

SOIL AND LEAF WATER POTENTIAL OF *QUERCUS SEMECARPIFOLIA* AT PHULCHOWKI HILL, NEPAL

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ABSTRACT

Quercus semecarpifolia is a high altitude oak and dominant species of central Himalayan vegetation. In the central Himalaya, plants are subjected to a prolonged dry period, thus developing moisture stress. Soil water potential at 15 cm and 30 cm depth, predawn and midday leaf water potential and their relationship with stomatal conductance and phenological behaviour was studied at Phulchowki Hill, Kathmandu to evaluate the drought adaptation strategy of *Q. semecarpifolia* in a pure stand at 2130 m elevation. The natural ecosystem of Himalayan region has a characteristic climatic pattern of concentrated rainfall and a prolonged dry season which have a strong effect on the adaptability of this species. It maintained a high predawn leaf water potential ($\Psi_{L\ pd}$) and stomatal conductance (g_w) despite low soil water Ψ and $\Psi_{L\ pd}$. Lowest Ψ_s and $\Psi_{L\ pd}$ were observed in March 1999, when there was almost no rain for five months. Mean $\Psi_{L\ pd}$ and $\Psi_{L\ md}$ were (-1.79 and -2.29 MPa, respectively). Patterns of $\Psi_{L\ pd}$ and $\Psi_{L\ md}$ correlated significantly with soil Ψ , and phenology as $\Psi_{L\ pd}$ often increased during leafing but not with g_w .

Key words: Drought adaptation, oak, Phulchowki hill, *Quercus semecarpifolia*, stomatal conductance and water potential.

INTRODUCTION

Quercus semecarpifolia, a high altitude oak, is an evergreen dominant species of central Himalayan vegetation, and is distributed from southwest China to Afghanistan, at elevations of 2100 to 3800 m asl. It occurs in moist temperate and sub-alpine regions with heavy snowfall and moderate rainfall, and is absent from the dry regions of the inner Himalayas (Negi and Naithani 1995). *Q. semecarpifolia* is also considered as one of the oldest vegetation of Himalayan zone which invaded the prairieland of the Himalayas and became the dominant species of then sub-alpine and alpine forest (Singh and Singh 1992). In fact,

oaks occupy a very prominent place in the ecosystem of not only the Himalayan region but according to Gailing *et al.* (2009) *Quercus* spp. are a model for forest tree species, being one of the most important forest genera in northern hemisphere.

The natural vegetation of central Himalayas reflects a strong and extensive environmental gradient. The climate is characterized by concentrated rainfall from mid-June to mid-September. Such warm season rainfall and complimentary eight to nine months of drought are likely to have profound effects on adaptation and ecosystem processes (Singh and Singh 1992, Zobel

and Singh 1997). The structural and physiological adaptations to drought determine the growth and survival of forest tree species in dry climates (Tenhunen *et al.* 1987). Role of the environment, particularly drought in controlling the distribution and performance of species is poorly understood in Himalayan region. As plant growth is chiefly associated with the maintenance of a favourable water status, such prolonged dry period may be a limiting factor for the growth and development of this species.

Phulchowki Hill has typical warm temperate monsoon climate with three seasons round the year: cold and dry winter (October to February), pre monsoon dry summer (March to May) and monsoon (June to September). There is no perennial source of water above 1600m in Phulchowki Hill.

Water moves from the soil through the plants to the atmosphere along a gradient of water potential (Ψ), the lowest Ψ in the plants being at the leaf surface (Lambers *et al.* 1998). Tree Ψ and its components play an important role in the physiology and metabolism of the plants (Kramer and Boyer 1995). The predawn water potential is considered as a good indicator of soil water availability and is an important reflection of plant water status. Predawn water potential varies along the environmental gradients indicating how plants integrate soil water availability; hence it is an useful measure of plant water status (Hinckley *et al.* 1983, Waring and Schlesinger 1985) and may correlate with maximum stomatal conductance (Reich and Hinckley 1989). Predawn Ψ also reflects the water extraction capacity by root systems of trees (Aranda *et al.* 2000) and one of the most important expressions of the water relations in higher plants is the maintenance of an efficient water conducting system based on its hydraulic conductance. Also the changes in tissue elasticity in response to drought modify the relationship between turgor pressure and cell

volume that may contribute to drought tolerance (Zlatev and Lidon 2012). Hence turgor maintenance is of critical importance because the turgor necessary for leaf expansion must develop in these trees despite low water availability (Kramer and Boyer 1995). Osmotic adjustment which increases the osmotic force thus promoting water absorption is recognized as an effective component of drought resistance (Martinez *et al.* 2007) and it provides a mean of maintaining cell wall water status.

