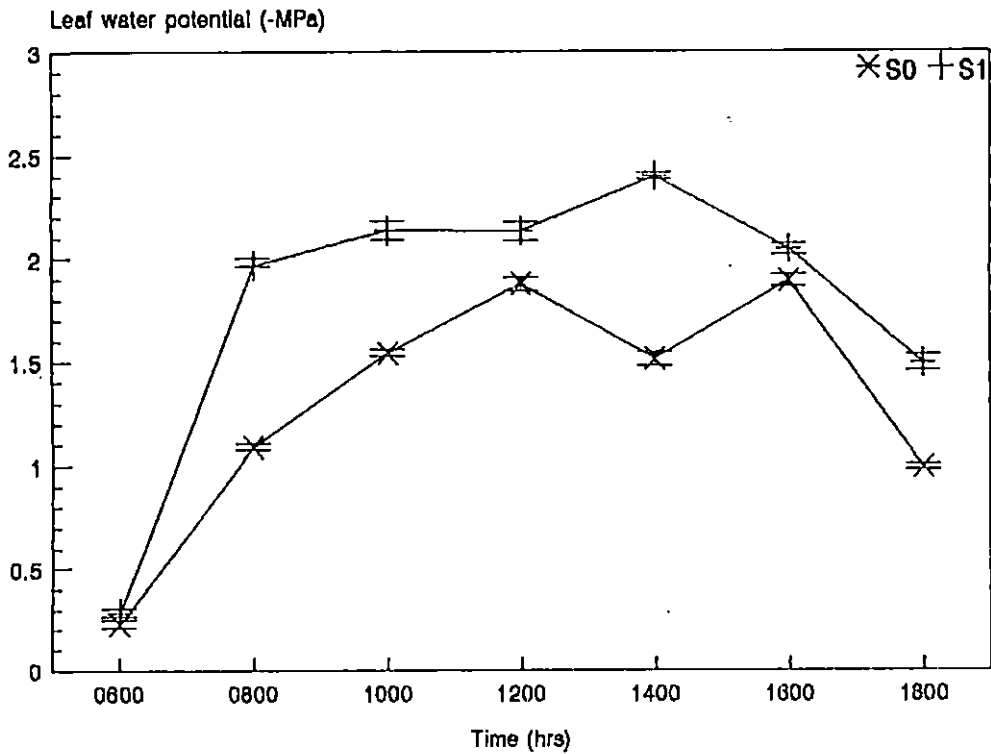
Fig.9. Diurnal variations in the leaf water potential of *S. macrophylla* seedlings as affected by different levels of water stress

stress. At 6 DAS, S_2 plants experienced no significant variations in their leaf temperature when compared to control.

4.3.2.4 Leaf water potential

The diurnal variations in the leaf water potential (ψ) of *S. macrophylla* seedlings are given in Fig. 9 and Appendix V. Leaf water potential (ψ) decreased as the water stress increased. Even mildly water stressed (S_1) plants were showing much lower values than the control. Lower values of ψ were recorded during 1200 to 1600 hrs for both S_0 and S_1 plants.

4.3.2.5 Relative water content (RWC)

The relative water content in *S. macrophylla* seedlings as observed during 0800 and 1400 hrs at different levels of stress are given in Table 24. The predawn RWC did not show any significant variation among the treatments. At 1400 hrs, all the water stressed treatments (S_1, S_2 and S_3) were having significantly lower RWC when compared to control. However S_1, S_2 and S_3 were on par.

4.3.2.6 Net photosynthesis

The diurnal variations in net photosynthesis was more or less similar in the various treatments (Fig. 10). However, there were marked differences among the photosynthetic rate due to the influence of water stress, with highest value in control and lowest in severely stressed (S_3) plants. There was

Net photosynthesis (μ mol cm^{-2} s^{-1})
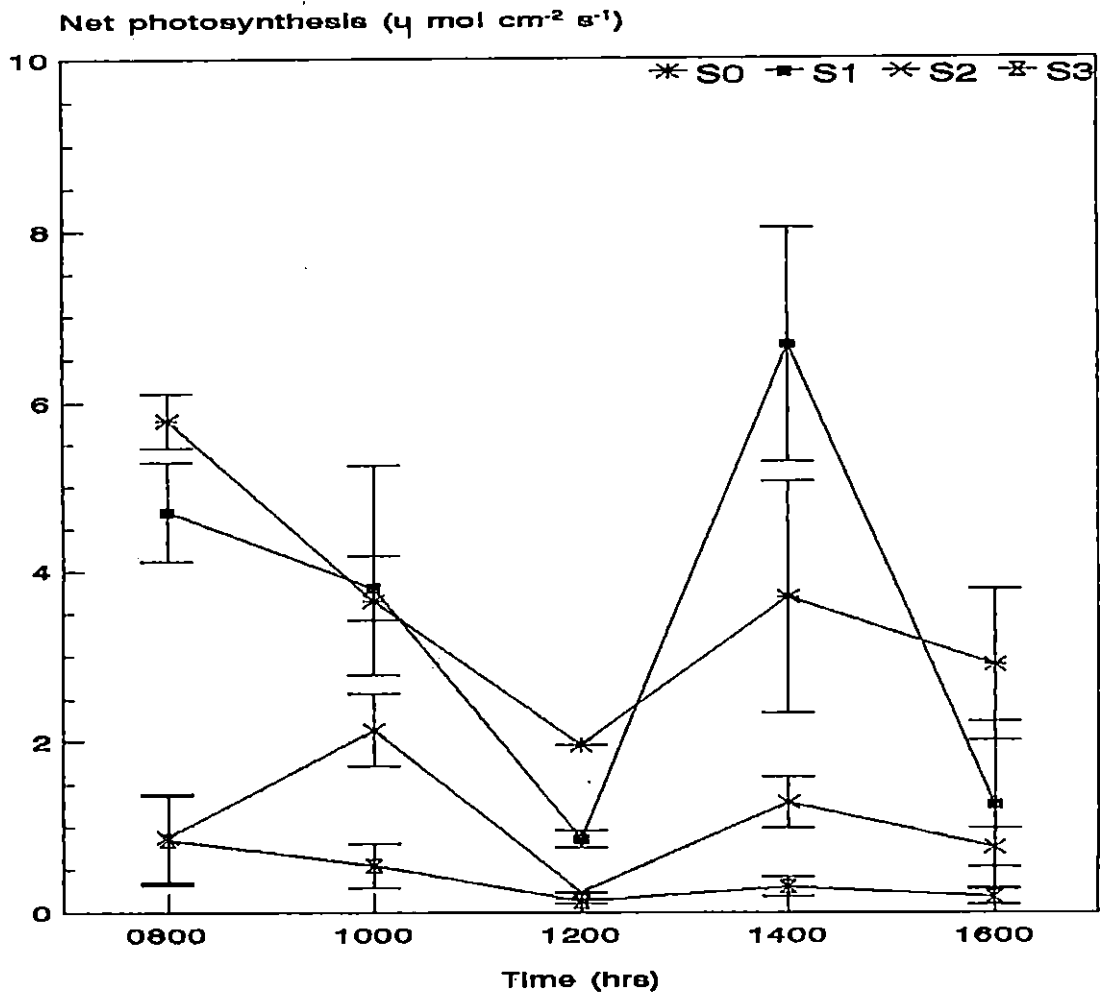
Fig.10. Diurnal variations in the net photosynthesis of *S. macrophylla* seedlings as affected by different levels of water stress

a decline in the net photosynthesis at 1200 noon irrespective of the treatments. However, there was a rise in the values again at 1400 hrs which then declined towards dusk.

4.3.3 Biochemical attributes

4.3.3.1 Chlorophyll content

The chlorophyll 'a', chlorophyll 'b' and total chlorophyll content of *S. macrophylla* seedlings experiencing water stress at different levels are given in Table 28. Water stress significantly affected the chlorophyll content of the plants. Chlorophyll 'a' content was reduced in all the water stressed (S_1, S_2 and S_3) plants but S_1 and S_2 were on par. The trend was repeated in the case of chlorophyll 'b' and total chlorophyll content with severe reductions in severely stressed (S_3) plants.

4.3.3.2 Proline content

The proline content in the fresh leaves of *S. macrophylla* seedlings at different stress stages are given in Table 28. The proline content increased in the leaves as the level of water stress increased. All the water stressed treatments recorded values above control and were significantly different among each other.

Table 28   Biochemical attributes of *S. macrophylla* seedling as affected by different levels of water stress at the end of the growth period

Stress levels	Chlorophyll 'a' (mg g^{-1})	Chlorophyll 'b' (mg g^{-1})	Total Chlorophyll (mg g^{-1})	Proline (μg g^{-1})	Soluble protein (mg g^{-1})
S_0	0.90	0.21	1.11	4.10	4.13
S_1	0.56	0.13	0.89	5.24	5.88
S_2	0.70	0.19	0.68	5.86	7.85
S_3	0.32	0.05	0.37	7.13	10.07
F	**	**	**	**	**
LSD (0.05)	0.21	0.07	0.25	0.33	0.22
SEM±	0.06	0.02	0.08	0.10	0.07

* Significant at 5% level   ** Significant at 1% level

Table 29 Inter-correlation matrix of total dry matter production and other plant characters in *S. macrophylla*

Character	LA	LW	CD	SW	RW	RSR	SLA	TDMP
LN	0.740**	0.691**	0.954**	0.752**	0.604**	0.035	0.352	0.733**
LA		0.940**	0.683**	0.869**	0.745**	0.033	0.677**	0.856**
LW			0.759**	0.926**	0.843**	0.049	0.710**	0.922**
CD				0.871**	0.845**	0.238	0.217	0.877**
SW					0.918**	0.029	0.434	0.997**
RW						0.231	0.311	0.946**
RSR							-0.175	0.068
SLA								0.416

* Significant at 1% level   ** Significant at 0.1% level   LA - Leaf area
RW - Root weight   LW - Leaf weight   RSR - Root shoot ratio
SW - Shoot weight   CD - Collar diameter   TDMP - Total drymatter production
SLA - Specific leaf area

Table 30 Inter-correlation matrix of net photosynthesis and other physiological parameters in *S. macrophylla*

Characters	LT	CON	TRN	CIN	NP
QNT	0.948**	0.091	0.294	0.219	0.104
LT		-0.055	0.143	0.258	-0.114
CON			0.947**	0.150	0.866**
TRN				0.284	0.805**
CIN					0.024

* Significant at 1% level   ** Significant at 0.1% level   LT - Leaf temperature   CON - Conductance
CIN - Internal CO_2 QNT - Quantum influx   NP - Net photosynthesis   TRN - Transpiration

4.3.3.3 Soluble protein

The total soluble protein content in the leaves of *S. macrophylla* at different stress levels (Table 28) showed significant variation. Water stress increased the soluble protein contents with the highest value in S_3 and lowest in control plants.

4.4 *Pterocarpus marsupium* (Bijasal)

4.4.1 Growth attributes

4.4.1.1 Plant height

The mean values on plant height of *Pterocarpus marsupium* seedlings at 30, 60, 90 and 120 DAP are given in Table 31. No significant differences in plant height was observed at 30 and 60 DAP. However, a reducing trend in plant height as water stress increased was observed from 60 DAP onwards. At 90 DAP, water stress significantly reduced the plant height below the control, but S_1, S_2 and S_3 were on par. Severely stressed (S_3) plants recorded the minimum height at 120 DAP, which was significantly lower to all other treatments.

4.4.1.2 Rooting depth

The rooting depth observed in *P. marsupium* seedlings at different growth stages as affected by different levels of water stress are presented in Table 31. There was no significant variation in the rooting depth observed at any of the growth stages.

Table 31   Plant height, rooting depth and collar diameter of *P. marsupium* seedlings as affected by different levels of water stress

Stress levels	Plant height (cm)				Rooting depth (cm)				Collar diameter (mm)			
	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP
S_0	39.0	56.3	97.5	129.0	33.8	43.0	41.8	66.5	6.3	9.0	14.9	17.5
S_1	45.5	56.3	69.5	122.2	35.5	36.5	40.0	57.1	6.8	8.6	8.9	11.0
S_2	40.3	43.0	63.8	95.5	42.0	42.5	44.5	57.6	8.0	8.6	9.8	10.4
S_3	48.0	45.8	50.0	59.0	38.5	45.8	50.5	55.7	8.5	8.7	9.5	8.2
F	NS	NS	*	**	NS	NS	NS	NS	NS	NS	**	*
LSD (0.05)	-	-	38.5	28.4	-	-	-	-	-	-	2.1	4.7
SEM±	5.2	9.1	12.4	7.2	3.6	4.7	7.6	5.4	1.4	0.84	0.54	1.2

* Significant at 5% level   ** Significant at 1% level   NS - Not significant

4.4.1.3 Collar diameter

The mean values of collar diameter of *P. marsupium* seedlings grown under different levels of water stress are given in Table 31. There was no significant difference among the treatments at 30 or 60 DAP. However there was significant reduction in the collar diameter at 90 and 120 DAP due to the effect of water stress. The collar diameter of the water stressed plants (S_1, S_2 and S_3) were below the control. At 120 DAP, the minimum value was recorded by severely stressed (S_3) plants and the maximum, by control.

4.4.1.4 Number of leaves

The number of leaves per plant was reduced drastically due to the effect of water stress (Table 32) in *P. marsupium* seedlings. Significant variation was observed at all the stages of growth. At 30 DAP, the number of leaves in all the water stressed plant (S_1, S_2 and S_3) were less than that of control plants. A similar trend was observed at 60 DAP also. At both these stages (30 and 60 DAP), S_2 and S_3 were on par. Water stress significantly reduced the number of leaves at 90 DAP also. At the end of the cycle (120 DAP), water stress severely reduced the number of leaves.

4.4.1.5 Leaf Area

The leaf area per plant of *P. marsupium* seedlings (Table. 32) did not show significant variation due to the influence of water stress at the initial stages (30 DAP). However, from 60 DAP onwards, there were significant

able 32   Number of leaves, leaf area, leaf weight and specific leaf area of *P. marsupium* seedling as affected by different levels of water stress

Stress levels	Number of leaves (no plant⁻¹)				Leaf area (cm² plant⁻¹)				Leaf weight (g)				Specific leaf area (m² g⁻¹)			
	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP
S_0	20.5	18.5	22.0	25.0	197	1184	3695	3145	2.0	12.7	24.1	19.7	1.1	0.96	1.5	1.6
S_1	15.0	11.5	15.0	15.5	260	697	890	1268	2.4	7.6	9.5	8.5	1.0	0.92	0.94	1.5
S_2	8.5	8.0	12.0	11.0	192	523	704	995	2.2	5.0	6.1	7.6	0.89	1.1	1.2	1.3
S_3	5.5	4.0	6.5	7.5	437	363	348	724	2.0	4.4	3.2	3.3	2.2	0.83	1.1	2.3
F	**	**	**	**	NS	*	**	**	**	*	**	**	*	NS	**	*
LSD (0.05)	5.5	5.4	4.9	2.4	-	493	183	310	2.2	7.5	3.1	2.3	0.66	-	0.22	0.75
SEM±	1.4	1.4	1.3	0.61	65	126	47	79	0.55	1.9	0.78	0.58	0.17	0.06	0.05	0.19

* Significant at 5% level   ** Significant at 1% level   NS - Not significant

differences due to the effect of water stress. At 60 DAP, leaf area was significantly reduced in all the water stressed plants (S_1, S_2 and S_3). At 90 DAP, the influence of water stress was so severe that the leaf area reduced drastically and all the water stress levels were significantly different among each other.

4.4.1.6 Leaf weight

The leaf dry weight recorded for *P. marsupium* at different stages of growth are presented in Table 32. During the initial stage (30 DAP), there was no significant variations, but severely stressed (S_3) plants recorded significantly high value above all the other treatments. Water stress reduced the leaf height from 60 DAP onwards. At 60 DAP, though water stress reduced the leaf weight, S_1, S_2 and S_3 plants were on par. The leaf weight in moderately (S_2) and severely stressed (S_3) plants were significantly below the other plants at 90 DAP. A severe reduction in leaf weight due to water stress was also observed towards the end of the growth period (120 DAP).

4.4.1.7 Specific leaf area

The specific leaf area recorded for *P. marsupium* at different stages of growth in given in Table 32. At 30 DAP, water stress increased the specific leaf area of severely stressed (S_3) plants as compared to control. No significant variation was observed at 60 DAP. However, significant increase was observed in specific leaf area due to water stress at 120 DAP

whereas at 90 DAP water stress reduced the specific leaf area of the seedlings.

4.4.1.8 Shoot weight

The dry weight of shoot recorded for *P. marsupium* seedlings at different stages of growth are presented in Table 33. During the initial stages (30 DAP), significant variations was observed only for severely stressed (S_3) plants. From 60 DAP onwards, the shoot weight was decreased in all plants with increasing levels of water stress. At 60 and 90 DAP, shoot weight of all the water stressed plants (S_1, S_2 and S_3) were significantly below the control.

4.4.1.9 Root weight

The dry weight of root in *P. marsupium* seedlings at 30 DAP was reduced due to the effect of water stress levels of S_1 and S_2 (Table 33). At 60 and 90 DAP, root weight was significantly affected in all the water stressed plants. Moderately and severely stressed (S_2 and S_3) plants recorded significantly lower root weights than all the other treatments. At 120 DAP also, the same trend was repeated with highest value recorded in unstressed control and lowest in severely stressed (S_3) plants.

4.4.1.10 Root - shoot ratio

The root - shoot ratio in *P. marsupium* at different growth stages (Table 33) did not show significant variation among the treatments at any of

Table 33 Shoot weight, root weight, root/shoot ratio and total dry matter production in *P. marsupium* seedlings as affected by different levels of water stress

Stress levels	Shoot weight (g)				Root weight (g)				Root/shoot ratio				Total dry matter production (g)			
	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP
S_0	5.3	29.6	34.1	63.1	11.5	17.1	30.4	36.7	2.2	1.0	1.1	0.87	16.8	46.8	84.5	99.8
S_1	5.9	16.4	18.7	31.7	8.6	10.3	16.4	18.1	1.5	1.3	1.8	0.86	14.4	26.6	35.1	49.8
S_2	4.4	9.8	17.7	27.8	9.3	6.9	15.4	12.3	2.4	1.5	1.6	0.61	13.7	16.7	33.1	40.0
S_3	15.4	5.2	11.1	8.2	18.0	5.0	11.1	9.3	1.2	1.3	1.4	2.1	33.4	13.2	22.2	17.5
F	*	**	**	**	*	**	**	**	NS	NS	NS	*	*	**	**	**
LSD (0.05)	5.2	9.0	17.3	18.2	8.7	4.9	4.5	4.7	-	-	-	1.1	12.6	8.9	13.2	17.5
SEM±	1.3	2.3	4.4	4.6	2.2	1.2	1.2	1.2	0.41	0.35	0.43	0.29	3.2	2.3	3.4	4.5

* Significant at 5% level   ** Significant at 1% level   NS - Not significant

Table 34   Relative growth rate, net assimilation rate and relative water content of leaves of *P. marsupium* seedlings as affected by different levels of water stress

Stress levels	Relative Growth Rate (mg g^{-1} wk^{-1})			Net Assimilation Rate (mg cm^{-2} wk^{-1})			Relative Water Content (%)	
	30-60 DAP	60-90 DAP	90-120 DAP	30-60 DAP	60-90 DAP	90-120 DAP	0800 (hrs)	1400 (hrs)
S_0	10.3	6.1	3.6	0.31	0.11	0.10	51.43	59.28
S_1	5.6	5.4	2.8	0.16	0.08	0.08	50.89	55.83
S_2	4.3	4.0	2.9	0.09	0.09	0.07	58.36	46.02
S_3	4.0	3.8	2.0	0.05	0.06	0.06	52.59	35.32
F	*	*	**	*	*	**	NS	**
LSD (0.05)	3.5	1.6	0.48	0.14	0.06	0.03	-	6.97
SEM±	0.88	0.41	0.12	0.04	0.01	0.01	3.62	2.13

* Significant at 5% level   ** Significant at 1% level   NS - Not significant

the growth stages except at 120 DAP. At 120 DAP, severely stressed (S_3) plants were showing significantly higher values than all the other treatments.

4.4.1.11 Total dry matter production

The total dry matter production in *P. marsupium* seedlings did not varied significantly at 30 DAP (Table 33). From 60 DAP onwards, water stress significantly reduced the dry matter production. At 60 DAP, S_2 and S_3 plants recorded significantly lower values than other treatments. Total dry matter production was reduced significantly in severely stressed (S_3) plants at 120 DAP. S_1 and S_2 plants, though produced lower dry matter than control, were on par.

4.4.1.12 Relative Growth Rate (RGR)

The mean RGR of *P. marsupium* seedlings in response to water stress are given in Table 34. RGR showed significant reductions at all the stages of growth due to water stress. During 30-60 DAP, even mild water stress severely reduced the RGR of *P. marsupium* seedlings. Severe water stress (S3) reduced RGR much during all the stages of growth.

4.4.1.13 Net Assimilation Rate (NAR)

The mean values on the NAR for *P. marsupium* seedlings are given in Table 34. NAR was reduced significantly by water stress at all levels

during 30-60, 60-90 and 90-120 DAP intervals. Severe reductions were observed in severely stressed (S3) plants during the above mentioned growth stages.

4.4.2 Physiological parameters

4.4.2.1 Leaf Diffusive Resistance (LDR)

The mean leaf diffusive resistance as influenced by different levels of water stress in *P. marsupium* seedlings are presented in Table 35. The predawn LDR at the beginning of the stress (I DAS) itself varied significantly among the treatments. However, the midday measurements showed significant rise only in severely water stressed (S_1) plants. At the end of 3 days of water stress (S_1), plants showed significant rise in predawn and midday leaf diffusive resistance. Six days of water stress (S_2) induced significantly higher LDR as compared to the control and mildly stressed (S_1) plants both at 0800 and 1400 hrs. The values recorded through out the stress period for the moderately stressed plants were significantly above the other plants except for the measurement during 1400 hrs at 1 DAS. In the plants water stressed for nine days (S_3), the LDR at both predawn and midday LDR were above all the other plants.

