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Drought Resilience of *Pinus kesiya* Royle ex Gordon Populations in Manipur, North-East India

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***Abstract*:** This study evaluated water-use efficiency (WUE) and drought-stress-related traits in two *P. kesiya* populations, the Eastern (Andro) and Western (Langol), from the valley region of Manipur. The populations were sampled from sites with bioclimatic and edaphic conditions that were significantly similar but in reproductive isolation. Five trees per population were sampled for needle and wood cores for measuring wood moisture content (WMC), stomatal number per length (SNL), relative water content (RWC), and proline concentration, along with growth traits viz. height, girth at breast height. Significant differences were observed in SNL, WMC, and proline content, but not in RWC. Andro showed higher SNL (67) than Langol (57.11), suggesting greater stomatal conductance and potentially lower WUE under drought conditions. Langol's slightly lower SNL and higher proline (0.19 mM, albeit Andro's 0.14 mM) indicate a water conservation strategy and stronger biochemical defenses against drought stress. Andro's higher WMC (46.18) than Langol's 33.10 supports hydraulic resilience. Both populations maintained high RWC, indicating effective leaf hydration. These findings highlight *P. kesiya's* physiological plasticity, with Langol adapted to drier conditions and Andro suited to wetter environments, informing afforestation and forest management strategies in North-East India amid escalating climate change impacts.

***Keywords*:** *Pinus kesiya,* Water-use efficiency, Drought tolerance, Climate change, Forest resilience.

1. INTRODUCTION

Climate change profoundly alters global forest ecosystems, with projections indicating increased frequency and intensity of droughts, elevated temperatures, and erratic precipitation patterns (IPCC, 2022), severely affecting the biodiversity of tropical and subtropical regions of India, such as the North-Eastern Region (NER). NER, encompassing eight states and characterized by its unique subtropical wet forests, faces additional pressures of drastic changes from anthropogenic activities such as shifting cultivation (jhum) and deforestation, which interact synergistically with climate change to degrade forest health (Chaturvedi et al., 2011; Roy et al., 2021; Gogoi & Lahon, 2022). Along with these pressures, the NER has also been experiencing heightened climate variability, including prolonged dry seasons and reduced monsoon reliability, which exacerbates drought stress on vegetation (Singh & Kumar, 2022; Roy et al., 2021). These changes pose severe threats to endemic forests and keystone species like *Pinus kesiya* Royle ex Gordon (Khasi Pine), a dominant conifer that plays critical roles in carbon sequestration, soil

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stabilisation, and local livelihoods (Patricio & Tulod, 2010).

Drought resilience in trees involves a suite of physiological, biochemical, and morphological adaptations that enable survival and productivity under water-limited conditions (McDowell et al., 2008; Allen et al., 2010). Water-use efficiency (WUE), the ratio of carbon assimilated to water transpired, is a pivotal indicator of drought tolerance, enabling plants to optimise growth while minimising water loss (Bramley et al., 2013; Frank et al., 2015). In conifers, WUE is modulated by traits such as stomatal density (or number per length in needle leaves), relative water content (RWC), wood moisture content (WMC), and osmo-protectant accumulation like proline (Szabados & Savouré, 2010; Corcuera et al., 2012; Duan et al., 2024). Proline, in particular, acts as an osmo-protectant, stabilizing cellular structures and mitigating oxidative damage during water deficits (Delauney & Verma, 1993; Newton et al., 1986; Shabnam et al., 2016). RWC reflects leaf hydration status and is a predictor of drought-induced mortality (Sapes & Sala, 2021; Keyvan, 2010; Blackman et al., 2023), while WMC indicates hydraulic capacitance and resilience to embolism (Ziemińska et al., 2020). Stomatal traits regulate gas exchange and transpiration, with lower densities often conferring higher WUE (Kouwenberg et al., 2003; Hepworth et al., 2015; Pirasteh-Anosheh et al., 2016; Bertolino et al., 2019). In the context of NER, where climate models predict a 1-2°C temperature rise and 10-20% precipitation decline by mid-century (Murthy et al., 2011), understanding intraspecific variation in these traits is essential for predicting species responses.

