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ORIGINAL ARTICLE

Bark thickness variation in five young South African-grown *Pinus* species and hybrids

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Abstract

Key message **Understanding bark allocation in juvenile stages of commercially viable *Pinus* trees can be useful in dating wood formation, thus improving the accuracy of correlating wood quality to environmental factors.**

Abstract Bark is an important and multifunctional part of plant anatomy that has been researched mostly in the context of fire history, timber resource assessments and more recently as a bioresource. Few studies have comprehensively examined bark thickness in some commercially valuable *Pinus* species. More importantly, the role of bark in accurately dating wood formation has seldom been researched. This study was conducted to model and compare bark thickness variation between different species of young South African-grown *Pinus* trees including *Pinus radiata* var. radiata D. Don., *Pinus elliottii* Engelm., *Pinus elliottii* × *Pinus caribaea* var. hondurensis, *Pinus patula* × *Pinus tecunumanii* (Low Elevation), and *Pinus patula* × *Pinus tecunumanii* (High Elevation). Measurements were taken at 1.6 and 2.3 years including absolute and relative bark thickness and distribution along the stem. Results showed species-specific variation in absolute and relative bark thickness with the highest means recorded in *Pinus elliottii* × *Pinus caribaea* and lowest in *Pinus radiata*. A positive linear relationship was observed between bark thickness and diameter, consistent with all species and ages. Absolute bark thickness decreased along the stem from bottom to top while more nuanced patterns of variation were observed for relative bark thickness. These findings underscore the importance of understanding bark thickness in young trees for various applications, including dating wood formation, anticipatory breeding strategies for quality wood and predicting stand quality among others.

Keywords Bark thickness · Bark taper · Wood formation · Early selection · Young *Pinus*

Introduction

Bark is an important and multifunctional part of plant anatomy (Paine et al. 2010; Poorter et al. 2014; Rosell 2019; Fedorov and Ryazanova 2021). It comprises all tissues outside the vascular cambium that, among other things, play a protective, conductive and supportive role for the plant (Niklas 1999; Morris and Jansen 2017; Rosell 2019; Carrasco et al. 2022; Shtein et al. 2023). Several studies have been conducted to investigate bark thickness but with a particular focus on the fire history of different ecosystems (Pausas 2015a; Musić et al. 2019; Rodman et al. 2020; Berendt, de Miguel-Diez, et al. 2021; Costa et al. 2021; Shearman and Varner 2021; Yilmaz, Ozdemir and Makineci 2021; Cywicka et al. 2022; Singh et al. 2022) or on quantifying wood volume under bark (Sonmez et al. 2007; Jankovský et al. 2019; Sedmíková et al. 2020; Costa et al. 2021; Mirski et al. 2021; Yilmaz, Ozdemir and Makineci 2021; Konôpka et al. 2022; Hansen et al. 2023).

In the case of fire resistance, the majority of the studies found that bark thickness and properties vary depending on several factors, including the species, age and environment in which the trees are growing (Zeibig-Kichas et al. 2016; Pile et al. 2017; Kidd and Varner 2019; Kurt, Calikoglu and Isik 2021; Shearman & Varner 2021; Singh et al. 2022; Hansen et al. 2023; Jankovský et al. 2023). It has also been observed that plants in fire-prone ecosystems invest more resources in developing thicker bark than ecosystems that experience less fire. Although not the only consideration (Paine et al. 2010; Mugisha 2011; Bastien and Ganteaume 2020; Zhu et al. 2024), fire remains a critical criterion for

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classifying and understanding bark variability in many plant species (Pausas 2017; Pellegrini et al. 2017; Shearman et al. 2018; Trugman et al. 2018; Merschel et al. 2021; Moris et al. 2022).

