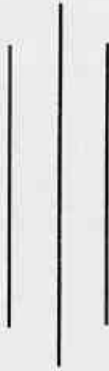




**ANALYSIS OF WATER RELATIONS AND PHENOLOGY IN  
*BAUHINIA VARIEGATA* L., *LARGERSTROEMIA INDICA* L. AND  
*CELTIS AUSTRALIS* L. IN KIRTIPUR, KATHMANDU.**



**A DISSERTATION SUBMITTED FOR THE PARTIAL FULFILLMENT OF THE  
REQUIREMENT FOR THE MASTER OF SCIENCE IN BOTANY**



**BY  
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KATHMANDU, NEPAL  
2003**



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INSTITUTE OF SCIENCE AND TECHNOLOGY  
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Kirtipur, Kathmandu  
NEPAL

## RECOMMENDATION

This is to certify that the dissertation work entitled **Analysis of Water Relations and Phenology of *Bauhinia variegata* L., *Celtis australis* L. and *Lagerstroemia indica* L.** in Kirtipur, Kathmandu, submitted by Miss Sandhya Tripathi for the partial fulfillment of M.Sc. in Botany, has been carried out under my supervision. The entire work is based on the results of her own work and has not been submitted for any other degree to the best of my knowledge.

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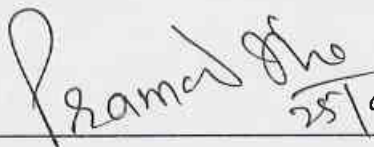
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## Letter of Approval

The dissertation paper submitted by Miss Sandhya Tripathi entitled “**Analysis of Water Relations and Phenology of *Bauhinia variegata* L., *Lagerstroemia indica* L. and *Celtis australis* L. in Kirtipur, Kathmandu**” has been accepted as a partial fulfillment of Masters in Botany.

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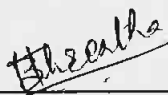
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.....  
Sandhya Tripathi

## ABSTRACT

Seasonal variation in water relation parameters and phenological processes of *Bauhinia variegata* L., *Celtis australis* L. and *Lagerstroemia indica* L. were studied in Coronation Garden of Tribhuvan University, Kirtipur, Kathmandu, Nepal. The measurement was carried out from August 2002 to June 2003 at monthly interval. Parameters like leaf relative water content, P-V curve analyses, leaf conductance, specific leaf mass and phenology were determined.

Leaf relative water content was always higher throughout the year in all the species studied but wide variation between leaf relative water content and relative water content at zero turgor was observed. Osmotic potential decreased with increasing pressure potential during the dry season which facilitates the plants to extract water easily. Bulk modulus of elasticity decreased in this season. Plants never reached to its turgor loss point during the study period. Both osmotic and elastic adjustment equally worked for all species. But with the initiation of leaf fall (from winter), osmotic adjustment was found more pronounced in *Bauhinia variegata* and the elastic adjustment differed at different seasons of the year.

Leaf conductance was low in winter (December and January) in all species. The lower values of hydraulic conductivity, specific conductivity, leaf specific conductivity and Huber value in the species indicate the xylem embolism with the initiation of dry period. SLM was low in March in *B. variegata* and *C. australis* but in December in *L. indica*. Most of the phenological activities took place in the dry months (March - April) of the year in all the species except flowering (June) in *L. indica*.

## ACRONYMS AND ABBREVIATIONS

$A_l$	Leaf area
$A_{we}$	Effective xylem area
BP	Balance pressure
$g_s$	Leaf conductance
$g_{sd}$	Leaf conductance at mid-day
$g_{sm}$	Leaf conductance at morning
HV	Huber value
$K_h$	Hydraulic conductivity
$K_l$	Leaf specific conductivity
$K_s$	Specific conductivity
LRWC	Leaf relative water content
$LRWC_{pd}$	Predawn leaf relative water content
$LRWC_{md}$	Mid-day leaf relative water content
MPa	Megapascal
P-V curve	Pressure Volume curve
Q	Light intensity
r	Karl Pearson coefficient of correlation
RH	Relative humidity
RWC	Relative water content
$RWC_z$	Relative water content at zero turgor
SLA	Specific leaf area
SLM	Specific leaf mass
VPD	Vapour pressure deficit
$\overline{X}$	Coefficient of leaf area
$\overline{X}$	Arithmetic mean
$\Delta T$	Change in temperature
$\epsilon$	Bulk modulus of elasticity
$\sigma$	Standard deviation
$\psi_l$	Leaf water potential
$\psi_p$	Pressure potential
$\psi_{pf}$	Pressure potential at full turgor
$\psi_{pz}$	Pressure potential at zero turgor
$\psi_s$	Osmotic potential
$\psi_{sf}$	Osmotic potential at full turgor
$\psi_{soil}$	Soil water potential
$\psi_{sz}$	Osmotic potential at zero turgor

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# 1. INTRODUCTION

## 1.1 BACKGROUND

On global basis, water is a paramount factor in determining the distribution of species, and the responses and adaptations of species to water stress are critical for its success in any environmental niche (Lange *et al.*, 1972). Its availability is the single most important environmental factor limiting the growth and distribution of trees (Zimmermann *et al.*, 1971; Hinckley *et al.*, 1991; Kramer and Boyer, 1995). Terrestrial plants are exposed to water regimes that change seasonally and diurnally. If they are to survive, they must adjust physiologically and/or anatomically and have a broad range of tolerance or avoid times of limited water (Barbour *et al.*, 1999). Low water availability limits the productivity of many natural ecosystems particularly in dry climate. Loss in crop yield due to water stress exceeds loss due to all other biotic and environmental factors (Lambers *et al.*, 1998). Carbon isotope discrimination method in *Acacia koa* also showed that decrease in productivity is due to decreased water availability rather than nitrogen or other nutrient deficiency (Ares and Fownes, 1999). All plants, to varying degree, can also acclimatize to an environment where water is scarce; thus a full understanding of biophysical, physiological and molecular aspect of plant water relation is essential if we aim to improve the performance of economically important plants in dry environments (Lambers *et al.*, 1998).

Plant water deficit influences all the aspect of plant organization viz, metabolism, physiology as well as gross morphology. Growth of plants probably is limited more often by internal water deficits than by any other single internal factors. Water relation of trees are as important to their successful growth as the biochemical processes involved in synthesis of food and its transformation into new tissues (Kramer and Kozlowski, 1960).

Variation in forest productivity, biomass, leaf properties, structure and diversity is well documented for many regions of the world, which is directly influenced by the availability of water (Zobel *et al.*, 1995). Seasonal variation in tree water status appears to be the principal determinant of both phenology and distribution of tree species in tropical dry forests (Borchert, 1994 a). Leaf shedding, flowering and shoot emergence (flushing) were strongly correlated with seasonal changes in tree water status, which varied with the

availability of sub-soil water and a variety of biotic factors such as structure and life span of leaves, time of leaf shedding, wood density and stem water storage capacity, and depth and density of root system. Species distribution is also determined by their differences to tolerate drought; those with lower tolerance being confined to moist sites (Kramer and Boyer, 1995). Similarly, site dependent differences in soil water availability, not seasonal rain fall, are principle environmental causes of variations in tree water status, phenology and distribution of tree species (Borchert, 1994 a).

Himalayan ecosystem includes vegetation from both tropics and temperate region. The Himalayan climate is famous for the concentrated rainfall, three to four months during June to September. Such concentrated warm season rainfall and the complementary eight to nine months of drought are likely to have a profound effects on adaptations and ecosystem processes (Zobel and Singh, 1997). Thus, study on the Himalayan trees subjected to drought can contribute to the understanding of local patterns of species distribution and performance, as well as plant water relation in general. This study deals with seasonal variation in water potential, xylem conductance and leaf conductance, leaf relative water content and specific leaf mass along with phenology in *Bauhinia variegata*, *Celtis australis* and *Lagerstroemia indica* in planted area of Coronation Garden, Tribhuvan University, Kirtipur, Kathmandu.

## 1.2 PLANT WATER STATUS

The exchange of water and energy between plant communities growing under natural conditions and their environment determines, to a considerable extent, not only the characteristics of the physical micro-environment but also the characteristics and functions of the plant themselves. In particular the water relations of plants influence and are influenced by these exchanges and in general precipitation frequently appear to dominate the micro-environment (Slatyer, 1963)

'Water status' refer to any measure of the general state of a plant in relation to water, and is therefore used in a relative sense. It may refer to plant's water potential, its relative water content or its turgor (Passioura, 1982). The water status is based on a physically defined reference rather than a biological one (Kramer and Boyer 1995). The status of water in soils, plants, and the atmosphere is commonly described in terms of water

potential ( $\psi$ ). Therefore plant water status is assessed as plant water potential which is the work necessary to raise the bound water to the potential level of pure water.

Water potential is the important parameter of plant water relations (Larcher, 1995) to describe plant and soil water status on common physical basis (Chaves, 1991). Water potential in any part of the system is the algebraic sum of the osmotic potential ( $\psi_{\pi}$ ), and the hydrostatic pressure ( $\psi_p$ ).

i.e.  $\psi_w = \psi_{\pi} + \psi_p$ .

The osmotic potential is the chemical potential of water in a solution due to the presence of dissolved materials. It has a negative value. The hydrostatic pressure refers to the physical pressure exerted on water in the system, and it may have positive or negative values and its effect depends both on the living or dead cells.

Therefore, measurement of water potential has gained widespread acceptance as the most useful approach to the quantification of water status (Pallardy *et al.*, 1991). However, no single measure of plant water status can be expected to be correlated with numerous effects of plant water stress (Kramer, 1988). So, other variables like xylem conductance, P-V analysis and relative water content (RWC), are important indicators in assessing the plant water status.

### 1.3 PRESSURE VOLUME (P-V) CURVE ANALYSIS

The pressure volume (P-V) curve is widely used parameter to analyse the plant water relations (Koide *et al.*, 1989; Pallardy *et al.*, 1995). It is obtained by plotting reciprocal of the water potential of sample tissue (obtained by pressure chamber) and RWC. The curve displays the relationship between water potential components and water content of the tissues (Pallardy *et al.*, 1991; Larcher, 1995; Zobel 1996) which are not constant and vary among species and with the environment of the plant. From the P-V curve several parameters of plant water relations including osmotic and turgor potentials at different levels of hydration, tissue elasticity, and osmotic and elastic adjustment during the water stress can be analysed (Tyree and Hammel, 1972; Koide *et al.*, 1989; Pallardy *et al.*, 1991).

P-V relation also gives the elastic modulus ( $\epsilon$ ) of the leaf or shoot (Tyree and Hammel, 1972). The elasticity of cell wall determines the rate of change of turgor pressure of a cell with respect to change in water content (Cheung *et al.*, 1975; Passioura, 1982)

Relative water content (RWC) is a simple way of expressing the quantity of water of plant tissue (Boyer 1969; Kramer 1988, Pallardy *et al.*, 1991). RWC is the water content (on percentage basis) relative to the water content of the same tissue at full turgor. It is commonly used as an indicator of plant water status and is related to water potential. Thus Pressure-Volume analysis i) shows how components of water potential changes as the RWC decline and ii) measures the elasticity of tissues.

## 1.4 STOMATAL CONDUCTANCE

The stomata occupy a central position in the pathway for both the loss of water from plants and the exchange of  $\text{CO}_2$ . It is commonly assumed that they therefore provide the main short-term control of both transpiration and photosynthesis (Jones and Sutherland 1991; Jones 1998). One of the important effects of internal water deficit is closure of stomata. Among all the factors affecting the movement of guard cells, water deficit is most important and thus it has been found that stomatal aperture is a sensitive indicator of internal water balance of plants (Kramer and Kozlowski, 1960). Plants also control their water status by regulating the size of stomatal openings, which modify the rate of water loss; reducing water loss can reduce the effect of limited soil moisture on water potential (Zobel and Singh, 1995).

Stomatal conductance of leaf surface to water vapour is an important indicator of plant water relation (Schulze, 1988). The regulation of stomatal conductance is generally considered to be the main mechanism by which plant controls water loss and their hydration level (Cowan 1982), and stomatal control is often thought to be the first line of defense against water stress. Therefore stomatal conductance to water stress is a key variable in many studies related to plant water balance and photosynthetic relation (Percy *et al.*, 1989).

## 1.5 XYLEM CONDUCTANCE

Xylem conductance is the measure of efficiency of xylem to conduct water. Hydraulic conductivity, specific conductivity, leaf specific conductivity and Huber value are measured to characterize xylem conductance. These parameters give information on functional efficiency of xylem, vulnerability to embolism and hydraulic sufficiency of xylem to supply water to leaves.

Water deficit in the plant is created when the loss of water from the transpiring area is greater than the absorption by the roots. In such condition, replenishment of the water loss from shoots by transpiration required an efficient water conducting system (Kramer and Boyer 1995). Thus, hydraulic architecture can potentially limit the flow of water to leaves controlling leaf water potential, stomatal conductance and gas exchange (Tyree and Ewers, 1996).

Rapid growth in many species is predicted on high hydraulic conductivity or low transpiration rates, which allow for maximum turgor potential in growing tips (Dixon *et al.*, 1988). Thus, high leaf specific conductivity value may be part of necessary strategy for rapid growth (Tyree and Ewers, 1996).

Water movement in plant takes place along the water potential gradient by diffusion from cell to cell (short distance transport) and by conduction (long distance transport) through the xylem. The amount of water moved through the vascular system in unit time is dependent on the specific properties of the xylem, such as conducting area (cross-sectional area of vessels) and flow resistances, on the physiological state of the plant (e.g. degree of stomatal opening) and an environmental conditions. Larger the conducting area, higher the flow velocity (Larcher, 1995).

Hydraulic conductivity is the ability of the tissue to supply water to the growing cells. Hydraulic conductivity ( $K_h$ ) per unit pressure gradient is equal to the ratio between the water flux through an excised stem segment and the pressure gradient causing the flow.

Huber value, (HV) is the ratio of xylem conducting area ( $A_{xyl}$ ) and the leaf surface area or leaf mass of the transpiring parts of the plant that are supplied with water by this conducting tissue. HV is more informative than the total cross sectional area in water



relation of the whole plant. It is particularly large in plants that lose large quantities of water by transpiration. Furthermore, HV is matched to the size of the plant, and it also modifies during growth to meet local moisture conditions (Larcher, 1995).

Specific conductivity ( $K_s$ ) is the measure of porosity of the wood. It depends on the diameter of the conducting element and its type of perforation (Larcher 1995).  $K_s$  indicates how functional the xylem is as it is the rate of sap flow caused by unit pressure gradient through unit area of the xylem. According to Huber (1928), the specific conductivity of branches of the trunk decreases from bottom to top. This is compensated for by a considerable increase in relative conducting surface from the base to the top of the trunk. The resistance to water movement is not proportional to the length of the stem because of changes in specific conductivity (Kramer and Kozlowski, 1960)

Leaf specific conductivity ( $K_l$ ) is the measure of hydraulic sufficiency of the segment to supply water of leaves distal to the segment (Tyree and Ewers, 1996).  $K_l$  can be used to explain the specific difference in stomatal responses to humidity and soil water availability (Bond and Kavanagh, 1999).

## **1.6 LEAF RELATIVE WATER CONTENT (LRWC)**

Leaf relative water content (LRWC) is a simple parameter to express plant water status. It is a superior parameter for understanding the impact of drought on physiological process (Sinclair and Ludlow, 1985). Species from different habitat has similar responses of photosynthesis to changes in RWC (Kaiser, 1987). Measurement of RWC can be an important tool to estimate plant growth and biomass production of commercial tree plantations (Naidu and Swamy, 1995).

Measurement of LRWC at predawn ( $LRWC_{pd}$ ) and mid-day ( $LRWC_{md}$ ) gives the diurnal change in leaf water status.  $LRWC_{pd}$  gives the water status of leaf when it has maximum amount of water in diurnal cycle.  $LRWC_{md}$  gives the water status when the leaf has minimum amount of water.



## 1.7 SPECIFIC LEAF MASS (SLM)

The leaves of evergreen species have higher leaf specific mass ( $\text{g/cm}^2$ ) and lower nitrogen and phosphorus contents on mass basis than the deciduous species (Mooney *et al.*, 1984; Sobrado, 1991). Leaf structural character influences leaf energy and water balance. Longer photosynthetic period probably compensate for the high energy cost of evergreen leaves, with their high SLM (Kikuzawa, 1995). Evergreen leaves lose mass gradually, without senescing, during late winter and spring, by contrast, deciduous leaves begin to lose mass before the end of rainy season and senesce rapidly during autumn (Ralhan and Singh 1987). In evergreen senescence is hastened by new growth in spring, whereas deciduous species senesce during the drying, cooling, and shortening days after the monsoon. High SLM leaves worked better in resource poor environments where retention of captured resource was a higher priority, while low SLM leaves worked best in resource rich environment, and short lived and vulnerable to herbivory (Wilson *et al.*, 1999).

## 1.8 PHENOLOGY

The variation in water availability causes significant differences in the phenology of the trees, since the trees are largest structural component and the dominant producer in forest. Phenology is a season-wise distribution of different phases of plants such as leaf flushing, leaf fall, bud break, flowering, fruiting, etc. Phenological study is the relationship between climatic factors and seasonal biological events (Leith, 1974; Kikuzawa 1995; Barbour *et al.*, 1999). The onset and duration of particular phases of development vary from year to year, depending on the weather (Larcher, 1995). Thus, phenological observations provide background information on functional rhythms of plants and plant communities (Ralhan *et al.*, 1985; Singh and Singh, 1992).

Leaf shedding during the early dry season and flowering or flushing immediately after the leaf shedding is the characteristic of most trees in tropical dry forest (Borchert, 1994 a). Seasonal patterns of tree development have therefore a major influence on ecosystem properties and are mainly determined by the duration and intensity of seasonal drought (Borchert, 1995).

Leaf shedding, flowering and shoot growth (flushing) were strongly correlated with seasonal changes in tree water status, which varied with the availability of subsoil water

and variety of biotic factors such as structure and life span of leaves, time of leaf shedding, wood density, and capacity for stem water storage and depth and density of root systems (Borchert, 1994 a). Therefore water stress is a precursor inducing phenological activities during the summer drought. Water level in such trees is managed by plant through the elimination of transpirational water loss during leaf shedding in conjunction with exploitation of more soil water through the internal adjustments. Hence all phenological events to be explained depend on the water status of stem tissues in the supporting branches (Borchert, 1994 b).

Himalayan climate is unique in having concentrated rainfall within short period, limited variation in day length and year around moderate temperature and this feature had led to observe the variations in the phenological events. Most of the Himalayan trees are phenologically active during the dry season i.e. March to May (Ralhan *et al.*, 1985). Leaves in the Himalaya both evergreen and deciduous develop generally during the dry season and are mature when the condition are warm and wet (Singh and Singh 1992). The leaf shedding is similar to dry tropical forests (Zobel and Singh, 1997). These aspects of leaf phenology like evergreen and deciduous, timing of development and senescence of leaf in turn have been linked to variations in the tree water relations (Escudero and Del Arco, 1987) and such observation strongly plays a dominant role in structuring temporal pattern of the expansion and abscission of leaves and other organs.

## 1.9 JUSTIFICATION

Himalayan climate is unique in having the concentrated rainfall, three to four month during June to September and complementary eight to nine months of drought which are likely to have profound effects on the adaptations and ecosystem processes (Zobel and Singh, 1995, 1997). The response of Himalayan trees to drought can contribute to understanding the local patterns of species distribution and performance, as well as to plant water relations in general. Therefore, an understanding of water relations is one of the necessary pre-requisites for the development of varieties of plants which will survive in the areas of longer drought; and this can only be achieved by an intensive study of the regulatory and adaptive processes which leads to change in water relations in a plant in response to environmental changes (Zimmermann and Steudle, 1978).

Distribution and ecological success of plants have complex relations with plant water relations, and one cannot judge the fitness of plant for drought based on single characteristics. Similarly, no single measure of plant water status can be expected to be well correlated with the numerous effects of plant water stress. Thus, one can interpret water relations data effectively only by understanding a suite of characteristics of a group of species that compete with each other, along with details about their other adaptive behaviour and environment.

Very few works have been carried out in water relations of tropical trees (Zobel and Singh, 1997) where the rainfall is concentrated in warm season, as compared to temperate trees where the precipitation is evenly distributed or concentrated in winter (Bannister and Kissel, 1986; Abrams and Menges, 1992; Lowenstein and Pallardy, 1993). Not much is known about water relations of trees in Nepal Himalaya. But now few works have been started. Since the present study area lies in the subtropical belt in Central Nepal, the study will be important to trace the significance of water deficits during drought for governing phenology of trees of Nepal Himalaya.

## **1.10 OBJECTIVES**

This work was performed with the following objectives:

1. To study the seasonal changes in different water relation parameters and establish correlation among them if any.
2. To know the timing of drought stress and understand possible mechanism of drought resistance.
3. To estimate the variation in specific leaf mass (SLM), leaf relative water content (RWC) and correlate these parameters with water relation.
4. To detect the effect of tree water relation on phenomorphological phases.

## **1.11 LIMITATION**

Duration of the study is one year only, as a part of master degree in Botany.

## 2. LITERATURE REVIEW

### 2.1 HISTORICAL BACKGROUND

The first important physiological work on trees was done by Stephen Hales (1727) in his publication “Vegetable Statick” (Kramer and Boyer, 1995). He measured transpiration and root and stem pressures and found that the transpiration rate varied with species, temperature, time of day and light intensity.

