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RESEARCH

Seasonal variations of leaf ecophysiological traits and strategies of co-occurring evergreen and deciduous trees in white oak forest in the central Himalaya

Rajendra Kr. Joshi · Rajman Gupta · Ambuj Mishra · Satish Chandra Garkoti

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Abstract The present study investigates the seasonal variations in leaf ecophysiological traits and strategies employed by co-occurring evergreen and deciduous tree species within a white oak forest (*Quercus leucotrichophora* A. Camus) ecosystem in the central Himalaya. Seasonal variations in physiological, morphological, and chemical traits were observed from leaf initiation until senescence in co-occurring deciduous and evergreen tree species. We compared various parameters, including net photosynthetic capacity (A_{area} and A_{mass}), leaf stomatal conductance (gsw_{area} and gsw_{mass}), transpiration rate (E_{area} and E_{mass}), specific leaf area (SLA), mid-day water potential (Ψ_{md}), leaf nitrogen (N) and phosphorus (P) concentration, leaf total chlorophyll concentration, photosynthetic nitrogen- and phosphorus-use efficiency (PNUE and PPUE), and water use efficiency (WUE) across four evergreen and four deciduous tree species. Our findings reveal that evergreen and deciduous trees exhibit divergent strategies in coping with seasonal changes, which are crucial for their survival and growth. Deciduous trees consistently exhibited significantly higher photosynthetic rates, transpiration rates, mass-based N and P concentrations (N_{mass} and P_{mass}), mass-based chlorophyll concentration (Chl_{mass}), SLA, and leaf Ψ_{md}, while maintaining lower leaf structural investments throughout the year compared to evergreen trees. These findings indicate that deciduous trees achieve greater assimilation rates per unit mass and higher nutrient-use efficiency. Physiological, morphological, and leaf N and P concentrations were higher in the summer (fully expanded leaf) than in the fall (senesced leaf). These insights provide valuable contributions to our understanding of tree species coexistence and their ecological roles in temperate forest ecosystems, with implications for forest management and conservation in the Himalayan region.

Keywords Evergreen and deciduous trees · Acquisitive and conservative strategies · Leaf longevity · Leaf phenology · Photosynthesis and stomatal conductance · Water potential

R. K. Joshi · R. Gupta · A. Mishra · S. C. Garkoti (✉)
School of Environmental Sciences, Jawaharlal Nehru University, New Delhi 110067, India
e-mail: sgarkoti@yahoo.com

R. K. Joshi
Department of Environmental Sciences, Daulat Ram College, University of Delhi, New Delhi 110007, India

Introduction

Forests, as essential components of terrestrial ecosystems, play a pivotal role in global biogeochemical cycles, carbon sequestration, and the maintenance of biodiversity (Berner & Law, 2016; Buotte et al., 2020; Joshi & Garkoti, 2020). They are particularly diverse in montane regions, such as the central Himalaya, where a multitude of tree species coexist, each adapted to specific ecological niches and characterized by unique ecophysiological traits (Maharjan et al., 2021; Joshi et al., 2023). Evergreen and deciduous tree species represent two distinct strategies for coping with the challenges of seasonal variations in environmental conditions, including temperature, moisture, and light availability (Choat et al., 2006; Tomlinson et al. 2014; Bai et al., 2015; Wang et al., 2022). In this context, leaf ecophysiological traits and strategies of co-occurring tree species within a forest community have been the subject of intense research owing to their crucial role in shaping species coexistence and ecosystem functioning (He et al., 2023; Visakorpi et al., 2022). Seasonal variations in these traits and strategies provide valuable insights into the adaptations of tree species to changing environmental conditions, thereby helping us comprehend the response of forests to ongoing climate change (Beyschlag & Ryel, 2007; Harrison et al., 2010; Legg, 2021; Visakorpi et al., 2022; Hu et al., 2023).

Leaf ecophysiological traits are fundamental indicators of a tree's response to its environment (Ackerly et al., 2000; Khan et al., 2022; Wang et al., 2022). These traits encompass a wide range of physiological processes, including photosynthesis, transpiration, nutrient allocation, and water-use efficiency. Seasonal variations in these traits may provide crucial insights into the mechanisms governing tree adaptations and acclimation (Bai et al., 2015; Choat et al., 2006; Ishida et al., 2010). For evergreen species, which maintain leaves throughout the year, the challenge lies in sustaining leaf function during periods of reduced resource availability, such as the cold and dry winter months. Deciduous species, on the other hand, invest heavily in leaf production during the growing season and must coordinate leaf shedding and regrowth to optimize resource use efficiency (Negi & Singh, 1992; Negi, 2006; Devi & Garkoti, 2013; Vico et al., 2015; Estiarte & Peñuelas, 2015; Joshi & Garkoti, 2023). Numerous studies have documented that deciduous plants tend to adopt a more resource-acquisitive strategy by increasing their leaf nutrient concentrations and specific leaf area (SLA) (Choat et al., 2006; Tomlinson et al., 2014; Bai et al., 2015; Wang et al., 2022). For instance, deciduous trees often exhibit higher leaf nitrogen concentrations (N), a vital element for plant growth, in comparison to co-occurring evergreen trees. This increased leaf N in deciduous plants is commonly associated with higher SLA and light-saturated photosynthetic rates, which enable them to achieve greater carbon assimilation rates when environmental conditions are favorable. Conversely, the evergreen leaf habit is often considered a more 'conservative' approach to leaf strategy (Reich et al., 1997; Wright et al., 2004). An advantage of retaining their leaves year-round is that evergreen species can maintain photosynthesis in adverse seasons when deciduous species cannot, thereby exhibiting resilience in unfavorable conditions (Reich et al., 1997; Wright et al., 2004; Ishida et al., 2005; Tomlinson et al., 2014).