The diurnal variations in the leaf diffusive resistance (LDR) of *P. marsupium* seedlings due to water stress is given in Fig. 11 and Appendix VI. The LDR showed a sharp decline from 0600 to 0800 hrs for

Table 35 Leaf diffusive resistance (m mol m^{-2} s^{-1}) in *P. marsupium* seedlings as affected by different levels of water stress through a nine day cycle

Stress levels	1 DAS		2 DAS		3 DAS		4 DAS		5 DAS	
	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)
S_0	2.94	7.36	2.57	6.47	2.94	7.41	2.75	6.40	2.63	6.33
S_1	4.24	6.48	3.69	5.65	3.98	11.95	4.41	3.94	3.90	6.56
S_2	7.05	8.06	4.72	11.60	4.96	19.94	9.94	30.67	14.75	45.23
S_3	5.33	10.19	4.77	12.53	5.68	17.06	7.40	20.37	8.96	41.19
F	**	**	**	**	**	**	**	**	**	**
LSD (0.05)	0.99	1.64	0.97	2.64	0.93	1.66	1.25	2.94	1.32	2.70
SEM±	0.33	0.55	0.32	0.88	0.31	0.56	0.41	0.98	0.44	0.90

Stress levels	6 DAS		7 DAS		8 DAS		9 DAS	
	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)
S_0	2.87	6.01	3.06	5.07	3.41	4.44	3.14	5.72
S_1	4.05	14.83	4.34	4.17	4.34	6.62	4.12	18.14
S_2	19.28	65.19	7.34	6.59	4.80	11.26	5.68	19.74
S_3	11.63	47.07	13.15	64.43	18.15	84.79	23.28	111.75
F	**	**	**	**	**	**	**	**
LSD (0.05)	1.43	3.46	1.32	1.91	1.18	2.93	2.11	7.85
SEM±	0.48	1.15	0.44	0.64	0.40	0.98	0.71	2.61

** Significant at 1% level   DAS Days after the beginning of stress

all the treatments. The values recorded for moderate (S_2) and severely (S_3) plants were above that of control (S_0) and mildly stressed (S_1) plants. A further decline was observed in S_0 and S_1 plants whereas S_2 and S_3 plants showed a rising trend in LDR after 0800 hrs. Values for control were more or less steady until 1600 hrs, which then rose. Mildly stressed (S_1) plants deviated from the control curve from 1000 hrs onwards owing to a rise in the diffusive resistance. Both S_2 and S_3 plants recorded maximum values at 1400 hrs wherein, S_3 plants showed a prominent peak. Between 1600 to 1800 hrs, the LDR in S_2 and S_3 plants decreased whereas in S_0 and S_1 plants, it increased.

4.4.2.2 Transpiration rate

The transpiration rate of *P. marsupium* seedlings recorded at 0800 and 1400 hrs are presented in Table 36. At the start of the water stress cycle (1 DAS), mildly stressed (S_1) plants showed significantly lower transpiration rate at 0800 hrs whereas the transpiration at 1400 hrs was on par with the control. After three days of water stress both predawn and midday transpiration rate of mildly stressed plants were significantly lower than that of control plants. Significant reduction in transpiration rates due to water stress was observed in both predawn and midday measurements of S_2 (water stressed for six days) plants during all the six days. Plants stressed for nine days (S_3) also exhibited a severe reduction in

Table 36 Transpiration rate ($\mu g\ H_2O\ cm^{-2}\ s^{-1}$) in *P. marsupium* seedlings as affected by different levels of water stress through a nine day cycle

Stress levels	1 DAS		2 DAS		3 DAS		4 DAS		5 DAS	
	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)
S_0	5.22	5.04	5.74	5.20	5.15	4.87	5.09	5.31	5.49	6.17
S_1	3.71	5.58	4.12	5.32	4.45	2.60	4.06	7.51	5.02	4.68
S_2	2.34	3.34	3.23	2.60	3.33	1.64	1.87	1.26	1.28	0.78
S_3	3.21	3.33	3.21	2.52	3.14	2.03	2.71	1.96	2.38	0.83
F	**	**	**	**	**	**	**	**	**	**
LSD (0.05)	0.90	1.05	0.82	0.96	0.54	0.47	0.59	0.39	0.54	0.32
SEM±	0.30	0.35	0.28	0.32	0.18	0.16	0.20	0.13	0.18	0.11

Stress levels	6 DAS		7 DAS		8 DAS		9 DAS	
	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)
S_0	6.00	6.71	5.62	7.25	5.28	8.62	5.51	7.14
S_1	4.44	2.41	3.90	7.94	4.44	4.82	4.47	2.38
S_2	0.91	0.39	2.60	5.47	3.33	2.61	3.20	1.67
S_3	1.81	0.75	1.44	0.40	0.95	0.54	0.73	0.24
F	**	**	**	**	**	**	**	**
LSD (0.05)	0.48	0.52	0.51	0.78	0.58	1.44	0.40	0.45
SEM±	0.16	0.17	0.17	0.26	0.19	0.48	0.13	0.15

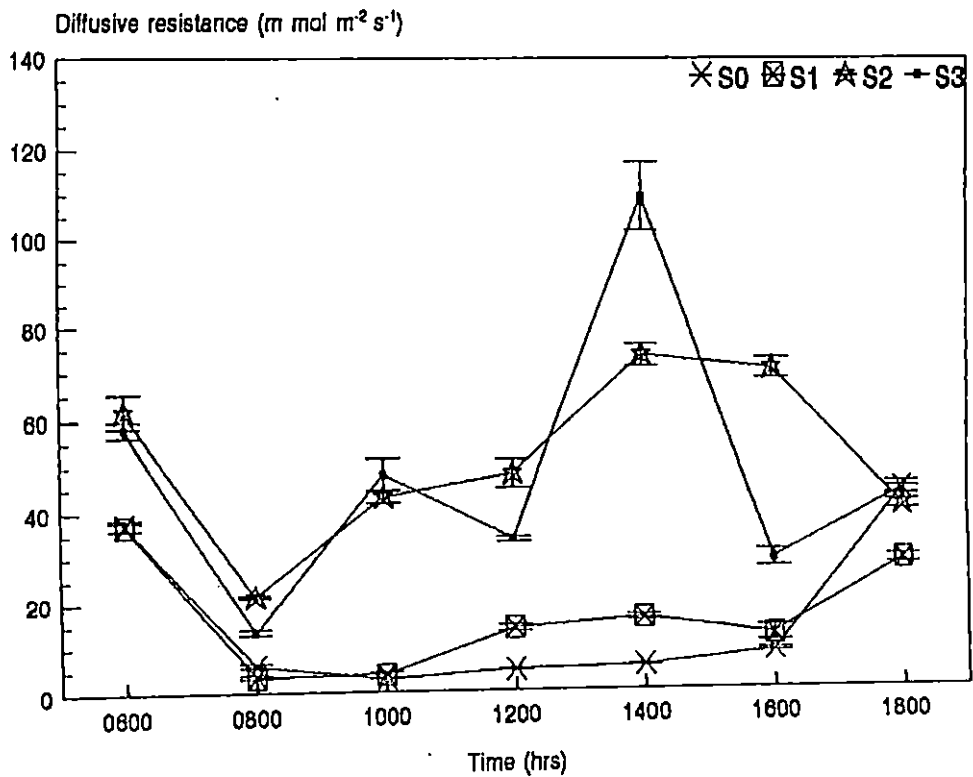** Significant at 1% level   DAS Days after the beginning of stress

Fig.11. Diurnal variations in the leaf diffusive resistance of *P. marsupium* seedlings as affected by different levels of water stress
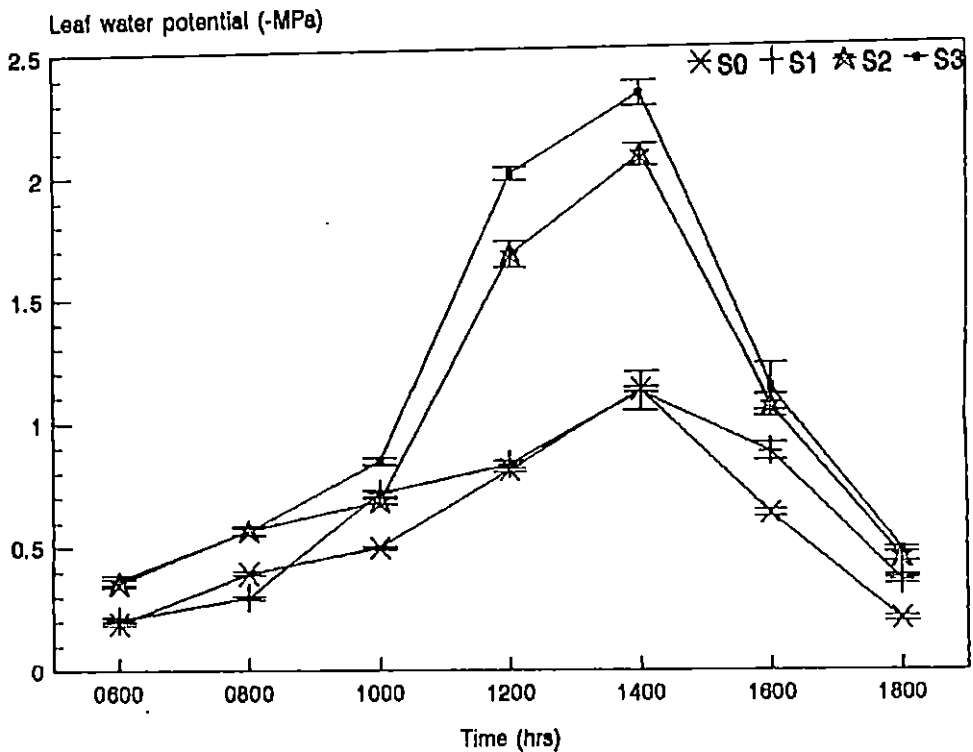
Fig.12. Diurnal variations in the leaf water potential of *P. marsupium* seedlings as affected by different levels of water stress

Table 37 Leaf temperature (°C) in *P. marsupium* seedlings as affected by different levels of water stress through a nine day cycle

Stress levels	1 DAS		2 DAS		3 DAS		4 DAS		5 DAS	
	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)
S_0	27.20	39.30	29.76	37.10	27.24	37.96	27.04	38.48	27.14	37.88
S_1	27.94	37.26	29.90	36.58	27.00	37.94	27.08	38.86	27.28	37.84
S_2	28.18	38.68	29.68	36.32	27.72	38.24	27.44	38.84	27.64	38.04
S_3	28.34	38.80	29.76	36.86	27.92	38.60	27.96	38.98	27.60	38.12
F	*	**	NS	*	**	**	**	*	*	*
LSD (0.05)	0.99	0.79	-	0.52	0.23	0.32	0.27	0.39	0.36	0.23
SEM±	0.33	0.26	0.10	0.17	0.18	0.11	0.09	0.13	0.12	0.08

Stress levels	6 DAS		7 DAS		8 DAS		9 DAS	
	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)
S_0	28.14	40.08	27.32	38.30	27.26	38.0	27.04	38.50
S_1	27.42	37.84	27.60	36.96	28.18	36.44	27.20	38.42
S_2	27.96	39.64	27.56	37.84	29.04	38.04	27.52	38.54
S_3	28.36	39.54	27.78	38.36	29.12	38.52	28.00	38.72
F	*	*	*	*	**	**	**	*
LSD (0.05)	0.63	0.97	0.33	0.90	0.56	0.61	0.30	0.20
SEM±	0.21	0.66	0.11	0.30	0.19	0.20	0.10	0.07

* Significant at 5% level ** Significant at 1% level NS - Not significant DAS Days after the begining of stress

transpiration as the days of stress increased. A severe reduction was noticed at the end of the cycle (9 DAS) which was significantly below all the other plants.

4.4.2.3 Leaf temperature

The leaf temperature observed in *P. marsupium* seedlings during the water stress are presented in Table 37. The predawn leaf temperature of water stressed plants (S_1, S_2 and S_3) at 1 DAS was found to be significantly above that of control. However, at 1400 hrs there was no significant variations, except for S_1 which recorded a slightly lower value. At 3 DAS, in mildly stressed (S_1) plants, the predawn leaf temperature were significantly below the control whereas the midday leaf temperatures were on par with control. The leaf temperatures were significantly lower in moderately stressed (S_2) plants at 6 DAS during both the measurements of the day. At the end of the stress cycle (9 DAS) severely stressed (S_3) plants recorded significantly higher leaf temperature than the control both at 0800 and 1400 hrs.

4.4.2.4 Leaf water potential

The variations in the leaf water potential (ψ) due to water stress in *P. marsupium* seedlings are shown in Fig. 12 and Appendix VI. The ψ of control (S_0) and mildly stressed (S_1) plants did not vary much and the pattern of variations were similar. In the case of moderately and severely stressed (S_2 and S_3) plants, the ψ declined steeply from 1000 hrs onwards with

Net photosynthesis (μ mol cm⁻² s⁻¹)
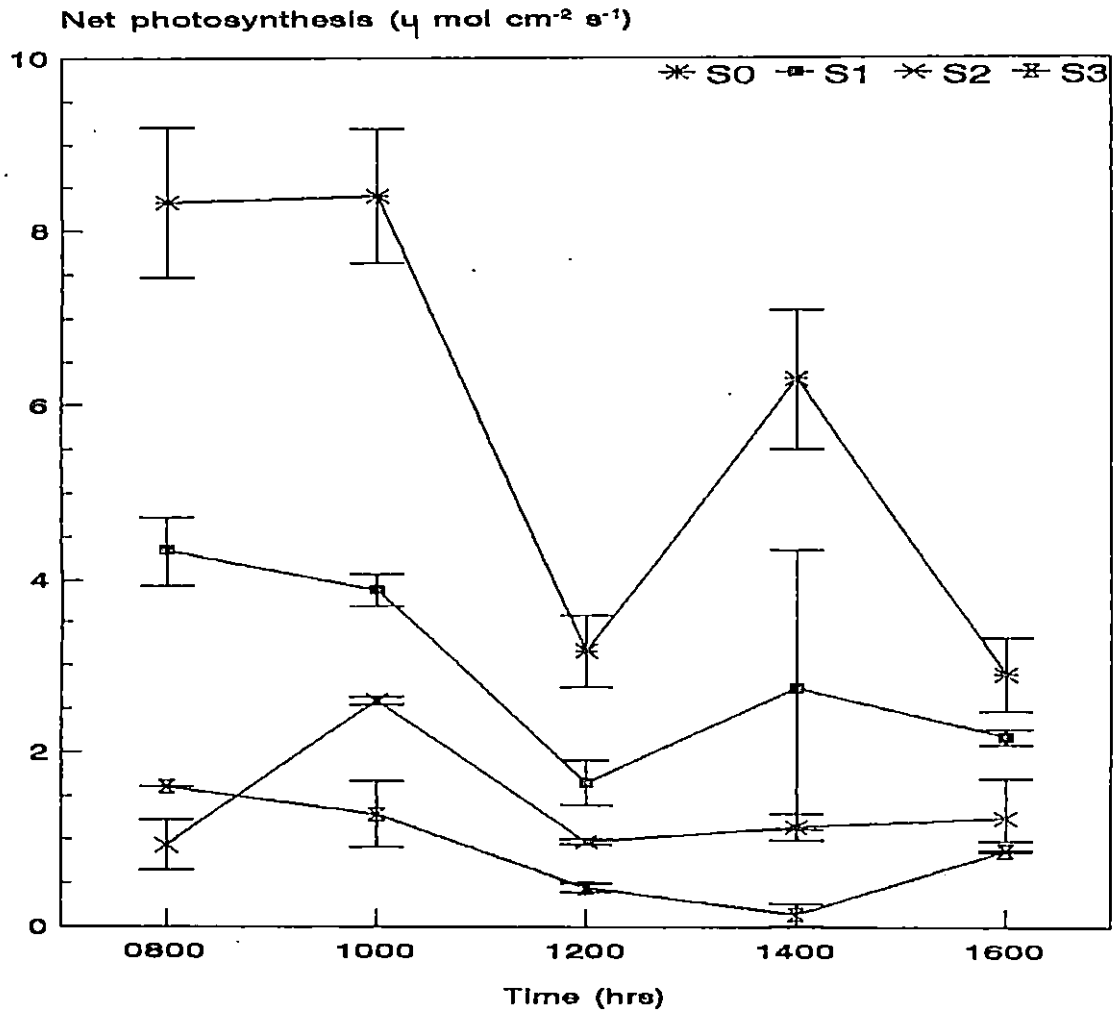
Fig.13. Diurnal variations in the net photosynthesis of *P. marsupium* seedlings as affected by different levels of water stress

minimum ψ recorded at 1400 hrs. The variations from 1000 to 1600 hrs in severely stressed plants were prominent when compared to the control.

4.4.2.5 Relative water content (RWC)

The data on relative water content, in the leaves of *P. marsupium* seedlings experiencing water stress at different levels are given in Table 34. There was no significant variation in RWC among the treatments at 0800 hrs. At 1400 hrs, severely stressed (S_2 and S_3) plants showed significantly lower RWC when compared to control. The lowest relative water content was observed in severely stressed (S_3) seedlings.

4.4.2.6 Net photosynthesis

The diurnal variations in the net photosynthesis of *P. marsupium* seedlings experiencing water stress at different levels are given in Fig. 13. The control plants recorded maximum photosynthesis with a prominent decline at 1200 hrs. This decline was observed in the water stressed plants also. Moderately (S_2) and severely stressed (S_3) plants were similar in the pattern of variations with values lower than control and mildly stressed (S_1) plants. The variations in S_1 plants was more like that of control, with a slight increase in the net photosynthesis at 1400 hrs which then declined by evening hours.

4.4.3 Biochemical attributes

4.4.3.1 Chlorophyll content

The chlorophyll 'a', chlorophyll 'b' and total chlorophyll content in the leaves of *P. marsupium* seedlings experiencing stress at different levels are shown in Table 38. Water stress significantly reduced the chlorophyll 'a' content in the leaves. However S_1 and S_2 plants were on par. The severely stressed (S_3) plants showed significantly lower value as compared to plants in other treatments. The same trend was observed in the case of chlorophyll 'b' and total chlorophyll. The highest value was recorded by the control and lowest by the severely stressed (S_3) plants.

4.4.3.2 Proline content

Proline content in the fresh leaves of *P. marsupium* as influenced by different levels of water stress are given in Table 38. Water stress increased proline content in the leaves of all the plants. There was a proportionate increase in the proline content with increase in the levels of water stress. All the treatments were significantly different among themselves.

4.4.3.3 Soluble protein

The soluble protein contents in the leaves of *P. marsupium* seedlings were significantly influenced by the water stress treatments (Table 38). Soluble protein content were lower than control in all the water stressed

Table 38 Biochemical attributes of *P. marsupium* seedlings as affected by different levels of water stress at the end of the growth period

Stress levels	Chlorophyll 'a' (mg g^{-1})	Chlorophyll 'b' (mg g^{-1})	Total Chlorophyll (mg g^{-1})	Proline (μg g^{-1})	Soluble protein (mg g^{-1})
S_0	1.00	0.19	1.20	5.49	4.70
S_1	0.92	0.13	1.04	6.34	4.58
S_2	0.85	0.12	0.97	7.30	4.53
S_3	0.49	0.05	0.54	8.09	4.42
F	**	**	**	**	**
LSD (0.05)	0.08	0.06	0.11	0.20	0.06
SEM±	0.02	0.02	0.03	0.06	0.02

** Significant at 1% level

Table 39   Inter-correlation matrix of total dry matter production and other plant characters in *P. marsupium*

Character	LA	LW	CD	SW	RW	RSR	SLA	TDMP
LN	0.688**	0.707**	0.499*	0.664**	0.705**	-0.154	-0.136	0.694**
LA		0.961**	0.866**	0.936**	0.879**	-0.421	0.185	0.941**
LW			0.823**	0.917**	0.829**	-0.440	0.289	0.911**
CD				0.893**	0.841**	0.517*	0.094	0.898**
SW					0.889**	-0.593**	0.119	0.988**
RW						-0.311	0.015	0.949**
RSR							-0.307	-0.514*
SLA								0.087

* Significant at 1% level   ** Significant at 0.1% level   LA   - Leaf area
RW   -   Root weight   LW   - Leaf weight   RSR   -   Root shoot ratio
SW   -   Shoot weight   CD   - Collar diameter   TDMP   -   Total drymatter production
SLA   -   Specific leaf area

Table 40   Inter-correlation matrix of net photosynthesis and other physiological parameters in *P. marsupium*

Characters	LT	CON	TRN	CIN	NP
QNT	0.878**	-0.127	0.433*	-0.138	0.267
LT		-0.297	0.184	-0.153	-0.075
CON			0.478*	0.176	0.516**
TRN				-0.053	0.844**
CIN					0.023

* Significant at 1% level   ** Significant at 0.1% level   LT - Leaf temperature   CON - Conductance
CIN - Internal CO_2 QNT - Quantum influx   NP - Net photosynthesis   TRN - Transpiration

plants, with the lowest content in severely stressed (S_3) plants. However, S_1 and S_2 plants were on par.

4.5 *Tectona grandis* (Teak)

4.5.1 Growth attributes

4.5.1.1 Plant height

The plant height of *Tectona grandis* seedlings at 30, 60, 90 and 120 DAP are presented in Table 41. Water stress significantly reduced the plant height at 60 DAP in mild (S_1) and moderately (S_2) stressed plants. However, the observations on severely stressed plants could not be taken as the plants dried up consequent with water stress after six days. Both at 90 and 120 DAP also, plant height was reduced significantly by water stress with drastic reductions in moderately stressed (S_2) plants.

4.5.1.2 Rooting depth

The rooting depth of *T. grandis* seedlings at different growth stages as affected by water stress are presented in Table 41. There was no significant variation in the rooting depth of the seedlings due to water stress upto moderate level at any of the growth stages.

4.5.1.3 Collar diameter

The collar diameter of *T. grandis* as affected by different levels of water stress are presented in Table 41. There were significant difference

Plate 5   One year old *P. marsupium* seedlings grown under
          different   levels of water stress for 90 days

Plate 6   One year old *T. grandis* seedlings grown under
          different   levels of water stress for 90 days

Table 41 Plant height, rooting depth and collar diameter of *T. grandis* seedlings as affected by different levels of water stress

Stress levels	Plant height (cm)				Rooting depth (cm)				Collar diameter (mm)			
	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP
S_0	73.8	91.3	67.8	73.8	43.3	44.8	56.8	59.3	12.4	14.7	15.2	15.1
S_1	63.8	55.3	53.5	59.3	47.8	44.5	46.5	56.0	10.6	12.8	12.1	13.4
S_2	63.3	49.9	47.0	48.4	56.8	46.4	46.5	57.3	9.7	12.0	11.3	11.0
S_3	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR
F	NS	**	*	*	NS	NS	NS	NS	*	**	*	*
LSD (0.05)	-	9.3	15.6	13.8	-	-	-	-	2.4	0.93	1.9	1.7
SEM±	22.3	2.4	8.0	6.7	5.8	1.2	7.1	6.2	1.7	0.24	1.1	0.81

* Significant at 5% level   ** Significant at 1% level   NS - Not significant

NR - Not recorded as the S_3 plants dried off when water stress was continued for more than six days

due to the effect of water stress. During the initial stage itself (30 DAP), mild (S_1) and moderate (S_2) water stress reduced the collar diameter of the seedlings. A similar effect was observed during 60, 90 and 120 DAP also. Moderately water stressed (S_2) plants recorded the minimum values.

