



Journal of Biological Sciences

ISSN 1727-3048

science
alert

ANSI*net*
an open access publisher
<http://ansinet.com>

Ecophysiological and Growth Responses of Elm, *Ulmus pumila*, to Different Water Tables

^{1,2}Xiongwen Chen

¹Center for Forestry and Ecology, P.O. Box 1927, Alabama A & M University, Normal, AL 35762, USA

²Laboratory of Quantitative Vegetation Ecology, Institute of Botany,
Chinese Academy of Sciences, Beijing 100093, People's Republic of China

Abstract: The relationships between tree ecophysiological activity and underground water table need to be studied because a huge number of trees died in arid and semi-arid area during recent years for the decreasing water table due to increasing water consumption. In this study, the water table was represented by the distance from soil surface to water surface. Study on the effect of water tables on the ecophysiological characteristics and growth of *Ulmus pumila* saplings was conducted by a short-term experiment. Saplings at water tables of -5 (under water), 3, 9, 15 and 22 cm were abbreviated as U-5, U3, U9, U15 and U22. Present results indicated that water table did affect the ecophysiological and growth response of *U. pumila*. All U-5 died after one week. U9 and U15 had higher net photosynthesis rates than those of U3 and U22. The diurnal mean transpiration rate of U3 was significantly lower than that of U9, U15 and U22, respectively. The diurnal mean stomatal resistance of U3 was significantly higher than that of U9, U15 and U22, respectively. U22 had the highest increment in main root length and there was good correlation between water level and main root length. U15 had the highest increment in stem height. Maintaining proper water table would result in higher net photosynthesis, water use efficiency, plant height and root length, but relative lower transpiration rate for *U. pumila* saplings. These results would have implications for water management at arid and semi-arid area for vegetation survival and regeneration. Seedlings and saplings should not be submerged for a long time during irrigating. Ecophysiological measurements can indicate the underground water table. Maintaining proper underground water table at arid and semi-arid area would be helpful to the growth of plant species and vegetation.

Key words: Main root length, net photosynthesis, transpiration rate, water use efficiency

INTRODUCTION

Elm, *Ulmus pumila* L. is an important and popular tree species at the arid and semi-arid area in China^[1]. It is shade-intolerant and tends to live at the deep, drained and fertile soil, but it can also grow in the dry, infertile and salt-alkaline soil so that it is usually distributed near or far away from river banks in the arid and semi-arid area. Many trees, including *U. pumila*, have died at this area in China during the recent years because of the decreasing underground water table due to environmental change (such as, increased air temperature and decreased precipitation) and overuse of groundwater. The typical example was that a huge number of trees died at the watershed of Tarim River, Xinjiang, China and the local government had to release water from the nearby lakes and reservoirs to preserve the vegetation there. Therefore, how to maintain the proper water table to preserve the current vegetation in the arid and semi-arid area is urgent to the local government. Ewanchuk and Bertness^[2] suggested that water table can cause different plant

communities. The long-term responses of the riparian vegetation along reservoirs and run-of-river margin to water level regulation indicated that water level have long-term effect on the ecological integrity and biodiversity of the vegetation^[3]. The extent of the Tana riverine forest is determined by the water-table depth of the river and consequently the composition, structure and dynamics of the forests are influenced by the hydrological characteristics of the river system^[4,5]. Flooding is found to be the overriding factor controlling regeneration of *Quercus lyrata* in a seasonally flooded karst depression^[6]. Water decline will have effects on growth allocation and concentrations of endogenous gibberellins in black cottonwood saplings^[7]. The responses of leaf respiration to temperature and leaf characteristics of three deciduous tree species vary with water availability and trees at the dry site have higher rates of leaf respiration and lower assimilation than trees at the wet site^[8]. Also there are many researches about ecophysiological response of *Eucalyptus* species to different watering regimes^[9,10]. Although little direct

research was reported on tree species, such as *U. pumila*, about the relationship between plant growth and water table at arid and semi-arid area in China, it can be hypothesized based on the above literatures that ecophysiological activities and growth of *U. pumila* in the arid and semi-arid area would be determined by water table (in this research the water table is defined as distance from soil surface to water surface), higher rate of photosynthesis and lower main root length may be related with lower water table; lower rate of photosynthesis, lower stomatal conductance and longer main root may be related with higher water table. The aim of this research was to test this hypothesis and find out the effects of water table on the ecophysiological and growth response of *U. pumila* saplings, then, determine what kind of water level will be suitable for the plant growth.