In timber production forests, bark assessment has generally been motivated by the perception of bark as a waste product which reduces the value of logs and causes inaccurate valuations of log resources (Marshall et al. 2006; Kitikidou et al. 2014; Musić et al. 2019; Berendt, de Miguel-Diez, et al. 2021). However, more recently, bark has been used in the generation of energy, for other biomolecules, and as mulch or growth medium (Bauer et al. 2020; Fedorov and Ryazanova 2021; Jankovský et al. 2023). As part of the current transition to greener economies, the commercial value of bark is expected to increase. Furthermore, the mechanical role bark plays in maintaining posture in early plant life was highlighted in early research (Niklas 1999) but not studied in depth. Some recent studies have reported that bark controls stem orientation, particularly in the early stages of plant growth (Rosell et al. 2017), and this has been demonstrated for some tropical tree species, such as *Cecropia*, *Virola* and *Simarouba* (Clair et al. 2019; Lehnebach et al. 2020). This means that understanding bark allocation and distribution in juvenile stages can be useful for predicting stand quality. Tree breeders can also select bark traits earlier in plant life to improve forest management and anticipate yields. Early selection of commercial tree species based on their bark properties will be important not only for volumetric analysis but also because with climate change, the threat of wildfires to commercial forestry will only increase (Kraaij et al. 2018; Liu et al. 2021; Xulu, Mbatha and Peerbhay 2021). Understanding bark allocation is also important in fine-scale research focused on dating wood formation to relate wood quality and environmental factors prevailing at the time of wood formation (Drew and Pammenter 2007; Drew and Downes 2009; Drew et al. 2009). Especially where diameter growth outside bark is recorded periodically, understanding bark growth facilitates accurate isolation of wood and bark. We did not find any studies that have studied bark thickness in this context.

As discussed above, accurately estimating and predicting bark thickness is, therefore, important for many different objectives (Berendt et al. 2021a, b; Wilms et al. 2021). Most studies have examined bark thickness of older trees and at breast height (Yilmaz, Ozdemir and Makineci 2021; Konôpka et al. 2022). Some studies argue that stems less than 10 cm in diameter should be preferred for bark measurements because trees at this growth stage are more susceptible to bark-related vulnerabilities, such as fires and pathogens (Hoffmann et al. 2012; Hempson et al. 2014; Hammond et al. 2015; Pile et al. 2017). Also in smaller trees, the relationship between bark and diameter is more linear and can be assessed more accurately (Poorter et al. 2014; Midgley and Lawes 2016; Kidd and Varner 2019; Singh et al. 2022). The linkage of a particular species to bark distribution is evident even in young trees and different characteristics can be observed between species (Lawes et al. 2011; Hammond et al. 2015; Lehnebach et al. 2020; Rodriguez-Perez et al. 2022; Singh et al. 2022). Despite the growing importance of bark in the green economy, few comprehensive studies have been conducted on young trees of the commercially valuable pine species.

In the South African context, two species of pines are of primary importance for timber production. For many years, *P. patula* and *P. radiata* were the most commonly planted softwood species, in summer rainfall and winter rainfall regions respectively (Hongwane et al. 2017; FES 2020). However, these species have been found to be most susceptible to attack by the pitch canker fungus, threatening their sustainability in commercial forestry (Wingfield et al. 2008; Mitchell et al. 2012, 2014; Steenkamp et al. 2014; Santana et al. 2016). As a result, several species and hybrids including *P. patula* × *tecunumanii* and *P. elliottii* × *caribaea* have been developed, tested and are being adopted in different regions of South Africa (Roux et al. 2007; Kanzler et al. 2012; Ford et al. 2014; Kanzler, Nel and Ford 2014; Hongwane et al. 2018). In addition to resistance to the pitch canker fungus, studies have also been conducted to determine the wood properties of these species (Hongwane et al. 2017, 2018; Nilsson et al. 2020). Although some studies have been conducted to examine bark thickness in commercial pines in South Africa (de Ronde and du Plessis 2002; Van Laar 2007; Crous et al. 2009; Hempson et al. 2014; Odhiambo et al. 2014), limited attention has been paid to the hybrids. Fire and pathogens pose significant and ongoing threats to the sustainability of commercial forestry in South Africa, challenges that are expected to intensify with climate change (Kraaij et al. 2018; Wingfield et al. 2020). Investigating variation in bark thickness during the early developmental stages of commercially important *Pinus* species is essential. This knowledge can help forest managers optimize site-species matching, ultimately enhancing resilience to fire and pathogen outbreaks. By prioritizing these strategies, the continuity of commercial timber supply can be better safeguarded against these environmental and biological stressors over the long term.

