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**Research Article****MAINTENANCE OF TURGOR IN RESPONSE TO DROUGHT IN *SCHIMA WALLICHII* AND *QUERCUS SEMECARPIFOLIA* AT PHULCHOWKI HILL, KATHMANDU, NEPAL**

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DOI: 10.7897/2321-6328.01302

Article Received on: 02/08/13

Accepted on: 10/10/13

Abstract

In the central Himalaya, plants are subjected to a prolonged dry period, thus developing moisture stress. Maintenance of turgor, tissue water relations and response to drought were studied at Phulchowki Hill, Kathmandu, Nepal by pressure-volume curve analysis in two Himalayan tree species (*Schima wallichii* at 1400 m elevation, and *Quercus semecarpifolia* at 2130 m). Variations were found for turgor maintenance in these two species. Both osmotic potential at zero turgor (Ψ_{sz}) and osmotic potential at full turgor (Ψ_{st}) declined in dry months and decline was greater in the summer months of 1999 when pre monsoon rain was negligible. *Q. semecarpifolia* showed high osmotic adjustment at Ψ_{sz} , -2.45 MPa than *S. wallichii* (-1.24 MPa). Similarly osmotic adjustment at Ψ_{st} was -1.89 MPa in *Q. semecarpifolia*, and -1.07 MPa in *S. wallichii*. Pressure potential at full turgor (Ψ_{pt}) was also high in *Q. semecarpifolia* (2.18 MPa) in the dry month. Comparatively, *S. wallichii* showed elastic adjustment with high elasticity of cell walls while *Q. semecarpifolia* had rigid cell walls. *Q. semecarpifolia* lost turgor at 76 – 95 % relative water content while *S. wallichii* at 66 – 89 %. Among these two species *S. wallichii* maintained turgor by both elastic and osmotic adjustments while *Q. semecarpifolia* showed osmotic adjustment for the maintenance of turgor during the dry months and showed high drought tolerance.

Keywords: Drought tolerance, elastic adjustment, elasticity, osmotic adjustment, osmotic potential, pressure potential, *Q. semecarpifolia*, *Schima wallichii*, turgor.

INTRODUCTION

Plant water status is determined by cell and tissue water status¹. Changes in tissue elasticity in response to drought modify the relationship between turgor pressure and cell volume that may contribute to drought tolerance². Pressure – volume curve is the most widely used analysis for determining plant water relations parameters³. The trees of Nepal Himalaya are exposed to a prolonged drought of 8-9 months and even so, majority of phenological activities (leaf initiation, expansion, flowering and fruiting) occurs during the end of dry season^{4,5}. Hence turgor maintenance is of critical importance because the turgor necessary for leaf expansion must develop in these trees despite low water availability⁶. Maintenance of turgor in the plants is facilitated by elastic and osmotic adjustments as such adjustments at lower tissue water potential prevent mechanical damages to plasma membrane. Osmotic adjustment which increases the osmotic force thus promoting water absorption is recognized as an effective component of drought resistance⁷ and it provides a mean of maintaining cell wall water. Elastic adjustment results from the cell wall elasticity, which depends on the chemical interactions between various components of the wall⁸. The pattern and seasonality of precipitation in the Himalaya differ from that of other temperate forests where leaf expansion in most of the woody trees occurs before the dry season and turgor maintenance is of less importance in such cases. The climate of Nepal Himalaya is characterized by concentrated rainfall during monsoon from mid-June to mid- September. Such

concentrated warm season rainfall and the complementary eight to nine months of drought are likely to have profound effects on adaptation and ecosystem processes^{9,10}. Although osmotic adjustment has been documented in many woody plants, the knowledge of relative importance of tissue water relations parameters for turgor maintenance particularly in Himalayan trees is negligible¹¹⁻¹³. Hence this study was focused with the main objectives to find out:

- Effects of drought on osmotic and elastic adjustments and in the maintenance of turgor
- The relative importance of elastic and/or osmotic adjustments for drought resistance and completion of phenological activities during the dry periods