MATERIALS AND METHODS

Plant material and growth conditions: In this study, *Ulmus pumila* is an ecotype that lives at dry and infertile soil. The experiment was conducted at the semi-opened greenhouse (free air and sun-light could enter, but rain could not enter) in Institute of Botany of the Chinese Academy of Sciences, Beijing, China, from March to October 2000. More than 40 saplings of *U. pumila* with buds but no leaves at a nearby seedling bed were chosen at the similar size of 10-15 cm in height, 0.2-0.3 cm in diameter and 3.5 to 5.0 cm of main root length. All the saplings were from the same seed source. The age of the saplings was about 2 years. Each selected sapling was labeled and the height, stem diameter and length of main root were recorded. The stem diameter of every sapling was measured at 2 cm above the soil surface at three directions by vernier caliper, then, a marker was made. All these saplings were transplanted into large plastic pipes (PVC) at 5 different lengths and were filled with the original soil. The diameter of the plastic pipes was 12 cm and lengths were 15, 23, 29, 35 and 42 cm. There were more than 8 saplings for each cylinder size. One sapling occupied one pipe. For each pipe size the inside soil was of the similar weight and the soil weight was proportional to the pipe length. The soil weight in each pipe size was 1.5, 2.3, 2.9, 3.5 and 4.2 kg, respectively, and the standard deviations were less than 5 g. Based upon the results of analysis, the soil properties were: pH 7.2, organic matter 7%, N: P: K was 1: 1.3: 1.4, total S was 0.6%, NO_3^- was $570 \mu\text{g g}^{-1}$ and field water capacity was 53%. After the transplantation the soil was irrigated to the full water capacity at every 4-5 days by water without any fertilizer. All the saplings were under semi-shade condition, the Photosynthetic Photon Flux Density

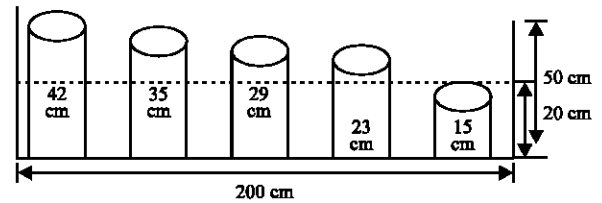


Fig. 1: Profile of the plastic tank and different height of PVC tubes. The number on each cylinder represents the height of each cylinder. The dotted line indicates water surface in tank. Eight replicates were arranged in the same way. There was no interaction between each sapling

(PPFD) was about $500 \mu\text{mol m}^{-2}\text{s}^{-1}$ and the air temperature was from 25 to 35°C. After one month 8 surviving saplings and each with 1 to 2 leaves were chosen for each cylinder length. The height and stem diameter of each seedling were recorded again. After that, all these cylinders with saplings were moved into a big plastic tank (250 cm length×80 cm width×50 cm height). The tank was filled with water and the water was maintained at 20 cm constantly, then, five water tables (distance from soil surface to water surface) (-5, 3, 9, 15 and 22 cm) were formed (Fig. 1). Saplings in water were chosen because we would like to know whether flooding would affect the ecophysiological characters and growth of saplings. This is important for forest preservation and regeneration by releasing water from nearby reservoirs, because during water release many seedlings and saplings were flooded. The tank water was constantly maintained at 20 cm by filling water. Because the greenhouse was semi-opened, the environmental condition, such as temperature and radiation regimes, varied with the local climate. During the experimental period PPFD at noon was about $1350\text{-}850 \mu\text{mol m}^{-2}\text{s}^{-1}$ and the air temperature was 20-40°C. This condition was similar with natural conditions of seedlings in the nearby forests.

Measurements and statistical analysis: After about four months three top leaves (the leaf was suitable for measuring) of each sapling were measured for rates of net photosynthesis, transpiration and stomatal resistance by CI-301 portable photosynthesis system (CID, USA) three times every hour from 9 am to 16 am for two continuous days with similar climate condition (Aug. 19 and 20). Generally the seasonal leaf abscission would occur on earlier time in November, however, this experiment was ended on Oct. 5 in order to obtain all leaves. Each sapling was harvested and the diameter, height and the length of main root were measured. After all, each sapling was

separated into leaf, branch and root. The dry weight was determined to within 0.01 g after 24 h at 90°C. The increment in height and main root during the experiment could be separated by the color.

