

## Treeline species in Western Himalaya are not water stressed: a comparison with low elevation species

ASHISH TEWARI\*, SHRUTI SHAH, NANDAN SINGH & AMIT MITTAL

*Department of Forestry & Environmental Science, D.S.B. Campus, Kumaun University, Nainital, India*

**Abstract:** Water potential (predawn  $\{\Psi_{pd}\}$  and midday  $\{\Psi_{md}\}$ ), osmotic potential at full turgor (OP<sub>f</sub>) and zero turgor (OP<sub>z</sub>) turgor, relative water content at zero turgor (RWC<sub>z</sub>) and leaf conductance were measured for four species, *Quercus semecarpifolia* Sm., *Abies spectabilis* D. Don., *Betula utilis* D. Don and *Rhododendron campanulatum* D. Don in the Tungnath treeline ecotone, located between 3200 and 3450 m elevation. Similar parameters were studied in four species, *Pinus roxburghii* Sarg., *Myrica esculenta* Thumb., *Quercus leucotrichophora* A. camus and *Rhododendron arboreum* Wall. of low elevations located between 1720 m and 2100 m to compare the degree and timing of stress and adaptational features. The treeline ecotone soils were moister than low elevation forest soil in all seasons and years. In all the four treeline ecotone species  $\Psi_{pd}$  remained above  $-1.1$  MPa indicating the potential absence of severe water stress. The low elevation species (LES) had lower daily change in water potential in comparison to treeline species (TLS). Daily change was significantly correlated with  $\Psi_{pd}$ . The  $\Psi_{pd}$  water potential during the summer season in undercanopy evergreen species *M. esculenta* was close to  $-2.2 \pm 0.05$  MPa and  $-1.93 \pm 0.02$  MPa in Y<sub>r1</sub> and Y<sub>r2</sub>. The winter to spring/ summer time rise in  $\Psi_{pd}$  was a more pronounced in the LES than the in TLS and coincided with the lowering of osmotic potential. The morning leaf conductance in all seasons of TLS ranged between  $28.75 \pm 1.45$  and  $329.2 \pm 8.98$  m mol m<sup>-2</sup> sec<sup>-1</sup>. The TLS maintained a high rate of leaf conductance during spring and summer season.

**Key words:** Leaf conductance, osmotic potential, relative water content, water potential.

**Guest editor:** S.P. Singh

### Introduction

Drought is amongst the most important climatic events which can severely impact natural ecosystems. The Himalayas are warming at a faster rate than the global average due to global warming (Yao & Zhang 2012). The treeline of the Himalayan region are highest in the northern hemisphere (Miehe *et al.* 2007; Shi & Wu 2013), therefore, trees occurring there experience a different physical environment than treelines of other mountains. Due to monsoonal pattern of rainfall, Himalayan tree species experience drought of several months (Zobel & Singh 1997). Trees growing in the treeline ecotone

are exposed to various environmental stresses like short growing season and adverse climatic conditions which influence the tree water relations (Körner 2003; Mayr *et al.* 2006; Tranquillini 1979). During winters, water uptake is low due to frozen soil but comparatively high atmospheric temperature enhances evaporation resulting in drier soils (Larcher 1972; Mayr *et al.* 2006; Pisek & Larcher 1954; Tranquillini 1976, 1980;)

Water moves across a gradient from the soil through the plants to the atmosphere, water potential being the highest in the soil and lowest at the leaf surface (Lambers *et al.* 1998). Stem predawn water potentials  $\Psi_{pd}$  give an indication of

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\*Corresponding Author; e-mail: atewari69@gmail.com

the soil water availability and is a useful measure of plant water status (Reich & Hinckley 1989).

There is some evidence that water deficit in treeline ecotone can reach lethal level in the north hemisphere during winters (Tranquillini 1976). For example, in *Picea abies*, water potentials can fall below  $-4.0$  MPa (Mayr *et al.* 2002). However, during the growing season tree water potential of treeline does not reach critical levels to affect the normal plant function (Anfodillo *et al.* 1998). Enhanced evapo-transpiration rate with rising global temperature and uncertainty associated with precipitation, earlier snow melt and more rain than snow may combine to create a more drought stressed condition for plants in a warming climate. Extended period of water stress would eventually lead to death of young individuals of some tree species at the drier sites (leeward sites) as already shown for white bark pine (Miller *et al.* 2012).

Low soil temperature can impair water uptake in alpine treeline species particularly during the winter season. In *Picea glauca* growing at treeline at Alaska water uptake reduction occurs when soil temperature is close to  $9$  °C (Goldstein *et al.* 1985). During winters water uptake is usually blocked in stands with limited snow (Tranquillini 1979). Embolism in root xylem may occur specially during the spring and autumn season in the top soil layer due to repeated freezing and thawing effect. The fine roots are more vulnerable to embolism (Hacke *et al.* 2000; Kavanagh *et al.* 1999; Sperry & Ikeda 1997).

The conductivity of leaf surface to water vapour is an important integrator of the plant water condition (Hinckley *et al.* 1983; Schulze 1986; Smith & Hollinger 1991). Leaf conductance during the growing season in treeline species is generally not restricted. *Larix deciduas* can maintain a high stomatal conductance than the species of lower altitudes, as it requires an increased leaf conductance to compensate for the short growth period (Benecke 1981).

Osmotic adjustment is an effective adaptation that the tree species employ to overcome drought, as it can contribute in the maintenance of turgor during periods of drought and therefore can enhance the chances of competing with other species in treeline areas (Badalotti 2000).

The Himalayan treeline species have generally not been studied for the impact of drought and its possible repercussions on tree phenology and physiology. Most eco-physiological data for treeline species has been collected from European temperate region where drought conditions are very

different from those of Himalayas.

In the present paper we have tried to assess (I) the level of stress that is encountered by the treeline species (TLS) of western Himalayan region in comparison with lower elevation species (LES) and to find out whether it becomes low enough to affect their physiological functions. (II) How these tree species react to droughts and the drought adaptation mechanisms they employ is another issue that we have addressed here.

We hypothesize that TLS will be less affected by water stress than LES because of relatively lower evapotranspiration losses in tree line area (Körner 2012). However, loss of snow with climatic warming in future may intensify tree line drought during pre-monsoon period. This study is the first attempt on developing understanding of tree water relations in treeline ecotone of Himalayas and provides data which would be used to determine the impact of changes like loss of snow and accelerated upward migration of fast growing species of lower elevations.

## Material and methods

### *Study Area & Climate*

**Study Site:** The studied treeline site (Tungnath)  $30^{\circ}49'22''$ N latitude and of  $79^{\circ}21'47''$ E longitude occurs between 3200 and 3560 m asl elevation. The tree species selected for the present study in the treeline site were *Quercus semecarpifolia*, *Abies spectabilis*, *Betula utilis*, *Rhododendron campanulatum*. The data in the treeline site was collected during the year 2016 and 2017 (Two years) (Table 1).

The low elevation sites were located between  $29^{\circ}23'21''$  and  $29^{\circ}24'40''$ N and  $79^{\circ}29'34''$  and  $79^{\circ}28'14''$ E along an elevation transect between 1720 and 2100 m asl. The LES includes *Pinus roxburghii*, *Myrica esculenta*, *Quercus leucotrichophora* and *Rhododendron arboreum* and they belong to subtropical to warm temperate forest zones. The data in the low elevation site was collected during the year 2014 and 2015 (Two years) (Table 1).