Pinus kesiya, distributed across altitudes of 350-2900 m, exhibits phenotypic plasticity, but population-level adaptations remain understudied (Fan et al., 2019). Previous research on conifers highlights that populations from drier sites often exhibit conservative water-use strategies, such as reduced stomatal conductance and elevated proline levels, which enhance survival but may limit growth (Olano et al., 2014). Conversely, wetter-site populations may prioritise hydraulic efficiency, as in higher WMC (Holbrook, 1995; Fan et al., 2019).

Therefore, the present study aimed to provide a foundation for drought resilience breeding programs on *P. kesiya* populations by expanding on prior works (1) to quantify variation in SNL, RWC, WMC, and proline content between two populations of Manipur; (2) to correlate these traits with growth parameters and bioclimatic data and soil characters; and (3) to discuss implications for climate change adaptation in NER's forests.

2. MATERIALS AND METHODS

2.1. Study Area

The study was conducted in two *P. kesiya* populations within the Central Forest Division of Manipur, India *viz.* Langol (Imphal West, 24.82°N, 93.95°E, ~800 m asl) and Andro (Imphal East, 24.74°N, 94.04°E, ~900 m asl). Both sites represent subtropical wet forests with a pronounced dry season from November to March and receive annual rainfall of ~1200-1400 mm (IMD, 2023). Bioclimatic variables, including mean annual temperature (18-25°C), precipitation of the driest quarter (~100-150 mm), and isothermality, were extracted from the WorldClim database (Hijman et al., 2005).

2.2. Field Sampling

Field sampling adhered to the National Working Plan Code (2023) guidelines, ensuring minimal disturbance in these reserved forests. Five trees (with GBH >50 cm) per population were randomly selected, maintaining a minimum distance of 50 m along a North-South transect to capture maximum diversity (Vaishnav et al., 2021). Trees were of similar age (estimated 20-30 years via increment borers) and health. Three replicates needle bunches were collected from mid-canopy branches using pole pruners for biochemical and morphological analyses. Wood cores (5 mm diameter) were extracted at breast height (1.3 m) using a Haglof increment borer for WMC assessment (Ziemińska et al., 2020). Growth traits: height (H), girth at breast height (GBH), bark thickness (Bt), and clear bole height (CBH were measured with a clinometer, measuring tape, and bark gauge, respectively. GPS coordinates were recorded with the help of a Garmin eTrex-30 device for geospatial integration with climate data. Sampling was conducted in March (the dry-season peak) to capture stress responses (Pumijumnong & Wanyaphet, 2006; Fan et al., 2019).

2.3. Laboratory Work

Proline was extracted from fresh needles using a modified eco-friendly ninhydrin protocol (Carillo & Gibon, 2011; Shabnam et al., 2016) and quantified by spectrophotometry at 520 nm against L-proline standards. Using epidermal impressions and microscopy, SNL was determined on both needle abaxial and adaxial surfaces (Kouwenberg et al., 2003; Hepworth et al., 2015). RWC was calculated as '(fresh weight - dry weight)/(turgid weight - dry weight) × 100' (Sapes & Sala, 2021; Li et al., 2024). WMC was measured gravimetrically on wood cores after ovendrying at 105°C (Ziemińska et al., 2020). All measurements were replicated 3 times per tree, whereas wood core samples were replicated only 2 times.

Table 1. Bioclimatic variables of the two sampled populations derived from Worldclim data (Worldclim.org)

Bioclimatic variable	Langol	Andro
Annual Mean Temperature [°C]	22.6	22.6
Mean Monthly Temperature Range [°C]	10.4	10.4
Isothermality (2/7) (* 100)	49.6	49.1
Temperature Seasonality (STD * 100)	346.4	342
Max Temperature of Warmest Month [°C]	30.6	30.9
Min Temperature of Coldest Month [°C]	9.7	9.7
Temperature Annual Range (5–6) [°C]	20.9	21.2
Mean Temperature of Wettest Quarter [°C]	25.6	25.4
Mean Temperature of Driest Quarter [°C]	18.7	18.7
Mean Temperature of Warmest Quarter [°C]	25.7	25.5
Mean Temperature of Coldest Quarter [°C]	17.6	17.6
Annual Precipitation [mm]	1578	1632
Precipitation of Wettest Month [mm]	343	356
Precipitation of Driest Month [mm]	0	0
Precipitation Seasonality (CV)	87.4	91.9
Precipitation of Wettest Quarter [mm]	899	966
Precipitation of Driest Quarter [mm]	52	48
Precipitation of Warmest Quarter [mm]	706	781
Precipitation of Coldest Quarter [mm]	64	59

