

**SEASONAL VARIATIONS IN GAS EXCHANGE AND
PLANT WATER RELATIONS IN *QUERCUS
SEMECARPIFOLIA* IN SUBALPINE FORESTS OF THE
CENTRAL HIMALAYA**

मध्य हिमालय के उप अति-उच्च पर्वतीय वनों में *क्वारकस सेमीकारपीफोलिआ* में
वायवीय विनिमय एवं पादप जल संबंध में ऋतुवीय परिवर्तन

Thesis submitted to Jawaharlal Nehru University for the award of degree of

MASTER OF PHILOSOPHY

By

AMBUJ MISHRA



Under supervision of

PROF. SATISH CHANDRA GARKOTI

SCHOOL OF ENVIRONMENTAL SCIENCES, JAWAHARLAL NEHRU
UNIVERSITY NEW DELHI, INDIA-110067

2021

Certificate 1

Certificate 2

**With the blessings of the goddess of knowledge,
Jagat Janani Maa Saraswati:**



**सरस्वति महाभागे विद्ये कमललोचने ।
विद्यारूपे विशालाक्षि विद्यां देहि नमोऽस्तु ते ॥**

Obeisance to the mighty Himalaya:



अनन्तरत्नप्रभवस्य यस्य हिमं
न सौभाग्यविलोपि जातम् ।
एको हि दोषो गुणसन्निपाते,
निमज्जतीन्दोः किरणेष्विवाङ्कः ॥

ACKNOWLEDGEMENT

First I am thankful to the Almighty Maa Saraswati, Goddess of knowledge and wisdom for giving me the strength to have successfully completed my MPhil dissertation work.

*I would love to express my gratitude to my mother **Smt. Meenakshi Mishra**, my father **Shri Umakant Mishra**, my elder sister **Richa Mishra**, younger brother **Ankur Mishra** without their unbelievable support, encouragement and sacrifice; I would never come so far. Their trust gives me new strength to lead such a beautiful life.*

*I give me immense pleasure to acknowledge my heartiest thanks to my supervisor **Prof. Satish Chandra Garkoti**, Professor, school of Environmental Sciences, Jawaharlal Nehru University, New Delhi; for his unparalleled and excellent guidance. Not only his guidance fostered my brain to think towards the result oriented way, also his constant inspiration and persistent enthusiasms have enabled me to complete my dissertation work.*

*I am thankful to **Prof. Umesh Kulshrestha**, Dean, School of Environmental Sciences, JNU for providing me facilities and support during the course of my dissertation work.*

*It am thankful to **Prof. Krishna Gopal Saxena**, Professor, SES, JNU for his valuable ideas, guidance and, encouragement given to me and providing great support each and every time whenever I need him. He was also Advisory Committee (RAC) member for my M.Phil.*

*I express my heartfelt, warmest and humble thanks to **Prof. Jayant Kumar Tripathi**, Professor, SES, JNU for providing his constant encouragement and support, not only as a teacher but as guardian as well.*

*I want to express my thanks to **Dr. Toolika Prasad**, Assistant professor, AIRF, JNU for her support and guidance as Research Advisory Committee (RAC) member for my MPhil.*

*It is with fathomless gratitude that I express my benevolent thanks to **Mr. Balbir Panwar** for providing logistic and all necessary support during field work.*

*It is extremely important to mention my heartiest gratitude toward the companions of my extremely regressive and tough field work along with the lab work and writings, **Mr. Rajendra Joshi and Mr. Rajman Gupta** providing me constant encouragement and great moral support every time. We ate, worked and slept together even in limited resources at field work by encouraging each other for the optimum output. We generated, shared and executed our ideas together for the better research study.*

*I also want to thanks my lab mates, **Anand Shanker, Priya Hansda, Shailendra Kumar, Dr. Mukesh Kumar, Padma Ladon, Shipra Singh, Pinki Doley and Dr. Deepak Chaudhari** who provided healthy and fearless working and learning environment which was very helpful in carrying out my dissertation work.*

I am also thankful to all faculty members of SES, JNU for their constant support advised they have rendered to me whenever I needed.

*I extend my special thanks to **Mr. Amit Kumar Patel, Saurabh Singh, Mudita Chaturvedi, Akanksha** who provided healthy and fearless working and learning environment which was very helpful in carrying out my dissertation work.*

*I avail this opportunity to thank Administrative Officer, SES, JNU; **Mr. Vinod Kumar and Mr. Kunal** and all the office staff for providing the necessary official support and facility.*

*I want to thank **DFO, Kedarnath Wildlife Sanctuary, Uttarakhand and Forest Department, Uttarakhand** for providing the necessary permission and help while doing my field work.*

*It is with deep sense of affection and love; I would like to thank friends **Priya, Kalyan Biswal, Manjul, Chetan, Deepika, Sheshmani, Kavya and Vishwas Kukreti** for their invaluable support, guidance and encouragement which have has made my living experience in JNU a really pleasant one.*

Last but not the least, it goes without saying, the indebted to a number of friends and well wishers who have extended their cooperation and help in preparation of this thesis. Thank you and all.

Ambuj Mishra

Date:.....

Contents

1. Introduction	2
2. Objective	11
3. Material and Methods	13
3.1. Site description	13
3.2. Sampling design and Methodology	15
3.2.1. Ecophysiological traits measurements	16
3.2.2. Soil Moisture	17
3.2.3. Chlorophyll estimation	18
3.2.4. Statistical analysis	18
4. Results	20
4.1. Diurnal and seasonal variations in environmental variables	20
4.2. Influence of seasonality and varying light environments on leaf gas exchange	22
4.3. Diurnal variation of leaf gas exchange	25
4.4. Influence of seasonality in varying light environments on water potential	28
4.5. Influence of seasonality and varying light environments on Chlorophyll content.	30
5. Discussion	33
5.1. Influence of seasonality and varying light environments on gas exchange	33
5.2. Diurnal variations of gas exchange in varying light environments	34
5.3. Influence of seasonality and varying light environments on plant water potential ...	37
5.4. Influence of seasonality and varying light environments on Chlorophyll content and its relation with the plant's adaptive strategy to optimize photosynthesis.	38
6. Conclusion.	42
7. Annexure	45
Photo plate:	45
8. Reference	47

LIST OF FIGURES

Figure 1 Mean monthly precipitation and temperature in the study area.	13
Figure 2 Location map of study area.....	15
Figure 3 Diurnal seasonal variation of photosynthetic photon flux density (PPFD).....	21
Figure 4 Diurnal seasonal variation in rate of photosynthesis (A_{max}).....	24
Figure 5 Diurnal seasonal variation in transpiration rate (E).	24
Figure 6 Diurnal seasonal variation in stomatal conductivity (gsw).	25
Figure 7 Diurnal seasonal variation in C_i/C_a	27
Figure 8 Diurnal seasonal variation in leaf temperature (T_{leaf}).	27
Figure 9 Seasonal variation in plant water potential (Ψ) at predawn (pd) and mid-day (md).....	28
Figure 10 Seasonal variation in chlorophyll a, b, total chlorophyll and chlorophyll a/b.	31
Figure 11 Photo Plate.....	45

LIST OF TABLES

Table 1 Seasonal variation in maximum rate of photosynthesis (A_{max}), rate of transpiration (E), stomatal conductivity (gsw), ratio of intercellular CO_2 and atmospheric CO_2 (C_i/C_a), leaf water potential at predawn (Ψ_{pd}) and at mid-day (Ψ_{pd}) among two varying light environments, S and N.....	23
Table 2 Seasonal variation in soil moisture (in %) for <i>Q. Semecarpifolia</i> among two varying light environments, S and N..	29

1.INTRODUCTION

1. Introduction

Forests are the important land resource, provide food and shelter to animal species, provide watershed protection, avert soil erosion, improve the quality of the environment and mitigate climate change (Sabogal et al., 2015). As per the recent report by FAO and UNEP (2020), forests form 4.06 billion hectares (31 percent) of the global land area, distributed unequally around the world, with large variations in their structure and function. Forests are variably sensitive to environmental factors due to their distribution along dissimilar and complex topographical landscapes with the wide variations in species composition, environmental conditions, and availability of resources (Cantlon, 1953; Pook and Moore, (1966); Bale and Charley, 1994; Xu et al., 2020; Murphy et al., 2021). Despite the evidences of the effect of topography on forest systems at landscape level, only few reports are available regarding the impact of varied topography on physiology and tree growth within catchment areas of the mountain ecosystem. The topographic influence of topoclimate and catchment hydrology may certainly play a significant role in shaping forest feedback to future climate conditions. Topoclimates construct habitats that may either buffer against unfavorable geographic climate circumstances (microrefugia) or intensify climate stress even in the presence of suitable conditions. Particularly, due to highly uneven topography and strong elevation gradient in the mountain ecosystem, the potential variations in soil moisture availability and other physiochemical characteristics-timing, and form of precipitation, shape the structure and function of the forest (Pelletier et al., 2018; Murphy et al., 2021).

Temperature and moisture conditions are well known to change across the topographic positions. As a result, sites with varying topographical attributes endorse a diverse range of forest

types (Wang et al., 2019). The Impact of inter-seasonal variability of precipitation, air temperature, humidity, and soil moisture on forest productivity, is associated with the topographic variability (for instance hill-slope position, slope, and aspect), results in expected differences in the incoming solar radiation (Rosenberg et al., 1983; Desta et al., 2004; Bennie et al., 2008; Pelletier et al., 2018; Murphy et al., 2021). Stephenson, (1990); Hinckley et al., (2014) and Yetemen et al., (2015) postulate, in the northern hemisphere, equator facing, southern aspect experience rapid and early snow melt along with relatively faster and early soil drying in the growing season than pole facing, north aspect. This is due to more directly striking incoming solar radiation in the southern aspect than the north one; such that, it enhances the evaporation rates in the southern aspect, hence, causes relatively more water stress conditions compared to northern aspect. Similarly, Desta et al., (2004), Gutiérrez-Jurado et al., (2006) and Geroy et al., (2011) observed the impact of varying incoming solar radiation on soil water retention and storage in varying slope aspects. Further, regional and microclimatic dissimilarities also cause variability in the incoming solar radiations, which in turn result in variations in composition of forest community, species distribution along elevation gradient and forest productivity (Whittaker and Niering, 1965; Coblenz and Riitters, 2004; Måren et al., 2015; Murphy et al., 2020). Murphy et al., (2020) observed and indicated that solely abiotic factors are not responsible for the aspect-based differences in the soil water availability, but the complex interactions between the biotic and abiotic factors together with canopy and geologic construction also influence availability of soil moisture. Furthermore, he postulated that seasonal shift in sun angle, air temperature, soil moisture and tree species influence the physiological performance of the plants, mediated by the differences in slope and aspect.

Topographic positions significantly influence the ecophysiological performances. Variation in topography offers microrefugia which can lead the environment alteration. As a result, topographic positions can affect the ecophysiological performances along with the other microclimatic variables, such as light, CO₂ concentration, water availability, temperature, available nutrients (Lüttge, 2008; Santanoo et al., 2019; Vincent, 2020). In addition, topographic heterogeneity causes irregularities in the photoperiod. Variation in photoperiod (day length) regulates the seasonal as well as microclimatic variations in environmental factors causing unevenness in physiological activities of the plants like leaf gas exchange and plant water relations (Keeling et al., 1996; Bauerle, 2012; Way and Montgomery, 2015; Barnard et al., 2017; Blackman, 2017; Huang et al., 2020), which in turn influence the growth and photosynthetic processes (Goulden et al., 1996; Randerson et al., 1999; Angert et al., 2005; Piao et al., 2008; Matthews et al., 2017). Therefore, topography is an important environmental factor which regulates the plant ecophysiological traits (leaf gas exchange and plant water relation).

Gas Exchange is a one of key physiological processes of a leaf that indicates the strength and growth patterns of the plant (Santanoo et al., 2019; Tankari et al., 2019). Leaf gas exchange parameters are highly variable set of plant ecophysiological traits that change diurnally and seasonally (Garkoti et al., 2000; Zobel et al., 2001; Garkoti et al., 2002; Garkoti et al., 2003; Ishida et al., 2010; Matthews et al., 2017; Santanoo et al., 2019), predominantly influenced with the several environmental factors such as photo period, intensity and quality of light, air temperature, relative humidity, soil water and nutrient availability (Lüttge, 2008; Urban et al., 2017; Santanoo et al., 2019; Vincent, 2020). These changes in environmental factors rapidly alters the rate of CO₂ uptake as well as other physiological (Matthews et al., 2017; Aspinwall et

al., 2021) and phenological traits (Wang et al., 2016; Wadgyamar et al., 2018; Lee et al., 2020) of the plant.

Plant physiological responses are interlinked and contribute to the plant's survival and productivity. For instance, stomata react to environmental cues by controlling the opening and closing of guard cells, which has two key functions; first is to allow the uptake of carbon dioxide; second to limit the loss of water due to evapotranspiration; by which it regulates the rate of photosynthesis and rate of transpiration simultaneously. Stomatal conductivity decreases to slow down water loss from the leaves during drought conditions (Slatyer, 1967) and frost drought stress (Kume and Tanaka, 1996; Garkoti et al., 2003; Poudyal et al., 2004; Cavender-Bares, 2007; Urban et al., 2017). This also responds negatively against rate of photosynthesis (Knapp and Smith, 1987; Tinoco-Ojanguren and Percy, 1993; Lawson et al., 2010; Lawson and Blatt, 2014; Arve et al., 2011) similarly.

There are several microclimatic factors that influence the functioning of stomata. Light and water are the predominantly regulating factor among all. When the light intensity is higher, the rate of photosynthesis rises to absorb more CO₂ and dissipate heat in response. When the luminosity is higher than the threshold, it causes overheating of the system, called non-photochemical quenching (NPQ) and subsequent exhaustion of the photosynthetic machinery (Miralles-Crespo et al., 2011). Such quick alterations in environmental factors result in diurnal variations in the ecophysiology of plants. Meanwhile it is important to know that the intensity of light, required to open stomata is very low as compared to the intensity required to start photosynthesis. The maximum stomatal conductance and photosynthesis observed to be highest

at mid-day when luminosity is highest and plants assimilate several folds higher CO₂ than released during respiration (El-Sharkawy & Hesketh 1965; El-Sharkawy et al., 1968).

For both broadleaf and conifers, Brodribb (1996) reported lower stomatal conductance for low water potential or water stress conditions. This limits the uptake of CO₂ from the atmosphere and declines the magnitude of the ratio of intercellular CO₂ concentration and atmospheric CO₂ concentration (C_i/C_a). But this scenario changes mysteriously when the magnitude of C_i/C_a increases with the continuation of such drier condition and stomatal conductivity approaches to zero. This may be due to respiration increases beyond the compensation point on the stomatal closer. Stomata, subsequently photosynthetic machinery, respond quickly to the changing light environment (Knapp and Smith, 1987; Pearcy, 1990; Barradas et al., 1994; Tinoco-Ojanguren and Pearcy, 1993; Kirschbaum et al., 1998; Lawson et al., 2003).

Plant water potential provides understanding about the equilibrium between availability of soil water, the rate of evapotranspiration by the leaf, and the plant's ability to supply water, efficiently to the leaves (Bhaskar and Ackerly, 2006). Water potential responds quickly, according to the required changes in plant physiology and phenology to overcome the several unfavorable environmental changes by regulating stomatal and other related functions, and maintains plant survival so that plant may present optimum productivity (Garkoti et al., 2000; Zobel et al., 2001; Garkoti et al., 2002; Garkoti et al., 2003; Paudyal et al., 2004; Bargaliand Tewari, 2004; Singh et al., 2006; Tewari et al., 2016; Tewari et al., 2018). Besides the plant physiological health, measurement of water potential also provides clear clues of favorability of soil abiotic stress. Measurement of pre-dawn water potential indicates the soil water availability

and is a useful measure of plant water status (Reich and Hinckley, 1989). During the growing season plant shows lower leaf to atmospheric water deficit. Therefore, measurements of water potential for the growing season give substantially higher values (Anfodillo et al., 1998); while for several types of stress like drought (Abrams, 1990) and frost stress (Mayr et al., 2006; Urban et al., 2017) it gives lower water potential.

