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The impact of climate on the dominant height and climate thresholds for *P. elliottii*, *P. taeda*, *P. patula*, and *P. patula x P. tecunumanii* plantation forests

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Abstract

Plantation forests were introduced into South Africa to satisfy the regional demand for wood-based products, which are largely found in the Mpumalanga province. To better understand the impacts of climate on the dominant height growth of commercially important plantation species, enumeration data collected from 2012 to 2023 was scrutinised, representing 34740 plots in 2082 plantation compartments. Statistically significant multiple linear regression models were developed to predict dominant heights for *Pinus elliottii*, *Pinus taeda*, *Pinus patula,* and *Pinus patula x Pinus tecunumanii* hybrids using climate variables as independent factors. Mean annual maximum temperature was statistically significant when modelling dominant height for *P. elliottii,* while winter maximum temperature was significant for *P. taeda*, *P. patula,* and *P. patula x P. tecunumanii*. Rainfall was found to be significant for *P. elliottii* and *P. taeda*, while spring rainfall was found to be more important when modelling dominant height for *P. patula*. Interestingly, autumn rainfall was found to have a negative impact on dominant height growth of *P. taeda* and *P. patula*, while rainfall was not significant in *P. patula x P. tecunumanii*. The findings imply that the southern pines have water thresholds, while Mexican pines are more temperature limited than water limited.

Key words: climate, tree height, *Pinus elliottii*, *Pinus taeda*, *Pinus patula*, *Pinus tecunumanii*

Introduction

South Africa is a water scarce country with limited native forests for wood production (Van Wilgen and Richardson 2012). Cumulatively, *Pinus elliottii*, *Pinus taeda,* and *Pinus patula*, represent 82% of the planted pine plantation forests in South Africa (Forest Economic Services CC. 2020). More recently, large areas have been established with *P. patula x Pinus tecunumanii* hybrids, due to their fast growth and natural resistance to the pathogen *Fusarium circinatum*, which causes large scale mortality in new plantings of *P. patula* (Hodge and Dvorak 2007; Mitchell et al. 2012; Kanzler et al. 2014).

Pine species represent 49% of the plantation forests in South Africa, of which the majority are located in the Mpumalanga province (Forest Economic Services CC. 2020; Van der Merwe et al. 2023*a*). The Mpumalanga forestry region is climatically diverse and can be broadly divided into the Lowveld and Highveld forestry regions. The Lowveld has irregular topography, is fractioned by the Drakensberg Mountain range, and receives more rainfall annually due to its closer proximity to the eastern seaboard (Muller et al. 2017; Van der Merwe et al. 2023*c*). The Highveld region has more uniform terrain conditions, little or no mountains, and comparatively receives less rainfall (Van der Merwe et al. 2023*c*).

Tree height growth occurs when resources required to maintain tree roots, stem, and leaves are satisfied, and is therefore limited to the available photosynthate after these primary processes have achieved energy equilibrium (Ryan and Yoder 1997; West et al. 1999; Ryan et al. 2006; Gonzalez-Benecke et al. 2014). Therefore, both temperature and water availability can limit tree growth (Hacker and Bilan 1992; Niklas and Spatz 2004; Ryan 2010; Koirala et al. 2021; Silva et al. 2022; White et al. 2022). Climate is known to impact tree growth and therefore introduced species in South Africa are typically planted in areas with similar conditions to their native habitat to ensure optimal survival and growth (Louw and Scholes 2006; Nedlo et al. 2009; Manson et al. 2013). Deployment of tree species to specific geo-climatic environments is known as site species matching (Schönau and Schulze 1984; Bernardo Pirovani et al. 2018; Peltier and Ogle 2020). Therefore, forest growers have characterised the inherent growing conditions of plantation forests by means of climate modelling and soil surveys, to ensure the successful deployment of plantation forests and accurate prediction of future timber stock manufacturing (Wang et al. 2007; Louw et al. 2011; Koirala et al. 2021).

Climate change may however impact the local climate of the forestry regions. South Africa is deemed a "climate change hotspot" (Engelbrecht et al. 2015; Betts et al. 2018; Hoegh-Guldberg et al. 2018; Engelbrecht and Monteiro 2021), with forecasts predicting a faster rate of heating than global averages. Together with expected increases in temperatures, regional downscaled models show generally drier conditions in the medium- and long-term future of South Africa (Engelbrecht et al. 2015; Engelbrecht and Monteiro 2021). In addition, it is predicted that rainfall variability will increase and extreme events such as droughts and floods will become more frequent and more intense (Engelbrecht et al. 2015). These changing climatic conditions could therefore have significant negative effects on plantation forestry production.

Plantation site productivity is broadly characterised at a compartment level by a site index (SI), which is defined as the dominant height at a predefined age (Louw and Scholes 2006; Wang et al. 2007; Tarmu et al. 2020). Plantation forests are enumerated regularly over the course of their growing cycle to predict future volumes of timber stock (Santiago-García et al. 2017; Santiago-García et al. 2020). This study aims to model dominant height for *P. elliottii*, *P. taeda*, *P. patula*, and *P. patula x P. tecunumanii* trees in South Africa, using recently developed climate models (Van der Merwe et al. 2023*c*) and historic enumeration data. Furthermore, SI at a plantation age of 20 years was projected for the Lowveld and Highveld forestry regions, respectively. The study investigated if climatic variables impact the growth of plantation forests in South Africa and how climate and height measurements can be used to improve site by species matching (Leibing et al. 2009; Notivol et al. 2020; Bauman et al. 2021).