**Climate:** The climate of treeline site is characterized by severe frosts, and hail storms for almost eight months in the year (September–April). Snow fall is from December to March and snow melt occurs during April and May which helps in keeping the soil moist prior to the monsoon period. Maximum rainfall is in July–August (Nautiyal *et al.* 2001). In the study site the mean annual temperature varies between  $-8.91$  °C to  $25.6$  °C. The average annual precipitation was about 2410

**Table 1.** A list of study sites.

Location	Site	Species	Latitude & Longitude	Elevation (m)	Aspect
Treeline	Tungnath	<i>Q. semecarpifolia</i> Sm. <i>A. spectabilis</i> D.Don. <i>B. utilis</i> D.Don. <i>R. campanulatum</i> D.Don	30°49'22"N 79°21'47"E	3200–3450	Southern
Low elevation	Mangoli chirpine	<i>P. roxburghii</i> Sarg. <i>M. esculenta</i> Thumb.	29°23'21"N 79°29'34"E	1720–1750	Southern
	Kilburry oak	<i>Q. leucotrichophora</i> A. camus <i>R. arboreum</i> Wall	29°24'40"N 79°28'14"E	2000–2100	Southern

mm of which 90% was received during June to September (Rai *et al.* 2012). According to Joshi *et al.* (unpublished data) 3800 mm of rainfall occurred during the year 2017, which is exceptionally high for the sites.

In the low elevation site average annual precipitation was 2258 mm of which two third occurred during rainy season. Mean annual temperature was 15.2 °C with mean minimum temperature of coldest month 4.6 °C (January) and mean maximum temperature of warmest month 25.9 °C (June) during the study period.

**Soil Moisture:** Soil samples were collected from five representative locations from 0–10 cm (surface layer), 10–20 cm (middle layer) and 20–30 cm (deeper layer) depth from each site. Soils from different depths were packed in polythene bags and brought to the laboratory for soil analysis. For soil moisture content estimation, five replicates of 50 g soil were dried at 100 °C till constant weight. The moisture content was determined on dry weight basis following Jackson (1958).

**Tree water potential ( $\Psi$ ),** Pressure volume curves and leaf conductance were measured on five representative trees of each of the selected species across the seasons. Sample trees were 15–25 m tall and measurements were made on twigs located 2 to 3 m from the ground. However *R. campanulatum* plants were 1–2 m tall.

**Twig Water Potential:** Pressure chamber (PMS Instrument Co. model 1000, range 70 bars) was used for the determination of water potential and the development of Pressure-Volume Curves (P-V curves). In this study water potential measurements were made for two years on selected sites and species in different seasons. The water potential ( $\Psi$ ) was measured at predawn ( $\Psi_{PD}$ ) (5.30–6.30 am) and in the midday (1.30–2.30 pm) ( $\Psi_{MD}$ ) following Tewari (1999) and Zobel *et al.* (2001).

Pressure volume curves (PV curves) and

Components of water potential: PV curves were prepared to develop a relationship between components of water potential and Relative water content (RWC %). PV curves were prepared following the bench drying method from overnight saturated twigs. From PV curves, the osmotic potential at full turgor ( $OP_t$ ), the osmotic potential at zero turgor ( $OP_z$ ) and RWC% at turgor loss point ( $RWC_z$ ) were determined following Pallardy *et al.* (1991) and Tewari (1998).

Osmotic adjustment is generally calculated as the decline in osmotic potential over the drought period (difference between the value at the beginning of drought and that at the peak of drought). We calculated decline in osmotic potential (zero and full turgor) separately for different seasons rainy, autumn, winter, late spring and summer, as environmental and phenological factors unrelated to drought also affects change in osmotic adjustment (Abrams 1988). Here we have applied the term osmotic adjustment for an obvious decline in osmotic potential over a period falling between two sampling dates of drought irrespective of its intensity.

**Leaf Conductance:** Leaf conductance measurements were made seasonally, using AP<sub>4</sub> porometer (Delta-T Devices). The porometer was calibrated against a perforated plastic plate of known conductance (Poudyal *et al.* 2004; Webb 1991). Data were collected from 03 leaves/ individual on the sunny sides of tree and from approximately similar height, in the morning and afternoon (10.30–11.30 AM & 1.30–2.30 PM) following Tewari (1998) and Garkoti *et al.* (2000).

**Statistical analysis:** The data were subjected to analysis of variance with a 95% confidence level using SPSS version 2016. Species, seasons and year were the factors used for ANOVA. Correlation coefficient was used for expressing relationship between different variables.

**Table 2.** Depth wise variation in soil moisture content (%) across different sites seasons and years.

Site	Soil depth (cm)	Yr <sub>1</sub>				Yr <sub>2</sub>					
		Summer	Rainy	Autumn	Winter	Spring	Summer	Rainy	Autumn	Winter	
Treeline site											
Tungnath	00–10	39.4 ± 2.96	59.9 ± 2.1	74.2 ± 2.53	44.4 ± 2.56	49.6 ± 0.38	36.2 ± 1.92	66.13 ± 1.01	42.9 ± 1.25	53.6 ± 1.02	
		38.4 ± 1.14	56.4 ± 1.9	48.7 ± 2.05	47.3 ± 0.81	53.3 ± 0.82	39.9 ± 1.17	71.23 ± 1.24	32.7 ± 0.36	47.8 ± 1.90	
	10–20	36.3 ± 3.24	57.9 ± 1.39	34.9 ± 1.41	32.15 ± 2.52	55.8 ± 0.99	44.0 ± 1.63	82.2 ± 1.38	33.28 ± 0.37	35.5 ± 0.13	
		20–30	21.4 ± 1.56	45.6 ± 3.04	21.2 ± 0.74	19.9 ± 0.71	15.4 ± 3.94	19.9 ± 1.80	40.81 ± 1.00	21.0 ± 0.83	20.8 ± 0.90
	Low elevation site	Mangoli (chirpine)	23.8 ± 4.03	44.7 ± 1.92	27.1 ± 0.67	23.5 ± 1.29	14.2 ± 2.80	22.4 ± 4.31	43.6 ± 4.56	23.7 ± 0.72	24.9 ± 1.58
			20–30	23.7 ± 4.96	47.9 ± 2.08	28.2 ± 0.31	25.2 ± 1.40	15.5 ± 2.98	22.3 ± 4.99	45.2 ± 0.70	25.8 ± 0.69
Kilburry (oak)		20.4 ± 1.05	32.8 ± 0.88	19.8 ± 0.10	6.4 ± 0.61	24.0 ± 0.97	18.6 ± 0.41	32.1 ± 1.00	20.5 ± 0.38	6.83 ± 0.64	
		10–20	20.2 ± 1.24	36.3 ± 0.23	20.2 ± 0.72	7.2 ± 0.67	23.6 ± 0.87	17.7 ± 0.47	35.3 ± 0.32	23.7 ± 0.50	7.6 ± 0.62
	20–30	21.3 ± 0.9	36.3 ± 0.98	23.0 ± 0.66	7.4 ± 0.46	23.4 ± 1.18	16.2 ± 1.06	34.7 ± 1.00	26.3 ± 0.71	8.45 ± 0.71	