Although the anatomical, phytogeographical and ecological view of Haberlandt (1884), Schimper (1898), Warming (1896) and Clements (1907) challenged plant biologists of the early 20<sup>th</sup> century with an array of speculation and hypotheses about plant response and adaptation to habitat factors, further development along these lines was slow for some time. In the beginning of the 19<sup>th</sup> century de Saussure (1804) found that absorption of minerals by plants was not proportional to the absorption of water and different solutes were not absorbed in the same proportions in which they occurred in the soil, suggesting that root differs in permeability of various solutes. Development of an “*Osmotic Theory*” by Dutrochet in 1837 was the first to accurately measure osmotic pressure. In the middle of 19<sup>th</sup> century, the works of Sachs (1882 a, b) and his contemporaries can be considered a cornerstone in the development of concepts in water relations. His investigations were related with the effects of soil moisture, soil aeration, and soil temperature on water absorption and root growth.

In the beginning of 20<sup>th</sup> century, Brown and Escombe (1900) described diffusion of water through stomata to be a purely physical process. Publication of “*Transpiration and Ascent of Sap in Plants*” by Dixon (1914) was a landmark in the study of water relation of plants. However for the first quarter of this century, ecological research remained mainly descriptive, with little serious correlation of plant distribution and habitat factors, and physiological research remained confined to the laboratory. With few notable exceptions, the pioneers who took physiological experimentation to the field included the plant chemist at the Carnegie Institution's Desert Research Laboratory: Richards (1915), Spoehr (1919), Fitting (1911) and Shreve (1914) who investigated plant water relation under desert conditions. Wood (1925) studied salinity and water relations of Australian halophytes. Turesson (1922) introduced genecology as a tool in ecological plant

physiology. These workers were then followed by the true founders of the discipline i.e. Huber (1935), Lundegardh (1924), Pisek and Cartellieri (1939), Stocker (1928) and Walter (1931) in Europe; Maximov (1923) in Russia; Evenari and Richter 1937 and Oppenheimer (1932) in Israel; Daubenmire (1947) in United States; and Beadle (1925) in Australia.

Development of Thermocouple Psychrometer (Spanner, 1951; Monteith and Owen, 1958; Richards and Ogata, 1958) and pressure chamber by Scholander *et al.*, (1964, 1965) made the measurement of water potential easy and today these are used to characterise the plant water status. Using pressure chamber today, one can easily measure very accurately osmotic potential, pressure potential, cell wall elasticity and relative water content.

## 2.2 MAJOR PUBLICATIONS

Several books have been published on eco-physiology, particularly in water relations and stress physiology since the first publication of “Vegetation Statick” by Stephen Hales in 1727. Some of the major publications (books) on eco-physiology and water relations are: *Physiology of Trees* by Kramer and Kozlowski (1960), *Water Metabolism in Plants* by Kozlowski (1961), *Water Deficits and Plant Growth*, (vol. 1-7) by Kozlowski (1968-1983), *Plant-Water Relationships*, by Slatyer (1967), *The Physiological Ecology of Woody Plants*, by Kozlowski (1972), *Methods of Studying Plant Water Relations*, by Slavik (1974), *The Physiology and Bio-chemistry of Drought Resistance in Plants* by Paleg and Aspirals (1981), *Water Relations of Plants* by Kramer (1983), *Xylem Structure and Ascent of Sap* by Zimmermann (1983), *The Physiological Ecology of Woody Plants* by Kozlowski *et al.*, (1991), *Forest Tree Eco-physiology* by Lassoie and Hinckley (1991), *Water Relations of Plants and Soils* by Kramer and Boyer (1995), *Physiological Plant Ecology* by Larcher (1995), *Plant Physiological Ecology* by Lambers *et al.*, (1998) and *Environmental Biophysics* by Campbell and Norman (1998).

## 2.3 RECENT WORKS

In recent time, some of the prominent scientists working on water relations and phenology are: R. Borchert (University of Kansas, Lawrence, USA), M.T. Tyree (USDA, Forest Service, Northeastern Forest Experiment Station, Vermont, USA), D.B. Zobel (Oregon State University, Corvallis, USA), K. Kikuzawa (Hokkaido Forestry Research

Institute, Hokkaido, Japan), A.G. Netting (University of New South Wales, Sydney, Australia), S.P. Singh (Kumaon University, Nainital, India), etc.

In Nepal, the study on water relations and phenology is being carried out since 1998 through a joint project of Prof. D.B. Zobel (Oregon State University, Oregon, USA) with Prof. P.K. Jha (Central Department of Botany, Tribhuvan University, Kathmandu, Nepal). Since then water relations and phenology have been studied in *Castanopsis tribuloides* (Adhikari, 2000), *Shorea robusta* (Mainali, 2000, Tripathi 2001), *Pinus roxburghii* (Shrestha, 2001), *Schima wallichii* (Bhattarai, 2001, Pokharel, 2001), *Alnus nepalensis* and *Cotoneaster bacillaris* (Upreti 2002) and *Cinamomum camphora* and *Quercus lanata* (Nepal, 2002).

### 2.3.1 Plant Water Potential

The effect of drought on phenology, growth and physiological processes, as well as the water relations of white Oak (*Quercus alba* L.), and eight other species in oak hickory forest were studied by Hinckley *et al.*, (1979). They found that growth was reduced, die-back increased, net photosynthetic rate depressed to near the compensation point and phenological patterns in the next year were altered.

Calkin and Pearcy (1984) observed the seasonal decreases in plant water potentials which was greatest in evergreen (*Heteromeles arbutifolia*), intermediate in winter deciduous (*Cercis occidentalis*) and least in drought deciduous (*Aesculus californica*).

Calson *et al.*, (1994) studied plant-soil water relation on forestry and silvipastoral system in Oregon, USA and found that grazing of understorey vegetation might reduce water stress of trees during dry periods by reducing transpirational water use by the forage plants. Dawson (1996) concluded that small trees had lower overall rates of water loss at leaf and canopy levels than large trees.

The response of *Pinus sylvestris* L. to drought and stomatal control of transpiration and hydraulic conductance was studied by Irvine *et al.*, (1998). Their study suggest that, in response to soil water deficit, mature scot pine closes its stomata sufficiently to prevent the development of substantial xylem embolism. Reduced growth in the year after a severe soil water deficit is most likely to be the result of reduced assimilation in the year



of the drought, rather than to any residual embolism carried over from one year to the next.

Auge *et al.*, (1998) compared the lethal leaf water potential as a surrogate of foliar dehydration tolerance and maximum capacity for osmotic adjustment among 12 temperate deciduous tree species. Among these species, decreasing lethal leaf water potential was significantly correlated with increasing capacity for osmotic adjustment. In addition to water relation parameters and strategies that plants use (e.g. osmotic and elastic adjustment) to neutralize drought stress, plants have evolved many physiological, morphological, anatomical and phenological characteristics for responding to and resisting drought stress (Auge *et al.*, 1998).

Ares and Fowness (1999) studied changes in stand structure, productivity, canopy development, growth efficiency and intrinsic water use efficiency (WUE) of native tree *Acacia koa* across a gradient of decreasing rainfall (2600-700 mm) with increasing elevation (700-2000m) on the island of Hawaii. They found that long term structural and growth adjustments as well as changes in WUE are important mechanism of *A. koa* in response to water limitation.

Chone *et al.*, (2001) determined the leaf water potential at dawn (dawn  $\psi$ ), leaf water potential (leaf  $\psi$ ) and stem water potential (stem  $\psi$ ) of mature leaves to know the water status of non-irrigated vine in vineyards during growing season. Stem  $\psi$  was the most discriminating indicator for both moderate and severe water deficits. The difference between stem  $\psi$  and leaf  $\psi$  ( $\Delta\psi$ ) provides an indirect measurement for mean leaf transpiration which varied with soil moisture conditions and vapour pressure deficit in the atmosphere.

### **2.3.2 Pressure – Volume (P-V) Curve Analysis**

Elasticity of cell wall determines the rate of change of turgor pressure of a cell with respect to changes in water. A cell with more rigid wall (lower elasticity) drops its turgor pressure (and therefore water potential) more in response to a given change in water content. Tissues with higher elasticity are able to maintain adequate osmotic water

content even at lower water potential, which have high adaptive value to a plant species with high water stress during its life cycle (Chueng *et al.*, 1975).

Robert *et al.* (1980) used the pressure – volume method to study the leaf water relationship in four widespread forest tree species (*Ilex opaca* Ait., *Cornus florida* L., *Acer rubrum* L. and *Liriodendron tulipifera*). Water potential components (turgor osmotic and matric) were obtained by the analysis of P-V curves and recorded highest (least negative) initial osmotic potentials (the value of the osmotic component at full turgidity) at the start of the growing season. These value decreased (becoming progressively more negative) as the season progressed through a drought period. Following a period of precipitation at the end of the drought period, initial osmotic potential increased towards the value measured earlier in the season.

Tissue water relations and seasonal changes in leaf water potential components of an evergreen tree, two evergreen shrubs, two deciduous tree and deciduous vine were compared by Sobrado (1986). They analysed water relation using pressure – volume curves and showed that evergreen species could develop a higher leaf turgor and lose turgor at lower leaf water potentials than deciduous species. This was related to a lower osmotic potential at full turgor in evergreen ( $\cong -3.0\text{MPa}$ ) than in deciduous ( $\cong -2.0\text{MPa}$ ) species, rather than to elastic proportion of leaf tissue.

Kubiske and Abrams (1990) have indicated that artificial rehydration may significantly alter P-V relationships such as the plateaus effect, resulting in erroneous measurements of tissue, elasticity and osmotic potentials. They also suggested that linear regression of P-V at and above the turgor loss point may be used to extrapolate saturated weight from non-rehydrated samples at various moisture deficits thus eliminating the plateau effect and other potential rehydration problems.

Fan *et al.* (1994) compared the relative contribution of elastic and osmotic adjustments to turgor maintenance of woody species (i.e. seedlings of *Pinus backsiana* Lamb., *Picea mariana* (Mia) B.S.P., and *Eucalyptus grandis* W. Hill ex Maiden.), and concluded that elastic adjustment ( $<-3.7\text{ MPa}$ ) was more important for turgor maintenance than osmotic adjustment ( $<-0.13\text{ MPa}$ ), maximum bulk modulus of elasticity but not osmotic potential at full turgor, was significantly correlated with the RWC and water potential at zero



turgor in droughted seedlings. Both the inherent capacity for turgor maintenance of a species under drought and its ability to adjust to repeated drought should be considered in genetic selections for drought tolerance.

Zobel (1996 a) developed pressure – volume curves for twigs of three deciduous, three evergreen broadleaf, four pine and two other conifer species in the southern Appalachian mountains, U.S.A. He found that water relations parameter usually varied with leaf form, and occasionally with sampling location. Patterns of variation among leaf forms differed for each combination of parameters and season: the strongest generality was that leafy deciduous twig and pines had high tissue elasticity, whereas evergreen broad leaf species had low elasticity. Also they concluded that evergreen broadleaf species had a consistently high relative water content at zero turgor.

Marsal and Girona (1997) studied the effects of water stress cycles on turgor maintenance processes in pear leaves (*Pyrus communis*) and concluded that the leaf water potential, and relative water content at the turgor loss point of control leaves tended to decrease from spring to summer. Changes in leaf osmotic potential at full turgor and in symplast water fraction did not explain the seasonal decrease in leaf water potential.

From P-V curve analysis of two mediterranean species (*Phlomis fruticosa* L. and *Cistus creticus* L.) Grammatikopoulos (1999) reported the less pronounced summer reduction of water potential at turgor loss point. During summer, gradual decrease in osmotic potential and apoplastic RWC (xylem sap), increase in tissue elasticity were observed. So both species used combination of osmotic and elastic adjustment in order to maintain their turgidity during dry period. The summer leaf of *P. fruticosa* tolerates dehydration quite successfully, surviving at RWC value as low as 17%. This improved dehydration tolerance of the summer leaves was attributed to possession of physiological and /or biophysical adaptation to water stress, reflected in lower osmotic potential at full turgor and at turgor loss point.

Adhikari (2000) observed osmotic adjustment to be the most effective strategy of tolerating drought rather than elastic adjustment in *Castanopsis tribuloides*. However *Shorea robusta* used both osmotic and elastic adjustment to maintain turgidity during dry period of the year (Mainali, 2000).

By comparing water relations of mediterranean shrubs, Tognetti *et al.*, (2000) showed that all the species studied (*Erica arborea* L., *Myrtus communis* L. and *Juniperus communis* L.) maintained higher turgor potential under elevated CO<sub>2</sub> during drought, so that growth should be affected less than for plants exposed to drought in ambient CO<sub>2</sub>. Elevated CO<sub>2</sub> had the potential to alter the competitive relationships, in terms of tissue water relations, by differentially altering the mechanism to withstand stress period. Thus it might represent an important factor in controlling species composition and diversity.

*Schima wallichii* showed least osmotic adjustment in comparison to higher elastic adjustment in phenologically active period i.e. during summer drought (Bhattarai, 2001). Similarly, *S. wallichii* is highly stressed during summer than winter season and during summer both elastic and osmotic adjustment have significant roles for drought tolerance (Pokharel, 2001). He also found phenological processes highly correlated with drought.

Zobel *et al.* (2001) developed P-V curve for seedling of *Chamaesyce lawsoniana* A. Murr. and  $\psi_{sf}$ , RWC<sub>2</sub> and index of tissue elasticity (IE) were calculated.

Nepal (2002) found both osmotic adjustment and elastic adjustment in phenologically active period in *Quercus lanata* and *Cinnamomum camphora* but only osmotic adjustment in *Quercus lanata*. Similarly, Uprety (2002) observed osmotic adjustment in *Alnus nepalensis* and both elastic and osmotic adjustment in *Cotoneaster bacillaris* in dry months.

### 2.3.3 Stomatal Conductance

Stomatal closure is a drought avoidance mechanism and this mechanism represents trade off between continued transpiration and photosynthetic activity (Levitt, 1972). Thus stomata have evolved as regulatory valves to minimize water loss for a given amount of carbon gained (Bradford and Hsiao, 1982).

Sheriff (1979) in the review "Stomatal aperture and the sensing of the environment by guard cells" concluded that guard cells cannot lose water directly to the atmosphere, so that stomatal responses to humidity is mediated through metabolic responses to guard cells to water stress in epidermis to whole leaf water stress.

The vulnerability of xylem conduits to cavitation theoretically determines the maximum flow rate of water through plants, and hence maximum transpiration ( $E$ ), stomatal conductance ( $g_s$ ), and leaf area ( $A_L$ ). Sperry *et al.*, (1993) while studying the field-grown *Betula occidentalis* found that reduction of  $K$  at constant  $E$  would reduce leaf water potential below the threshold bringing about stomatal closure probably via abscisic acid (ABA) released into the leaf apoplast. Modulation of  $g_s$  could maintain leaf  $\psi$  approximately constant near the threshold value.

The effects of soil and atmospheric water deficits are main variable determining stomatal closure in native mediterranean species in field (Castell and Terrudas 1995). Maier and Koch (1995) studied stomatal control and abscission of needles in spruce of Northern Alps and found the association of low leaf turgor values with shedding of green needles. The loss of stomatal control changed the drought avoidance abilities of the foliage, and as a consequence, low turgor level occurred and premature needle abscission was induced.

Changes in water relations, gas exchange, and carbohydrates of white spruce seedling was studied by Wang and Zwiazek (1995). They found that both net photosynthesis and stomatal conductance showed a significant linear relationship with minimum air and soil temperature, and there was a significant linear relationship between net photosynthesis and stomatal conductance.

The work of Borel *et al.* (1997) on stomatal conductance and ABA concentration in the xylem sap of barley lines of contrasting genetic origins concluded that stomatal control had a low genetic variability in the studied range of lines, in spite of the large genetic difference between lines. Prior *et al.* (1997) showed that  $g_s$  was always higher in the morning than in the afternoon, irrespective of the season in *Eucalyptus tetrodonta* sampling of a wet dry savanna in northern Australia.

Pataki *et al.* (1998) studied the canopy architecture and water relation in response to progressive defoliation in *Pinus taeda* L. They showed that the canopy stomatal conductance and whole plant liquid phase as calculated from sap flux were influenced by the rate of growth as indicated by the annual basal area increment. It has implications for predicting whole plant responses to herbivory, as well as for evaluating relationship between stomatal conductance to water vapour and other hydraulic parameters.

Stomatal responses to water availability in soil, leaf and atmosphere are highly interactive and specific. Bond and Kavanagh (1999) studied four woody species and hypothesized that species differences in stomatal response to humidity and soil water availability can be explained by two parameters: leaf specific hydraulic conductance and threshold water potential. They constructed a simple hydraulic model based on these two parameters which predicted stomatal behaviour that were similar to the published reports.

Salleo *et al.* (2000) studied the xylem cavitation and hydraulic control of stomatal conductance in *Laurus nobilis* L. They suggested that regulation of stomatal conductance is generally considered as a mechanism by which plants control their water loss and maintain hydration level. However, the origin of signals controlling stomatal conductance is still unclear. During soil drying, roots generate some chemical signals (e.g. ABA) which reaches to leaves and induces stomatal closure before any measurable change in leaf water potential. This showed very little role, if any, of leaf water potential in controlling stomatal conductance. However, evidence also exists in favour of stomatal responses to factors influencing leaf water potential rather than leaf water potential itself, such as xylem cavitation. They also concluded that the hydraulic signals (e.g. leaf water potential, xylem cavitation, etc.) may represent the primary events for stomatal regulation in response to sudden changes (such as diurnal) in environmental variables; however during long term water stress (e.g. seasonal drought), it is integrated with more important chemical signals leading to stable reduction in stomatal conductance.

Interrelationships between water potential and stomatal conductance were studied in *Pyrus communis* L. by Naor (2001). Stomatal conductance was found highly correlated with leaf water potential ( $r^2 = 0.54$ ), but much better correlation was found with stem water potential ( $r^2 = 0.80$ ). Decreasing RWC of leaves progressively decreased stomatal conductance, slowing  $\text{CO}_2$  assimilation which eventually stopped, after which  $\text{CO}_2$  is evolved (Lawlor, 2002).

Seasonal dynamics of net photosynthesis ( $A_{\text{net}}$ ) in 2 years old seedlings of *Pinus burtia* Ten., *Pinus pinea* L. and *Pinus pinaster* Ait. were investigated by Awada *et al.* (2003). They found that the stomatal conductance was generally lower in shaded seedlings than in seedlings grown in the sun, except on days with high vapor pressure deficit. Similarly,

total chlorophyll concentration per unit leaf area, specific leaf area (SLA) and height significantly increased in *P. pinea* in response to shade, but not in *P. pinaster* or *P. brutia*.

### 2.3.4 Xylem Conductance

Zimmermann (1978) suggested that very large  $K_t$  values in the trunks of dicotyledons trees were the result of large vessels which had low resistance to water flow. Hydraulic architecture of Eastern Hemlock (*Tsuga canadensis*) was studied by Ewers and Zimmermann (1984). They measured leaf specific conductivities, Huber values, specific conductivities and tracheid diameters throughout the trunk and crown of 9 to 96 year old trees. Their study revealed decreased leaf specific conductivity acropetally with higher value for trunk than for branches and was controlled by wood anatomical features, particularly the tracheid diameter in conifers. The differential water supply was due to larger Huber value in the leaves and to particular narrow tracheids at branch junctions. Gartner *et al.* (1990) recorded that excised stem segments of vines had higher specific hydraulic conductivities than did trees during the dry season in a deciduous forest in Jailsco, Mexico.

Joyce and Steiner (1995) observed the hydraulic parameters of *Fraxinus americana* and recorded the highest leaf-specific conductivity ( $K_l$ ) in the main stem than in branches, primary than in secondary branch axis, terminal leaf bearing shoot than in adjacent lateral shoot, two years old branch than in one year, and south facing branches than in north facing branches. They concluded that all these variabilities in leaf specific conductivity was primarily due to the variation in mean vessel diameter. This was also supported by the occurrence of vulnerability segmentation i.e. roots, stems and petioles having different vulnerabilities in *Acer saccharum* by Tsuda and Tyree (1997). Hydraulic characteristics of *Acer* provided the ability to conserve soil water by shedding leaves and allow the roots to survive on dry soil.

Tyree and Cochard (1996) monitored summer and winter embolism in oak and its impact in water relation. They found that the impact of embolism was reduction in hydraulic conductivity in the vascular system. Oaks seemed to operate close to the point of xylem dysfunction but they protected themselves against embolism by stomatal regulation which kept water potential above that causing runaway embolism.



Cochard *et al.* (1997) compared the hydraulic properties and leaf gas exchange of *Fraxinus excelsor* L. branches differing in their age and vertical crown position, and suggested that, in *Fraxinus* leaf gas exchange and leaf areas were coupled with xylem hydraulic capacities probably through a control of bud activity.

Bunce and Ziska (1998) reported decreased hydraulic conductance in plants at elevated carbon dioxide and indicated that both reversible and irreversible decrease in hydraulic conductance can occur at elevated carbon dioxide concentrations, and that both could be response to reduced transpiration rate, rather than to carbon dioxide concentration itself. Hubbard *et al.* (1999) observed the effect of xylem conductance on photosynthetic rate and productivity and proposed that decrease in net photosynthetic rate during tree maturation was due to decreased xylem hydraulic conductance.

Broddrib and Field (2000) observed strong positive correlation between leaf specific conductivity and maximum photosynthetic capacity, suggesting that maximum photosynthetic rate was constrained by their vascular supply. The leaf specific conductivity of conifer wood overlap broadly with that of associated vessel bearing and vessel-less angiosperms indicating a degree of hydraulic convergence in co-existing plants.

Meinzer *et al.* (2001) reviewed the water transport in trees and emphasized recent developments and controversies related to the uptake, transport and loss of water by trees. They revealed that passive, hydraulic redistribution of water from moisture to drier portions of the soil profile via plant root systems may have a substantial impact on vertical profiles of soil water distribution, partitioning of water within and among species, and on ecosystem water balance. They emphasized and proposed that there was a dynamic equilibrium between embolism formation and repair throughout the day and that daily release of water from xylem via cavitation might serve to stabilize leaf water balance by minimizing the temporal imbalance between water supply and demand.