There are many reports available on the effect of topography, seasonality and microclimatic variables on leaf gas exchange and plant water relation from different forest systems (Pearcy, 1987; Goulden et al., 1996; Grossnickle et al., 2005; Piao et al., 2008; Ishida et al., 2010; Bauerle et al., 2012; Matthews et al., 2017; Urban et al., 2017; Santano et al., 2019; Mendes et al., 2020), Such studies are also available on various oak species (Gazal et al., 2009; Wolkerstorfer et al., 2011; Rodríguez-Calcerrada et al., 2012) globally in various mountain ecosystems.

Our knowledge related to variations of ecophysiological traits along the topography at the Himalayan Forest ecosystems is still limited. The Himalaya shares one fifth part of the India's total geographical area and primarily contributes to forest resource of the country. It is the youngest and highest mountain, vary in terms of seasonal, climatic, and ecological behavior to other mountain ecosystems of the world (Zobel and Singh, 1997, Singh and Singh, 1987). In fact, there are seasonal and climatic variations to a large extent in Himalaya itself due to vast topographical complexity and contrast. Because of which, contrasting sub-regions of the mountain system respond differently to even slight variation in the climate (Dad et al., 2021). Often the same forest ecosystem exhibits significant inter and intra-specific variability in environmental factors due to the formation of microclimatic zones in same catchment. Besides

this, in a same catchment of a mountain ecosystem of Indian Himalaya, inter-annual climate variability has also been reported consistently (Dimri, 2013; Sanwal et al., 2013; Hamal et al., 2020; Dad et al., 2021, Gutam et al., 2021).

Reported studies in Himalaya revealed that the contrasting slope aspects vary in received solar radiation (Ghimire et al., 2010; Paudel and Vetaas, 2014). In the Himalaya, south aspect is substantially warmer and soil drying is more rapid as a result of more incoming solar radiation than other aspects; subsequently governs the differences in forest composition, growth and photosynthetic productivity (Måren et al., 2015; Singh, 2018; Singh 2020). Many studies in Himalaya reported that north aspect exhibits relatively higher species diversity, forest density, growing stock and higher vertical allocation of forest (Måren et al., 2015; Singh 2018; Pandita et al., 2019; Singh 2020).

Limited information is available on the dynamics, growth patterns, and plant physiology of the Himalayan species in response to the above discussed microclimatic and seasonal variability.

In mid and higher elevations of the central Himalayas, oak species (*Quercus* spp.) are dominant vascular plants and form a major part of forest ecosystems (Singh and Singh, 1987; Zobel and Singh, 1997, Negi and Negi, 2021). *Quercus semecarpifolia* Sm., also known as Brown Oak, is a multipurpose tree species of ecological significance in the sub-alpine ecosystem in the Indian Himalaya, constituting a substantial part of the forests at elevation range between 2800 and 3700 m a.s.l. (Singh et al., 2021; Zobel and Singh, 1997). Singh et al. (1997) described this late successional species as greatest forest forming species in subalpine region of the Indian Himalaya.

The recent study by Negi and Negi (2021) reveals a significant increase in density of various oak species except for *Q. semecarpifolia*. It has been observed a vulnerable ecological status and failure of brown oak in the Himalaya due to huge decline of density and regeneration status (Singh et al., 1997; Negi and Rawal, 2017; Negi and Negi, 2021). Consequently, it becomes a matter of immediate concern to study the physiological responses of brown oak against several environmental changes to understand and implement various required forest management actions to conserve this forest-forming treeline species in sub-alpine Himalaya. Overall, our knowledge about the influence of topography on ecophysiology of central Himalayan native tree species *Q. semecarpifolia* is still limited.

2.Objective

2. Objective

The main aim of the present study was to understand the effects of topographic complexity on *Q. semecarpifolia*'s eco-physiological responses with seasonal variation in air, leaf temperature, photosynthetic photon flux density (PPFD) and moisture availability. To address this, we characterized the seasonal variation in leaf water potential and seasonal as well as diurnal variation in leaf photosynthesis in *Q. semecarpifolia* growing on north and south facing aspects with varying light environments in a same catchment of Kedarnath valley of the Central Himalaya. We hypothesized that the magnitude of plant physiological performance mediated by the differences in slope aspect and subsequently by light environment would vary with seasonal and diurnal shifts in sun angle, air temperature and soil moisture. We expected that, *Q. semecarpifolia* would maintain higher rates of leaf photosynthesis under higher light, warmer and drier conditions of south facing aspect than the contrasting north facing aspect.

- The specific objectives of our study was to investigate seasonal and diurnal changes in CO₂ assimilation rates, stomatal conductance and water potential of the subalpine evergreen broadleaf tree species, *Q. semecarpifolia* Sm., under varying light environments due to contrasting slope aspect.

➤

3.MATERIAL AND METHODS

3. Material and Methods

3.1. Site description

Present study was undertaken in the Chopta Tungnath forest area at elevation range of 2800 to 2950-m a.s.l. The study sites were located at the border of Rudraprayag and Chamoli districts at Chopta in Kedarnath Forest division (Kedarnath Wildlife Sanctuary). The study site is situated at 30°28'56.2"N latitude 79°12'43.9"E longitude in subalpine forest.

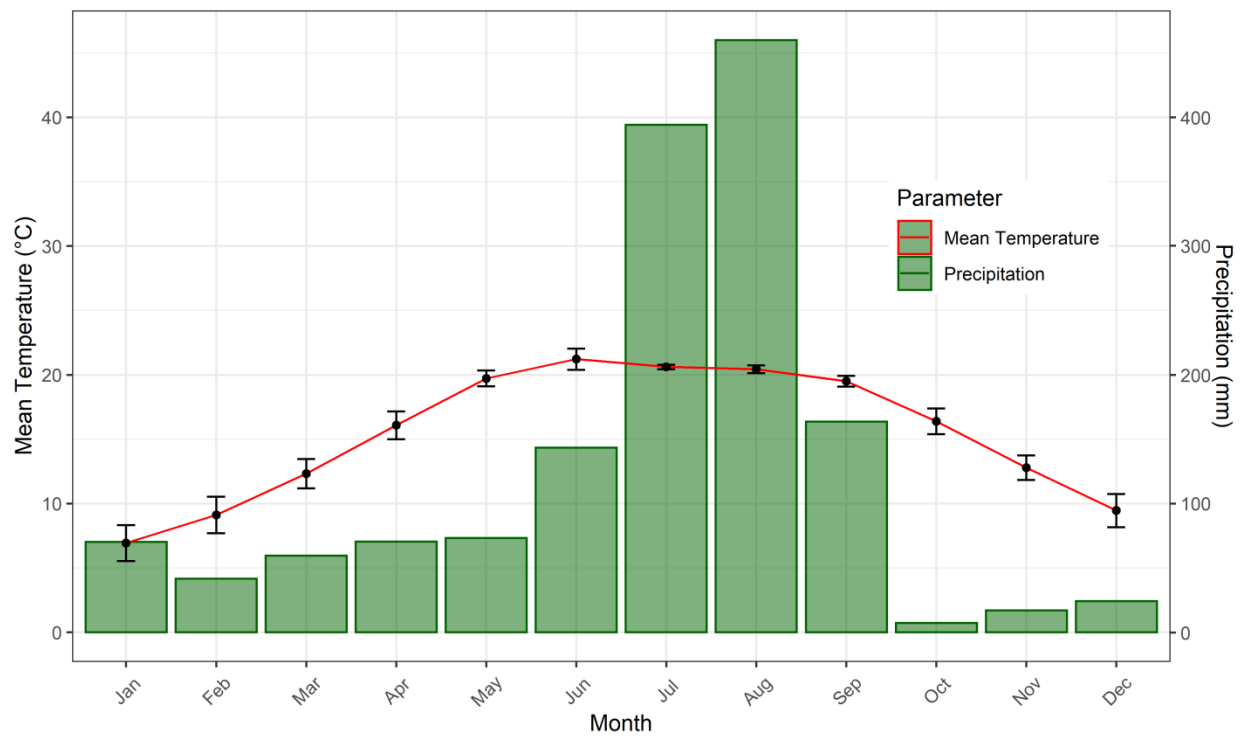


Figure 1 Mean monthly precipitation and temperature in the study area (daily precipitation data (obtained from IMD) for the year 2017 to 2020 has been obtained and averaged and monthly average temperature (from January 2011 to March 2021) has been obtained from European Copernicus Data Services (ECMWF ERA-5 data).

Climate of the selected study area is subalpine with snow fall from December to February. As per the stationed meteorological data by IMD (2017-2021), the study area receives 1525.18 ± 144.38 mm average annual rainfall (ranges between 1384.9 and 1684.4 mm from 2017-2020)

(Fig.1). Maximum rainfall occurs during monsoon (from mid June to late September) (460.03 ± 40.09 to 143.45 ± 79.86 mm average) (Fig. 1). Month of October to December consistently receive minimum values of precipitation (ranges between 24.13 ± 29.53 to 7.33 ± 13.52 mm) (Fig. 1). Rainy season accounts for one-third of the annually received rainfall. Mean annual relative humidity ranged from 15% to 86% (Gairola et al., 2010, Tewari et al., 2018). In the months of December, January and February the region is covered with snow, which sometimes extends till end of March. In the year 2019 and 2020 also, such extension of snow fall, till the month of March has been seen. January has minimum average day time temperature and considered as coldest month ($6.92 \pm 1.39^\circ\text{C}$, Fig.1). June is the warmest moth of the year with average day time temperature $21.21 \pm 0.82^\circ\text{C}$ (Fig. 1). May to September are comparatively warmer months in the year. Overall there are three main distinctly visible seasons; the cool-chilly winters (mid-November to March), the moderately hot but comparatively drier summer (mid-April to June); and wet but warm rainy season (July to September). Besides these key seasons, pragmatically there are the middle periods interconnecting rainy season with winter, likewise winter and summer reported as autumn (October to November) and spring (mid-February to mid-April). The snow melts during mid-March to mid-April, resulting in high soil moisture which supports regeneration and plant growth (Rai et al., 2010, Tewari et al., 2018).

There was 18 to 35 percent variation in slope with undulating topography and comparatively steeper slopes along with north and south aspects. The soil colour was brown-black and mainly podzolic and was usually gravelly. Occurrence of large boulders was common in the area. The study site lies in the central axis of the greater Himalaya. Rock type was metamorphic, including gneisses, granites and schist, which is also recognized as the central crystalline (Joshi and Garkoti, 2021).

The study area was dominated by *Quercus semecarpifolia*, a subalpine broad leaved tree species native to the Himalaya, and *Abies pindrow*, a multiyear coniferous species. *Rhododendron arboreum* was the majorly associated tree species of *Q. semecarpifolia* and *A. pindrow*.

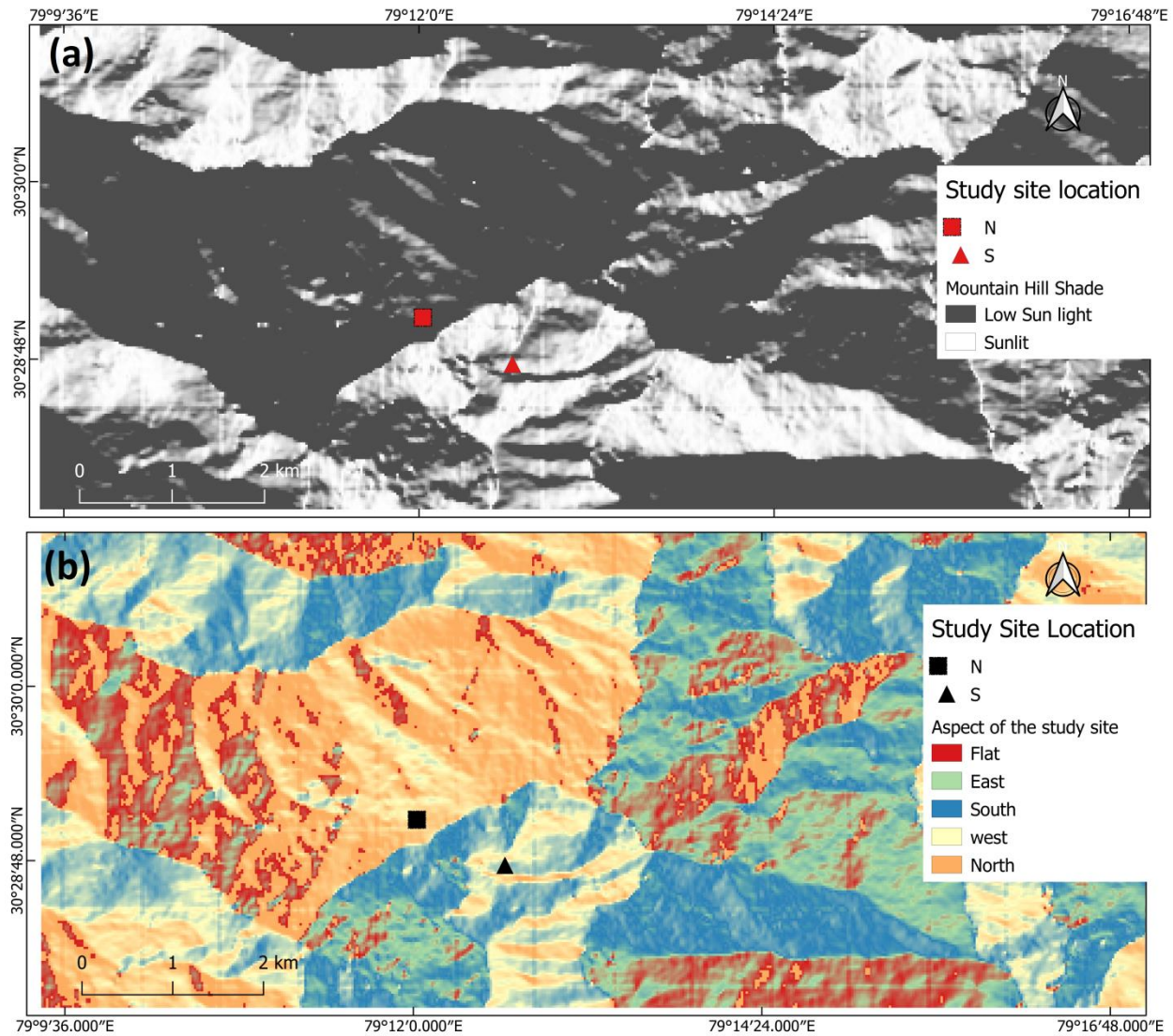


Figure 2 Location map of study area (a & b) showing aspects and low light and higher light sub-sites at Chopta, Tungnath.

3.2. Sampling design and Methodology

Reconnaissance of the study area has been done before start of the sampling and the two representative sites were selected; one in N and one in S aspect of the same catchment of the

mountain. We selected and tagged five- mature trees of *Q. semecarpifolia* on each of the both selected sites at the N and S aspect of the same catchment for all the ecophysiological trait measurements (Fig. 2 (b)). To minimize the age effect, in both the aspects the trees with same circumference at breast height (CBH, 80-120 cm) were selected and tagged,. The S aspect was well sun lit aspect with optimum light environment, while N aspect was less light receiving aspect with comparatively shorter photo period (day length) than the S (Fig. 2 (a)). Both the sites differed significantly on duration and timings of the sunshine. S aspect receives sunshine much early in the morning than the N, while N aspect where sunshine reaches late in the morning keeps receiving sunshine till sunset.

3.2.1. Ecophysiological traits measurements

3.2.1.1. Leaf Gas Exchange measurements

Leaf gas exchange measurements were performed on cloudless days for each sampling season. Total 5-9 fully expanded matured, sun-exposed, terminal canopy leaves were marked and tagged in each individual tree out of total 10 permanently tagged individual trees following Choat et al., (2006); Ishida et al., (2010) and Murphy et al., (2020).