## Result

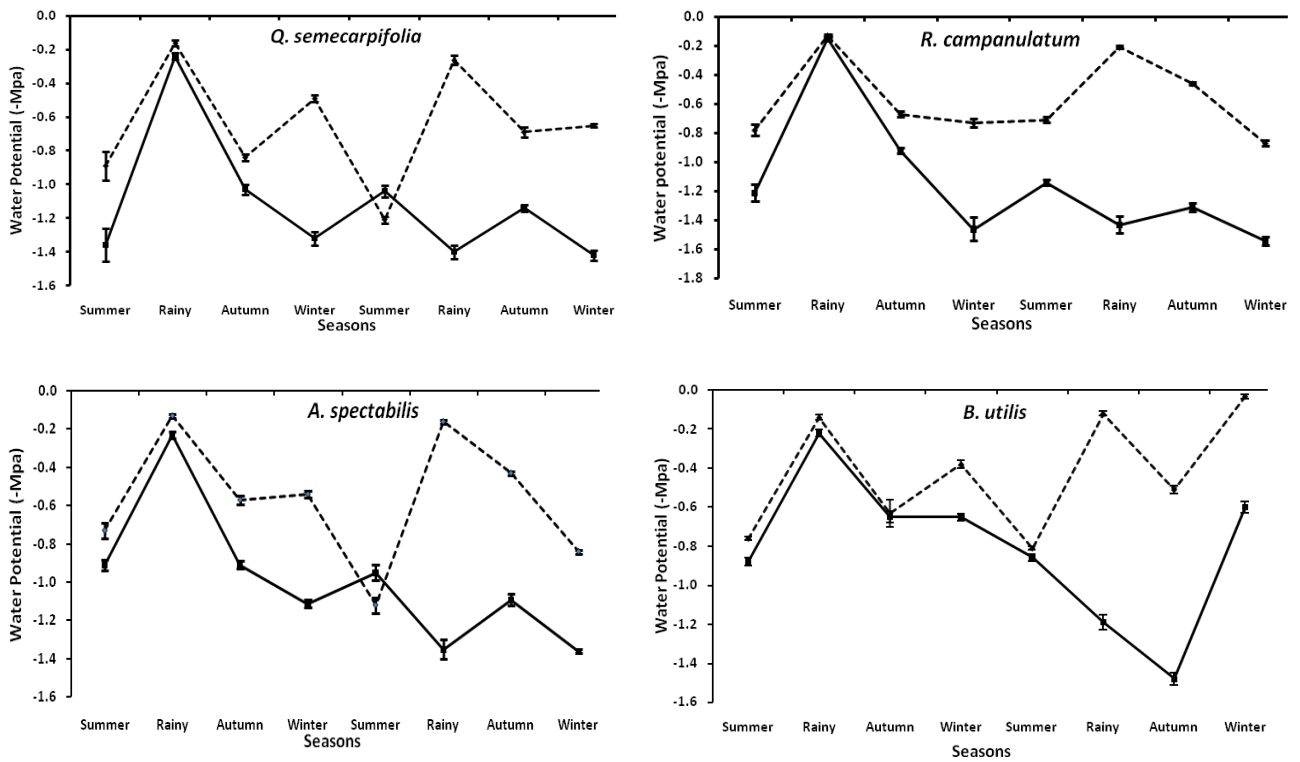
**Soil Moisture:** Soil moisture was highly variable across the sampling dates and differed significantly ( $P < 0.01$ ). The treeline forest soils were moister than soils of LES. At the TLS across all soil depths and seasons the soil moisture ranged between  $32.7 \pm 0.36$  and  $74.2 \pm 2.53\%$  (Table 2). At the LES in chir pine forest in the top soil layer moisture content ranged between  $19.9 \pm 0.71$  and  $45.6 \pm 3.04\%$  and in banj oak site between  $6.4 \pm 0.61$  and  $32.8 \pm 0.88\%$  (Table 2). Comparison of soil moisture during the winter seasons indicates that the chir pine forest soil was moister than the banj oak forest soil in all depths. ANOVA showed soil moisture varied significantly across sites and years ( $P < 0.01$ ). Interestingly, soils tended to be drier in surface layer than deeper layer in low elevation forest sites, while at treeline, soils tended to be drier in deeper layers particularly during autumn and winter season.

**Tree Water Potential ( $\Psi$ ):** In the TLS the tree water potential ( $\Psi$ ) varied significantly across species and seasons ( $P < 0.01$ ). Across all seasons and the two study years, the  $\Psi_{pd}$  of all species remained above 1.0 MPa indicating the absence of

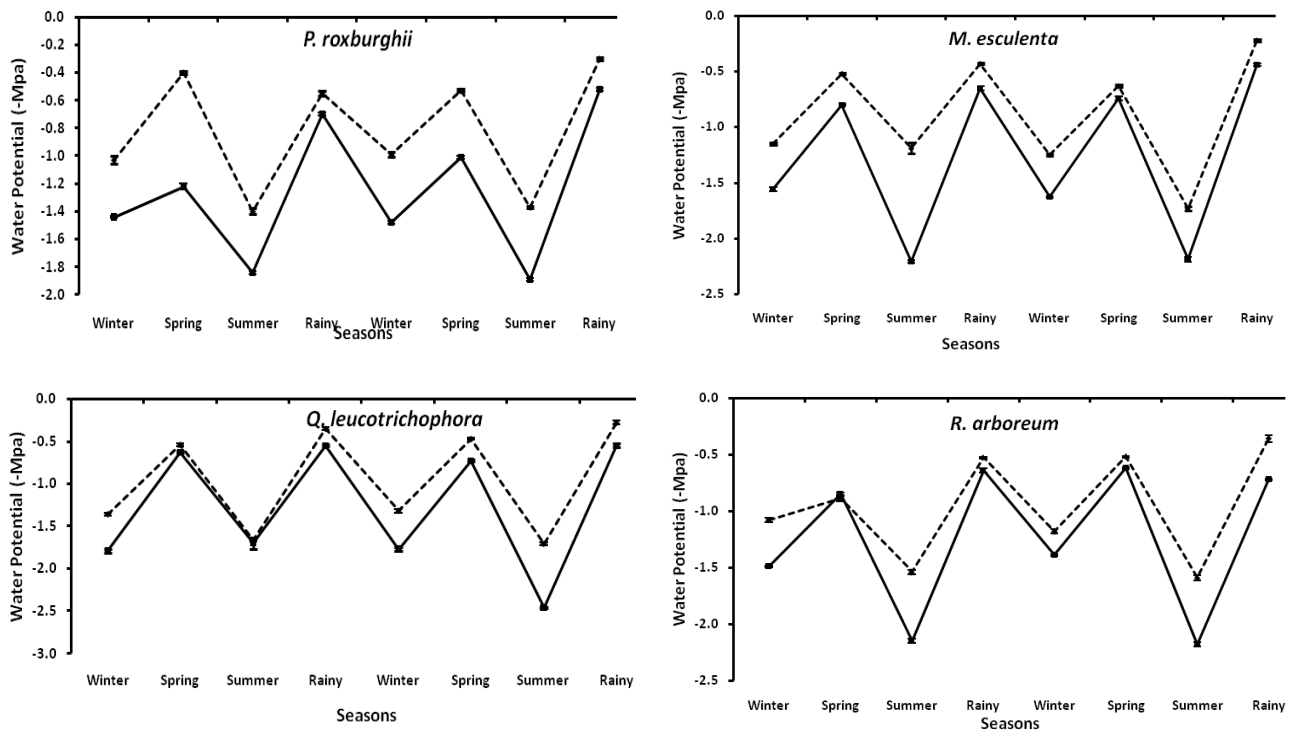
severe stress. The lowest predawn tree water potential values indicate that LES suffered roughly twice as much water stress as did treeline species. It was only in the summer season of Yr<sub>2</sub> the  $\Psi_{pd}$  in *Q. semecarpifolia* and *A. spectabilis* had declined below  $-1.0$  MPa. Minimum values of  $\Psi_{pd}$  for all species were observed during the summer season followed by the comparatively dry autumn season. Maximum  $\Psi_{pd}$  was during the rainy season the period during which more than 80% of annual rainfall occurs. Tree  $\Psi_{md}$  varied significantly among species and seasons ( $P < 0.01$ ) (Fig. 1).