Materials and methods

Study area, sampling strategy, and measurement data

The study was conducted in the Mpumalanga forestry region of South Africa, which is grouped according to the Lowveld and Highveld sub-regions (Fig. 1). The Lowveld is mountainous, has irregular terrain, and receives up to 1500 mm of rainfall annually (Van der Merwe et al. 2023*c*; Van der Merwe et al. 2024). The Highveld has relatively regular terrain, is generally situated at a higher altitude, and receives less than 1000 mm of rainfall annually (Van der Merwe et al. 2023*c*).

A total of 2082 plantation compartments were enumerated, spanning ages from 3 to 25 years over the period from 2012 to 2023 (Fig. 1, Table 1, and Supplementary Table S1). The enumerated plots were circular, covering an area of 500 m^2 per plot, and were replicated within each even-aged compartment until 6–7% of the total compartment surface area was enumerated. Enumeration points were selected according to a grid system, dividing the plantation area into evenly sized polygons and determining the centroids of each polygon using ArcMap software (ESRI 2021).

Species and enumeration age of the corresponding trees were obtained from historic plantation records. The *P. patula x P tecunumanii* hybrids were established with a mixture of *P. tecunumanii* pollen that included both high and low altitude ecotypes, as was common practice during the time of commercial deployment of the hybrid pines. Enumeration measurements included dominant height, diameter at breast height, and tree count per hectare, however only dominant height measurements were assessed in this study. Centroid coordinates were determined for each enumerated compartment using QGIS software Version 3.24.1. Seasonal annual climate, including T-max (mean maximum temperature), T-min (mean minimum temperature), P-median (median rainfall) was obtained for each centroid position using existing climate models for the region (Van der Merwe et al. 2023*c*). The monthly demarcations of the respective seasons can be seen in Supplementary Table S2 (Van der Merwe et al. 2023*c*). Compartment stocking ranged between 1111 and 1333 trees per hectare. Over the course of the plantation rotation, compartments were systematically thinned to a mean stocking density of 800 trees per ha followed by a second thinning to a target planting of 500 trees per ha, while maintaining a mean target basal area of 24 m^2 per ha, as the trees matured. Pruning treatments included three stages of branch pruning; a first pruning to a height of 1.5 m, a second pruning to a height of 3.5 m, and a third pruning to a height of 5.5 m. Branch pruning was typically initiated according to tree size with the aim to maximize clear wood formation by restricting the knotty core of the pruned tree sections to less than 12 cm. Hence, pruning was initiated according to the growth rate of trees.

Data processing

All statistical analyses and data processing were completed using R version 3.4.1: A language and environment for statistical computing. Identification of significant climate variables for developing multiple linear regression models to predict dominant height was accomplished via stepwise regression, which also scrutinised the respective models by using the Bayesian information criterion ("leaps") (Lumley 2020). Only variables with significant probabilities ($\alpha = 0.05$), while maintaining a significant model intercept, were included in the final models. Resultant multiple linear regression models were developed for the respective species ("lm") (R Core Team 2023). Model residuals were tested for normality ("qqPlot") (Almeida et al. 2018). Model accuracies was determined by means of root mean square error and the resultant R-squared values. Landscape projections were completed for dominant height at age 20 years, by harnessing existing climate models and the newly developed dominant height models from this

Fig. 1. Enumerated plantation area according to species, including *Pinus elliottii* (red), *Pinus taeda* (yellow), *Pinus patula* (green), *Pinus patula x Pinus tecunumanii* (blue) and the not sampled area (grey), within the Lowveld and Highveld forestry regions, respectively. Figures were created using ESRI ArcGIS version 10.8.2 and assembled from the following data sources: compartment species from compartment lists (Microforest), compartment boundaries layer (York Timbers). Base maps from ArcMap, World Terrain Base, courtesy of ESRI ArcGIS (ESRI 2021).