This study was conducted to model and compare bark thickness variation between different species of young South African-grown *Pinus* trees, specifically to improve the dating of wood formation in young tree stems. Accurately accounting for bark thickness is crucial in the process of dating wood formation, as it ensures the precise estimation of wood formation timing (Drew and Downes 2009; Drew et al. 2009). Correctly determining when wood formation occurred is essential for linking wood properties to growth conditions. The specific objectives of this study were to

compare bark thickness between the species, assess the variation of bark thickness with age and model changes in bark thickness at varying diameters and heights along the stem.

Methods

The study was conducted using a fertilizer × species trial established on Delheim farm, in Stellenbosch area, Western Cape, in August 2021. The five species of pine studied were *Pinus radiata* var. radiata D. Don. (*P. radiata*), *Pinus elliottii* Engelm. (*P. elliottii*), *P. elliottii* Engelm. × *P. caribaea* var. hondurensis (*P. ell* × *car*), *P. patula* × P. tecunumanii Low Elevation (*P.pat* × *tecL*), and *P. patula* × *P. tecunumanii* High Elevation (*P. pat* × *tecH*). *P. tecunumanii* low and high elevation represent subpopulations occurring below and above an altitude of 1, 500 m respectively (Dvorak et al. 2000). The species were randomly assigned as main plots, each main plot consisted of 8 × 8 tree rows, thus 64 trees, and this was slip longitudinally into two subplots of 32 trees each. The trees were planted at a spacing of 3 × 3 m apart. Two fertilizer treatments (high N:K – 2.8 and low N:K – 1.6) were randomly assigned to the subplots on each half of the main plots. For the high N:K treatment, a controlled release fertilizer blend of 186:72:67 g/kg of NPK with some Ca, Mg and trace elements was applied at rate of 150 g per tree. The low N:K treatment consisted of a blend of 139:91:88 g/kg (also with Ca, Mg and trace elements) applied at a rate of 75 g per tree. The N and K constituents of the fertilizer mixture were polymer-coated (controlled release) products. Fertilizers were applied in two lateral strips on either side of the transplant, at a depth of about 5 cm below the soil surface, and the closest part of the fertilizer strip approximately 5 cm from the root plug (Loewe-Muñoz et al. 2024). All the treatments were replicated three times each in two blocks with high wind exposure and low wind as the blocking factor. For brevity, in this paper, the term "species" will be used when referring to the five species and hybrids combined. A detailed map of the experimental site included in Appendix 1.

Bark thickness was measured twice (March and November) during the second year of growth. No bark sampling was conducted in the first year to avoid inflicting wounds that would deter growth and potentially compromise survival. In March 2023, when the trees were 1.6 years (19 months) old, 142 trees (at least two from each sub plot) were randomly selected for bark sampling (Table 1). Their height was measured using a tape measure attached to a wooden rod. Two perpendicular diameter measurements were taken at a point 50 mm above the ground using a digital caliper with an accuracy of 0.01 mm. Stem diameter was obtained as the average of the two measurements. At the point of diameter measurement, a rectangular section of the bark was extracted from the stem with a sharp blade (Fig. 1b). Absolute bark thickness was measured with an INSIZE digital micrometer with an accuracy of 0.001 mm. This method was suitable for these young stems owing to the relatively uniform bark along the circumference. Relative bark thickness was obtained as a percentage of the ratio of absolute bark thickness to the bole diameter (Midgley and Lawes 2016). Bole diameter (diameter under bark) was determined by subtracting double bark thickness from the diameter over bark.