The central Himalayan region, renowned for its rich biodiversity and unique ecological features, harbors diverse forest ecosystems that play a crucial role in maintaining ecological balance. Among these, the white oak forest stands as a prominent representative, featuring a fascinating interplay between evergreen and deciduous tree species. With its steep altitudinal gradients, the central Himalayan region offers a unique opportunity to investigate the ecological strategies of evergreen and deciduous tree species in response to the pronounced seasonality (Negi & Singh, 1992; Negi, 2006; Poudyal et al., 2004). The region is home to diverse vegetation, with white oak (*Quercus leucotrichophora* A. Camus) forests covering approximately 12,000 km^2 being one of the dominant forest types (Dhyani et al., 2020). The white oak forest is particularly noteworthy due to the co-occurrence of evergreen and deciduous tree species within the same ecosystem. The coexistence of the species with different leaf phenologies raises intriguing questions regarding how these species adjust their ecophysiological strategies in response to the seasonal climate variations that occur at high elevations. White oak forests are emblematic of the region's temperate ecosystems and provide critical ecosystem services, including carbon sequestration, habitat provision, and water regulation, the coexistence of evergreen and deciduous tree species in these forests provides an ideal setting for studying how different leaf ecophysiological traits and strategies contribute to their success and the functioning of the ecosystem (Joshi & Garkoti, 2023; Joshi et al., 2024; Mishra et al., 2024; Sigdel et al., 2023; Singh et al., 2023). The central Himalayan region experiences distinct seasonal changes in temperature, precipitation, and photoperiod, which pose unique challenges to the evergreen and deciduous species. These challenges may drive divergent strategies among species to cope with these seasonal fluctuations. Evergreens may exhibit higher leaf longevity and increased drought tolerance, while deciduous species may prioritize rapid growth and energy conservation through leaf shedding.

Seasonal variations in environmental factors pose distinct challenges for plant species, influencing their adaptive strategies to ensure survival and growth. In the context of the central Himalayan white oak forest, the interplay between evergreen and deciduous trees unveils a compelling narrative of ecological resilience and adaptation. Understanding the nuances of leaf ecophysiological traits becomes imperative to unravel the mechanisms governing these species' responses to the dynamic seasonal changes prevalent in the region. This study aims to elucidate the seasonal dynamics of key leaf ecophysiological traits, such as photosynthetic rates, stomatal conductance, and leaf water potential, among others, in both evergreen and deciduous tree species. By examining these traits across different seasons, we seek to unravel the distinct adaptive strategies employed by these trees to cope with the contrasting environmental conditions experienced throughout the year. In this context, the present study aims to investigate the seasonal variations in leaf ecophysiological traits and leaf strategies of co-occurring evergreen and deciduous tree species in a white oak forest in the central Himalaya. Specifically, we hypothesize that these two functional groups will exhibit distinct patterns of leaf trait variations across seasons, reflecting their differing resource acquisition and utilization strategies. Additionally, we expect that the evergreen species will maintain higher leaf trait values during winter, while deciduous species may show greater plasticity in response to changing environmental conditions. To test the above hypothesis, we have the following predictions: (1) leaf water potential, area and mass-based leaf-level gas exchange (stomatal conductance, photosynthetic rate, transpiration rate) would differ between co-occurring evergreen and deciduous tree species, (2) evergreen trees have lower nutrient efficiency consequently lower photosynthetic rates compared to deciduous trees.

Materials and methods

Study area

The study was conducted within the Ukhimath region, situated at coordinates 30°31′36.7″ N and 79°6′42.0″ E, and an elevation of 1612 m above sea level. The study sites are located close to the Kedarnath Wildlife Sanctuary, in the western region of the central Himalaya (Fig. 1), providing a unique and ecologically diverse environment for the investigation of various flora and fauna species in this pristine and high-altitude ecosystem. The climate in the study area is defined by its cold temperate and seasonal nature. Throughout the year, the average minimum and maximum temperatures exhibit noticeable variations, reaching a low of − 1.1 °C in January and ascending to a peak of 13.4 °C in July. Notably, the mean maximum temperature experiences a gradual ascent from 11.6 °C in January to a warmer 24.4 °C in June. These temperature fluctuations contribute to the distinctiveness of the region's climate, shaping its overall climatic profile. Throughout the study period, monthly rainfall varied from 7.3 mm in November to 637.1 mm in July (Fig. 1). Over the study period, the cumulative yearly rainfall in the study area amounted to 1983 mm, with over 70–80% of this occurring during the monsoon season (July–September), and moderate to heavy snowfall during December through February. The main canopy height is 15 m, with a few emergent trees reaching heights exceeding 20 m.

With a leaf area index (LAI) of 5.5 m2 m¯2 and a corresponding tree density of 980 trees per hectare, as documented by Joshi and Garkoti in 2020, the study

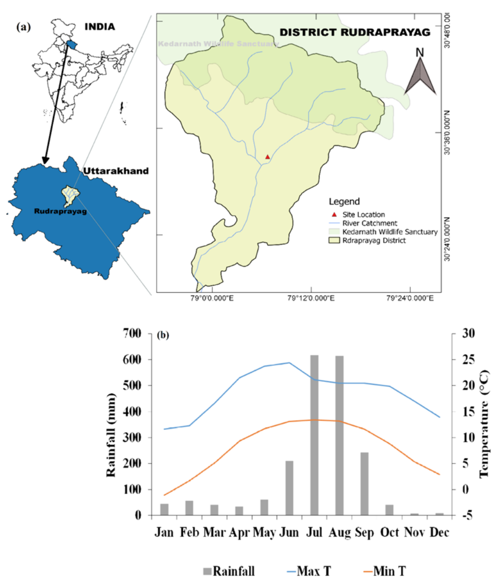

Fig. 1 Location of the study area (**a**) and patterns of monthly temperature and rainfall (**b**) at Ukhimath Central Himalaya

provides a comprehensive overview of the vegetation cover in the specified area. The soil in the study area was classified as sandy loam, brown podzolic, and mixed with pebbles and gravel (Joshi & Garkoti, 2021).

Tree species and ecophysiological traits measurement

Four evergreen species were chosen for this study: *Quercus leucotrichophora* A. Camus, *Rhododendron arboreum* Sm, *Myrica esculenta* Buch.-Ham. ex D.Don, and *Quercus floribunda* Lindl. ex A. Camus. Additionally, four winter-deciduous species, namely *Alnus nepalensis* D. Don, *Pyrus pashia* Linnaeus, *Lyonia ovalifolia* (Wall.) Drude, and *Symplocos paniculata* Miq, were selected. All of these tree species were commonly found at the study sites. The evergreen tree species had a leaf lifespan of approximately 1 year, while the deciduous species retained their leaves for a period ranging from six to 9 months. During winter, the deciduous tree species remained leafless for three to 4 months (Table 1).

The leaf ecophysiological traits were measured in 2019 during spring (February to April), summer (May to July), autumn (September to November), and winter (December to February) to represent different leaf phenology. For each species, we selected five representative trees with similar diameters at breast height, which were mature and fully exposed to sunlight for sampling. Measurements were conducted between 9:30 AM and 12:00 Noon local solar time to minimize sources of diurnal heterogeneity and avoid midday depression in three to five fully expanded healthy leaves. Since the canopy was not easily reachable due to the absence of canopy cranes or towers, we chose fully mature leaves from sun-exposed terminal canopy branches to measure leaf water potential, gas exchange, and leaf functional traits (Ishida et al., 2023; Zhang et al., 2013). The leaf phenophases encompassed various categories, such as leaf initiation (spring), full leaf expansion (summer), full expansion and maturity (autumn), and leaf senescence (autumn and winter).