Sun light intensity changed diurnally along the sampling seasons (Fig. 2). Diurnal trends of gas exchange measurements were recorded during 6am, 8am, 10am, 12pm, 2pm, 4pm and 6pm, by using instrument, IRGA (open circuit Infrared Gas Analyzer), Portable Photosynthesis System, Li-Cor 6800, Lincoln, NE, USA. Measurements were taken under natural condition of leaf temperature (T_{leaf} °C) and Photosynthetic Photon Flux Density (**PPFD**, $\mu\text{mol m}^{-2}\text{s}^{-1}$) with 6 cm² chamber of red-blue light emitting diodes of IRGA.

Diurnal leaf gas exchange parameters such as, leaf transpiration rate **E** ($\text{mmol H}_2\text{O m}^{-2}\text{s}^{-1}$), CO₂ assimilation rate or maximum photosynthetic rate **A_{max}** ($\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$), stomatal conductivity

g_{sw} ($\text{mol H}_2\text{O m}^{-2}\text{s}^{-1}$) and intercellular CO_2 concentration C_i ($\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$) were measured for Autumn, Winter, Spring and Summer, representing different leaf phenological stages. Ratio of C_i/C_a (intercellular and atmospheric CO_2 concentration) was calculated to evaluate stomatal acclimation.

3.2.1.2 Water Potential (ψ) measurement

Leaf predawn and midday water potential (Ψ leaf) was measured seasonally with a pressure chamber (Model 1000, PMS Instrument, Corvallis, OR). Three-Five sun-exposed terminal twigs (<15 cm long) were excised from the marked trees, among each ten (5 individual trees at N aspect and 5 individual trees at S aspect) tagged trees, and placed in sealed polythene bags before measurement of leaf water potential (Ψ leaf). The water potential (Ψ) was measured at predawn (Ψ_{pd}) at 5.30–6.00 am, and in the midday at 1.00–2.00 pm, (Ψ_{md}) following Garkoti et al., (2000); Zobel et al., (2001); Garkoti et al., (2002); Garkoti et al., (2003); Singh et al., (2006) and Tewari et al., (2018).

3.2.2. Soil Moisture

The soil moisture content was measured as a percentage dry weight with the gravimetric method by oven drying of soil till constant weight. For each season soil samples were taken from 5 representative locations from each of the both the selected aspects (S and N aspect) from three depths (0-10cm; 10-20cm; and 20-30). Immediately soil was kept in zip-lock poly-bags, sealed tightly and brought to laboratory for taking fresh weight. Samples were oven dried at 70°C till constant weight and soil moisture content was calculated following Jackson (1958) and Joshi and Garkoti, (2021):

$$\text{soil moisture (\%)} = \frac{\text{freshweight of soil} - \text{dryweight of soil}}{\text{dryweight of soil}} \times 100$$

3.2.3. Chlorophyll estimation

Chlorophyll content was estimated seasonally. 0.1 gram of 5-8 fresh leaf samples were taken (cleaned thoroughly and contaminations were removed) from each individual sample tree for Chlorophyll (Chlorophyll a, b and total chlorophyll) estimation. Chlorophyll content was estimated using dimethylsulfoxide (DMSO), following Hiscox and Israelstam (1979). Chlorophyll a and b concentrations were calculated using reading on spectrophotometer (Shimadzu UV-1201, Kyoto, Japan) at 665 nm and 645 nm, respectively (Barnes et al., 1992; Wellburn 1994). Total chlorophyll was calculated by adding the concentration of Chlorophyll a and b. We also calculated chlorophyll a/b ratio to check the brown oak's strategy and response against varying light environment (Niinemets, 2007; Yang et. al., 2016).

3.2.4. Statistical analysis

All statistical analysis was performed in programming language R (version 4.0) and MS-Excel 2007. Significant differences in leaf gas exchange, Water potential, leaf chlorophyll (a, b and total chl) content and soil moisture were tested with two way ANOVA (analysis of variance). Tukey post hoc analysis was carried out to determine the impact of season and aspect on the measured parameters. All the statistical analysis was performed after testing the normality and homogeneity of the data with log transformation, if required. All the numerical measurements were expressed in mean value \pm standard error/standard deviation. All analysis parameters were considered significantly different when $p < 0.05$.

4.RESULTS

4. Results

4.1. Diurnal and seasonal variations in environmental variables

We observed a significant difference of illumination in terms of PPFD between the studied aspects. N aspect experienced average 85-90% reduction in PPFD than the S aspect (Fig. 3). The data recorded for diurnal photosynthetic photon flux density (PPFD) provides a bell shaped and left-skewed bell shaped curve with significant difference (at $p < 0.05$) between the S and the N aspect, respectively for all the observed seasons. In the S aspect, the magnitude of PPFD started increasing from zero at pre-dawn and reached at its peak at 12 pm to 2 pm (mid-day) with maximum values and then continuously dropped sharply to minimum values (near zero) at evening 6 pm (Fig. 3). While in the N aspect the PPFD reached peaked at 4 pm then dropped sharply to near zero at 6 pm for all the studied seasons (Fig. 3). For both the aspects, recorded peak values of PPFD were consistently higher for summer season ($1945.76 \pm 125.12 \mu\text{mol m}^{-2}\text{s}^{-1}$ for S and $142.7 \pm 7.27 \mu\text{mol m}^{-2}\text{s}^{-1}$ for N); but the minimum values observed were recorded in autumn ($1274.76 \pm 79.07 \mu\text{mol m}^{-2}\text{s}^{-1}$) for S aspect and in winter ($43.48 \pm 2.69 \mu\text{mol m}^{-2}\text{s}^{-1}$) for N aspect (Fig. 3). Leaf temperature (T_{leaf}) followed the similar diurnal and seasonal trends with PPFD and across the seasons, significantly lower values of T_{leaf} were observed at N aspect than the S aspect (Fig. 8). Across the seasons, 40-50% reduction in T_{leaf} was observed at N aspect than the S. The temperature values were the highest at mid day and the lowest at early morning across the seasons and aspects (Fig. 8).

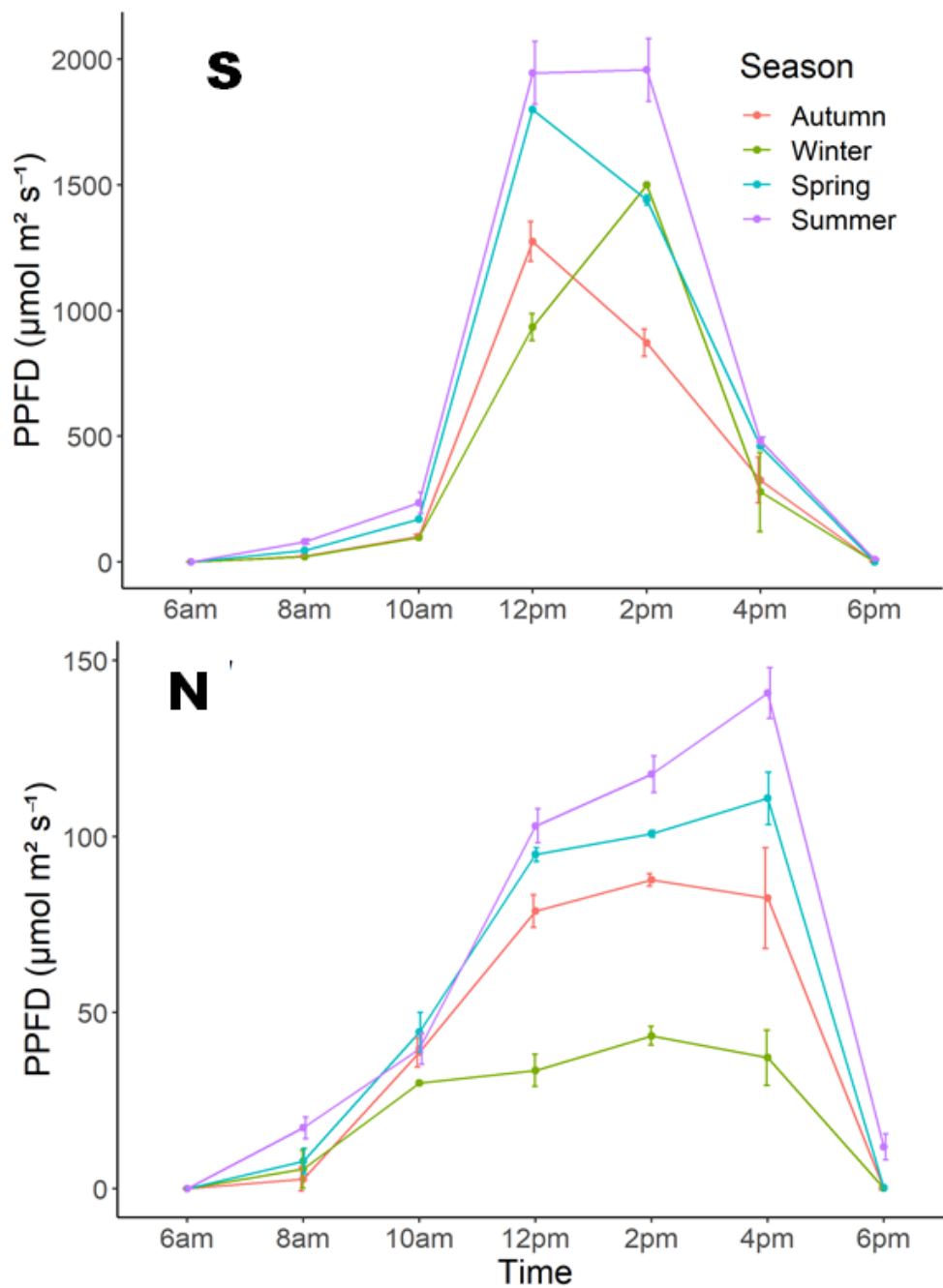


Figure 3 Diurnal seasonal variation of photon flux density (PPFD) in $\mu\text{mol m}^2 \text{s}^{-1}$, of two selected varying light environments (two different aspects), S and N. Values are in mean \pm sd.

4.2. Influence of seasonality and varying light environments on leaf gas exchange

Forest aspects resulting a significant illumination difference and prolonged exposure of leaves to different light intensities resulted in substantially different magnitude of ecophysiological parameters of the north and south aspect. The CO₂ assimilation or rate of photosynthesis (A_{\max} ; $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) was significantly higher ($p < 0.05$) in summer (9.99) followed by spring (7.43), autumn (6.67) and was lowest in the winters (5.68) in well sunlit aspect S (Table 1, Fig. 4). Approximately 50% reduction in photosynthetic rate was recorded in the winters than the summers in S aspect. Similar reduction between summer (4.09) and winter (2.62) was found in the N aspect which received relatively less photosynthetically active radiation (PAR). In N aspect, A_{\max} in spring (2.92) was significantly lower than the autumn (3.35) (Table 1, Fig. 4). Similar trends were observed in stomatal conductivity g_{sw} ($\text{mol H}_2\text{O m}^{-2} \text{ s}^{-2}$) and were significantly ($p < 0.05$) higher (Table 1, Fig. 6) in summer (0.078) followed by the spring (0.76) > autumn (0.75) and winter (0.037) in S aspect. Likewise in N with low light environment g_{sw} was significantly ($P < 0.05$) higher in summers (0.065) followed by spring (0.061), autumn (0.055) and winter (0.041). Transpiration rate (E) ($\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-2}$) significantly ($p < 0.05$) differed both in S and N aspects with values: summer (2.40), spring (2.20), autumn (1.9) and winter (0.69) in S aspect, and summer (1.2) and lower in winter (0.67); spring (0.88) and autumn (0.74) in N aspect (Fig.5). In both S and N aspects, C_i/C_a was significantly ($p < 0.05$) the higher in winter (0.68 and 0.88, respectively) and lowest in summer (0.52 and 0.82, respectively) (Fig. 7). But for N aspect, C_i/C_a found significantly ($p < 0.05$) higher than the S aspect for all the studied seasons (Fig. 7).

Light Environment	Season	A_{max}	E	gsw	Ci/Ca	Ψ_{pd}	Ψ_{md}
		$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	$\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$	$\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$		MPa	MPa
S	Autumn	5.75 ± 0.54 ^{Ac}	1.9 ± 0.39 ^{Ac}	0.075 ± 0.004 ^{Ac}	0.63 ± 0.06 ^{Bb}	-0.80 ± 0.02	-1.12 ± 0.04
	Winter	3.88 ± 1.19 ^{Ad}	0.69 ± 0.22 ^{Ad}	0.037 ± 0.0069 ^{Ad}	0.68 ± 0.09 ^{Ba}	-0.88 ± 0.02	-1.51 ± 0.02
	Spring	6.84 ± 0.44 ^{Ab}	2.20 ± 0.12 ^{Ab}	0.076 ± 0.0057 ^{Ab}	0.56 ± 0.02 ^{Bc}	-0.60 ± 0.02	-1.14 ± 0.02
	Summer	8.64 ± 0.96 ^{Aa}	2.40 ± 0.09 ^{Aa}	0.078 ± 0.0023 ^{Aa}	0.52 ± 0.01 ^{Bd}	-0.67 ± 0.02	-1.38 ± 0.04
N	Autumn	3.35 ± 0.59 ^{Bb}	0.74 ± 0.12 ^{Bc}	0.055 ± 0.012 ^{Bd}	0.85 ± 0.03 ^{Abc}	-0.72 ± 0.02	-1.07 ± 0.03
	Winter	2.62 ± 0.67 ^{Bd}	0.67 ± 0.082 ^{Bd}	0.041 ± 0.011 ^{Bb}	0.88 ± 0.03 ^{Aa}	-0.94 ± 0.01	-1.33 ± 0.05
	Spring	2.92 ± 0.80 ^{Bc}	0.88 ± 0.029 ^{Bb}	0.061 ± 0.011 ^{Bc}	0.86 ± 0.03 ^{Ab}	-0.54 ± 0.03	-1.02 ± 0.03
	Summer	4.09 ± 1.06 ^{Ba}	1.2 ± 0.27 ^{Ba}	0.065 ± 0.008 ^{Ba}	0.84 ± 0.03 ^{Ac}	-0.56 ± 0.02	-1.18 ± 0.02
Season		F = 113.520 <i>p</i> = ***	F = 216.60 <i>p</i> = ***	F = 110.08 <i>p</i> = ***	F = 107.07 <i>p</i> = ***	F = 1561.61 <i>p</i> = ***	
Light environment		F = 126.161 <i>p</i> = ***	F = 238.73 <i>p</i> = ***	F = 32.27 <i>p</i> = ***	F = 820.06 <i>p</i> = ***	F = 875.18 <i>p</i> = ***	

Table 1 Seasonal variation in maximum rate of photosynthesis (A_{max}), rate of transpiration (E), stomatal conductivity (gsw), Ratio of intercellular CO₂ and atmospheric CO₂ (Ci/Ca), leaf water potential at predawn (Ψ_{pd}) and at mid-day (Ψ_{md}) among two varying light environments S and N for *Q. semecarpifolia* is presented in the table. For all the shown parameters in the table, the optimum representative values are given. Different small letters given indicate the significant difference under four seasons, and the capital letter between the combination of two light environments at *p* value ≤ 0.05 using Tukey's HSD post hoc test. The values are in mean ± se of sample from the each combination of the treatment (Season-Light environments). Results of the variance test (two-way ANOVA) in terms of F value and *p* value at 95% confidence interval are given below the table separately for the combination of the season and light environment.