The lowest  $\Psi_{md}$  were generally encountered by treeline species during summer and winter seasons with values ranging between  $-0.88 \pm 0.02$  MPa (*B. utilis*) and  $-1.95 \pm 0.04$  MPa (*A. spectabilis*) (Fig. 1).

Water potentials in LES varied significantly across seasons and species ( $P < 0.01$ ). *P. roxburghii* had the minimal  $\Psi_{pd}$  during the summer season ( $-1.7 \pm 0.02$  MPa and  $-1.81 \pm 0.01$  MPa, Fig. 2). The under canopy species *M. esculenta* had  $\Psi_{pd}$  values  $-2.2 \pm 0.05$  MPa and  $-1.93 \pm 0.02$  MPa during the summer season of Yr<sub>1</sub> and Yr<sub>2</sub>. The species encountered another drought of slightly less magnitude during the winter season. *Q. leucotrichophora* and *P. roxburghii* during the summer



**Fig. 1.** Variation in predawn ( $\Psi_{PD}$ , dotted line) and midday ( $\Psi_{MD}$ , Solid line) Water potential (MPa) in treeline species (TLS).



**Fig. 2.** Variation in predawn ( $\Psi_{PD}$ , Dotted line) and midday ( $\Psi_{MD}$ , Solid line) Water potential (MPa) in lower elevation species (LES).

**Table 3.** Seasonal changes in Osmotic Potential at full turgor ( $OP_f$ ), and at zero turgor ( $OP_z$ ) and Relative water content at zero turgor ( $RWC_z$ ) % in treeline and low elevation species.

$\Psi$ Components	Rainy	Autumn	Winter	Spring	Summer
Treeline Species					
<i>Q. semecarpifolia</i>					
OP Full	$-1.24 \pm 0.08$	$-1.74 \pm 0.18$	$-1.94 \pm 0.69$	$-2.5 \pm 0.09$	$-1.04 \pm 0.20$
OP Zero	$-1.78 \pm 0.42$	$-2.30 \pm 0.07$	$-3.10 \pm 0.47$	$-3.8 \pm 0.20$	$-1.45 \pm 0.20$
RWC%	$78.63 \pm 4.12$	$58.89 \pm 5.99$	$72.34 \pm 5.25$	$69 \pm 1.53$	$54.63 \pm 1.46$
<i>R. campanulatum</i>					
OP Full	$-1.24 \pm 0.29$	$-1.76 \pm 0.2$	$-1.40 \pm 0.31$	$-1.7 \pm 0.06$	$-0.74 \pm 0.02$
OP Zero	$-1.6 \pm 0.58$	$-2.15 \pm 0.34$	$-2.24 \pm 0.02$	$-2.7 \pm 0.12$	$-1.54 \pm 0.11$
RWC%	$91.66 \pm 1.74$	$88.23 \pm 0.97$	$89.73 \pm 2.97$	$75.3 \pm 1.20$	$73.20 \pm 4.01$
<i>A. spectabilis</i>					
OP Full	$-1.04 \pm 0.62$	$-1.76 \pm 0.12$	$-1.05 \pm 0.17$	$-1.6 \pm 0.12$	$-0.72 \pm 0.19$
OP Zero	$-1.52 \pm 0.58$	$-2.10 \pm 0.06$	$-1.48 \pm .01$	$-2.7 \pm 0.26$	$-1.54 \pm 0.42$
RWC%	$90.16 \pm 4.09$	$91.02 \pm 1.21$	$79.02 \pm 4.82$	$75.3 \pm 2.03$	$52.18 \pm 5.77$
<i>B.utilis</i>					
OP Full	$-0.94 \pm 0.14$	$-1.51 \pm 0.14$	$-1.32 \pm 0.12$	$-2.6 \pm 0.09$	$-1.38 \pm 0.15$
OP Zero	$-1.43 \pm 0.37$	$-2.50 \pm 0.12$	$-2.16 \pm 0.23$	$-3.4 \pm 0.15$	$-2.07 \pm 0.14$
RWC%	$88.14 \pm 1.90$	$78.86 \pm 6.14$	$78.28 \pm 4.3$	$65.7 \pm 1.20$	$88.76 \pm 2.6$
Low Elevation Species					
<i>P. roxburghii</i>					
OP Full	$-1.3 \pm 0.02$	$-0.83 \pm 0.03$	$-1.69 \pm 0.03$	$-1.41 \pm 0.01$	$-1.18 \pm 0.02$
OP Zero	$-1.6 \pm 0.06$	$-1.46 \pm 0.06$	$-2.24 \pm 0.03$	$-2.47 \pm .02$	$-1.83 \pm 0.01$
RWC%	$84.0 \pm 1.58$	$78.5 \pm 1.58$	$79.36 \pm 0.66$	$82.24 \pm 0.76$	$84.94 \pm 0.84$
<i>M. esculenta</i>					
OP Full	$-0.88 \pm 0.03$	$-1.27 \pm 0.04$	$-1.38 \pm 0.01$	$-1.92 \pm 0.01$	$-2.46 \pm 0.02$
OP Zero	$-1.36 \pm 0.03$	$-1.47 \pm 0.03$	$-1.97 \pm 0.03$	$-2.45 \pm 0.02$	$-2.88 \pm 0.01$
RWC%	$90.96 \pm 1.45$	$81.38 \pm 1.5$	$90.94 \pm 0.55$	$86.14 \pm 0.71$	$82.6 \pm 1.02$
<i>Q. leucotrichophora</i>					
OP Full	$-1.27 \pm 0.01$	$-1.43 \pm 0.02$	$-2.2 \pm 0.01$	$-2.40 \pm 0.01$	$-2.08 \pm 0.01$
OP Zero	$-1.67 \pm 0.02$	$-1.79 \pm 0.01$	$-2.35 \pm 0.02$	$-2.82 \pm 0.02$	$-2.81 \pm 0.01$
RWC%	$85.12 \pm 0.84$	$83.68 \pm 0.81$	$74.32 \pm 1.13$	$71.88 \pm 0.41$	$82.66 \pm 0.87$
<i>R. arboreum</i>					
OP Full	$-0.74 \pm 0.01$	$-1.9 \pm 0.01$	$-1.94 \pm 0.02$	$-2.16 \pm 0.02$	$-1.8 \pm 0.01$
OP Zero	$-1.47 \pm 0.02$	$-1.65 \pm 0.02$	$-2.44 \pm 0.02$	$-2.38 \pm 0.11$	$-2.36 \pm 0.02$
RWC%	$84.12 \pm 0.99$	$85.46 \pm 0.54$	$84.1 \pm 1.36$	$94.14 \pm 0.22$	$74.34 \pm 0.84$