Table 1 Number of trees sampled for bark measurement per species

Species	March 2023	November 2023
P. elliottii	34	24
P. ell × *car*	20	24
P. pat × *tecH*	28	24
P.pat × *tecL*	24	24
P. radiata	36	24

In November 2023, when the trees were 2.3 years (27 months) old, 120 trees from the same trial were destructively sampled including two trees per treatment group (Table 1). This made it possible for bark thickness to be measured at different positions along the stem. The trees were cut at the root collar and the stems were stripped of needles and branches. Bark was measured along the main stem from the root collar (0%) and then from 25%, 50%, 75% of the length of the main stem and from the tip (100%) (Fig. 1c). At each point along the stem, diameters were measured in two axial directions. Then, the bark was removed, and the diameters were remeasured at the same locations (accuracy ± 0.1 mm). Absolute bark thickness was calculated as half of the difference between the diameters over and under bark. Relative bark thickness was calculated as a percentage of the ratio of absolute bark thickness to the bole diameter.

Data analysis

Shapiro–Wilk tests were used to confirm normal distribution of variables and Bartlett's test of sphericity was used to test equality of variances. Because the data did not meet the theoretical assumptions for parametric tests, significant differences in bark properties among the species were tested by the nonparametric Kruskal–Wallis test (with post hoc Dunn test). The growth (diameter and height) between the two ages was analyzed using descriptive statistics and compared by species. An independent samples t-test was used to verify the existence of differences between bark thickness measured at 1.6 and 2.3 years for each species. The relationship between bark thickness and diameter over



Fig. 1 **a** The research trial, **b** rectangular bark section removed for measurement at 1.6 years, **c** bark measurement along stem diameter for measurement at 2.3 years

bark was examined using correlations and simple linear regression models. A simple linear model was fitted using the pooled data for all species to produce one regression line. This model was compared with another analysis of covariance model that allowed the slopes and intercepts to vary for each species. To obtain fit statistics for each species, models were fitted for each species with and without disaggregation by age. Models were evaluated using the coefficient of determination (R^2), root mean square error (RMSE), mean absolute error (MAE), and Akaike information criterion (AIC). Before interpretation, model residuals were checked for normality and homogeneity of variance using the Shapiro–Wilk and Breusch–Pagan test respectively. Analysis of variance (ANOVA) was used to test the significance of the differences in bark thickness at the different relative positions along the stem. Where significant differences were found, a post hoc Tukey HSD test was performed to isolate the pairwise differences. All tests were performed at a significance level of 0.05 and data analysis was conducted using R programming language – v4.3.0 (R Core Team 2024).

Results

Difference in bark thickness among the species

The diameter and the height of the trees at the end of the study ranged from 9 to 85 mm and 6 cm to 350 cm, respectively. Between 1.6 and 2.3 years, the fastest mean growth in diameter was recorded in *P. pat*×*tecL* from 17.3 to 38.3 mm (121%) while the slowest was recorded in *P. elliottii* from 19.2 to 33.1 (72%). Height increment was the highest for *P. ell*×*car* from 70.8 to 141 cm (99%) and the lowest for *P. elliottii* (83.7–112 cm) and *P. pat*×*tecH* (118–160 cm), both of which increased by 35%. *P. elliottii* had the slowest growth both in diameter and height.

There was no significant effect of the fertilizer and the blocking effect on both absolute and relative bark thickness (Kruskal–Wallis test: $p > 0.05$). At both 1.6 and 2.3 years, there were statistically significant differences in absolute bark thickness (Figs. 2 and 3) among the species (Kruskal–Wallis test: $p < 0.001$). At 1.6 years, the only significant difference was between *P. ell*×*car* and