2.4. Data Analysis

Descriptive statistics and correlations (Pearson's) were performed using Microsoft Excel and PAST v4.0 (Hammer et al., 2001). Significance level was determined at $p < 0.05$. Trait correlations with bioclimatic variables were analysed via regression models ® v4.2).

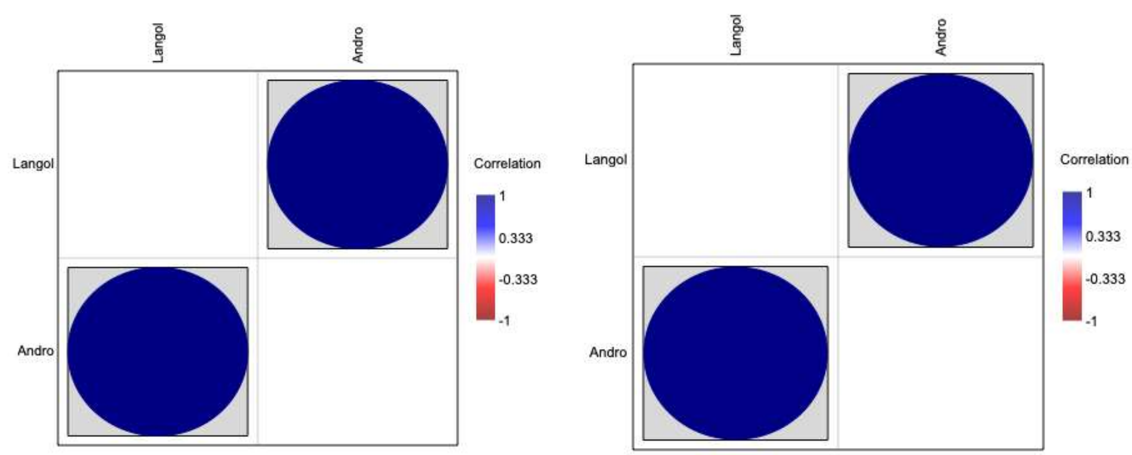
3. RESULTS AND DISCUSSION

3.1. Bioclimatic Variables, Soil Variables, and Growth Characteristics

The bioclimatic variables from the two sampled

Table 2. Physical and chemical properties of soil at 25cm depth derived from (www.soilgrid.org)

Parameter	Langol	Andro
Organic carbon density (hg/m^3)	183	191
Soil organic carbon (dg/kg)	163	152
Bulk density (cg/cm^3)	127	125
Clay content (g/kg)	348	364
Coarse fragment (cm^3/dm^3)	209	183
Sand (g/kg)	299	282
Silt (g/kg)	353	353
Volume water content at -10kpa ($(10^{-2} cm^3 cm^{-2})*10$)	394	407
Volume water content at -33kpa ($(10^{-2} cm^3 cm^{-2})*10$)	342	356
Volume water content at -1500kpa ($(10^{-2} cm^3 cm^{-2})*10$)	173	182
Cation exchange capacity (at pH 7)	163	152
Nitrogen (cg/kg)	190	161
pH of water	5.3	5.4



(a) (b)