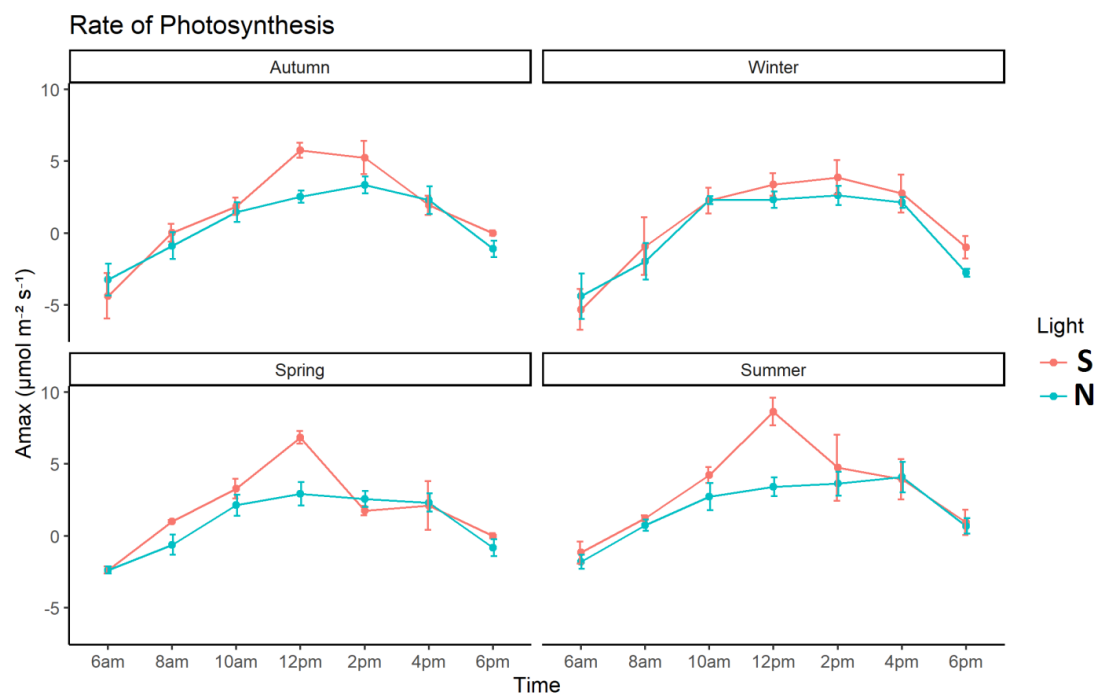


Figure 4 Diurnal seasonal variation in CO_2 assimilation rate (rate of photosynthesis) A_{max} for *Q. semecarpifolia* among two varying light environments, S and N. values are in mean \pm sd.

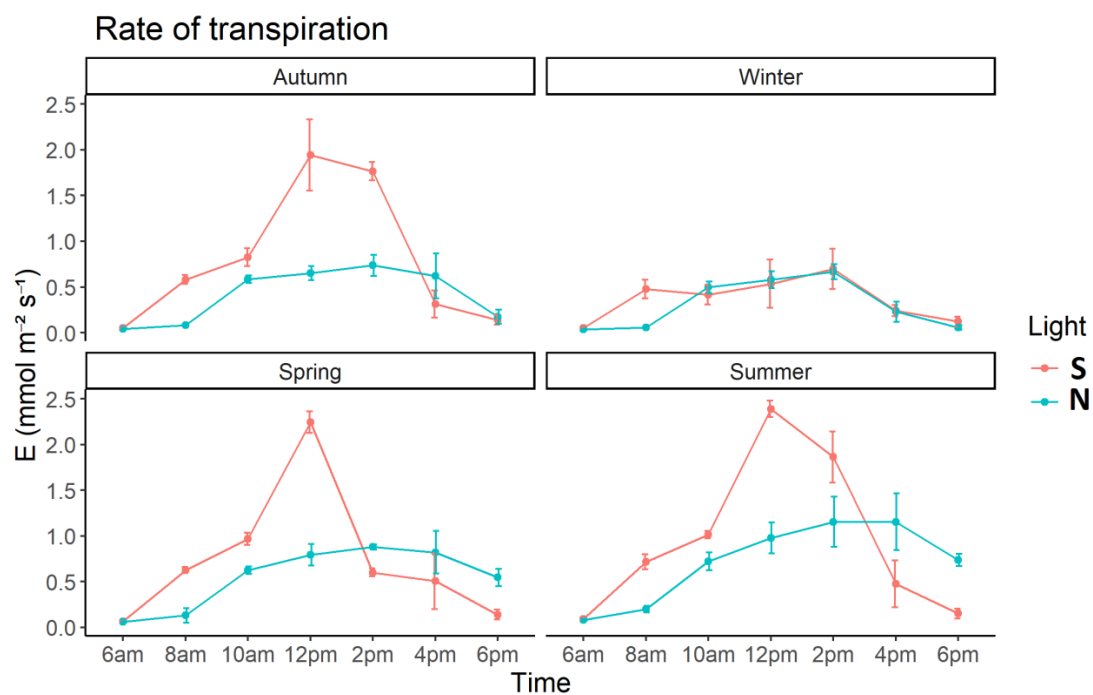


Figure 5 Diurnal seasonal variation in Transpiration rate (E) for *Q. semecarpifolia* among two varying light environments, S and N. values are in mean \pm sd.

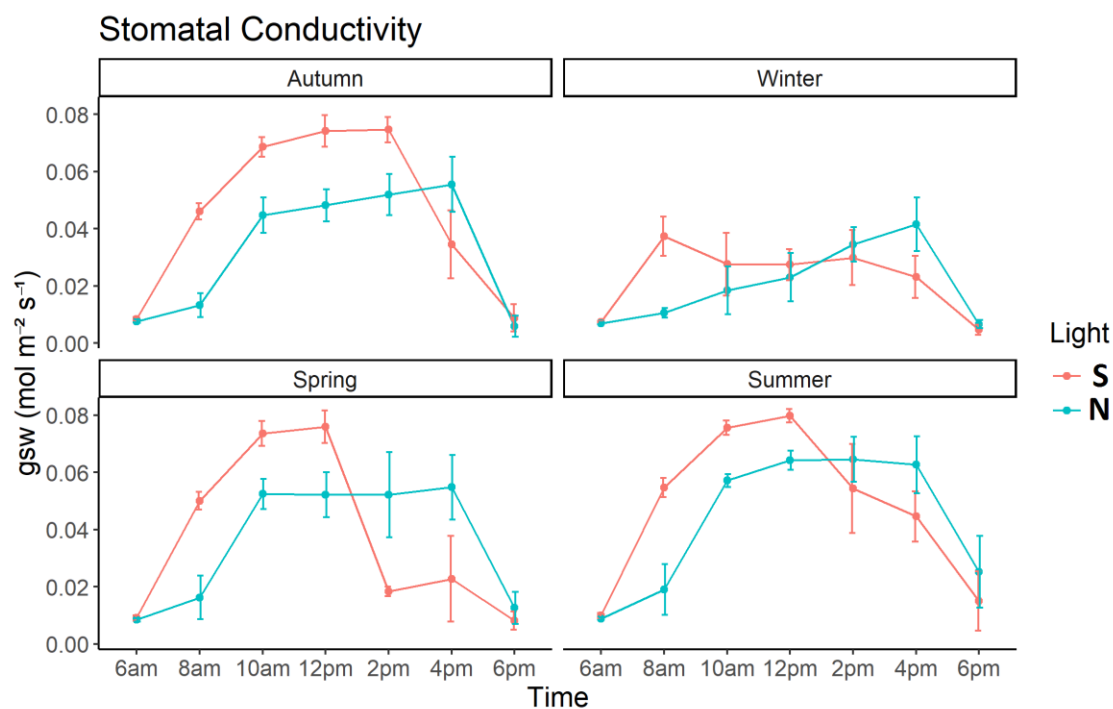


Figure 6 Diurnal seasonal variation in Stomatal Conductivity (g_{sw}) for *Q. semecarpifolia* among two varying light environments, S and N. values are in mean \pm sd.

4.3. Diurnal variation of leaf gas exchange

Diurnal A_{max} (Fig. 4), E (Fig. 5) and g_{sw} (Fig. 6) were highly influenced with the diurnal change in PPFD (Fig. 3). In S aspect, all the three parameters gradually increased and reached to maximum values at 12 pm during autumn, winter and summer. During winter maximum values were recorded at 2 pm. In aspect N, diurnal A_{max} (Fig. 4), E (Fig. 5) and g_{sw} values were higher at 4 pm, for all studied seasons except winter. In general, substantial difference between diurnal gas exchange parameters of both the studied aspects for all the observed seasons except winter. Diurnally, it was not observed comparatively much significant difference in gas exchange parameters (A , E , g_{sw}) between both the studied light environments for winter season (Fig. 4, 5 and 6, respectively). The A_{max} at S aspect decreased significantly from peak values at 12 pm to 2 and 6, respectively).

pm, (peak values of PPFD were also recorded at 12 pm for all studied seasons in S) during spring (at 12 pm: $6.48 \mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$; at 2pm: $1.74 \mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$) and in summer (at 12 pm: $8.64 \mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$; at 2pm: $4.37 \mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$) (Fig. 4). Similar patterns of decrease were found in E (Fig. 5) and gsw (Fig. 6) for the same aspect for spring and summer season. Post mid-day (4 pm and 6pm) values of A_{max} were either not significantly different between both the light environments, S and N (Fig. 4) in all the studied seasons. There was no significant difference in gas exchange parameters (A_{max} , E and gsw) in S and N aspects during early morning (6 am) and evening (6 pm) for all the seasons except E for spring and summer at evening (6 pm). The recorded values of E at 6 pm were significantly ($p < 0.05$) lower for S than the N for spring (0.14 and $0.55 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ for S and N respectively) and summer (0.15 and $0.74 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ for S and N, respectively) season. Post mid-day transpiration rate, E was significantly ($p < 0.05$) lower for sun lit light aspect S than the low light environment aspect N for all the seasons except winter (Fig. 5). Similar trends were recorded in gsw across the seasons except for 6 pm; it recorded no significant difference in gsw between S and N at 6 pm (Fig. 6). In winter season all the recorded gsw, post 8 am were significantly higher for N than the S, except 6 pm.

C_i/C_a ratios showed similar diurnal pattern for all the observed seasons, however, diurnally its magnitudes were significantly lower ($p < 0.05$) in aspect S aspect in comparison to the N aspect for all the seasons (Fig. 7). Diurnal patterns of C_i/C_a ratios were inverse bell shaped (Fig. 7) and inverse to the diurnal patterns of A_{max} , E and gsw (Fig. 4, 5 and 6, respectively). The ratio of C_i/C_a were significantly higher at predawn (≥ 2), compared to the mid-day (≤ 1) and post mid-day ($1.5 \geq 1$) (Fig. 7). Diurnally, lowest ratio of C_i/C_a were observed, when maximum CO_2 assimilation A_{max} was at its peak and gsw was highest. At pre-dawn, when PPFD (Fig. 3)

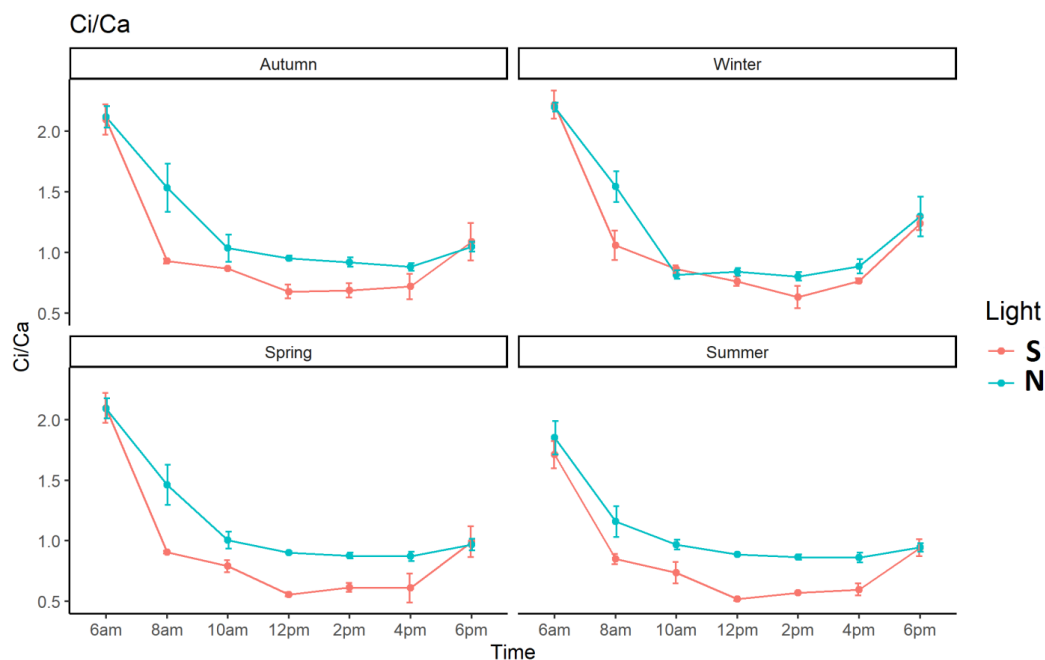


Figure 7 Diurnal seasonal variation in ratio between intercellular CO₂ concentration (Ci) and atmospheric CO₂ (Ca) concentration (gs/w) for *Q. semecarpifolia* among two varying light environments, S and N. values are in mean ± sd.

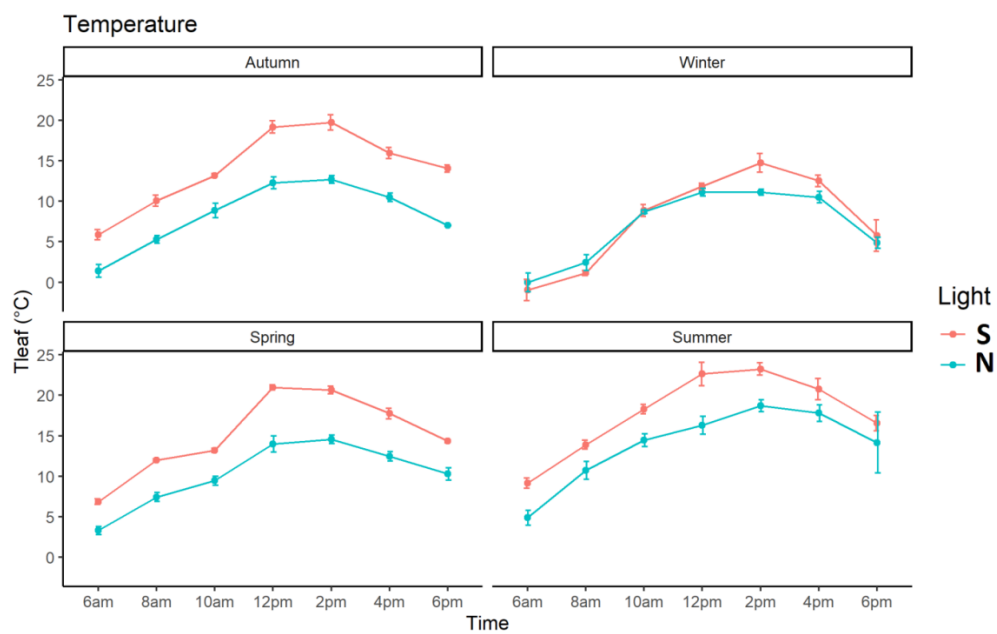


Figure 8 Diurnal seasonal variation in leaf temperature (T_{leaf}) for *Q. semecarpifolia* among two varying light environments, S and N. values are in mean ± sd.

approached to zero and stomata were still closed with near zero values of stomatal conductivity g_{sw} (Fig. 6), the exceptionally higher values of C_i/C_a were recorded (Fig. 7). All the gas exchange parameters were observed to be influenced with the diurnal trends of PPFD.