season had relatively low  $\Psi_{pd}$  values. This species also encountered a moderate stress during the winter season with values close to  $-1.3$  MPa (Fig. 1). The under canopy species *R. arboreum* had the lowest  $\Psi_{pd}$  values during the summer season followed by the winter season with  $\Psi_{pd}$  values marginally lower than the dominant *Q. leucotrichophora*. At the lower altitude the most negative  $\Psi_{md}$  were during the summer and winter

season across all species. The values in these seasons ranged between  $-1.39 \pm 0.01$  and  $-2.46 \pm 0.01$  MPa.

The daily change ( $\Delta\Psi = \Psi_{md} - \Psi_{pd}$ ) differed significantly among species and seasons ( $P < 0.01$ ). The magnitude of diurnal change across all TLS was maximum during the growing season from spring to autumn. The species varied in seasons and magnitude of diurnal change. *B. utilis*, the only

**Table 4.** The lowest pre-dawn water potential  $\Psi_{pd}$  (-MPa) and maximum daily change  $\Delta\Psi$  among all seasons and years in the treeline species (TLS) and low elevation species (LES).

Species	Lowest $\Psi_{pd}$ (-MPa)	$\Delta\Psi$ (MPa)
<i>Q. semecarpifolia</i>	-1.21 (Summer, Yr <sub>2</sub> )	1.13 (Rainy Yr <sub>2</sub> )
<i>R. campanulatum</i>	-0.87 (Winter, Yr <sub>2</sub> )	1.22 (Rainy Yr <sub>2</sub> )
<i>A. spectabilis</i>	-1.12 (Summer, Yr <sub>2</sub> )	1.19 (Rainy Yr <sub>2</sub> )
<i>B. utilis</i>	-0.81 (Summer, Yr <sub>2</sub> )	1.07 (Rainy Yr <sub>2</sub> )
<i>P. roxburghii</i>	-1.81 (Summer, Yr <sub>2</sub> )	0.64 (Autumn Yr <sub>2</sub> )
<i>M. esculenta</i>	-1.93 (Summer, Yr <sub>2</sub> )	0.41 (Winter Yr <sub>1</sub> )
<i>Q. leucotrichophora</i>	-1.71 (Summer, Yr <sub>2</sub> )	0.75 (Summer Yr <sub>2</sub> )
<i>R. arboreum</i>	-1.84 (Summer, Yr <sub>1</sub> )	0.31 (Autumn Yr <sub>1</sub> )

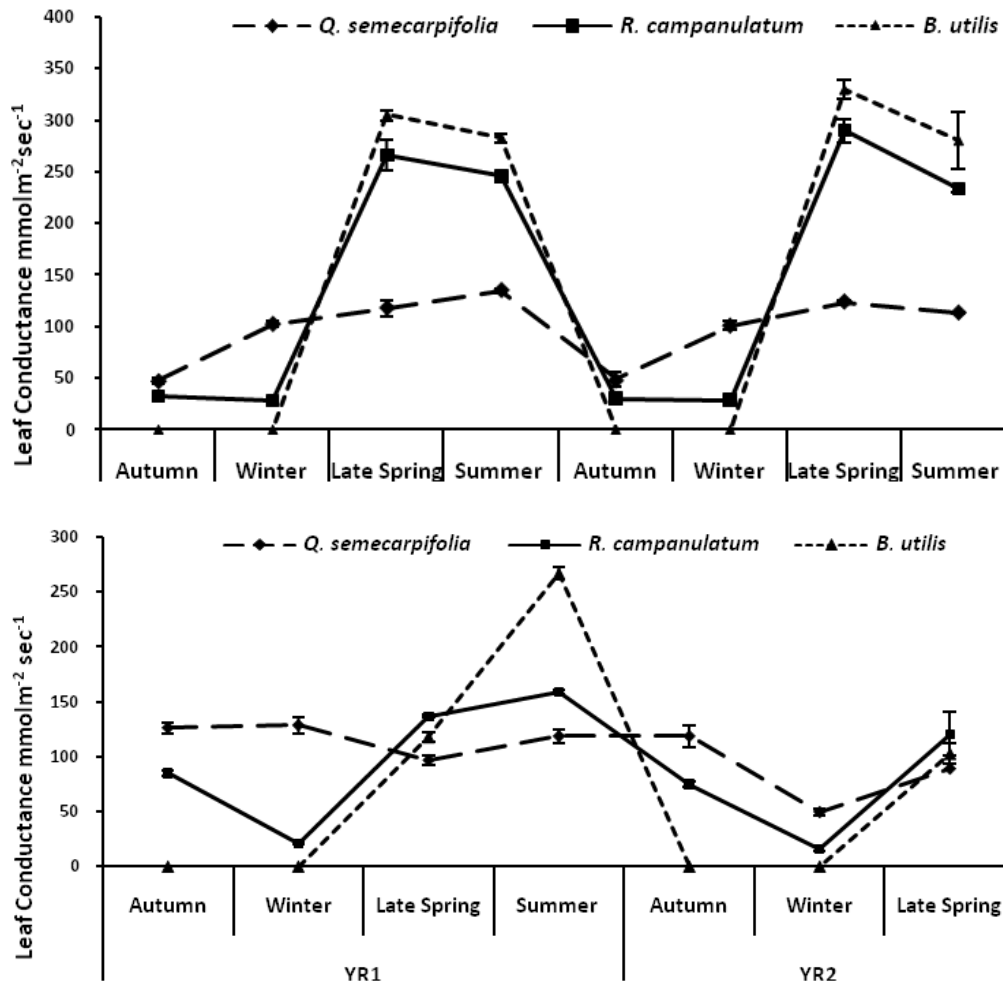
deciduous species had the highest daily change during the rainy and autumn season of Yr<sub>2</sub> (1.07 and 0.97 MPa respectively). In LES the magnitude of daily change was lower than in TLS and varied between 0.41 MPa and 0.75 MPa compared to 1.07 to 1.22 MPa in TLS (Table 4). This indirectly represents the ability of the TLS to keep the stomata open and conduct water freely and carry on leaf conductance. There was a significant correlation between the  $\Delta\Psi$  and  $\Psi_{pd}$  ( $P < 0.01$ ,  $r = 0.80$ ).