MATERIALS AND METHODS**Study Site and Species**

The study was carried out at Phulchowki Hill (27°33'N, 85°22'E), 10 km southeast of Kathmandu, Nepal. It is a part of sub-Himalayan Mahabharat region with an altitudinal range of 1400 – 2715 m with extensive diverse forests mostly dominated by broad-leaved evergreen trees. It covers an area of approximately 50 square km consisting of a vast range of flora. The natural vegetation of Phulchowki Hill is characterized by three distinct evergreen broad-leaved forest types: mixed *Schima-Castanopsis* forest at the base (1400 m – 1800 m), Oak - Laurel forest (1800 m – 2400 m) and evergreen oak forest (2000 m above). The study area 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 1600 m in Phulchowki Hill. Mean long- air temperature ranges between 2.6 - 18.7 °C in winter and 15.8 - 28.2 °C in summer. Mean long-term annual rainfall is 1882 mm with about more than 80 % of this occurring between mid-June and mid-September. Relative humidity at 6:30 AM is > 90 % in July, with a minimum of 63 % in April¹². Two evergreen species *Schima wallichii* (DC) Korth and *Quercus semecarpifolia* Smith were selected. These species are dominants in two vegetation types. *S. wallichii* was studied at 1400 m, representative of the upper subtropical forest of central Nepal and *Q. semecarpifolia* at 2130 m, representing the lower and upper temperate zone forests. *Q. semecarpifolia*, a widespread dominant throughout the Himalaya in cool-temperate and sometimes subalpine forests, was studied here at its lower elevation limit. Both species are dominants in the canopy, reaching 25 - 30 m tall. P-V curve analyses were made for 23 times for each species during the period of December 1998 to April 2001 at monthly interval. One monsoon month's observation was performed in September 1999. The reason for September data collection was to quantify whether or not there is any recovery from the drought.

Twigs with healthy leaves were collected from the secondary branch from each sample tree mostly after 1600 h. The cut ends were immediately immersed in water and covered by black polythene sheet and brought to the laboratory. Twigs were kept overnight in a cool dark place and allowed to saturate for 12 - 14 h. P - V curve analysis was performed using Pressure chamber (Model 1000, PMS Instrument Company, Corvallis, Oregon, USA) by free transpiration techniques¹⁴. The turgor loss point for Relative Water Content (RWC_z), osmotic potential (Ψ_s) at zero turgor (Ψ_{sz}), and full turgor (Ψ_{sf}) were determined from the curve. Pressure potential (Ψ_p) for each sample time was calculated by subtracting Ψ_s from water potential ($\Psi = -BP$). To calculate the index of elasticity (ϵ), all values of Ψ_p above zero turgor were plotted against RWC; the slope of a linear regression line through these points was used as ϵ . Occasionally, newly emerged leaves of the twigs broke due to repeated handling; in such cases, the broken portion was weighed separately both fresh and dry, and calculations were adjusted to account for the loss. An index of Desiccation Tolerance (IDT) which can estimate the net effect of RWC at turgor loss, osmotic potential at zero turgor and high tissue elasticity was computed using these three tissue properties that confer desiccation tolerance: low RWC_z, Ψ_{sz} and high tissue elasticity⁸. 'Plateaus' occurred in a few samples. The plateaus are apparently associated with apoplastic water accumulated in the intercellular spaces of the leaf near full saturation and act to buffer changes in leaf xylem pressure potential as tissue dehydrates¹⁵. Plateaus were corrected in data sets by assuming that the beginning of the steep decline in water potential represents full turgor¹⁶.

Statistical Analysis

Data were analyzed using ANOVA and a least significant test (LSD) with a 95 % confidence interval. Factors in the ANOVA were species, months, years and their interactions. Least square means were estimated and Spearman correlation (ρ) was used to study the relationship between variables. The statistical package used for the analysis was Stat Graphics

Plus ver. 4.0 (Statistical Graphics Corp., Rockville, MD, USA).