4.5.1.4 Number of leaves

The number of leaves per plant as influenced by water stress at different stages of growth in *T. grandis* seedlings are shown in Table 42. Water stress significantly reduced the number of leaves in mild and moderately stressed plants at 30, 60 and 120 DAP. At 90 DAP, though water stress reduced the number of leaves in moderately stressed (S_2) plants, mildly stressed plants were on par with the control. The intensity of reduction increased with age and the maximum reduction in the number of leaves was observed during 120 DAP.

4.5.1.5 Leaf Area

Water stress reduced the leaf area significantly in *T. grandis* (Table 42), at all the stages of growth. The reduction in leaf area was severe even at moderate water stress.

4.5.1.6 Leaf weight

The leaf dry weight observed in *T. grandis* seedlings at different stages of growth are given in Table 42. There were significant variation among the

Table 42   Number of leaves, leaf area, leaf weight and specific leaf area of *T. grandis* seedling as affected by different levels of water stress

Stress levels	Number of leaves (no plant⁻¹)				Leaf area (cm² plant⁻¹)				Leaf weight (g)				Specific leaf area (m² g⁻¹)			
	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP
S_0	18.0	25.0	20.0	32.0	3869	3020	2726	3706	33.1	29.5	24.5	23.2	1.2	1.0	1.1	1.6
S_1	12.0	14.0	17.5	14.5	2445	1870	1865	2912	21.1	16.3	16.3	20.4	1.2	1.2	1.2	1.4
S_2	7.0	10.0	8.5	8.0	1620	1301	1266	1753	13.9	9.4	7.9	13.1	1.2	1.4	1.6	1.4
S_3	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR
F	*	**	**	**	*	**	**	**	**	**	**	**	NS	NS	**	**
LSD (0.05)	7.7	5.2	3.8	2.4	1180	241	175	118	7.3	4.7	3.4	0.82	-	-	0.30	0.07
SEM±	2.0	1.3	0.97	0.61	300	61	44	30	1.9	1.2	0.86	0.21	0.14	0.11	0.08	0.02

* Significant at 5% level   ** Significant at 1% level   NS - Not significant

NR - Not recorded as the S_3 plants dried off when water stress was continued for more than six days

treatment at all the different growth stages. Water stress at moderate levels reduced the leaf weight severely in moderately stressed plants. At 120 DAP, the leaf weight was reduced from 23.2 g in control plants to 13.1 g in moderately stressed plants.

4.5.1.7 Specific leaf area

The specific leaf area of *T. grandis* seedlings as influenced by different levels of water stress are shown in Table 42. At 30 and 60 DAP, no significant variation was observed in specific leaf area due to water stress. At 90 DAP, water stress significantly increased the specific leaf area of moderately stressed (S_2) plants above control, whereas at 120 DAP, a significant decrease in specific leaf area was observed both in mild and moderately stressed plants.

4.5.1.8 Shoot weight

The shoot dry weight recorded for *T. grandis* at different stages of growth as affected by different levels of water stress are given in Table 43. The shoot weight was reduced significantly in mild and moderately stressed plants at 30 and 60 DAP due to water stress. During 90 and 120 DAP, only moderately stressed (S_2) plants showed significant reduction in shoot weight as compared to control. At all the different stages of growth, reduction in shoot weight of moderately stressed plants were severe.

4.5.1.9 Root weight

The root dry weight of *T. grandis* seedlings grown under different water stress levels are presented in Table 43. There were significant variations in the root dry weight of *T. grandis* during different stages of growth. At 30 DAP, though the root weight was reduced in water stressed plants, mild and moderately stressed plants were on par. At 60, 90 and 120 DAP, mild and moderate water stress reduced the root weight that, the plants were significantly different among each other. At 90 and 120 DAP, severe reductions were observed in root weight of moderately stressed plants.

4.5.1.10 Root - Shoot ratio

The root - shoot weight ratios of *T. grandis* seedlings grown under different levels of water stress are shown in Table 43. There was a significant increase in the root - shoot ratio in mild and moderately stressed plants at 30 and 60 DAP itself. However, at 90 DAP, moderately stressed plants (S_2) showed an increase. A reverse trend was observed at 120 DAP. The root- shoot ratio of control plants were higher than that of the water stressed plants at 120 DAP. Nevertheless, the variations at 120 DAP were not significant.

4.5.1.11 Total dry matter production

The mean values on the total dry matter production of *T. grandis* seedlings grown under different levels of water stress are given in Table 43.

Table 43   Shoot weight, root weight, root/shoot ratio and total dry matter production in *T. grandis* seedlings as affected by different levels of water stress

Stress levels	Shoot weight (g)				Root weight (g)				Root/shoot ratio				Total dry matter production (g)			
	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP	30 DAP	60 DAP	90 DAP	120 DAP
S_0	63.9	61.7	39.9	43.9	67.7	56.4	65.8	58.1	1.1	1.8	4.3	2.7	131.5	118.1	105.6	102.0
S_1	39.5	41.0	36.0	44.1	56.0	52.0	37.6	44.9	1.4	2.1	1.9	1.9	95.5	93.1	73.5	89.4
S_2	30.7	25.1	19.0	28.5	55.8	46.5	31.8	32.1	1.8	3.0	2.9	2.1	86.5	71.6	50.9	60.6
S_3	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR
F	*	**	*	*	*	**	**	**	*	**	*	NS	*	**	**	*
LSD (0.05)	15.9	7.3	13.9	11.9	6.1	4.2	5.8	10.9	0.49	0.51	1.4	-	19.8	7.6	19.5	21.7
SEM±	4.0	1.9	3.5	3.0	1.6	1.1	1.5	2.8	0.12	0.13	0.36	0.30	5.0	1.9	5.0	5.5

* Significant at 5% level   ** Significant at 1% level   NS - Not significant

NR - Not recorded as the S_3 plants dried off when water stress was continued for more than six days

Table 44 Relative growth rate, net assimilation rate and relative water content of leaves of *T. grandis* seedlings as affected by different levels of water stress

Stress levels	Relative Growth Rate $(mg\ g^{-1} wk^{-1})$			Net Assimilation Rate $(mg\ cm^{-2}\ wk^{-1})$			Relative Water Content (%)	
	30-60 DAP	60-90 DAP	90-120 DAP	30-60 DAP	60-90 DAP	90-120 DAP	0800 (hrs)	1400 (hrs)
S_0	0.77	0.60	0.65	0.15	0.10	0.07	91.87	81.48
S_1	0.25	0.23	0.19	0.01	0.02	0.002	81.42	72.08
S_2	0.19	0.22	0.16	0.01	0.01	0.002	79.02	60.94
S_3	NR	NR	NR	NR	NR	NR	NR	NR
F	**	*	**	**	**	**	*	**
LSD (0.05)	0.08	0.26	0.18	0.03	0.03	0.03	9.50	9.73
SEM±	0.02	0.07	0.05	0.01	0.01	0.01	2.90	2.98

* Significant at 5% level   ** Significant at 1% level

NR - Not recorded as the S_3 plants dried off when water stress was continued for more than six days

The influence of water stress was found significant during the different stages of growth. During the initial stage itself (30 DAP), water stress significantly reduced the total dry matter production in mild and moderately stressed plants. The same trend was observed during 60 and 90 DAP also. At 120 DAP also the same trend was observed even the reduction in total dry matter production at mild-water stress was not significant.

4.5.1.12 Relative Growth Rate (RGR)

The relative growth rate (RGR) of *T. grandis* seedlings as affected by different levels of water stress are given in Table 44. During all the growth intervals (30-60, 60-90 and 90-120 DAP), mild and moderate water stress reduced the RGR. The reductions were severe at moderate levels of water stress as compared to control.

4.5.1.13 Net Assimilation Rate (NAR)

The mean values on net assimilation rate (NAR) of *T. grandis* seedlings are given in Table 44. Water stress at both mild and moderate levels reduced the NAR significantly during all the growth stages with severe reduction observed in moderately stressed plants. .

4.5.2 Physiological parameters

4.5.2.1 Leaf Diffusive Resistance (LDR)

The leaf diffusive resistance of *T. grandis* seedlings as affected by different levels of water stress are presented in Table 45. In the case of

Table 45   Leaf diffusive resistance (m mol m^{-2} s^{-1}) in *T. grandis* seedlings as affected by different levels   of water stress through a nine day cycle

Stress levels	1 DAS		2 DAS		3 DAS		4 DAS		5 DAS		6 DAS	
	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)
S_0	2.20	3.20	3.09	3.43	3.32	3.01	4.64	5.30	4.75	4.03	4.65	3.89
S_1	3.05	3.16	2.94	3.51	2.91	6.38	3.91	28.11	5.39	3.81	5.34	5.15
S_2	2.46	2.61	3.02	3.45	2.72	5.57	3.35	43.28	5.45	33.09	9.62	35.36
S_3	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR
F	*	*	NS	NS	NS	*	NS	**	*	**	**	**
LSD (0.05)	0.67	1.37	-	-	-	2.71	-	13.58	2.46	7.57	3.28	4.51
SEM±	0.22	0.46	0.22	0.51	0.29	0.91	0.91	4.57	0.82	2.52	1.19	1.50

*Significant at 5% level   ** Significant at 1% level   NS - Not significant   DAS   Days after the beginning of stress

NR - Not recorded as the S_3 plants dried off when water stress was continued for more than six days

S_1 plants (with 3 days water stress), though there was no significant variation in the predawn LDR measurements, midday values were significantly above the control plants. Plants water stressed for six days (S_2) showed significant variations in LDR as compared to control. Water stress significantly increased both the predawn and midday LDR values over control in moderately stressed (S_2) plants at 6 DAS.

The diurnal variations in the leaf diffusive resistance of *T. grandis* seedlings experiencing stress at different levels are given in Fig. 14 and Appendix VII. There was a decline in the LDR values from 0600 to 0800 hrs irrespective of the water stress levels. Plants under the control did not show significant variation in LDR from 0800 to 1600 hrs, which then increased with the sunset. Pattern of variation in mild (S_1) and moderately (S_2) stressed plants were similar but the values showed significant increase as compared to control. Leaf diffusive resistance showed a sharp rise from 1000 hrs onwards with maximum values at 1400 hrs. In both the treatments (S_1 and S_2), a prominent decline in LDR was observed at 1600 hrs which then increased towards dusk.

4.5.2.2 Transpiration rate

The transpiration rate recorded for *T. grandis* seedlings during the water stress cycle are given in Table 46. At 1 DAS, there was no significant variation in the predawn transpiration rates. Midday transpiration rates of

Table 46　Transpiration (μg H_2O cm^{-2} s^{-1}) in *T. grandis* seedlings as affected by different levels of water stress through a nine day cycle

Stress levels	1 DAS		2 DAS		3 DAS		4 DAS		5 DAS		6 DAS	
	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)
S_0	4.15	6.17	5.10	5.60	2.91	6.08	2.04	4.79	2.66	5.31	2.59	5.62
S_1	3.60	6.24	3.53	6.04	3.25	3.71	3.01	0.92	2.71	6.07	2.60	4.65
S_2	3.81	6.89	3.40	5.44	3.74	4.50	2.24	0.41	1.54	0.70	1.47	0.58
S_3	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR
F	NS	*	NS	NS	NS	*	NS	**	*	**	*	**
LSD (0.05)	-	1.90	-	-	-	1.67	-	1.61	1.02	1.79	0.92	2.43
SEM±	0.45	0.63	0.97	0.71	0.36	0.56	0.53	0.54	0.34	0.60	0.31	0.81

*Significant at 5% level　** Significant at 1% level　NS - Not significant　DAS　Days after the beginning of stress

NR - Not recorded as the S_3 plants dried off when water stress was continued for more than six days

Table 47 Leaf temperature (°C) in *T. grandis* seedlings as affected by different levels of water stress through a nine day cycle

Stress levels	1 DAS		2 DAS		3 DAS		4 DAS		5 DAS		6 DAS	
	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)	0800 (hrs)	1400 (hrs)
S_0	26.4	32.0	25.7	30.7	26.2	31.7	25.5	32.1	24.8	31.6	25.5	31.1
S_1	26.6	32.1	25.7	30.8	26.3	32.0	25.5	32.4	24.8	31.6	25.5	31.1
S_2	26.6	32.2	25.8	31.1	26.2	32.5	20.5	32.2	24.8	31.8	25.7	31.3
S_3	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR
F	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
LSD (0.05)	-	-	-	-	-	-	-	-	-	-	-	-
SEM±	0.19	0.18	0.21	0.23	0.18	0.28	2.57	0.35	0.10	1.60	0.19	0.32

NS - Not significant   DAS Days after the beginning of stress

NR - Not recorded as the S_3 plants dried off when water stress was continued for more than six days
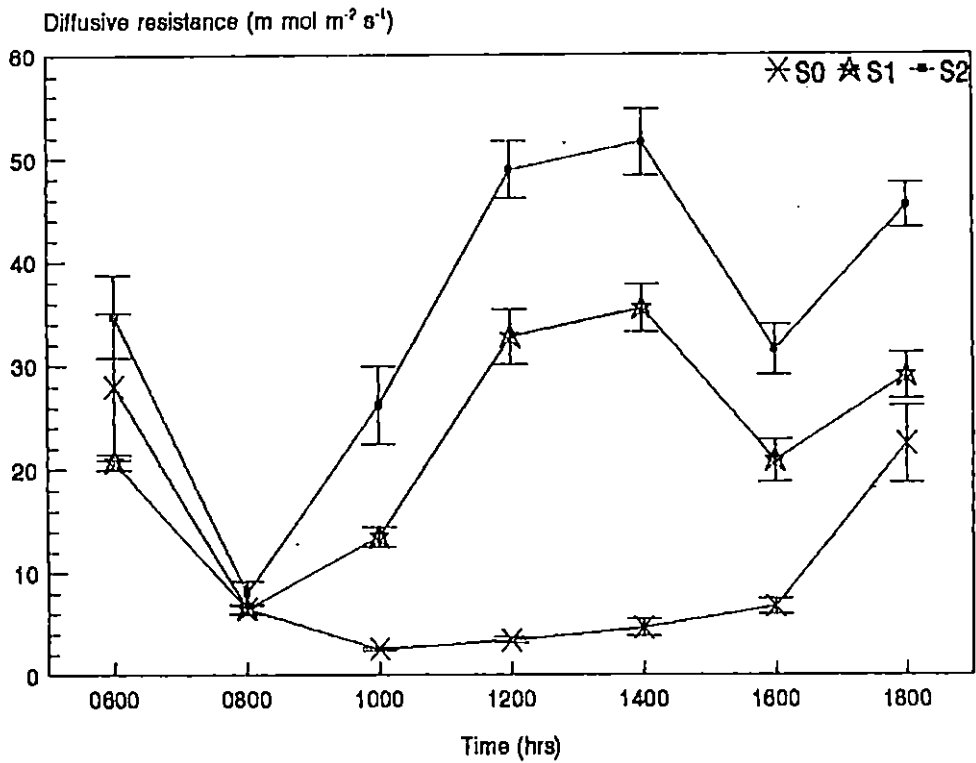
Fig.14. Diurnal variations in the leaf diffusive resistance of *T. grandis* seedlings as affected by different levels of water stress
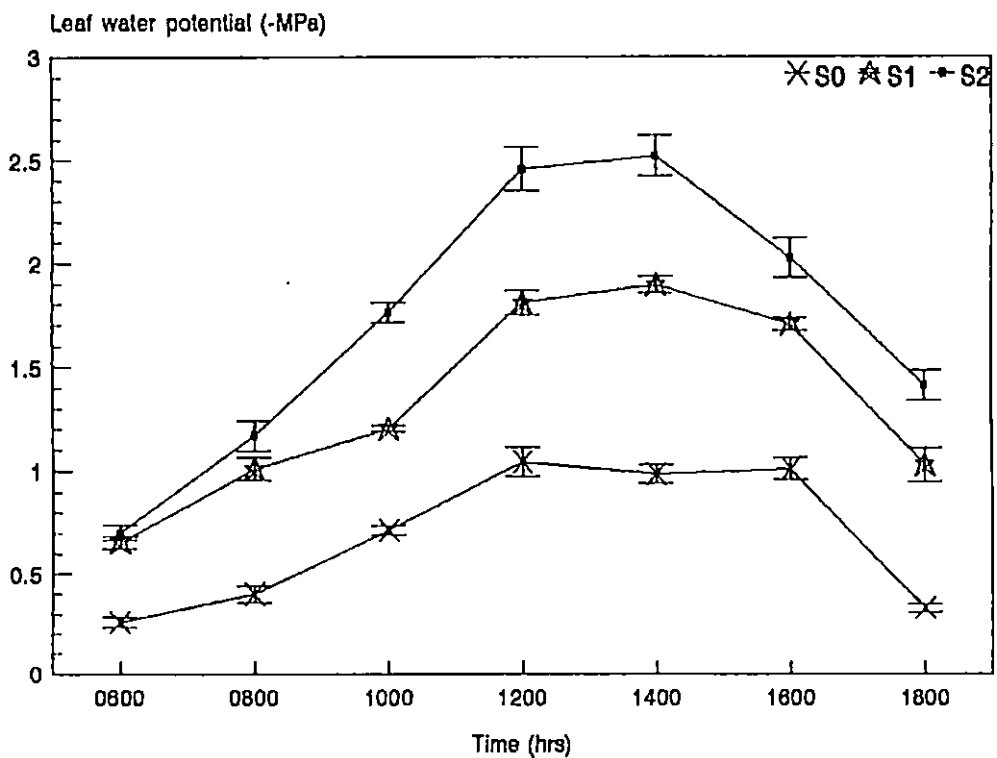

Fig.15. Diurnal variations in the leaf water potential of *T. grandis* seedlings as affected by different levels of water stress

mildly stressed plants were significantly reduced below control at 3 DAS. Transpiration rate at both 0800 and 1400 hrs were significantly lower in plants water stressed for six days (S_2) at six DAS.

4.5.2.3 Leaf temperature

The leaf temperature recorded for *T. grandis* seedlings in respect to different water stress cycles are given in Table 47. There was no significant variations in the leaf temperature observed due to the effect of water stress during any of the days.

4.5.2.4 Leaf water potential

The diurnal variations in the leaf water potential (ψ) of *T. grandis* seedlings experiencing water stress at different levels are given in Fig. 15 and Appendix VII. The pattern of variation in ψ was similar in all the treatments with maximum values recorded by control and minimum, by the moderately stressed (S_2) plants. Mild and moderately stressed (S_1 and S_2) plants were well below that of control with minimum of 2.5 MPa recorded during 1400 hrs in S_2 plants. A rise in the leaf water potential (ψ) towards the evening hours was observed in all the plants.

4.5.2.5 Relative water content

The relative water content in the leaves of *T. grandis* seedlings exposed to different water stress levels are given in Table 44. The relative water

Table 48   Inter-correlation matrix of total dry matter production and other plant characters in *T. grandis*

Character	LA	LW	CD	SW	RW	RSR	SLA	TDMP
LN	0.727**	0.653**	0.802**	0.617**	0.494*	0.104	0.565**	0.609**
LA		0.878**	0.504*	0.776**	0.619**	-0.238	0.796**	0.766*
LW			0.480*	0.928**	0.739**	-0.313	0.839**	0.916**
CD				0.468*	0.395	0.388	0.401	0.472*
SW					0.688**	-0.488*	0.678**	0.933**
RW						-0.089	0.338	0.904**
RSR							-0.201	-0.333
SLA								0.569**

* Significant at 1% level   ** Significant at 0.1% level   LA   - Leaf area
RW   -   Root weight   LW   - Leaf weight   RSR   -   Root shoot ratio
SW   -   Shoot weight   CD   - Collar diameter   TDMP - Total drymatter production
SLA   - Specific leaf area

Net photosynthesis (μ mol cm^{-2} s^{-1})

✳ S0 ✳ S1 ✳ S2

Time (hrs)
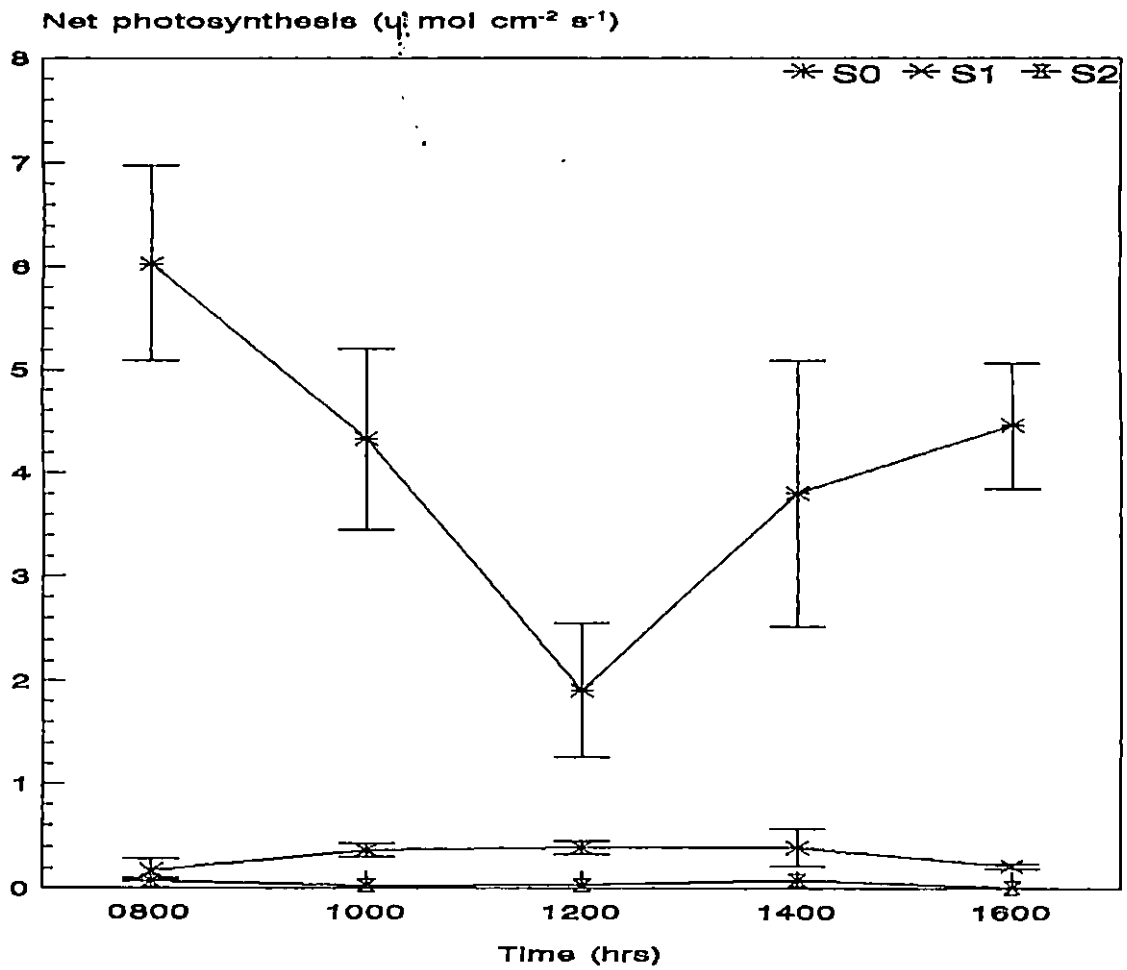
Fig.16. Diurnal variations in the net photosynthesis of *T. grandis* seedlings as affected by different levels of water stress

content in mild and moderately stressed (S_1 and S_2) plants were below that of control during both 0800 and 1400 hrs.