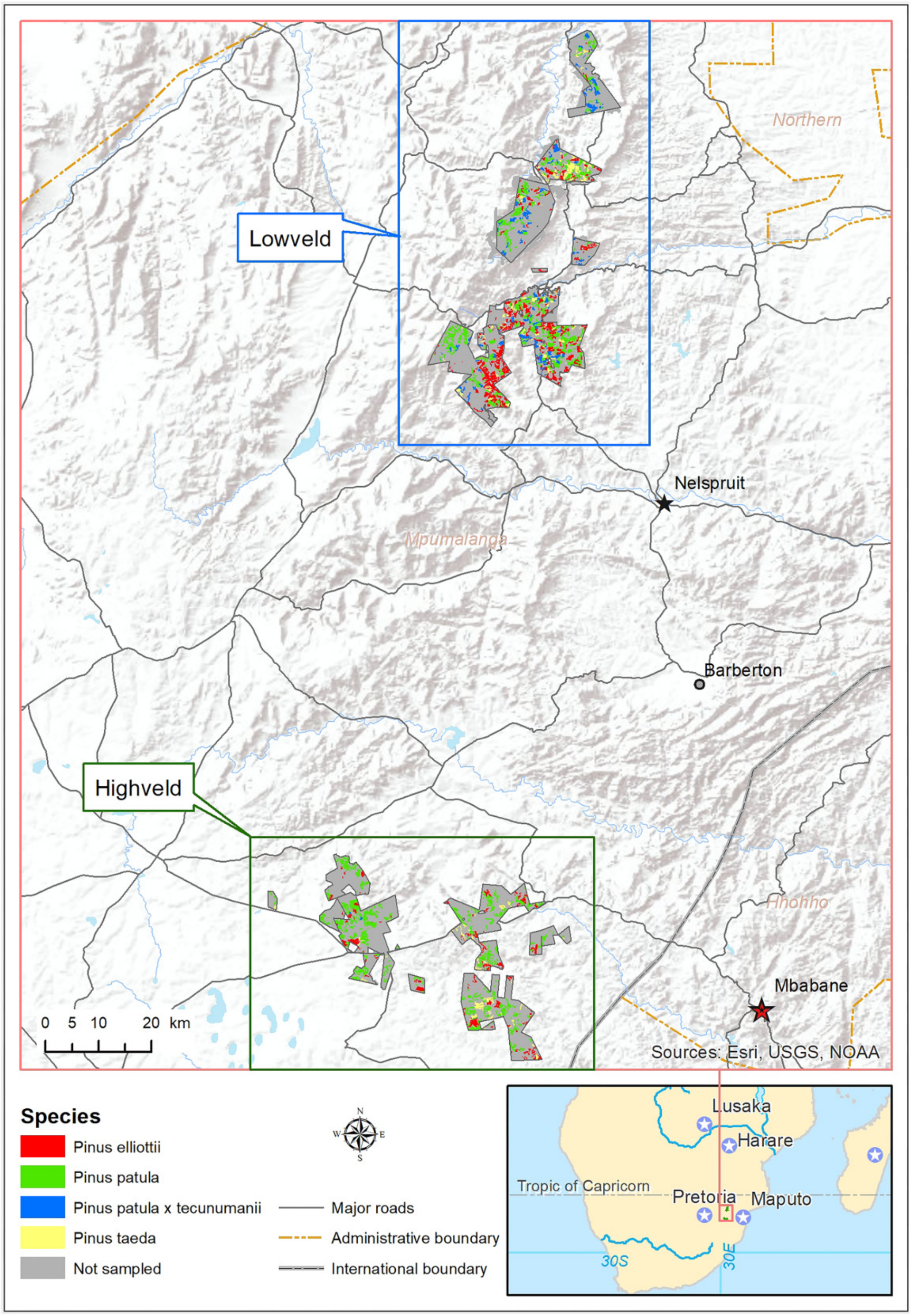


Table 1. Summary of the enumeration compartment features for the different species of pine.

Species	Plantation count	Plantation area (ha)	Plot count	Measured area (ha)	Sample %
P. elliottii	619	7290	9840	487	6.7%
P. taeda	234	2755	3901	194	7.0%
P. patula	1013	13267	17285	857	6.5%
P. patula x P. tecunumanii	217	2949	3714	184	6.2%

study (“raster”) (Hijmans 2023; Van der Merwe et al. 2023*c*). The newly developed models were used to project dominant height of the respective sample plots to a normalised age of 20 years. The amount of theoretical annual growing days (GD) and growth temperature (GT) in a calendar year for the respective enumerated sites were derived by using the predicted climate and existing models (Louw et al. 2011). GD can be defined as the number of days with sufficient water available to facilitate evapotranspiration, while GT refers to the mean monthly temperature, weighted according to the monthly GD (Louw et al. 2011; Van der Merwe et al. 2023*a*).

Four principle component analyses were completed to determine the key variables and relationships between variables impacting dominant height growth of the species at a normalised tree age of 20 years. Only climate variables that were found to significantly impact height growth were included in the model (“lfda”, “ggfortify”, “rcompanion”) (Tang et al. 2016; Tang and Li 2019; Wei and Simko 2021; Mangiafico 2024).

A Pearson’s correlation coefficient matrix was calculated to establish the correlation between annual climatic variables (“corrplot”) (Wei and Simko 2021). In addition, threshold models were developed using Cate–Nelson analysis, incorporating annual maximum temperature (T-max) and the projected dominant height at age 20 years (“CateNelson”) (Cate and Nelson 1971; Mangiafico 2013). Cate–Nelson analysis determined the threshold annual maximum temperature and rainfall at which the respective species achieve optimal growth. This analysis determined critical-*x* (climate variable) and critical-*y* (dominant height) values by repetitively dividing the data into two groups and comparing the sum of squares of the respective iterations. The critical *x* and *y* values were determined by maximising the amount of data points within the second and fourth quadrants of an *x*–*y* plot in the case of a positive trend, or first and third quadrants in the case of a negative trend (Cate and Nelson 1971; Lee 2016). Model accuracy was quantified using the χ^2 test, also known as the Cramer’s V statistic (Lee 2016).

Results and discussion

Climate is widely recognised to be one of the most significant variables impacting the growth of plantation-grown pine trees (Bauman et al. 2021; Nava-Nava et al. 2022; van der Merwe et al. 2023*a*). Typically, tree height growth is significantly impacted by the most limiting resource affecting photosynthesis, as tree growth is restricted when the atmospheric demand for moisture or potential evaporation exceeds water availability (Dye 2001; Louw and Scholes 2006; Downes and Drew 2008; Belay 2016; Urban et al. 2017).

Seasonal climate impacts on dominant height growth

The study aimed to develop dominant height models for plantation grown *P. elliottii*, *P. taeda*, *P. patula*, and *P. patula x P. tecunumanii*, while including tree age and climate variables as independent variables. Multiple linear regression models were developed by identifying significant climatic variables impacting tree height growth by means of stepwise regression. Independent variables investigated included tree age at enumeration, together with annual maximum temperature (T-max), annual minimum temperature (T-min), seasonal maximum, and minimum temperatures for summer, autumn, winter, and spring, respectively. Furthermore, seasonal precipitation and mean annual precipitation (MAP) were included for the respective sample sites. However, no precipitation values were included for winter, as the study area is located in a summer rainfall region, with little or no precipitation during the winter months (Van der Merwe et al. 2023*c*). The final models with variable probabilities and model R-square values for the respective species are summarised in Table 2. Furthermore, actual versus predicted plots are presented in Fig. 2. Tree age was found to be the most important variable predicting tree height, with varying importance of climatic conditions per species, which further highlights the importance of genotype by environment (G × E) interaction on tree growth (Brawner et al. 2014; Zhai et al. 2015). The specific outcomes for each species examined are describe independently. Historic height measurements were archived per compartment, *i.e.*, the number of sample plots and sample area was specified with a single dominant height value and not for the respective sample plots per compartment. Therefore, random effects were not included in the final multiple linear regression models.