RESULTS

For both species sampled, the attributes of water relations parameters (Ψ_{sz} , Ψ_{sf} , RWC_z), osmotic amplitude ($\Psi_{sf} - \Psi_{sz}$) and Index of Elasticity (ϵ) differed significantly with species and months ($P < 0.001$ and $P < 0.01$ respectively) except ϵ with months. Both Ψ_{sz} and Ψ_{sf} were high (less negative) in *S. wallichii* and low in *Q. semecarpifolia*. Mean RWC_z and ϵ was significantly lower in *S. wallichii* than in *Q. semecarpifolia* (Table 1). In both species Ψ_{sz} and Ψ_{sf} were more negative mostly in dry months. Comparing the attributes of water relations on monthly basis, Ψ_{sz} and Ψ_{sf} were lowest in *Q. semecarpifolia* (-3.7 MPa) in April 2000 and (-3.03 MPa) in April 1999 and 2.78 MPa in March 2000 and 2.17 MPa in March 1999 respectively. Highest value of Ψ_{pf} in *Q. semecarpifolia* (2.81 MPa) and *S. wallichii* (2.08 MPa) was observed in April 1999 (Figure 2). Index of elasticity (ϵ) was also high in *Q. semecarpifolia* and low in *S. wallichii* during the dry months. Lowest ϵ in *S. wallichii* (2.58 MPa) was observed in April 2000 and in September 1999 in *Q. semecarpifolia* (4.3 MPa) (Figure 3). Relative water content at zero turgor (RWC_z) declined in both species during the dry months of 1999. Incidentally, this year was a very dry period with a negligible precipitation of 5.4 mm for five months. But in the later year of observation no consistent pattern of decline was found among these species. A small decrease was observed in RWC_z of *S. wallichii* in 2000 and 2001 dry months. RWC_z in *Q. semecarpifolia* did not decline in dry months except in the first year of observation when plant and soil water potential reached up to -2.6 MPa and -2.4 MPa respectively in March 1999¹³ (Poudyal *et al.* 2004). In the species sampled, *S. wallichii* maintained turgor to the lowest RWC_z (64.9 %) and *Q. semecarpifolia* (75.6 %) (Figure 1).

Mean IDT was 52.9 in *S. wallichii* and 45.9 in *Q. semecarpifolia* (Table 1). However, IDT showed a reflection of phenological activities (leaf flush and expansion) but was not related to the availability of water in plants (Figure 1).

Correlation among water relations attributes

Ψ_{sz} correlated significantly with soil at 15 cm (Ψ_{15}), soil at 30 cm (Ψ_{30}), predawn water potential (Ψ_{pd}) in *Q. semecarpifolia* but not in *S. wallichii*. Ψ_{sz} correlated with gw_{AM} in *Q. semecarpifolia*. Both Ψ_{sz} and Ψ_{sf} showed significant negative correlation with percentage starch content in twigs of different years, mostly in *S. wallichii* (Table 2). RWC_z in both species correlated with Ψ_{15} , Ψ_{30} , Ψ_{pd} , Ψ_{md} and Ψ_{sz} except with Ψ_{md} in *S. wallichii*. ϵ did not show significant correlation with Ψ_{pd} in both species and Ψ_{md} in *S. wallichii* (Source of correlation of different water relations parameters^{12,13}).

DISCUSSION

Variations in Ψ_{sz} , Ψ_{sf} , ϵ and RWC_z in the studied species might be attributed to the internal recycling of solutes during the dry periods and the timing of phenological activity. Osmotic adjustment is an important drought tolerance strategy exhibited by plants to maintain turgor. When water availability to plants decreases, cells adjust their water status by accumulating osmotically active compounds, which lower the osmotic potential and hence maintain turgor.

Table 1: Least-Square Means of Water Relations Attributes

Species	RWC _z	Ψ _{sz}	Ψ _{sf}	Ψ _{sf} -Ψ _{sz}	Ψ _{pf}	ε	IDT
<i>S. wallichii</i>	77.9 %	-1.82 MPa	-1.49 MPa	0.32 MPa	1.37 MPa	6.3 MPa	52.9
<i>Q. semecarpifolia</i>	82.9 %	-2.55 MPa	-2.04 MPa	0.51 MPa	1.86 MPa	11.9 MPa	45.9

Least-square means of water relations attributes: Relative Water Content at zero turgor (RWC_z), osmotic potential at zero turgor (Ψ_{sz}), osmotic potential at full turgor (Ψ_{sf}), osmotic amplitude (Ψ_{sf}-Ψ_{sz}), pressure potential at full turgor (Ψ_{pf}), Index of Elasticity (ε) and Index of Desiccation Tolerance (IDT) for two species.