Area-based physiological traits, including the photosynthetic rate (A_{area}; µmol CO_2 m^{-2} s^{-1}), stomatal conductance (gsw_{area}; mol H_2O m^{-2} s^{-1}), and transpiration rate (E_{area}; mol H_2O m^{-2} s^{-1}), were measured using an open-flow, portable infrared gas analyzer (IRGA) (Li-6800, Li-Cor, Lincoln, NE, USA) (Evans & Santiago, 2014) under ambient conditions. Air temperature (T air, °C), leaf temperature (T leaf, °C), humidity and photosynthetic photon flux density (PPFD, µmol m^{-2} $^{s-1}$) were recorded by the IRGA at each measurement using a 6-cm^2 chamber equipped with red–blue light-emitting diodes on clear, cloudless days. Measurements were initiated after ensuring that the intercellular CO_2 to ambient CO_2 ratios, vapor pressure difference (VPD), as well as the rates of photosynthesis and conductance, had stabilized for a minimum duration of 2 min (Joshi & Garkoti, 2023). After conducting gas exchange measurements, we harvested 30 or more mature leaves from

Table 1 Major phenological events of selected tree species in a Indian central Himalayan oak forest and tree family, leaf flushing, leaf drop, leafless month(s) and leaf lifespan (months). Season: four seasonal periods: spring (Feb–April), summer (May–July), autumn (Sep–Nov) and winter (Dec–Feb)

Species	Family	Leaf flushing	Leaf drop	Leafless month(s)	Leaf lifespan (months)
Evergreen					
Quercus leucotrichophora	Fagaceae	March–April	March–June	None	13–14
Rhododendron arboreum	Ericaceae	March–April	March–June	None	14–16
Myrica esculenta	Myricaceae	April–May	June–July	None	13–15
Quercus floribunda	Fagaceae	March–April	May–June	None	13–14
Deciduous					
Alnus nepalensis	Betulaceae	Jan–March	April–May	Jan–March	7–9
Pyrus pashia	Rosaceae	Feb–March	Nov–Dec	Jan–March	6–7
Lyonia ovalifolia	Ericaceae	Feb–March	Nov–Dec	Dec–March	6–8
Symplocos paniculata	Symplocaceae	Feb–March	Nov–Dec	Jan–March	6–7

each species and measured their surface areas using a leaf area meter (LI 3000C, LI-COR, Inc). The harvested leaves were then dried for a minimum of 48 h at 80 °C, and their dry weights were subsequently determined. Specific leaf area (SLA; m^2 kg^{-1}) was calculated as the ratio of leaf dry mass to leaf area. Mass-based assimilation rate (A_{mass}; μmol CO_2 m^{-2} s^{-1}), mass-based stomatal conductance (gsw_{mass}; mol H_2O m^{-2} s^{-1}), and mass-based transpiration rate (E_{mass}; mol H_2O m^{-2} s^{-1}) were calculated as follows: $A_{mass} = A_{area} \times SLA$; $gsw_{mass} = gsw_{area} \times SLA$; and $E_{mass} = E_{area} \times SLA$, respectively.

Leaf N and P concentrations were measured because they are essential nutrient elements for photosynthesis, specifically RUBISCO and ATP. The measured leaf functional traits included mass-based nitrogen (leaf N_m; g kg^{-1}), mass-phosphorus (leaf P_m; g kg^{-1}), and total chlorophyll (Chl; mg g^{-1}) concentrations. For chemical analysis, eight to ten leaf discs of a defined area (1.60 cm^2) were excised from the leaves (excluding the petiole), dried at 64 °C until constant weight was achieved, and then weighed for each species. During the analysis, all samples were triplicated and averaged. Leaf N concentrations were determined using the Kjeldahl method. Leaf P concentration was determined using ammonium molybdate and the absorbance was read at 660 nm (Shimadzu UV-1800, Shimadzu Corp., Kyoto, Japan). Fresh leaves were cleaned to remove contaminants, and 0.1 g of fresh leaf sample was used to extract chlorophyll using 5 ml of dimethylsulfoxide (DMSO), with five replicates for each tree and season. After preheating the sample test tube to 64 °C in a water bath for 4 h, the sample tissues were decolorized and cooled to room temperature. The absorbance of the supernatant was measured using a spectrophotometer (Shimadzu UV-1201, Kyoto, Japan). Chlorophyll a and b concentrations were calculated using readings at 665 nm and 645 nm (Barnes et al., 1992; Wellburn, 1994).

Area-based N and P concentrations (N_a, and P_a mg m^{-1}) were calculated mass based of N_m and P_m concentrations and multiplied by the specific leaf area (i.e., N_a and $P_a = N_m$ and $P_m \times SLA$). Photosynthetic resource-use efficiency traits were determined by calculating nitrogen-phosphorus use efficiency (PNUE or PPUE $= A_{area}/N_{area}$ or A_{area}/P_{area} μmol CO_2 N and P s^{-1} g^{-1}). Intrinsic water-use efficiency (WUEi; μmol CO_2 μmol^{-1} H_2O) was measured as the ratio of A_{area}/gsw_{area}, and water-use efficiency (WUE; μmol CO_2 μmol^{-1} H_2O) was derived as the ratio of A_{area}/E_{area} (Farquhar and Sharkey 1982). Leaf water potential (ΨL) was measured using a pressure chamber (Model 1000, PMS Instrument, Corvallis, OR, USA). Five sun-exposed terminal twigs (< 15-cm long) were excised and placed in sealed polythene bags before measuring leaf water potential (ΨL) during each sampling period.

Statistical analysis

We employed a two-way repeated-measures ANOVA along with Tukey tests for post hoc analysis to assess the differences in morphological and physiological leaf traits across growth forms (evergreen and deciduous), seasons (spring, summer, autumn, and winter), and their respective interactions. To evaluate the normality of residuals, we utilized the Shapiro–Wilk statistic. When deemed essential, adjustments to the data were made using the Box-Cox method. These analyses were performed using the R programming language, version 4.0 (R Core Team), and the MS Excel (2013) analytical software. All analyses present the data as the mean of five replicate values ± standard error. We also calculated Pearson's correlation coefficient to evaluate the relationships among the measured traits. Principal component analysis (PCA) was performed to identify the eco-physiological traits using 'FactoMineR' and 'Facto-extra' packages in R.