In recent years, many research suggest that forests in certain areas might become more vulnerable to drought in the future not only due to water depletion but because of the amplified effect of changes in climate variability and extremes resulting from global warming. In the last decade, forest species composition change due to drastic drought spell in different forest ecosystems have been reported worldwide (Breshears *et al.* 2005, 2009). Similarly some cases of altitudinal displacement of drought sensitive forest trees, from lower and drier altitude to higher and wetter one have also been reported (Penuelas *et al.* 2008, Lindner *et al.* 2010). Thus it is a challenge to comprehend the basic interactions of plants and their environment to predict responses for now and in future in milieu of expanding demands of growing population, global warming and climate change in both managed and natural ecosystem (Waring *et al.* 2011).

Hence this study was focussed with the main objectives to find out: the relative importance of plant water potential for drought resistance and completion of phenological activities during the dry periods.

MATERIALS AND METHODS

The study was carried out at Phulchowki Hill (27°33'N, 85°22'E), 10 km southeast of Kathmandu, Nepal. *Quercus semecarpifolia* was studied here at its lower elevational limit at 2130 m and forms a pure stand above 2400 m.

Soil water potential and leaf water potential were measured with a thermocouple psychrometer (Tru-Psi, Decagon, Pullman WA). Soil was measured at two depth 15 and 30 cm and leaf water potential was measured in leaves from three representatives at predawn (0500-0600 h) and midday (1300-1400 h).

Measurements were taken at a monthly interval for 24 times from December 1998 to January 2001. One monsoon month's observation was made in September 1999.

RESULTS

Soil water potential: Soil Ψ at both depth (Ψ_{15} and Ψ_{30}) were mostly less than -1.0 MPa except in March, April, May and June 1999. As a result of 5 months of absolute dryness Ψ_{15} was < -1.5 MPa from March (often called the Permanent Wilting Point) and in the following months till June 1999 (Fig. 1). Despite 6.0 mm rainfall on April 9, 1999, Ψ_{15} couldn't recover on April 10 when

measurement was taken. In contrast, the 2000 received more precipitation and Ψ_{15} was from -0.2 to -0.5 MPa. Mean Ψ_{15} and Ψ_{30} was -0.46 MPa and -0.44 MPa, respectively. There was significant difference in 1st and 2nd year of Ψ_{15} and Ψ_{30} (statistical source - Poudyal *et al.* 2003, 2004).

Leaf water potential: There was significant variation in $\Psi_{L\text{pd}}$ months and years ($P=0.001$). The minimum values of $\Psi_{L\text{pd}}$ and $\Psi_{L\text{md}}$ were observed in March 1999 (Fig. 1) and maximum $\Psi_{L\text{pd}}$ and $\Psi_{L\text{md}}$ were observed in June 2000 when monsoon starts. Predawn and midday leaf water potential showed a profound effect of precipitation on it and low value was observed during the dry summer month and mostly during the 1st year of drought. $\Psi_{L\text{pd}}$ reached a minimum value of -4.747 MPa (March 1999) and recovered upto -0.763 MPa (June 2000) (Fig. 1). There was a significant difference in 1st and 2nd year of $\Psi_{L\text{pd}}$ and $\Psi_{L\text{md}}$ ($P=0.001$).

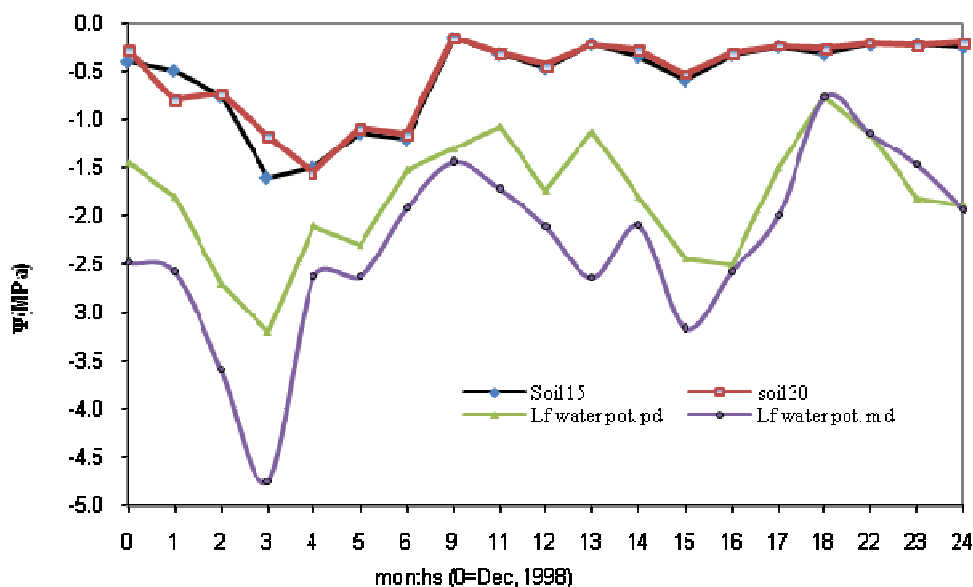


Fig. 1. Mean soil Ψ_{15} , Ψ_{30} , Leaf water potential at predawn and midday in *Q. semecarpifolia*.