Pinus elliottii

Dominant height (Ht_d) growth of *P. elliottii* was significantly impacted by annual maximum temperature and seasonal rainfall during the summer and spring months (Table 2, Fig. 2A, and Supplementary Fig. S1A). Trees were taller on sites with higher annual maximum temperatures (Table 2). In addition, Ht_d was also larger on sites that received more summer and spring rainfall, allowing for more available water during the active growing season (Foster and Brooks 2001; Wang et al. 2007).

Previous international studies found height growth of southern pines, which included *P. elliottii* trees, to be positively correlated with annual temperature and seasonal rainfall (Teskey et al. 1994; Loehle 1998; Huiqing et al. 2008; Harley et al. 2012). In fact, *P. elliottii* has been found to be physiologically active throughout the year at sites with sufficient solar radiation and temperature (Martin 2000). Height growth of *P. elliottii* has been found to be negatively impacted by dry growing conditions, due to conservative water use efficiency (Foster and Brooks 2001; Ford and Brooks 2003; Samuelson et al. 2012). Of the species investigated, *P. elliottii* was one of the species significantly impacted by seasonal rainfall, which illustrates the importance of water availability to ensure optimal growth for the species.

Pinus taeda

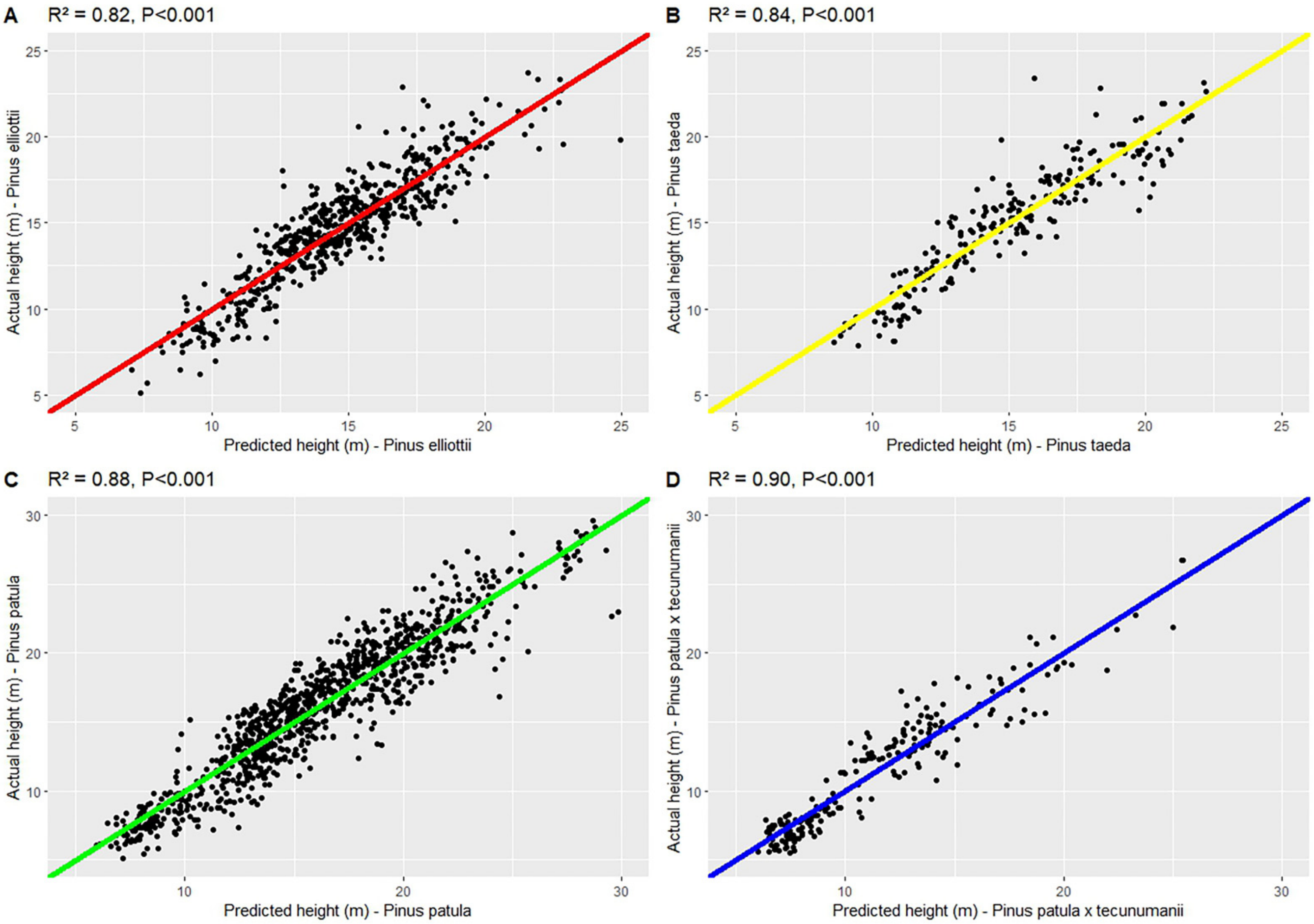
Dominant height growth of *P. taeda* was significantly impacted by winter maximum temperatures, MAP, and autumn rainfall (Table 2, Fig. 2B, and Supplementary Fig. S1B). Higher winter maximum temperatures and a higher annual rainfall were found to have a positive impact on dominant height

Table 2. Summary statistics for dominant height (Ht_d) regression independent variables per species. Significant = $*$ ($0.01 < P < 0.05$), highly significant = $**$ ($0.001 < P < 0.01$), and very highly significant $***$ ($P < 0.001$).