Table 2: Spearman Rank Correlation Coefficients of Different Water Relations Attributes

Attributes	Species	Correlated with						
		Ψ _{sz}	Ψ _{sf}	Ψ _{sf} -Ψ _{sz}	ε	IDT	Starch ₀	Starch ₁
RWC _z	<i>S. wallichii</i>	0.73 ***	0.68 ***	-0.60 **	0.81 ***	-0.98 ***	-0.50*	-0.47*
	<i>Q. semecarpifolia</i>	0.47 *	0.41 ns	-0.36 ns	0.67 **	-0.96 ***	-0.29ns	-0.55**
Ψ _{sz}	<i>S. wallichii</i>	ε		IDT	Starch ₀	Starch ₁		
		0.28 ns	-0.83 ***	-0.74***	-0.60***			
Ψ _{sf}	<i>Q. semecarpifolia</i>	-0.25 ns	-0.66 ***	-0.23 ns	-0.53**			
	<i>S. wallichii</i>	0.19 ns	-0.77 ***	-0.58**	-0.54**			
Ψ _{sf}	<i>Q. semecarpifolia</i>	-0.32 ns	-0.57 **	-0.28 ns	-0.50*			

Spearman rank correlation coefficients of different water relations attributes: RWC_z (Relative water content at zero turgor), Ψ_{sz} (osmotic potential at zero turgor), Ψ_{sf} (osmotic potential at full turgor) ε (Index of elasticity), IDT (Index of desiccation tolerance), starch₀ and starch₁ (percentage starch estimation in 0 and 1-year twig respectively) in two species. Significance values: ns = P > 0.05, * = 0.05 > P > 0.01, ** = 0.01 > P > 0.001, *** = P < 0.

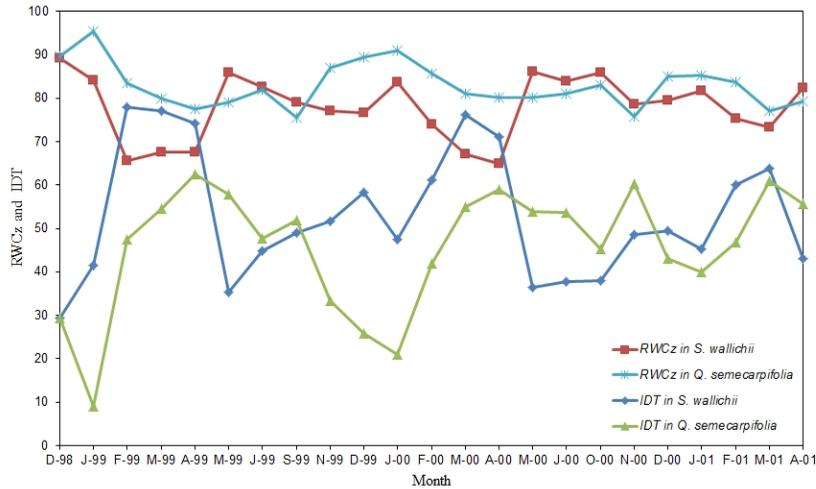


Figure 1: Relative water content percentage at zero turgor (RWC_z) and Index Of Desiccation Tolerance (IDT) in *S. wallichii* and *Q. semecarpifolia*.