**Water Potential Components:** The water potential parameters (Osmotic Potential at full turgor ( $OP_f$ ) and zero turgor ( $OP_z$ ) and Relative Water Content ( $RWC_z$ ) %) differed significantly across species and seasons ( $P < 0.01$ ). *Q. semecarpifolia* at the treeline showed osmotic adjustment persistently from rainy to the late spring season (-1.26 MPa at full turgor and -2.02 MPa at zero turgor). The  $RWC$  at turgor loss point for the species was the lowest during autumn season  $58.89 \pm 5.99\%$  and maximum at winter season  $72.34 \pm 5.25\%$ . *R. campanulatum* showed an osmotic adjustment between rainy to autumn season of -0.52 MPa at full turgor and a smaller adjustment from winter to late spring. However,  $OP_z$  for the species showed a continuous decline from the rainy to late spring time (-1.1 MPa). This species could maintain a high  $RWC_z$  at turgor loss point across all seasons. *A. spectabilis* showed a decline in osmotic adjustment at zero and full turgor between rainy to autumn season and a larger adjustment between winters to late spring. *B. utilis* the only deciduous species reduced its osmotic potential at full and zero turgor between rainy to autumn and from winters to late spring. The adjustment was more than -1.0 MPa both at full and zero turgor between the winters and late spring (Table 3).

All the LES except *M. esculenta* showed a decline in osmotic potential at full and zero turgor during winter and spring season. In *P. roxburghii*

the decline in osmotic potential was from autumn to winter season. *M. esculenta* reduced its osmotic potential from rainy to summer season and adjusted by -1.58 MPa at full turgor. In *Q. leucotrichophora* the decline was from rainy to spring season, the osmotic adjustment at full turgor being -1.13 MPa. *R. arboreum* behaved similarly as did *Q. leucotrichophora*, but the adjustment was more pronounced than *Q. leucotrichophora*. All the species could maintain a high  $RWC$  at turgor loss point which generally remained above 71.8% (Table 3). There was a significant correlation between the  $\Delta\Psi$  and  $\Psi_{pd}$  at low elevation site ( $P < 0.01$ ,  $r = 0.94$ ). The two oaks, *Q. semecarpifolia* and *Q. leucotrichophora* did not differ in the timing of osmotic adjustment which was between rainy to spring season, however, the degree of adjustment was more in the high altitude oak, -1.26 MPa at full turgor and -2.02 MPa at zero turgor compared to -1.13 MPa at full and -1.15 at zero turgor in *Q. leucotrichophora*. In *R. campanulatum* the adjustment at full and zero turgor was much lower than in *R. arboreum*.

**Leaf Conductance:** The instrument AP<sub>4</sub> type diffusion porometer could not measure the leaf conductance of conifers hence the conductance of only broad leaved species was measured. As the deciduous *B. utilis* was leafless during autumn and winter season leaf conductance in these two seasons were not estimated. Leaf conductance was measured over four seasons summer, autumn, winter and late spring over a two year period. Morning conductance varied significantly across seasons ( $P < 0.01$ ) but there was no significant variation across species. The afternoon conductance varied significantly across species as well as seasons ( $P < 0.01$ ). The TLS maintained a high rate of leaf conductance during late spring and summer season. The morning leaf conductance across all seasons and species of the treeline areas ranged



**Fig. 3.** Seasonal pattern of leaf conductance ( $\text{m mol m}^{-2} \text{sec}^{-1}$ ) in the treeline species (TLS). Upper graph is of morning leaf conductance and lower graph is of afternoon leaf conductance.

between  $28.75 \pm 1.45$  and  $329.2 \pm 8.98 \text{ m mol m}^{-2} \text{sec}^{-1}$ . *R. campanulatum* had the lowest leaf conductance during the autumn and winter season. The afternoon leaf conductance was generally lower for all species than the morning conductance (Fig. 3).

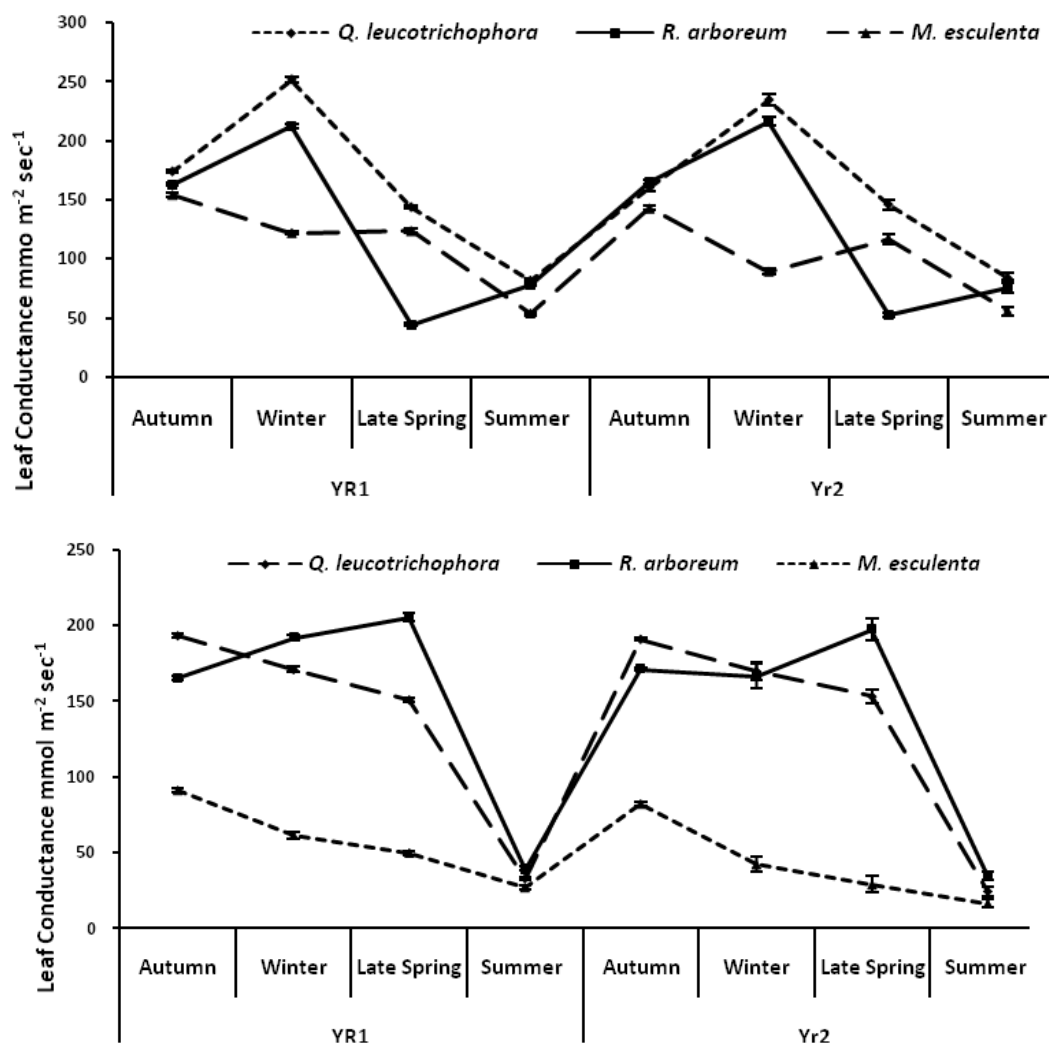
The morning leaf conductance for LES ranged between  $44.43 \pm 1.15$  and  $234.20 \pm 4.78 \text{ m mol m}^{-2} \text{sec}^{-1}$  across all species and seasons. The low altitude oak *Q. leucotrichophora* had relatively lower leaf conductance during the summer season compared to high altitude oak *Q. semecarpifolia*. The conductance of almost all species was lowest during the summer season when  $\Psi_{\text{pd}}$  was most negative. All the species generally showed one peak in conductance during the winter season and a small peak during the autumn season. The afternoon conductance was 50 to 60% lower than the morning conductance during the summer time and in *M. esculenta* during the autumn season

(Fig. 4). Significant correlation existed between  $\Psi_{\text{pd}}$  and morning leaf conductance ( $P < 0.01$ ,  $r = 0.45$ ) and afternoon conductance ( $P < 0.01$ ,  $r = 0.58$ ) at low elevation sites.