	Pinus elliottii						*Pinus taeda*						*Pinus patula*						*Pinus patula x Pinus tecunumanii*					
Variable	Est.	Std. Err.	*P*	Sign.	RMSE	R^2	Est.	Std. Err.	*P*	Sign.	RMSE	R^2	Est.	Std. Err.	*P*	Sign.	RMSE	R^2	Est.	Std.Err	*P*	Sign.	RMSE	R^2
(Intercept)	−17.28	2.39	0.000	***	1.40	0.82	−4.66	1.79	0.010	**	1.41	0.84	−6.17	1.52	0.000	***	1.76	0.88	−5.95	1.22	0.000	***	1.39	0.90
Age	1.07	0.02	0.000	***			1.00	0.03	0.000	***			1.24	0.02	0.000	***			1.49	0.04	0.000	***		
T-max	0.19	0.04	0.000	***			NS	NS	NS	NS			NS	NS	NS	NS			NS	NS	NS	NS		
T-min	NS	NS	NS	NS			NS	NS	NS	NS			NS	NS	NS	NS			NS	NS	NS	NS		
T-max (summer)	NS	NS	NS	NS			NS	NS	NS	NS			NS	NS	NS	NS			NS	NS	NS	NS		
T-max (autumn)	NS	NS	NS	NS			NS	NS	NS	NS			NS	NS	NS	NS			NS	NS	NS	NS		
T-max (winter)	NS	NS	NS	NS			0.30	0.07	0.000	***			0.33	0.05	0.000	***			0.38	0.07	0.000	***		
T-max (spring)	NS	NS	NS	NS			NS	NS	NS	NS			NS	NS	NS	NS			NS	NS	NS	NS		
T-min (summer)	NS	NS	NS	NS			NS	NS	NS	NS			NS	NS	NS	NS			NS	NS	NS	NS		
T-min (autumn)	NS	NS	NS	NS			NS	NS	NS	NS			NS	NS	NS	NS			NS	NS	NS	NS		
T-min (winter)	NS	NS	NS	NS			NS	NS	NS	NS			NS	NS	NS	NS			NS	NS	NS	NS		
T-min (spring)	NS	NS	NS	NS			NS	NS	NS	NS			NS	NS	NS	NS			NS	NS	NS	NS		
MAP	NS	NS	NS	NS			0.01	0.00	0.000	***			NS	NS	NS	NS			NS	NS	NS	NS		
Summer rainfall	0.01	0.00	0.000	***			NS	NS	NS	NS			NS	NS	NS	NS			NS	NS	NS	NS		
Autumn rainfall	NS	NS	NS	NS			−0.05	0.01	0.000	***			−0.02	0.00	0.000	***			NS	NS	NS	NS		
Spring rainfall	0.04	0.01	0.000	***			NS	NS	NS	NS			0.03	0.00	0.000	***			NS	NS	NS	NS		

Note: Rows containing "NS" indicate variables that were not significant ($p > 0.05$). Variables investigated include age, annual maximum temperature (T-max), annual minimum temperature (T-min), seasonal maximum and minimum temperatures, annual rainfall (MAP) and seasonal rainfall. RMSE, root mean square error; MAP, mean annual precipitation.

Fig. 2. Comparison of tree dominant height growth from multiple linear regression model predictions to the actual measured dominant height values for (A) *Pinus elliottii* (red), (B) *Pinus taeda* (yellow), (C) *Pinus patula* (green), and (D) *Pinus patula x Pinus tecunumanii* (blue) trees.



growth, potentially due to an extended growing season, facilitated by higher temperatures (Martin 1999; Urban et al. 2017). Overall, annual precipitation was found to be positively correlated with height growth (Table 2). However, autumn rainfall was found to have a negative impact on height growth, possibly due to more cloud cover days and limited solar radiation on sites receiving more rainfall in autumn, during the seasonal transition period (Tang et al. 2003; Alvarado-Barrientos et al. 2014).

Similar to previous studies, height growth of *P. taeda* was significantly impacted by climate (Teodoro Zamin et al. 2013). Temperature and more specifically sufficient temperature during the winter season have been found to significantly impact height growth, potentially due to a longer growing season (Downs and Borthwick 1956; Loehle 1998; Martin 1999; Tang et al. 2003; Teodoro Zamin et al. 2013). Dominant height growth of *P. taeda* was also significantly impacted and had a positive relationship with mean annual rainfall (MAP). These findings could be associated with lower water use efficiency as previously seen in southern pine species (Tang et al. 2003; Sameulson et al. 2012; Teodoro Zamin et al. 2013). The importance of sufficient soil water to maintain a positive stomatal water deficit in *P. taeda* has been reported (Ewers et al. 2001; Teskey et al. 2015). In fact, growth of *P. taeda* has been reported to stop, when grown in soils with moisture content below 40% (Dougherty et al. 1994).

Pinus patula

Winter maximum temperatures, and spring and autumn rainfall were found to be the most influential climatic variables, when predicting Ht_d for *P. patula* (Table 2, Fig. 2C, and Supplementary Fig. S1C). In particular, sites with higher winter maximum temperatures and more spring rainfall were found to have a positive impact on height growth, potentially due to an early onset of the growing season, while higher winter maximum temperatures may allow for an extended late growing season (Downs and Borthwick 1956) (Table 2). However, higher autumn rainfall had a negative impact on height growth, potentially due to radiation limitations associated with cloud cover during the autumn season (Alvarado-Barrientos et al. 2014) (Table 2). Thus, seasonal timing, rather than overall rainfall seems to have a more significant impact on the height growth of *P. patula*. Spring rainfall could lead to the onset of an early growing season, while autumn rainfall reduces radiation due to more frequent cloud cover (Van der Merwe et al. 2023*a*).