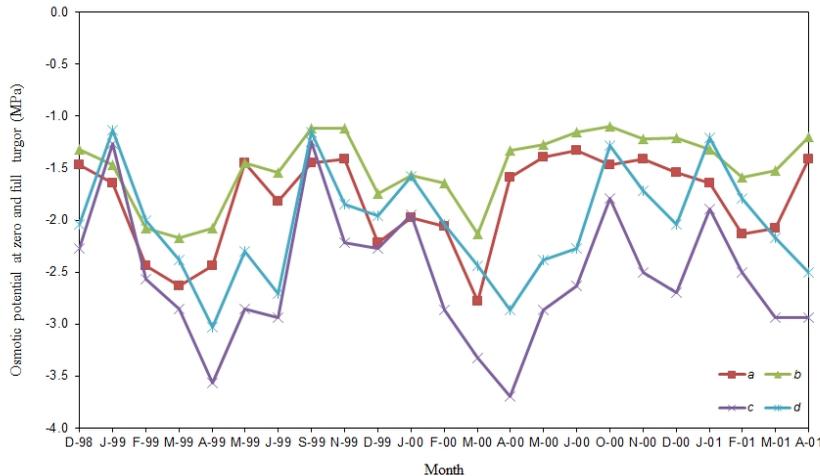


Figure 2: Osmotic potential at zero turgor (Ψ_{sz}) and full turgor (Ψ_{sf}) in *S. wallichii* and *Q. semecarpifolia*.

a = Ψ_{sz} in *S. wallichii*, b = Ψ_{sf} in *S. wallichii*, c = Ψ_{sz} in *Q. semecarpifolia* and d = Ψ_{sf} in *Q. semecarpifolia*.

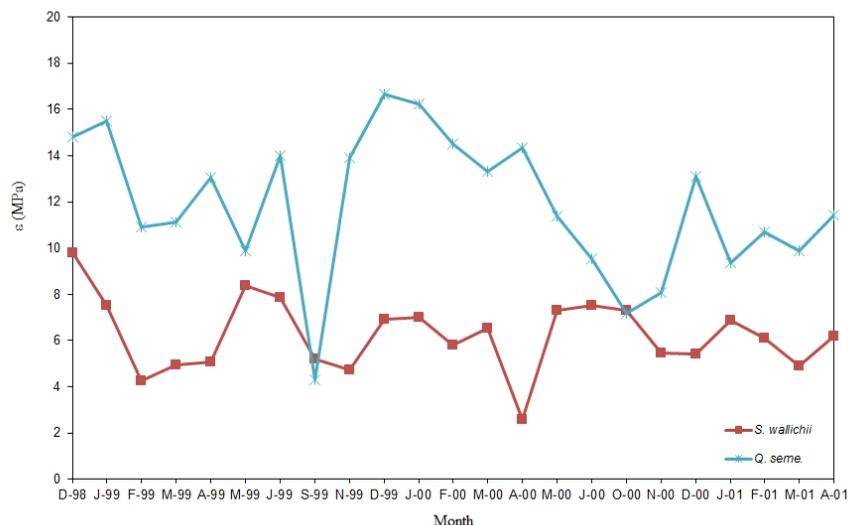


Figure 3: Index of elasticity (ϵ) in *S. wallichii* and *Q. semecarpifolia*.

Both species showed osmotic adjustment in 1999 when rainfall was 5.4 mm only for a period of five months (Dec-Apr). In fact, the year 1999 was detected to be a winter drought year, one of the six cases over a period of 33 years in Central Nepal¹⁷. Water stress was not very severe in the following years of observations as occasional replenishment was done by sporadic pre monsoon and winter precipitation. *Q. semecarpifolia* showed osmotic adjustment at Ψ_{sz} , -2.30 MPa while *S. wallichii* showed osmotic adjustment at -1.51 MPa in the 1st year of drought. *Q. semecarpifolia* showed significant correlation between Ψ_{sz} , and Ψ_{15} , Ψ_{30} , Ψ_{pd} , indicating an ability to accumulate solute concentrations during low water availability. A significant correlation between mean soil Ψ and Ψ_{sz} in the saplings of *Quercus* species¹⁸ and no correlation between predawn leaf Ψ and Ψ_{sz} for several oak species both under field and greenhouse conditions¹⁹ were reported. Mean Ψ_{sz} were -1.82 MPa and 2.55 MPa and mean Ψ_{sf} were -1.49 MPa and 2.04 MPa in *S. wallichii* and *Q. semecarpifolia*, respectively (Table 1). These values are lower than those reported²⁰ in ambient plot for *Quercus prinus*. In *S. wallichii*, Ψ_{sz} and Ψ_{sf} ranged between -1.33 MPa to -2.78 MPa and -1.10 to -2.17 MPa respectively. In literature^{21,22} reported a marginally higher Ψ_{sz} ranging between -1.43 to -2.6 MPa and 1.49 to -2.22 MPa while Ψ_{sf} ranged from -1.25 to -2.44 MPa and 1.21 to -1.96 MPa in Hetauda, south-western part of the country, at 487 m and 689 m respectively, when rainfall was optimum. *S. wallichii* with a declining RWC_z during the dry months showed a strong positive correlation with Ψ_{sz} ($\rho = 0.66$), Ψ_{sf} ($\rho = 0.56$) and ϵ ($\rho = 0.84$) and a significant negative correlation with osmotic amplitude ($\Psi_{sf} - \Psi_{sz}$) ($\rho = -0.65$) (Table 2), thus exhibiting both osmotic and elastic adjustment during the dry periods. *S. wallichii* showed both osmotic and elastic adjustment²¹ when water potential was high and only elastic adjustment was found while growing with comparatively lower tree water potential and high RWC_z ²². This indicates that, at lower elevation, *S. wallichii* faced water stress and more elastic cell walls were required to maintain turgor. In this study, *Q. semecarpifolia* exhibited a good osmotic adjustment despite of low RWC_z . Lowering of