Average and Standard Deviation (SD) of each indicator for 8 saplings at each water table was calculated. Statistical differences between means of every indicator at different pot sizes were determined by ANOVA at $p < 0.05$ level. For saplings at each water table the diurnal rates of net photosynthesis, transpiration and water use efficiency were the averages of 8 saplings at the same time during the two days. The average diurnal rate of photosynthesis was the mean rate of photosynthesis at different time points during two days. The differences of diurnal processes of net photosynthesis, transpiration and water use between treatments were compared by ANOVA and visual sense. Correlation analysis (CORR) was made between each indicator and water tables.

RESULTS

Effect of water table on the survival and growth of the saplings: All saplings of *U. pumila* at the water table of -5 cm (under water 5 cm) died after one week. However, the saplings at water tables of 3, 9, 15 and 22 cm survived.

Effect of water table on the net photosynthesis rate: If we use net photosynthetic rate (P_n) of the saplings at one time (such as noon) to represent the average P_n of the whole day, the mean P_n of U15 was the highest among these treatment ($p < 0.05$) (Fig. 2). However, the diurnal P_n of U3, U9, U15 and U22 were in Fig. 3. The average rates of diurnal P_n for U3, U9, U15 and U22 were 2.39, 5.21, 3.81 and 2.57 $\mu\text{mol m}^{-2}\text{s}^{-1}$, respectively. The saplings of U9 had the highest P_n . Therefore, P_n at one particular time

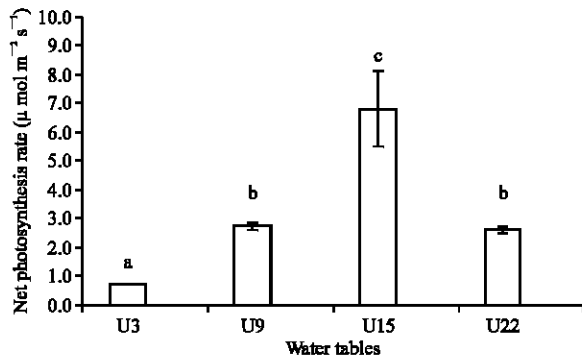


Fig. 2: The net photosynthesis rate of the saplings of *U. pumila* at noon in different water tables. U3, U9, U15 and U22 represent saplings at water tables of 3, 9, 15 and 22 cm. Columns with different letters are significant different at $p < 0.05$

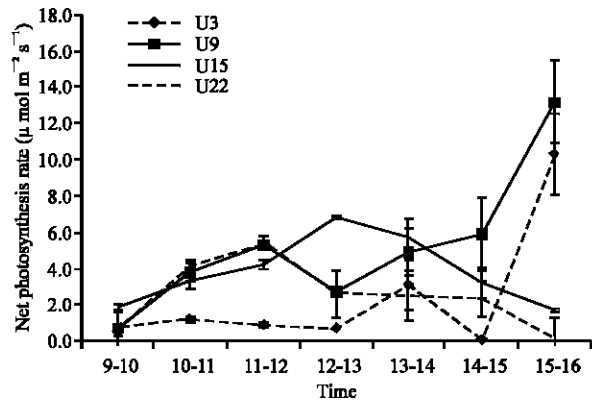


Fig. 3: The net photosynthesis rates of saplings of *U. pumila* at different water tables. Abbreviations are the same with Fig. 2

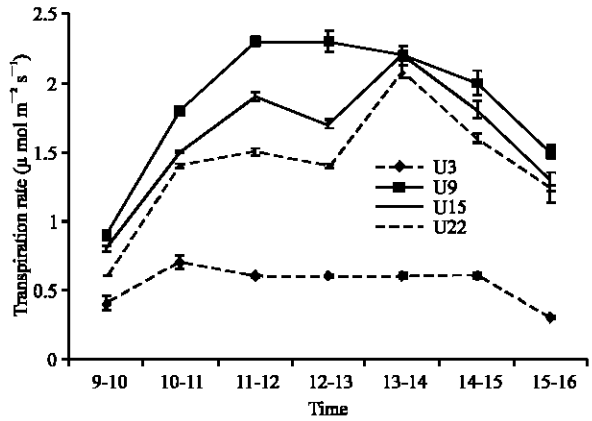


Fig. 4: The transpiration rates of saplings of *U. pumila* at different water tables. Legends and abbreviation are the same with Fig. 2

point could not represent the diurnal P_n exactly. P_n was higher at middle water levels, but it decreased when water table was above 15 cm.