Previous studies have determined temperature to be the most influential climatic variable on height growth of *P. patula*, with larger trees being found on warmer sites displaying a negative relationship between temperature and rainfall (Nava-Nava et al. 2022; van der Merwe et al. 2023*a*). Similar to the current study, spring and summer rainfall had a positive relationship with the height growth, while autumn rainfall had a negative relationship with height growth of *P. patula* (Van der Merwe et al. 2023*a*). For example, higher altitude sites found on the Highveld received less rainfall and were found to be warmer than Lowveld sites that received more rainfall, located at similar altitude (Van der Merwe et al. 2023*a*).

Pinus patula x P. tecunumanii

Winter maximum temperature was the single most important variable impacting height growth in the hybrid, and sites with higher winter maximum temperatures had larger trees; none of the rainfall variables were observed to impact height growth (Table 2, Fig. 2D, and Supplementary Fig. S1D). These results indicate that *P. patula x P. tecunumanii* grown in the Mpumalanga forestry region is not restricted by water availability. In addition, the findings inherently imply a better water use efficiency, as no regional water limitations impact the Ht_d model. However, enumerations for the hybrid were mostly limited to the Lowveld forestry region, with only two sites enumerated in the drier Highveld region (Van der Merwe et al. 2023*c*). Plantings of *P. patula x P. tecunumanii* have been limited in the Highveld region, due to frost related mortality in the region.

Research on the environmental factors impacting height growth of the newly developed *P. patula x P. tecunumanii* hybrid has been limited. Previous studies have shown that hybrid species, such as *P. patula x P. tecunumanii*, outperform pure pine species due to hybrid vigour (Nilsson et al. 2020). Additionally, studies conducted in Brazil, Columbia, Mexico, and South Africa have shown a positive correlation between height growth and temperature (Leibing et al. 2009; Kanzler et al. 2012; Nava-Nava et al. 2022; Van der Merwe et al. 2023*a*). The results from the current study provide further insights into the growth dynamics of this hybrid, revealing that it is not limited by water availability, but rather by temperature, especially during winter months.

Annual climate impacts on dominant height growth

Dominant height measurement projections were carried out by employing local terrain features to determine climate conditions for the respective enumerated compartments, using recently developed climate models (Van der Merwe et al. 2023*c*) (Supplementary Fig. S2).

Dominant height at age 20 was modelled for *P. elliottii*, *P. taeda*, *P. patula,* and *P. patula x P. tecunumanii* and projected for the Lowveld and Highveld landscape, according to the underlying climate conditions (Table 2, Supplementary Fig. S4 and S5). A summary of the height distribution of the respective species according to the respective Lowveld and Highveld forestry regions are shown in Supplementary Table S3.

Furthermore, dominant height was predicted at age 20 years for all of enumerated sample plots using the newly developed dominant height models (Supplementary Fig. S4 and S5). Dominant heights of the enumerated trees at a normalised tree age, allowed for the development of climate-dominant height threshold models. Three climate-independent variables were investigated, including annual maximum temperature (T-max), annual minimum temperature (T-min), and MAP. Model significance was determined according to the Chi-square-based Cramer's V statistic (Table 3). Model thresholds are visualised in Supplementary Figs. S6, S7, and S8.

Pinus elliottii

T-max had a relatively strong positive relationship with height growth of *P. elliottii,* and 75% of the observations were accounted for within the threshold quadrants (Cramer's $V = 0.48$, P-model $= 0.75$) (Table 3). Critical threshold T-max for dominant height growth was determined to be 22.3 °C and a threshold Ht_d of 24.4 m was observed. The results indicate that *P. elliottii* achieved superior growth above temperatures of 22.3 °C and the threshold height at this T-max is 24.4 m. The P-model value indicates that 75% of the measurements are explained between quadrants two and four (positive trend; Fig. 3).

T-min was found to have strong positive relationship with the height growth of *P. elliottii* and 89% of the observations were accounted for within the threshold quadrants (Cramer's $V = 0.61$, P-model $= 0.89$) (Table 3). Critical threshold T-min for dominant height growth was determined to be 11.1 °C and a threshold Ht_d of 23.2 m was observed. However, MAP was found to be the most influential climatic variable impacting Ht_d of *P. elliottii*. A very strong positive relationship with height growth of *P. elliottii* was observed and 96% of the observations were accounted for within the threshold quadrants (Cramer's $V = 0.87$, P-model $= 0.96$) (Table 3). Critical threshold MAP for dominant height growth was determined to be 828.8 mm and a threshold Ht_d of 23.5 m was observed.