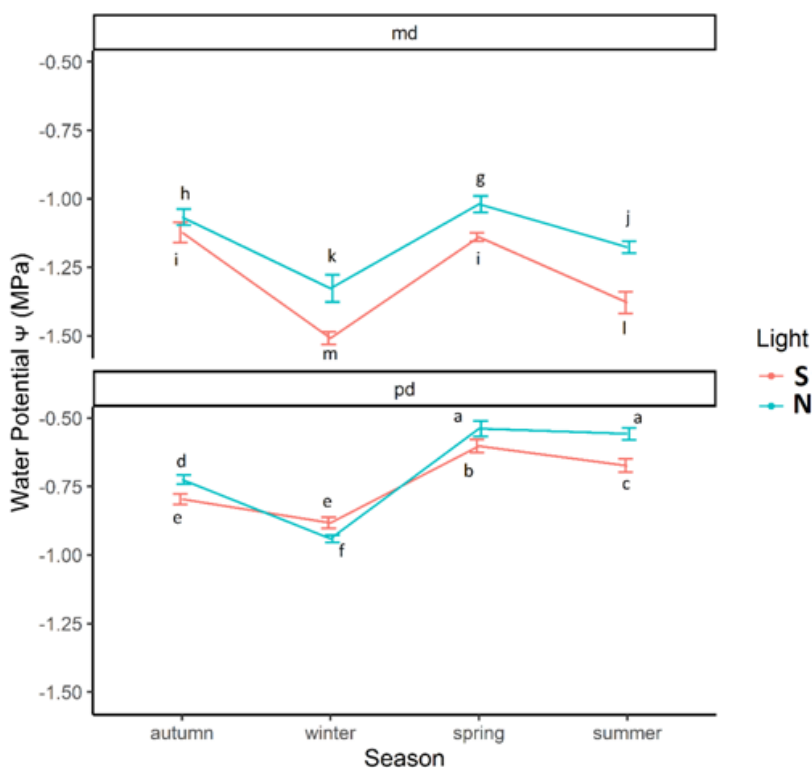


Figure 9 Seasonal variation in plant water potential (Ψ) at predawn (pd) and mid-day (md) for *Q. semecarpifolia* among two varying light environments, W and NE. values are in mean \pm se. Different letters indicated a significant difference under four seasons and two light environments (S and N) at p value ≤ 0.05 using Tukey's HSD post hoc test.

4.4. Influence of seasonality in varying light environments on water potential

Across the sites and seasons, plant water potential Ψ (MPa) for brown oak was significantly higher during the predawn than mid-day. In S aspect, the highest predawn Ψ (Table 1, Fig. 9) was recorded during spring season (-0.60), while the highest mid-day Ψ was found during autumn (-1.12). In N aspect, Ψ values during both predawn and midday were highest during spring season (-0.54 and -1.02, respectively). In both the aspects, the lowest predawn and midday

Soil Depth (S)	Autumn	Winter	Spring	Summer
0 to 10 cm	25.8±1.01	22.3±2.1	30.8±0.50	20.0±1.23
10 to 20 cm	26.2±0.64	25.5±1.72	25.1±1.24	23.8±0.5
20 to 30 cm	29.2±1.46	25.9±0.66	27.1±0.9	25.7±1.71
Soil Depth (N)	Autumn	Winter	Spring	Summer
0 to 10 cm	48.9±1.18	40.4±2.56	52.6±1.38	36.1±1.22
10 to 20 cm	36.7±2.06	37.3±2.01	47.3±1.82	39.9±1.17
20 to 30 cm	35.3±1.25	40.2±2.52	49.8±0.99	42.0±1.63

Table 2 Seasonal variation in soil moisture (in %) among two varying light environments, S and N. Values are in mean ± se, n = 5 for each depth per season for each light environment.

-water potential were recorded during winter (-1.51 and -0.88 in S aspect and(-0.94) and -1.33 in N aspect).

Overall, the following trends of plant water potential were observed during the study (Fig. 9):

Ψ predawn for S aspect was highest for spring, followed by summer, autumn and lowest for winter. Similarly the trends for N aspect were highest for spring, followed by summer, autumn and lowest winter. Trends of Ψ at midday for S aspect were autumn > spring > summer > winter; while for N aspect trends were: spring>autumn>summer>winter.

The soil moisture (Table. 2) was significantly higher in the N aspect than the sun lit aspect S. For both the studied aspects, spring was holding the highest soil moisture (N: 52.6 ± 1.38 ; S: 30.8 ± 0.50) followed by autumn (N: 48.9 ± 1.18 ; S: 25.8 ± 1.01) and winter (N: 40.4 ± 2.56 ; S: 22.3 ± 2.1), while summers observed lowest relative soil moisture (N: 36.1 ± 1.22 ; S: 20.0 ± 1.23) (Table. 2).

4.5. Influence of seasonality and varying light environments on Chlorophyll content

Substantial variations were recorded in leaf chlorophyll content (chlorophyll a, b, total chlorophyll and chlorophyll a/b) seasonally as well as with varying light environments (Fig. 10). Significantly higher ($p < 0.05$) chlorophyll content (chlorophyll a, b and total chlorophyll) was recorded in summer and the lowest in winter for both the studied aspects (Fig. 10). The observed trend of chlorophyll content was as follows: summer>autumn>spring>winter for both the studied aspects. The observed chlorophyll (Chlorophyll a, b and total chlorophyll) content was significantly ($p < 0.05$) higher in low light environment (N aspect) in comparison to the sun lit environment (S aspect)(Fig. 10). Significant decrease in chlorophyll a/b ratio was recorded in low light environment aspect N than the sun lit environment aspect S for all the studied seasons (Fig. 10).

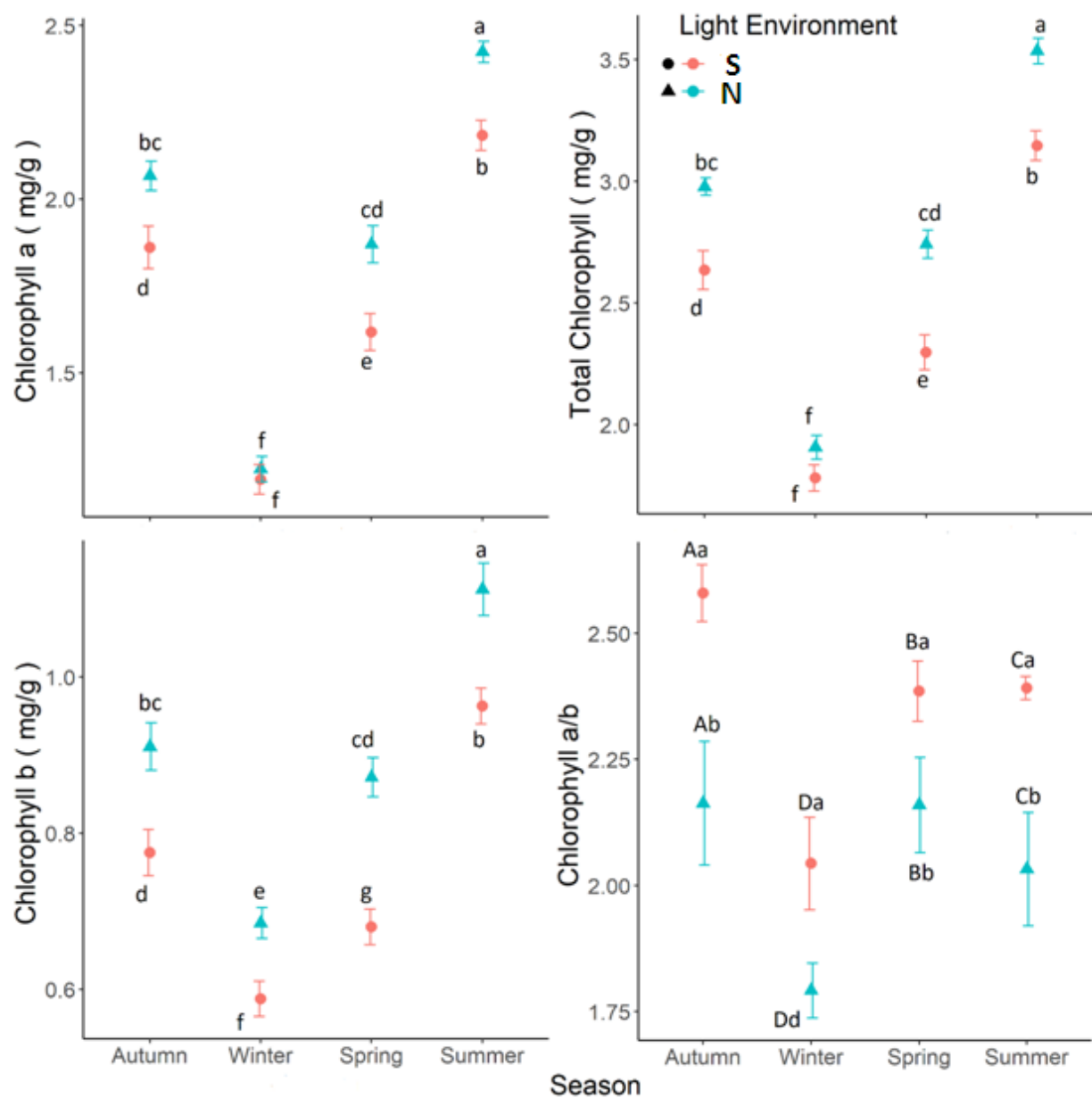


Figure 10 Seasonal variation in chlorophyll a, b, total chlorophyll and chlorophyll a/b (in mg/g) for *Q. semecarpifolia* among two varying light environments, W and NE. values are in mean \pm se. Different letters in chlorophyll a, chlorophyll b and total chlorophyll indicated a significant difference under four seasons and two light environments (S and N); for chlorophyll a/b the same capital letter represent the same combination and the different small letter indicate significant difference at p value \leq 0.05 using Tukey's post hoc test. Values are in mean \pm se ; n = 5 sample from each combination of the treatment (season- light environment).

5.DISCUSSION

5. Discussion

5.1. Influence of seasonality and varying light environments on gas exchange

In the present study spring and summer exhibited maximum photosynthetic rate (A_{\max}), transpiration rate (E) and stomatal conductivity (gsw)(Fig. 4, 5 and 6, respectively) due to the availability of optimum PPFD (Fig. 3) and optimum temperature (Fig. 8) for the subalpine oak, *Q. semecarpifolia*. Freezing winter exhibited lowest A_{\max} , E and gsw (Fig. 4, 5 and 6, respectively) due to subzero temperature at night and early morning along with below 15°C temperature at mid-day (Fig. 8). This is because; the chilling can disturb all vital constituents of photosynthesis including ETR (Electron Transport Reaction), subsequently Carbon reduction cycle and gsw (Frank et al., 1973). Paudyal et al., (2004) also reported the negative correlation of gsw of *Q. semecarpifolia* with low temperature and explained sensitivity of stomata with declined temperature. Moreover, declined leaf temperature decreases evaporative demand of the plants, results in altered E (Allen and Ort, 2007; Miralles-Crespo et al., 2011).

Higher C_i/C_a values (Fig. 7) in the winter indicated the season mediated response of stomatal activity. Winter rise in C_i/C_a values (Fig. 7) indicated the reduced activity of stomata in the cold temperature season and the higher stomatal activity in optimum temperature, resulted in lower values of C_i/C_a in summer. Xu and Baldocchi (2003) also reported the similar seasonal trends of the data for C_i/C_a (higher values in winter season). Rundel et al., (2002) elucidated the similar negative relationship between C_i/C_a and stomatal activity, along with the negative relationship of mid-day water potential with C_i/C_a . Magnitude of C_i/C_a was higher for low light aspect N (peak value of PPFD in N aspect was 142.7 ± 7.27 ; Fig. 3) than the sunlit aspect S (PPFD:

$1945.76 \pm 125.12 \mu\text{mol m}^{-2}\text{s}^{-1}$) across the seasons, which indicates negative relationship of Ci/Ca with light intensity and stomatal activity (Reindardt and Smith, 2016; Huang et al., 2021). Reports suggested that at low light, Ci/Ca exhibit the elevated values and show sharp reduction with the rise in the intensity of light till certain threshold, subsequently remains stagnant for any rise in intensity of light (Reindardt and Smith, 2016; Huang et al., 2021).

The present study revealed that seasonality plays a key role in dynamics of plant photosynthetic and other physiological traits. Overall, our data indicated that sunlight varied strongly with the seasons with more sun light in the summer than in the winter (Fig. 3), and with the difference being more pronounced in S aspect than the N (Fig. 3). All the observed plant eco-physiological traits in *Q. semecarpifolia* varied with the seasons and provided significantly higher magnitudes of plant ecophysiological traits (Fig. 4, 5 and 6) in S aspect due to the higher PPFD than the N of the same catchment. This indicated that the temperature and moisture are the important regulators of seasonal changes in leaf gas exchange; photoperiod and quality of light also predominantly modulates leaf activity and a major game changer in the productivity of the plant (Bauerle et al., 2012).

5.2. Diurnal variations of gas exchange in varying light environments

During all the sampling seasons, and both the studied aspects (S and N) diurnal ecophysiological activity was observed maximum at mid-day, particularly at S aspect. High influence of available light (Fig. 3) was clearly recorded in the diurnal data of the each observed season. Rise and fall of the rate of photosynthesis A_{max} (Fig. 4) was proportional to the rise and fall of PPFD (Fig. 3), along with the similar change in E (Fig. 5) and gsw (Fig. 6), for both the light environments (S and N aspects). This clearly indicated that the light played as a key factor in the productivity

differences in the different light environments at different time of the day. Both the studied light environments S and N aspects were highly different in quality and amount of the available light in similar season (Fig. 3), therefore, differed substantially in soil moisture (Table. 2) (Palhares et al., 2010; Flexas et al., 2012), air temperature (Taiz & Zeiger 2013), leaf temperature (Fig. 8) (Smith and Berry, 2013), humidity and leaf water deficits. Consequently plant varied substantially in A_{max} , E, gsw and leaf water potential Ψ (Fig. 9) (Pearcy and Sims, 1994; Pearcy et al., 1994; Pallardy, 2010; Ribeiro et al., 2018).

In spring and summer season, the received PPFD was greater (Fig. 3) among all the sampling seasons. For well sunlit environment S aspect in spring and summer season, it observed the mid-day depression in the rate of photosynthesis (Fig. 4), the E (Fig. 5) and gsw (Fig. 6), subsequent to the peak gas exchange at the window when the received PPFD (Fig. 3) was highest of the whole day. This was due to the fact that the primary photochemical reactions of PSII and PSI takes place at a much faster rate than ET (Electron Transport) and leaf's metabolism, when the plants is subjected to receive the excess light energy that of needed for photosynthesis. This leads to an energy imbalance between supply and demand for electron transport end products, generally results in photo-inhibition (Osmond, 1994; Miralles-Crespo et al., 2011; Bayat et al., 2018). This photo-inhibition is characterized by decline in quantum efficiency (number of moles, carbon-dioxide assimilated per mole photons absorbed) and ultimately decline in A_{max} (Osmond, 1987; long et al., 1994;). Raja Harun and Hardwick (1987) also reported the similar decline in photosynthesis in cacao leaves when continuously exposed to higher PPFD than full saturating photosynthetic intensity. Similar observations have also been reported and explained by several previous studies (Barber and Andersson, 1992; Aro et al., 1993; Vass et al., 2007; Pallardy, 2010; Gururani et al., 2015; Bayat et al., 2018). This sudden photo-inhibition and decline in gas

exchange may also be an early defense response against the oxidative damage due to continuous high light intensities (Vranová et al., 2002).

With the rise of the day, evaporative demand of the plant increases so the value of E (Fig. 5) also rises with the elevation in the value of PPFD (Fig. 3). With the higher values of PPFD, A_{\max} (Fig. 4) also grows higher and the stomatal conductivity increases (Fig. 6) to absorb more CO_2 from the atmosphere. Ci/Ca values (Fig. 7) are inversely related to the stomatal conductivity, g_{sw} (Brodribb, 1996). Therefore, high Ci/Ca ratio denoted the lower activity of stomata (Reindardt and Smith, 2016; Huang et al., 2021) and with zero approaching g_{sw} (Fig. 6). Generally, as intensity of light falls down, the utilization of carbon-dioxide for photosynthesis reduces. Similarly, the observed diurnal trends in Ci/Ca (Fig. 7) in the presented study indicated the inactivation or lower activity of stomata at early morning and evening with highest values of Ci/Ca and near zero values of A_{\max} , while highly active at mid-day with lowest values of Ci/Ca and highest A_{\max} (Reindardt and Smith, 2016; Huang et al., 2021). The majority of species open and close stomata during day time in response to the modifying abiotic or microclimatic environmental factors like light intensity, relative humidity and CO_2 concentration; for instance, it described above for the observed mid-day decline of g_{sw} along with the A_{\max} and E (Fig. 4, 5 and 6, respectively), in response to the highly saturated light condition at noon (Fig. 3). The study also represented the huge influence of different light environment along the different mountain aspect S and N on the Ci/Ca values and stomatal activity as it recorded significantly lower values of Ci/Ca in high light environment S than low light environment N, consistently throughout the day.