Cordero and Nilsen (2002) studied the limits to maximum water transport in three diffuse-porous evergreen shrubs exposed to frequent winter freeze-thaw events from the Appalachian mountains and to a severe summer drought from the Oregon Cascades and they measured the percent loss of hydraulic conductivity ( $K_h$ ), vulnerability curves to xylem embolism and freezing point temperatures of stems for 2 years. From the study,

they found that both drought-induced and winter induced embolism caused a significant reduction in hydraulic conductivity in all species during periods when drought or freeze-thaw events occurred in their native habitats. However, rapid recovery of  $K_h$  following freezing or drought maintained the species above their relatively low margins of safety for complete xylem dysfunction. Zimmermann *et al.* (2002) reviewed that pressure gradients, pressure potentials, ion concentration, volume flow as well as turgor pressure gradient were the major driving forces for water lifting in the xylem conduit.

### 2.3.5 Specific Leaf Mass (SLM)

Sobrado (1986) concluded that ratio of dry weight to leaf area of fully mature leaves were about 75 and 17 g cm<sup>-2</sup> in evergreen and deciduous species, respectively. This shows that SLM of evergreen species are higher than deciduous species. Prior *et al.* (1997) while studying the relation between the specific leaf area in deciduous tree (*Terminalia ferdinandiana*) of northern Australian Savannas and a co-occurring evergreen tree (*Eucalyptus tetrodonta*) found that SLA was higher in the deciduous species than in evergreen one.

McBurney (1992) found that the relationship between leaf thickness and water potential of *Brassica oleracea* was strongly influenced by leaf age, stress history and, in young leaves, by the effects of leaf growth. Study conducted by Lei and Lechowicz (1998) in 11 species of forest maples (*Acer* spp.) found that seedlings grown under the gap center (clear sky  $\approx$  20%), open sky irradiance region had significantly greater SLM, and higher  $g_s$  compared with those grown in either gap edge (2.5%) or gap center (cloudy 1.5%) regimes.

Wilson *et al.* (1999) concluded that high SLM leaves worked better in resource poor environments where retention of captured resource was a higher priority while low SLM leaves worked best in resource rich environment, and short lived and vulnerable to herbivory.

### 2.3.6 Leaf Relative Water Content

Occurrence of leaf water deficits usually causes measurable decrease in area and thickness of leaves. Closure of stomatal which unfortunately also reduces the

photosynthetic activity thus affecting the growth (Kramer and Kozlowski 1960; Kramer and Boyer 1995). Naidu and Swamy (1995) studied the relationship between leaf relative water content and biomass production in some deciduous species. Their study indicated that leaf relative water content of tree species varies with the seasonal changes in the environmental factors which in turn influences the biomass production in those tree species.

### **2.3.7 Phenology**

Modelling of plant phenology has a long tradition, starting from the early work of Reamur during the 18<sup>th</sup> century (Wang, 1960). Ralhan *et al.* (1985) described the phenology of tree components of natural forests occurring between 350 and 2150m in Kumaon Himalaya and found more evergreen than deciduous taxa. The degree of evergreenness increased with increasing elevation and decreasing summer dryness. They also observed that for most species (including all dominants) concentrated leaf drop and simultaneous leafing occurred during warm dry period of the year, and about half of the species showed multiple leafing.

Negi and Singh (1992) observed that evergreen species of the Himalayan region differ from the evergreen species with leaf span of several years; new leaves are produced simultaneously with leaves of the deciduous species at the similar rate during early summer (March and April), the driest period of the year. Factors determining these phenological characters were concentrated rainfall, limited variation in day length and year round moderate temperature.

Water relation alone cannot explain the full range of variation in foliar seasonality of hard wood species; it also depends on herbivory and carbon economy of trees. Wang *et al.* (1992) presented strong evidences in support of functional linkage between foliar phenology and hydraulic conductivity of 43 north temperate tree species. Not only the canopy development in the spring but also the timing of autumn senescence depended on hydraulic architecture.

Borchert (1994 a) observed that phenology, seasonal change in water status and water storage capacity of tree species were highly correlated. Most of the tropical dry forests flower or form new shoots soon after leaf shedding during the dry season, i.e., during a



period when trees are likely to be severely water stressed. Borchert (1994 b) monitored the changes in tree water status during the dry season in numerous trees in Costa Rica and put the evidence that elimination of xylem tension by leaf shedding and establishment of a higher solute content and high  $\psi_{\text{stem}}$  were prerequisites for flowering and bud break during drought. Elimination of transpirational water loss during leaf shedding in conjunction with utilization of residual water, osmotic adjustment of stem tissue and extension of roots into moist sub-soil layer enabled rehydration of stem tissue and subsequent flowering and flushing during dry season (Borchert, 1994 a). Rate and degree of rehydration varied strongly with the availability of water stored in tree trunk or in the sub-soil. Stored water buffered the impact of seasonal drought and enabled flowering and flushing during dry season.

Hanninen (1995) presented a framework for modeling bud burst phenology of trees from cool and temperate regions and demonstrated the importance of the concept of realism for modeling bud burst phenology of trees. Model realism addressed the essential environmental responses in the physiological phenomena related to the regulation of timing of bud burst.

Kikuzawa (1995) addressed leaf phenology as an optimal strategy for carbon gain in plants. Considering the photosynthetic rates, construction cost and maintenance cost, he proposed that leaves must be replaced when net gain of a leaf per unit time over the leaf's life span was maximum. In carbon optimization model, he suggested that it was more productive to shed a canopy and produce another leaf later in any event than to produce foliage capable of tolerating a prolonged period of low carbon gain potential.

Reich (1995) reviewed the patterns, causes and consequences of phenology of tropical forests. He described the pattern of foliar phenology in tropical lowland forests in relation to key climatic and edaphic gradient, moisture and discuss the physiological causes and ecological consequences of such patterns, and reviewed that phenology of dry forests could be more sensitive to elevated  $\text{CO}_2$  and temperatures. Elevated  $\text{CO}_2$  might delay the onset of leaf shedding and stimulate longer life span if stand level transpiration was reduced, whereas higher temperatures could lead to more rapid water depletion, longer leafless periods, and more strongly synchronized phenology. But in case of rainforest they might be relatively insensitive to moderate changes in  $\text{CO}_2$  or temperature.

William *et al.* (1997) monitored the phenology and predawn leaf water potential of woody species at wet dry tropical eucalypt savanna in Australia and found that leaf fall in all species was coincident with the attainment of seasonal minima in leaf water potential (-1.5 to -2.0 MPa in evergreen and semi-deciduous species). In all species leaf flushing commenced after rise of water potential following the attainment of seasonal minima in pre-drawn leaf water potential. In majority of species leaf flushing take place during or at the end of dry season. Soil water reserve is sufficient to support the whole plant rehydration that preceded leaf flushing in the absence of rain.

The role of water in the development and yield of coffee crop (*Coffea arabica* L.) was reviewed by Carr (2001). He confirmed that a period of water stress induced either by dry soil or dry air, was needed to prepare flower buds for blossoming which was then stimulated by rain or irrigation. Water must be freely available during the period of rapid fruit expansion to ensure large, high-quality seed yields. Shrestha (2001) observed higher water storage capacity and death of leaf tissue at the time of bud break which were important strategies developed by plant to maintain favourable water status during dry but phenologically active period in *Pinus roxburghii* Sarg.

### 3. SITE DESCRIPTION

#### 3.1 LOCATION

The study area is the Coronation Garden of Tribhuban University, Kirtipur. It is located at about 7 km south-west from the center of Kathmandu in between 27°40'N to 27°41'N latitude, and 85°16'E to 85°18'E longitude. The altitude ranges from 1280 m to 1400m and garden covers an area of 2.76 sq km.

#### 3.2 CLIMATE

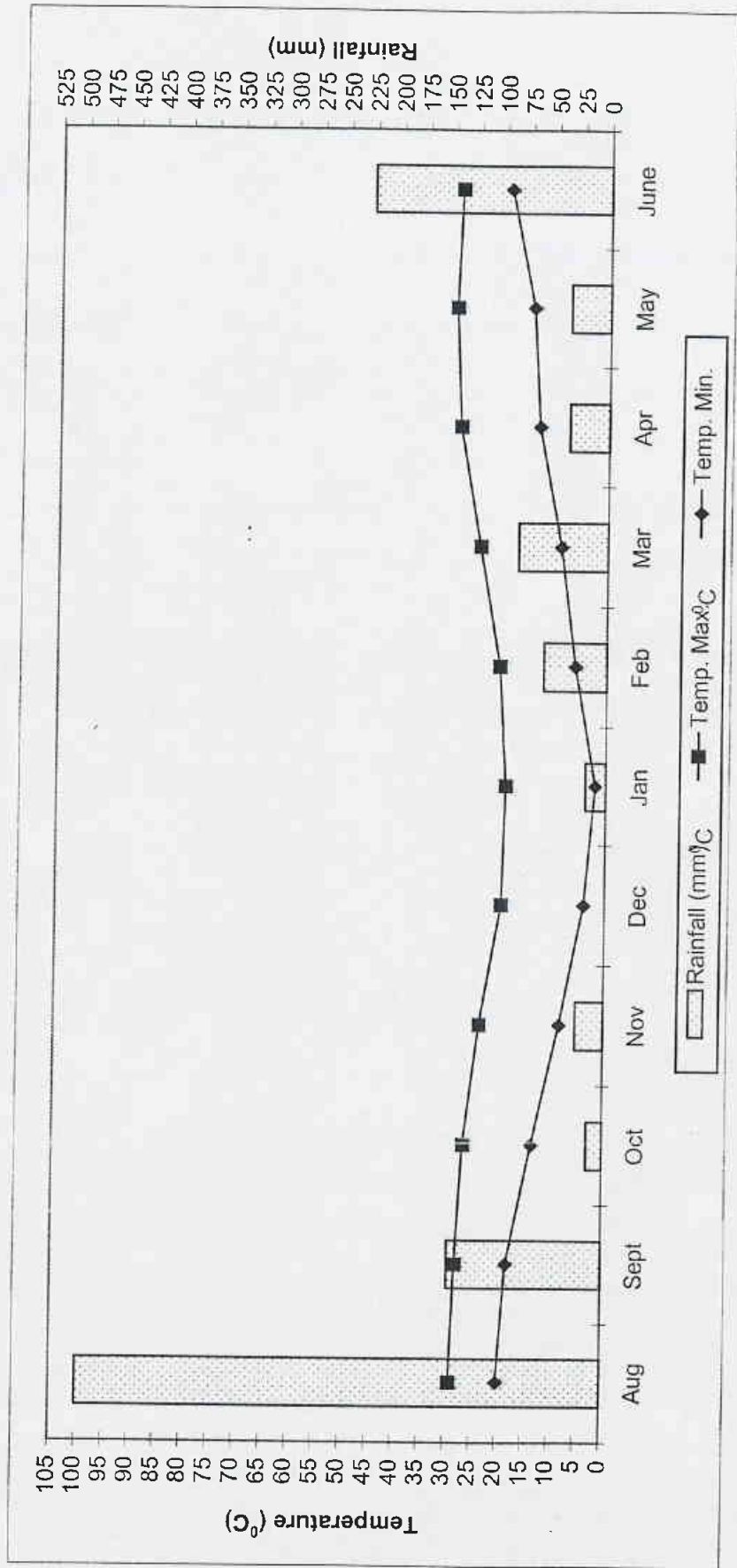
The study area has sub-tropical climate with cool and dry winter (October – February), hot and dry summer (March – May) and hot and humid monsoon (June – September). The climatic data were recorded at Tribhuvan International Airport station Kathmandu, 12 km far from the study area. The maximum rainfall was recorded in August (2002) with 499.9 mm. There was no rainfall in December. During the study period average lowest minimum temperature was 2°C in January and the average highest maximum was 29.6°C in May (Fig 1).

#### 3.3 SOIL

The soil of the area is sandy loam, brown to gray in colour with small stones. The pH ranges from 5.6 to 7.4. The water holding capacity of the soil is 58% (Nepal, 2002 and Uprety, 2002).

#### 3.4 VEGETATION

The study site lies in the sub-tropical latitude. But being a planted site the vegetation of the study area is characterized by the presence of *Alnus nepalensis*, *Castanopsis indica*, *Schima wallichii*, *Quercus lanata*, *Celtis spp.*, *Legustrum confusum*, *Cotoneaster bacillaris*, *Bauhinia variegata*, *Lagerstroemia indica*, etc. Few exotic species like *Populus euro-americana*, *Cinnamomum camphora*, *Callistemon lanceolatus*, *Casuarina equistilla*, *Thuja orientalis*, *Juniperus spp.*, *Salix babylonica*, etc are present in the area.



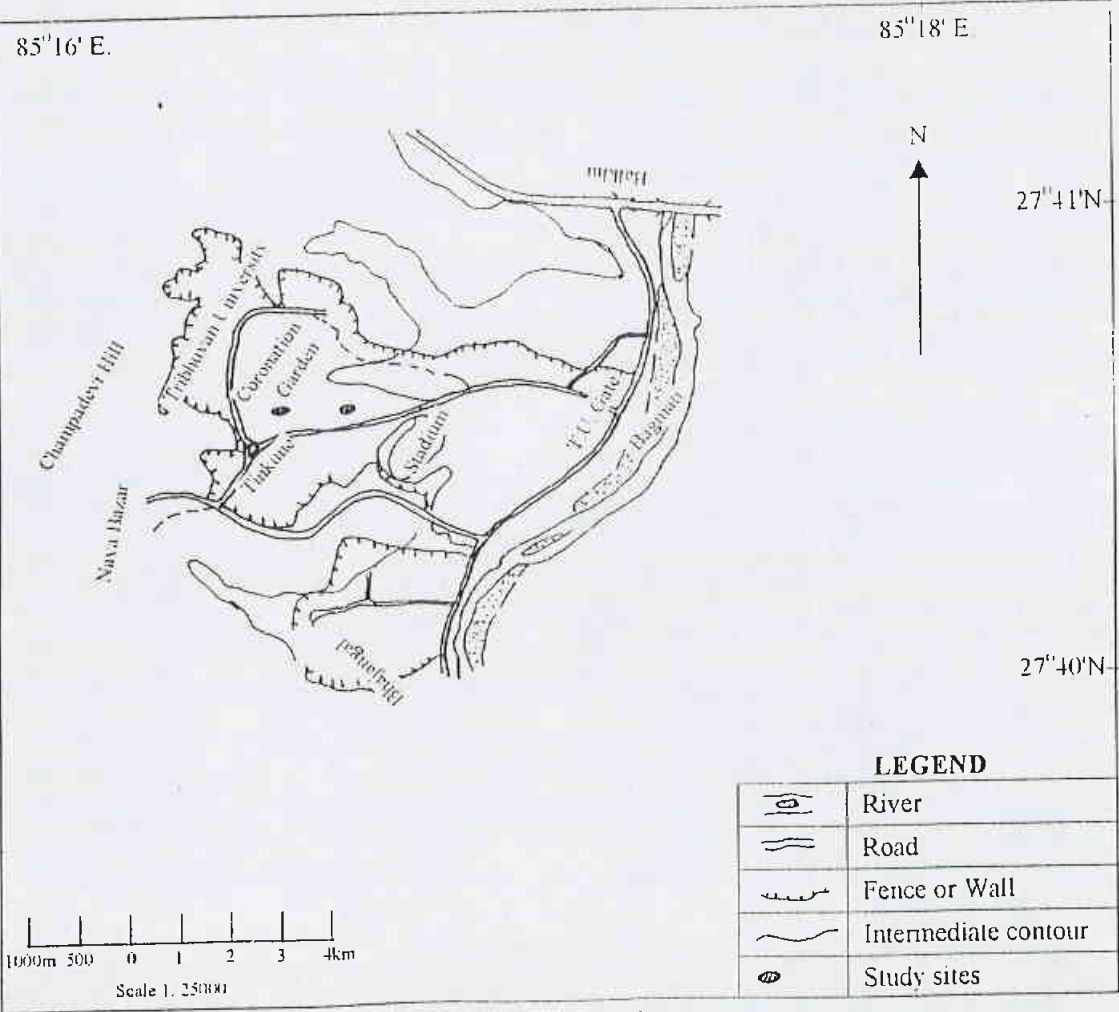
**Fig 1 : Climatic data of study site from August 2002 to June 2003**

(Source: Department of Hydrology and Meteorology, HMG/N)

3.5 SPECIES CHARACTERISTICS

*Bauhinia variegata* commonly known as variegated baulinea, of family Leguminosac, (locally known as ‘Koiralo’) is a medium size deciduous tree with glabrous stem. Leaves alternate, stipules present, 2-3 mm caducous, petioles 3-5 cm long with pubescent base. Leaf blade broadly ovate, 5 - 12 x 5 - 15cm, sub-coriaceous, abaxially glabrous, adaxially sparsely pubescent, cordate base with bifid apex (1/4 - 1/2). Inflorescence corymbose; flower white, showy and fragrant with variegated corolla (purplish in colour). Pods oblong, glabrous, 12-18x1.5-2.0 cm. It is distributed in west, central and east Nepal at an altitude of 150-1900 m. The flower buds are eaten as vegetable (Malla *et al.*, 1986). It has a wide fodder value in hilly areas. Also the leaves are used in making the plates (*tapari*).

*Celtis australis* L., locally known as ‘Khari’ belongs to the family Ulmaceae. It is a deciduous tree, about 16 m tall with spreading branches. Leaves stipulate, ovate,



Map of Study Area

Source: HMG of Nepal, Survey Department

lanceolate, acuminate coarsely serrate, dark green when dry. Flowers greenish yellow, polygamous. Male flower in the cluster of short raceme towards the base of the shoots. Female bisexual in the axil of upper leaves. Perianth 4-5 parted, deciduous. Stamens 4-5 ovary ovoid, disk wooly, style 2-armed. Fruit an ovoid drupe. Mostly it is distributed in temperate Himalaya, and in Nepal it is found in central region. It is cultivated as an ornamental shade tree (Malla *et al.*, 1986). This species is also used as fodder as well as it has fibre value.

*Lagerstroemia indica* L., commonly known as crape-myrtle, belongs to the family Lythraceae. Locally it is called as "Ashare Phool". It is a glabrous, deciduous small tree, 2-6 m high with smooth brown bark; leaves nearly sessile elliptic or oblong, 2-5 cm long; flowers on terminal panicles, petals white, pink or purple, fringed, 2-4 cm across. Flowering: May – September. The tree is native of Asia, North Australia, and American tropics. In Nepal, it is mostly found in eastern and central part. It is cultivated as ornamental tree in garden (Bajracharya *et al.*, 1997).



## 4. MATERIALS AND METHODS

Three trees of *Bauhinia variegata*, *Celtis australis* and *Lagerstroemia indica* were marked in the study site and the readings were taken from these plants from August 2002 to June 2003, at a monthly interval. All the parameters except stomatal conductance and phenological observations were measured by a series of laboratory works. Osmotic potential, pressure potential, bulk modulus of elasticity and relative water content at zero turgor were determined by analyzing the P-V curves developed from the collected samples. Other parameters measured were leaf relative water content, hydraulic conductivity, specific conductivity, leaf specific conductivity, Huber value and specific leaf mass.

### 4.1 PRESSURE VOLUME ANALYSIS

Pressure volume (P-V) analysis was typically performed using the pressure chamber by free transpiration technique. The curve obtained from this analysis is widely used to analyse plant water relation (Koide *et al.*, 1989; Pallardy *et al.*, 1991). P-V curves were used to illustrate the relationship between water potential and relative water content (RWC) which help to determine several properties of plant that may affect plant water relations (Plate 4.1).

For P-V analysis, water content and water potential of a twig were measured simultaneously and repeatedly where the water content is expressed as RWC and the water potential as balance pressure (BP) with negative sign.

Leafly twigs were collected from the experimental plants and cut end of twigs were immediately dipped in water. The samples were covered with plastic bags to reduce the transpiration and left for rehydration at least for 24h that allowed to absorb water under condition of minimum transpiration and water potential became less than -3 bars (Zobel, 1996 b).

The twig was recut to size appropriate to pressure chamber. Leaf surface was made dry by soaking with tissue paper, and dead and loose parts were removed, and the bark was stripped from the cut end. The twig was then fitted into the cork and weight (twig + cork)

was taken and finally BP was measured. Time, mass and BP were recorded. The twig was then hanged in an open area so as to allow free transpiration. After an interval of time (usually 5-10 min in first few readings, then 30 min of interval and finally upto one hour in later readings) the measurements of mass and BP were repeated. The process was continued till the leaf completely wilted or no exudation came from the twigs. After the last measurement the cork was removed from the sample twig and the cork was weighed. The twigs were dried at 80<sup>0</sup>C for about 24 hour and dry weight of the twigs was recorded. Then RWC was calculated for each measurement, using following relations

$$RWC(\%) = \frac{F - D}{S - D} \times 100$$

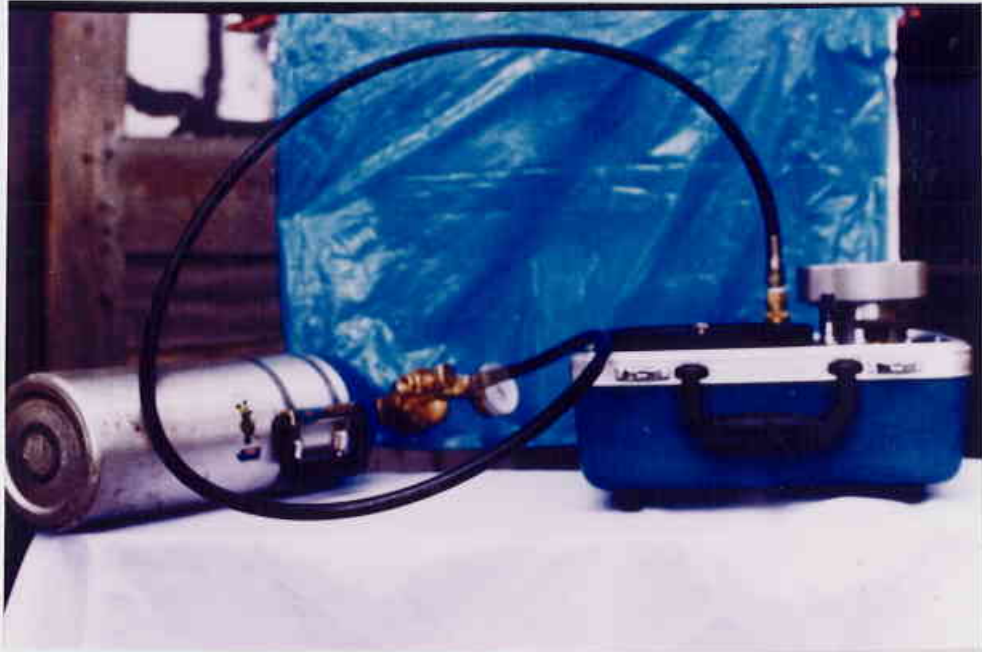
where,

F = sample + cork wt. for each time

S = sample + cork wt. for initial measurement (saturation weight).