Effect of water table on leaf water use: Water table did affect transpiration rate. Diurnal Mean Transpiration Rate (DMT) of U3 was significantly lower than that of U9 ($p = 0.0004$), U15 ($p = 0.0006$) and U22 ($p = 0.0019$), respectively (Fig. 4). However, DMT was not significantly different among U9, U15 and U22. The pattern of diurnal transpiration rate was similar for U9, U15 and U22 and transpiration rate increased in the morning and decreased at afternoon. However, the diurnal transpiration rate of U3 had no significant change during the day.

Diurnal Mean Water Use Efficiency (DMWUE) of U15 was significantly higher than that of U22 (Fig. 5). However, it was not significantly different between other pairs. Pattern of diurnal WUE was similar with diurnal P_n .

Table 1: Results of the morphological characteristics of *U. pumila* at different water tables (U3, U9, U15 and U22 represent saplings at water tables of 3, 9, 15 and 22 cm, respectively)*

	U3	U9	U15	U22
Root/shoot ratio	0.93 ^a (0.08)	0.95 ^a (0.10)	0.90 ^a (0.03)	0.94 ^a (0.08)
Increment in main root length (cm)	4.10 ^a (1.02)	12.10 ^{ab} (1.75)	14.60 ^b (1.13)	25.06 ^c (1.91)
Increment in diameter (cm)	0.18 ^a (0.10)	0.60 ^a (0.32)	0.71 ^a (0.41)	0.47 ^a (0.26)
Increment in height (cm)	0.30 ^a (0.13)	4.33 ^{ac} (2.95)	10.36 ^b (1.78)	8.5 ^b (0.83)

*Values of each index with same letter were not significantly different at $p < 0.05$, but with different letters were significantly different at $p < 0.05$; values in () were standard deviations of 8 replicates

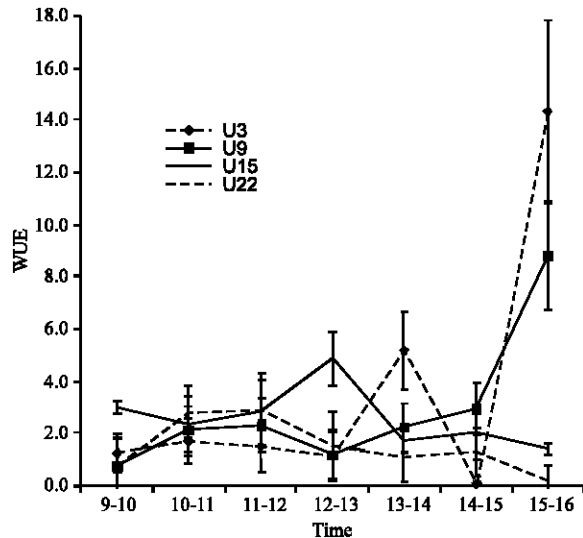


Fig. 5: WUE of the saplings of *U. pumila* at different water tables. Abbreviations are the same with Fig. 2

WUE increased in afternoon for U3 and U9, but it decreased for U15 and U22. The correlation between DMWUE and water table (WT) was $DMWUE = 3.9376 - 0.1048 WT$ ($F = 59.741$, $N = 48$, $R = -0.9837$, $p = 0.0163 < 0.05$). The unit of WT was cm.

Diurnal Mean Stomatal Resistance (DMSR) was significantly different between U3 and U9 ($p = 0.0031$), U3 and U15 ($p = 0.0004$), U3 and U22 ($p = 0.0005$), U15 and U22 ($p = 0.0468$) (Fig. 6), respectively. However, DMSR was not significantly different between other pairs. The correlation between DMSR and WT was $DMSR = 40.3573 - 1.4636WT$ ($F = 5.070$, $N = 48$, $R = -0.8468$, $p = 0.1532 > 0.05$). The unit of DMSR and WT were $\mu mol m^{-2} s^{-1}$ and cm, respectively.