5.3. Influence of seasonality and varying light environments on plant water potential

Presented plant Ψ values were predominantly dependent on the aspect mediated environmental variables i.e., temperature, soil moisture, relative humidity and available PAR, which are also the key factor of the seasonal dynamics of environmental condition.

The observed leaf water potential (Fig. 9) for brown oak were highly varied during the day, seasons and aspects. Both, seasonality and varying light conditions (varying aspects) alter temperature and relative humidity (Everham III et al., 1996), subsequently modulates the water potential and impacts CO₂ assimilation and plant growth (Boyer, 1993; Choi et al., 2013; Vesala et al., 2017). Both, predawn and mid-day water potential were lowest (indicating high plant stress) in winter season (Table. 1; Fig. 9) in both the studied sunlit and low light aspect, S and N respectively, resulted in declined A_{max} . During winter, frozen soil water caused embolism and obstructed water uptake. Parallely, comparatively higher atmospheric temperature enhanced evaporation resulting in drier soil and constituted frost draught effect and lowered leaf water potential (Frank et al., 1973; Mayer et al., 2006). Winter decline in leaf water potential in the Himalayan oak species is also reported by many studies (Garkoti et al., 2000; Singh et al., 2006; Tewari et al., 2018). Most favorable and high water potential (Fig. 9) was noticed during the spring season because of the comparably higher availability of soil moisture (Table. 2) due to post winter snow melt (Rai et al., 2010). No season recorded water potential lower than -1.51 ± 0.02 , indicated no severe water stress in the plant, also reported by earlier study at the similar sites (Tewari et al., 2018). The moist soil due to the melting snow perhaps keeps the Ψ elevated above the threshold necessary for the commencement of phenological activities (Tewari, 1998). Consequently, spring and summer both represented the growing season in the subalpine area of the study site, due to optimum temperature (Fig. 8) and rise in water potential (Fig. 9); as in

growing season it reported low water deficit and elevated water potential (Anfodillo et al., 1998). Predawn (Ψ_{pd}) and midday (Ψ_{md}) water potential were significantly higher for N aspect than the S aspect (Fig. 9) across the seasons. This was due to the significantly higher soil moisture availability (Table. 2) and lower temperature (Fig. 8), as a result of lower sunlight (Fig. 3) in N aspect than the S. Similar impact of varying light environment on water potential has also been reported by Young and Smith (1980).

5.4. Influence of seasonality and varying light environments on Chlorophyll content and its relation with the plant's adaptive strategy to optimize photosynthesis.

During the measurements Chlorophyll a, b and total chlorophyll (Fig. 10) consistently exhibited the higher values in low light environment aspect N than the light saturated and sunlit environment S, throughout the studied four seasons, in spite of the 80-90% lower PPFD (Fig. 3) and substantially lower leaf temperature (Fig. 8). It indicated the well adaptive modifications made by *Q. semecarpifolia* to maximize the CO₂ assimilation rate, even in lower light environment. The frosty winters caused frost draught (Frank et al., 1973; Mayer et al., 2006) condition for plant, which disrupted photosynthetic system (Zhuang et al., 2019) of the plant along with the decline in the chlorophyll a, b and total chlorophyll (chl a+b) content in both the studied light environments (Fig. 10). Similar decline in chlorophyll content has also been reported in plants due to low temperatures by Zhao et al., (2020). It observed in the present study that, in spite of such severe frost damage to the photosynthetic machinery in the winter season at subzero temperature, brown oak acclimatized and adjusted the amount of chlorophyll content (Fig. 10) substantially higher in N than S; and maintained the plant's photosynthetic efficiency nearly 50% to the peak efficient summer season (Table. 1).

The observed chlorophyll allocation ratio a/b (Fig. 10) in the present study, was significantly reduced in N than S light environment consistently, across the seasons. It exhibited an adaptive strategy of leaves to varying light environments across varying microclimatic conditions (Li et al., 2018b). Shady light environment or understory possesses more defused and reduced blue-violet light (Ostrom, 2005; Li et al., 2018b). Both the chlorophyll, a and b possess well build light absorption potential but their absorption peaks are different. Chlorophyll a absorbs higher light in red band, while Chlorophyll b in blue-violet (Lichtenthaler and Buschmann, 2001; Li et al., 2018b). *Q. semecarpifolia* reduced the amount of chl b in leaves, to improve and maintain its CO_2 assimilation rate (Fig. 4) and productivity in the low light environment N, having lower in the amount of incident blue-violet light.

Chlorophyll a and b harvest the sunlight at different wavelengths and the most essential constituents of the primary reaction (which is the first and one of the important part of whole photosynthetic reaction). Amount of total leaf chlorophyll (a + b) content and its ratio of allocation (chlorophyll a/b) directly influence the photosynthetic efficiency of the plant (Croft et al., 2017; Li et al., 2018). Plants adjust the amount and allocation ratio of leaf chlorophyll content to rearrange and optimize the photosynthesis by optimizing the absorption of light, according to the modifying seasonal and microclimatic environmental (atmospheric temperature, humidity and light environment) factors (Zhang et al., 2007; Croft et al., 2015; Li et al., 2018a; Li et al., 2018b). As a result, leaf chlorophyll content is highly influenced with seasonality and light environment, and a great indicator of the plant's adaptive adjustments to optimize photosynthesis (Yang et al., 2016). The present study indicated the extent of the adaptive adjustments made by *Q. semecarpifolia* to optimize its A_{max} throughout the studied seasons, by

modifying the magnitude of chlorophyll a, b, total chlorophyll and chlorophyll allocation ratio a/b.

6.CONCLUSION

6. Conclusion.

The studies to model the forest response to environmental alterations comprise of landscape level processes, but generally exclude finer scale dynamics, which may be similarly significant to ecosystem functions of the forest (Murphy et al., 2020). The present study revealed aspect regulated finer scale variations in leaf ecophysiology, evidenced by increased CO₂ assimilation rate A_{\max} of *Q. semecarpifolia*, growing under higher light, warmer and drier conditions of S aspect relative to the contrasting N facing aspect of the same catchment, in the subalpine forest of the central Himalaya. The provided data puts in new information to where and when carbon and water fluxes on the landscape are dependent variably on multi-scale inter-linkages between biotic, abiotic, and temporal domains.

In general, the seasonality and aspect driven light environments both posed remarkable changes in the leaf ecophysiology (i.e. leaf gas exchange and plant water relation). While, the effect of variation in light environment was more pronounced and affected the overall productivity of the plants more severely. This marked effect of light environment also affected the leaf physiology and productivity diurnally. Consequently, photosynthesis also varied severely throughout the day with the diurnal variation of quality and intensity of light. It has also been realized throughout the study that photosynthesis and other leaf gas exchange parameters are highly variable and highly influenced with microclimatic environmental factors like, air temperature, soil moisture, relative humidity, light quality, intensity and duration. Therefore, while predicting the gross primary productivity (GPP), it needs to take more site-specific, time specific (diurnal) and season specific data to take more accurate and precise account of the forest productivity. The presented study also provides the important clue that brown oak adapts itself and adjusts its physiological

traits against several abiotic stresses to maintain its productivity higher. One more important finding of the study is that, optimum PPFD was the governing factor to optimize the photosynthesis of the plant, but above a saturation point or a certain threshold, it becomes light stress and impacts photosynthesis negatively.

Several traditional methods are available and being used to predict and calculate forest productivity in terms of GPP and rate of carbon sequestration. But, with most of those available methods, either it may over estimate or under estimate the same, ignoring the highly variable nature of photosynthesis along different season, time, climatic and microclimatic zones. By estimating such seasonal and diurnal variations in the ecophysiological functions at finer scale, it may provide more precise GPP in the changing climate of Himalaya.

7. Annexure

7. Annexure

Photo plate:



Figure 11 (a). Sampling with LiCor-6800, for leaf gas exchange measurements during winter. (b). Sampling with PMS 600 for plant water potential measurements. (c). After sampling time with the team. (d). During measurements of leaf gas exchange for spring season.

8. REFERENCES

8. Reference

- Abrams, M.D., 1990. Adaptations and responses to drought in *Quercus* species of North America. *Tree physiology*, 7(1-2-3-4), pp.227-238.
- Allen, D.J. and Ort, D.R., 2001. Impacts of chilling temperatures on photosynthesis in warm-climate plants. *Trends in plant science*, 6(1), pp.36-42.
- Anfodillo, T., Rento, S., Carraro, V., Furlanetto, L., Urbinati, C. and Carrer, M., 1998. Tree water relations and climatic variations at the alpine timberline: seasonal changes of sap flux and xylem water potential in *Larix decidua* Miller, *Picea abies* (L.) Karst. and *Pinus cembra* L. In *Annales des sciences forestières* (Vol. 55, No. 1-2, pp. 159-172). EDP Sciences.
- Angert, A., Biraud, S., Bonfils, C., Henning, C.C., Buermann, W., Pinzon, J., Tucker, C.J. and Fung, I., 2005. Drier summers cancel out the CO₂ uptake enhancement induced by warmer springs. *Proceedings of the National Academy of Sciences*, 102(31), pp.10823-10827.
- Aro, E.M., Virgin, I. and Andersson, B., 1993. Photoinhibition of photosystem II. Inactivation, protein damage and turnover. *Biochimica et Biophysica Acta (BBA)-Bioenergetics*, 1143(2), pp.113-134.
- Arve, L.E., Torre, S., Olsen, J.E. and Tanino, K.K., 2011. Stomatal responses to drought stress and air humidity. In *Abiotic stress in plants-Mechanisms and adaptations*. IntechOpen.
- Aspinwall, M.J., Juenger, T.E., Rymer, P.D., Rodgers, A. and Tissue, D.T., 2021. Intraspecific variation in plant responses to atmospheric CO₂, temperature, and water availability. In *Photosynthesis, Respiration, and Climate Change* (pp. 133-169). Springer, Cham.
- Baatz, R., Sullivan, P.L., Li, L., Weintraub, S.R., Loescher, H.W., Mirtl, M., Groffman, P.M., Wall, D.H., Young, M., White, T. and Wen, H., 2018. Steering operational synergies in terrestrial observation networks: Opportunity for advancing Earth system dynamics modelling. *Earth System Dynamics*, 9(2), pp.593-609.
- Bale, C.L. and Charley, J.L., 1994. The impact of aspect on forest floor characteristics in some eastern Australian sites. *Forest Ecology and Management*, 67(1-3), pp.305-317.
- Barber, J. and Andersson, B., 1992. Too much of a good thing: light can be bad for photosynthesis. *Trends in biochemical sciences*, 17(2), pp.61-66.
- Bargali, K. and Tewari, A., 2004. Growth and water relation parameters in drought-stressed *Coriaria nepalensis* seedlings. *Journal of Arid Environments*, 58(4), pp.505-512.
- Barnard, D.M., Barnard, H.R. and Molotch, N.P., 2017. Topoclimate effects on growing season length and montane conifer growth in complex terrain. *Environmental Research Letters*, 12(6), p.064003.

- Barnes, J.D., Balaguer, L., Manrique, E., Elvira, S. and Davison, A.W., 1992. A reappraisal of the use of DMSO for the extraction and determination of chlorophylls a and b in lichens and higher plants. *Environmental and Experimental botany*, 32(2), pp.85-100.
- Barradas, V.L., Jones, H.G. and Clark, J.A., 1994. Stomatal responses to changing irradiance in *Phaseolus vulgaris* L. *Journal of Experimental Botany*, 45(7), pp.931-936.
- Bauerle, W.L., Oren, R., Way, D.A., Qian, S.S., Stoy, P.C., Thornton, P.E., Bowden, J.D., Hoffman, F.M. and Reynolds, R.F., 2012. Photoperiodic regulation of the seasonal pattern of photosynthetic capacity and the implications for carbon cycling. *Proceedings of the National Academy of Sciences*, 109(22), pp.8612-8617.
- Bauerle, W.L., Oren, R., Way, D.A., Qian, S.S., Stoy, P.C., Thornton, P.E., Bowden, J.D., Hoffman, F.M. and Reynolds, R.F., 2012. Photoperiodic regulation of the seasonal pattern of photosynthetic capacity and the implications for carbon cycling. *Proceedings of the National Academy of Sciences*, 109(22), pp.8612-8617.
- Bayat, L., Arab, M., Aliniaefard, S., Seif, M., Lastochkina, O. and Li, T., 2018. Effects of growth under different light spectra on the subsequent high light tolerance in rose plants. *AoB Plants*, 10(5), p.p052.
- Bennie, J., Huntley, B., Wiltshire, A., Hill, M.O. and Baxter, R., 2008. Slope, aspect and climate: spatially explicit and implicit models of topographic microclimate in chalk grassland. *Ecological modelling*, 216(1), pp.47-59.
- Bhaskar, R. and Ackerly, D.D., 2006. Ecological relevance of minimum seasonal water potentials. *Physiologia Plantarum*, 127(3), pp.353-359.
- Bjorkman, O., 1965. Comparative physiological studies of ecological races of *Solidago*. *Yb. Carnegie Instn Wash*, 64, pp.415-20.
- Björkman, O., 1966. The effect of oxygen concentration on photosynthesis in higher plants. *Physiologia Plantarum*, 19(3), pp.618-633.
- Blackman, B.K., 2017. Changing responses to changing seasons: natural variation in the plasticity of flowering time. *Plant physiology*, 173(1), pp.16-26.
- Boyer, J.S., 1993. Temperature and growth-induced water potential. *Plant, Cell & Environment*, 16(9), pp.1099-1106.
- Brodribb, T., 1996. Dynamics of changing intercellular CO₂ concentration (ci) during drought and determination of minimum functional ci. *Plant physiology*, 111(1), pp.179-185.
- Brown, T.B., Hultine, K.R., Steltzer, H., Denny, E.G., Denslow, M.W., Granados, J., Henderson, S., Moore, D., Nagai, S., SanClements, M. and Sánchez-Azofeifa, A., 2016. Using phenocams to monitor our changing Earth: toward a global phenocam network. *Frontiers in Ecology and the Environment*, 14(2), pp.84-93.
- Cantlon, J.E., 1953. Vegetation and microclimates on north and south slopes of Cushtunk Mountain, New Jersey. *Ecological Monographs*, 23(3), pp.241-270.

- Cantlon, J.E., 1953. Vegetation and microclimates on north and south slopes of Cushetunk Mountain, New Jersey. *Ecological Monographs*, 23(3), pp.241-270.
- Cantlon, J.E., 1953. Vegetation and microclimates on north and south slopes of Cushetunk Mountain, New Jersey. *Ecological Monographs*, 23(3), pp.241-270.
- Cavender-Bares, J., 2007. Chilling and freezing stress in live oaks (*Quercus* section *Virentes*): intra-and inter-specific variation in PS II sensitivity corresponds to latitude of origin. *Photosynthesis Research*, 94(2), pp.437-453.
- Champion, H.G. and Seth, S.K., 1968. *A revised survey of the forest types of India*. Manager of publications. Government of India. pp.404.
- Choi, H.K., Iandolino, A., da Silva, F.G. and Cook, D.R., 2013. Water deficit modulates the response of *Vitis vinifera* to the Pierce's disease pathogen *Xylella fastidiosa*. *Molecular Plant-Microbe Interactions*, 26(6), pp.643-657.
- Coblentz, D.D. and Riitters, K.H., 2004. Topographic controls on the regional-scale biodiversity of the south-western USA. *Journal of Biogeography*, 31(7), pp.1125-1138.
- Croft, H., Chen, J.M., Froelich, N.J., Chen, B. and Staebler, R.M., 2015. Seasonal controls of canopy chlorophyll content on forest carbon uptake: Implications for GPP modeling. *Journal of Geophysical Research: Biogeosciences*, 120(8), pp.1576-1586.
- Croft, H., Chen, J.M., Zhang, Y. and Simic, A., 2013. Modelling leaf chlorophyll content in broadleaf and needle leaf canopies from ground, CASI, Landsat TM 5 and MERIS reflectance data. *Remote Sensing of Environment*, 133, pp.128-140.
- D'Ambrosio, N., Arena, C. and De Santo, A.V., 2006. Temperature response of photosynthesis, excitation energy dissipation and alternative electron sinks to carbon assimilation in *Beta vulgaris* L. *Environmental and experimental botany*, 55(3), pp.248-257.
- Dad, J.M., Muslim, M., Rashid, I. and Reshi, Z.A., 2021. Time series analysis of climate variability and trends in Kashmir Himalaya. *Ecological Indicators*, 126, p.107690.
- Desta, F., Colbert, J.J., Rentch, J.S. and Gottschalk, K.W., 2004. Aspect induced differences in vegetation, soil, and microclimatic characteristics of an Appalachian watershed. *Castanea*, 69(2), pp.92-108.
- Dimri, A.P., 2013. Interannual variability of Indian winter monsoon over the Western Himalayas. *Global and planetary change*, 106, pp.39-50.
- El-Sharkawy, M. and Hesketh, J., 1965. Photosynthesis among species in relation to characteristics of leaf anatomy and CO₂ diffusion resistances. *Crop Science*, 5(6), pp.517-521.
- El-Sharkawy, M.A., Loomis, R.S. and Williams, W.A., 1968. Photosynthetic and respiratory exchanges of carbon dioxide by leaves of the grain amaranth. *Journal of Applied Ecology*, pp.243-251.