DISCUSSION

Seasonal variation of leaf water potential ($\Psi_{L_{pd}}$ and $\Psi_{L_{md}}$) illustrated the pattern of precipitation as the lowest value was found in March 1999, the driest period when there had been only 5.4 mm rainfall at the end of five months. Similar result was shown by soil Ψ at both depths. Similar observation was made by Zobel *et al.* (2001) in oaks in the Central Indian Himalaya during the dry season of 1995, when soil Ψ reached a minimum of -3.51 MPa, in contrast to the average < -1.8 MPa. Poudyal *et al.* (2004) reported that Ψ_{15} and tree Ψ_{pd} reached minimum values of -4.9 MPa and -1.6 MPa respectively in *C. indica* in March 1999 growing at a lower elevation of 1400m. Drought was also stern during the pre-monsoon dry season of 1999 in Kumaun, in the central Indian Himalaya, west of Nepal where Ψ_{pd} reached -5.5 MPa in *Q. floribunda* (Singh *et al.* 2000).

Ψ_{30} was higher than Ψ_{15} and correlated significantly with Ψ_{15} and specified the same seasonal patterns of variation.

Predawn Ψ has been considered a good indicator of Ψ_s (Kramer and Boyer 1995, Paulilo *et al.* 1998) because equilibrium may be established in the soil-plant-atmosphere continuum before dawn. $\Psi_{L_{pd}}$ and $\Psi_{L_{md}}$ were lower than soil Ψ at both depths, mostly in winter, when low temperature might decrease water movement from the soil into the roots, reducing leaf Ψ . As the pathway of water from the soil to the atmosphere takes place along a gradient of water potential (Ψ), the lowest Ψ in the plants is at the leaf surface (Lambers *et al.* 1998). Due to the evaporative demand during dry seasons, Ψ among the plant gradient becomes more pronounced as tree water Ψ was -1.6 and -2.4 MPa in morning and afternoon (Poudyal *et al.* 2004) in comparison to -3.2 and -4.75 MPa ($\Psi_{L_{pd}}$ and $\Psi_{L_{md}}$ respectively) in March 1999. After the monsoon (July to September), cold and dry winter (October to February) prevails and temperature difference between predawn and afternoon increases by and large and hence due to the evaporative demand leaf Ψ decreased even though soil Ψ and tree Ψ was comparatively high (Fig. 1).

Similarly, the effect of dryness is more effectual in leaf than in soil as both $\Psi_{L_{pd}}$ and $\Psi_{L_{md}}$ showed decreasing tendency from February 1999 onwards and reached minimum in March 1999 as in soil Ψ , but in April 1999, soil Ψ replenished due to the previous day 6.00 mm rain, which was not found in $\Psi_{L_{pd}}$ and $\Psi_{L_{md}}$. Similarly, the diurnal change in predawn and midday leaf Ψ was minimum in June, October and November 2000, which could be attributed different climatic effects as temperature, light and relative humidity. In June 2000, the predawn temperature was 19.2°C with RH 79.7% while the midday temperature was 22.1°C and RH decreased to 66.8%. Also the stomatal conductance was higher in morning than in the afternoon during these months (Poudyal *et al.* 2004) which can be responsible for minimum diurnal change. Poudyal *et al.* (2004) reported higher value of predawn and midday tree Ψ in *Q. semecarpifolia* during the same period.

A diurnal change ($\Psi_{md} - \Psi_{pd}$), which is the ability of plants to recover water Ψ diurnally that is lost through leaf conductance, reflected seasonal variation as it increased during dry months. Further low illumination on hazy days played its role in decreasing diurnal change mostly in winter months. Mean diurnal change in leaf Ψ was -0.50 MPa which was comparatively lower than tree water Ψ (-0.77 MPa), (Poudyal *et al.* 2004). Rain water is available to the roots of the plants for a certain period then it either percolates down or evaporates from the surface, which lowers the soil Ψ after precipitation is over. However, occasional replenishment of Ψ_s was done by pre-monsoon and winter precipitation in the 2nd year of observation due to sporadic pre monsoon and winter precipitation.