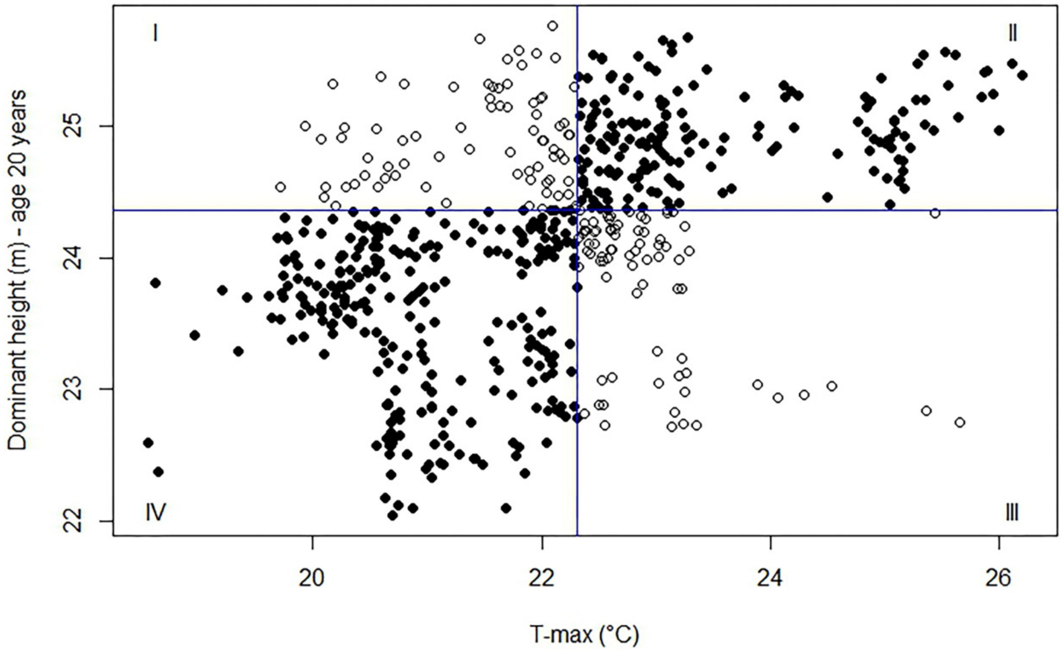
Recent studies have indicated that *P. elliottii* possesses the necessary physiological and metabolic mechanisms to cope with warmer temperatures and drought conditions (Celeste Dias et al. 2022). However, findings from this study suggest that *P. elliottii* grown in Mpumalanga is most sensitive to MAP among the species investigated in this study (Table 3, Supplementary Fig. S8). Furthermore, the relatively high temperature thresholds and positive relationship between Ht_d and temperature suggest that the species will benefit from future warming climates, provided sufficient water is available for tree growth (Table 3, Supplementary Fig. S6, S7, and S8). The results suggest that *P. elliottii* height growth is more sensitive and positively related to growth days (GD) than growth temperature (GT), as precipitation and T-min were generally found to be positively correlated with GD and weakly related to GT (Supplementary Fig. S3) (Van der Merwe et al. 2023*a*).

Table 3. Climate and dominant height threshold values for annual maximum temperature (C-T-max), annual minimum temperature (C-T-min), mean annual precipitation (C-MAP), and the resultant dominant height (C-Ht_d) at age 20 years, categorised by species.

Variable	Species	C-T-max (° C)	C-$\mathrm{Ht_d}$ (m)	*P*-model	Cramer.V	Trend
T-max	*P. elliottii*	22.3	24.4	0.75	0.48	Positive
	P. taeda	23.3	24.2	0.88	0.46	Positive
	P. patula	20.4	26.9	0.92	0.73	Positive
	P. patula x P. tecunumanii	21.6	31.0	1.00	1.00	Positive
Variable	Species	C-T-min (° C)	C-$\mathrm{Ht_d}$ (m)	P-model	Cramer.V	Trend
T-min	*P. elliottii*	11.1	23.2	0.89	0.61	Positive
	P. taeda	11.2	23.1	0.76	0.57	Positive
	P. patula	11.6	27.6	0.84	0.67	Negative
	P. patula x P. tecunumanii	12.0	31.4	0.81	0.58	Negative
Variable	Species	C-MAP (mm)	C-$\mathrm{Ht_d}$ (m)	P-model	Cramer.V	Trend
MAP	*P. elliottii*	828.8	23.5	0.96	0.87	Positive
	P. taeda	916.7	23.2	0.84	0.70	Positive
	P. patula	868.0	27.7	0.84	0.69	Negative
	P. patula x P. tecunumanii	990.0	30.0	0.71	0.04	Negative

Note: Summary statistics are provided, including *P*-model values, indicating the number of observations accounted for within the respective opposing quadrants, and the Chi-square-based Cramer's V statistic, measuring the strength of association between the variables. Cramer's V statistic values of 0.00–0.10 are considered negligible (no association), 0.10–0.20 weak, 0.20–0.40 moderate, 0.40–0.60 relatively strong, 0.60–0.80 strong, and 0.80–1.00 very strong. Additionally, the relationship trend (positive or negative) between the respective climate variables and dominant height growth was indicated (Lee 2016).

Fig. 3. Cate–Nelson analysis visualisation including the T-max threshold at 22.3 °C, at a tree height threshold of 24.4 m. All the visualisation of the computed thresholds for the respective species can be seen in Supplementary Fig. S6, S7, and S8.



Pinus taeda

T-max also had a relatively strong positive relationship with height growth of *P. taeda* and 88% of the observations were accounted for within the threshold quadrants (Cramer's V = 0.46, *P*-model = 0.88) (Table 3). Critical threshold T-max for dominant height growth was determined to be 23.3 °C and a threshold Ht_d of 24.2 m was observed. T-min was found to have strong positive relationship with the height growth of *P. taeda* and 76% of the observations were accounted for within the threshold quadrants (Cramer's V = 0.57, *P*-model = 0.76) (Table 3). Critical threshold T-min for dominant height growth was determined to be 11.2 °C and a threshold Ht_d of 23.1 m was observed. Similar to the results for *P. elliottii*, MAP was found to be the most influential climatic variable impacting Ht_d of *P. taeda*. A strong positive relationship between MAP and height growth of *P. taeda* was observed, and 84% of the observations were accounted for within the threshold quadrants (Cramer's V = 0.87, *P*-model = 0.96) (Table 3). The critical threshold for MAP influencing dominant height growth was identified as 916.7 mm, marking the highest rainfall threshold value among the species investigated. A height threshold (Ht_d) of 23.2 m was observed.

The results indicate that the growth of *P. taeda* plantations in the region, is fundamentally limited by rainfall and overall water availability (Table 3). The findings are supported by previous studies that reported stunted or halted growth of *P. taeda* under water-limiting conditions (Dougherty et al. 1994; Ewers et al. 2001; Teskey et al. 2015). However, a positive relationship between both T-max and T-min was also observed (Table 3). In fact, positive temperature responses for both T-min and T-max were found to be at the highest temperature thresholds of all the species investigated (T-max: 23.3 °C; T-min: 11.2 °C). The findings suggest that *P. taeda*, has high temperature-growth thresholds, while a positive soil water deficit is maintained. Therefore, water availability is essential for the species to maintain a positive growth trend, at higher temperatures. The findings indicated that dominant height growth in southern pine species, including *P. taeda*, is more constrained and positively correlated with rainfall and associated GD than with GT. This is attributed to the positive relationships observed between rainfall, T-min, and GD (Supplementary Fig. S3).