4.5.2.6 Net photosynthesis

The diurnal variation in the net photosynthesis from 0800 to 1600 hrs in *T. grandis* seedlings are shown in Fig. 16. Throughout the day net photosynthesis recorded in control plants was higher than that recorded in water stressed plants. A midday decline was observed at 1200 hrs in the control plants. The net photosynthesis in mild and moderately (S_1 and S_2) plants were negligible and photosynthesis with S_2 plants during most of the day were zero.

4.6 Anatomical characters

The anatomical characters of the leaves of the different species grown under different levels of water stress are shown in Plates 7 to 18. Leaves of *A. triphysa* grown under water stress showed progressive degeneration of palisade layers. A deterioration of chlorophyll pigments could also be observed as the levels of water stress increased. There was an increase in the amount of mechanical tissues like collenchyma, sclerenchyma and xylem elements.

Plate 7   Cross section of *A. triphysa* leaf grown under
           three day water stress cycle (x 100)

Plate 8   Cross section of *A. triphysa* leaf grown under
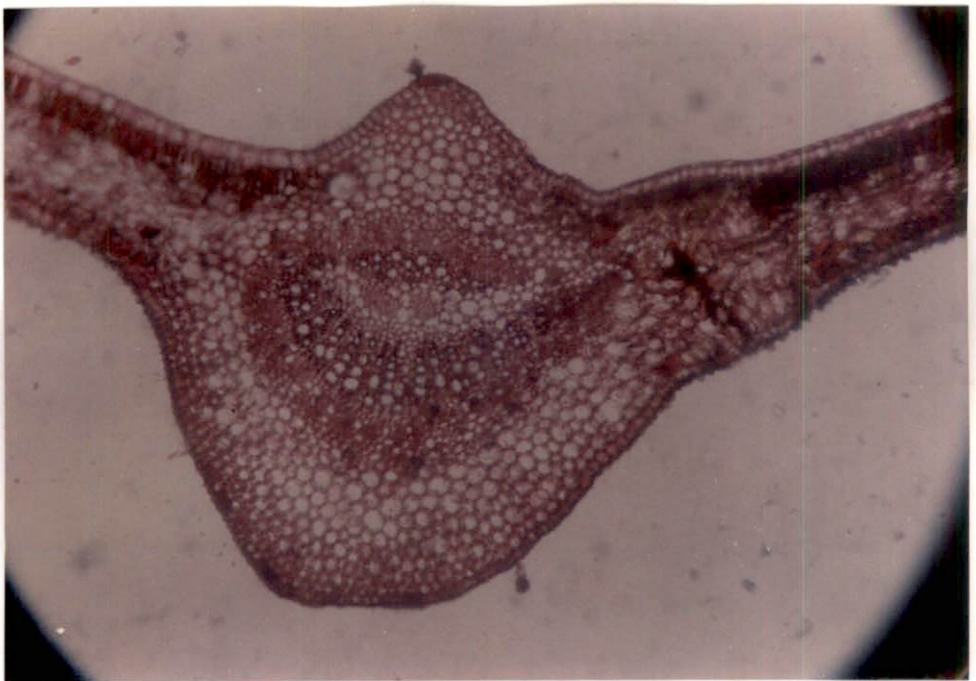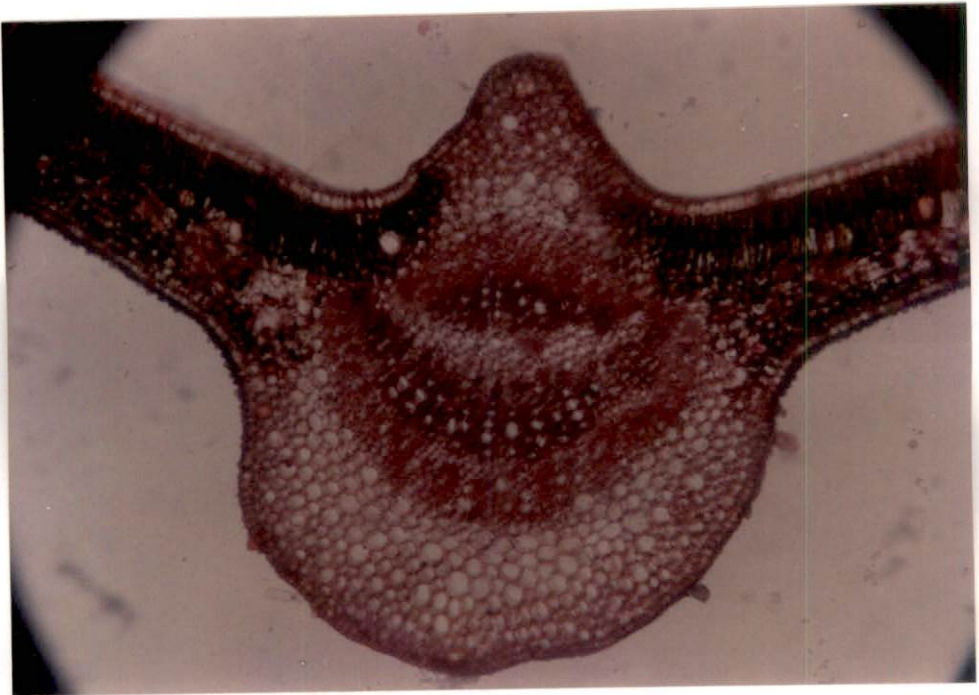   six day water stress cycle (x 100)

Plate 9 Cross section of *A. mangium* leaf grown under well watered (control) condition (x 100)

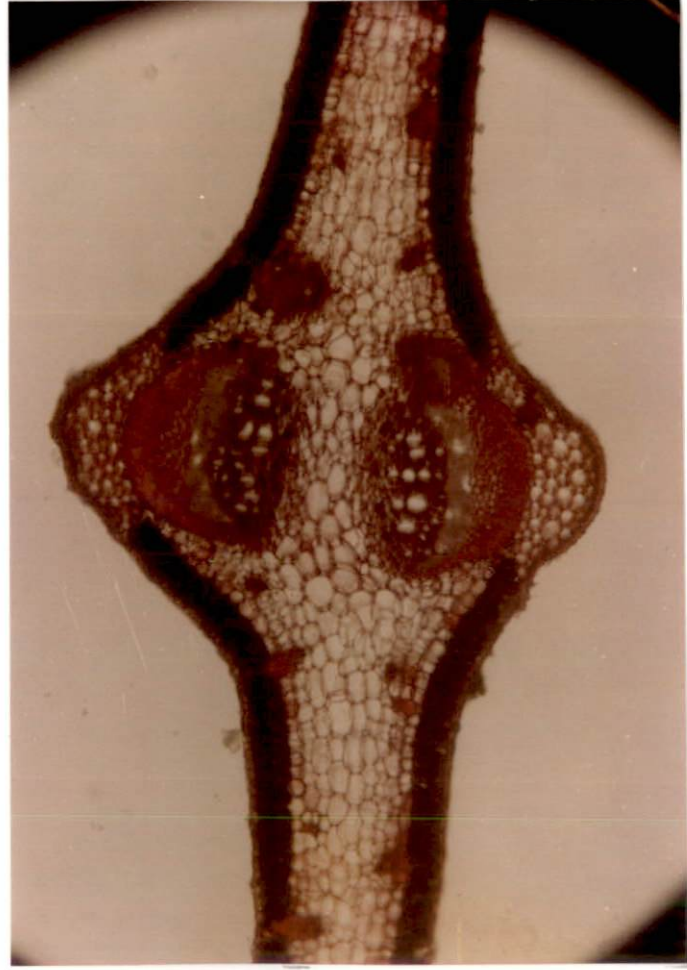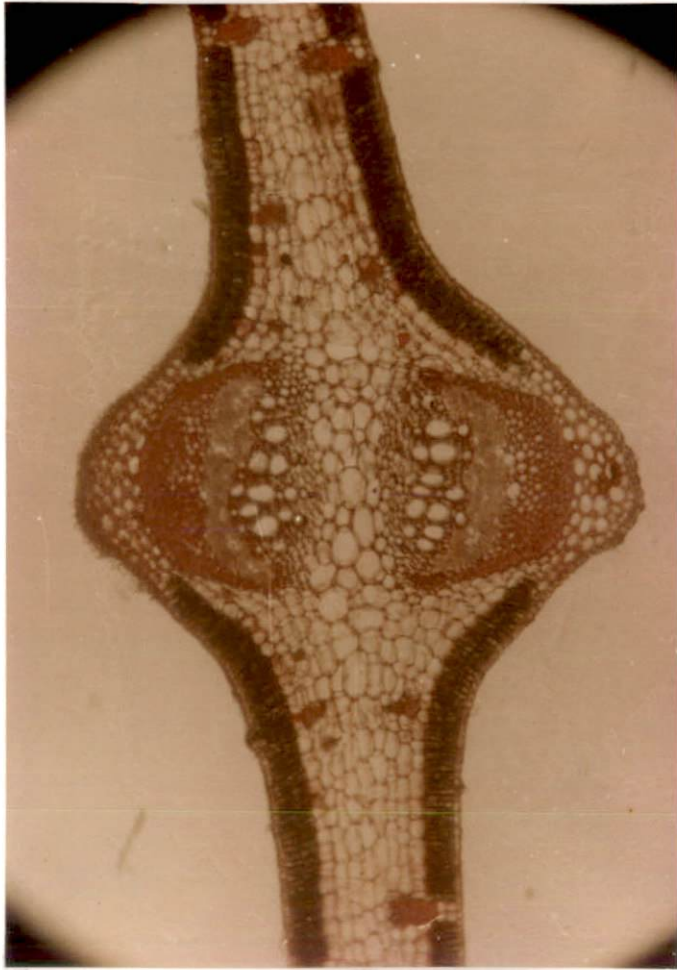Plate 10 Cross section of *A. mangium* leaf grown under nine day water stress cycle (x 100)

Plate 11   Cross section of *S. macrophylla* leaf grown
             under well watered condition (x 100)

Plate 12   Cross section of *S. macrophylla* leaf grown
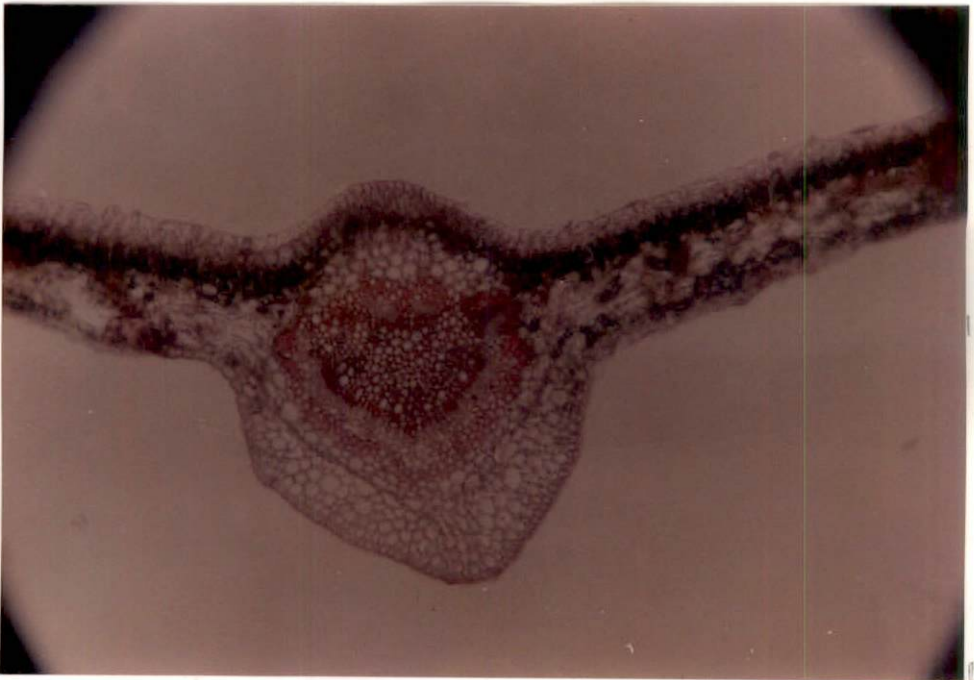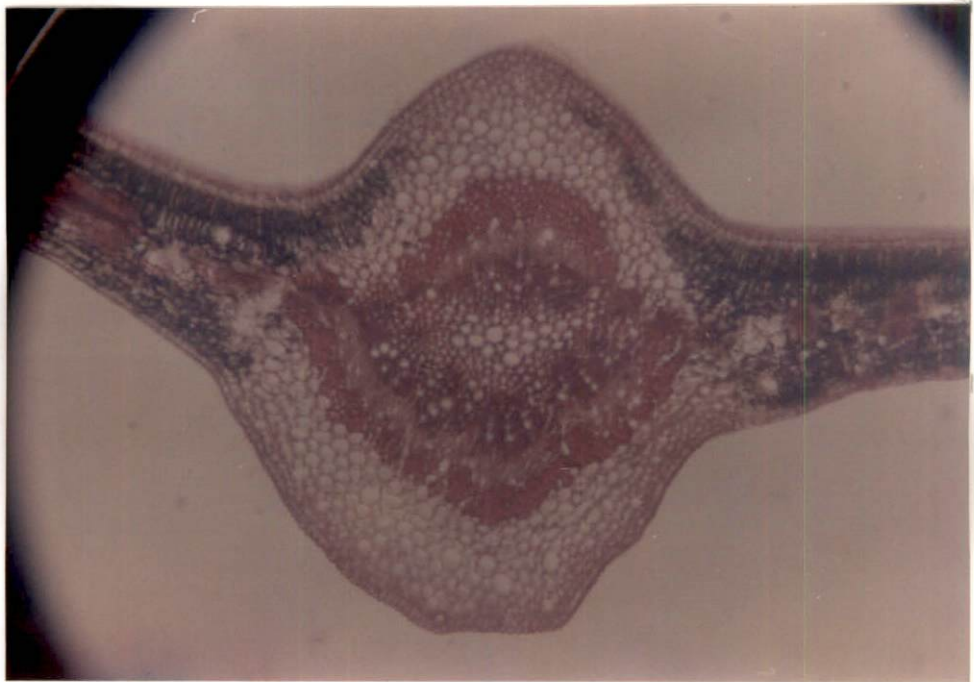   under nine day water stress cycle (x 100)

Plate 13   Cross section of *S. macrophylla* leaf grown
            under well watered condition (x 450)

Plate 14   Cross section of *S. macrophylla* leaf grown
            under nine day water stress cycle (x 450)
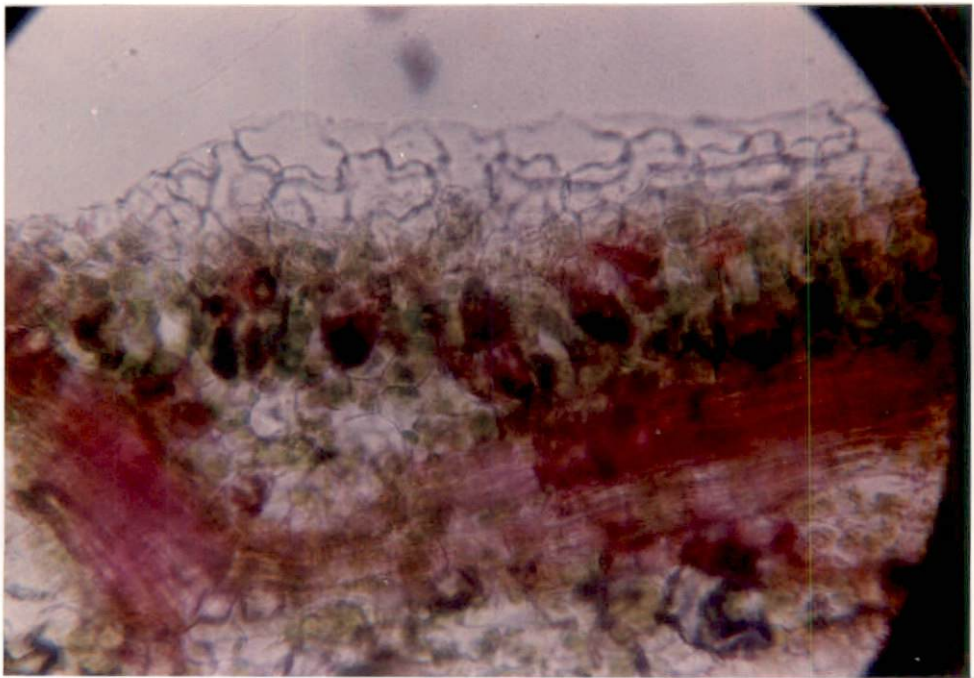
Plate 15   Cross section of *P. marsupium* leaf grown
            under well watered condition (x 50)

Plate 16   Cross section of *P. marsupium* leaf grown
            under nine day water stress cycle (x 100)
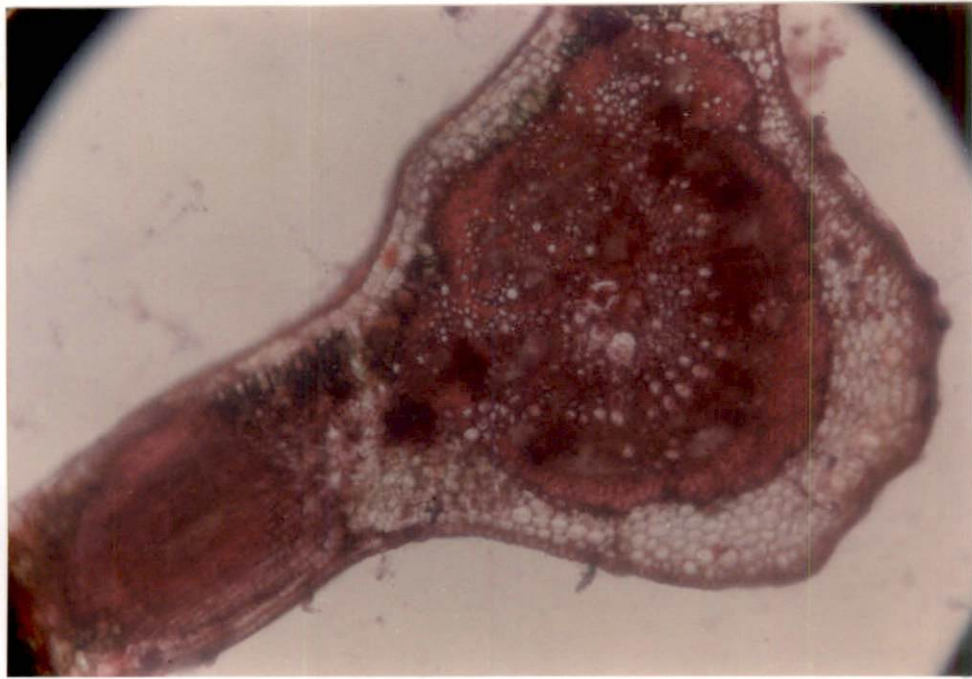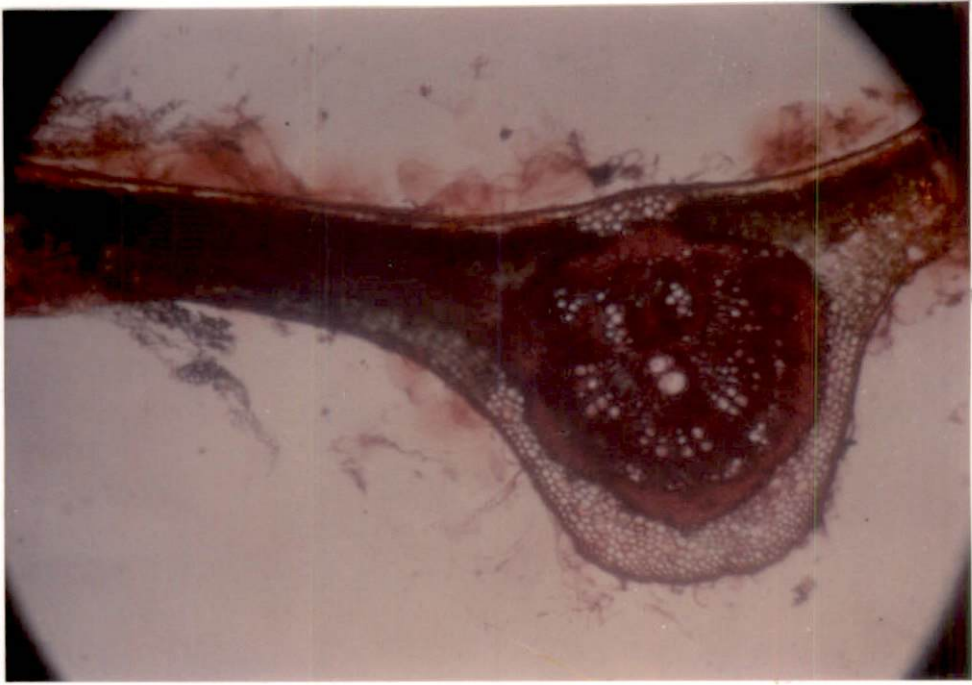
Plate 17   Cross section of *T. grandis* leaf grown
            under well watered condition (x 100)

Plate 18   Cross section of *T. grandis* leaf grown
            under six day water stress cycle (x 100)
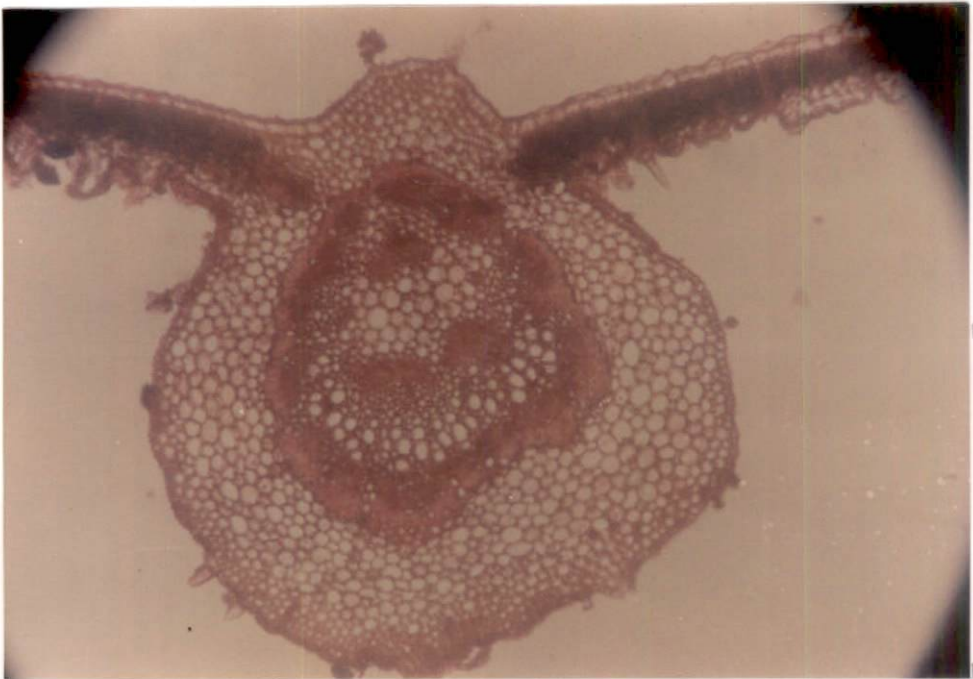
Plate 17   Cross section of *T. grandis* leaf grown
            under well watered condition (x 100)

Plate 18   Cross section of *T. grandis* leaf grown
            under six day water stress cycle (x 100)

The anatomical features of the phyllodes of *A mangium* grown under water deficit situations are shown in Plates 9 and 10. There was not much degeneration of chlorophyll pigments in the mesophyll layers. An increase in the amount of mechanical tissues was observed in the phyllodes of *A. mangium*. Water stressed plants showed an increase in the thickness of cuticle when compared to unstressed plants.