Results

Seasonal variation in leaf ecophysiology traits

Results revealed that evergreen and deciduous species exhibited contrasting leaf gas exchange traits through the season. Throughout the entire growing season, deciduous trees consistently demonstrated significantly greater mass (A_{mass}) and area-based (A_{area}) CO_2 assimilation rate, transpiration rates (E_{area}, and E_{mass}), and stomatal conductance (gsw_{area} and gsw_{mass}) compared to evergreen trees (Fig. 2). The values of A_{area} measured during the summer season ranged from 5.2 μmol CO_2 m^{-2} s^{-1} in *M. esculenta* to 13.5 μmol CO_2 m^{-2} s^{-1} in *L. ovalifolia*. The gsw_{area} varied from 0.18 mol m^{-2} s^{-1} in *R. arboreum* to 0.29 mol m^{-2} s^{-1} in *L. ovalifolia*, while

E_{area} ranged from 2.8 mol m^{-2} s^{-1} in *R. arboreum* to 7.2 mol m^{-2} s^{-1} in *L. ovalifolia.* The average A_{area} in deciduous species was 38.89% higher than the evergreen species (7.71 ± 0.74 vs. 4.98 ± 0.56 μmol CO_2 m^{-2} s^{-1}), the difference being statistically significant ($P<0.05$). The mass-based (A_{mass}) CO_2 assimilation rate in deciduous species was significantly higher than evergreen species (45.69 ± 5.67 vs. 29.69 ± 4.23 μmol CO_2 kg^{-1} s^{-1}, respectively). A 21 to 49% increment in deciduous species and 27 to 54% increment in evergreen species in A_{area} were observed between the spring to summer season. A 41 to 60% decline in deciduous species and 34 to 70% decline in A_{area} were observed between summer to autumn and summer to winter season value, respectively. Because deciduous species were leafless for 3 or 4 months of the year, a declined A_{area} was 100% between summer to winter season.

PNUE, PPUE, WUE, and WUEi demonstrated substantial differences between deciduous and evergreen species during the spring, summer, autumn, and winter. Specifically, PNUE and PPUE were significantly higher in deciduous tree species than in evergreen species, while WUE and WUEi displayed the opposite trend (Fig. 3). Across season, WUEi, WUE, PNUE, and PPUE increased from spring to summer and decreased thereafter with leaf age. Across species, *A. nepalensis* and *S. paniculata* demonstrated highest average values for PNUE and PPUE. *M. esculenta* displayed the highest average value of WUEi, and WUE (Fig. 3).

Seasonal variation in leaf chemical and morphological traits

The area-based concentrations of nitrogen (N_{area}), phosphorus (P_{area}), total chlorophyll (Chl), and SLA varied significantly between deciduous and evergreen species and among seasons ($P<0.001$), with significant season × species interactions. The deciduous trees exhibited significantly higher N_{area}, P_{area}, total Chl, and SLA compared to the evergreen trees. Among species highest N_{area}, P_{area} was recorded for *A. nepalensis* and the lowest for *Q. floribunda*. In deciduous species, specific leaf area (SLA) varied from 4.2 ± 0.14 (*S. paniculata* in autumn) to

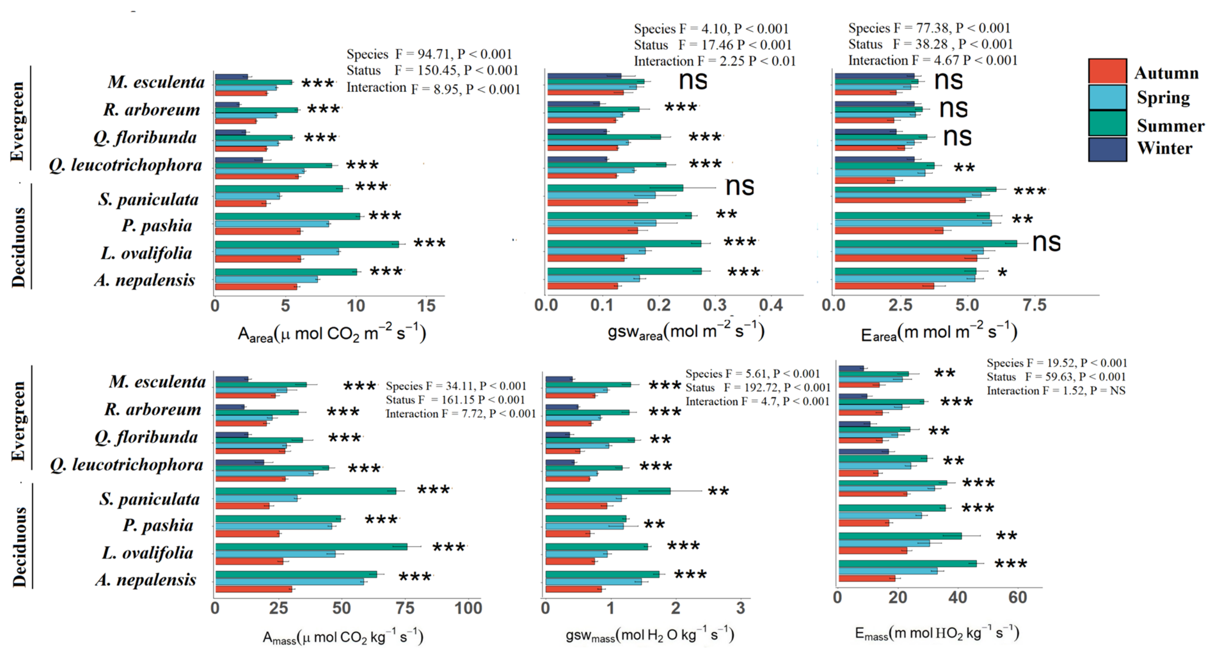

Fig. 2 Seasonal variations in area-based and mass-based photosynthesis assimilation (A_{area} and A_{mass}), stomatal conductance (gsw_{area} and gsw_{mass}) and transpiration rate (E_{area} and E_{mass}) for four evergreen species (*Quercus leucotrichophora*, *Rhododendron arboreum*, *Myrica esculenta*, *Quercus floribunda*) and four deciduous species (*Lyonia ovalifolia*, *Alnus nepalensis*, *Pyrus pashia*, *Symplocos paniculata*). Values are means ($n=5$, ± SE). All statistical significances were recognized by $P<0.05$ (***$P<0.001$, **$P<0.01$, *$P<0.05$, n.s.: $P \geq 0.05$)