Pinus patula

Temperature, specifically T-max, was identified to be the most influential climate variable affecting height growth of *P. patula*. The T-max threshold model showed a strong positive relationship between T-max and height growth of *P. patula*, with 92% of observations falling within the threshold quadrants (Cramer's V = 0.73, *P*-model = 0.92) (Table 3). The critical threshold for T-max was determined to be 20.4 °C at a threshold (Ht_d) of 26.9 m. Conversely, T-min exhibited a strong negative relationship with height growth of *P. patula*, with 84% of observations within the threshold quadrants (Cramer's V = 0.67, *P*-model = 0.84), and a critical threshold of 11.6 °C and Ht_d of 27.6 m. Similarly, MAP displayed a strong negative relationship with 84% of observations within the threshold quadrants (Cramer's V = 0.69, *P*-model = 0.84), with a critical threshold of 868.0 mm and Ht_d of 27.7 m observed for dominant height growth of *P. patula* (Table 3). It however remains unclear if the negative relationship between Ht_d, T-min, and MAP was more related to temperature or rainfall, due to a strong colinear relationship between these two independent variables.

The results indicated that *P. patula* is most limited by T-max. *P. patula* grew tallest on sites with higher T-max and the results are substantiated by previous studies (Nava-Nava et al. 2022; Van der Merwe et al. 2023*a*; Van der Merwe et al. 2023*b*; Van der Merwe et al. 2024). In addition, *P. patula* was the most responsive to T-max and had the lowest T-max threshold value of the investigated species. A negative relationship was observed between Ht_d and T-min. The Pearson's correlation coefficient matrix revealed a negative relationship between T-min and sites with higher rainfall, a finding supported by previous studies (Van der Merwe et al. 2023*a*) (Supplementary Fig. S3). Similar to previous studies, *P. patula* was found to be moderately drought tolerant, and in fact more drought tolerant than *P. elliottii* and *P. taeda*, which further supported the observations in this study (Sudhakara Reddy and Natarajan 1996). The results indicate that *P. patula*, grown in the Mpumalanga forestry region, currently faces limitations not in water supply, but in maximum temperature. The findings imply that *P. patula*'s height growth is more responsive to GT than GD, since T-max was found to be positively correlated with GT and weakly correlation with GD (Supplementary Fig. S3).

Pinus patula x Pinus tecunumanii

T-max was found to be the most significant climatic variable impacting height growth of *P. patula x P. tecunumanii*. A very strong positive relationship was observed between T-max and height growth of *P. patula x P. tecunumanii*, and 100% of the observations were accounted for within the threshold quadrants (Cramer's V = 1.00, *P*-model = 1.00) (Table 3). Critical threshold T-max for dominant height growth was determined to be 21.6 °C and a threshold Ht_d of 31.0 m was observed. T-min had a relatively strong negative relationship with height growth of *P. patula x P. tecunumanii* and 81% of the observations were accounted for within the threshold quadrants (Cramer's V = 0.58, *P*-model = 0.81) (Table 3). Critical threshold T-min for dominant height growth was determined to be 12.0 °C and a threshold Ht_d of 31.4 m was observed. MAP had a negligible influence on height growth of *P. patula x P. tecunumanii*, although 71% of the observations were accounted for within the threshold quadrants (Cramer's V = 0.04, *P*-model = 0.71) (Table 3).

The results indicate that *P. patula x P. tecunumanii* significantly benefits from warm–dry conditions, as growth was superior on warmer sites with greater T-max. In addition, sites with lower T-min had larger trees and it is not clear if this observation is related to a colinear relationship between rainfall and T-min. The findings are supported by previous studies, which found *P. tecunumannii* to be more drought tolerant compared to *P. elliottii*, *P. taeda*, and *P. patula* which could explain why the *P. patula x P. tecunumanii* performed better on warm–dry sites (Hodge and Dvorak 1999; Dvorak et al. 2000; Kanzler et al. 2012; Kanzler et al. 2014). Furthermore, no significant threshold models were developed for the relationship between MAP and Ht_d, which further substantiates the drought tolerance of this species. The results indicate that *P. patula x P. tecunumanii* plantations in the Mpumalanga province of South Africa have not encountered growth limitations, due to water availability. Of the species investigated, *P. patula x P. tecunumanii* was the fastest growing, least impacted by rainfall, and grew best in warm conditions, which makes this hybrid the most promising for future deployment considering the anticipated impacts of global warming (Kanzler et al. 2012; Kanzler et al. 2014) (Supplementary Fig. S4 and S5). Although the *P. tecunumanii* pollen used for the development and deployment of this hybrid was not segregated according to low and high ecotypes, no trend deviation in climatic suitability was observed during analysis of the commercially deployed populations investigated in this study.

Conclusion

The study emphasises the importance of understanding the impact of climate on the growth of pine plantation forests. In addition, the study identified species-specific climate limitations, and provides valuable insights into the underlying climate drivers impacting successful deployment and growth of commercially important introduced pine plantation species in South Africa. Future studies should focus on modelling the future climate of the Mpumalanga forestry region and assessing how climate changes may influence decision-making in the selecting of introduced pine species for site-species matching. In addition, geoclimatic limitations for tree growth including the interaction between soil water availability and climate should be further investigated and scrutinised.

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Competing interests

The authors declare that they have no conflicts of interest regarding this article.

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Supplementary material

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