In *S. macrophylla,* leaves of the control plants (zero water stress) showed a good amount of chlorophyll in definitely arranged palisade and spongy layers of the mesophyll. As the severity of water stress increased from mild to severe, considerable decrease in the amount of spongy parenchyma and a progressive deterioration of chlorophyll pigments with the mesophyll tissue was observed (Plate 14). There was a decrease in the number of palisade layers as the water stress levels intensified. An increase in the amount of mechanical tissues like collenchyma, sclerenchyma and xylem elements was also observed in response to water stress.

A degeneration of the chlorophyll pigments with increasing water stress was observed in the leaves of *P. marsupium* seedlings. There was an increase in the amount of mechanical tissues in water stressed plants.

There was an increase in the cuticle thickness of *T. grandis* leaves due to water stress (Plate 18). Chlorophyll pigments showed degeneration in the mesophyll layers. An increase in the xylem elements and other supporting tissues like collenchyma and sclerenchyma was also observed in response to water stress. The decrease in palisade layers and degeneration of chloroplast is evident from plates 17 and 18.

Discussion

DISCUSSION

5.1 Growth parameters

Plant height was reduced significantly in *Ailanthus triphysa* at both 30 and 90 DAP due to the effect of water stress (Table 1). However, at the end of the growing period, the effect of water stress was not significant. In *Acacia mangium* seedlings, there was a significant reduction in the plant height during 90 and 120 DAP and the reduction was in the tune of 21 and 46 per cent in moderately and severely stressed plants at 120 DAP (Table 9). The reduction in plant height of *Swietenia macrophylla* and *Pterocarpus marsupium* also showed significant variations at 90 and 120 DAP (Table 17 & 25). The intensity of reduction at 120 DAP for severely stressed plants were in the order of 37 and 54 per cent below that of control in *S. macrophylla* and *P. marsupium* respectively. Plant height of *Tectona grandis* did not show significant variations due to water stress up to moderate level, except for a significant reduction at 60 DAP (Table 33). Severe water stress killed the plants. The primary effect of water stress is the reduction in turgor which retards the cell elongation. This in turn affect the internodal elongation of plants. Pessin (1938) and Wenger (1952) found that various species of southern pine (*Pinus palustris, P. elliotti, P. taeda, P. echinata*) were sensitive to shoot growth when subjected to restricted irrigation. Reduction in stem elongation due to water stress was also reported in loblolly pine (Cannell *et al.*,1978), *Picea rubens* (Robert and Cannon, 1992) and *Liriodendron tulupifera* (Cannon *et al.*,1993) seedlings.

In the present study, the plant height of *A. mangium, P. marsupium* and *S. macrophylla* decreased considerably, whereas that of *T. grandis* and *A. triphysa* showed a reduction of lesser magnitude (Fig. 17). The overall comparison of the five species indicated that the plant height was not much influenced by the water stress levels in *A. triphysa* and *T. grandis* eventhough *T. grandis* wilted and dried when kept without watering for six days or more. In other species a steep decrease in plant height with increasing water stress was observed.

The rooting depth, in general was not affected much due to water stress in any of the species. However, significant variation in rooting depths were observed at 30 DAP in *A. triphysa* and at 90 DAP in *T. grandis* seedlings (Tables 1 & 41). Eventhough there is a possibility for reduction in root growth due to restricted watering regimes, in the present study, the rewatering cycles may be so short that the roots could resume its growth. Similar observation was reported by Waring and Schlesinger (1985) . Water stress in *A. mangium* is reported to increase the root growth capacity (Awang and De Chavez, 1993). This is contrary to the findings of this study and it could be due to the short rewatering cycles as mentioned above.

The collar diameter registered significant reduction in *A. triphysa* seedlings at 30 and 120 DAP (Table 1) and in *A. mangium* at 90 and 120 DAP (Table 11). In *A. triphysa*, water stress reduced collar diameter by 4, 18 and
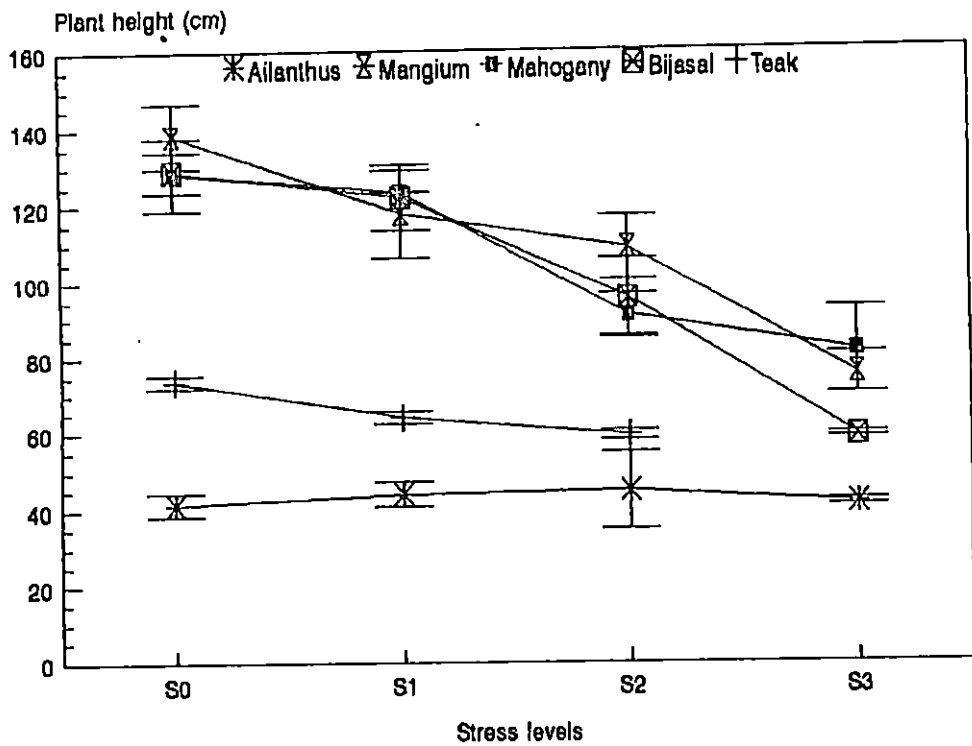
Fig.17. Plant height at 120 DAP as influenced
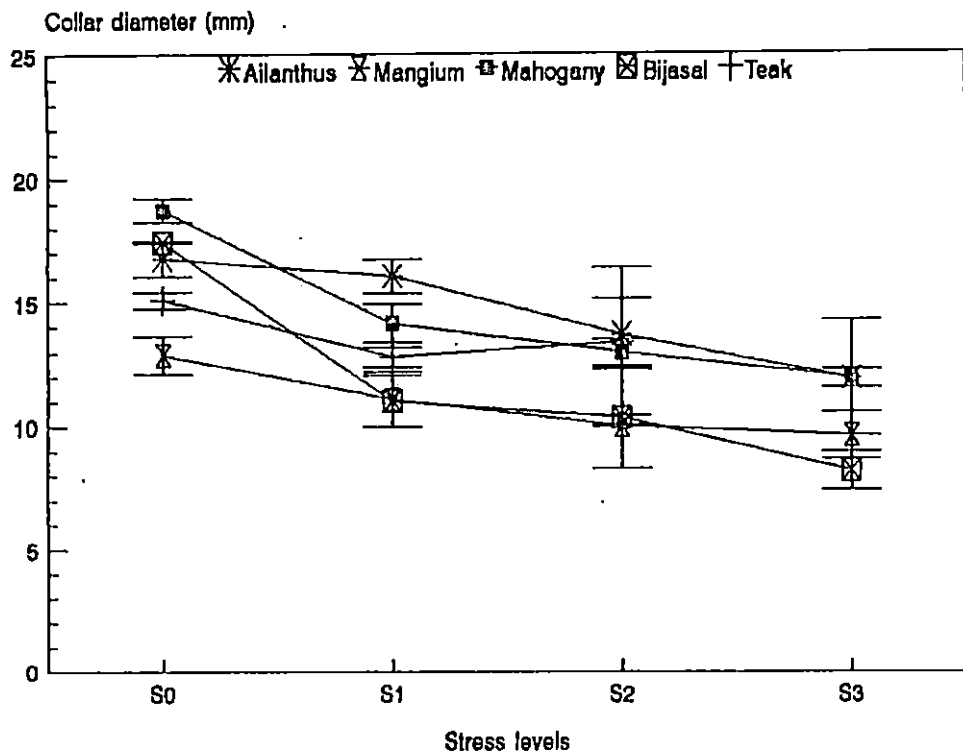by different levels of water stress

Fig.18. Collar diameter of tree seedlings at 120 DAP as
influenced by different levels of water stress

29 per cent respectively in mild, moderate and severely water stressed plants. In *A. mangium*, the reduction was to the tune of 14, 22 and 25 per cent respectively at 120 DAP. In *S. macrophylla* and *T. grandis* seedlings, significant reduction was observed at 120 DAP (Tables 21 & 41). Collar diameter of *P. marsupium* showed significant reduction at 90 and 120 DAP (Table 31). At 120 DAP, collar diameter was decreased by 37 per cent in mild, 41 per cent in moderate and 53 per cent in severely stressed plants. *S. macrophylla* and *P. marsupium* showed a sharp decrease even with mild levels of water stress (Fig. 18). In other three species the decrease in collar diameter at this level of water stress was marginal and negligible. When the water stress was further increased (S_2 & S_3), all the five species responded more or less similarly, showing a steady marginal decrease in collar diameter with increasing stress levels. *S. macrophylla* and *P. marsupium* appear to be very sensitive to water stress as far as the girth of the plant is concerned. Upto 90 per cent of annual variation in the xylem increment of forest trees has been attributed to water deficits in arid regions and upto 80 per cent in humid regions (Zahner, 1968). Several aspects of cambial activity, including division of fusiform cambial cells and xylem mother cells as well as enlargement and differentiation of cambial derivatives, are very sensitive to changes in water balance. The adverse interference on cambial growth of *Acacia auriculiformis* due to water stress was observed by Kallarackal and Somen (1992). Girth increment showed good correlation with other water stress responses like higher stomatal resistance and

lower water potentials. So the decrease in the collar diameter observed may be the result of reduced cambial activity due to water stress.

The number of leaves, leaf area and leaf dry weight showed a decreasing trend in response to water stress in all the five species. Mild water stress reduced the number of leaves by 25 per cent, moderate water stress by 31 per cent and severe stress by 61 per cent in *A. triphysa* at the end of the growing period. At 120 DAP, the reduction in severely stressed plants were to the tune of 56, 78, 70 and 75 per cent for *A. mangium*, *S. macrophylla* and *P. marsupium* seedlings respectively. In *T. grandis*, even at moderate stress the reduction in number of leaves was to the extent of 75 per cent. Zahner (1968) has reported that water stress induces senescence and early abscission which when combined with reduced leaf primordia initiation result in a reduced number of leaves per plant. A reduction in the number of leaves in response to water stress was observed in *Eucalyptus maculata* and *E. brockwayii* (Myers and Landsberg, 1989) and *Fagus sylvatica* (Cermak *et al.*, 1993). A comparison of the five species indicate (Fig. 19) that the steepest decrease in number of leaves due to water stress was in *A. mangium* and *T. grandis*. When the water stress levels increased to S_2 and S_3, *S. macrophylla* and *A. mangium* showed further sharp decrease, whereas the other three species showed only a steady marginal decrease. In general the number of leaves, leaf area and leaf dry weight of *S. macrophylla*, *A. mangium* and *T. grandis* were more sensitive to water stress as compared to the other two species.

The leaf area was also reduced due to water stress in all the species, but the intensity of reduction varied. At 120 DAP, the leaf area was reduced by 57, 78, 78 and 77 per cent in severely stressed *A. triphysa, A. mangium, S. macrophylla,* and *P. marsupium* respectively. In *T. grandis* 53 per cent reduction in leaf area was observed even at moderate levels of water stress (S_2). The reduction in leaf area could be primarily due to the reduced number of leaves in the seedlings (Tables 2, 12, 22, 32 & 42). A significant positive correlation (Tables 9, 19, 29, 39 & 48) was observed between the number of leaves and leaf area in all the species. This coupled with factors like reduction in leaf size and increased leaf abscission due to water stress might have contributed to the reduced leaf area. Boyer (1976) attributed the reduction in leaf size as the main reason for the reduction of leaf area in water stressed plants whereas Ludlow and Muchow (1990) attributed the reduction in leaf area to increased leaf abscission. A steep decline in leaf area was observed due to water stress in *P. marsupium* and *S. macrophylla* even at mild water stress (Fig. 20). In *S. macrophylla* the steep decrease continued with further increase in water stress level to S_2 and S_3. However, in *P. marsupium* water stress above S_1 showed only a marginal decrease in leaf area. The leaf area of *A. mangium* decreased sharply when the water stress level was increased from S_1 to S_2. In the other two species the response was marginal and smallest response was in *A. triphysa*. This sudden decrease in leaf area might be a mechanism of the species to reduce water loss in response to restricted water availability. *S. macrophylla* which maintained highest leaf area
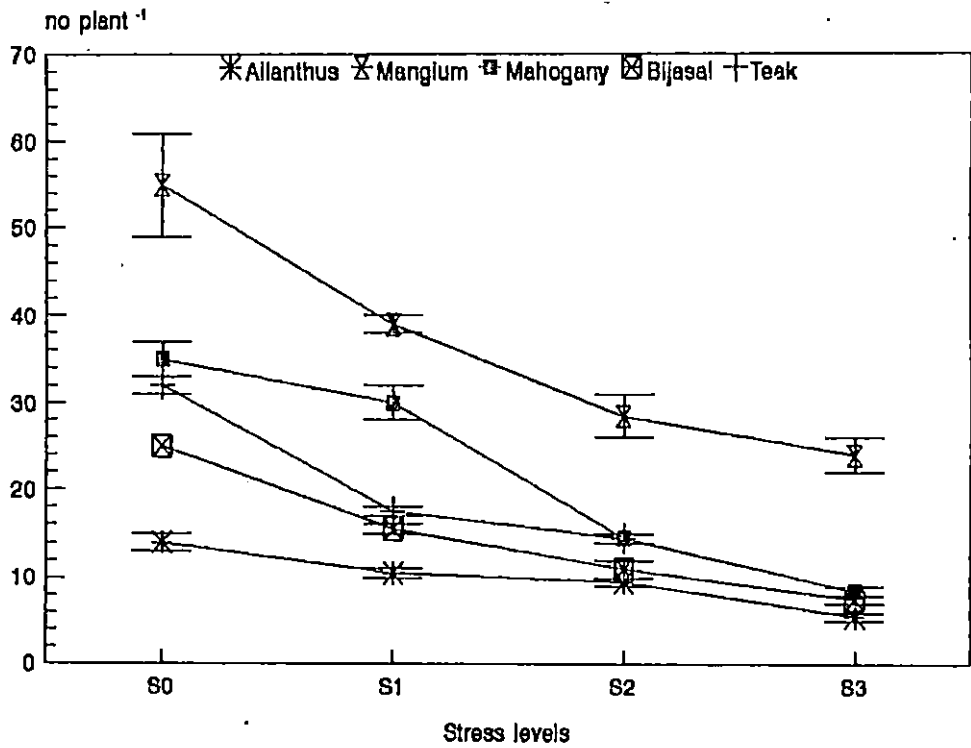
Fig.19. Number of leaves per plant at 120 DAP as influenced by different levels of water stress
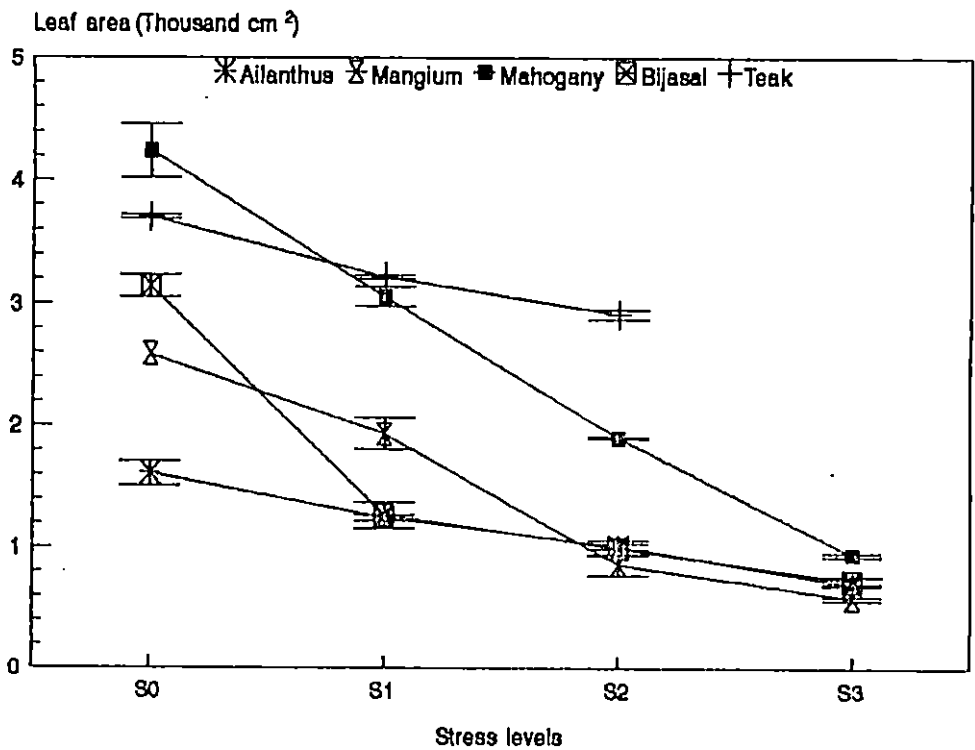

Fig.20. Leaf area per plant at 120 DAP as influenced by different levels of water stress

quickly decreased it under water stress whereas *T. grandis* maintained its leaf area even under water stressed situation resulting in a higher transpiration and permanent wilting of the plants within six days of dry period. This argument can also be supported by the data on LDR in *T. grandis* (Fig. 14). These results indicate that *T. grandis* showed permanent wilting when the soil moisture tension (SMT) approached 5 bars (S_2) whereas other four species survived without wilting even when the SMT approached 10 bars (S_3) (Fig. 1).

The leaf dry weight of all the species showed significant reductions due to water stress during different growth stages. Severe water stress reduced the leaf dry weight to a great extent in all the species. The reduction in leaf dry weight could be attributed to the reduction in number of leaves per plant and the leaf area (Tables 2, 12, 22, 32 & 42).

The number of leaves, leaf area and leaf dry weight which showed a sharp decline (Fig. 19, 20 & 21) in *A. mangium* and *S. macrophylla* seedlings indicate their inability to withstand water deficits during seedling stages. In *A. mangium* Supriadi and Valli (1988) observed wilting and stunted growth of the *A. mangium* seedlings due to water stress. *A. triphysa* seedlings did not show severe reduction in number of leaves, leaf area and leaf dry weight as observed in other species indicating that the species can tolerate water deficit situations.