- Everham III, E.M., Myster, R.W. and VanDeGenachte, E., 1996. Effects of light, moisture, temperature, and litter on the regeneration of five tree species in the tropical montane wet forest of Puerto Rico. *American Journal of Botany*, 83(8), pp.1063-1068.
- FAO and UNEP. 2020. The State of the World's Forests 2020. Forests, biodiversity and people. Rome. <https://doi.org/10.4060/ca8642en>
- Flexas, J., Barbour, M.M., Brendel, O., Cabrera, H.M., Carriquí, M., Díaz-Espejo, A., Douthe, C., Dreyer, E., Ferrio, J.P., Gago, J. and Gallé, A., 2012. Mesophyll diffusion conductance to CO₂: an unappreciated central player in photosynthesis. *Plant Science*, 193, pp.70-84.
- Frank, A.B., Power, J.F. and Willis, W.O., 1973. Effect of Temperature and Plant Water Stress on Photosynthesis, Diffusion Resistance, and Leaf Water Potential in Spring Wheat 1. *Agronomy journal*, 65(5), pp.777-780.
- Fritts, H., 2012. *Tree rings and climate*. Elsevier.
- Gairola, S., Sharma, C.M., Ghildiyal, S.K. and Suyal, S., 2011. Tree species composition and diversity along an altitudinal gradient in moist tropical montane valley slopes of the Garhwal Himalaya, India. *Forest Science and Technology*, 7(3), pp.91-102.
- Gairola, S., Sharma, C.M., Rana, C.S., Ghildiyal, S.K. and Suyal, S., 2010. Phytodiversity (Angiosperms and Gymnosperms) in Mandal-Chopta forest of Garhwal Himalaya, Uttarakhand, India. *Nature and Science*, 8(1), pp.1-17.
- Garkoti, S.C., Akoijam, S.B. and Singh, S.P., 2002. Ecology of water relations between mistletoe (*Taxillus vestitus*) and its host oak (*Quercus floribunda*). *Tropical Ecology*, 43(2), pp.243-249.
- Garkoti, S.C., Zobel, D.B. and Singh, S.P., 2000. Comparison of water relations of seedlings and trees of two Himalayan oaks. *International Journal of Ecology and Environmental Sciences*, 26, pp.213-222.
- Garkoti, S.C., Zobel, D.B. and Singh, S.P., 2000. Comparison of water relations of seedlings and trees of two Himalayan oaks. *International Journal of Ecology and Environmental Sciences*, 26, pp.213-222.
- Garkoti, S.C., Zobel, D.B. and Singh, S.P., 2003. Variation in drought response of sal (*Shorea robusta*) seedlings. *Tree physiology*, 23(15), pp.1021-1030.
- Gautam, D., Karki, J., Gaire, N.P., Roth, B.E., Bhattarai, S., Thapa, S., Sharma, R.P., Li, J., Tong, X. and Liu, Q.J., 2020. Intra-and interannual climate variability drives the radial growth of *Pinus wallichiana* in the Nepalese Himalayas. *Plant Ecology & Diversity*, 13(5-6), pp.391-400.
- Gazal, R.M., Kubiske, M.E. and Connor, K.F., 2009. Leaf gas exchange of mature bottomland oak trees. *Res. Pap. SRS-45. Asheville, NC: US Department of Agriculture Forest Service, Southern Research Station. 8 p., 45.*

- Geroy, I.J., Gribb, M.M., Marshall, H.P., Chandler, D.G., Benner, S.G. and McNamara, J.P., 2011. Aspect influences on soil water retention and storage. *Hydrological Processes*, 25(25), pp.3836-3842.
- Ghimire, B., Mainali, K.P., Lekhak, H.D., Chaudhary, R.P. and Ghimeray, A.K., 2010. Regeneration of *Pinus wallichiana* AB Jackson in a trans-Himalayan dry valley of north-central Nepal. *Himalayan Journal of Sciences*, 6(8), pp.19-26.
- Goulden, M.L., Munger, J.W., Fan, S.M., Daube, B.C. and Wofsy, S.C., 1996. Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. *Science*, 271(5255), pp.1576-1578.
- Grossnickle, S.C., Fan, S. and Russell, J.H., 2005. Variation in gas exchange and water use efficiency patterns among populations of western redcedar. *Trees*, 19(1), pp.32-42.
- Gururani, M.A., Venkatesh, J. and Tran, L.S.P., 2015. Regulation of photosynthesis during abiotic stress-induced photoinhibition. *Molecular plant*, 8(9), pp.1304-1320.
- Gutiérrez-Jurado, H.A., Vivoni, E.R., Harrison, J.B.J. and Guan, H., 2006. Ecohydrology of root zone water fluxes and soil development in complex semiarid rangelands. *Hydrological Processes: An International Journal*, 20(15), pp.3289-3316.
- Hamal, K., Sharma, S., Baniya, B., Khadka, N. and Zhou, X., 2020. Inter-annual variability of winter precipitation over Nepal coupled with ocean-atmospheric patterns during 1987–2015. *Frontiers in Earth Science*, 8, p.161.
- Hiscox, J.D. and Israelstam, G.F., 1979. A method for the extraction of chlorophyll from leaf tissue without maceration. *Canadian journal of botany*, 57(12), pp.1332-1334.
- Huang, J.G., Ma, Q., Rossi, S., Biondi, F., Deslauriers, A., Fonti, P., Liang, E., Mäkinen, H., Oberhuber, W., Rathgeber, C.B. and Tognetti, R., 2020. Photoperiod and temperature as dominant environmental drivers triggering secondary growth resumption in Northern Hemisphere conifers. *Proceedings of the National Academy of Sciences*, 117(34), pp.20645-20652.
- Huang, M.Y., Wong, S.L. and Weng, J.H., 2021. Rapid Light-Response Curve of Chlorophyll Fluorescence in Terrestrial Plants: Relationship to CO₂ Exchange among Five Woody and Four Fern Species Adapted to Different Light and Water Regimes. *Plants*, 10(3), p.445.
- Ishida, A., Harayama, H., Yazaki, K., Ladpala, P., Sasrisang, A., Kaewpakasit, K., Panuthai, S., Staporn, D., Maeda, T., Gamo, M. and Diloksumpun, S., 2010. Seasonal variations of gas exchange and water relations in deciduous and evergreen trees in monsoonal dry forests of Thailand. *Tree Physiology*, 30(8), pp.935-945.
- Jackson, M.L., 2005. *Soil chemical analysis: advanced course*. UW-Madison Libraries Parallel Press.
- Joshi, R.K. and Garkoti, S.C., 2021. Influence of Nepalese alder on soil physico-chemical properties and fine root dynamics in white oak forests in the central Himalaya, India. *Catena*, 200, p.105140.

- Keeling, C.D., Chin, J.F.S. and Whorf, T.P., 1996. Increased activity of northern vegetation inferred from atmospheric CO₂ measurements. *Nature*, 382(6587), pp.146-149.
- Kirschbaum, M.U.F., Gross, L.J. and Pearcy, R.W., 1988. Observed and modelled stomatal responses to dynamic light environments in the shade plant *Alocasia macrorrhiza*. *Plant, Cell & Environment*, 11(2), pp.111-121.
- Knapp, A.K. and Smith, W.K., 1987. Stomatal and photosynthetic responses during sun/shade transitions in subalpine plants: influence on water use efficiency. *Oecologia*, 74(1), pp.62-67.
- Knapp, A.K. and Smith, W.K., 1987. Stomatal and photosynthetic responses during sun/shade transitions in subalpine plants: influence on water use efficiency. *Oecologia*, 74(1), pp.62-67.
- Kramer, P.J. and Kozlowski, T.T., 1960. Physiology of trees. *Physiology of trees*.
- Kume, A. and Tanaka, C., 1996. Adaptation of stomatal response of *Camellia rusticana* to a heavy snowfall environment: Winter drought and net photosynthesis. *Ecological Research*, 11(2), pp.207-216.
- Lawson, T. and Blatt, M.R., 2014. Stomatal size, speed, and responsiveness impact on photosynthesis and water use efficiency. *Plant physiology*, 164(4), pp.1556-1570.
- Lawson, T., Oxborough, K., Morison, J.I. and Baker, N.R., 2003. The responses of guard and mesophyll cell photosynthesis to CO₂, O₂, light, and water stress in a range of species are similar. *Journal of experimental botany*, 54(388), pp.1743-1752.
- Lawson, T., von Caemmerer, S. and Baroli, I., 2010. Photosynthesis and stomatal behaviour. In *Progress in botany* 72 (pp. 265-304). Springer, Berlin, Heidelberg.
- Lee, H.K., Lee, S.J., Kim, M.K. and Lee, S.D., 2020. Prediction of Plant Phenological Shift under Climate Change in South Korea. *Sustainability*, 12(21), p.9276.
- Li, Y., He, N., Hou, J., Xu, L., Liu, C., Zhang, J., Wang, Q., Zhang, X. and Wu, X., 2018a. Factors influencing leaf chlorophyll content in natural forests at the biome scale. *Frontiers in Ecology and Evolution*, 6, p.64.
- Li, Y., Liu, C., Zhang, J., Yang, H., Xu, L., Wang, Q., Sack, L., Wu, X., Hou, J. and He, N., 2018b. Variation in leaf chlorophyll concentration from tropical to cold-temperate forests: association with gross primary productivity. *Ecological Indicators*, 85, pp.383-389.
- Lichtenthaler, H.K. and Buschmann, C., 2001. Chlorophylls and carotenoids: Measurement and characterization by UV-VIS spectroscopy. *Current protocols in food analytical chemistry*, 1(1), pp.F4-3.
- Long, S.P., Humphries, S. and Falkowski, P.G., 1994. Photoinhibition of photosynthesis in nature. *Annual review of plant biology*, 45(1), pp.633-662.

- Lüttge U., 2008. Plant Physiology. Editor(s): Jørgensen, S. E., Fath, B. D., *Encyclopedia of Ecology*, Academic Press. Pp. 2837-2845. ISBN 9780080454054.
<https://doi.org/10.1016/B978-008045405-4.00535-8>
- Måren, I.E., Karki, S., Prajapati, C., Yadav, R.K. and Shrestha, B.B., 2015. Facing north or south: Does slope aspect impact forest stand characteristics and soil properties in a semiarid trans-Himalayan valley?. *Journal of arid environments*, 121, pp.112-123.
- Matthews, J.S., Viallet-Chabrand, S.R. and Lawson, T., 2017. Diurnal variation in gas exchange: the balance between carbon fixation and water loss. *Plant Physiology*, 174(2), pp.614-623.
- Mayr, S., Hacke, U., Schmid, P., Schwienbacher, F. and Gruber, A., 2006. Frost drought in conifers at the alpine timberline: xylem dysfunction and adaptations. *Ecology*, 87(12), pp.3175-3185.
- Mendes, K.R., Campos, S., da Silva, L.L., Mutti, P.R., Ferreira, R.R., Medeiros, S.S., Perez-Marin, A.M., Marques, T.V., Ramos, T.M., de Lima Vieira, M.M. and Oliveira, C.P., 2020. Seasonal variation in net ecosystem CO₂ exchange of a Brazilian seasonally dry tropical forest. *Scientific Reports*, 10(1), pp.1-16.
- Miao, Y., Cai, Y., Wu, H. and Wang, D., 2021. Diurnal and Seasonal Variations in the Photosynthetic Characteristics and the Gas Exchange Simulations of Two Rice Cultivars Grown at Ambient and Elevated CO₂. *Frontiers in plant science*, 12, p.559.
- Miralles-Crespo, J., Martínez-López, J.A., Franco-Leemhuis, J.A. and Banón-Arias, S., 2011. Determining freezing injury from changes in chlorophyll fluorescence in potted oleander plants. *HortScience*, 46(6), pp.895-900.
- MUNNÉ-BOSCH, S.E.R.G.I., Nogues, S. and Alegre, L., 1999. Diurnal variations of photosynthesis and dew absorption by leaves in two evergreen shrubs growing in Mediterranean field conditions. *New Phytologist*, 144(1), pp.109-119.
- Murphy, P.C., Knowles, J.F., Moore, D.J., Anchukaitis, K., Potts, D.L. and Barron-Gafford, G.A., 2020. Topography influences species-specific patterns of seasonal primary productivity in a semiarid montane forest. *Tree Physiology*, 40(10), pp.1343-1354.
- Nautiyal, M.C., Nautiyal, B.P. and Prakash, V., 2001. Phenology and growth form distribution in an alpine pasture at Tungnath, Garhwal, Himalaya. *Mountain research and Development*, 21(2), pp.168-174.
- Negi, M. and Negi, V.S., 2021. Temporal changes in Oak forests over last three decades in western Himalaya, India. *Trees, Forests and People*, p.100146.
- Negi, M. and Rawal, R.S., 2017. POPULATION STRUCTURE AND IMPLICATIONS FOR FUTURE COMPOSITION OF WESTERN HIMALAYAN OAK FORESTS. *HIMALAYAN ECOLOGY*, 25, p.94.
- Niinemets, U., 2007. Photosynthesis and resource distribution through plant canopies. *Plant, cell & environment*, 30(9), pp.1052-1071.

- Oliver, C.D. and Larson, B.C., 1996. *Forest stand dynamics: Updated edition*. John Wiley and sons.
- Osmond, C.B., 1987. Photosynthesis and carbon economy of plants. *New Phytologist*, 106, pp.161-175.
- Osmond, C.B., 1994. What is photoinhibition? Some insights from comparisons of shade and sun plants. In: Baker, N.R. and Bowyer, J.R., Eds., *Photoinhibition of Photosynthesis. From Molecular Mechanisms to the Field*, BIOS Scientific Publishers, Oxford, 1-24.
- Ostrom, B., 2005. Effect of Forest Structure on the Understory Light Environment and Growth Potential of Oak Seedlings in a Closed Canopy Riparian Forest (Doctoral dissertation).
- Palhares, D., Franco, A.C. and Zaidan, L.B.P., 2010. Photosynthetic responses of Cerrado plants during the rainy and dry seasons. *Revista Brasileira de Biociências*, 8(2), pp.213-220.
- Pallardy, S.G., 2010. *Physiology of woody plants*. academic press. pp- 107-167. doi: <http://doi.org/10.1016/B978-012088765-1.50006-3>
- Pandita, S., Kumar, V. and Dutt, H.C., 2019. Environmental variables vis-a-vis distribution of herbaceous tracheophytes on northern sub-slopes in Western Himalayan ecotone. *Ecological Processes*, 8(1), pp.1-9.
- Paudel, S. and Vetaas, O.R., 2014. Effects of topography and land use on woody plant species composition and beta diversity in an arid Trans-Himalayan landscape, Nepal. *Journal of Mountain Science*, 11(5), pp.1112-1122.
- Pearcy, R.W. and Sims, D.A., 1994. Photosynthetic acclimation to changing light environments: scaling from the leaf to the whole plant. *Exploitation of environmental heterogeneity by plants. Ecophysiological Processes Above-and Belowground*, pp.145-174.
- Pearcy, R.W., 1987. Photosynthetic gas exchange responses of Australian tropical forest trees in canopy, gap and understory micro-environments. *Functional Ecology*, pp.169-178.
- Pearcy, R.W., 1990. Sunflecks and photosynthesis in plant canopies. *Annual review of plant biology*, 41(1), pp.421-453.
- Pearcy, R.W., Chazdon, R. L., Gross, L. J., and Mott, K. A. 1994. Photosynthetic utilization of sunflecks: a temporally patchy resource on a time scale of seconds to minutes. In *Exploitation of environmental heterogeneity by plants*, M. M. Caldwell and R. W. Pearcy, eds., Academic Press, San Diego. pp.175-208.
- Pelletier, J.D., Barron-Gafford, G.A., Gutiérrez-Jurado, H., Hinckley, E.L.S., Istanbuluoglu, E., McGuire, L.A., Niu, G.Y., Poulos, M.J., Rasmussen, C., Richardson, P. and Swetnam, T.L., 2018. Which way do you lean? Using slope aspect variations to understand Critical Zone processes and feedbacks. *Earth Surface Processes and Landforms*, 43(5), pp.1133-1154.
- Piao, S., Ciais, P., Friedlingstein, P., Peylin, P., Reichstein, M., Luysaert, S., Margolis, H., Fang, J., Barr, A., Chen, A. and Grelle, A., 2008. Net carbon dioxide losses of northern ecosystems in response to autumn warming. *Nature*, 451(7174), pp.49-52.