osmotic potential during the dry periods enabled the plant to maintain turgor. Osmotic adjustment during drought has been demonstrated in many species of *Quercus* in North America (*Q. alba*, *Q. macrocarpa* and *Q. stellata*)¹⁵. *Q. semecarpifolia* showed osmotic adjustment of -2.45 MPa at Ψ_{sz} and -1.88 MPa at Ψ_{sf} . An osmotic adjustment value lower than the present observation was reported²³ which ranged between -1.47 to -2.0 MPa at Ψ_{sz} and -0.5 to -1.8 MPa at Ψ_{sf} in *Q. leucotrichophora* and *Q. floribunda*, the central Himalayan oaks. A sharp decline in field Ψ_{sf} (3.5 MPa) and Ψ_{sz} (-4.2 MPa), a value approximately 1.5 times lower than the normal summer value was reported during the dry months of 1999 in Central Himalayan oaks namely *Q. leucotrichophora* and *Q. floribunda*²⁴. The bulk modulus of elasticity (ϵ) was low in *S. wallichii* and high in *Q. semecarpifolia* in the dry months (Figure 3). Lower ϵ value during drought indicates tissue ability to shrink more during dehydration and elastic adjustment results from the modification in cell walls, which make them more elastic, thereby facilitating tissue shrinkage during dehydration. With increasing drought stress, ϵ has been found to decrease. Changes in tissue elasticity in response to drought, which modify the relationship between turgor pressure and cell volume, might be a drought tolerance strategy². RWC_z , which is a measure of the plant's ability to maintain turgor in the presence of increasing water deficits, declined with the beginning of dry months in *S. wallichii* in the studied years while in *Q. semecarpifolia*, RWC_z decreased in the 1st year of drought only. The capacity to maintain a high RWC under drought was observed^{25,26}. RWC_z did not correlate with soil and predawn tree Ψ in the studied species thus suggesting a possible increase in water uptake from soil through deep roots. Despite a good osmotic adjustment, *Q. semecarpifolia*, with more rigid cell walls (high ϵ), could not show elastic adjustment during the drought period. In *Q. semecarpifolia* a gradual decrease in Ψ_{sz} and Ψ_{sf} with increase in Ψ_{pf} was observed during the dry period. Such increase in Ψ_{pf} accompanied by decrease in RWC_z , in the first year of drought spell, indicates a pronounced augment in osmotic adjustment. Hence *Q. semecarpifolia*, which had very low Ψ_{pd} and Ψ_{md} ¹³ seemed