## Discussion

The TLS were much less water stressed than LES across all seasons. There is a marked difference in temperature and soil water availability of the two study areas. In treeline areas the snow melt from winter snowfall keeps the soil moist during spring and summer season, prior to monsoon rains. The low elevation sites are characterized by an approximately three months of heavy rainfall from mid June to mid September and the remaining 9 months with little rainfall or no rain. The severity of drought can be assessed by the minimum level of  $\Psi$  and the best indicators can be the lowest  $\Psi_{\text{pd}}$  on a particular site and sampling date.





**Fig. 4.** Seasonal pattern of leaf conductance ( $\text{m mol m}^{-2} \text{sec}^{-1}$ ) in the low elevation species (LES). Upper graph is of morning leaf conductance and lower graph is of afternoon leaf conductance.

The studied forest forming evergreen species generally have one year leaf life and the new leaves that the trees put forth during March–April seems to induce leaf drop (Rahhan *et al.* 1985). In the LES the winter to spring time rise (0.19–0.82 MPa) or stability of tree water potential was a pronounced feature which coincided with the timing of maximum phenological activities. In TLS the rise in  $\Psi_{\text{pd}}$  occurred, but was from winter to late spring season (April–May). The rise amongst all species ranged between 0.2 MPa to 0.42 MPa and was of a lower magnitude than LES. The wet soils from the melting snow possibly keeps the water potential higher above the threshold required for the commencement of phenological activities. This spring/ summer time rise could also be due to thinning of the canopy (about 25% in oaks and 40–50% in other species) and resultant reduction in

transpiration rate (Tewari 1998). This data and those of Williams *et al.* (1997) on Savanna trees support the Reich-Borchert hypothesis that leaf flushing is determined by change in internal water status of the whole plant. However this  $\Psi_{\text{pd}}$  rise in Himalayan trees is generally lower than the woody species of drier climate such as Australian savannah (Williams *et al.* 1997). In Australian savannah the leaflessness is suggested to be an adaptation that species employ to raise  $\Psi_{\text{pd}}$  between  $-1.0$  and  $-0.5$  MPa (William *et al.* 1997) for producing leaves during dry season.

The values of  $\Psi_{\text{pd}}$  in *Q. leucotrichophora* and *Q. semecarpifolia* ranged between  $-0.16$  and  $-1.71$  MPa. These are on the higher side when compared with the range of values reported for oaks in literature  $-1.98$  MPa and  $-2.26$  MPa to  $0.39$  MPa for *Q. rubra* and *Q. velutina* (Bahari *et al.* 1985). For

*Q. rubra* in mesic and xeric sites the reported values were  $-1.5$  MPa and  $-2.39$  MPa, respectively (Kubliske & Abrams 1992). The  $\Psi_{pd}$  of some other Himalayan species of mid altitude varied between  $-0.49$  (*Pinus roxburghii*) and  $-0.86$  MPa (*Cornus macrophylla*) (Singh *et al.* 2006).

The pre-dawn water potentials in all studied TLS remained above  $-1.0$  MPa.  $\Psi$  in TLS of different parts of world has not been found to reach critically low level of  $\Psi$  to affect the normal plant function (below  $-2.0$  MPa) during the growing season (Anfodillo *et al.* 1998; Körner 2012). Anfodillo *et al.* (1998) have reported  $\Psi_{pd}$  close to  $-1.0$  MPa during exceptionally dry period and peak mid day value between  $-1.5$  and  $-1.9$  MPa. The most negative water potential (value) is reported for *Larix decidua*, but in *Pinus cembra* and *Picea abies* remained above  $-1.5$  MPa (Körner 2012). However, Mayor *et al.* (2002) have reported low water potential ( $-4$  MPa) in tall trees of *Picea abies*. Richard & Bliss (1986) observed water potential as low as  $-5.3$  MPa in *Larix lyallii* in the Rocky Mountains. Except for a few such studies, the trees of tree line experience only small periods of mild constraints of water which are much less than the tree growing at lower elevations. Problems in water supply can occur during winter months in TLS when the ground is frozen, hampering water uptake required for foliar maturation and induced winter desiccation in young individuals without snow protection above the tree line (Mayor 2007). However, in the Tungnath TLS such low water potentials were not found during winter season.

The TLS species differed from LES also seasonal patterns of water potential. In all TLS species the  $\Delta\Psi$  was maximum during the rainy season. However, in Yr1 the  $\Delta\Psi$  was negligible in all species due to overcast conditions in this season. The magnitude of  $\Delta\Psi$  particularly in growing season was higher in TLS in comparison to LES. The  $\Delta\Psi$  generally peaked when  $\Psi_{pd}$  was generally above  $-0.5$  MPa and tended to decline with increasing stress. However, *A. spectabilis* could maintain a  $\Delta\Psi$  of  $0.83$  MPa when the  $\Psi_{pd}$  was  $-1.12$  MPa in Yr2. In a study by Poudyal *et al.* 2004 *Q. semecarpifolia* had a daily change of  $0.77$  MPa when  $\Psi_{pd}$  was  $-0.40$  MPa. Fotelli *et al.* (2000) reported  $\Delta\Psi$  values up to  $1.5$  MPa in Mediterranean oaks during drought.

At the low altitude during the summer season *P. roxburghii* closed its stomata when  $\Psi_{pd}$  had declined to  $-1.7$  MPa and below as evident from the  $\Delta\Psi$ ;  $0.14$  MPa in Yr1 and  $0.8$  MPa in Yr2. *Q. leucotrichophora* could maintain a daily change

of  $0.53$  MPa when  $\Psi_{pd}$  was  $-1.67$  in Yr1 and  $0.75$  MPa when  $\Psi_{pd}$  was  $-1.71$  MPa. *Q. leucotrichophora* tends to keep its stomata open and conduct water freely as evident from the  $\Delta\Psi$  value even at low  $\Psi_{pd}$ . In LES the spring time  $\Delta\Psi$  was amongst the lowest in all the evergreen broad leaved species. This could be attributed to new leaf flush in these species with under developed stomata resulting in less water loss through transpiration (Poudyal 2013). In the under canopy species of low elevation *M. esculenta* and *R. arboreum* during the peak summer time when  $\Psi_{pd}$  has declined to  $-2.0$  MPa the  $\Delta\Psi$  in both the species had become negligible ( $0.1$  to  $0.8$  MPa) signifying their ability to avoid drought by closing their stomata. Singh *et al.* (2006) have reported  $\Delta\Psi$  values ranging between  $0.06$  and  $0.90$  MPa, for *P. roxburghii*, *R. arboreum* and *Q. leucotrichophora*.