D = dry wt. + cork wt.

The RWC was plotted against the inverse of balance pressure (1/BP) for each measured and the curve thus formed were analyzed to find different components of plant water relation.



**Plate 4.1: Pressure chamber fitted with nitrogen cylinder.**



## 4.1.1 Components of Plant Water Potential

### 4.1.1.1 Osmotic potential

As discussed in Kramer and Boyer (1995),  $\psi_s$  approximates  $-RTn/v$ , where  $R$  is the gas constant,  $T$  is temperature,  $n/v$  is the molar concentration of solutes.

$$\text{Thus, } \frac{1}{\psi_s} = -v \frac{1}{nRT}$$

Where,  $n$  represents number of mole solutes and  $v$  is the volume of cell.

In turgor loss time,

$$\frac{1}{BP} = -v \frac{1}{nRT}$$

$$\text{or, } \frac{1}{BP} = v \frac{1}{nRT}$$

When pressure is applied the water moves out from the cell thus affecting  $v$  but the number of solutes ( $n$ ) remains the same. As  $T$  and  $n$  are constant,  $nRT$  is a constant. So, graph of  $1/BP$  over  $v$  becomes linear. A linear portion of  $P$ - $V$  curve represents changes in  $\psi_s$  along with cell volume. The linear portion and its regression line was used to calculate  $\psi_s$  at full turgor (at a point where the extrapolation of linear portion meets the abscissa) and at zero turgor (at a point where the curve meets linear).

### 4.1.1.2 Turgor

At zero turgor point,  $P$ - $V$  curve changes its nature. The  $PV$ -curve is smooth curve at any positive turgor which measure  $\psi_s$  and  $\psi_p$ . The calculated  $\psi_s$  was subtracted from  $\psi_w$  ( $\psi_w = -BP$ ) to determine  $\psi_p$  at any RWC.

In few samples 'Plateaus' occurred. The 'plateaus' are apparently associated with apoplastic water that is accumulated in the intercellular spaces of leaf near full turgidity, and act to buffer changes in the leaf xylem pressure potential as tissue dehydrates (Parker and Pallardy, 1987). A plateau from either natural or artificial rehydration violates the requirements of constant apoplastic water content and causes an abnormally rapid decrease in RWC relative to that in  $\psi_w$  (Tyree and Hammel, 1972; Parker and Pallardy, 1987). It is reported that the presence of plateaus or 'free water' in the region of high  $\psi_e$

where  $\psi_w$  remains stable or decline only slightly with tissue dehydration (Bahari *et al.*, 1985). Data sets with plateaus were corrected by assuming that the beginning the steep decline in water potential represented full turgor.

#### 4.1.1.3 Relative Water Content (RWC) at Zero Turgor

RWC at the point where P-V curve becomes linear (turgorloss point) was determined as RWC at zero turgor.

#### 4.1.1.4 Bulk Modulus of Elasticity ( $\epsilon$ )

The bulk modulus of elasticity ( $\epsilon$ ) is the proportionality parameter between the observed change in pressure,  $\Delta P$ , and the change in relative cell volume,  $\Delta v/v$ , where  $v$  is the cell volume (Zimmermann, 1978). RWC was taken as surrogate of cell volume.

$$\begin{aligned}\epsilon &= \frac{\Delta P}{\frac{\Delta V}{V}} \\ &= \frac{\Delta P}{\frac{RWC_f - RWC_z}{RWC_f}} \\ &= \frac{\Delta P}{100 - RWC_z} \times 100\end{aligned}$$

Where,

$\Delta P$  = pressure change between full turgor and zero turgor, which is equal to turgor pressure at full turgor.

$\Delta v$  = change in volume with  $\Delta P$

$RWC_f$  = RWC at full turgor (100%).

$RWC_z$  = RWC at zero turgor.

## 4.2 STOMATAL CONDUCTANCE

The stomatal conductance (leaf conductance) was measured in the field by using portable steady state diffusion porometer (model AP<sub>4</sub> ΔT Devices Ltd., Cambridge, England). Three trees for each species were selected. From each tree, five healthy leaves were

selected. Moisture, if present on the leaf surface, was soaked with blotting paper before measuring the conductance. The conductance of lower surface of leaves were recorded (Plate 4.2).



**Plate 4.2: AP<sub>4</sub> Porometer used for the study.**

The leaf conductance was recorded twice a day: first reading in the morning (at 9:00 – 10:00 a.m) when the intensity of sunlight becomes sufficient for water loss by the leaf and second reading was taken at mid-day (1:00 – 2:00 p.m.) when the water stress was at maximum.

The porometer worked by measuring the time taken by leaf to release sufficient water vapour to change the relative humidity in a small chamber by a fixed amount. This was compared with a calibration plate of known resistance in order to derive the stomatal conductance of the leaf. Finally the instrument reads leaf conductance as number of moles of water transpired by unit leaf surface in unit time.

### **4.3 XYLEM CONDUCTANCE**

To measure the xylem conductance, about 2 years old twigs were cut from the experimental plants and the cut end were immediately dipped in the bottle filled with water. The twigs were then taken to laboratory. About 15 cm of straight portion of stem was cut under water. Bark of the lower end was removed and it was fitted to plastic tube connected with reservoir containing oxalic acid (0.1M, 1.26 g/l) solution. The segment

was allowed to remain vertical till the solution started to drop from the free end (i.e. upper end). Paraffin tape was used to check leakage, if any (Plate 4.3).

During the measurement the twig segment was placed horizontally at fixed level. A small plastic tube closed with paraffin tape at one end and loosely packed with tissue paper was weighed and the free end of segment was soaked by tissue paper. After one minute the plastic tube was again weighed; the difference gave the flow rate. The same process was repeated until nearly constant flow rate was recorded.



**Plate 4.3: Twig segment fitted with vertical column of oxalic acid solution.**



**Plate 4.4: Twig segment fitted with vertical column of saffranin solution to stain effective xylem area.**

The stem segment was then transferred to another tube containing 0.1% saffranin solution attached to the reservoir (Plate 4.4). The saffranin was then allowed to flow through the segment. Once the saffranin started flowing from the free end, the segment was removed. Then the length of twig, upper and lower end diameter of xylem as well as pith diameter

of both the end of the segment was measured. The segment was then cut transversely at the center with sharp blade and the percentage of xylem stained (i.e. active xylem) was observed with visual estimation. The length of the stem segment as well as the height of reservoir from the twig level (pressure head) was also measured.

The area of leaves beyond the mid-point of the segment was calculated by multiplying the length, breadth and coefficient factor. Coefficient factor (x) was determined by examining 40 leaves of more or less uniform size classes. The leaf is placed on a graph paper and its margin is outlined. Then the area was obtained by counting the squares within the outline. Then all the parameters of xylem conductance i.e. Pressure Gradient (PG), Effective Xylem Area ( $A_{we}$ ), Huber Value (HV), Hydraulic Conductivity ( $K_h$ ), Specific Conductivity ( $K_s$ ) and Leaf Specific Conductivity ( $K_L$ ) were calculated.

**4.3.1 Pressure Gradient (PG):** It was obtained by following formula,

$$PG(KPa / mm) = \frac{\text{Pressure Head (cm)}}{10.2} \times \frac{1}{\text{length of segment (mm)}}$$

$$PG(MPa / m) = \frac{\text{Pressure Head (cm)}}{10.2} \times \frac{1}{\text{length of segment (m)}} \times \frac{1}{1000}$$

**4.3.2 Effective Xylem Area ( $A_{we}$ ):**

$A_{we} (m^2) = \text{Average Xylem Area} \times \text{Proportion of Stained Xylem}$

Average Xylem Area ( $m^2$ ) =  $\pi/8 (dlw^2 - dlp^2 + dsw^2 - dsp^2)$

Where,

dlw = diameter of wood at large end

dlp = diameter of pith at large end

dsw = diameter of wood at smaller end

dsp = diameter of pith at smaller end

**4.3.3 Huber Value (HV):**

Huber value is the ratio of wood cross-sectional area and leaf area distal to the middle of the segment (Tyree and Ewers, 1996).

$$HV = \frac{\text{Average Xylem Area}}{\text{Leaf Area}}$$

Where, leaf area =  $l \times b \times x$

$l$  = length of leaves

$b$  = breadth of leaves

$x$  = coefficient factor

(i.e.  $x = 0.6367$  for *Celtis australis*;  $0.69038$  for *Lagerstroemia indica* and;  $0.99449$  for *Bauhinia variegata*).

#### 4.3.4 Hydraulic Conductivity ( $K_h$ ):

Hydraulic conductivity ( $K_h$ ) is equal to the ratio of water flux through an excised stem segment and to pressure gradients causing the flow (Tyree and Ewers, 1996).

$$K_h (\text{Kg m Sec}^{-1} \text{ MPa}^{-1}) = \frac{\text{Flow rate}}{\text{Pressure gradient}}$$

#### 4.3.5 Specific Conductivity ( $K_s$ ):

Specific conductivity ( $K_s$ ) is a measure of the porosity of wood which is equal to  $K_h$  divided by effective xylem area ( $A_{we}$ ).

$$K_s (\text{Kg.m}^{-1}\text{Sec}^{-1} \text{ MPa}^{-1}) = \frac{K_h}{A_{we}}$$

#### 4.3.6 Leaf specific Conductivity ( $K_l$ ):

Leaf specific conductivity  $K_l$  is equal to  $K_h$  divided by leaf area distal to the segment ( $A_l$ ).

$$K_l (\text{Kg m}^{-1} \text{ Sec}^{-1} \text{ MPa}^{-1}) = \frac{K_h}{A_l}$$

$$A_l = \text{leaf area} = l \times b \times x$$

Where  $x$  = coefficient factor.

### 4.4 LEAF RELATIVE WATER CONTENT (LRWC)

The leaf relative water content (LRWC) was determined by selecting 5 healthy leaves from each species (in triplicate). Five healthy leaves from each sample tree was taken which was immediately kept in a small plastic bag and zipper of the plastic was tightly closed. In the laboratory, fresh weight of leaves were taken along with the plastic weight. Then the leaves were saturated by keeping the leaves in between the wet blotting paper for 24 hours. After 24 hours, the leaf surface was soaked with dry blotting paper and saturation weight of the leaves were taken. The leaves were then kept for oven drying at  $80^{\circ}\text{C}$  for 24 hours and finally dry weight of the leaves were taken. The same method was



done for each species in triplicate. The leaf relative water content (LRWC) was determined by following formula:

$$\text{LRWC (\%)} = \frac{\text{Fresh wt.} - \text{Dry wt.}}{\text{Sat. wt.} - \text{Dry wt.}} \times 100$$

Where, fresh wt. of leaves = wt. of leaves and plastic – wt. of the plastic

LRWC was determined both in predawn as well as midday condition.

#### 4.5 SPECIFIC LEAF MASS (SLM)

Five leaves from each tree were collected from the healthy twig of a tree both in predawn and in midday. The area of leaves was calculated by multiplying length, breadth and coefficient factor. Leaves were oven dried at 80°C for at least 24 h and dry mass was measured. Using the following formula, SLM was calculated.

$$\text{SLM (g cm}^{-2}\text{)} = \frac{\text{Dry mass of leaves}}{\text{Surface area of leaves}}$$

#### 4.6 PHENOLOGY

The phenological events (bud break, leaf flushing, flowering and fruiting, leaf fall) were recorded twice a month and sometimes once a week during phenologically active months (e.g. March, April) in sample trees.

#### 4.7 STATISTICAL ANALYSIS

##### 4.7.1 Mean

The single value representing many replicates in experiments is arithmetic mean ( $\bar{X}$ ) which is calculated as follows:

$$\bar{X} = \frac{\sum x}{n}$$

Where, x = Measured value of an item.

n = size of a sample



**4.7.2 Standard Deviation**

Standard deviation ( $\sigma$ ) measures the variability that indicates, by how much all the values in a distribution typically deviates from the mean. As described by Hosmand (1988),

$$\sigma = \sqrt{\frac{\sum (x - \bar{x})^2}{n - 1}}$$

**4.7.3 Coefficient of Correlation**

The strength of the linear relationship between two variables X and Y can be measured by coefficient correlation (r). The Karl Pearson sample correlation coefficient as described by Hosmand (1988),

$$r = \frac{\sum xy - n\bar{x}\bar{y}}{\sqrt{(\sum x^2 - n\bar{x}^2)(\sum y^2 - n\bar{y}^2)}}$$

The correlation coefficient can assume values between -1 and +1 inclusive. +1 and -1 values of r refer to perfect positive (direct) and negative (inverse) linear correlation, respectively between variables of interest. When r equals of zero, there is no linear correlation.

## 5. RESULTS

### 5.1 PRESSURE – VOLUME ANALYSIS

Seasonal fluctuation was observed in all the parameters obtained from the P-V curve analysis in *Bauhinia variegata* (Fig 2). Throughout the year  $\psi_{sf}$  and  $\psi_{sz}$  showed similar pattern of seasonal variation.  $\psi_{sf}$  and  $\psi_{sz}$  were recorded lowest during November i.e. – 2.22 MPa and –2.5 MPa respectively.  $\psi_{sf}$  had weak positive correlation with SLM ( $r=0.52$ ) and negative correlation with  $K_h$  ( $r=-0.63$ ). Similarly,  $\psi_{sz}$  showed poor positive correlation with  $LRWC_{md}$  ( $r=0.54$ ) while it showed strong negative correlation with  $\psi_{pf}$  ( $r=-0.93$ ).

The highest and lowest  $\psi_{pf}$  were recorded in November (2.12 MPa) and June (0.76 MPa) respectively. The value fluctuates significantly from August to September, reaching maximum in November. The  $\psi_{pf}$  showed strong positive correlation with  $K_l$  ( $r=0.59$ ).

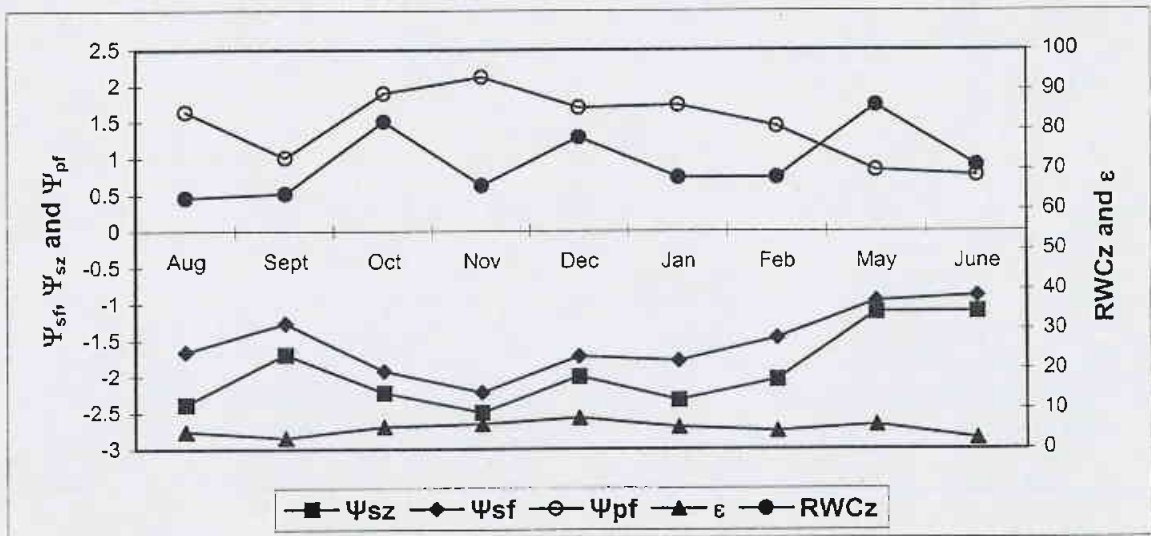


Fig 2. Parameters obtained from pressure–volume analysis. [Osmotic potential at zero turgor ( $\psi_{sz}$ ), Osmotic potential at full turgor ( $\psi_{sf}$ ), Pressure potential at full turgor ( $\psi_{pf}$ ), Relative water content at zero turgor ( $RWC_z$ ) and Bulk modulus of elasticity ( $\epsilon$ )] for *Bauhinia variegata* from August 2002 to June 2003.

The lowest value of  $\epsilon$  was observed in June (2.64 MPa) and highest in December (7.72 MPa), whereas the  $RWC_z$  were recorded the lowest in August (63%) and highest in May (86%) with much variation in other months (Fig 2)  $RWC_z$  had very weak positive

correlation with  $\epsilon$  ( $r=0.50$ ) and good correlation with  $g_{sm}$  ( $r=0.62$ ), but had no significant correlation with other parameters.  $\epsilon$  had high positive correlation with HV ( $r=0.73$ ) and  $K_i$  ( $r=0.73$ ), weak with  $K_h$  ( $r=0.59$ ) and had no significant correlation with other parameters (Table 1).

In case of *C. australis* also,  $\psi_{sf}$  and  $\psi_{sz}$  showed similar pattern of seasonal variation. Both  $\psi_{sf}$  and  $\psi_{sz}$  showed higher value in March (-1.21 MPa and -1.49 MPa) and lowest value in December (-1.81 MPa and -2.32 MPa) respectively.  $\psi_{pf}$  achieved its highest value during December (1.79 MPa) and the lowest in March (1.06 MPa) (Fig 3).

$\psi_{sf}$  had strong positive correlation with  $\psi_{sz}$  ( $r=0.95$ ),  $g_{sd}$  ( $r=0.93$ ),  $g_{sm}$  ( $r=0.67$ ) and poor with  $LRWC_{md}$  ( $r=0.50$ ). It has strong negative correlation with  $\psi_{pf}$  ( $r=0.96$ ) and  $\epsilon$  ( $r=0.63$ ).  $\psi_{sz}$  showed significant positive correlation with  $g_{sd}$  ( $r=0.89$ ) and  $g_{sm}$  ( $r=0.85$ ) and strong negative correlation with  $\psi_{pf}$  ( $r=-0.96$ ). Likewise,  $\psi_{pf}$  has strong negative correlation with  $g_{sm}$  ( $r=-0.97$ ) and  $g_{sd}$  ( $r=-0.75$ ) (Table 2).

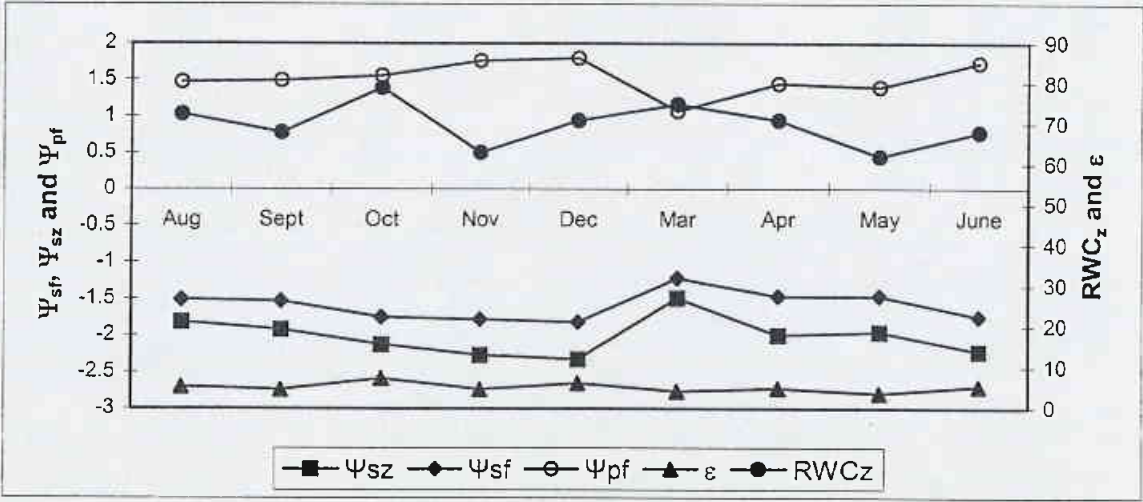


Fig 3. Parameters obtained from pressure–volume analysis. [Osmotic potential at zero turgor ( $\psi_{sz}$ ), Osmotic potential at full turgor ( $\psi_{sf}$ ), Pressure potential at full turgor ( $\psi_{pf}$ ), Relative water content at zero turgor ( $RWC_z$ ) and bulk modulus of elasticity ( $\epsilon$ )] in *Celtis australis* from August 2002 to June 2003.

$RWC_z$  for *C. australis* has highest value in October (79%) and lowest in May (62%).  $RWC_z$  showed much fluctuation in all months.  $RWC_z$  had strong correlation with  $\epsilon$  ( $r = 0.68$ ) and slightly with  $g_{sm}$  ( $r = 0.55$ ). The highest value of  $\epsilon$  was observed in October

(7.4 MPa) and lowest in May (3.67 MPa) correlating negatively with  $LRWC_{md}$  ( $r = -0.74$ ), but had no significant correlation with other parameters (Table 2).