Effect of water table on morphological characteristics:

The root/shoot ratio was not significantly different among U3, U9, U15 and U22 ($p > 0.05$) (Table 1). However, main root length (MRL) was significantly different between U3 and U15 ($p = 0.0003$), U3 and U22 ($p = 0.0001$), U9 and U22

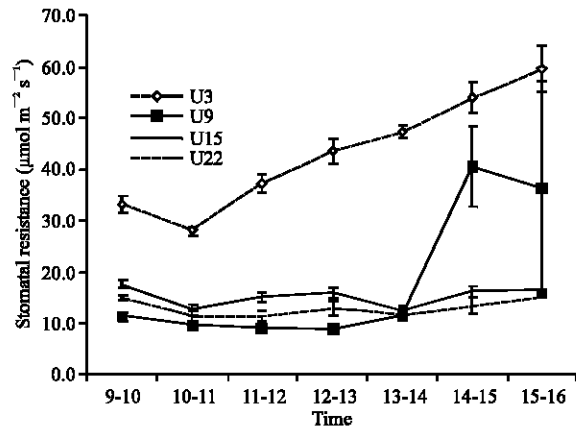


Fig. 6: The stomatal resistance of the saplings of *U. pumila* at different water tables. Abbreviations are the same with Fig. 2

($p = 0.011$), U15 and U22 ($p = 0.0045$), respectively. It was similar for the increment of MRL. The correlation between MRL and WT could be expressed as $MRL = 5.3310 + 1.0393 WT$ ($F = 59.563$, $N = 24$, $p = 0.0164 < 0.05$, $R = 0.9836$). The units of both MRL and WT were cm.

The increment in diameter was not significantly different among U3, U9, U15 and U22. However, the increment in height was significantly different between U3 and U15 ($p = 0.003$), U3 and U22 ($p = 0.005$), U9 and U15 ($p = 0.0123$), respectively. As the water table increased, the increment in plant height increased; but if the water table was higher than 15 cm, the increment in height decreased.

DISCUSSION

All saplings of *U. pumila* under water (water table = -5 cm) died after one week. However, the saplings at water tables of 3, 9, 15 and 22 cm could survive and grow. This indicated the water tolerance of *U. pumila* was low. There are many reasons for the death of the submerged *U. pumila*, the possible reasons might be the low diffusion of oxygen in water, the oxygen concentration in the submerged roots was not enough as those above water table although *U. pumila* could transfer oxygen-rich air from the leaves to the submerged roots^[11]. A number of metabolic and physiological changes would be caused by hypoxia under flooding. Gravatt and Kirby^[12] found that the maintenance of low leaf starch concentrations and high pre-flood root tissue starch concentrations were important characteristics allowing flood-tolerant species to survive in flooded soil. McLeod *et al.*^[13] indicated that P_n of *Quercus michauxii*

was immediately reduced by freshwater flooding. Rood *et al.*^[7] suggested that GA₃ (gibberellins) was consistently reduced in plants experiencing water table decline. That's why *U. pumila* was distributed at the arid and semi-arid area. It was also the evidence that water table could affect the survival of plant species. During the water release in the arid and semi-arid area in China many seedlings and saplings were flooded because of their positions in river beds or depression areas. This experiment indicated the long time submerging would damage seedlings and saplings. This is important for forest survivals and their regeneration in the arid and semi-arid area.

When comparing the change of ecophysiological response, the diurnal processes or averages were more accurate than just measurements on a particular time. In this research if only the mean P_n at noon were compared, then, the mean P_n of U15 was significantly higher than that of U9, U15 and U22. However, if the diurnal mean net photosynthetic rate (DMP) of saplings at different water levels were compared, then, U9 had the highest DMP. Therefore, by comparing P_n at one particular time could not get the right result unless the diurnal processes were compared. The progress pattern of diurnal P_n of all saplings could be divided into two types. One type was that P_n increased at afternoon, such as U3 and U9. Another type was that P_n decreased at afternoon, such as U15 and U22. Therefore, P_n of *U. pumila* was higher when the water table was appropriate, such as between 9 to 15 cm. If the water table was too high the saplings could not get enough water, then, P_n would decrease. This was inconsistent with the hypothesis. The implication of this result was important, if we would like to preserve the vegetation in the arid and semi-arid area, then, we should maintain the proper water level. Too high and too low water table would both decrease the rate of net photosynthesis of trees.