Figure 1. a) Significant *($p<0.05$)* Pearson's correlation between the bioclimatic variables of the two study sites determined the homogeneity of the bioclimatic conditions in the sites. b) significant *($p<0.05$)* Pearson's correlation between the physical and chemical properties of the soil of the two study sites determined the homogeneity of the soil properties of the sites

populations (Langol and Andro) show high similarity, with annual mean temperatures of 22.6°C for both sites, identical minimum temperatures of the coldest month (9.7°C), and comparable precipitation patterns (e.g., annual precipitation of 1578 mm in Langol vs 1632 mm in Andro (Table 1). The soil's physical and chemical properties also show high similarity (Table 2). The significant Pearson's correlation ($p < 0.05$) between the bioclimatic variables and soil properties indicates homogeneous environmental and edaphic conditions across the sites (Figure 1). ANOVA revealed no significant differences among populations in growth traits: GBH, CBH, H, and Bt. The homogeneity of bioclimatic and soil conditions across the two sites supports the hypothesis that trait divergences arise from reproductive isolation and subtle microclimatic influences rather than from environmental heterogeneity.

3.2. Proline Content (Pro)

Proline content was higher in Langol (0.19 mM) than in Andro (0.14 mM) (Table 7), aligning with its role as an osmo-protectant under drought (Szabados & Savouré, 2010; Khoma et al., 2021). It reflects the mirror patterns observed in *Pinus pinaster* (Corcuera et al., 2012) and *Pinus taeda* (Newton et al., 1986), in which drier sites accumulate more proline to enhance cellular stability under water deficits (Table 4). There was no significant variation between populations (or among trees within populations). Pearson's correlation analysis showed a significant negative correlation between proline content and WMC, but no significant correlations with stomatal number/length (SNL) or RWC (Table 5). The lack of significant between-population differences in proline content, coupled with its negative correlation with WMC, aligns with proline's role during water deficits (Dien et al., 2019; Kijowska et al., 2023; Poury et al., 2023). Similar to the observation of overexpression of proline metabolism exhibiting enhanced drought resistance and proline degradation response sensitively to changing moisture content (Szabados & Savouré, 2010; Khoma et al., 2021). This negative correlation with WMC underscores proline's compensatory role during moisture stress, supporting Langol's water-conserving phenotype and increased drought resilience.

3.3. Stomatal Number/Length (SNL)

The Andro population exhibited a higher mean SNL (67.00) than Langol (57.11) (Table 4), implying lower WUE in Andro due to increased transpiration (Hepworth et al., 2016; Pirasteh-Anosheh et al., 2016). Lower SNL in Langol aligns with drought adaptations in conifers (Kouwenberg et al., 2003; Miyazawa et al., 2006; Moran et al., 2017; Petek et al., 2023). No significant difference in SNL was found between populations, but significant variation was found among trees within populations.

Table 3. Variation based on growth characters of the two populations of the sample trees

Locations	Accessions	GBH (cm)	CBH (m)	H (m)	Bt (cm)
Langol	MNCF_CC2	107	3.43	11.3	1.23
Langol	MNCF_CC3	60	2	5.48	1.13
Langol	MNCF_CC4	101	2	6.85	1.26
Langol	MNCF_CC6	110	5.5	10.9	1.13
Andro	MNAN_HH1	79	2	8.49	1.2
Andro	MNAN_HH2	68	2	8.49	1.2
Andro	MNAN_HH3	147.5	3	12.33	1.83
Andro	MNANLM1	89	2	8.22	0.97
Andro	MNANLM2	83.5	1.5	9.45	1.1

H – height, GBH – girth at the breast height, CBH – clear bole height, Bt – bark thickness

Table 4. Mean values with standard deviation of the functional traits

Population	Pro (mM)	SNL	RWC (%)	MC (%)
Langol	0.19±0.09	57.11±12.14	91.95±13.83	33.10±3.65
Andro	0.14±0.06	67.00±10.03	89.85±1.77	46.18±3.74

Pro- Proline content, SNL- Stomatal number/length, RWC- Relative Water content of leaves, WMC- Wood Moisture Content

Table 5. Correlations between functional traits, based on Pearson's linear correlation coefficients (below the diagonal) and p-values (above the diagonal), confirmed a significant negative correlation between Proline content (Pro) and wood moisture content (WMC)