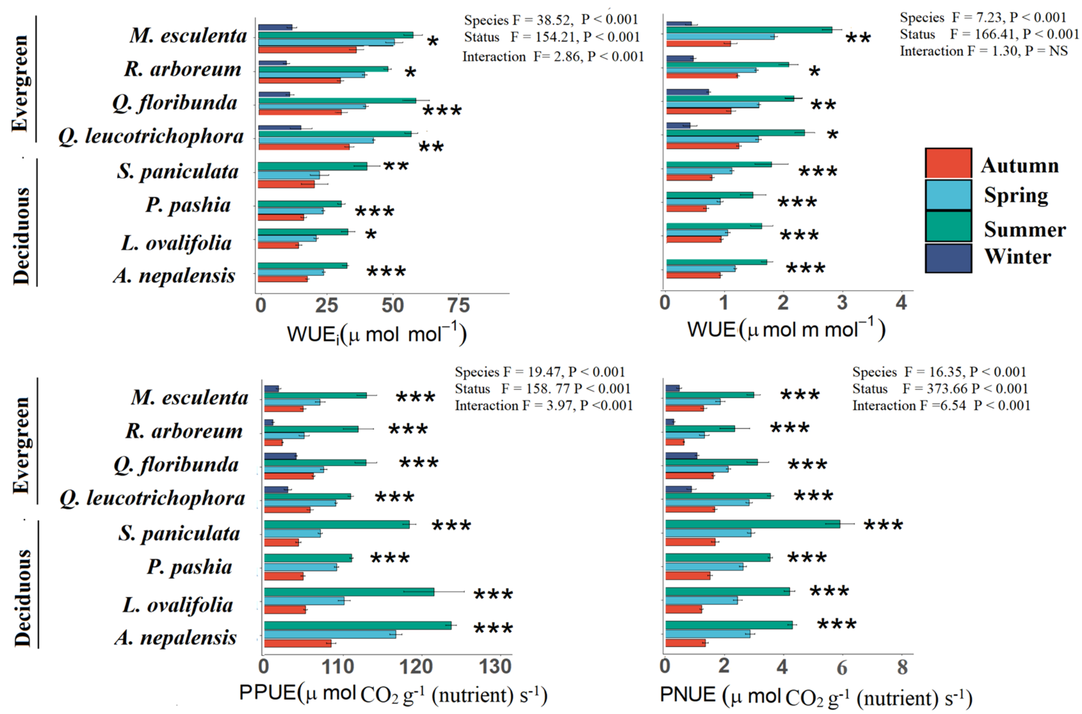

Fig. 3 Seasonal variations in intrinsic water use efficiency (WUE_i), water use efficiency (WUE), photosynthetic N-, and P-use efficiency (PNUE and PPUE) for four evergreen species (*Quercus leucotrichophora*, *Rhododendron arboreum*, *Myrica esculenta*, *Quercus floribunda*) and four deciduous species (*Lyonia ovalifolia*, *Alnus nepalensis*, *Pyrus pashia*, *Symplocos paniculata*). Values are means ($n=5, \pm$SE). All statistical significances were recognized by $P<0.05$ (***$P<0.001$, **$P<0.01$, *$P<0.05$, n.s.: $P\geq0.05$)

8.78 ± 0.32 m^2 kg^{-1} (*A. nepalensis* in summer). Evergreen species exhibited SLA ranging from 3.63 ± 0.16 (*Q. floribunda* in winter) to 6.8 ± 0.23 m^2 kg^{-1} (*M. esculenta* in summer) (Fig. 4). For deciduous species, ranged from 2.92 ± 0.12 (*S. paniculata* in autumn) to 6.1 ± 0.11 g m^{-2} (*A. nepalensis* in summer). Among evergreen species, N_{area} varied from 2.47 ± 0.13 (*Q. floribunda* in winter) to 5.71 ± 0.21 g m^{-2} (*R. arboretum* in summer). *Q. floribunda* exhibited the lowest and *A. nepalensis* the highest P_{area}. In the winter season, *M. esculenta* had the lowest, while *L. ovalifolia* in summer had the highest total Chl content.

Seasonal variation in water potential

The midday water potential (Ψ_{md}) was significantly influenced by species and season, as indicated in Fig. 5. During the summer season, when leaves were fully expanded, the midday water potential (Ψ_{md}) remained consistently above − 2.0 MPa across all trees. Specifically, in the summer, the midday water potential for deciduous species was notably higher than for evergreen species. It ranged from − 1.62 MPa (*R. arborium*) to − 1.93 MPa (*Q. leucotrichophora*) among the evergreen trees and from − 1.11 MPa (*S. paniculata*) to − 1.74 MPa (*A. nepalensis*) among the deciduous trees, as depicted in Fig. 5.

Correlation between leaf traits

A significant positive correlation was observed between mass and area-based A, E, and gsw. Mass-based A, E, and gsw also exhibited positive correlations with N_{area}, P_{area}, and SLA. SLA was positively correlated with N_{area}, P_{area}, whereas SLA did not show any correlation with WUE and WUEi. In addition, SLA and N_{area}, and P_{area} were positively correlated with PNUE and PPUE. In addition, N_{area}, and P_{area} were positively correlated with total Chl