Similarly, in *Largerstroemia indica*,  $\psi_{sz}$  and  $\psi_{sf}$  showed similar pattern of seasonal variation.  $\psi_{sf}$  and  $\psi_{sz}$  were recorded lowest during December (-1.75 MPa and -2.27 MPa) and lowest in March (-1.58 MPa and -1.01 MPa) respectively.  $\psi_{pf}$  also achieved its highest value during December (1.70 MPa) and the lowest in March (0.88 MPa).

$\psi_{sf}$  had positive correlation with  $g_{sm}$  ( $r = 0.60$ ) and  $g_{sd}$  ( $r = 0.70$ ).  $\psi_{sz}$  was weakly correlated with  $LRWC_{md}$  ( $r = 0.50$ ) but it showed strong negative correlation with  $\psi_{pf}$  ( $r = -0.86$ ). Likewise,  $\psi_{pf}$  had strong correlation with  $\epsilon$  ( $r = 0.71$ ). This negatively correlated with SLM ( $r = -0.59$ ) and  $g_{sd}$  ( $r = -0.53$ ).

$RWC_z$  for *L. indica* had lowest value in April (70%) while it had maximum value in June (82%). Similarly, highest value of  $\epsilon$  was observed in October (6.97 MPa) and lowest in March (3.40 MPa).  $RWC_z$  had strong correlation with  $\epsilon$  ( $r=0.71$ ) and negatively correlated with SLM ( $r=-0.68$ ).  $\epsilon$  also showed strong negative correlation with SLM ( $r = -0.867$ ) (Table 3).

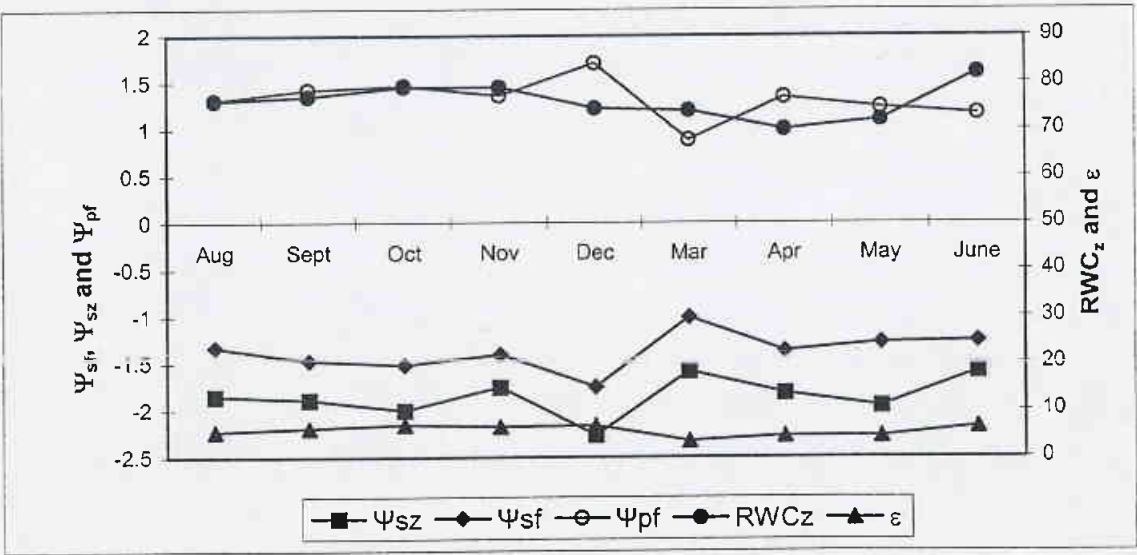


Fig 4. Parameters obtained from pressure – volume analysis. [Osmotic potential at zero turgor ( $\psi_{sz}$ ), Osmotic potential at full turgor ( $\psi_{sf}$ ), Pressure potential at full turgor ( $\psi_{pf}$ ), Relative water content at zero turgor ( $RWC_z$ ) and bulk modulus of elasticity ( $\epsilon$ )] in *Largerstroemia indica* from August 2002 to June 2003.

5.2 LEAF RELATIVE WATER CONTENT (LRWC)

In *Bauhinia variegata*, LRWC showed little fluctuation in different season (Fig 5). LRWC both in predawn and mid-day were highest in June (99.67% and 98.97% respectively) and in general lowest in September (96.45% and 89.45% respectively) for both predawn and mid-day with the exception of March (LRWC<sub>pd</sub>=96.24%, for single sample tree) LRWC<sub>pd</sub> showed negative correlation with  $g_{sd}$  ( $r=-0.779$ ) whereas LRWC<sub>md</sub> showed positive correlation with  $g_{sd}$  ( $r=0.602$ ) and  $\psi_{sz}$  ( $r=0.544$ ).

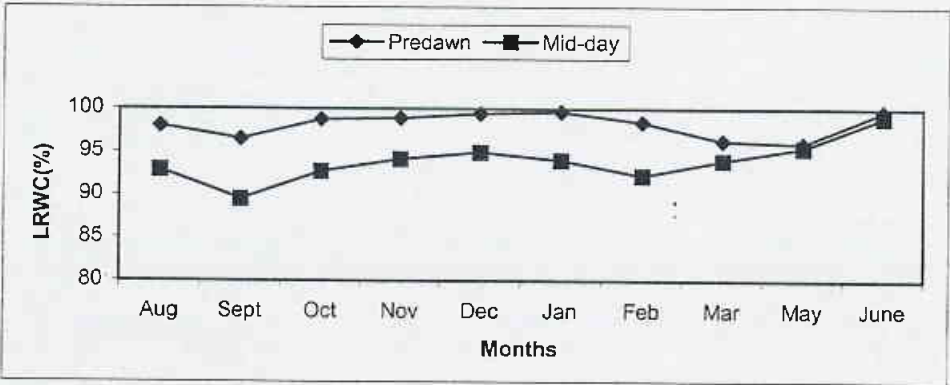


Fig 5: Leaf relative water content in *Bauhinia variegata* from August 2002 to June 2003.

In *Celtis australis* (Fig 6), LRWC at predawn was highest in June (99.34%) and lowest in August (91.84%). Similarly, LRWC at mid-day was highest in March (98.22%) and lowest in December (88.94%). LRWC<sub>pd</sub> was positively correlated with  $K_l$  ( $r=0.664$ ) and strong negatively correlated with HV ( $r=-0.804$ ). Likewise, LRWC<sub>md</sub> had weak positive correlation with  $\psi_{sf}$  ( $r=0.505$ ) and negative correlation with  $\epsilon$  ( $r=-0.744$ ),  $K_s$  ( $r=-0.556$ ) and  $g_{sm}$  ( $r=-0.571$ ).

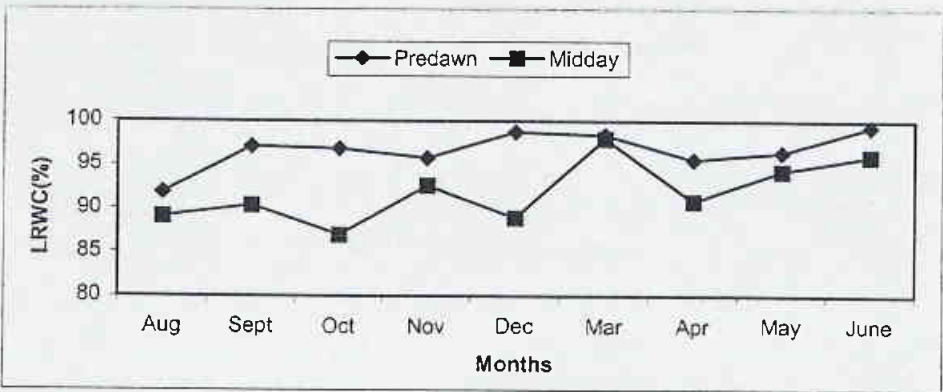


Fig 6: Leaf relative water content in *Celtis australis* from August 2002 to June 2003.

LRWC in *L. indica* showed little fluctuation in different months (Fig 7). LRWC was lowest in August for both predawn and mid-day (i.e. 94.84% and 87.97% respectively). But predawn LRWC was highest in June (99.27%) and mid-day LRWC in May (97.12%). LRWC<sub>pd</sub> was positively correlated with  $g_{sm}$  ( $r=0.551$ ) and  $g_{sd}$  ( $r=0.606$ ). LRWC<sub>md</sub> showed positive correlation with LRWC<sub>pd</sub> ( $r=0.644$ ) and  $\psi_{sz}$  ( $r=0.506$ ).

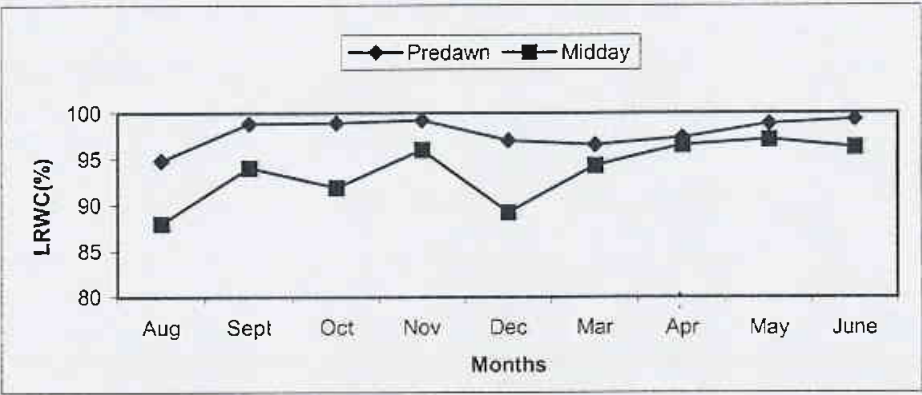


Fig 7: Leaf relative water content in *Lagerstroemia indica* from August 2002 to June 2003.

### 5.3 LEAF CONDUCTANCE

Leaf conductance ( $g_s$ ) showed much fluctuation in different months (Fig 8). In *B. variegata*,  $g_s$  at morning was highest in October ( $603.66 \text{ mmol.m}^{-2}\text{s}^{-1}$ ) and lowest in

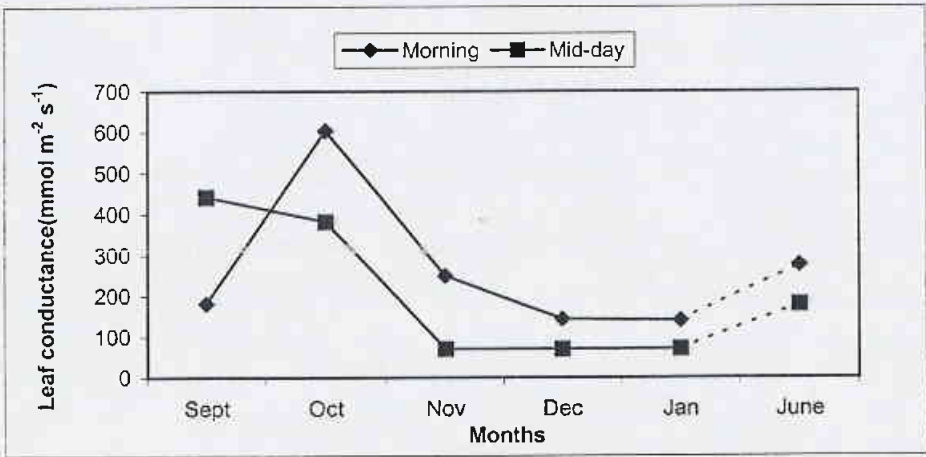


Fig 8: Leaf conductance in *Bauhinia variegata* from September 2002 to June 2003.

January ( $139.8 \text{ mmol.m}^{-2}\text{s}^{-1}$ ).  $g_s$  at mid day was recorded highest in September ( $442.6 \text{ mmol.m}^{-2}\text{s}^{-1}$ ) and lowest in December ( $69.2 \text{ mmol.m}^{-2}\text{s}^{-1}$ ).  $g_s$  at morning was generally higher than that of  $g_s$  at mid-day but reverse condition was observed in September. The  $g_s$  increased in October and then gradually decreased in November, December and January



and finally increased in June.  $g_s$  at morning showed positive correlation with  $RWC_z$  ( $r = 0.627$ ) and negative correlation with SLM ( $r = -0.518$ ).  $g_s$  at mid-day has positive correlation with  $g_{sm}$  ( $r = 0.522$ ) and negative correlation with  $K_l$  ( $r = -0.607$ ), HV ( $r = -0.614$ ),  $\epsilon$  ( $r = -0.557$ ) and  $K_h$  ( $r = -0.507$ ).

In *C. australis*, leaf conductance ( $g_s$ ) showed much fluctuation both in morning and mid-day in different months (Fig 9).  $g_s$  at morning was least in December (98.9  $\text{mmol.m}^{-2}\text{s}^{-1}$ ) and highest in October (603.5  $\text{mmol.m}^{-2}\text{s}^{-1}$ ). The  $g_{sm}$  was least in January (43.6  $\text{mmol.m}^{-2}\text{s}^{-1}$ ) and highest in September (367.2  $\text{mmol.m}^{-2}\text{s}^{-1}$ ).  $g_{sd}$  was recorded high in June (222.4  $\text{mmol.m}^{-2}\text{s}^{-1}$ ) while in other months it was less in comparison to  $g_{sm}$ .  $g_s$  at morning showed strong positive correlation with  $K_h$  ( $r = 0.834$ ),  $K_s$  ( $r = 0.819$ ),  $\psi_{sz}$  ( $r = 0.852$ ),  $\psi_{sf}$  ( $r = 0.676$ ) and also with  $RWC_z$  ( $r = 0.550$ ). Similarly, it showed strong negative correlation with  $\psi_{pf}$  ( $r = -0.970$ ) and HV ( $r = -0.596$ ).  $g_s$  at day strongly correlates with  $\psi_{sf}$  ( $r = 0.935$ ),  $\psi_{sz}$  ( $r = 0.899$ ),  $K_h$  ( $r = 0.860$ ), SLM ( $r = 0.867$ ),  $K_s$  ( $r = 0.747$ ),  $g_{sm}$  ( $r = 0.638$ ) and  $K_l$  ( $r = 0.509$ ).  $g_s$  at mid-day showed negative correlation with  $\psi_{pf}$  ( $r = -0.759$ ).

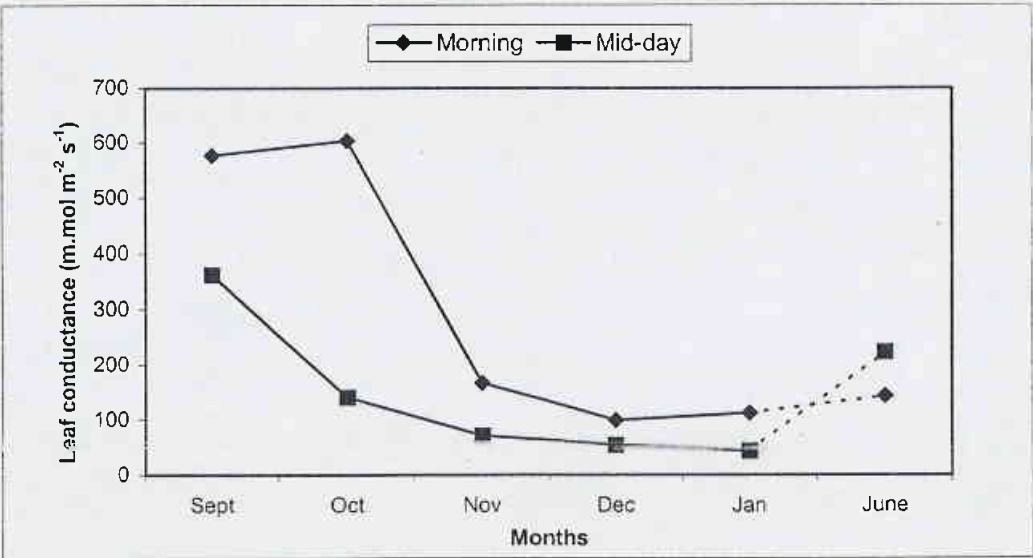


Fig 9: Leaf conductance in *Celtis australis* from September 2002 to June 2003.

In *L. indica*, leaf conductance both at morning and mid-day was lowest in January (81.92 – 20.76  $\text{mmol.m}^{-2}\text{s}^{-1}$ ). In this month conductance was measured for single plant due to leaf fall in other marked plants.



Similarly,  $g_{sm}$  was highest in September ( $474 \text{ mmol.m}^{-2}\text{s}^{-1}$ ) and  $g_{sd}$  was highest in October ( $372.8 \text{ mmol.m}^{-2}\text{s}^{-1}$ ).  $g_s$  at morning positively correlated with  $\psi_{sf}$  ( $r = 0.607$ ),  $K_h$  ( $r = 0.780$ ),  $K_s$  ( $r = 0.799$ ) and negatively with HV ( $r = -0.745$ ) and  $K_l$  ( $r = -0.703$ ). Similarly,  $g_{sd}$  showed positive correlation with  $g_{sm}$  ( $r = 0.770$ ),  $\psi_{sf}$  ( $r = 0.704$ ),  $RWC_z$  ( $r = 0.636$ ),  $K_h$  ( $r = 0.565$ ) and  $K_s$  ( $r = 0.569$ ) and it showed negative correlation with HV ( $r = -0.790$ ),  $K_l$  ( $r = -0.749$ ) and  $\psi_{pf}$  ( $r = -0.535$ ).

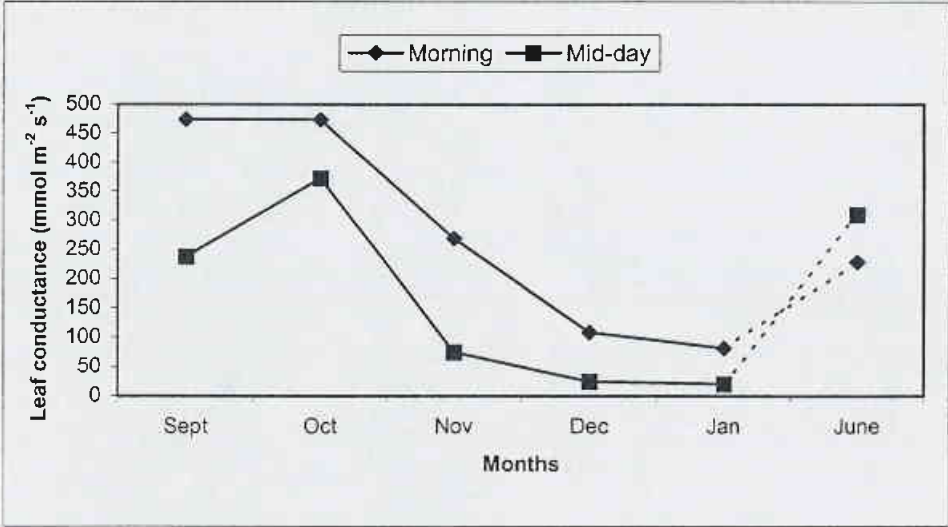


Fig 10: Leaf conductance in *Largerstroemia indica* from September 2002 to June 2003.

### 5.4 XYLEM CONDUCTANCE

In *B. variegata*, hydraulic conductivity ( $K_h$ ) was found highest during October ( $55.0 \times 10^{-6} \text{ kg.m.sec}^{-1} \text{ MPa}^{-1}$ ) and lowest in September ( $4.901 \times 10^{-6} \text{ kg.m.sec}^{-1} \text{ MPa}^{-1}$ ). Leaf specific conductivity ( $K_l$ ) and Huber Value (HV) showed the same pattern of variation. Both were maximum in December ( $20.796 \times 10^{-3} \text{ kg.m}^{-1} \text{ sec}^{-1} \text{ MPa}^{-1}$  and  $11.307 \times 10^{-3}$  respectively) and minimum in September ( $0.034 \times 10^{-3} \text{ kg m}^{-1} \text{ sec}^{-1} \text{ MPa}^{-1}$  and  $0.157 \times 10^{-3}$  respectively).  $K_s$  was highest in November ( $26.396 \text{ kg. m}^{-1} \text{ sec}^{-1} \text{ MPa}^{-1}$ ) and lowest in September ( $0.551 \text{ kg.m}^{-1} \text{ sec}^{-1} \text{ MPa}^{-1}$ ). All the parameters showed much variation during the different seasons (Fig 11).  $K_h$  and  $K_s$  had positive correlation ( $r=0.961$ ). HV also showed significant correlation with  $\epsilon$  ( $r=0.737$ ).  $K_h$  showed significant correlation with  $\psi_{sf}$  ( $r = -0.633$ ). Likewise  $K_s$  was positively correlated with  $\psi_{pf}$  ( $r=0.677$ ).

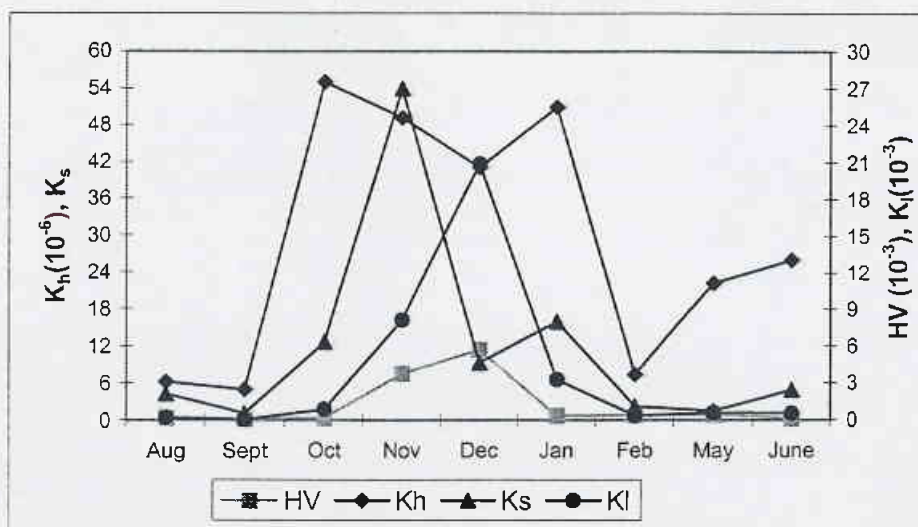


Fig 11. Various parameters of xylem conductance. [Huber Value (HV), hydraulic conductivity ( $K_h$ ,  $\text{kg.m.sec}^{-1} \text{MPa}^{-1}$ ), specific conductivity ( $K_s$ ,  $\text{kg.m}^{-1}\text{sec}^{-1} \text{MPa}^{-1}$ ) and leaf specific conductivity ( $K_l$ ,  $\text{kg.m}^{-1}\text{sec}^{-1}\text{MPa}^{-1}$ )] in *Bauhinia variegata* from August 2002 to June 2003.