- Pook, E.W., 1966. The influence of aspect on the composition and structure of dry sclerophyll forest on Black Mountain, Canberra. ACT. *Australian Journal of Botany*, 14(2), pp.223-242.
- Pook, E.W., Moore, cW.E., 1966. The influence of aspect on the composition and structure of dry sclerophyll forest on Black Mountain, Canberra. ACT. *Australian Journal of Botany*, 14(2), pp.223-242.
- Poudyal, K., Jha, P.K., Zobel, D.B. and Thapa, C.B., 2004. Patterns of leaf conductance and water potential of five Himalayan tree species. *Tree Physiology*, 24(6), pp.689-699.
- Rai, I.D., Adhikari, B.S. and Rawat, G.S., 2012. Floral diversity along sub-alpine and alpine ecosystems in Tungnath area of Kedarnath wildlife sanctuary, Uttarakhand. *Indian Forester*, 138(10), pp.927-940.
- Raja Harun, R.M. and Hardwick, K., 1988. The effects of prolonged exposure to different light intensities on the photosynthesis of cocoa leaves. In *Proc. 10th Int. Cocoa Res. Conf., Santo Domingo, Dominican Republic* (pp. 205-209).
- Randerson, J.T., Field, C.B., Fung, I.Y. and Tans, P.P., 1999. Increases in early season ecosystem uptake explain recent changes in the seasonal cycle of atmospheric CO₂ at high northern latitudes. *Geophysical research letters*, 26(17), pp.2765-2768.
- Reich, P.B. and Hinckley, T.M., 1989. Influence of pre-dawn water potential and soil-to-leaf hydraulic conductance on maximum daily leaf diffusive conductance in two oak species. *Functional Ecology*, pp.719-726.
- Reinhardt, K. and Smith, W.K., 2016. Chlorophyll fluorescence and photosynthetic gas exchange under direct versus diffuse light in evergreen conifer (*Picea pungens*) shoots and broadleaf shrub (*Rhododendron ponticum*) leaves. *Plant Ecology*, 217(4), pp.443-450.
- Ribeiro, J.E.D.S., Barbosa, A.J.S., Lopes, S.D.F., Pereira, W.E. and Albuquerque, M.B.D., 2018. Seasonal variation in gas exchange by plants of *Erythroxylum simonis* Plowman. *Acta Botanica Brasilica*, 32, pp.287-296.
- Rodríguez-Calcerrada, J., Limousin, J.M., Martin-StPaul, N.K., Jaeger, C. and Rambal, S., 2012. Gas exchange and leaf aging in an evergreen oak: causes and consequences for leaf carbon balance and canopy respiration. *Tree Physiology*, 32(4), pp.464-477.
- Rosenberg, N.J., Blad, B.L. and Verma, S.B., 1983. *Microclimate: the biological environment*. John Wiley & Sons.
- Rundel, P.W., Gibson, A.C., Midgley, G.S., Wand, S.J.E., Palma, B., Kleier, C. and Lambrinos, J., 2002. Ecological and ecophysiological patterns in a pre-altiplano shrubland of the Andean Cordillera in northern Chile. *Plant Ecology*, 169(2), pp.179-193.
- Sabogal, C., Besacier, C. and McGuire, D., 2015. Forest and landscape restoration: Concepts, approaches and challenges for implementation. *Unasylva*, 66(245), p.3.
- Santanoo, S., Vongcharoen, K., Banterng, P., Vorasoot, N., Jogloy, S., Roytrakul, S. and Theerakulpisut, P., 2019. Seasonal variation in diurnal photosynthesis and chlorophyll

- fluorescence of four genotypes of cassava (*Manihot esculenta* Crantz) under irrigation conditions in a tropical savanna climate. *Agronomy*, 9(4), p.206.
- Sanwal, J., Kotlia, B.S., Rajendran, C., Ahmad, S.M., Rajendran, K. and Sandiford, M., 2013. Climatic variability in Central Indian Himalaya during the last ~ 1800 years: Evidence from a high resolution speleothem record. *Quaternary International*, 304, pp.183-192.
- Sendall, K.M., Vourlitis, G.L. and Lobo, F.A., 2009. Seasonal variation in the maximum rate of leaf gas exchange of canopy and understory tree species in an Amazonian semi-deciduous forest. *Brazilian Journal of Plant Physiology*, 21, pp.65-74.
- Singh, A., Samant, S.S. and Naithani, S., 2021. Population ecology and habitat suitability modelling of *Quercus semecarpifolia* Sm. in the sub-alpine ecosystem of Great Himalayan National Park, north-western Himalaya, India. *South African Journal of Botany*, 141, pp.158-170.
- Singh, J.S. and Singh, S.P., 1987. Forest vegetation of the Himalaya. *The Botanical Review*, 53(1), pp.80-192.
- Singh, P. and Negi, G.C.S., 2018. Treeline species phenology: shoot growth, leaf characteristics and nutrient dynamics. *Tropical Ecology*, 59(2), pp.297-311.
- Singh, S.P., Rawat, Y.S. and Garkoti, S.C., 1997. Failure of brown oak (*Quercus semecarpifolia*) to regenerate in central Himalaya: a case of environmental semisurprise. *Current Science*, pp.371-374.
- Singh, S.P., Zobel, D.B., Garkoti, S.C., Tewari, A. and Negi, C.M.S., 2006. Patterns in water relations of central Himalayan trees. *Tropical Ecology*, 47(2), pp.159-182.
- Singh, S.P., Zobel, D.B., Garkoti, S.C., Tewari, A. and Negi, C.M.S., 2006. Patterns in water relations of central Himalayan trees. *Tropical Ecology*, 47(2), pp.159-182.
- Singh, U., Phulara, M., David, B., Ranhotra, P.S., Shekhar, M., Bhattacharyya, A., Dhyani, R., Joshi, R., Pal, A.K., 2018. Static treeline of Himalayan silver fir since last several decades at Tungnath, western Himalaya. *Trop Ecol* 59(2):351–363
- Singh, V., 2020. Environmental Plant Physiology: Botanical Strategies for a Climate Smart Planet. CRC Press.
- Slayter, R.O., 1967. *Plant-water relationships*. Academic Press, New York.
- Smith, W.K. and Berry, Z.C., 2013. Sunflecks?. *Tree physiology*, 33(3), pp.233-237.
- Taiz, L. and Zeiger, E., 2013. Plant Physiology= Fisiologia Vegetal. *Editores Artemed: Porto Alegre, Brazil*.
- Tankari, M., Wang, C., Zhang, X., Li, L., Sothar, R.K., Ma, H., Xing, H., Yan, C., Zhang, Y., Liu, F. and Wang, Y., 2019. Leaf gas exchange, plant water relations and water use efficiency of *Vigna unguiculata* L. Walp. Inoculated with *Rhizobia* under Different Soil Water Regimes. *Water*, 11(3), p.498.

- Tewari, A., 1998. *Timing of Drought: Effects on Water Relation of Certain Major Forest Types of Lower and Middle Central Himalaya* (Doctoral dissertation, Ph D Dissertation]. Nainital (India): Botany Department, Kumaon University).
- Tewari, A., 1999. Tree water relations study in Sal (*Shorea robusta* Gaertn.) forest in Kumaon Central Himalaya. *Journal of Environmental Biology*, 20(4), pp.353-357.
- Tewari, A., Bhatt, J. and Mittal, A., 2016. Influence of tree water potential in inducing flowering in *Rhododendron arboreum* in the central Himalayan region. *iForest-Biogeosciences and Forestry*, 9(5), p.842.
- Tewari, A., Shah, S., Singh, N. and Mittal, A., 2018. Treeline species in Western Himalaya are not water stressed: a comparison with low elevation species. *Tropical Ecology*, 59(2).
- Tewari, A., Shah, S., Singh, N. and Mittal, A., 2018. Treeline species in Western Himalaya are not water stressed: a comparison with low elevation species. *Tropical Ecology*, 59(2).
- Tinoco-Ojanguren, C. and Percy, R.W., 1993. Stomatal dynamics and its importance to carbon gain in two rainforest *Piper* species. *Oecologia*, 94(3), pp.395-402.
- Tinoco-Ojanguren, C. and Percy, R.W., 1993. Stomatal dynamics and its importance to carbon gain in two rainforest *Piper* species. I. VPD effects on the transient stomatal response to lightflecks. *Oecologia*, pp.388-394.
- Urban, L., Aarouf, J. and Bidel, L.P., 2017. Assessing the effects of water deficit on photosynthesis using parameters derived from measurements of leaf gas exchange and of chlorophyll a fluorescence. *Frontiers in plant science*, 8, p.2068.
- Vass, I., Cser, K. and Cheregi, O., 2007. Molecular mechanisms of light stress of photosynthesis. *ANNALS-NEWYORK ACADEMY OF SCIENCES*, 1113, p.114.
- Vesala, T., Sevanto, S., Grönholm, T., Salmon, Y., Nikinmaa, E., Hari, P. and Hölttä, T., 2017. Effect of leaf water potential on internal humidity and CO₂ dissolution: reverse transpiration and improved water use efficiency under negative pressure. *Frontiers in plant science*, 8, p.54.
- Vincent, C., Morillon, R., Arbona, V. and Gómez-Cadenas, A., 2020. Citrus in changing environments. In *The Genus Citrus* (pp. 271-289). Woodhead Publishing.
- Vranová, E., Inzé, D. and Van Breusegem, F., 2002. Signal transduction during oxidative stress. *Journal of experimental botany*, 53(372), pp.1227-1236.
- Wadgyamar, S.M., Ogilvie, J.E., Inouye, D.W., Weis, A.E. and Anderson, J.T., 2018. Phenological responses to multiple environmental drivers under climate change: insights from a long-term observational study and a manipulative field experiment. *New Phytologist*, 218(2), pp.517-529.
- Wang, C., Tang, Y. and Chen, J., 2016. Plant phenological synchrony increases under rapid within-spring warming. *Scientific Reports*, 6(1), pp.1-7.

- Wang, H. and Shang, Q., 2020. The combined effects of light intensity, temperature, and water potential on wall deposition in regulating hypocotyl elongation of *Brassica rapa*. *PeerJ*, 8, p.e9106.
- Wang, S., Qi, G. and Knapp, B.O., 2019. Topography affects tree species distribution and biomass variation in a warm temperate, secondary forest. *Forests*, 10(10), p.895.
- Way, D.A. and Montgomery, R.A., 2015. Photoperiod constraints on tree phenology, performance and migration in a warming world. *Plant, cell & environment*, 38(9), pp.1725-1736.
- Wellburn, A.R., 1994. The spectral determination of chlorophylls a and b, as well as total carotenoids, using various solvents with spectrophotometers of different resolution. *Journal of plant physiology*, 144(3), pp.307-313.
- Whittaker, R.H. and Niering, W.A., 1965. Vegetation of the Santa Catalina Mountains, Arizona: a gradient analysis of the south slope. *Ecology*, 46(4), pp.429-452.
- Wolkerstorfer, S.V., Wonisch, A., Stankova, T., Tsvetkova, N. and Tausz, M., 2011. Seasonal variations of gas exchange, photosynthetic pigments, and antioxidants in Turkey oak (*Quercus cerris* L.) and Hungarian oak (*Quercus frainetto* Ten.) of different age. *Trees*, 25(6), pp.1043-1052.
- Wu, J., Chavana-Bryant, C., Prohaska, N., Serbin, S.P., Guan, K., Albert, L.P., Yang, X., van Leeuwen, W.J., Garnello, A.J., Martins, G. and Malhi, Y., 2017. Convergence in relationships between leaf traits, spectra and age across diverse canopy environments and two contrasting tropical forests. *New Phytologist*, 214(3), pp.1033-1048.
- Xu, L. and Baldocchi, D.D., 2003. Seasonal trends in photosynthetic parameters and stomatal conductance of blue oak (*Quercus douglasii*) under prolonged summer drought and high temperature. *Tree physiology*, 23(13), pp.865-877.
- Yang, J., El-Kassaby, Y.A. and Guan, W., 2020. The effect of slope aspect on vegetation attributes in a mountainous dry valley, Southwest China. *Scientific reports*, 10(1), pp.1-11.
- Yang, X., Tang, J., Mustard, J.F., Wu, J., Zhao, K., Serbin, S. and Lee, J.E., 2016. Seasonal variability of multiple leaf traits captured by leaf spectroscopy at two temperate deciduous forests. *Remote Sensing of Environment*, 179, pp.1-12.
- Yang, X., Tang, J., Mustard, J.F., Wu, J., Zhao, K., Serbin, S. and Lee, J.E., 2016. Seasonal variability of multiple leaf traits captured by leaf spectroscopy at two temperate deciduous forests. *Remote Sensing of Environment*, 179, pp.1-12.
- Yang, X., Tang, J., Mustard, J.F., Wu, J., Zhao, K., Serbin, S. and Lee, J.E., 2016. Seasonal variability of multiple leaf traits captured by leaf spectroscopy at two temperate deciduous forests. *Remote Sensing of Environment*, 179, pp.1-12.
- Zapata-Rios, X., Brooks, P.D., Troch, P.A., McIntosh, J. and Guo, Q., 2015. Influence of terrain aspect on water partitioning, vegetation structure and vegetation greening in high-elevation catchments in northern New Mexico. *Ecohydrology* 9 (5): 782-795.

- Zhang, Y., Chen, J.M. and Thomas, S.C., 2007. Retrieving seasonal variation in chlorophyll content of overstory and understory sugar maple leaves from leaf-level hyperspectral data. *Canadian Journal of Remote Sensing*, 33(5), pp.406-415.
- Zhao, Y., Han, Q., Ding, C., Huang, Y., Liao, J., Chen, T., Feng, S., Zhou, L., Zhang, Z., Chen, Y. and Yuan, S., 2020. Effect of low temperature on chlorophyll biosynthesis and chloroplast biogenesis of rice seedlings during greening. *International journal of molecular sciences*, 21(4), p.1390.
- Zhuang, K., Kong, F., Zhang, S., Meng, C., Yang, M., Liu, Z., Wang, Y., Ma, N. and Meng, Q., 2019. Whirly1 enhances tolerance to chilling stress in tomato via protection of photosystem II and regulation of starch degradation. *New Phytologist*, 221(4), pp.1998-2012.
- Zobel, D.B. and Singh, S.P., 1997. Himalayan forests and ecological generalizations. *BioScience*, 47(11), pp.735-745.
- Zobel, D.B., Garkoti, S.C., Singh, S.P., Tewari, A. and Negi, C.M.S., 2001. Patterns of water potential among forest types of the central Himalaya. *Current Science*, pp.774-779.