successful in maintaining turgor by osmotic adjustment. Besides *Q. semecarpifolia* showed osmotic adjustment in the winter months also without a marked decline in RWC_z . Such winter osmotic adjustment and a significant correlation between Ψ_{sz} and morning stomatal conductance¹³ in *Q. semecarpifolia* indicates plant's strategy to ensure water availability to maintain high assimilation rates through unremitting stomatal conductance during dry winter months. P-V variables, in the both studied species showed a close phenological affinity. All the phenological processes involve cell expansion, which is most sensitive to water stress²⁷. Due to the peculiar pattern and seasonality of precipitation, these species are exposed to a prolonged drought of 8-9 months and even so majority of phenological activities occur during the dry season¹³. Osmotic potentials at both turgors decreased at the time of leaf and twig emergence in *S. wallichii* and *Q. semecarpifolia* and osmotic adjustment along with leaf senescence as prerequisite for bud break before rain for tropical trees in dry environment was reported²⁸. In the studied species, turgor pressure at full (Ψ_{pf}) exceeded the threshold value²⁹ of 0.4 MPa and ranged from 1.07 to 2.02 MPa in *S. wallichii* and 0.81 to 2.71 MPa in *Q. semecarpifolia*. In both species high Ψ_{pf} was related with the phenological activities and hence could be attributed to the elasticity of cell walls during the period of leaf and shoot emergence, development and other cambial activities. In *S. wallichii*, in the first year of drought and leaf expansion period i.e., February-March there was decline in RWC_z , Ψ_{sz} and Ψ_{st} and increase in Ψ_{pf} which signifies greater ability to adjust elastic modulus. Elastic shrinkage is more important for drought resistance than osmotic adjustment as higher elasticity indicates greater inherent ability to shrink when dehydrated. As both elastic and osmotic adjustments help the plant to maintain turgor, *S. wallichii* successfully performs all the phenological activities (leaf flush, flowering and fruiting) that occur during the dry months. *S. wallichii* had a high IDT during the dry months when RWC_z and Ψ_{sz} were low; and elasticity increased because the phenological activities (leaf emergence, development, flowering and fruiting) were accomplished from February to April. *Q. semecarpifolia* showed high Index of Desiccation Tolerance (IDT) during dry periods. Desiccation tolerance is associated with low Ψ_{sz} , low RWC_z and low ϵ (high elasticity)⁸. For this, high IDT was shown by *Q. semecarpifolia* during leaf development in the month of September 1999. Both Ψ_{st} and Ψ_{sz} in the studied species showed significant negative correlation with percentage starch estimation of twigs of different years (Table 2). This suggests the conversion of starch into soluble carbohydrates, which in turn might have acted as osmotic solutes and contributed to osmotic regulation during these months when plants were water stressed. *S. wallichii* with a low ϵ , RWC_z and osmotic potentials reflected an inherent drought tolerance ability which was supported by its capacity to lower stomatal conductance during drought¹³. High elasticity in *S. wallichii* helps in maintaining turgor during low water supply. *S. wallichii*, which had a low Huber value and Specific Conductivity with a low water supply to the leaves and a significant negative correlation between RWC_z and wood water content¹², indicated its dependence on the stem water storage for rehydration, a prerequisite for bud break. *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 tree Ψ . Further it increases the gradient between soil and water potential, thereby promoting more effective water uptake from drying soils as exhibited by high xylem conductivity¹². Thus osmotic adjustment in *Q. semecarpifolia* seemed to be a drought tolerant strategy to maximize photosynthesis in dry periods provided by an amicable environment of warm temperature, greater illumination and mature leaves with high stomatal conductance.

ACKNOWLEDGEMENTS

I would like to express my sincere thanks to Prof. Dr. P. K. Jha, Tribhuvan University, and Prof. Dr. D. B. Zobel, Oregon State University, for their guidance. I would also like to acknowledge Dr. B. B. Shrestha, K. Mainali, N. Adhikari, K. Parajuli, K. Pokharel and R. Tripathy for their help during the field study and National Science Foundation for funding.

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Cite this article as:

Poudyal, Kanta. Maintenance of turgor in response to drought in *Schima wallichii* and *Quercus semecarpifolia* at Phulchowki hill, Kathmandu, Nepal. *J Biol Sci Opin* 2013; 1(3):145-150 <http://dx.doi.org/10.7897/2321-6328.01302>

Source of support: Nil; Conflict of interest: None Declared