The DMT of U3 was the lowest, but it was the highest for U9. It indicated the proper water table would increase transpiration rate of the saplings, such as, from 3 to 9 cm. On the other hand, too low (such as 3 cm) or too high (such as 15 and 22 cm) water tables would decrease transpiration rate. Other experimental results also indicated the hypothesis that plants in dry habitats have a conservative water use strategy^[14-16]. This study also showed that plants in wetter condition would also have a conservative water use strategy. Plant adaptations to varying water availability seemed to be more complex. Roots would send a stress signal to the transpiring leaves. At too low or too high water table plant was both in water stress, then, it decreased its physiological activities and consumed less water, but at a proper water

table, the physiological activities of plant can reach its maximum. In this study, at water tables from 9 to 15 cm, saplings had higher transpiration rate and P_n. Therefore, maintaining proper water table would result in higher transpiration rate and P_n.

DMWUE had good correlation with water table in this experiment. However, if we deleted the time point of 15 to 16 pm, when U3 had highest P_n but with high standard error, then, we would find that U15 had the highest Water Use Efficiency (WUE). From water table 9 to 15 cm transpiration rate decreased about 13.84%, but WUE decreased only about 10.78%. It means that at water table 15 cm, saplings of *U. pumila* had higher WUE but less transpiration rate; maintaining water table near 15 cm would be economical for saplings growth. DMSR of U3 was significantly higher than that of U9, U15 and U22, respectively, and the DMSR of U22 was also significantly higher than that of U15. Therefore, U9 and U15 had less stomatal resistance. Under lower or higher water table (such as, 3 and 22 cm) the stomatal resistance was higher. This was also inconsistent with the hypothesis. Changes in stomatal resistance were induced by metabolic signals (ABA)^[17-19]. In condition of good water and oxygen supply, stomata resistance was less (e.g., U9 and U15). This result could explain the diurnal process of transpiration and net photosynthesis. U3 and U22 had higher stomatal resistance and transpiration rate and P_n of them were lower. On the contrary, U9 and U15 had higher transpiration rate and P_n because of their lower stomatal resistance. Franca *et al.*^[20] indicated that as substrate water content decreased below 30%, stomatal conductance decreased linearly to its minimum value. Stomatal closure might be a common drought avoidance response allowing plants to keep water in their tissues^[21]. However, it would also restrict the entry of CO₂ to mesophyll cells and consequently would reduce net photosynthetic rates^[20]. However, for the species inhabited at wet sites, they usually had high stomatal conductance and high transpiration rate^[22].

Although the ecophysiological responses of the saplings at different water levels were quite different, the root/shoot ratios were not significantly different among U3, U9, U15 and U22. The result could also be questioned whether the evaporative demand could be linked to carbon allocation strategies, where a more efficient water-conducting structure of the trees enabled maintenance of larger foliage mass with the same sapwood^[23]. The changes in allocation should be connected with the conductivity of the wood^[23]. However, there was significant correlation between the main root length of the saplings and water levels. The main root length and its increment would increase as the water table

increased. The reason seemed clear because the saplings need long root to get available water. This was coincident with the hypothesis. The increment of diameter was not significantly different among the saplings at different water levels. U15 had the highest increment of height. The possible reason for the not significant change in diameter but significant increment in height and main root length might be: (I) the experiment lasted only one growing season and (ii) height and root growth were more sensitive to water table than diameter growth, the saplings grew faster in height and root length than in diameter.

Overall, the short-term experiments indicated that the ecophysiological response and growth characteristics of *U. pumila* had a close relationship with the water table. They may be used as indicators of underground water table. Long time flooding would damage some saplings. Maintaining proper water table would increase net photosynthesis, water use efficiency and higher height growth but with relatively low transpiration rate. The results had an implication for maintaining and regenerating of the vegetation at arid and semi-arid area.

ACKNOWLEDGMENTS

This research was partially supported by China National Key Basic Research Program (G1999043507) and NSF CREST project No. 0420541 at Alabama A and M University. Thanks to Mr. Y. Yang of Beijing Forestry University for his help during the experiment.