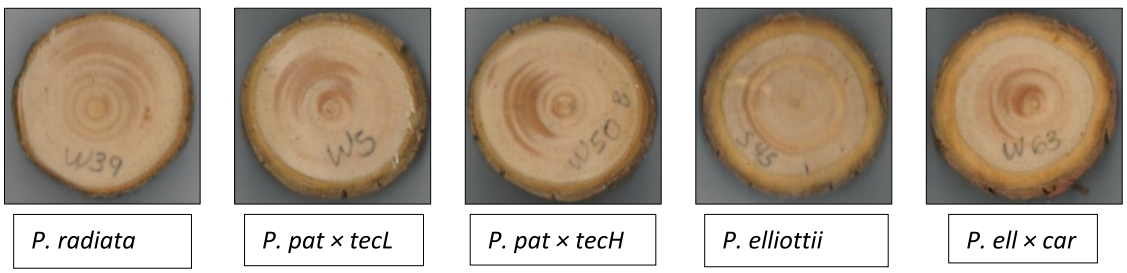


Fig. 2 Cross sections of the species at 2.3 years arranged from species with lowest mean bark thickness (*P. radiata*) to highest (*P. ell*×*car*)

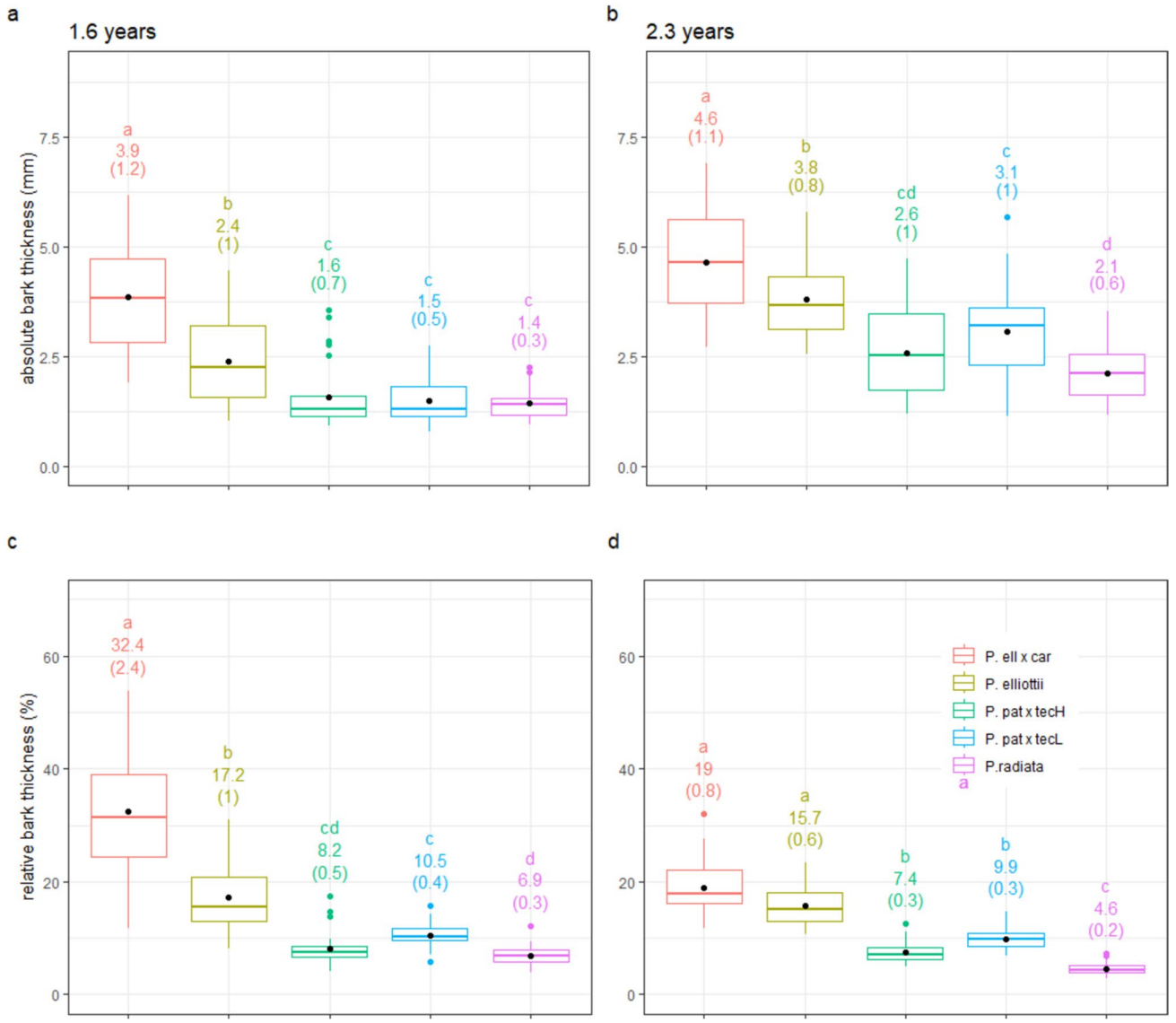


Fig. 3 Boxplots for absolute (**a** and **b**) and relative (**c** and **d**) bark thickness by age (letter – level of significance; inset point and number – mean; number in parenthesis – standard deviation)

P. elliottii while *P. pat* × *tecL, P. pat* × *tecH* and *P. radiata* had low variation in bark thickness. However, at 2.3 years, *P. pat* × *tecL* and *P. radiata* became significantly different from each other while the other pairs remained as they were at 1.6 years. While *P. ell* × *car* had the highest mean bark thickness at both ages, *P. radiata* had the lowest values, Fig. 2.

Bark thickness relative to diameter varied between 4.9 and 51.86%. The variability among the species was statistically significant at both ages (Kruskal–Wallis test: $p < 0.001$). The comparative differences in mean absolute and relative bark thickness between species stayed fairly consistent between 1.6 and 2.3 years (see Fig. 3). However, it is notable that while for most species, the variation in absolute bark thickness increased from 1.6 to 2.3 years, the variation in relative bark thickness decreased.

As expected, there was an increase in mean absolute and a decrease in mean relative bark thickness between ages 1.6 and 2.3 years. For all the species, the increase in bark thickness was statistically significant ($p < 0.05$). Bark deposition more than doubled in *P. pat* × *tecL* (113%) and was also reasonably higher in *P. pat* × *tecH* (82%) as shown in Fig. 4a.

The decrease in relative bark thickness was significant in *P. ell* × *car* (t (27) = 5.7, $p < 0.001$) *and P. radiata*