In *C. australis*, all the parameters of xylem conductance showed much fluctuation in different months (fig. 12). HV was lowest in August ( $1.823 \times 10^{-4}$ ) and highest in March ( $42.613 \times 10^{-4}$ ).  $K_h$  and  $K_s$  reached maximum in September ( $186.574 \times 10^{-6} \text{ kg.m.sec}^{-1} \text{MPa}^{-1}$  and  $9.172 \text{ kg.m}^{-1} \text{sec}^{-1} \text{MPa}^{-1}$  respectively). Both  $K_h$  and  $K_s$  decreased to minimum in March ( $4.761 \times 10^{-6} \text{ kg.m.sec}^{-1} \text{MPa}^{-1}$  and  $0.337 \text{ kg.m}^{-1} \text{sec}^{-1} \text{MPa}^{-1}$  respectively). Likewise,  $K_l$  achieved its maximum value in September ( $17.39 \times 10^{-4} \text{ kg.m}^{-1} \text{sec}^{-1} \text{MPa}^{-1}$ ) and minimum in August ( $0.899 \times 10^{-4} \text{ kg.m}^{-1} \text{sec}^{-1} \text{MPa}^{-1}$ ).

HV was correlated negatively with  $\text{LRWC}_{\text{pd}}$  ( $r = -0.804$ ) and  $g_{\text{sm}}$  ( $r = -0.596$ ).  $K_h$  was strongly correlated with  $K_l$  ( $r=0.681$ ),  $g_{\text{sm}}$  ( $r=0.834$ ) as well as  $g_{\text{sd}}$  ( $r=0.860$ ). Similarly  $K_s$  also showed strong positive correlation with  $K_l$  ( $r=0.740$ ),  $g_{\text{sm}}$  ( $r=0.819$ ) and  $g_{\text{sd}}$  ( $r=0.747$ ).  $K_s$  was negatively correlated with  $\text{LRWC}_{\text{md}}$  ( $r = -0.556$ ).  $K_l$  also showed positive correlation with  $\text{LRWC}_{\text{pd}}$  ( $r=0.664$ ) and  $g_{\text{sd}}$  ( $r=0.509$ ).  $K_h$  and  $K_s$  also showed strong correlation ( $r=0.953$ ) to each other.

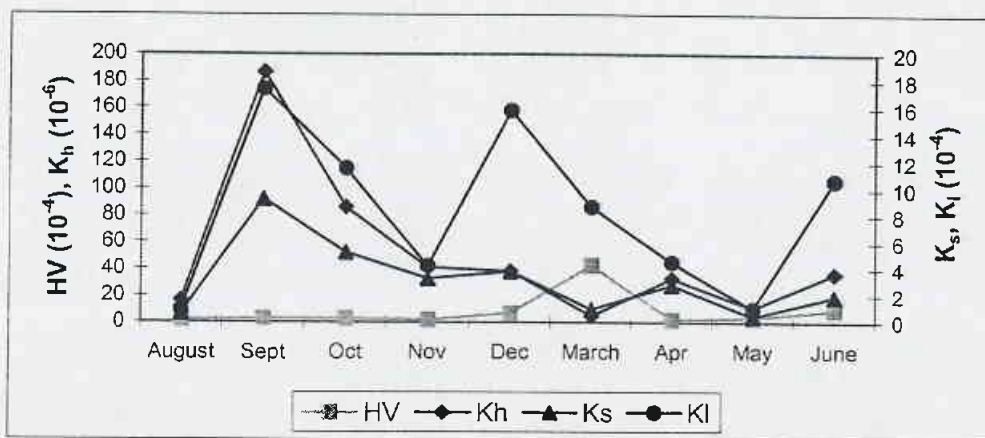


Fig 12. Various parameters of xylem conductance. [Huber value (HV), hydraulic conductivity ( $K_h$ ,  $\text{kg.m sec}^{-1} \text{MPa}^{-1}$ ), specific conductivity ( $K_s$ ,  $\text{kg.m}^{-1}\text{sec}^{-1}\text{MPa}^{-1}$ ) and leaf specific conductivity ( $K_l$ ,  $\text{kg.m}^{-1} \text{sec}^{-1} \text{MPa}^{-1}$ )] in *Celtis australis* from August 2002 to June 2003.

Similarly, much variation in xylem conductance parameter was observed in different months in *L. indica* (fig. 13). HV was highest in December ( $20.396 \times 10^{-3}$ ) followed by March ( $13.6 \times 10^{-3}$ ) and lowest in April ( $1.243 \times 10^{-3}$ ).  $K_h$  was maximum in September ( $16.271 \times 10^{-5} \text{kg.m.sec}^{-1} \text{MPa}^{-1}$ ) and minimum in August ( $2.185 \times 10^{-5} \text{kg.m.sec}^{-1} \text{MPa}^{-1}$ ). Specific conductivity and leaf specific conductivity were maximum in April ( $K_s$ ,  $7.788 \text{kg.m}^{-1} \text{sec}^{-1} \text{MPa}^{-1}$  and  $K_l$ ,  $53.118 \times 10^{-3} \text{kg.m}^{-1} \text{sec}^{-1} \text{MPa}^{-1}$  respectively). But  $K_s$  was minimum in August ( $0.834 \text{kg.m}^{-1} \text{sec}^{-1} \text{MPa}^{-1}$ ) and  $K_l$  in June ( $0.354 \times 10^{-3} \text{kg.m}^{-1} \text{sec}^{-1} \text{MPa}^{-1}$ ).

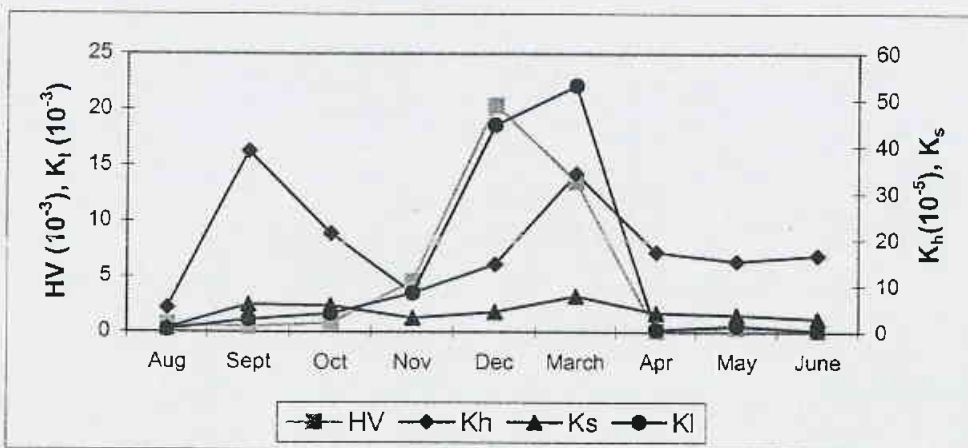


Fig 13: Various parameters of xylem conductance. [Huber Value (HV), hydraulic conductivity ( $K_h$ ,  $\text{kg.m.sec}^{-1} \text{MPa}^{-1}$ ), specific conductivity ( $K_s$ ,  $\text{kg.m}^{-1} \text{sec}^{-1} \text{MPa}^{-1}$ ) and leaf specific conductivity ( $K_l$ ,  $\text{kg.m}^{-1} \text{sec}^{-1} \text{MPa}^{-1}$ )] in *Largetroemia indica* from August 2002 to June 2003.

HV was correlated positively with  $K_l$  ( $r = 0.940$ ) and negatively with  $g_{sm}$  ( $r = -0.745$ ) and  $g_{sd}$  ( $r = -0.790$ ).  $K_h$  and  $K_s$  had high correlation ( $r = 0.846$ ).  $K_h$  also showed positive correlation with  $g_{sm}$  ( $r = 0.780$ ) and  $g_{sd}$  ( $r = 0.565$ ).  $K_s$  also showed significant correlation with  $K_l$  ( $r = 0.563$ ),  $g_{sm}$  ( $r = 0.799$ ), and  $g_{sd}$  ( $r = 0.569$ ).  $K_l$  was negatively correlates with  $g_{sm}$  ( $r = -0.703$ ) and  $g_{sd}$  ( $r = -0.749$ )

### 5.5 SPECIFIC LEAF MASS (SLM)

Specific leaf mass (SLM) was found to be highest in January and lower in February ( $8.303 \times 10^{-3} \text{ g.cm}^{-2}$  and  $5.853 \times 10^{-3} \text{ g.cm}^{-2}$  respectively) in *B. variegata* (fig. 14). SLM decreased from August to October and increased till January. From the January to March the SLM again decreased till March and then rose till June. SLM showed weak positive correlation with  $\psi_{sf}$  ( $r=0.523$ ) and negative correlation with  $g_{sm}$  ( $r=0.518$ ).



Fig 14. Specific leaf mass of *Bauhinia variegata* from August 2002 to June 2003.

In *C. australis*, SLM achieved its maximum value in December ( $8.212 \times 10^{-3} \text{ g.cm}^{-2}$ ) and minimum in March ( $3.252 \times 10^{-3} \text{ g.cm}^{-2}$ ). SLM showed positive correlation with  $g_{sd}$  ( $r=0.867$ ) and negative correlation with  $RWC_z$  ( $r=0.527$ ).

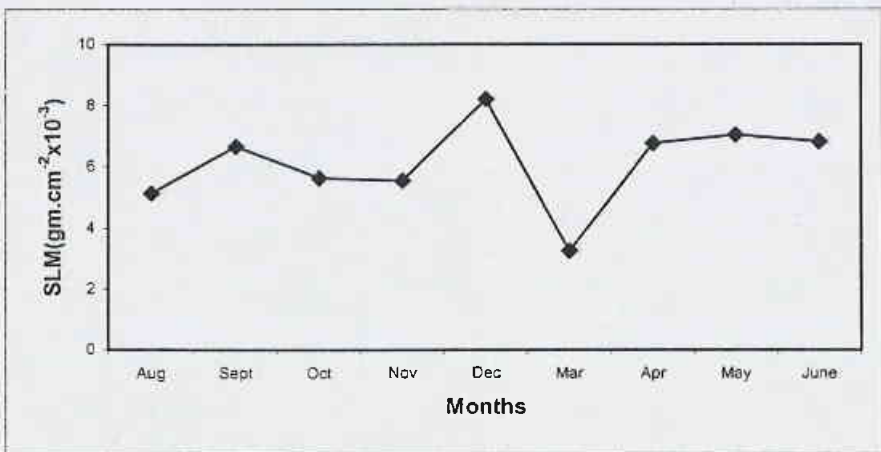


Fig 15. Specific leaf mass of *Celtis australis* from August 2002 to June 2003.

Similarly, in *L. indica*, SLM was found to be highest in April ( $5.285 \times 10^{-3} \text{ g.cm}^{-2}$ ) and lowest in December ( $1.128 \times 10^{-3} \text{ g.cm}^{-2}$ ). SLM showed decreasing order in values from August to October. SLM also decreased continuously from April to June. SLM showed negative correlation with  $\text{RWC}_z$  ( $r = -0.680$ ) and  $\epsilon$  ( $r = -0.867$ ).

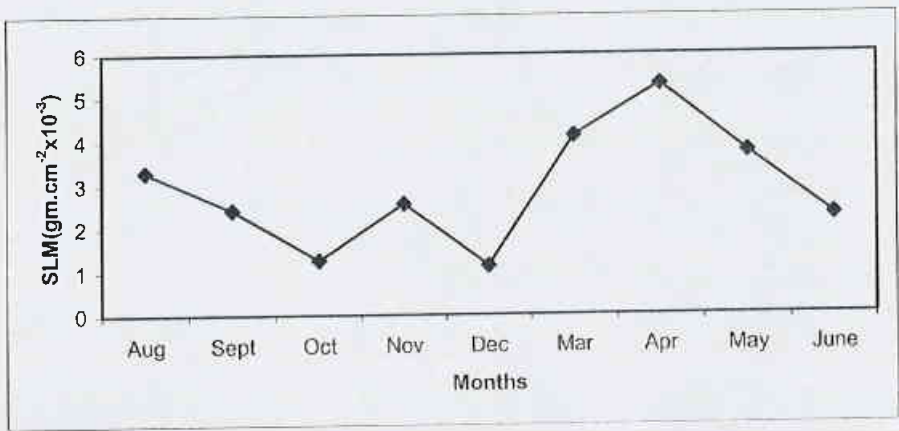


Fig 16: Specific leaf mass of *Lagerstroemia indica* from August 2002 to June 2003.

### 5.6 PHENOLOGY

The most phenological activities were found to occur from the mid winter (December) to dry summer month (March) in *B. variegata* (fig. 17). Leaf fall started at the end of September, gradually increasing towards in the following months and became completely leafless at the end of February to the beginning of March with the exception of one tree out of three experimental tree where the leaf senescence completed in April. In general, complete leaf less condition was observed from March to April. Simultaneously from the April new leafing ( $\cong 5\%$ ) started in two trees and at the last of April in third tree. So, in *B. variegata*, leaf life span is nearly one year. Flower bud initiated in December and remained dormant throughout the winter. Bud break and flowering started at the end of March and completed by the end of May. Thus, bud break, flowering as well as leaf flushing in *B. variegata* occurred during drought period.

In *Celtis australis*, the phenological observation were mostly concentrated for leaf fall and leaf flushing since the experimental plants were at sapling stage and did not flower. Continuous leafing as well as leaf senescing had started at the end of August and leaf fall started in February. New leafing started from the mid of March and became mature in April.





**Plate 5.1: Mature leafing in *Celtis australis*.**

New leafing in *L. indica* started in mid-March, and reached at peak in mid April. Flower bud appeared in June and flowering was observed in late June. Flowering in this species lasted the beginning of September. Fruiting started from the September and was retained until May. Leaf senescence began from late September, which became reddish – orange in colour by late December. But the plant was completely leafless from January to late March.

The phenological events were quite different in *L. indica* than in other two species studied. In this plant, after the complete maturation of first crop of leaf, minor leaf flushing took place three times and the process lasted for a week. Such multiple leafing was more prominent in the isolated tree which was fully exposed to sunlight.



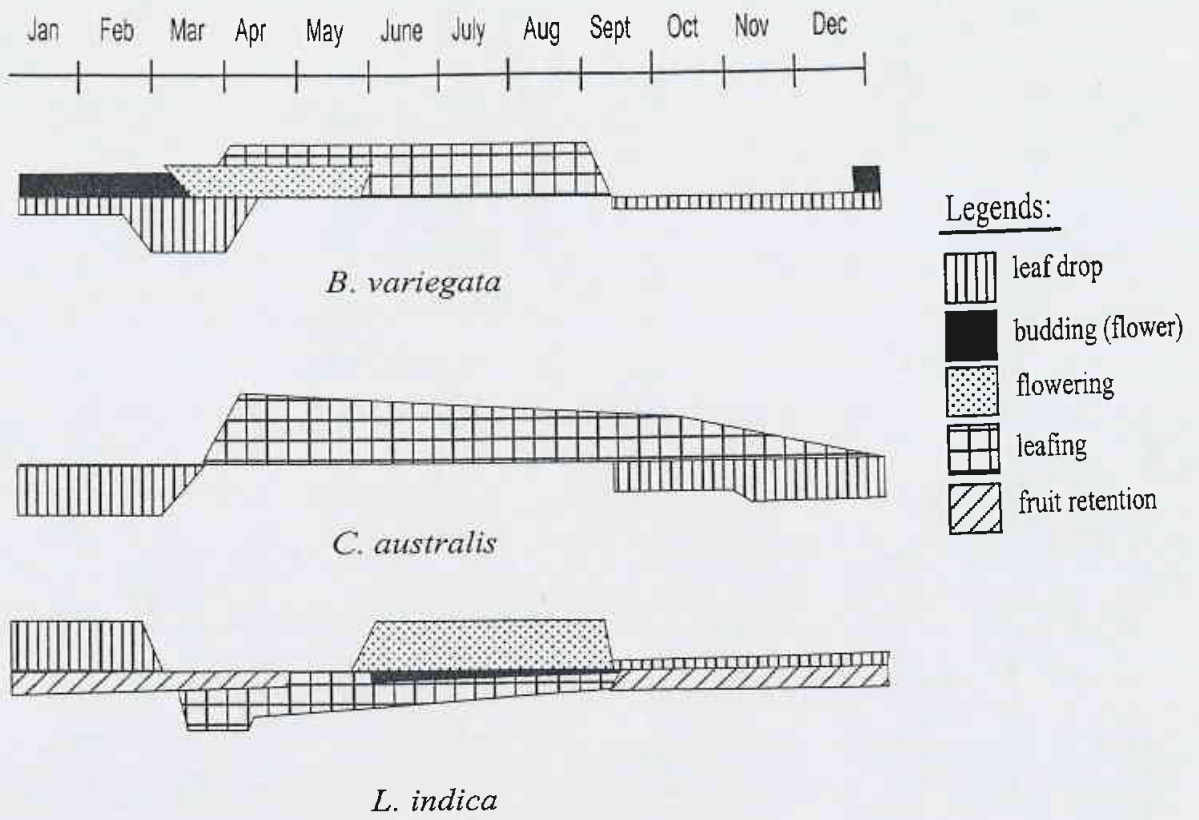


Fig. 17. Phenograms of *B. variegata*, *C. australis* and *L. indica*.



Plate 5.2 Leaf initiation in *Lagerstroemia indica*.



Plate 5.3 Flowering in *Lagerstroemia indica*.





**Plate 5.4: Flowering in *Bauhinia variegata*.**



**Plate 5.5: New leafing in *Bauhinia variegata*.**

Table 1: Karl Pearson coefficient of correlation between various parameters of *Bauhinia variegata*.

Parameters	$\psi_{sf}$	$\psi_{sz}$	$\psi_{rf}$	RWC <sub>z</sub>	$\varepsilon$	HV	K <sub>h</sub>	K <sub>s</sub>	K <sub>l</sub>	SLM	g <sub>sm</sub>	g <sub>sd</sub>	LRWC <sub>pd</sub>
$\psi_{sz}$	0.049												
$\psi_{pf}$	-0.246	-0.939**											
RWC <sub>z</sub>	-0.302	0.432	-0.156										
$\varepsilon$	-0.350	-0.380	0.598	0.502									
HV	-0.369	-0.280	0.464	0.121	0.737*								
K <sub>h</sub>	-0.633	-0.346	0.594	0.383	0.599	0.410							
K <sub>s</sub>	-0.442	-0.544	0.677*	-0.201	0.396	0.498	0.610						
K <sub>l</sub>	-0.344	-0.236	0.408	0.185	0.737*	0.961**	0.429	0.315					
SLM	0.523	0.157	-0.319	-0.394	-0.442	-0.400	-0.266	-0.134	-0.330				
g <sub>sm</sub>	-0.091	-0.189	0.217	0.627	-0.026	-0.361	0.363	0.006	-0.405	-0.518			
g <sub>sd</sub>	0.320	0.285	-0.375	0.070	-0.557	-0.614	-0.507	-0.495	-0.607	-0.200	0.522		
LRWC <sub>pd</sub>	-0.267	-0.386	0.481	-0.168	0.182	0.347	0.378	0.302	0.409	0.242	-0.008	-0.779	
LRWC <sub>nd</sub>	0.001	0.544	-0.339	0.440	0.120	0.137	0.263	0.039	0.150	0.214	-0.052	0.602	0.283

\*\* Correlation is significant at the 0.01 level (2-tailed)

\* Correlation is significant at the 0.05 level (2-tailed)

Table 2: Karl Pearson coefficient of correlation between various parameters for *Celtis australis*.

Parameters	$\psi_{sf}$	$\psi_{sz}$	$\psi_{pf}$	RWC <sub>z</sub>	$\varepsilon$	HV	K <sub>h</sub>	K <sub>s</sub>	K <sub>l</sub>	SLM	g <sub>sm</sub>	g <sub>sd</sub>	LRWC <sub>pd</sub>
$\psi_{sz}$	0.951**												
$\psi_{pf}$	-0.962**	-0.962**											
RWC <sub>z</sub>	0.126	0.301	-0.299										
$\varepsilon$	-0.631	-0.472	0.463	0.680*									
HV	0.158	0.300	-0.110	0.185	0.044								
K <sub>h</sub>	-0.203	-0.132	0.169	0.047	0.193	-0.235							
K <sub>s</sub>	-0.353	-0.301	0.314	0.080	0.325	-0.329	0.953						
K <sub>l</sub>	-0.321	-0.240	0.259	0.302	0.421	-0.457	0.681*	0.740*					
SLM	-0.332	-0.496	0.421	-0.527	-0.092	-0.221	0.407	0.293	0.039				
g <sub>sm</sub>	0.676	0.852	-0.970	0.550	0.265	-0.596	0.834*	0.819*	-0.354	0.393			
g <sub>sd</sub>	0.935*	0.899*	-0.759	-0.059	-0.400	-0.075	0.860*	0.747	0.509	0.867	0.638		
LRWC <sub>pd</sub>	-0.174	-0.220	0.124	0.012	0.077	-0.804**	0.119	0.178	0.664	-0.022	-0.438	0.074	
LRWC <sub>ind</sub>	0.505	0.401	-0.440	-0.424	-0.744*	-0.283	-0.439	-0.556	-0.279	-0.100	-0.571	0.185	0.386

\*\* Correlation is significant at the 0.01 level (2-tailed)

\* Correlation is significant at the 0.05 level (2-tailed)

Table 3: Karl Pearson coefficient of Correlation between various parameters for *Largerstroemia indica*.