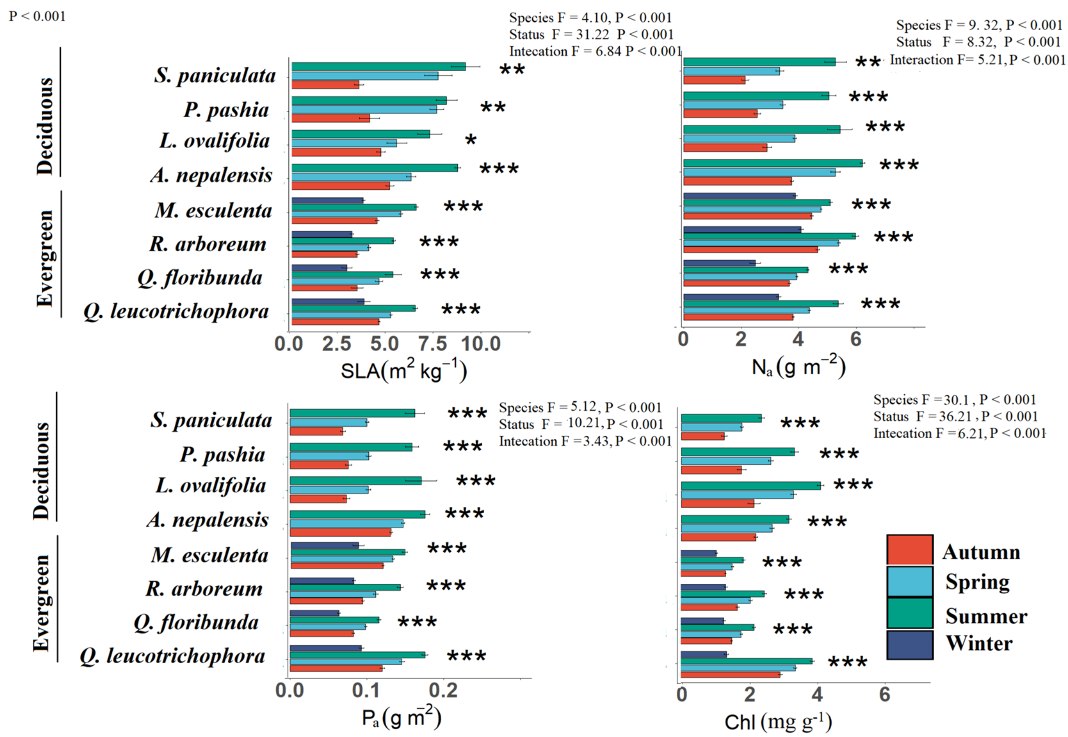

Fig. 4 Seasonal variations in specific leaf area (SLA), mass-based leaf N, mass-based leaf P, chlorophyll (Chl) for four evergreen species (*Quercus leucotrichophora*, *Rhododendron arboreum*, *Myrica esculenta*, *Quercus floribunda*) and four deciduous species (*Lyonia ovalifolia*, *Alnus nepalensis*, *Pyrus pashia*, *Symplocos paniculata*). Values are means ($n = 5, \pm$ SE). All statistical significances were recognized by $P < 0.05$ (***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, n.s.: $P \geq 0.05$)

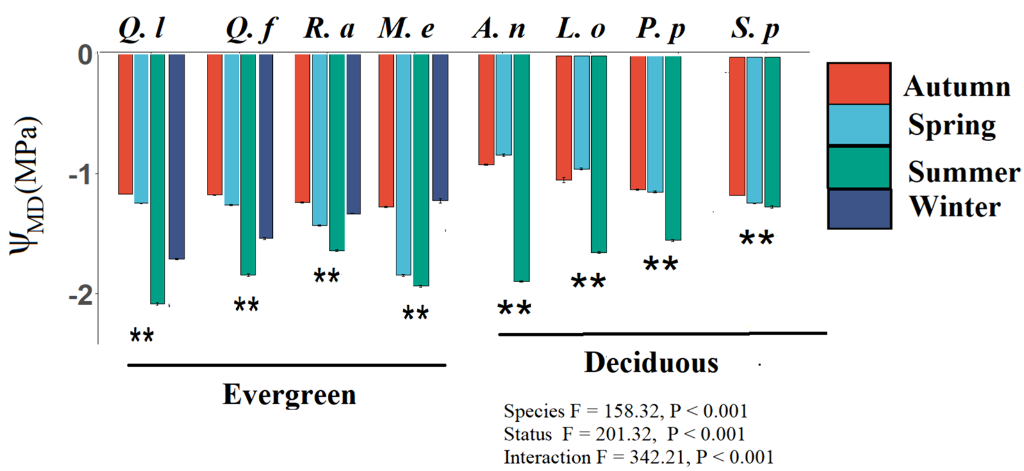

Fig. 5 Seasonal variations in mid-day water potential for four evergreen species and four deciduous tree species. Values are means ($n = 5, \pm$ SE). All statistical significances were recognized by $P < 0.05$ (***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, n.s.: $P \geq 0.05$). Note Q.l: *Quercus leucotrichophora*; R.a: *Rhododendron arboreum*; M.e: *Myrica esculenta*: Q.f: *Quercus floribunda*) and four deciduous species (L.o: *Lyonia ovalifolia*; A.n: *Alnus nepalensis*; P.p: *Pyrus pashia*; S.p: *Symplocos paniculata*)

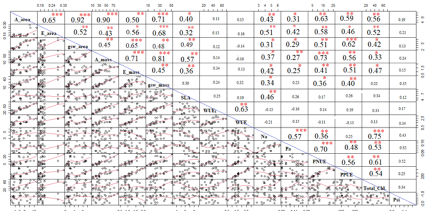

Fig. 6 Correlation for leaf ecophysiological traits across all species and season

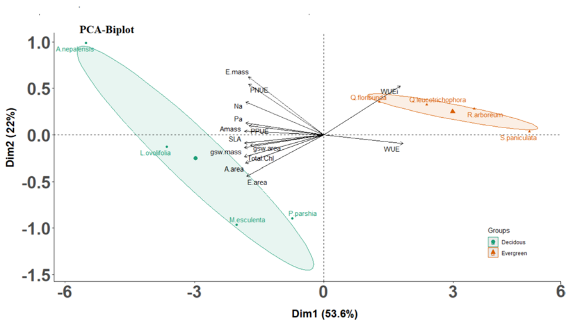

Fig. 7 Principal component analysis (PCA) of studied leaf ecophysiological traits of evergreen and deciduous trees

contents. Correlation analysis also demonstrates a negative relationship between WUE, WUE_i, and E, A, as well as gsw (Fig. 6). The PCA revealed distinct patterns of variation in leaf ecophysiological traits between evergreen and deciduous species. The first and second axes of principal component analysis (PCA) explained, respectively, 53.6% and 22% of the variation in the ecophysiological traits measured (Fig. 7). The first PCA axis was defined by gas exchange (A_{mass}, A_{area}, gsw), leaf nutrients N and P and photosynthetic nutrient use efficiency traits (PNUE, and PPUE). The gas exchange traits were positively correlated with leaf nutrient concentration. The second PCA axis reflected variation in WUE and WUE_i. The PCA also revealed a clear separation between the ecophysiological traits in species and generated two groups. Deciduous species tended to exhibit higher scores along PC1, indicating a greater photosynthetic capacity and nutrient use efficiency. PC2 explained 22% of the total variance and primarily captured variations in leaf water-use efficiency (WUE). Evergreen species exhibited higher scores along PC2, suggesting a stronger reliance on water-conserving strategies.