Population	Pro (mM)	SNL	RWC (%)	MC (%)
Pro (mM)		0.08	0.05	0.01*
SNL	-0.31		0.99	0.06
RWC (%)	-0.35	-0.00		0.44
MC (%)	-0.53*	0.41	-0.18	

*Significant at $p < 0.05$

Pro- Proline content, SNL- Stomatal number/length, RWC- Relative Water content of leaves, WMC- Wood Moisture Content

3.4. Relative Water Content (RWC)

RWC of leaves was slightly higher in Langol (91.95 %) than in Andro (89.85 %) (Table 5). In the RWC, no significant variation between populations was observed, but significant differences among trees within populations were observed. The non-significant differences in RWC between populations indicate that leaf hydration levels are maintained consistently in both Langol and Andro, reflecting effective water-retention mechanisms. Although not significantly correlated with other traits, the trend of negative associations with proline suggests a potential trade-off where higher RWC might reduce the need for osmo-protectants, contributing to overall drought tolerance strategies in these populations. RWC exhibited significant within-population variation, serving as a reliable marker of hydration status and drought response. Declines in RWC under stress are common, but resilient plants recover rapidly post-drought. The stability across populations, despite intraspecific variability, indicates inherent tolerance, as RWC correlates positively with root traits and overall survival. RWC reductions during drought highlight adaptive strategies such as stomatal regulation. This trait's pattern suggests both sites are drought-suitable, with populations capable of maintaining turgor through other biochemical adjustments (Fu et al., 2017; Meena & Kaur, 2019; Haghpanah, 2024).

3.5. Wood Moisture Content (WMC)

WMC was markedly higher in Andro (46.18%) than in Langol (33.10%), reflecting better water-use efficiency of Langol (Table 4). There was significant variation between populations, but no significant differences among trees within populations. A significant negative correlation was found with proline, while correlations with SNL and RWC (Table 5) were non-significant, suggesting that as WMC declines, proline compensates to stabilise cellular functions. This is consistent with findings that drought intensity alters biomass distribution, favouring roots for improved water uptake (Wang et al., 2024). Therefore, the langol population with lower WMC is more suited to prolonged drought, as it promotes adaptive mechanisms like dehydration tolerance

This study hypothesises that, despite similar bioclimatic conditions, reproductive isolation between the Andro (Eastern) and Langol (Western) populations of *P. kesiya* in Manipur has led to divergent drought adaptation strategies. Specifically, we posit that the Langol population, potentially exposed to microclimatic drier spells due to soil differences (sandy loam *vs* clay loam), will exhibit traits indicative of higher drought tolerance, including lower SNL, higher proline accumulation, and lower WMC, reflecting a water-conserving phenotype. In contrast, the Andro population is expected to show traits favouring growth under moist conditions, such as higher SNL and WMC, but potentially lower WUE under stress. This hypothesis is grounded in evolutionary ecology principles, where local selection pressures drive trait divergence (Choat et al., 2018; Anderegg et al., 2016). Justifying the aims, this research addresses a critical gap in NER's conifer studies by integrating multiple WUE traits to inform climate-resilient reforestation. Amid projections of intensified droughts (Aragão et al., 2018), identifying tolerant genotypes could enhance forest management, biodiversity conservation, and carbon sinks in vulnerable regions (Patricio & Tulod, 2010; Olano et al., 2014; Duan et al., 2024).

4. CONCLUSION

The analysis of bioclimatic, edaphic, growth, and functional trait data from the Langol and Andro populations of *Pinus kesiya* demonstrates overall similarity in environmental conditions and morphological development, affirming their adaptation to a shared subtropical climate with pronounced seasonal variations of the functional traits (Pro, SNL, RWC, WMC). Andro appears more suitable for the tree species studied. This is evidenced by lower proline content (indicating reduced osmotic stress), higher stomatal number/length (suggesting improved photosynthetic potential), more stable relative leaf water content (lower variability), and significantly higher wood moisture content (enhancing hydration and structural resilience). In contrast, Langol shows signs of mild stress (elevated Pro and variable RWC) and lower WMC, which may compromise long-term performance despite similar growth outcomes. If selecting for optimal physiological health, Andro is recommended; however, site-specific management could mitigate differences.