Parameters	$\psi_{sf}$	$\psi_{sz}$	$\psi_{pf}$	RWC <sub>z</sub>	$\varepsilon$	HV	K <sub>h</sub>	K <sub>s</sub>	K <sub>l</sub>	SLM	g <sub>sm</sub>	g <sub>sd</sub>	LRWC <sub>m</sub>
$\psi_{sz}$	-0.082												
$\psi_{pf}$	0.044	-0.861**											
RWC <sub>z</sub>	0.296	0.270	0.033										
$\varepsilon$	0.268	-0.401	0.718	0.715*									
HV	-0.247	-0.353	0.166	-0.181	-0.047								
K <sub>h</sub>	0.125	0.187	-0.280	-0.053	-0.238	0.099							
K <sub>s</sub>	0.316	0.050	-0.236	-0.167	-0.277	0.367	0.846**						
K <sub>l</sub>	-0.152	-0.113	-0.134	-0.209	-0.275	0.940**	0.306	0.563					
SLM	-0.331	0.485	-0.590	-0.680*	-0.867**	-0.275	0.042	-0.001	-0.107				
g <sub>sm</sub>	0.607	0.178	-0.213	0.190	-0.047	-0.745	0.780	0.799	-0.703	0.181			
g <sub>sd</sub>	0.704	0.417	-0.535	0.636	0.214	-0.790	0.565	0.569	-0.749	0.009	0.770		
LRWC <sub>m</sub>	0.241	0.077	0.096	0.435	0.412	-0.323	0.200	0.109	-0.352	-0.352	0.551	0.606	
LRWC <sub>d</sub>	-0.120	0.506	-0.435	-0.123	-0.338	-0.392	0.206	0.191	-0.285	0.492	0.195	0.276	0.644

\*\* Correlation is significant at the 0.01 level (2-tailed)

\* Correlation is significant at the 0.05 level (2-tailed)



## 6. DISCUSSION

Present study showed seasonal variation in water relation parameters specific leaf mass (SLM) and phenological behaviours in *Bauhinia variegata* L., *Celtis australis* L. and *Lagerstroemia indica* L., growing in Coronation garden of Tribhuvan University, Kathmandu, Nepal.

Osmotic potential ( $\psi_s$ ), pressure potential ( $\psi_p$ ) and tissue elasticity ( $\epsilon$ ), and relative water content of zero turgor ( $RWC_z$ ) were determined from the analysis of Pressure – Volume curves. As the soil dries, causing soil water potential to decline, live cell adjust their water status by accumulating osmotically active compounds, which reduce the osmotic potential and therefore helps to maintain the turgor. As a result of the increased concentration of osmotic solutes, cells have a higher turgor when fully hydrated (Lambers *et al.*, 1998). In the present study, the plant appears to exhibit good osmoregulation in response to drought. Throughout the late monsoon to late winter (except the extreme drought, March and April are senescencing period with complete leaf fall), the osmotic potential at zero turgor ( $\psi_{sz}$ ) and osmotic potential at full turgor ( $\psi_{sf}$ ) were least in *B. variegata*. Both  $\psi_{sz}$  and  $\psi_{sf}$  were least in November (-2.5 MPa, -2.222 MPa). Such results of osmotic adjustment in response to drought were also obtained by Saliendra and Meinzer (1991), Ishida *et al.* (1992), Kumari and Veeranjanyulu (1996) and Peltier and Marigo (1999).  $\psi_s$  decreased throughout the winter both passively by concentrating the existing tissue solute through dehydration, and actually increasing the amount of solutes in cells (Tyree and Jarvis, 1982). One of the common adaptational strategies employed by species having ability to tolerate low water potential is to employ osmotic adjustment (Abrams, 1990) and in the present study it was observed by the initiation of senescence of leaves in *B. variegata* L. Both  $\psi_{sf}$  and  $\psi_{sz}$  appear to symbolize the osmotic adjustment because they follow similar seasonal variation, however they didn't show any correlation.

In case of *Celtis australis* L. and *Lagerstroemia indica* L., the trend of osmotic potential was found different to that of *Bauhinia variegata* L. Throughout the year, both osmotic potential at zero turgor ( $\psi_{sz}$ ) and osmotic potential at full turgor ( $\psi_{sf}$ ) were least in December (-2.325 MPa and -1.818 MPa for *Celtis australis* and -2.272 and -1.754 MPa in *L. indica*) and higher in March (-1.492 and -1.219 MPa in *C. australis*, and -1.587 and



in *L. indica*) and higher in March (-1.492 and -1.219 MPa in *C. australis*, and -1.587 and -1.01 MPa in *L. indica*). However, the increase in  $\psi_s$  during the dry period of the year does not indicate the osmoregulation. But in the present study, the lower values of osmotic potential both  $\psi_{sz}$  and  $\psi_{sf}$  may be due to the lack of water availability and tissue dehydration. It can also be supported by the climate, as precipitation was nil during December in the study site. Therefore, the decrease in  $\psi_s$  in December also have significant role in osmoregulation since both  $\psi_{sz}$  and  $\psi_{sf}$  showed positive correlation with each other ( $r=0.951$ ) in *C. australis*, however there is no significant correlation between  $\psi_{sz}$  and  $\psi_{sf}$  in case of *L. indica* L.

Similar results of osmotic adjustment in response to drought from the same site were obtained by Nepal (2002) in *Quercus lanata* and *Cinnamomum camphora* and Upreti (2002) in *Alnus nepalensis* and *Cotoneaster bacillaris*.

Increased water stress during early dry season generally cause a decline in water potential and induces leaf shedding (Borchert, 1995). A leaf abscission is morphological response to substantial drought (Mooney and Dunn, 1970b). The leaves at the top of the tree are in more unfavourable environment than at the base of the tree, because xylem pressure decreases at least 0.1 bar with every meter of height (Zimmermann, 1978), and perhaps due to this reason leaf fall started at the top and descended downward in case of *Bauhinia variegata* and *Lagerstroemia indica*.

Live cells must maintain a positive hydrostatic pressure (i.e. remain turgid) to be physiologically active (Lambers *et al.*, 1998). Since most of the phenological processes occurred in drought, maintenance of turgor pressure is critical to plant life since its loss inhibits growth (Hsiao, 1973). It was clearly observed in *B. variegata* in the present study. In *B. variegata*, the value of  $\psi_{pf}$  were greater than 1 MPa except in May and June and the highest value was found in November (2.122 MPa) corresponding to the lowest value of osmotic potential (-2.5 MPa and -2.222 MPa). Also, during this period, flower bud appeared and therefore maintenance of turgidity is important in this case and thus the  $\psi_{pf}$  was higher during November. Similarly, in *C. australis*  $\psi_{pf}$  was highest in December (1.793 MPa) when the corresponding osmotic potential were least in this month (-2.325 MPa and -1.818 MPa). Similar results were also found in *L. indica* with highest value of  $\psi_{pf}$  in December (1.704 MPa). In general, in all the three species, major phenological

processes (bud break, flowering and leafing) coincided with drought during March and April. This signifies the necessity of turgor during phenologically active period. As the leaves become mature,  $\psi_{pf}$  dropped to least value which is in consistent with the present study for all the species (Appendices 1, 2, 3). Similar result has been obtained by Tewari (1998) in *Shorea robusta* at the foot hills of Kumaun Himalaya, south of Nainital.

Cell wall elasticity is an important adaptational behaviour during the phenological process occurring mostly in drought seasons. Elastic modulus ( $\epsilon$ ) is a function of cell turgor and water content (or cell volume), and therefore changes in the slope of relationship between turgor and relative water content, provide a measure of elastic adjustment. Elastic adjustment results from the modification in the cell wall which make them more elastic there by facilitating tissue shrinkage during dehydration (Blake and Tschaplinski, 1992).  $\epsilon$  is inversely proportional to elasticity of cell wall i.e. smaller  $\epsilon$  value indicates greater elasticity (Fan *et al.*, 1994). In the present study, lower value of  $\epsilon$  was found in May for *C. australis* (3.671 MPa) and in April in case of *L. indica* (3.403 MPa) respectively during the phenologically active period. This was a general phenomenon observed by Patakas *et al.* (1970 b), where cell became more extensible during growth and development but once the organ attains the maturity, the cell becomes less and less extensible. Therefore, a small elastic modulus (low rigidity of cell wall) contributed to turgor maintenance both in *C. australis* and *L. indica* in the similar way as decrease in osmotic potential.

In *B. variegata* L.,  $\epsilon$  had lowest value in June (2.644 MPa). Higher tissue elasticity in this month was due to the addition of new tissue because the immature and differentiating tissues have higher elasticity. Highest value of  $\epsilon$ , recorded in December (7.722 MPa) was due to the presence of mature tissue. Since the plant was not under the water stress, annual variation in  $\epsilon$  was simply due to the presence of tissue of different degree of maturation in annual cycle. Similar results were obtained by Nepal, (2002) in *Quercus lanata* and *Cinnamomum camphora* from the same site. Also the seasonal trend of  $\epsilon$  in *B. variegata* is in good agreement with the result of Tewari (1998) in *Shorea robusta* where he obtained higher values of  $\epsilon$  during winter and early summer and low values during the monsoon and post-monsoon period.

Elastic and osmotic adjustments help plants to maintain turgor during the drought (Blake and Tschaplinski, 1992). In *B. variegata* osmotic adjustments was found more pronounced than elastic adjustments in winter where as in *C. australis* and *L. indica* both elastic and osmotic adjustments were found to be significant. The osmotic adjustment may be advantageous to plant in longer terms as accumulation of organic solutes can be re-metabolized after water stress is no more existing (Weixing *et al.*, 1992).

Plant maintains turgidity during dry period by lowering relative water content at zero turgor ( $RWC_z$ ). Thus, cell can hold much water in symplast volume beyond zero turgor, and the turgor pressure beyond incipient plasmolysis is also higher. In *B. variegata*,  $RWC_z$  ranged from 63% to 87%; 62% to 79% in *C. australis* and 70% to 82% in *L. indica*. During the phenologically active period, there should be high turgor pressure for cell expansion, and this was induced by lowering  $RWC_z$ . As  $RWC_z$  is meant to maintain turgor, it exhibited good positive correlation with  $\epsilon$  in *C. australis* ( $r = 0.680$ ) and *L. indica* ( $r = 0.715$ ) but weak in *B. variegata* ( $r = 0.502$ )

Leaf relative water content (LRWC) was used as a surrogate of plant water potential. LRWC was always higher than  $RWC_z$  as obtained from P-V curve analysis for all three species indicating that plants were not water stressed throughout the year. The narrowest difference (i.e. 7.96%) was found in *C. australis* in October. In the same month tissue was least elastic and leaf fall began. The widest difference between  $LRWC_{md}$  and  $RWC_z$  was also found in May for *C. australis*. In the same month,  $RWC_z$  was lowest (62%) and tissue elasticity was highest. So the sharp decline in  $RWC_z$  in May was due to increased elasticity. This enabled the plant to continue growth (eg. leaf flushing) in such dry month. Change in  $\psi_{sf}$  over the year was least in *C. australis*. So, this plant maintains favourable water balance by elastic adjustment. Change in  $\psi_{sf}$  and  $\epsilon$  were highest in *B. variegata*,  $\psi_{sf}$  was lowest in November but tissue elasticity was highest in June. Though the plant was not water stressed both osmotic and elastic adjustment could be the potential strategies to tolerate water stress but at different seasons of the year. In *L. indica* tissue elasticity was highest in March and  $RWC_z$  dropped to minimum in April, indicating that elastic adjustment could be an important mechanism to maintain favourable water status in tree.

Leaves show variation in water content in diurnal cycle. Generally, the minimum water content occurs in early afternoon when the transpiration reached to maximum, but the

maximum water content often occurs near the middle of the night and decreased again towards the morning (Karmer and Kozlowski, 1960).

The relative water content of leaves of different species varied slightly in different months. In all the three species, predawn leaf relative water content (LRWC<sub>pd</sub>) was higher than mid-day leaf relative water content. In all the species (*B. variegata*, *C. australis* and *L. indica*), LRWC in both predawn and midday was higher which was not in accordance with seven species studied by Naidu and Swamy (1995) where LRWC never reach their maximum values throughout their study period. But as found by Naidu and Swamy in seven tree species, all the species in general show higher LRWC in winter. Higher LRWC in winter may be due to limited transpirational water loss associated with low temperature, low light intensity and shorter sunshine hours prevailed during winter.

In *B. variegata*, LRWC<sub>md</sub> is correlated with  $g_{sd}$  ( $r = 0.602$ ). When the water from the leaves is transpired excessively, stomata close and ultimately decreasing the  $g_{sd}$ . Similarly, in *C. australis*, LRWC<sub>pd</sub> was highly correlated with  $K_l$  ( $r = 0.664$ ), which indicated that LRWC was controlled by water supply by the stem.

Xylem conductance was studied by measuring the parameters like Huber value (HV), Hydraulic Conductivity ( $K_h$ ), Specific Conductivity ( $K_s$ ) and Leaf Specific Conductivity ( $K_l$ ). These parameters showed marked seasonal variation in all three species.

The best correlation ( $r = 0.846$ ) existed between  $K_h$  and  $K_s$  in *L. indica* and ( $r = 0.953$ ) in *C. australis* and also with *B. variegata* ( $r = 0.610$ ). The gradual decrease in values as the season became drier was due to drought induced embolism in the xylem conduit suggesting that xylem embolism increased with progressive drought and diminishes stem cross sectional area available for water transport (Holbrook et.al., 1995). Embolism is important because embolized conduits reduce the hydraulic conductivity of the xylem in woody plants which may be induced by drought, excessive transpiration, or winter cycle of freezing and thawing of xylem water (Tyree and Sperry, 1989). Marked seasonal decline in hydraulic conductivity of drought deciduous species was also found by Sobrado (1993). In present study the embolism was more pronounced in *L. indica* than in *C. australis* and *B. variegata*.

Huber value (HV) which is considered as relative conducting area (i.e. xylem area to leaf area) is high in plants that lose large quantities of water in transpiration (Larcher, 1995). In the present study, the correlation between HV and  $K_i$  ( $r = 0.916$ ) in *B. variegata* and ( $r = 0.940$ ) in *L. indica* shows good agreement with Larcher (1995). The gradual increase in HV during the winter season (November and December) in *B. variegata* as well as *L. indica* (Appendix 10 and 12) may be due to winter wood formation. Similar result was obtained by Bhattarai (2001) in *Schima wallichii*, Tripathi (2001) in *Shorea robusta* in Hetauda, Nepal (2002) and Uprety (2002) in *Quercus lanata* and *Alnus nepalensis* in Kirtipur.

The specific conductivity ( $K_s$ ) depends on the diameter of the conducting element (Larcher, 1995) and the porosity of the wood (Tyree and Ewers, 1996). The highest value of  $K_s$  was found in November ( $26.936 \text{ kg.m}^{-1}.\text{sec}^{-1}.\text{MPa}^{-1}$ ) in *B. variegata* and in September ( $9.172 \text{ kg.m}^{-1}.\text{sec}^{-1}.\text{MPa}^{-1}$ ) in *C. australis*. In both the species, the value of  $K_s$  was found decreasing from November and September, which might be due to embolism. But in case of *L. indica*, the value was higher in March ( $7.783 \text{ kg.sec}^{-1}.\text{m}^{-1}.\text{MPa}^{-1}$ ), which might be due to rapid supply of water to newly formed leaf.

Similarly, leaf specific conductivity ( $K_l$ ) showed positive correlation with HV ( $r = 0.961$ ) in *B. variegata*. The value was highest in the December ( $20.796 \times 10^{-3} \text{ kg.m}^{-1}.\text{sec}^{-1}.\text{MPa}^{-1}$ ) which was due to sufficient water supply to the leaves distal to the segment even the leaves are in extreme senescing stage. In *C. australis*, the  $K_l$  was highest in September ( $17.39 \times 10^{-4} \text{ Kg.m}^{-1}.\text{sec}^{-1}.\text{MPa}^{-1}$ ) and it was due to high correlation between  $K_h$  ( $r = 0.681$ )  $K_s$  ( $r = 0.740$ ),  $\text{LRWC}_{\text{pd}}$  ( $r = 0.664$ ) and  $g_{\text{sd}}$  ( $r = 0.509$ ). In *L. indica*, similar to specific conductivity ( $K_s$ ), it was higher in April ( $53.118 \times 10^{-3} \text{ Kg.sec}^{-1}.\text{m}^{-1}.\text{MPa}$ ). When new leafing was initiated the hydraulic sufficiency of the segment to supply water to the leaves of distal end was high giving the higher value in April. It showed positive correlation with  $K_s$  ( $r = 0.563$ ), HV ( $r = 0.940$ ) but negatively correlated with  $g_s$  at morning and day ( $r = -0.793$  and  $r = -0.749$  respectively).

Specific leaf mass (SLM) increased with increasing leaf maturation in *B. variegata*. In February and March leaves were senescing so the SLM had low value. During monsoon, the plant leaf fully expanded by getting sufficient water and therefore the value was found in ascending order from May, June and August. Fully opened stomata aided to reach the



photosynthesis rate at its peak and therefore greater mass was accumulated in January, and then decreased in February and March (in one sample tree) due to senescence. Higher value of SLM is also correlated with light intensity (Q), which was also found in present study. Similar findings were obtained by Shiraishi et.al.. (1996), Lei and Lechowicz (1998), Mainali (2000), Bhattarai (2001), Tripathee (2001) and Nepal (2002) and Uprety (2002). During the late summer, late monsoon, and in winter SLM was higher concomitantly with higher irradiance. In *B. variegata* SLM did not show significant correlation with other parameters except  $\psi_{sf}$  ( $r = 0.523$ ).

In *C. australis*, lower value of SLM in March ( $3.252 \times 10^{-3} \text{ g/cm}^2$ ) was due to immature leaves. Similarly, during the monsoon, the values were higher indicating higher rates of dry matter accumulation by photosynthesis under favourable condition. SLM showed strong correlation with  $g_{sd}$  ( $r = 0.867$ ). SLM in case of *L. indica* showed somewhat different pattern from the other two species where the SLM was high in winter. This species has low SLM in winter i.e. December ( $1.128 \times 10^{-3} \text{ gcm}^{-2}$ ), which was due to senescence. The color of the leaves became reddish orange. The value was higher in April, which was due to higher photosynthesis under the condition higher light intensity and moderate water supply.

Regulation of leaf conductance is generally considered as a mechanism by which plants control their water loss and maintain the hydration level. Leaf conductance ( $g_s$ ) depends both on availability of moisture in the soil and vapour pressure on the air (Lambers et al., 1998). In *B. variegata*, stomatal conductance ( $g_s$ ) both in morning and midday was higher in October (603.66 and 382.13  $\text{mmol.m}^{-2}.\text{s}^{-1}$ ). In *C. australis*,  $g_{sm}$  was higher in October (603.5  $\text{mmol.m}^{-2}.\text{s}^{-1}$ ) and  $g_{sd}$  was higher in September (367.2  $\text{mmol.m}^{-2}.\text{s}^{-1}$ ). Similarly, in *L. indica*,  $g_{sm}$  was highest in September (474  $\text{mmol.m}^{-2}.\text{s}^{-1}$ ) and  $g_{sd}$  was highest in October (372.8  $\text{mmol.m}^{-2}.\text{s}^{-1}$ ). In general, stomatal conductance was higher in September and October during which sufficient moisture was available in soil with frequent precipitation (Appendices 7, 8 and 9). In all the species, gradual decrease in leaf conductance during winter was due to leaf senescence. Leaf conductance was in general, higher in the morning than in mid-day. In morning, plants show saturation and soil show its field capacity (Lambers et al., 1998), and also there is sufficient light to cause the stomata open, and thus show higher conductance. As the intensity of the light increases at noon, temperature also increases which reduces the leaf conductance by closing the stomata



(Larcher 1995). Similarly, stomata also close partially in many cases when the air humidity is low and evaporative demand is high, although the water status of the bulk leaf tissue is above the closure threshold value (Bradford and Hsiao, 1982).

Decrease in leaf conductance was controlled more by decrease in soil water potential than leaf water potential. It is found that stomatal closure is correlated with higher concentration of abscisic acid (ABA) in leaves due to decrease in soil water potential (Lambers *et al.*, 1998). Closure of stomata by  $K^+$  as the leaf under goes water stress has also been found (Hsiao, 1973).

Exceptionally,  $g_{sm}$  was found lower than  $g_{sd}$  in the same months (eg. September for *B. variegata*, June for *C. australis* and *L. indica*) which was due to unstable weather prevailing on the day of measurement. This finding was not in consistent with the finding of Prior *et al.* (1997) where  $g_s$  was always higher in the morning than in afternoon. Similar results were found in *Schima wallichii* (Pokharel, 2001), *Shorea robusta* (Tripathee, 2001), *Quercus lanata* and *Cinnamomum camphora* (Nepal, 2002) and *Alnus nepalensis* and *Cotoneaster bacillaris* (Upreti, 2002).