$\Psi_{L_{pd}}$ ranged from -0.78 MPa to -3.2 MPa and $\Psi_{m_{pd}}$ from -0.78 MPa to -4.75 MPa. Poudyal *et al.* (2004) reported a range of Ψ_{pd} : -0.1 MPa to -1.7 MPa during the same period. A similar range of tree Ψ_{pd} , i.e. -0.2 MPa to -1.6 MPa in *Q. leucotrichophora* by Tewari (2000) and from -0.4 MPa to -1.1 MPa in *Q. leucotrichophora* and *Q. floribunda* Lindl. (Zobel *et al.* 2001) In March

1999, when Ψ_{15} and $\Psi_{L_{pd}}$ reached minimum values, other Himalayan tree species viz; *Q. lanata*, *Rhododendron arboreum*, *C. indica* and *Schima wallichii* showed similar results (Poudyal *et al.* 2004).

Relationship with stomatal conductance and phenology: There was occasional rise in $\Psi_{L_{pd}}$ in the studied species during the dry season which could be related to the phenological development of the species beside intermittent pre monsoon rain and reduced stomatal conductance. An alternative explanation for the rise in leaf Ψ_{pd} in May and June 2000 and January 2001 is the thin canopy, caused by lopping of the trees by villagers who collected fodder for farm animals from the forest thus decreasing conducting surface.

Q. semecarpifolia, which has the longest leaf emergence and expansion period (March to mid – September) raised $\Psi_{L_{pd}}$ during the period of maximum leaf expansion. Such increase in $\Psi_{L_{pd}}$ agrees with Reich and Borchert's (1984) hypothesis, which states that phenomorphology varies as a consequence of differences in water availability and changes in internal water status.

Stomatal responses to water availability in soil, leaf and atmosphere are highly interactive. Hinckley *et al.* (1983) found a decrease in stomatal conductance during dry periods as a reciprocal function of the predawn leaf water potential in oaks. Stomatal conductance decreased in dry months when tree water potential were at their lowest (Poudyal *et al.* 2004).

The conductivity of water from the leaf to air is probably the most sensitive and earliest indicator of the physiological status of the whole plant (Smith and Hollinger, 1991). Significant correlation ($P = 0.02$) was found for stomatal conductance (g_w) with $\Psi_{L_{md}}$.

Q. semecarpifolia exhibited maintenance of high stomatal conductance over low predawn leaf water Ψ i.e. $122.7 \text{ mmol m}^{-2}\text{s}^{-1}$ at -3.2 MPa in March 1999. The range of $g_{w_{AM}}$ was between 94 and $327 \text{ mmol m}^{-2}\text{s}^{-1}$ (Poudyal *et al.* 2004). Despite

low soil-water availability in dry months, this oak kept its stomata open and kept so till December when maximum g_w was observed (Poudyal *et al.* 2004). Higher water use efficiency, which decreased the $\Psi_{L_{pd}}$ in December 1999, is reflected by a negative correlation between VPD and g_w . Such interdependency is reported by Aphalo and Jarvis (1991) in oaks and Gao *et al.* (2003) in coniferous pines.

Phenological development is related to tree water status during leaf expansion (Meinzer *et al.* 1983). Because some phenological activities are inhibited by moderate water stress (Borchert 1994a), phenological processes (leaf emergence, leaf expansion, flowering, and fruiting) took place primarily at the end of the dry season (Poudyal *et al.* 2012a), which indicates that this evergreen tree cannot rehydrate during a leafless dry season, as Borchert (1994a,b,c) describes for American dry tropical trees. But perhaps the low leaf Ψ during the dry season was enough to allow tissue development, or the occasional rise in $\Psi_{L_{pd}}$ during the dry season in response to sporadic rainfall, reduced leaf area, or changes that increase water uptake was sufficient to allow phenological development.

In conclusion, *Q. semecarpifolia*, a high altitude inhabitant had low $\Psi_{L_{pd}}$, high g_w , low tissue elasticity and high osmotic potential. At higher altitude lower temperatures and more cloud prevails which, could support high g_w even during soil drying. Further, low osmotic potential maintains a good osmotic adjustment thus compensating low tissue elasticity. *Q. semecarpifolia* showed high osmotic adjustment in response to low water availability, an ability to accumulate significantly high solute concentrations, where as an inelastic cell could be a potential advantage in maintaining cell/tissue integrity at lower soil and leaf Ψ (Poudyal *et al.* 2012b). Further it increases the gradient between soil and water potential, thereby promoting more effective water uptake from drying soils as exhibited by high xylem conductivity (Poudyal *et*

al. 2003). Thus, *Q. semecarpifolia* displayed different combinations of water relation parameters as low leaf and tree Ψ over high g_w to maximize photosynthesis in dry periods provided by an amicable environment of warm temperature, greater illumination and mature leaves with high stomatal conductance and a good osmotic adjustment, which seemed to be a drought tolerant strategy to survive in the drought prone Himalayas.

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