REFERENCES

1. Institute of Botany, Chinese Academy of Sciences (Ed.), 1972. *Iconographia Cormophytorum Sinicorum*. Tomus I. Science Press, Beijing.
2. Ewanchuk, P.J. and M.D. Bertness, 2004. The role of waterlogging in maintaining forb panes in northern New England salt marshes. *Ecology*, 85: 1568-1574.
3. Nilsson, C., R. Jansson and U. Zinko, 1997. Long-term responses of river-margin vegetation to water-level regulation. *Science*, 276: 798.
4. Marsh, C.W., 1978. Tree phenology in a gallery forest on the Tana river, Kenya. *East Afr. Agric. For. J.*, 43: 305-316.
5. Maingi, J.K. and S.E. Marsh, 2002. Quantifying hydrologic impacts following dam construction along the Tana River, Kenya. *J. Arid Environ.*, 50: 53-79.
6. McCarthy, S.E. and J.P. Evans, 2000. Population dynamics of overcup oak (*Quercus lyrata*) in a seasonally flooded karst depression. *J. Torrey Bot. Soc.*, 127: 9-18.
7. Rood, S.B., K. Zanewich, C. Stefura and J.M. Mahoney, 2000. Influence of water table decline on growth allocation and endogenous gibberellins in black cottonwood. *Tree Physiol.*, 20: 831-836.
8. Turnbull, M.H., D. Whitehead, D.T. Tissue, W.S.F. Schuster, K.J. Brown and K.L. Griffin, 2001. Responses of leaf respiration to temperature and leaf characteristics in three deciduous tree species vary with site water availability. *Tree Physiol.*, 21: 571-578.
9. Tuomela, K., S.G. Johansson, J. Kuusipalo and O. Luukkanen, 1993. Morphological and physiological comparison of three provenances of *Eucalyptus microtheca* grown in eastern Kenya. *East Afr. Agric. For. J.*, 58: 35-41.
10. Hohansson, S. and K. Tuomela, 1996. Growth of sixteen provenances of *Eucalyptus microtheca* in regularly irrigated plantation in eastern Kenya. *For. Ecol. Manage.*, 82: 11-18.
11. Barclay, A.M. and R.M.M. Crawford, 1982. Plant growth and survival under strict anaerobiosis. *J. Exp. Bot.*, 33: 541-549.
12. Gravatt, D.A. and C.J. Kirby, 1998. Pattern of photosynthesis and starch allocation in seedlings of four bottomland hardwood tree species subjected to flooding. *Tree Physiol.*, 18: 411-417.
13. McLeod, K.W., J.K. McCarron and W.H. Conner, 1999. Photosynthesis and water relations of four oak species: Impact of flooding and salinity. *Trees*, 13: 178-187.
14. Read, J. and G. Farquhar, 1994. Comparative studies in *Nothofagus*. Leaf carbon isotope discrimination. *Fun. Ecol.*, 5: 684-695.
15. Zhang, J.W., Z. Feng, B.M. Cregg and C.M. Schumann, 1997. Carbon isotopic composition, gas exchange and growth of three populations of ponderosa pine differing in drought tolerance. *Tree Physiol.*, 17: 461-466.
16. Palmroth, S., F. Beminger, E. Nikinmaa, J. Lloyd, P. Paulkkinen and P. Hari, 1999. Structural adaptation rather than water conservation was observed in Scots pine over a range of wet to dry climates. *Oecologia*, 121: 302-309.
17. Gowing, D.J.G., H.G. Jones and W.J. Davies, 1993. Xylem-transported abscisic acid: The relative importance of its mass and its concentrations in the control of stomatal aperture. *Plant Cell Environ.*, 16: 453-459.
18. Schulze, E.D. and M. Küppers, 1979. Short-term and long-term effects of plant water deficits on stomatal response to humidity in *Corylus avellana* L. *Planta*, 146: 319-326.

19. Zhang, J., U. Schurr and W.J. Davies, 1987. Control of stomatal behaviour by abscisic acid with apparently originates in the roots. *J. Exp. Bot.*, 38: 1174-1181.
20. Franca, M.G.C., A.T.P. Thi, C. Pimentel, R.O.P. Rossiello, Y. Zuily-Fodil and D. Laffray, 2000. Differences in growth and water relations among *Phaseolus vulgaris* cultivars in response to induced drought stress. *Environ. Exp. Bot.*, 43: 227- 237.
21. Ludlow, M.M., 1980. Adaptive Significance of Stomatal Responses to Water Stress. In: *Adaptation of Plants to Water and High Temperature Stress* (Turner, N.C. and P.J. Kramer (Eds.)). Wiley, New York, pp: 123-138.
22. Eschenbach, C. and L. Kappen, 1999. Leaf water relations of black alder (*Alnus glutinosa* (L.) Gaertn.) growing at neighbouring sites with different water regimes. *Trees*, 14: 28-38.
23. Berninger, F., A. Makela and P. Hari, 1996. Optimal control of gas exchange during drought: Empirical evidence. *Ann. Bot.*, 77: 469-476.