All the phenological activities (bud break, flowering, leaf fall and leafing) were concentrated in the drier months of the year (December to April) in *B. variegata*, *C. australis* and *L. indica*. But bud break and flowering in case of *L. indica* was observed in late May and June. The phenologically active periods were observed long in all the three species. Leaf fall started at the end of September and complete leaf fall was observed in March in *B. variegata* as well as *L. indica*. In *C. australis*, leaf senescence started from late August and completed in late February. Leaf fall is the functional strategy to maintain favorable tissue water status for growing tissue because decreased leaf surface area conserved water from transpirational loss. The results of Castell and Terrudas (1995) also showed the similar strategy. Leaf shedding during the early dry season and leafing immediately after the leaf shedding was found in all species studied, which is the characteristics of most trees in tropical dry forest (Borchert, 1994 ab) as well as Himalayan trees (Ralhan *et al.*, 1985).

Increasing water scarcity during the early dry season generally causes a decline in water potential and leaf shedding. Rehydration of leafless twig is a prerequisite for the

subsequent opening of vegetative and flower buds (Borchert, 1995). In *B. variegata*, complete leaf fall occurred in March which was successively followed by bud break, flowering and leaf flushing. But in one sample tree, leaf fall was completed in April thus delaying the flowering and new leaf formation. In shaded condition, plants produce leaves that can utilize low light effectively but not high light and this is beneficial for such plants to extend leaf longevity (Kikuzawa, 1995). If drought-resistant leaves of trees at moist are retained well in the dry season, leaf flushing or flowering triggered by leaf fall occurs over an extended period. In such species difference in drought resistance of leaves and in soil water reserves determine tree water balance during the dry season (Borchert, 1995) and hence, indirectly, variation in vegetative phenology results in staggered flowering. Similar observations were observed in case of *B. variegata*. Tree growing at moist sites retained their leaves longer than their conspecifics at dry sites as found by Borchert (1994 b).

In *B. variegata* leaf abscission started from upper part of the crown, and large flowers opened on the bare, upper branches while the lower branches still carry old, strongly dessicated leaves lacking stomatal conductance. Similar results were also cited by Reich and Borchert (1984) in deciduous trees of dry tropical forest. Cell expansion in growing buds or flowers, supposedly sensitive to water stress, thus takes place in a crown or in branches bearing strongly water stressed senescent leaves (Borchert, 1994 b) which was found in *B. variegata*. Here, in this situation, stem tissues rehydrate before or soon after leaf shedding and new shoots with lateral and terminal flowers develop during dry season.

With the increase in  $K_h$  flowering process began from March in *B. variegata*. This type of relation was also reported in deciduous hard woods (Wang *et al.*, 1992)

Different phenological events occurred in different months in *L. indica*. Even though leaf fall and new leaf flushing (secondary leaf formation) was initiated from late September and becomes completely senescent in December. But during the same month again new leafing was found. This event was found to occur thrice a time and such leaf last for one week. This was found in all trees but was most frequent in tree at drier site. Such pattern of multiple leafing was also observed by Ralhan *et al.* (1985) revealing an evolutionary strategy enabling the species to utilize more efficiently the favourable periods of potentially unfavourable seasons such as winter.

Leafing in *L. indica* was similar to that of dry tropical forest. But flowering in case of *L. indica* was different from the *B. variegata* in the sense that bud break and flowering was observed in June. The most likely environmental change controlling the periodicity of tree growth and flowering are the first heavy rainfalls after prolonged dry season, causing the rehydration of flower as well as expansion of leaves as observed in most tropical dry forests (Borchert, 1994 a,b) and this finding was consistent with the *L. indica*.

## 7. CONCLUSION

Seasonality and climatic conditions had strong control over water status of plants. Marked variation in water relation parameters were observed in different seasons in *Bauhinia variegata* L., *Celtis australis* L. and *Lagerstroemia indica* L.

Values obtained from the P-V curves analysis showed osmotic adjustment as well as elastic adjustment in all species. Before the complete leaf fall, least values of osmotic potential were found in all the species which facilitates the plant to extract the water easily from dry soil. This can also be observed by drought avoidance mechanism as evident from leaf shedding during dry months. In *B. variegata* only osmotic adjustment was found. But in *C. australis* and *L. indica* both osmotic and elastic adjustment was found. *C. australis* and *L. indica* showed higher tissue elasticity in phenologically active period (May and April, respectively) indicating the elastic adjustment. Both osmotic and elastic adjustments were important strategies for drought tolerance.  $RWC_z$  in all the species showed marked difference, the maximum difference was found in *B. variegata* (63% to 86%). Lower value of  $RWC_z$  was important in maintaining for plant growth during dry months. Leaf relative water content for all the species was higher in all the season and it differed between the predawn and midday values. But it was insignificant because it didn't show any variation with the seasonal change in water status as shown by other parameters. However, there was wide difference between LRWC and  $RWC_z$  of the twig for all species.

Seasonal variation in hydraulic conductance occur in all the species, the values being higher in September (*C. australis* and *L. indica*) and October (*B. variegata*). Lower values were obtained when drought progressed and plant faces water stress. Similarly, stomatal conductance was higher in September (*L. indica*) and in October (*B. variegata* and *C. australis*).

All the species were deciduous and most of the phenological events reached its peak during dry periods of the year except flowering in *L. indica* which takes place during monsoon. SLM was distinct in all the three species, the value being large at leaf maturation and lower at leaf senescence.

Thus, it is concluded that, though the studied species are planted they showed both drought tolerance and avoidance mechanisms and therefore growth and development remain unaffected even in severe drought condition.

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## APPENDICES

**Appendix 1: Leaf Relative Water Content (LRWC, %), seasonal variation. Values are mean with = standard deviation. Leaf Relative water content measured at two times of a day; Predawn (before sunrise) and mid-day (12:00 - 1:00 P.M), Sample size = 3 for *Bauhinia variegata*.**

Month	LRWC(%)	
	Predawn	Mid-day
August	97.96	92.84
September	96.45	89.453
October	98.73	92.71
November	98.90	94.14
December	99.40	94.93
January	99.62	93.98
February	98.40	92.19
March	96.24*	93.97*
May	95.93	95.42
June	99.67	98.97

Note: \*LRWC for single tree sample

**Appendix 2: leaf Relative Water Content (LRWC, %), seasonal variation. Values are mean with = standard deviation. Leaf Relative water content measured at two times of a day; Predawn (before Sunrise) and mid-day (12:00 - 1:00 P.M), Sample size = 3 for *Celtis australis*.**

Month	LRWC(%)	
	Predawn	Midday
August	91.848	89.08
September	97.07	90.34
October	96.83	86.96
November	95.78	92.59
December	98.76	88.94
March	98.41	98.22
April	95.61	90.83
May	96.42	94.31
June	99.34	96.01

**Appendix 3: Leaf Relative Water Content (LRWC, %), seasonal variation. Values are mean with = standard deviation. Leaf relative Water content measured at two times of a day; predawn (before Sunrise) and mid-day (12:00 - 1:00 P.M.), sample size = 3 for *Largarstroemia indica*.**

Month	LRWC(%)	
	Predawn	Midday
August	94.82	87.97
September	98.82	94.05
October	98.92	91.932
November	99.21	95.98
December	97*	89.25*
March	96.54	94.31
April	97.30	96.50
May	98.82	97.12
June	99.27	96.23

\*LRWC for single sample.



**Appendix 4: Parameters obtained from P-V curve analysis. Seasonal variation in Osmotic potential at zero turgor ( $\psi_{sz}$ , MPa), osmotic potential at full turgor ( $\psi_{sf}$ , MPa), water potential at full turgor ( $\psi_{wf}$ , MPa), pressure potential at full turgor ( $\psi_{pf}$ , MPa), relative water content at zero turgor ( $RWC_z$ , %) and bulk modulus of elasticity ( $\epsilon$ , MPa) for *Bauhinia varegata*.**

Month	$\Psi_{sz}$	$\Psi_{sf}$	$\Psi_{pf}$	$RWC_z$	$\epsilon$
August	-2.38	1.66	1.64	63	4.432
September	-1.694	-1.265	1.015	64	2.819
October	-2.222	-1.923	1.898	82	5.638
November	-2.5	-2.222	2.122	66	6.241
December	-2.0	-1.724	1.699	78	7.722
January	-2.325	-1.785	1.735	68	5.421
February	-2.04	-1.47	1.445	68	4.515
May	-1.111	-0.961	0.836	86	5.971
June	-1.109	-0.892	0.767	71	2.644

**Appendix 5: Parameters obtained from P-V curve analysis. Seasonal variation in osmotic potential at zero turgor ( $\psi_{sz}$ , MPa), Osmotic potential at full turgor ( $\psi_{sf}$ , MPa), water potential at full turgor ( $\psi_{wf}$ , MPa), pressure potential at full turgor ( $\psi_{pf}$ , MPa), Relative water content at zero turgor ( $Rwc_z$ , %) and Bulk modulus of elasticity ( $\epsilon$ , MPa) for *Celtis australis*.**

Month	$\Psi_{sz}$	$\Psi_{sf}$	$\Psi_{pf}$	$RWC_z$	$\epsilon$
August	-1.818	-1.515	1.465	72.5	5.327
September	-1.923	-1.538	1.488	68	4.65
October	-2.127	-1.754	1.554	79	7.4
November	-2.272	-1.785	1.76	63	4.756
December	-2.325	-1.818	1.793	71	6.182
March	-1.492	-1.219	1.069	75	4.276
April	-2.0	-1.47	1.445	71	4.982
May	-1.96	-1.47	1.395	62	3.671
June	-2.222	-1.754	1.729	68	5.403

**Appendix 6: Parameters obtained from P-V curve analysis. Seasonal variation in Osmotic potential at zero turgor ( $\psi_{sz}$ , MPa) Osmotic potential at full turgor ( $\psi_{sf}$ , MPa), water potential at full turgor ( $\psi_{wf}$ , MPa), pressure potential at full turgor ( $\psi_{pf}$ , MPa), relative water content at zero turgor ( $Rwc_z$ , %), and Bulk modulus of elasticity ( $\epsilon$ , MPa) for *Lagerstroemia indica*.**

Month	$\Psi_{sz}$	$\Psi_{sf}$	$\Psi_{pf}$	$RWC_z$	$\epsilon$
August	-1.851	-1.333	1.308	76	5.45
September	-1.886	-1.470	1.42	77	6.173
October	-2.0	1.515	1.465	79	6.976
November	-1.754	-1.408	1.358	79	6.466
December	-2.272	-1.754	1.704	74.5	6.682
March	-1.587	-1.01	0.885	74	3.403
April	-1.818	-1.369	1.344	70	4.48
May	-1.960	-1.282	1.232	72	4.4
June	-1.587	-1.265	1.165	82	6.472

**Appendix 7: Stomatal conductance and controlling parameters. Monthly variation at morning (9 - 10:00 a.m.) and mid-day (12:00 - 1:00 p.m.) values are means with = standard deviation. Sample size = 5 for *Bauhinia variegata*.**

Month	Stomatal conductance ( $\mu\text{ mol m}^{-1}\text{ s}^{-1}$ )		Leaf temprature $^{\circ}\text{C}$		Light intensity on leaf ( $\mu\text{ mol. m}^{-2}\text{ s}^{-1}$ )		R.H. set (%)	
	Mor.	M-day	Mor.	M-day	Mor.	M-day	Mor.	M-day
Sept	181.361±4.19	442.6±141.73	26.34±0.16	28.86±0.17	510.66±372.08	193.33±47.75	65	60
Oct	603.66±103.06	382.133±42.09	26.67±0.74	26.98±0.33	306.6±153.90	108.66±20.40	65	60
Nov	248.8±61.67	70.1±21.42	20.77±0.18	25.32±0.89	242±113.92	82.66±13.27	58	53
Dec	143.26±29.15	69.2±12.32	17.38±0.13	22.10±0.64	570.33±219.44	393.66±291.57	55	45
Jan	139.8±41.81	70.56±6.34	13.09±0.51	18.25±1.46	732.6±199.33	593.26±309.21	58	54
June	276.2±94.8	179.9±13.1	32.9±0.56	27.98±0.68	773±382.6	205.3±23.5	69	65

**Appendix 8: Stomatal conductance and controlling parameters. Monthly variation at morning (9:00 - 10:00 a.m.) and Mid-day (12:00 - 1:00 p.m.) values are means with = standard deviation. Sample size = 5 for *Celtis australis*.**

Month	Stomatal conductance ( $\mu\text{ mol m}^{-1}\text{ s}^{-1}$ )		Leaf temprature $^{\circ}\text{C}$		Light intensity on leaf ( $\mu\text{ mol. m}^{-2}\text{ s}^{-1}$ )		R.H. set (%)	
	Mor.	M-day	Mor.	M-day	Mor.	M-day	Mor.	M-day
Sept	577.13±243.33	362.2±28.32	27.96±0.29	28.64±0.63	323.66±275.57	132.33±21.51	65	60
Oct	603.5±82.5	141.2±29.2	27.92±0.34	27.58±0.76	326.9±19.9	104±1	65	60
Nov	166.6±21.4	70.9±9.5	19.57±0.49	27±0.7	88.5±11.5	71±10	58	53
Dec	98.9±13.7	54.3±9.5	16.28±0.62	20.6±0.28	70.5±21.5	51.4±4.4	55	45
Jan	111.85±28.35	43.6±0.3	11.75±0.93	19.81±1.15	83.5±1.5	56.2±5.8	58	54
June	143.1±0.7	222.4±49.0	32.5±0.14	27.48±0.12	560.5±198.9	197.8±62.8	69	65

**Appendix 9: Stomatal conductance and controlling parameters. Monthly variation at morning (9:00 - 10:00 a.m.) and Mid day (1:00 - 2:00 p.m.) and values are means with = standard deviation. Sample size = 5 for *Largenstroemica indica*.**

Month	Stomatal conductance ( $\mu\text{ mol m}^{-1}\text{ s}^{-1}$ )		Leaf temprature $^{\circ}\text{C}$		Light intensity on leaf ( $\mu\text{ mol. m}^{-2}\text{ s}^{-1}$ )		R.H. set (%)	
	Mor.	M-day	Mor.	M-day	Mor.	M-day	Mor.	M-day
Sept	474±51.39	237.7±16.5	27.75±0.63	28.86±0.12	221.66±142.36	119.3±64.0	65	60
Oct	473.4±169.10	372.8±164.32	27.27±0.74	26.33±0.53	249±114.3	529.46±253.54	65	60
Nov	268.5±19.99	74.8±16.94	20.64±0.23	26.33±0.53	173±120.43	368.6±134.33	58	53
Dec	108.4±29.95	24.4±11.34	17.68±0.44	21.58±0.32	318.5±42.61	486.9±518.65	55	45
Jan	81.92±0*	20.76±0	13.82±0	21.96±0	657.6±0	1326±0	58	54
June	228.7±29.36	310±39	27.44±1.16	26.77±0.26	144.6±100.88	197.6±53.45	69	65

\* g<sub>s</sub> for single sample tree.

**Appendix 10: Seasonal variation in various parameters of xylem conductance: Huber value (HV), Hydraulic conductivity ( $K_h$ , kg.m sec<sup>-1</sup>. MPa<sup>-1</sup>), specific conductivity ( $K_s$ , kg.m<sup>-1</sup> sec<sup>-1</sup>, MPa<sup>-1</sup>) and leaf specific conductivity ( $K_l$ , kg.m<sup>-1</sup> sec<sup>-1</sup>, MPa<sup>-1</sup>). Sample size = 1 for *Bauhinia variegata*.**

Month	(HV)	$K_h$	$K_s$	$K_l$
August	$0.357\times10^{-3}$	$6.190\times10^{-6}$	2.099	$2.056\times10^{-4}$
September	$0.157\times10^{-3}$	$4.901\times10^{-6}$	0.551	$0.348\times10^{-4}$
October	$0.343\times10^{-3}$	$55.0\times10^{-6}$	6.297	$8.648\times10^{-4}$
November	$7.494\times10^{-3}$	$49.16\times10^{-6}$	26.936	$80.75\times10^{-4}$
December	$11.307\times10^{-3}$	$40.99\times10^{-6}$	4.597	$207.965\times10^{-4}$
January	$0.745\times10^{-3}$	$50.9\times10^{-6}$	7.953	$32.59\times10^{-4}$
February	$0.836\times10^{-3}$	$7.352\times10^{-6}$	1.096	$3.670\times10^{-4}$
May	$0.869\times10^{-3}$	$22.222\times10^{-6}$	0.759	$5.943\times10^{-4}$
June	$0.245\times10^{-3}$	$26.111\times10^{-6}$	2.418	$5.337\times10^{-4}$

**Appendix 11: Seasonal variation in various parameters of xylem conductance: Huber value (HV), Hydraulic conductivity ( $K_h$ , kg.m sec<sup>-1</sup>. MPa<sup>-1</sup>), specific conductivity ( $K_s$ , kg.m<sup>-1</sup> sec<sup>-1</sup>, MPa<sup>-1</sup>) and leaf specific conductivity ( $K_l$ , kg.m<sup>-1</sup> sec<sup>-1</sup>, MPa<sup>-1</sup>).Sample size = 1 for *Celtis australis*.**

Month	(HV)	$K_h$	$K_s$	$K_l$
August	$1.823\times10^{-4}$	$16.27\times10^{-6}$	0.650	$0.889\times10^{-4}$
September	$2.527\times10^{-4}$	$186.574\times10^{-6}$	9.172	$17.39\times10^{-4}$
October	$2.932\times10^{-4}$	$85.984\times10^{-6}$	5.215	$11.469\times10^{-4}$
November	$1.833\times10^{-4}$	$41.056\times10^{-6}$	3.260	$4.183\times10^{-4}$
December	$6.965\times10^{-4}$	$38.095\times10^{-6}$	3.777	$15.788\times10^{-4}$
March	$42.613\times10^{-4}$	$4.761\times10^{-6}$	0.973	$8.623\times10^{-4}$
April	$2.015\times10^{-4}$	$32.926\times10^{-6}$	2.786	$4.492\times10^{-4}$
May	$3.364\times10^{-4}$	$10.569\times10^{-6}$	0.427	$1.007\times10^{-4}$
June	$9.146\times10^{-4}$	$36.764\times10^{-6}$	1.946	$10.683\times10^{-4}$

**Appendix 12: Seasonal variation in various parameters of xylem conductance: Huber value (HV), Hydraulic conductivity ( $K_h$ , kg.m sec<sup>-1</sup>. MPa<sup>-1</sup>), specific conductivity ( $K_s$ , kg.m<sup>-1</sup> sec<sup>-1</sup>, MPa<sup>-1</sup>) and leaf specific conductivity ( $K_l$ , kg.m<sup>-1</sup> sec<sup>-1</sup>, MPa<sup>-1</sup>). Sample size = 1 for *Lagerstroemia indica*.**

Month	(HV)	$K_h$	$K_s$	$K_l$
August	$0.649\times10^{-3}$	$2.185\times10^{-5}$	0.834	$0.461\times10^{-3}$
September	$0.48\times10^{-3}$	$16.271\times10^{-5}$	5.917	$2.702\times10^{-3}$
October	$0.816\times10^{-3}$	$8.902\times10^{-5}$	5.731	$3.975\times10^{-3}$
November	$4.633\times10^{-3}$	$3.547\times10^{-5}$	3.018	$8.392\times10^{-3}$
December	$20.396\times10^{-3}$	$6.111\times10^{-5}$	4.379	$44.661\times10^{-3}$
March	$13.6\times10^{-3}$	$14.28\times10^{-5}$	7.788	$53.118\times10^{-3}$
April	$0.124\times10^{-3}$	$7.222\times10^{-5}$	4.115	$0.486\times10^{-3}$
May	$0.391\times10^{-3}$	$6.406\times10^{-5}$	3.717	$1.383\times10^{-3}$
June	$0.143\times10^{-3}$	$6.96\times10^{-5}$	2.870	$0.354\times10^{-3}$

Appendix 13: seasonal variation in specific leaf mass (SLM, gm.cm<sup>-2</sup>). Values are mean. Sample size = 5, for all the species taken.

Month	Specific leaf mass (SLM)		
	<i>Bauhinia variegata</i>	<i>Celtis australis</i>	<i>Largerstroemia indica</i>
August	8.096×10 <sup>-3</sup>	5.127×10 <sup>-3</sup>	3.3×10 <sup>-3</sup>
September	7.286×10 <sup>-3</sup>	6.659×10 <sup>-3</sup>	2.411×10 <sup>-3</sup>
October	5.990×10 <sup>-3</sup>	5.621×10 <sup>-3</sup>	1.265×10 <sup>-3</sup>
November	6.645×10 <sup>-3</sup>	5.542×10 <sup>-3</sup>	2.552×10 <sup>-3</sup>
December	6.24×10 <sup>-3</sup>	8.212×10 <sup>-3</sup>	1.128×10 <sup>-3</sup>
January	8.303×10 <sup>-3</sup>	-	-
February	5.853×10 <sup>-3</sup>	-	-
March	5.444×10 <sup>-3</sup>	3.252×10 <sup>-3</sup>	4.107×10 <sup>-3</sup>
April	-	6.766×10 <sup>-3</sup>	5.285×10 <sup>-3</sup>
May	7.144×10 <sup>-3</sup>	7.046×10 <sup>-3</sup>	3.735×10 <sup>-3</sup>
June	7.919×10 <sup>-3</sup>	6.824×10 <sup>-3</sup>	2.271×10 <sup>-3</sup>

\*SLM for single sample tree

Appendix 14: Variation of Climatic Data from August 2002 to June 2003 in Kathmandu Recorded at Tribhuvan International Airport.

Month	Temperature(°C)		Mean Rainfall (mm)
	Maximum	Minimum	
August	29.0	19.8	499.9
September	28.1	18.2	148.0
October	26.7	13.5	15.0
Nov	23.8	8.4	26.5
Dec	19.8	4.0	0
Jan	19.2	2	19.5
Feb	20.5	6	60.3
Mar	24.5	8.9	85.9
Apr	28.6	13.3	38
May	29.6	14.6	37.7
June	28.7	19.1	227.3

Source: Department of Hydrology and Meteorology, HMG/N for rainfall and temperature.