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CRediT authorship contribution statement

Z. Philamazan Peace Shimray: Field data collection; laboratory work, data curation; result compilation; writing original draft of the manuscript. Hira Soraisam: Field data collection; laboratory work, data curation; result compilation; writing original draft of the manuscript. Vivek Vaishnav: Conceptualisation, Supervision, Validation, visualisation, review and editing.

Data availability statement

All data generated or analysed during this study are included in this published article. However, any additional data are available from the corresponding author upon request.

Conflict of interest

The authors declare that they have no conflict of interest.

REFERENCES

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., & Cobb, N. (2010). A global overview of drought- and heat-induced tree mortality reveals emerging climate-change risks for forests. *Forest ecology and management*, *259*(4), 660-684.

Anderegg, W.R., Klein, T., Bartlett, M., Sack, L., Pellegrini, A.F., Choat, B., & Jansen, S. (2016). Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. *Proceedings of the National Academy of Sciences*, *113*(18), 5024-5029.

Aragão, L.E.O.C., Anderson, L.O., Fonseca, M.G., Rosan, T.M., Vedovato, L.B., Wagner, F.H., Silva, C.V.J., Silva Junior, C.H.L., Arai, E., Aguiar, A.P., Barlow, J., Berenguer, E., Deeter, M.N., Domingues, L.G., Gatti, L., Gloor, M., Malhi, Y., Marengo, J.A., Miller, J.B., ... Saatchi, S. (2018). 21st century drought-related fires counteract the decline of Amazon deforestation carbon emissions. *Nature Communications, 9*(1), Article 536. https://doi.org/10.1038/s41467-017-02771-y

Bertolino, L.T., Caine, R.S., & Gray, J.E. (2019). Impact of stomatal density and morphology on water-use efficiency in a changing world. *Frontiers in Plant Science*, *10*, 225.

Blackman, C.J., Billon, L.M., Cartailler, J., Torres-Ruiz, J.M., & Cochard, H. (2023). Key hydraulic traits control the dynamics of plant dehydration in four contrasting tree species during drought. *Tree Physiology*, *43*(10), 1772-1783.

Bramley, H., Turner, N.C., & Siddique, K.H.M. (2013). Water use efficiency. In *Genomics and breeding for climate-resilient crops* (Vol. 2, pp. 225–268). Springer. https://doi.org/10.1007/978-3-642-37048-9_6

Carillo, P., & Gibon, Y. (2011). Protocol: extraction and determination of proline. *PrometheusWiki*, *2011*, 1-5.

Chaturvedi, R.K., Gopalakrishnan, R., Jayaraman, M., Bala, G., Joshi, N.V., Sukumar, R., & Ravindranath, N.H. (2011). Impact of climate change on Indian forests: a dynamic vegetation modeling approach. *Mitigation and adaptation strategies for global change*, *16*(2), 119-142.

Choat, B., Brodribb, T.J., Brodersen, C.R., Duursma, R.A., López, R., & Medlyn, B.E. (2018). Triggers of tree mortality under drought. *Nature*, *558*(7711), 531-539.

Corcuera, L., Gil-Pelegrín, E., & Notivol, E. (2012). Differences in hydraulic architecture between mesic and xeric Pinus pinaster populations at the seedling stage. *Tree Physiology*, *32*(12), 1442-1457.

Delauney, A.J. & Verma, D.P.S. (1993). Proline biosynthesis and osmoregulation in plants. *The Plant Journal, 4*, 215-223.

Dien, D.C., Mochizuki, T., & Yamakawa, T. (2019). Effect of various drought stresses and subsequent recovery on proline, total soluble sugar and starch metabolisms in Rice (Oryza sativa L.) varieties. *Plant Production Science*, *22*(4), 530-545.

Duan, H., Shao, C., Zhao, N., Wang, D., Resco de Dios, V., & Tissue, D.T. (2024). The role of leaf superoxide dismutase and proline on intra-specific photosynthesis recovery of Schima superba following drought. *Scientific Reports*, *14*(1), 8824.