Discussion

Seasonal variation in leaf ecophysiology traits

The results of this study provide valuable insights into the seasonal dynamics of leaf gas exchange traits in evergreen and deciduous tree species. The contrasting patterns observed between these two groups shed light on the adaptive strategies employed by these plants to cope with changing environmental conditions throughout the year. One of the key findings of this study is the consistently higher leaf gas exchange rates in deciduous trees compared to evergreen trees throughout the growing season. Deciduous trees exhibited significantly greater mass and area-based photosynthetic rates, transpiration rates, and stomatal conductance. This pattern suggests a more efficient utilization of resources for carbon assimilation and water transpiration in deciduous species, potentially contributing to their overall growth and survival (Choat et al., 2006; Ishida et al., 2010). The significant increase in A_{area} in deciduous species, with rates being 38.89% higher than evergreen species, highlights the greater photosynthetic activity. The corresponding increase in gsw_{area} and E_{area} further supports the idea of enhanced water and CO_2 exchange in deciduous trees during the summer months (Kutsch et al., 2009; Pivovaroff et al., 2016; Albert et al., 2018; Joshi & Garkoti, 2023). Both deciduous and evergreen species exhibited a substantial increment in A_{area} between the spring to summer seasons, indicative of a vigorous growth phase. However, a subsequent decline in A_{area} was observed as the seasons transitioned from summer to autumn and summer to winter. This decline was more pronounced in deciduous species, reaching 41 to 60%, while evergreen species showed a range of 34 to 70%. The drastic reduction in A_{area} during the transition from summer to winter in deciduous species can be attributed to their leafless state during this period. The deciduous strategy involves maximizing photosynthetic rates during favorable conditions while minimizing resource loss during periods of leaflessness. In contrast, evergreen species maintain a more consistent but comparatively lower level of physiological activity throughout the year. The correlation between mass photosynthetic rate (A_{mass}) and other traits like E_{mass} and gsw_{mass} suggests that tree species with higher leaf mass invest more in photosynthetic rates and maintain greater transpiration rates. These fluctuations may be linked to factors such as temperature, light availability, and water availability (Albert et al., 2018; Pivovaroff et al., 2016). These fluctuations may be linked to factors such as temperature, light availability, and water availability.

Deciduous trees are known for their distinct seasonal leaf shedding and regrowth patterns (Devi & Garkoti, 2013). The consistently higher mass and area-based photosynthetic rates observed in deciduous trees compared to evergreen trees highlight their ability to capture and utilize sunlight more efficiently during the growing season (Tomlinson et al., 2013; Bai et al., 2015; Sancho-Knapik et al., 2021). In this study, deciduous species exhibit leaves with high mass-based photosynthetic rates (A_{mass}) and SLA. Deciduous species optimize light capture by investing heavily in leaf area relative to dry matter, which results in carbon gain at the expense of a shorter leaf lifespan. These plants shed their leaves during the winter season (Ávila-Lovera et al., 2019; Eamus, 1999; Eamus & Prichard, 1998; Eamus & Prior, 2001; Ishida et al., 2023; Powers & Tiffin, 2010; Sobrado, 1991). Conversely, evergreen species have leaves with low SLA and relatively lower A_{mass} values compared to deciduous species. Several other evergreen species exhibit a similar pattern (Ávila-Lovera et al., 2019; Eamus, 1999; Eamus & Prichard, 1998; Eamus & Prior, 2001; Ishida et al., 2023; Powers & Tiffin, 2010; Sobrado, 1991). These plants retain their leaves for more than a year, enabling them to continue photosynthesizing during the winter season, albeit at reduced rates.

Additionally, the higher transpiration rates in deciduous trees signify their greater water loss through stomatal openings (Burghardt & Riederer, 2003; Marchin et al., 2023). The increased transpiration rate in deciduous tree species is often associated with the larger leaf area during the growing season. Conversely, with the persistent foliage, evergreen trees exhibit lower photosynthetic and transpiration rates than their deciduous counterparts. This adaptation allows them to conserve water and maintain a more consistent level of photosynthesis year-round. Evergreen trees often thrive in environments with lower water availability and may play a vital role in stabilizing ecosystems during drought (Garkoti et al., 2001; Tomlinson et al., 2013).

The differences observed in stomatal conductance (gsw_{area}) among tree species further emphasize the trade-offs between water conservation and carbon gain. Deciduous trees generally exhibited higher gsw_{area} values, indicating a more open stomatal structure that facilitates increased photosynthesis but also leads to greater water loss. On the other hand, evergreen trees tend to have lower gsw_{area}, conserving water but potentially limiting their photosynthetic potential (Bai et al., 2015; Ishida et al., 2014; Pivovaroff et al., 2016; Torngern et al., 2021; Wright et al., 2004). The variations in photosynthetic N- and P-use efficiency (PNUE and PPUE) among species, seasons, and their interaction indicate the adaptability of different tree species. The deciduous species exhibited significantly higher PNUE and PPUE than the evergreen species, suggesting a more efficient use of nitrogen and phosphorus resources during photosynthesis (Bai et al., 2015; DeLucia & Schlesinger, 1995). This difference may be attributed to the deciduous species' ability to shed leaves during unfavorable seasons (winter), conserve nutrients, and optimize resource allocation when conditions are more favorable for growth (Devi & Garkoti, 2013; Manzoni et al., 2015; Marchin et al., 2010).

Conversely, water use efficiency (WUE) and intrinsic water use efficiency (WUEi) displayed an opposite trend, with evergreen species are demonstrating higher values. This outcome suggests that evergreen species have evolved mechanisms to maximize carbon gain per unit of water consumed, likely through reduced transpiration rates and more conservative water use (Fu et al., 2012; Soh et al., 2019). Among the species studied, *A. nepalensis* and *S. paniculata* trees are having the highest average values of PNUE and PPUE. In contrast, *M. esculenta* displayed the highest average values of WUEi and WUE. These species-specific differences emphasize the importance of considering individual plant traits when assessing physiological responses. This adaptation is particularly advantageous in environments with limited water availability, where evergreen species can maintain photosynthetic activity year-round.