The dry weight of shoot in all the five species showed a decreasing trend with increasing water stress levels. In *A. triphysa* severe water stress reduced the shoot weight by 61 per cent as compared to control at 120 DAP (Table 3). The reductions were in the tune of 64, 72, and 87 per cent for *A. mangium, S. macrophylla,* and *P. marsupium* respectively (Tables 13, 23, & 33). In *T. grandis,* though the plants showed symptoms of permanent wilting at severe water stress (S_3) it showed only 35 per cent reduction in the shoot dry weight at moderate water stress (S_2). The reduction in shoot weight could be due to the cumulative effect of reduction in plant height, collar diameter, leaf number and leaf area due to water stress. The correlation matrices of the different species (Tables 9, 19, 29, 39 & 48) showed good positive correlation of the above characters with the shoot dry weight. There are a number of reports (Driessche, 1991; Roberts and Cannon, 1992) which cites decrease in shoot dry weight due to water stress in species like *Pseudotsuga menzeisii, Pinus contorta, Picea glauca* etc. The response of the different species to water stress (Fig. 22) indicate that *S. macrophylla* which showed the steepest decline even with mild water stress is the most sensitive. The reduction in shoot dry weight of *A. mangium* was slow and steady. However, in *A. triphysa,* the decrease in shoot dry weight was marginal and negligible indicating the tolerance of the species. In *T. grandis* also the decrease in shoot dry weight was only marginal up to moderate water stress, eventhough the species showed symptoms of permanent wilting when the water stress was further increased.
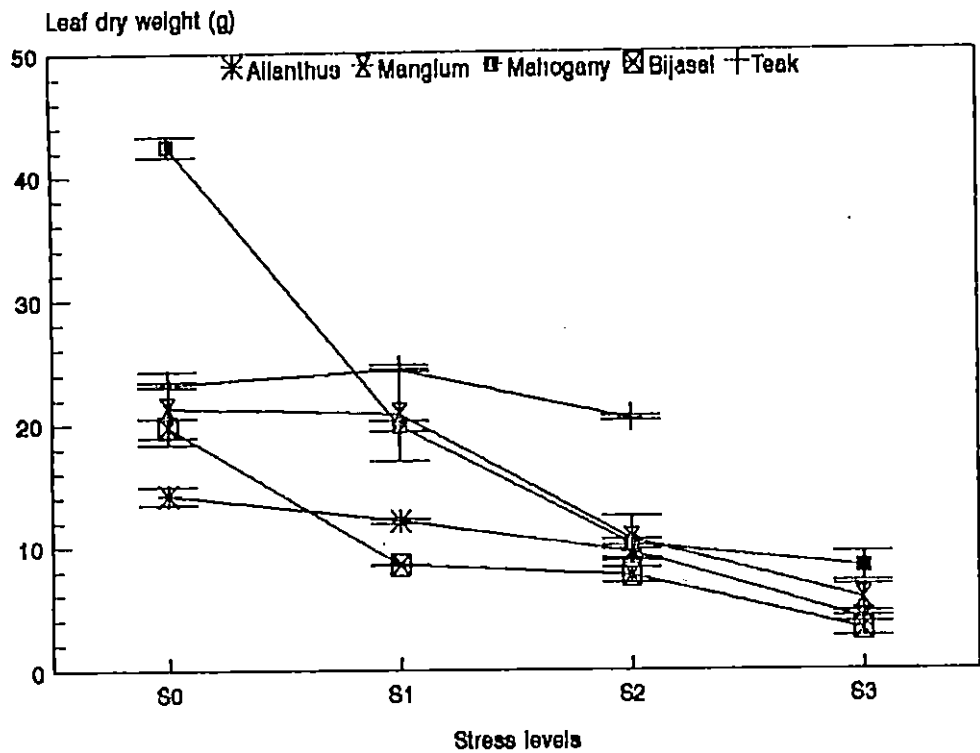
Fig.21. Leaf dry weight per plant at 120 DAP as influenced by different levels of water stress
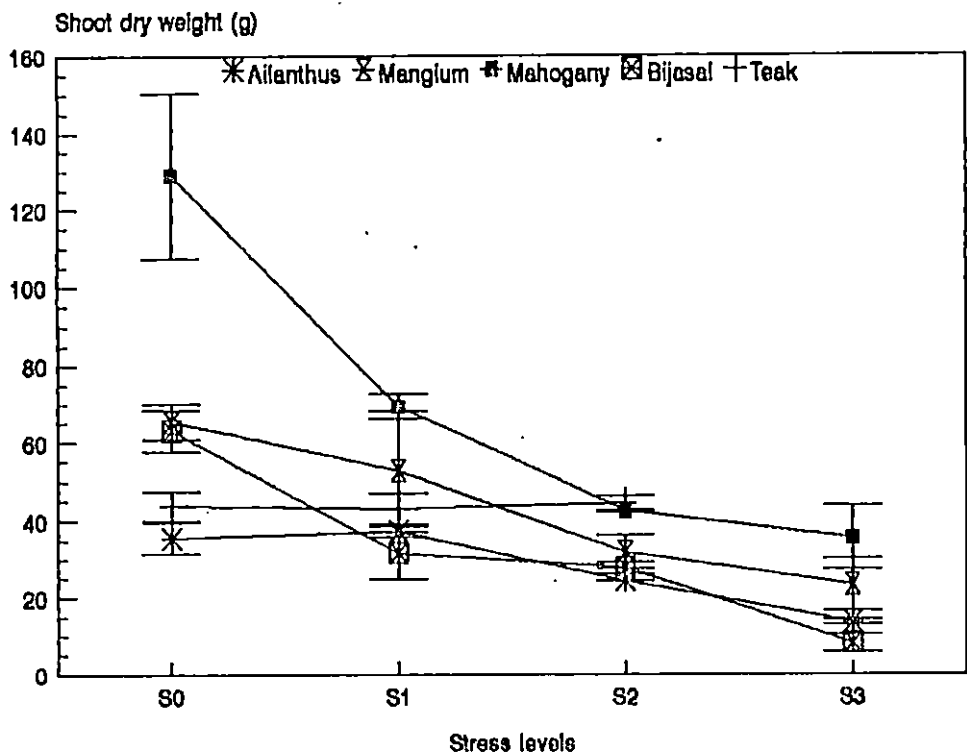

Fig.22. Shoot dry weight of tree seedlings at 120 DAP as influenced by different levels of water stress

The dry weight of roots also showed significant reductions due to water stress in all the species. In *A. triphysa,* about 75 per cent reduction in root weight was observed at 60 DAP. *Swietenia macrophylla* and *P. marsupium* also showed severe reduction in root dry weight at 120 DAP with a reduction of 65 and 45 per cent in severely stressed plants at 120 DAP (Tables 23 & 33). As the rooting depths were not appreciably affected by water stress in any of the species, the decrease in root weight might be the result of the decreased root regeneration under high soil water stress. Decreased root regeneration with increasing soil moisture tension was observed in northern red oak (Larson and Whitmore, 1970) and in white pine seedlings (Day and Mac Gillivray, 1975). Seiler and Johnson (1984) reported reduced root dry weight in *Alnus glutinosa* seedlings in response to water stress. The overall comparison of the five species revealed that root dry weight declined steeply in *S. macrophylla* and *P. marsupium* even with mild water stress (Fig. 23). However, further reduction was gentle and slow with increasing levels of water stress. A steady decrease of root dry weight with increasing water stress levels was observed in *T. grandis.* In *A. triphysa* and *A. mangium,* the decrease was marginal and negligible. The sharp reduction in the shoot and root weight of *S. macrophylla* seedlings with water stress emphasises the sensitivity of the species to water stress. Root dry weight was also reduced considerably. Though the shoot weight of *A. mangium* seedlings were reduced with increasing water stress, the root weight was not affected much by water stress. May be that the partitioning of photosynthates *in A. mangium* seedlings were in favour

of the root growth, during periods of stress to cope up with the reduced water availability. In the case of *A. triphysa,* the variations in shoot and root dry weight were negligible when compared to other species indicating the ability of the species to establish in dry areas.

The root - shoot weight ratios of none of the species studied showed consistent variations in their response to water stress. Significant variations were observed at certain growth stages in species like *A. triphysa, A. mangium* and *P. marsupium.* Hence it is inferred that the root - shoot ratio in these species were not influenced much due to water stress as the shoot and root dry weights were decreased proportionately, except in *A. mangium.*

The total dry matter production was reduced considerably in all the species due to the effect of water stress with pronounced reduction in severely stressed plants. In *A. triphysa* and *T. grandis* seedlings, the rate of reduction was lesser in mildly stressed plants (6% and 10% respectively) and the intensity of reduction was increased to 60 and 41 per cent respectively in severely stressed plants. The reductions were in the tune of 64, 73 and 82 per cent in *A. mangium, S. macrophylla* and *P. marsupium* seedlings. Water deficits generally have a negative effect on the dry matter production in plants as it impairs with many of the physiological processes which determines the growth.
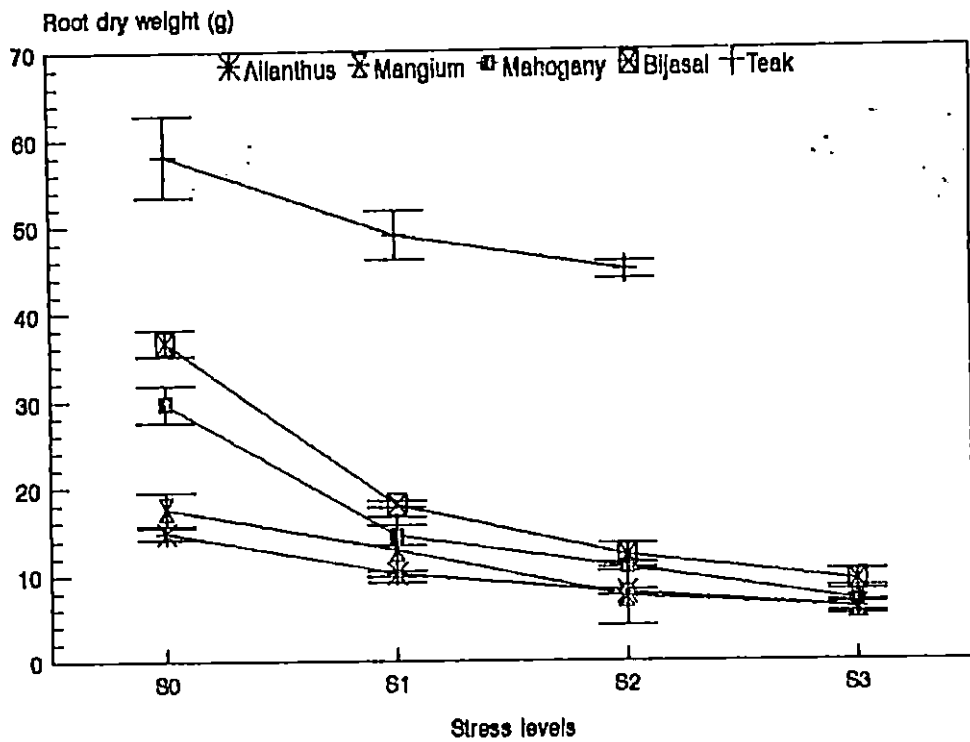
Fig.23. Root dry weight of tree seedlings at 120 DAP as influenced by different levels of water stress
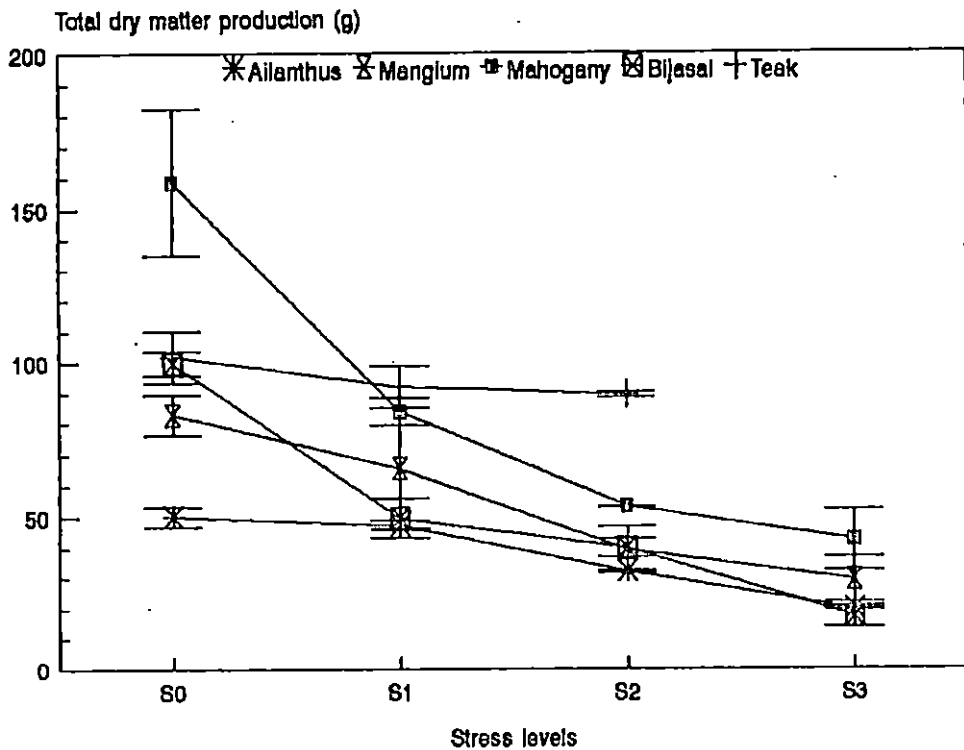

Fig.24. Total dry matter production in tree seedlings at 120 DAP as influenced by different levels of water stress

The reduction in dry matter production observed could be due to the decrease in the plant characters like leaf area, leaf dry weight, shoot dry weight, root dry weight etc which are positively correlated with the total dry matter production in different species (Tables 9, 19, 29, 39 & 48). The total dry matter production was reduced significantly even by mild water stress in *S. macrophylla* and *P. marsupium* seedlings (Fig.24). Further increase in stress evoked a slow and steady decrease in dry matter production. *Ailanthus triphysa* and *A. mangium* showed a steady slow decrease. In *T. grandis* also mild water stress resulted in a steady and slow decrease in dry matter production. However, moderate water stress seemed to reduce the total dry matter production drastically. When compared to other species, the reduction in dry matter production of *A. triphysa* seedlings was less indicating the tolerance of the species to water stress.

The relative growth rate (RGR) at 90-120 DAP interval showed a decreasing trend with increasing levels of water stress in different species (Fig.33). Under well watered conditions, the RGR of *T. grandis* was low, that of *A. triphysa, A. mangium* and *S. macrophylla* was medium and that of *P. marsupium* was high. RGR was not much affected by mild water stress in *A. triphysa* and *S. macrophylla* seedlings. Further reduction with increasing water stress levels were slow and steady. Eventhough the RGR of *A. triphysa* and *S. macrophylla* responded more or less similarly in response to water stress, the plant dry weight of *S. macrophylla* was decreased drastically due to water

Relative growth rate (mg g⁻¹ wk⁻¹)
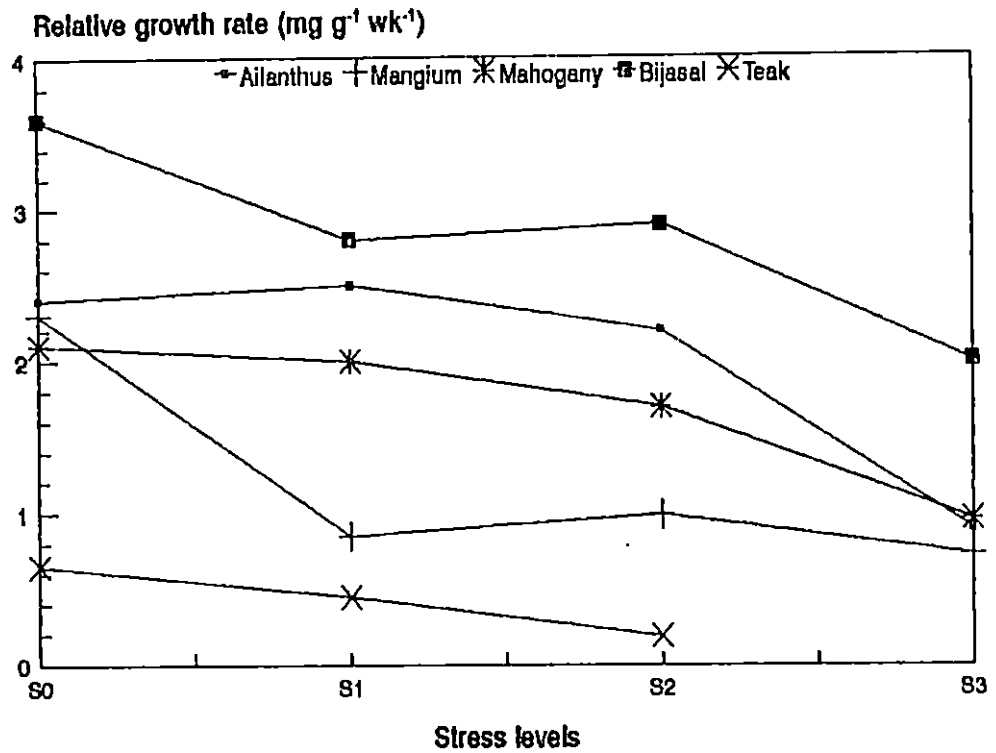

Fig.25. Relative growth rate at 90 - 120 DAP interval as influenced by different levels of water stress

Net assimilation rate (mg cm⁻² wk⁻¹)
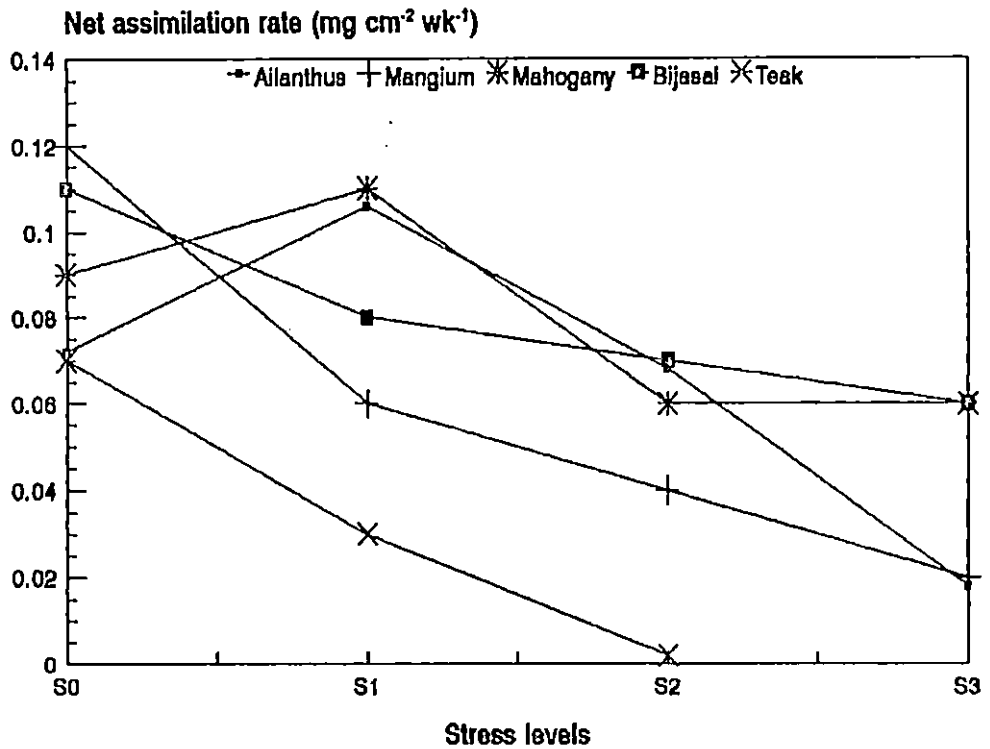
Fig.26. Net assimilation rate at 90 - 120 DAP interval as influenced by different levels of water stress

stress, whereas, in *A. triphysa*, the decrease in total dry matter production was only marginal. So in the long run, *A. triphysa* may perform better than *S. macrophylla* under water stressed situations. The negative effect of water stress on RGR of *T. grandis* was negligible. In *P. marsupium* and *A. mangium*, there was an increase in the RGR at moderate levels of water stress. The number of leaves, leaf area and leaf dry weight per plant in *A. triphysa* and *P. marsupium*, eventhough low under water stress situations the leaves maintained high efficiency with respect to dry matter production as indicated by the data on relative growth rate and net assimilation rate (Fig. 25 & 26) which were relatively stable as compared to *S. macrophylla* and *A. mangium*.

The net assimilation rates (NAR) showed steep decline with water stress for *A. mangium*, *T. grandis* and *P. marsupium* seedlings (Fig. 34). Sharp decline was observed even with mild water stress. It is noteworthy that mild water stress (S_1) increased the NAR in *A. triphysa* under mild water stress (S_1), inspite of having not much change in leaf area and leaf dry weight. This indicate relatively high dry matter production efficiency of the species under water stress situations. The data on the NAR of *P. marsupium* seedlings also suggest the increased efficiency of the available leaf area.

5.2. Physiological characteristics

The leaf diffusive resistance (LDR) showed an increasing trend with increasing water stress in all the species. The rise in LDR was steeper at

moderate and severe levels of water stress. Even at the beginning of the dry cycle (1 DAS), most of the species showed significantly higher LDR. The LDR values showed significant increase for all the species due to the effect of water stress and the rise in LDR was in proportion with the levels of water stress. The stomatal closure is usual when the turgor of guard cell decreases during relatively early stages of leaf water deficits, often long before leaves wilt (Kozlowski, 1976). Hence a steep increase in the LDR could be due to severe water deficit situation that might have developed in the leaves due to moderate and severe water stress cycles. Such closure of stomata with water deficit situation have been reported in many tree species (Pereira and Kozlowski, 1978; Kozlowski, 1982).

In the diurnal variations also, the values of LDR were much higher for water stressed plants in all the species. There was a pronounced midday stomatal closure for moderately stressed seedlings of *T. grandis* and moderately severely stressed plants of *A. triphysa*. (Fig. 14 & 2). In *A. mangium* and *P. marsupium*, though all the water stressed plants showed midday stomatal closure, it was more prominent in moderately and severely stressed plants (Fig. 5 & 11). It is clear from the results that as the water stress increases, plants reduce their water loss by stomatal regulation of transpiration. The stomatal response is more at higher levels of water stress in all the seedlings.

A comparison of the LDR of the different species (Fig. 27) showed that LDR in *S. macrophylla* and *A. mangium* increases steeply with water stress upto S_1 level. In *A. mangium*, further steep increase was observed with increasing levels of water stress whereas in *S. macrophylla*, mild and moderate levels did not show differences in LDR, but increased with severe water stress, indicating quick closure of stomata with water stress. The sensitivity of these species to water stress was also evident from the leaf water potential (Fig. 28) which declined sharply with water stress. Inspite of the quick response of the stomata to water stress, as deduced from the steep increase in the LDR in *S. macrophylla* and *A. mangium* in response to water stress, the plants were not able to maintain high leaf water potential. This indicate the poor ability of the species to absorb soil moisture under water stressed situations. This is also corroborated by the low root dry weight recorded in the species. In *T. grandis* and *A. triphysa* LDR increased slowly with increase in water stress indicating the sensitivity of the stomata of the species to water stress.