Fan ZX, et al. (2019). Growth responses of Pinus kesiya var. langbianensis to climate variability in the Ailao Mountains, Southwest China. *Dendrochronologia*, *53*, 39-46.

Frank, D.C., Poulter, B., Saurer, M., Esper, J., Huntingford, C., Helle, G., ... & Weigl, M. (2015). Water-use efficiency and transpiration across European forests during the Anthropocene. *Nature Climate Change*, *5*(6), 579-583.

Fu, Y., Ma, H., Chen, S., Gu, T., & Gong, J. (2017). Control of proline accumulation under drought via a novel pathway comprising the histone methylase CAU1 and the transcription factor ANAC055. *Journal of Experimental Botany, 69*, 579-588.

Gogoi, B., & Lahon, D. (2022). Impact of climate change on Biodiversity of Northeast India: An overview. *Indian Journal of Applied and Pure Biology, 37*(2), 322-331.

Haghpanah, M., Hashemipetroudi, S., Arzani, A., & Araniti, F. (2024). Drought tolerance in plants: Physiological and molecular responses. *Plants*, *13*(21), 2962.

Hammer, Ø., David, A.T., & Paul, D.R. (2001). Past: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*, *4*(1). http://palaeo-electronica.org/2001_1/past/issue1_01.htm.

Hepworth, C., Turner, C., Landim, M.G., Cameron, D., & Grey, J.E. (2016). Balancing water uptake and loss through the coordinated regulation of stomatal and root development. *PloS one*, *11*(6), e0156930.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology: A Journal of the Royal Meteorological Society*, *25*(15), 1965-1978.

Holbrook, N.M. (1995). Stem water storage. In *Plant stems* (pp. 151-174). Academic Press.

IPCC. (2022). Climate Change 2022: Impacts, Adaptation, and Vulnerability. *Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* [H.-O. Pörtner, D.C. Roberts, M. Tignor, E.S. Poloczanska, K. Mintenbeck, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, B. Rama (eds.)]. Cambridge University Press. Cambridge University Press, Cambridge, UK and New York, NY, USA, 3056 pp., doi:10.1017/9781009325844.

Keyvan, S. (2010). The effects of drought stress on yield, relative water content, proline, soluble carbohydrates and chlorophyll of bread wheat cultivars. *Journal of Animal and Plant Sciences, 8*(3), 1051-1060

Khoma, Y.A., Nesterenko, O.G., Kutsokon, N.K., Khudolieieva, L.V., Shevchenko, V.V., & Rashydov, N.M. (2021). Proline content in the leaves of poplar and willow under water deficit. *Regulatory Mechanisms in Biosystems*, *12*(3), 519-522.

Kijowska-Oberc, J., Dylewski, Ł., & Ratajczak, E. (2023). Proline concentrations in seedlings of woody plants change with drought stress duration and are mediated by seed characteristics: a meta-analysis. *Scientific Reports*, *13*(1), 15157.

Kouwenberg, L.L., McElwain, J.C., Kürschner, W.M., Wagner, F., Beerling, D.J., Mayle, F.E., & Visscher, H. (2003). Stomatal frequency adjustment of four conifer species to historical changes in atmospheric CO2. *American Journal of Botany*, *90*(4), 610-619.

Li, Z.K., Li, H.L., Gong, X.W., Wang, H.F., & Hao, G.Y. (2024). Prediction and mapping of leaf water content in Populus alba var. pyramidalis using hyperspectral imagery. *Plant Methods*, *20*(1), 184.

McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., & Yepez, E.A. (2008). Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought?. *New Phytologist*, *178*(4), 719-739.

Meena, Y.K., & Kaur, N. (2019). Towards an understanding of physiological and biochemical mechanisms of drought tolerance in plant. *Annual Research & Review in Biology*.

Miyazawa, S.I., Livingston, N.J., & Turpin, D.H. (2006). Stomatal development in new leaves is related to the stomatal conductance of mature leaves in poplar (Populus trichocarpa× P. deltoides). *Journal of Experimental Botany*, *57*(2), 373-380.