Seasonal variations in leaf chemical and morphological traits

One notable pattern observed is the temporal dynamics of traits during leaf development. As leaves expand, an initial increase in N, P, total Chl, and SLA indicates a period of active growth and photosynthetic investment (Poorter et al., 2019; Wang et al., 2020). However, this is followed by a subsequent decline during leaf senescence, reflecting the plant's reabsorption and withdrawal of resources from aging leaves. This difference suggests that deciduous trees may be more resource-demanding during the active growth period, whereas evergreen trees adopt a more conservative resource-use strategy, possibly to cope with extended periods of environmental stress or resource limitation (Reich et al., 1997; Eamus, 1999; Poorter and Bongers 2006; Bai et al., 2015). The peak in these traits, observed during the summer, reflects the optimal conditions for plant growth and photosynthesis. This highlights interspecific differences in nutrient acquisition and utilization. These variations could influence the competitive interactions between deciduous and evergreen species and their responses to changing environmental conditions (Bai et al., 2015; Joshi & Garkoti, 2023; Joshi et al., 2024). This suggests that deciduous trees allocate more nutrients to their leaves and have a higher chlorophyll content on a mass basis. The higher SLA in deciduous trees could be an adaptation to capture more sunlight during the growing season when leaves are present. Among deciduous species, *A. nepalensis* had the highest area-based leaf concentrations of N, P, total Chl, and SLA. This species-specific variation indicates that different tree species have distinct ecological strategies for nutrient allocation and light capture. Within evergreen species, *Q. floribunda* exhibited the lowest P_{area}, and *R. arboretum* had the highest N_{area}. This suggests that even within the same functional group, species may have unique nutrient strategies. This highlights interspecific differences in nutrient acquisition and utilization. *M. esculenta* had the lowest total chlorophyll content in winter among evergreen species. This finding aligns with expectations, as evergreen trees often reduce chlorophyll content during the winter months to minimize resource loss. However, this is followed by a subsequent decline during leaf senescence, reflecting the plant's reabsorption and withdrawal of resources from aging leaves. This pattern underscores the plants' efficient resource allocation strategies to maximize their fitness and resource use efficiency.

During the summer season, characterized by fully expanded leaves and presumably higher evaporative demand, it is observed that Ψ_{md} consistently remained above − 2.0 MPa across all tree species (Garkoti et al., 2003; Poudyal et al., 2004; Singh et al., 2006; Zobel et al., 2001). This indicates that the trees maintained relatively high water potential during the day, suggesting effective water uptake and management. Specifically, the results indicate that the differences in Ψ_{md} between evergreen and deciduous trees were more pronounced during the summer season when leaves were fully expanded. This suggests a potential adaptation or response to environmental conditions during the peak of the growing season. The midday water potential for deciduous species was significantly higher than that for evergreen species during the summer season. This difference may be attributed to the distinct physiological and ecological characteristics of deciduous and evergreen trees. Deciduous trees, which shed their leaves seasonally, demonstrated midday water potential values ranging from − 1.11 to − 1.74 MPa. This suggests that deciduous trees, in this particular study, were able to maintain a higher water potential during the day, possibly due to increased water uptake. Evergreen trees, characterized by retaining leaves throughout the year, exhibited midday water potential values ranging from − 1.62 to − 1.93 MPa. These values were notably lower compared to deciduous trees, indicating a different water-use strategy or physiological adaptation in response to the environmental conditions (Hasselquist et al., 2010; Ishida et al., 2014; Palomo-Kumul et al., 2021). Conversely, evergreen species may excel in more consistently humid or temperate conditions due to their ability to sustain water uptake and transpiration throughout the year.

The positive correlations between mass-based rates of photosynthesis, transpiration, and stomatal conductance with area-based nutrient concentrations (N and P) and specific leaf area (SLA) indicate that these physiological processes are closely linked to the plant's nutrient status and leaf structural characteristics (Niinements, 2007; Wright et al., 2003; Reich, 2014). Plants with higher nutrient concentrations and a greater SLA are likely to have more resources for photosynthesis and transpiration, leading to increased rates of these processes (He et al., 2009; Liu et al., 2023). The revelation that mass-based A, E, and gsw are more strongly influenced by area-based N, P, and SLA compared to their area-based counterparts, which underscores the importance of considering plant size and nutrient content when studying ecological processes (Bahar et al., 2017; Onoda et al., 2017; Han et al., 2020). The negative relationship between water use efficiency (WUE and WUEi) and transpiration (E) and stomatal conductance (gsw) suggests that plants with higher WUE values tend to exhibit reduced water loss through transpiration (Cooley et al., 2022; Guerrieri et al., 2019; Hatfield et al., 2019; Zhu et al., 2021). Moreover, various tree species may demonstrate distinct adaptive strategies in response to stomatal density, soil resource availability, including soil water and nutrient levels (Islam et al., 2024; Joswig et al., 2022). These differences may variably influence the growth, survival, and competitive ability of the coexisting species. Consequently, further investigations are required to investigate these hypotheses, unravel the underlying mechanisms and ecological consequences involved in empirically assessing these hypotheses, and gain deeper insights into associated mechanisms and ecological consequences. The results of the PCA highlight the contrasting ecophysiological strategies employed by evergreen and deciduous trees to cope with seasonal environmental variations. Evergreen species maintain relatively stable leaf traits throughout the year, indicating a conservative strategy optimized for resource retention and long-term survival. In contrast, deciduous species exhibit more flexible traits, adjusting their physiological processes in response to seasonal changes in environmental conditions.

Conclusion

For both deciduous and evergreen species, gas exchange parameters and leaf water potential were higher during the summer compared to the autumn or winter seasons. The co-occurring evergreen and deciduous trees in the white oak forest exhibited differences in physiological, morphological, and chemical traits. The deciduous trees displayed higher photosynthesis per unit mass and area, transpiration rate, stomatal conductance, PNUE, PPUE, and SLA compared to the evergreen trees. Our findings support that deciduous trees adopt an acquisitive leaf strategy, whereas evergreen trees exhibit a conservative leaf strategy. Furthermore, the present study provided evidence for the trade-off relationship among leaf physiological, morphological, chemical traits and water use efficiency. We observed relatively higher leaf N, P, and pigment concentrations, along with higher SLA and leaf area, in deciduous trees compared to the evergreen trees. These characteristics may effectively control leaf gas exchange parameters and demonstrate more suitable eco-physiological adaptation strategies. Additionally, leaf age has shown a significant negative influence on leaf physiological, morphological, and chemical traits, with higher values observed in summer compared to autumn and winter. Mature and fully expanded leaves in deciduous and evergreen species showed higher ecophysiological functions by assimilating more CO_2, leading to optimum productivity during the summer compared to the old and senescent leaves in autumn and winter. Further studies are required to gain a deeper understanding of the influence of soil moisture, and stomatal density on the ecophysiology of deciduous and evergreen species in the central Himalaya.

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Data availability The authors confirm that the data supporting the findings of this study are available within the article.

Declarations

Ethics approval All authors have read, understood, and have complied as applicable with the statement on "Ethical responsibilities of Authors" as found in the Instructions for Authors.

Consent for publication All authors gave their consent for publication in the journal.

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