Stomatal mechanism in *S. macrophylla* is not very efficient as compared to *A. mangium*. This was deduced from the LDR of *S. macrophylla* which showed sudden increase with mild water stress, but did not increase proportionately with further increases in water stress (Fig. 27) whereas in *A. mangium*, the LDR increased proportionately with increasing water stress levels upto S_3. The slowest stomatal response was found in *T. grandis* and the fastest in *A. mangium*. Inspite of the slow stomatal closure and high

Leaf diffusive resistance (m mol m⁻² s⁻¹)
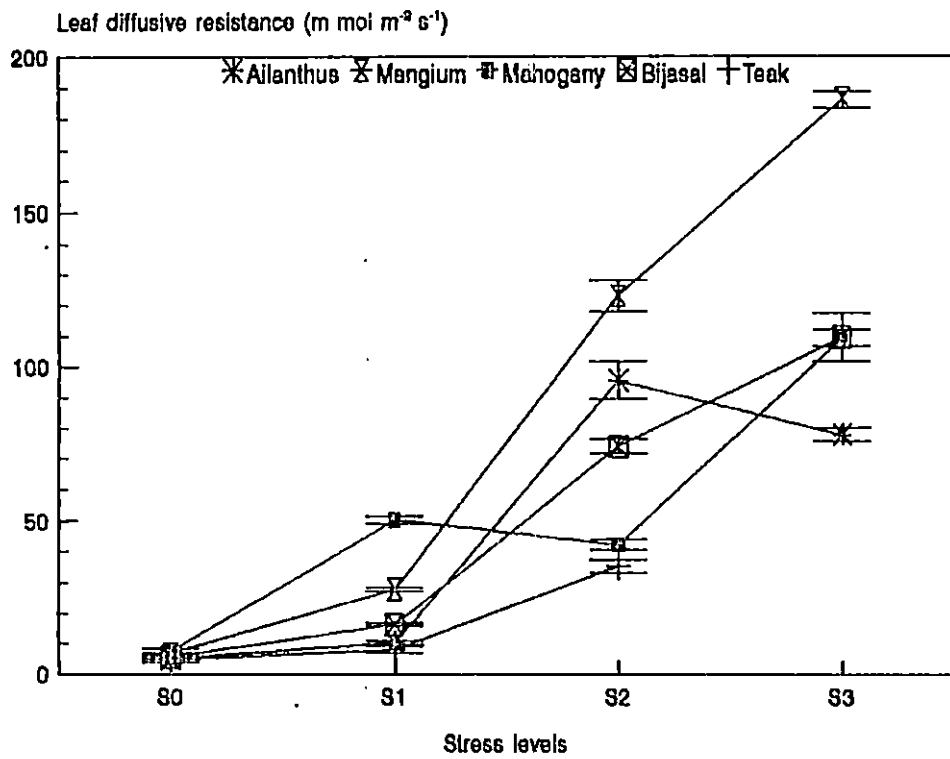

Fig.27. Leaf diffusive resistance of tree seedlings at 1400 hrs
as influenced by different levels of water stress

Leaf water potential (-MPa)
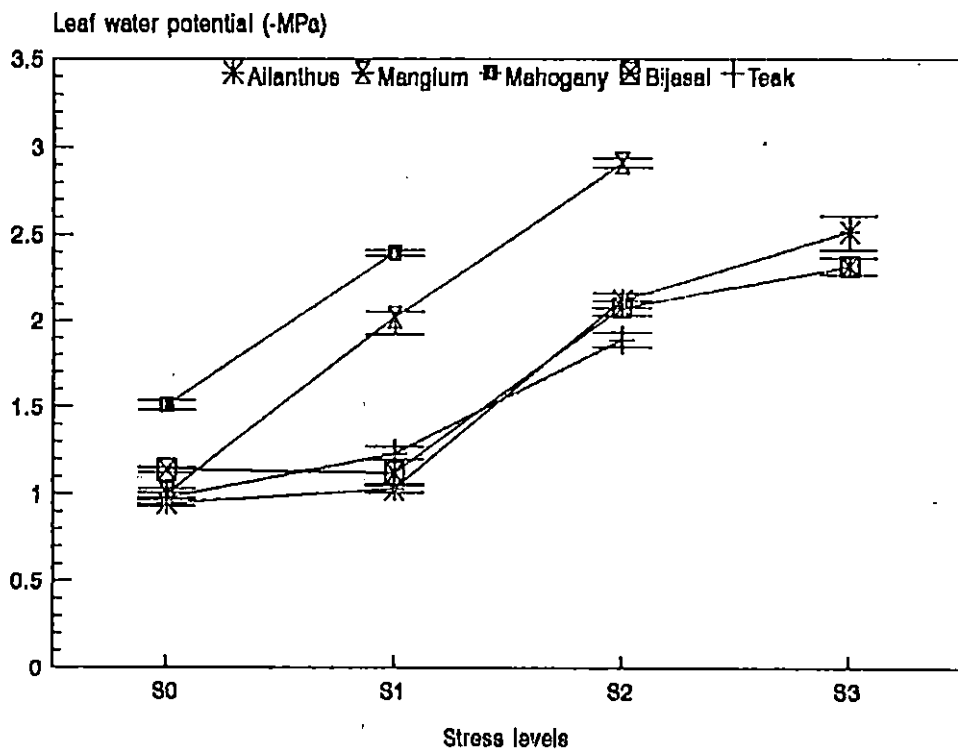
Fig.28. Leaf water potential of tree seedlings at 1400 hrs
as influenced by different levels of water stress

transpiration in *T. grandis*, it was able to maintain high leaf water potential because of the efficient utilisation of soil moisture with its well developed root system. This is corroborated by the high root dry weight observed in *T. grandis* (Fig. 23). Leaf diffusive resistance in *A. triphysa* and *P. marsupium* was not much increased due to mild water stress (S_1) indicating that the stomata was open at this level of water stress. This probably enabled more gas exchange through the stomata and could be one of the reasons for the high net photosynthesis observed in these two species even under water stressed situations (Fig. 29). These two species maintained a high leaf water potential under water stressed condition inspite of the low LDR indicating the inherent low transpiration of the species.

The leaf water potential (LWP) of control and mildly stressed plants were in the close range in *A. triphysa* (Fig. 3), *P. marsupium* (Fig. 12) and *T. grandis* (Fig. 15) seedlings. However, the moderate and severely stressed plants showed much lower leaf water potentials as compared to well watered plants. The LWP of severely stressed plants of *A. triphysa* was far below -2.5 MPa and that of *A. mangium* <-4.0 MPa. In *S. macrophylla*, even the moderately stressed plants were showing LWP less than -2.6 MPa. The leaf water potential of *S. macrophylla* and *A. mangium* showed a steep decline with increasing water stress (Fig. 28). The pattern of decline in the LWP was more or less similar for *A. triphysa*, *P. marsupium* and *T. grandis* seedlings upto S_1 level of water stress. Further increase in water stress, though

transpiration in *T. grandis*, it was able to maintain high leaf water potential (ψ) because of the efficient utilisation of soil moisture with its well developed root system. This is corroborated by the high root dry weight observed in *T. grandis* (Fig. 23). Leaf diffusive resistance in *A. triphysa* and *P. marsupium* was not much increased due to mild water stress (S_1) indicating that the stomata was open at this level of water stress. This probably enabled more gas exchange through the stomata and could be one of the reasons for the high net photosynthesis observed in these two species even under water stressed situations (Fig. 29). These two species maintained a high leaf water potential (ψ) under water stressed condition inspite of the low LDR indicating the inherent low transpiration of the species.

The leaf water potential (ψ) of control and mildly stressed plants were in the close range in *A. triphysa* (Fig. 3), *P. marsupium* (Fig. 12) and *T. grandis* (Fig. 15) seedlings. However, the moderate and severely stressed plants showed much lower ψ as compared to well watered plants. The ψ of severely stressed plants of *A. triphysa* was far below -2.5 MPa and that of *A. mangium* <-4.0 MPa. In *S. macrophylla*, even the moderately stressed plants were showing ψ less than -2.6 MPa. The leaf water potential of *S. macrophylla* and *A. mangium* showed a steep decline with increasing water stress (Fig. 28). The pattern of decline in the ψ was more or less similar for *A. triphysa*, *P. marsupium* and *T. grandis* seedlings upto S_1 level of water stress. Further increase in water stress, though decreased the ψ of

these species, the decrease was less compared to *S. macrophylla* and *A. mangium*. The three species maintained a far higher ψ (-0.99 to -2.52 MPa) at all the levels of water stress as compared to *S. macrophylla* and *A. mangium*, whereas the ψ was less than -4.0 MPa and -3.0 MPa respectively even at moderate (S_2) levels of water stress. This shows the ability of *A. triphysa* and *P. marsupium* to tolerate mild water stress (~ -0.1 MPa SMT). It is noteworthy that the net photosynthesis in *A. triphysa* and *P. marsupium* was relatively high at this stress level (Fig. 29).

In *A. mangium*, the ψ decreased to <-4.0 MPa when the water stress was increased to S_3 level (~ -1.0 MPa SMT). It may be noted that the plant biometric characteristics like collar diameter, number of leaves, leaf area, leaf dry weight, shoot dry weight, root dry weight etc. decreased steeply in *A. mangium* and *S. macrophylla* in response to water stress indicating that the two species were unable to maintain the leaf turgor under water stress situations resulting in poor growth of the plant. This is inspite of the adaptations like phyllodes instead of leaves, quick stomatal closure, low chloroplast disintegration, high accumulation of soluble protein and probable osmotic adjustment observed in *A. mangium*. Eventhough the leaf area decreased with water stress, leaf water potential (ψ) was not maintained as evidenced from the sharp decrease in the ψ. This may be because of the poor absorption of water due to poorly developed root system as deduced from the lower root dry weight (Table 13 & Fig. 23). So the popular belief of

A. mangium being a drought tolerant species should be accepted with caution at least in the seedling stage. In a related species, *A. auriculiformis* Kallarackal and Somen (1992) observed that the species transpired in large quantities inspite of having adaptations like phyllodes. Leaf water potential was considered as a direct indicator of leaf turgor and hence a good indicator of water status of plants. A sudden decline in the ψ as observed in *S. macrophylla* and *A. mangium* indicates the inability of the species to withstand water deficit situations. Hence from the present study, the above species were found to have difficulty in tolerating water stress at the seedling stages. This could be particularly true in the case of a mesophytic species like *S. macrophylla*. In the case of *A. mangium*, Supriadi and Valli (1988) have observed that the seedlings of the species were intolerant to water stress.

In *A. triphysa* and *P. marsupium* leaf water potential did not decrease appreciably with mild water stress. The leaf turgor was maintained by rapid adjustment of leaf area (Fig. 20). Further increase in water stress did not result in decrease in leaf area which may have resulted in continued transpiration. This may be the reason for the rapid decrease observed in the ψ when these two species were exposed to higher levels of water stress (S_2 and S_3). In *T. grandis*, leaf area decreased in response to mild water stress, however, water potential showed only a marginal decrease. When the water stress was increased to moderate and severe levels, there was a steep decrease in leaf water potential. The leaf area also decreased at these levels

of water stress indicating that the leaves remaining on the plants were transpiring freely. This view is supported by the slow stomatal response of the species as indicated by the low LDR in response to water stress.

In general, the water stressed plants showed a higher leaf temperature than the well watered plants in all the species. The diurnal variations of leaf temperature in severely stressed plants were also showing higher values. The elevation in the leaf temperature could be due to the decreased transpiration rate (Table 6, 16, 26, 36 & 46) caused by water stress as against a well watered plant which transpires optimum and makes the leaves cool. Elevation in leaf temperature was observed by Idso *et al.* (1978b) due to moisture deficit situation. Such situations would lead to a reduction in photosynthesis resulting in the decline of total dry matter production. Nevertheless, the leaf temperature alone cannot be considered as good indicator of water stress as there was no consistent pattern of variation.

Net photosynthesis of all the species were significantly influenced by water stress. Distinct variations could be observed with the control plants showing maximum photosynthesis. Nevertheless, a decline during mid hours of the day was observed in all species irrespective of the water stress treatments. Such midday reductions was observed in different species by Hanson and Dye (1980) and Tenhunen *et al.* (1980). Reduction in net photosynthesis was concomitant with the increasing water stress levels; with

severely stressed plants showing the least photosynthesis. The reduced net photosynthesis of the water stressed seedlings could be attributed primarily to the increased LDR. A significant positive correlation of the net photosynthesis with leaf conductance was found in all the different species in the present study (Tables 10, 20, 30 & 40). An increase in the leaf temperature also interferes negatively with the photosynthesis of the plants. Reduction in net photosynthesis was reported in several species in response to water stress (Kozlowski, 1982; Schulze, 1986).

The decline in net photosynthesis was steeper in *P. marsupium*, *A. mangium* and *T. grandis* indicating the higher sensitiveness of the photosynthetic mechanism of the species to water stress. Net photosynthesis showed least values for severely stressed *T. grandis* seedlings (Fig. 16) which recorded zero net photosynthesis at 1000, 1200 and 1600 hrs. At 0800 and 1400 hrs there was measurable photosynthesis. This is again evident from the sharp decrease in the net assimilation rates (NAR) of the species as read from Fig. 26. In the case of *A. triphysa* and *S. macrophylla* seedling also, a decline in net photosynthesis with water stress was observed. However, the NAR showed an increasing trend with mild water stress which then declined steeply with further increase of water stress. The relative growth rates showed decreasing trend (Fig. 25) for all the species concomitant with the reduction in net photosynthesis.
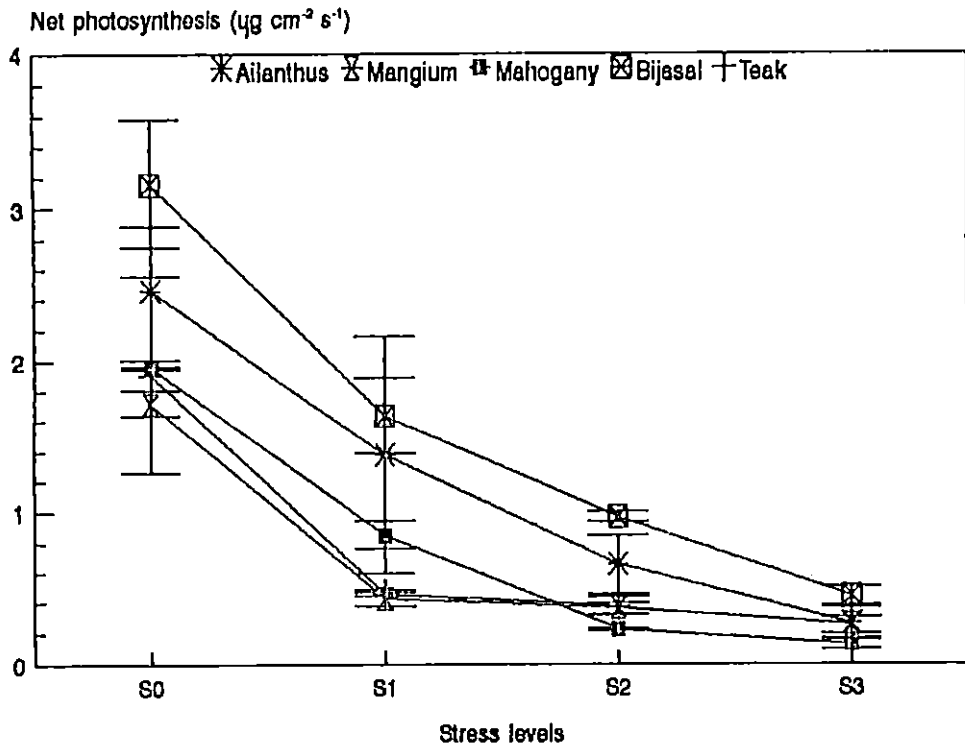
Fig.29. Net photosynthesis of tree seedlings at 1200 hrs as influenced by different levels of water stress
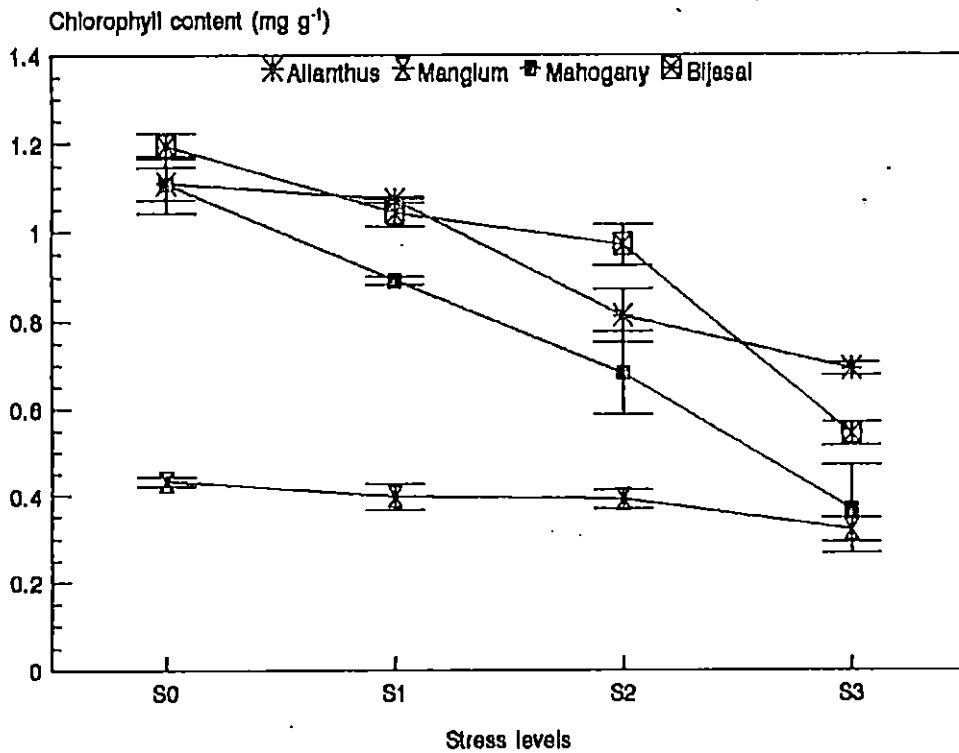
Fig.30. Total chloropyll content in the leaves of tree seedlings as influenced by different levels of water stress

In *T. grandis,* eventhough the LDR was low and the ψ high, net photosynthesis showed steep decrease even with mild water stress indicating the sensitivity of the species to water stress: The decrease in net photosynthesis observed in *T. grandis* may be because of the high chloroplast disintegration, which we have observed in the anatomical studies of the leaf (Plate 18) and/or other physiological reasons. The relatively stable relative growth rate and steeply decreasing net assimilation rate in T. grandis with increasing water stress indicate the poor efficiency of the leaves of *T. grandis* in producing photosynthates under water stressed situations. This is also evidenced from the sharp decrease in net photosynthesis in *T. grandis* in response to water stress.

The relative water content of *A. triphysa* seedlings did not show significant variations due to water stress (Table 4). In species like *A. mangium, S. macrophylla* and *P. marsupium,* though the RWC did not vary at 0800 hrs, water stress reduced the RWC at 1400 hrs (Tables 14, 24 & 34). In *A. mangium* and *S. macrophylla,* the reductions were severe in all water stressed plants whereas in *P. marsupium,* only moderately and severely stressed plants showed a steep decline. In *T. grandis,* the RWC was significantly reduced both at 0800 and 1400 hrs. A rapid decrease in the RWC is considered as a character of stress intolerant species, whereas stress tolerant species, especially sclerophytes tend to have a slower decrease in RWC as leaf water potential decreases (Cowan, 1981).

Hence a rapid decrease in the RWC of *S. macrophylla* and *A. mangium* seedlings during midday indicate that the species is intolerant to water stress.

5.3. Biochemical aspects

The chlorophyll 'a', chlorophyll 'b' and total chlorophyll contents were reduced due to water stress in all the species studied. The severity of reduction varied among the components and in the different species. In all the four species studied, the reduction in chlorophyll 'b' content was more intensive when compared to chlorophyll a and total chlorophyll (Tables 8, 18, 28 & 38). This implies that synthesis/disintegration of chlorophyll 'b' is more sensitive to water stress. Higher sensitiveness of chlorophyll 'b' was observed in *Grevellia robusta* by Nautiyal *et al.* (1993). The decrease in the chlorophyll content due to water stress could possibly be by the loosing of chloroplast membrane integrity (Vieira de Silva *et al.*, 1974) or due to the inhibition of biosynthesis of the precursor of chlorophyll (Makhmuda, 1983). The total chlorophyll content in the leaves of different species decreased with increasing water stress. In *S. macrophylla* and *P. marsupium* seedlings, a steep decline in the chlorophyll content was observed. However, the total chlorophyll content in *A. mangium* was not significantly affected due to water stress. This was evident from the cross section of the phyllodes (Plate 10) where little or no degeneration of chlorophyll pigments in the mesophyll was observed. Hence

it could be inferred that *A. mangium* might have some mechanism which prevents the degeneration of chlorophyll pigments which have to be further studied.

The free proline content in the leaves showed an increasing trend in all the species with increasing water stress levels (Fig. 31). *A. triphysa* and *P. marsupium* showed similar response with relatively higher proline content than *A. mangium* and *S. macrophylla*. As the proline content was increased in all the species studied, it can be considered as an after effect of water stress rather than an adaptation to combat water stress.