Osmotic potential at full and zero turgor varied significantly across species and season ( $P < 0.01$ ). As drought intensifies cells adjust their internal water status by accumulating osmotic active compounds resulting in lowering of osmotic potential which is helpful in maintaining turgor pressure. The studied species differed in degree of osmotic adjustment both at zero and full turgor. The high altitude treeline forming oak *Q. semecarpifolia* and deciduous *B. utilis* had lower osmotic potential during late spring both at zero and full turgor in comparison to *A. spectabilis* and *R. campanulatum*.

The TLS behaved differently in the extent and intensity of osmotic adjustment. In *Q. semecarpifolia* osmotic adjustment was from rainy to late spring. In *R. campanulatum*, *A. spectabilis* and *B. utilis* the adjustment occurred at two times in a year between rainy and autumn and winter to late spring. The adjustment was maximum in *Q. semecarpifolia*. In *B. utilis* the adjustment was above  $1.1$  MPa between rainy to autumn and winter to late spring. *A. spectabilis* and *P. roxburghii* differed in seasonality and extend of osmotic adjustment. In *P. roxburghii* the adjustment was from autumn to winter season whereas in *A. spectabilis* a smaller adjustment between rainy and autumn and a larger adjustment between winter and late spring. The magnitude of adjustment at zero and full turgor was greater in *A. spectabilis* than *P. roxburghii*. *Q. semecarpifolia* behaved similarly to LES oak, *Q. leucotrichophora* both in the season and extent of adjustment.

The under canopy species of low altitude *M. esculenta* and *R. arboreum* showed maximum osmotic adjustment which was comparable with the osmotic adjustment of *Q. leucotrichophora*. Singh

*et al.* (2006) for *P. roxburghii*, *Q. leucotrichophora* and *R. arboreum* have reported wider range of values of osmotic potential at full and zero turgor across seasons, the minimum osmotic potential values being more negative. According to Tewari (1998) the two Himalayan oaks *Q. leucotrichophora* and *Q. floribunda* showed osmotic adjustment from autumn to winter ranging between  $-0.5$  and  $-1.8$  MPa at full turgor and  $-1.47$  to  $-2.0$  MPa at zero turgor. These values are marginally lower than the reported values of oaks of the present study  $RWC_z$  which is an indirect measure of a plant capacity to maintain its turgor with declining  $\Psi$  was always high for all TLS except *Q. semecarpifolia* and *A. spectabilis* in which it had declined to  $54.63 \pm 1.43$  and  $52.18 \pm 5.77\%$  during the summer season. In the remaining two TLS the  $RWC_z$  was relatively high during the summer season when  $\Psi$  was most negative. All LES species could also maintain a high  $RWC_z$  ranging from  $74.34 \pm 0.84$  and  $82.66 \pm 0.87\%$  during the peak summer drought. The capacity of trees to maintain a high RWC under drought was also observed by Zlatev (2005) and Gorai *et al.* (2010).

The pronounced lowering of osmotic potential in the TLS during the autumn season and early summer indicate that their main strategy is to ensure water availability to maintain high rate of photosynthesis when days are warm and sunny with optimal humidity, soil is not significantly dry and leaves are fully mature. *Q. leucotrichophora*, *M. esculenta* and *R. arboreum* at the low elevation keep on gradually declining their osmotic potential across the drought seasons after the rainy season in autumn, winter, late spring and upto summer in *M. esculenta*, so that the phenological activities of the spring and summer season are not affected. This may be referred as slow osmotic adjustment strategy.

All broad leaved evergreen species kept their stomata open throughout the year however species differed in degree of fall in leaf conductance in response to adverse climatic conditions. Keeping stomata open as drought intensifies, allows a plant to continue photosynthesis and provide more dry matter for eventual use and growth. Maximum conductance for the *Q. semecarpifolia* was lower than reported for *Q. leucotrichophora* and *Q. floribunda* (Garkoti *et al.* 2000; Tewari 2000) and much lower than for the deciduous oak *Q. rubra*  $400 \text{ mmol m}^{-2} \text{ sec}^{-1}$  (Kubiske & Abrams 1992). Other oaks maintain high conductance with low water potential. For example *Q. dumosa* (L.) has a conductance of  $80 \text{ mmol m}^{-2} \text{ sec}^{-1}$  at  $-3.34$  MPa

(Hastings *et al.* 1989), *Q. coccifera* (L.) has a conductance of  $150 \text{ mmol m}^{-2} \text{ sec}^{-1}$  at  $-3$  MPa and *Q. douglasii* has a conductance of  $> 200 \text{ mmol m}^{-2} \text{ sec}^{-1}$  at  $-3.6$  MPa (Xu & Baldocchi 2003). Leaf conductance declined as drought intensified in the LES however, in the TLS maximum conductance occurred during the late spring and summer time. *B. utilis* maintained high morning conductance during late spring and summer time. *B. utilis* appears to make maximum use of the late spring and summer season and maintained high morning leaf conductance. In *R. arboreum* the morning conductance ranged between  $44.43 \pm 1.15$  and  $216.0 \pm 3.79 \text{ mmol m}^{-2} \text{ sec}^{-1}$  which are comparable with the range 28 to  $219 \text{ mmol m}^{-2} \text{ sec}^{-1}$  reported by Poudyal *et al.* (2004) and Tewari (1998).

To conclude, it is apparent from the study that water potential does not reach lethal level to curtail phenological and physiological activities in TLS. All the species could reduce their osmotic potential and maintain a favorable water potential gradient from the soil to the tree which assists in absorption of water particularly during the growing season. Among TLS, *R. campanulatum* has a weaker osmotic adjusting capacity and deciduous *B. utilis* makes maximum use of the period during which it has leaves as evident from its higher leaf conductance. At the low altitudinal sites the species faced relatively more severe water deficit than the treeline species with  $\Psi_{pd}$  declining up to  $-1.8$  MPa in the canopy species and  $-2.2$  MPa in undercanopy species. In the majority of species osmotic adjustment was between winters and late spring when soil moisture had started to decline and warming had commenced, with the initiation of phenological activities. The shallow rooted undercanopy species showed larger osmotic adjustment than the canopy species. All the species kept their  $\Psi_{pd}$  well above the critical level ( $-1.0$  MPa) at the time of leaf production. Several factors contribute to maintain high turgor at the time of leaf production such as osmotic adjustment, brief spell of rain storms and reduction in leaf foliage mass. With rising temperature due to global warming and enhanced evapo-transpiration rate the LES may face severe water deficit over the next few years. The young individuals would be more severely affected as they grow in the harsh micro environment affecting regeneration of the species.

## Acknowledgement

The authors are thankful Prof. S. P. Singh, Coordinator, NMHS-IHTRP for his constant

guidance and valuable inputs in improving the content of this manuscript, Head, Department of Forestry & Environmental Science, D.S.B. Campus, Kumaun University, Nainital for providing laboratory facilities. The Financial support received from National Mission on Himalayan Studies (NMHS), Ministry of Environment, Forest and Climate Change, Government of India, is gratefully acknowledged.

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