Moran, E., Lauder, J., Musser, C., Stathos, A., & Shu, M. (2017). The genetics of drought tolerance in conifers. *New Phytologist*, *216*(4), 1034-1048.

Murthy, I.K., Tiwari, R., & Ravindranath, N.H. (2011). Climate change and forests in India: adaptation opportunities and challenges. *Mitigation and adaptation strategies for global change*, *16*(2), 161-175.

National Working Plan Code (2023). MoEFCC, New Delhi, India

Newton, R.J., Sen, S., & Puryear, J.D. (1986). Free proline changes in Pinus taeda L. callus in response to drought stress. *Tree Physiology*, *1*(3), 325-332.

Olano, J.M., Linares, J.C., García-Cervigón, A.I., Arzac, A., Delgado, A.D., & Rozas, V. (2014). Drought-induced increase in water-use efficiency reduces secondary tree growth and tracheid wall thickness in a Mediterranean conifer. *Oecologia, 176*, 273-283.

Patricio, J.H.P., & Tulod, A.M. (2010). Carbon sequestration potential of Benguet pine (*Pinus kesiya*) plantations in Bukidnon, Philippines. *Journal of Nature Studies*, *9*(1), 99-104.

Petek, A., Petrík, P., Lamarque, L.J., Cochard, H., Burlett, R., & Delzon, S. (2023). Drought survival in conifer species is related to the time required to cross the stomatal safety margin. *Journal of Experimental Botany*, *74*(21), 6847-6859.

Pirasteh-Anosheh, H., Saed-Moucheshi, A., Pakniyat, H., & Pessarakli, M. (2016). Stomatal responses to drought stress. *Water stress and crop plants: A sustainable approach*, *1*, 24-40.

Poury, N., Seifi, E., & Alizadeh, M. (2023). Effects of salinity and proline on growth and physiological characteristics of three olive cultivars. *Gesunde Pflanzen*, *75*(4), 1169-1180.

Pumijumnong, N., & Wanyaphet, T. (2006). Seasonal cambial activity and tree-ring formation of Pinus merkusii and Pinus kesiya in Northern Thailand in dependence on climate. *Forest ecology and* *management*, *226*(1-3), 279-289.

Roy, A., Kolady, D., Paudel, B., Yumnam, A., Mridha, N., Chakraborty, D., & Singh, N.U. (2021). Recent trends and impacts of climate change in North-Eastern region of India:A review. *Journal of Environmental Biology*, *42*(6), 1415-1424.

Sapes, G., & Sala, A. (2021). Relative water content consistently predicts drought mortality risk in seedling populations with different morphology, physiology and times to death. *Plant, Cell & Environment*, *44*(10), 3322-3335.

Shabnam, N., Tripathi, I., Sharmila, P., & Pardha-Saradhi, P. (2016). A rapid, ideal, and eco-friendlier protocol for quantifying proline. *Protoplasma*, *253*(6), 1577-1582.

Singh, H., & Kumar, M. (2022). Climate change and its impact on Indian Himalayan forests: Current status and research needs. In *Climate change: impacts, responses and sustainability in the Indian Himalaya* (pp. 223-242). Cham: Springer International Publishing.

Szabados, L., & Savouré, A. (2010). Proline: a multifunctional amino acid. *Trends in plant science*, *15*(2), 89-97.

Vaishnav, V., Kumar, P., Shirke, P.A., & Rana, T.S. (2021). Genetic variation in carbon isotope discrimination-based water use efficiency of teak (Tectona grandis L. f.) and its association with growth and wood quality traits. *Trees*, *35*(3), 799-807.

Wang, X., Fan, Y., Yan, M., Tao, Z., He, D., Du, G., ... & Si, B. (2024). Direct characterization of deep soil water depletion reveals hydraulic adjustment of apple trees to edaphic changes. *Agricultural and Forest Meteorology*, *348*, 109932.

Ziemińska, K., Rosa, E., Gleason, S.M., & Holbrook, N.M. (2020). Wood day capacitance is related to water content, wood density, and anatomy across 30 temperate tree species. *Plant, Cell & Environment*, *43*(12), 3048-3067.