The soluble protein contents in the leaves of *A. mangium* and *A. triphysa* registered an increase with water stress. However, in *S. macrophylla* and *P. marsupium* seedlings, soluble protein content showed marked decrease with increase in water stress (Fig. 32). The decrease in the soluble protein content could be an indication of the absence of accumulation of drought stress proteins as advocated by Newton *et al.* (1991) in response to water stress. Hence such an adaptation to tolerate water stress by osmotic adjustment might be lacking in *S. macrophylla* and *P. marsupium*. The soluble protein in *P. marsupium* did not show significant changes in response to water stress. The increase in the protein content of *Ailanthus* and *A. mangium* seedlings may be
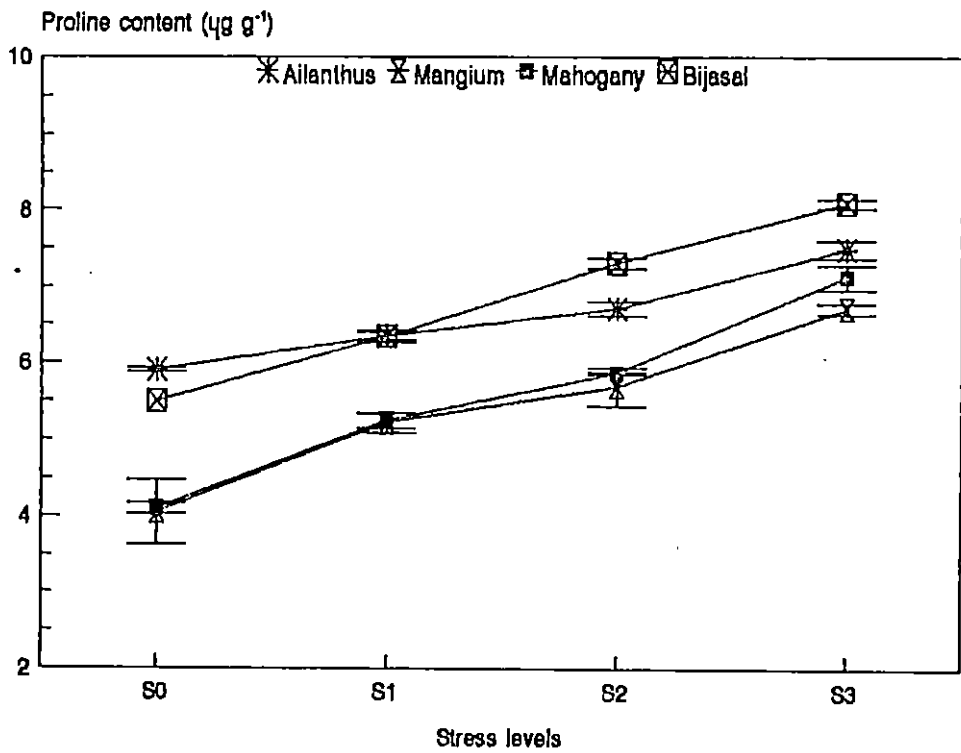
Fig.31. Proline content in the leaves of tree seedlings
as influenced by different levels of water stress
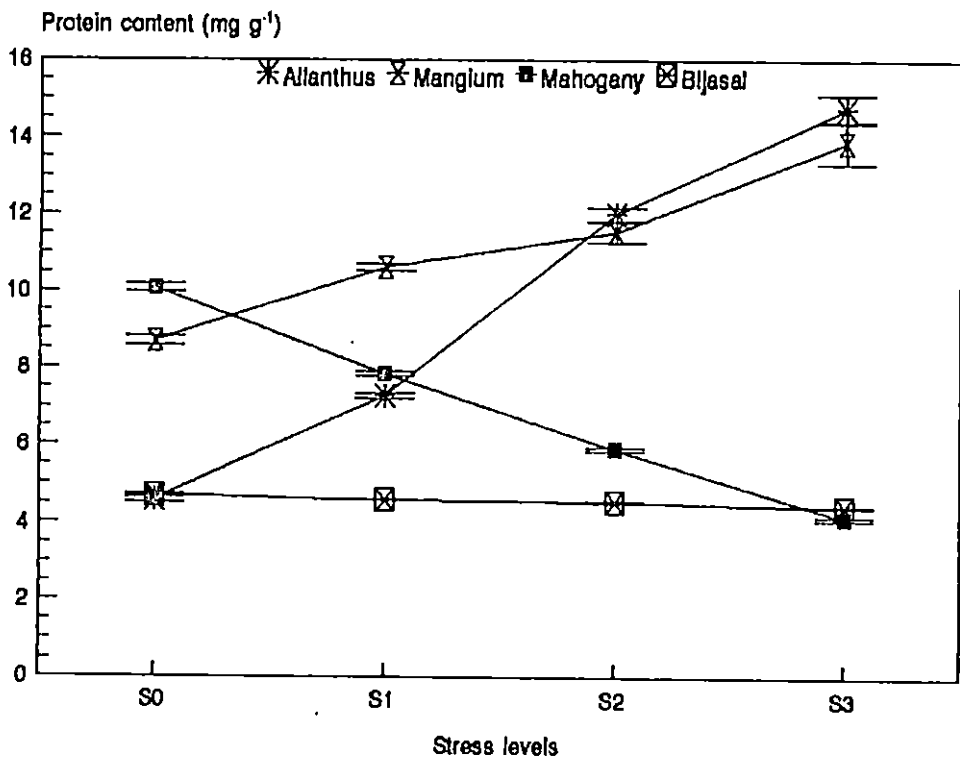
Fig.32. Soluble protein content in the leaves of tree seedlings
as influenced by different levels of water stress

an indication of the species' higher ability to tolerate stress by the production of additional 'drought stress proteins' and resultant osmotic adjustment which also calls for further investigation.

5.4 Anatomical characters

The anatomical differences observed in water stressed plants of the various species (Plates 7 to 18) showed distinct variations. A common observation in all species was that of an increase in the mechanical or supporting tissues like collenchyma, sclerenchyma and xylem elements. A decrease in the amount of spongy parenchyma cells and reduced, disintegrated palisade layers indicate that S. macrophylla seedlings are more sensitive to water stress. A decrease in the palisade layers was also observed in T. grandis seedlings. Nobel (1980) reported that environmental influences like water stress can cause variation in the number of layers of mesophyll cells and/or in the cellular dimensions. This result in different amount of internal leaf area being available for the absorption of CO_2 per unit of leaf surface area.

One of the interesting observations made on the leaves of all species except A. mangium was that of the degeneration of chlorophyll pigments in mesophyll layers in response to water stress. A progressive degeneration, as the stress levels increased (from mild to severe) was observed in A. triphysa, S. macrophylla, P. marsupium and T. grandis seedlings as the water stress

increased. Giles *et al.* (1974) reported that mesophyll cells were more sensitive to water stress and in about 75 per cent of mesophyll cells, the chloroplast become swollen under water stress conditions. In cotton leaves, a loss in chloroplast membrane integrity due to water deficit was reported by Vieira de Silva *et al.* (1974). In the present study also, mesophyll cells were more sensitive to water stress in species like *S. macrophylla. P. marsupium* and *T. grandis.* In *S. macrophylla,* the cells were highly sensitive to water stress as compared to other species, indicating the lower tolerance of the species to water deficit situation. It is interesting to note that even with severe water stress, the chloroplast were intact in *A. mangium* seedlings as observed from the cross section of the leaves (Plate 10).

Another important observation was that of the increase in cuticle thickness. In species like *A. mangium* and *T. grandis,* the cuticular thickness was increased due to water stress (Plates 10 & 18). Leaves with thick cuticle can reduce the transpiration rates in a water deficit situation and hence, the development of thick cuticle in the above species might be an adaptation to cope up with reduced water availability. Mishio (1992) reported higher drought resistance in species with increased cuticular thickness.

Summary

SUMMARY

A study was carried out at the College of Forestry, Vellanikkara to know the response of certain selected forestry and agroforestry tree seedlings to water stress. The study was conducted during the period 1994 to 1995. Various morphological, physiological, biochemical and anatomical characters in response to water stress were studied in *Ailanthus triphysa* (Dennst.) Alston, *Acacia mangium* Willd., *Swietenia macrophylla* King, *Pterocarpus marsupium* Roxb. and *Tectona grandis* L.F. The pot culture experiment was laid out in a Completely Randomized Design with four water stress levels ($\sim$ < 0.3, 1.0, 5.0, 10.0 bars) in each of the species. The highlights of the study are summarised hereunder.

1.   Water stress reduced the shoot elongation rate in all the five species with very high reduction under severe water stress. *Ailanthus triphysa* was found to be less affected by water stress with regard to shoot elongation.

2.   The collar diameter of the seedlings was reduced considerably by water stress. However, mild water stress had no effect on the collar diameter of *A. triphysa* and *T. grandis* seedlings.

3. The number of leaves and leaf area showed a decreasing trend with increasing water stress levels in all the species. Infact the number of leaves and leaf area was found to be the most sensitive morphological parameter to water stress. Severe reduction in number of leaves and leaf area in *Acacia mangium* and *Swietenia macrophylla* indicate the higher susceptibility of the species to reduced water availability especially in young stages.

4. Shoot-weight and root-weight decreased due to water stress and the reduction was severe in *S. macrophylla*. In *A. mangium* the root-weight was not much influenced by water stress.

5. The root-shoot weight ratios were not influenced by water stress appreciably in any of the species studied.

6. The total drymatter production was reduced considerably due to water stress in *S. macrophylla*, *P. marsupium* and *A. mangium* seedlings.

7. Water stress increased the leaf diffusive resistance in all the species. The rise was in proportion to the increasing levels of water stress. A midday closure of the stomata was observed in all the species under water stress and the closure practically absent in well watered (control) plants.

8. The transpiration rates were reduced in all the species with increasing levels of water stress and at severe water stress, the rates were very much reduced.

9. The leaf water potential (ψ) declined for all the species with increasing levels of water stress. In *S. macrophylla*, even with mild water stress, the LWP was -2.4 MPa during the mid hours of the day. *Acacia mangium* showed a sharp decline with increasing water deficit.

10. The photosynthetic rate of all the species under study was severely affected by water stress. A midday reduction of photosynthesis was observed in all the species. *Tectona grandis* seedlings were highly sensitive to water stress, with regard to net photosynthesis, that the rate was near zero in severely stressed plants for most time of the day.

11. The leaf temperature of all the species was increased by water stress. However, a consistent pattern was lacking.

12. The chlorophyll contents were reduced significantly at all levels of water stress in *A. triphysa, S. macrophylla* and *P. marsupium*. Synthesis of chlorophyll 'b' was found to be more sensitive to water stress in *A. triphysa, A. mangium, S. macrophylla* and *P. marsupium* seedlings.

13.   The accumulation of free proline was increased by water stress in all the four species studied.

14.   The soluble protein content increased in *A. triphysa* and *A. mangium* seedlings in response to water stress. In *P. marsupium*, the protein content showed only slight reductions, whereas *S. macrophylla* seedling showed a steep decline in the soluble protein content with increasing levels of water stress.

15.   Water stress increased the amount of mechanical or supporting tissues like collenchyma, sclerenchyma and xylem elements.

16.   Chlorophyll pigments showed degeneration in the mesophyll layers in all the species except in *A. mangium*, where the chloroplasts were unaffected by water stress.

17.   Anatomically *S. macrophylla* seedlings showed more sensitiveness to water stress by decreasing the amount of spongy parenchyma cells and a reduced, disintegrated palisade layer in the leaves.

The results lead to the following conclusions. The growth characteristics and physiological behaviour of all the five species were adversely affected due to water stress. Among the five species studied

S. macrophylla is the most sensitive species and did not show much adaptations to tolerate water stress. Eventhough *A. mangium* showed adaptations like quick closure of stomata, thick cuticle and low chloroplast disintegration when exposed to water stress, growth characteristics were found to be affected. So the species has to be tested for its water stress tolerance in a long term experiment. *Pterocarpus marsupium* is also found to be sensitive to water stress and all the growth characters were adversely affected. However, it showed relatively high net photosynthesis and relative growth rate. *A. triphysa* is the least sensitive species to water stress. Considering the relative growth rate and net photosynthesis, *A. triphysa* and *P. marsupium* are rated to perform well under dry situations. Among the five species studied *T. grandis* seedlings showed symptoms of permanent wilting when the water stress was increased from moderate (~5 Bar SMT) to severe (~10 Bar SMT) levels. Other species did not show permanent wilting even when the plants were not watered for nine days continuously (S_3). Growth characteristics in *T. grandis* was not much affected due to mild (S_1) levels of water stress eventhough the plants wilted and dried under severe water stress (S_3). Long term and extensive studies have to be conducted to understand the variation in response of these species to water stress during various phases of growth.

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Appendices

APPENDIX I

Weather parameters during the study period (June 1994 to September 1995)

Months	Mean monthly rainfall (mm)	Mean monthly temperature (°C)		Relative humidity		No. of rainy days
		Max.	Min.	FN	AN	
June '94	955.1	28.9	22.9	96	83	27
July '94	1002.1	28.6	22.4	96	85	29
Aug. '94	509.2	30.3	22.8	95	75	20
Sept.'94	240.5	31.8	23.2	92	64	8
Oct. '94	358.2	32.3	22.7	92	68	20
Nov. '94	125.3	31.8	23.3	77	58	5
Dec. '94	0	32.2	22.2	71	45	0
Jan. '95	0	32.9	22.4	76	41	0
Feb. '95	0.5	35.4	23.4	79	41	0
Mar. '95	2.8	37.6	23.8	83	37	0
Apr. '95	118.7	36.6	24.9	87	55	5
May '95	370.5	33.5	23.9	91	65	13
June '95	500.4	31.6	23.1	94	77	19
July '95	884.7	29.9	23.2	96	81	26
Aug. '95	448.7	30.6	23.7	94	78	22
Sept.'95	282.5	30.1	23.5	94	70	13

APPENDIX II
Weather data (weekly average) for the experiment period (December 1994 to May 1995)

Month	Week No.	Total rainfall (mm)	Temperature (°C)		Relative humidity (%)		Sun shine hours (mean)	Wind speed (mean) Kmph	Evapo-ration (mean) mm/day
			Max.	Min.	FN	AN			
Dec. 94	49	0	31.9	21.6	68	43	10.9	8.7	5.0
	50	0	32.1	20.1	71	41	10.8	8.8	5.4
	51	0	32.2	24.0	75	50	10.4	10.7	5.8
	52	0	31.9	23.1	68	44	10.3	12.8	6.1
Jan. 95	1	0	31.8	22.1	71	42	9.5	11.2	5.8
	2	0	33.3	21.5	88	49	8.5	4.3	4.1
	3	0	31.7	23.8	71	42	9.7	10.5	6.2
	4	0	32.5	22.2	77	34	10.4	9.6	6.6
	5	0	33.9	24.2	69	37	10.8	10.8	6.98
Feb. 95	6	0	34.7	23.4	71	37	10.3	10.2	7.5
	7	0	35.6	22.6	79	39	9.9	4.6	5.6
	8	0.5	36.1	23.4	89	50	9.7	3.8	4.9
	9	0	37.2	23.1	90	37	9.0	4.3	5.6
Mar. 95	10	1.8	36.9	23.8	86	38.6	8.6	4.6	5.5
	11	1.0	37.8	23.8	82	41	9.3	3.3	5.8
	12	0	38.9	23.7	75	33	10.3	5.2	7.6
	13	0	36.5	24.5	86	47	9.5	4.6	5.9
Apr. 95	14	54.8	37.5	24.4	86	49	8.9	4.4	6.0
	15	46.2	36.3	24.7	89	52	9.1	4.0	5.6
	16	12.6	35.7	25.0	87	60	8.9	3.9	5.2
	17	5.1	37.2	25.5	85	58	9.6	4.0	5.3
	18	110.0	35.4	24.5	89	61	7.6	3.4	-
May 95	19	290.9	31.3	23.8	96	74	1.3	3.8	6.3
	20	23.2	33.0	24.3	92	64	6.8	4.1	4.1
	21	0.6	33.8	23.8	87	61	8.8	3.7	4.6
	22	4.2	34.5	23.7	91	63	8.1	4.0	4.7

APPENDIX III

Mean values on diurnal variations in leaf diffusive resistance, leaf temperature and leaf water potential of *A. triphysa* seedlings as affected by different levels of water stress

Time (hrs)	Leaf diffusive resistance (m mol m^{-2} s^{-1})				Leaf temperature (°C)				Leaf water potential (MPa)		
	S_0	S_1	S_2	S_3	S_0	S_1	S_2	S_3	S_0	S_1	S_2
0600	27.6	27.5	49.8	47.3	26.4	25.0	24.9	25.9	-0.28	-0.30	-1.43
0800	7.9	5.8	26.4	55.8	27.2	25.1	25.1	26.9	-0.49	-0.48	-2.06
1000	3.6	7.1	52.5	78.3	30.2	30.0	30.0	31.3	-1.00	-1.07	-2.13
1200	3.3	10.9	75.2	130.2	31.8	32.1	32.3	34.9	-1.07	-1.17	-1.96
1400	4.9	10.4	95.7	78.0	33.3	33.4	34.1	35.9	-0.95	-1.04	-2.12
1600	5.7	6.3	54.2	82.5	33.2	33.1	32.0	35.0	-0.83	-0.79	-1.80
1800	23.3	25.4	60.8	85.3	30.9	31.0	29.4	31.7	-0.34	-0.56	-1.74

Mean values on diurnal variations in leaf diffusive resistance, leaf temperature and leaf water potential of *A. mangium* seedlings as affected by different levels of water stress

Time (hrs)	Leaf diffusive resistance ($m\ mol\ m^{-2}\ s^{-1}$)				Leaf temperature (°C)				Leaf water potential (MPa)		
	S_0	S_1	S_2	S_3	S_0	S_1	S_2	S_3	S_0	S_1	S_2
0600	15.3	16.8	51.7	92.8	25.0	25.0	25.2	26.6	-0.10	-0.18	-1.07
0800	4.9	13.7	34.6	45.7	26.7	26.2	25.0	26.5	-0.57	-1.22	-2.22
1000	4.4	23.5	47.5	139.6	30.4	30.7	30.3	32.1	-0.82	-1.61	-2.58
1200	5.9	38.3	78.4	128.6	33.1	34.6	33.1	35.6	-1.02	-2.00	-2.91
1400	6.7	27.9	123.1	186.4	34.5	33.7	34.3	36.0	-1.00	-2.02	-2.91
1600	9.6	21.7	67.4	94.0	33.5	32.1	32.4	35.5	-1.02	-1.10	-2.17
1800	27.6	34.6	96.0	71.2	29.6	30.4	30.0	31.4	-0.30	-0.61	-1.98

APPENDIX V

Mean values on diurnal variations in leaf diffusive resistance, leaf temperature and leaf water potential of *S. macrophylla* seedlings as affected by different levels of water stress

Time (hrs)	Leaf diffusive resistance (m mol m^{-2} s^{-1})				Leaf temperature (°C)				Leaf water potential (MPa)		
	S_0	S_1	S_2	S_3	S_0	S_1	S_2	S_3	S_0	S_1	S_2
0600	54.8	105.3	106.9	118.2	22.9	24.3	23.3	22.9	-0.23	-0.29	-
0800	24.2	6.1	12.2	15.7	24.9	29.1	30.7	26.8	-1.09	-1.99	-
1000	8.3	28.4	33.9	72.0	29.2	34.4	35.5	34.9	-1.54	-2.14	-
1200	7.3	26.1	36.7	64.3	31.8	38.3	37.4	36.9	-1.88	-2.13	<-2.6
1400	7.3	50.4	42.4	109.2	34.9	40.4	36.8	37.9	-1.52	-2.40	-
1600	9.4	71.8	80.3	27.0	33.4	39.8	35.5	34.2	-1.89	-2.05	-
1800	29.7	86.5	80.1	24.8	30.9	36.6	32.5	30.4	-1.00	-1.50	-

APPENDIX VI

Mean values on diurnal variations in leaf diffusive resistance, leaf temperature and leaf water potential of *P. marsupium* seedlings as affected by different levels of water stress

Time (hrs)	Leaf diffusive resistance (m mol m^{-2} s^{-1})				Leaf temperature (°C)				Leaf water potential (MPa)			
	S_0	S_1	S_2	S_3	S_0	S_1	S_2	S_3	S_0	S_1	S_2	S_3
0600	37.4	37.1	61.9	58.0	23.6	26.2	26.2	25.1	-0.19	-0.21	-0.36	-0.37
0800	6.0	3.5	21.5	13.5	25.3	29.2	30.4	27.5	-0.39	-0.30	-0.57	-0.56
1000	3.0	3.9	43.2	48.1	29.6	32.8	34.2	33.4	-0.50	-0.72	-0.69	-0.85
1200	4.7	14.2	48.1	33.8	34.0	36.1	37.4	33.6	-0.81	-0.83	-1.68	-2.00
1400	5.6	16.3	74.2	109.6	34.4	38.1	37.6	34.5	-1.14	-1.13	-2.07	-2.32
1600	8.7	12.4	71.4	29.2	33.8	38.5	33.1	33.0	-0.64	-0.89	-1.07	-1.15
1800	44.4	28.8	40.8	44.2	30.4	36.6	31.8	31.1	-0.21	-0.37	-0.46	-0.49

APPENDIX VII

Mean values on diurnal variations in leaf diffusive resistance, leaf temperature and leaf water potential of *T. grandis* seedlings as affected by different levels of water stress

Time (hrs)	Leaf diffusive resistance (m mol m^{-2} s^{-1})			Leaf temperature (°C)			Leaf water potential (MPa)		
	S_0	S_1	S_2	S_0	S_1	S_2	S_0	S_1	S_2
0600	28.0	20.7	34.8	24.5	24.3	24.3	-0.26	-0.66	-0.70
0800	6.5	6.5	8.0	25.1	26.5	26.5	-0.40	-1.01	-1.17
1000	2.5	13.5	26.8	28.1	30.0	30.4	-0.71	-1.20	-1.76
1200	3.4	32.8	48.9	29.8	31.7	32.5	-1.04	-1.81	-2.46
1400	4.6	35.5	51.6	30.1	32.4	32.9	-0.99	-1.90	-2.52
1600	6.7	20.8	31.5	31.3	31.8	31.8	-1.01	-1.71	-2.03
1800	22.4	29.0	45.4	32.8	30.2	30.2	-0.33	-1.03	-1.41

Observations on S_3 plants not recorded as the plants dried off when water stress was continued for more than 6 days

RESPONSE OF SELECTED FORESTRY AND AGROFORESTRY TREE SEEDLINGS TO WATER STRESS

BY

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ABSTRACT OF A THESIS

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ABSTRACT

An experiment was conducted at the College of Forestry, Kerala Agricultural University, Vellanikkara, Thrissur during the period from 1994 to 1995 with seedlings of *Acacia mangium* Willd., *Ailanthus triphysa* (Dennst.) Alston., *Pterocarpus marsupium* Roxb., *Swietenia macrophylla* King and *Tectona grandis* L.F. to study the response of the species to water stress.

The results showed that the growth characteristics and physiological behaviour of all the five species were adversely affected due to water stress. Among the five species studied *S. macrophylla* was the most sensitive species and did not show much adaptations to tolerate water stress. Eventhough *A. mangium* showed adaptations like quick closure of stomata, thick cuticle and low chloroplast disintegration when exposed to water stress, growth characteristics were found to be adversely affected due to water stress. So the species has to be tested for its water stress tolerance in a long term experiment. *Pterocarpus marsupium* was also found to be sensitive to water stress and all the growth characters were adversely affected. However, it showed relatively high net photosynthesis and relative growth rate. *Ailanthus triphysa* was the least sensitive species to water stress. Considering the relative growth rate and net photosynthesis, *A. triphysa* and *P. marsupium* are rated to perform well under dry situations. Among the five species studied *T. grandis* seedlings showed symptoms of permanent wilting when the water stress was increased from moderate (~ 5 Bar SMT) to severe (~ 10 Bar SMT) levels. Other species did not show permanent wilting even when the plants were not watered for nine days continuously (S_3). Growth characteristics in *T. grandis* was not much affected due to mild (S_1) levels of water stress eventhough the plants wilted and dried under severe water stress (S_3).