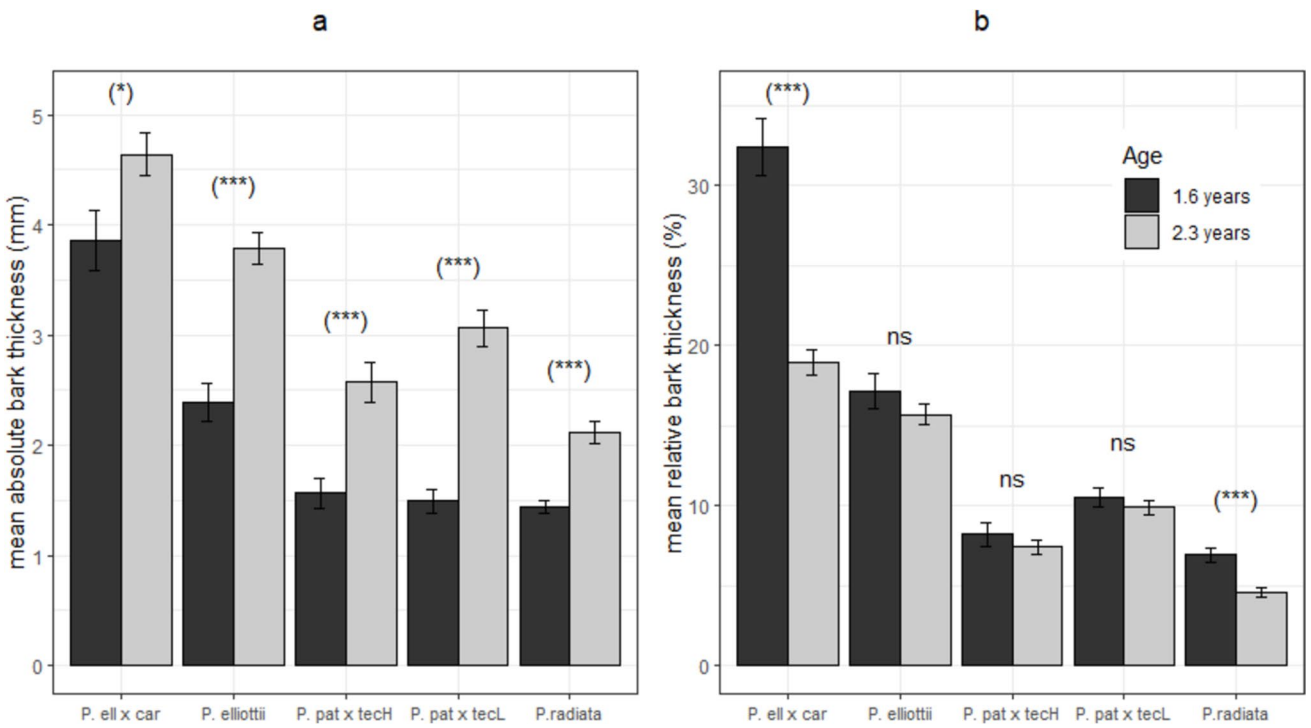


Fig. 4 Change in mean absolute (**a**) and mean relative bark (**b**) thickness with age among the species with standard error bars and significance level ((*)– $p < 0.05$, (***)– $p < 0.001$, ns not significant)

(t (59) = 7.1, $p < 0.001$). The mean relative bark thickness decreased by slightly over 30% for both species. For the remaining species studied, the decrease in mean relative bark thickness was not statistically significant and was less than 10%. Interestingly, the reduction in relative bark thickness for the hybrids was the lowest compared to the other species (Fig. 4b). Although *P. ell*×*car* had the thickest bark of all the species, bark growth between 1.6 and 2.3 years was only marginal at 18% compared to the other species. This resulted in a sharp decline in relative bark thickness. Similarly to *P. ell*×*car*, in *P. radiata*, there was a large decrease (34%) in relative bark thickness from 1.6 to 2.3 years.

Relationship between bark thickness and diameter

The analysis of covariance model in which the slopes and intercepts varied by species was much better ($R^2 = 0.83$, AIC = 538, RMSE = 0.558) than the model with pooled data ($R^2 = 0.16$, AIC = 1015, RMSE = 1.238). As expected, all species showed a positive linear relationship between absolute bark thickness and diameter (Fig. 5). Even when the data was disaggregated by age, there were still clear relationships between diameter and bark thickness for all the species with only slight variations in slope. Models with both ages together performed better (explained an extra 20% of variation in bark thickness) than models disaggregated by age.

The increase in bark thickness with diameter was the highest in *P. elliottii* which had the steepest slope (0.114) and lowest in *P. radiata* (0.029). The increase in bark thickness with diameter was higher in *P. pat*×*tecL* (0.081) than in *P. pat*×*tecH* (0.066). Except for *P. ell*×*car*, diameter explained at least 70% of the variation in bark thickness across all species. Relative bark thickness showed a strong decrease with stem diameter in *P. radiata* and *P. ell*×*car* while a weak negative correlation was observed in *P. elliottii, P. pat*×*tecH* and *P. pat*×*tecL.*

Variation in bark along the stem profiles

All species showed a decrease in absolute bark thickness along the stem except for *P. elliottii and P. radiata* where absolute thickness increased slightly at 25% and 75% relative height respectively (Fig. 6). The percentage decrease in bark thickness was the highest in *P. pat*×*tecL* from 3.19 to 1.15 mm (64%), while *P. radiata* had the smallest decrease from 2 to 1.37 mm (29%).

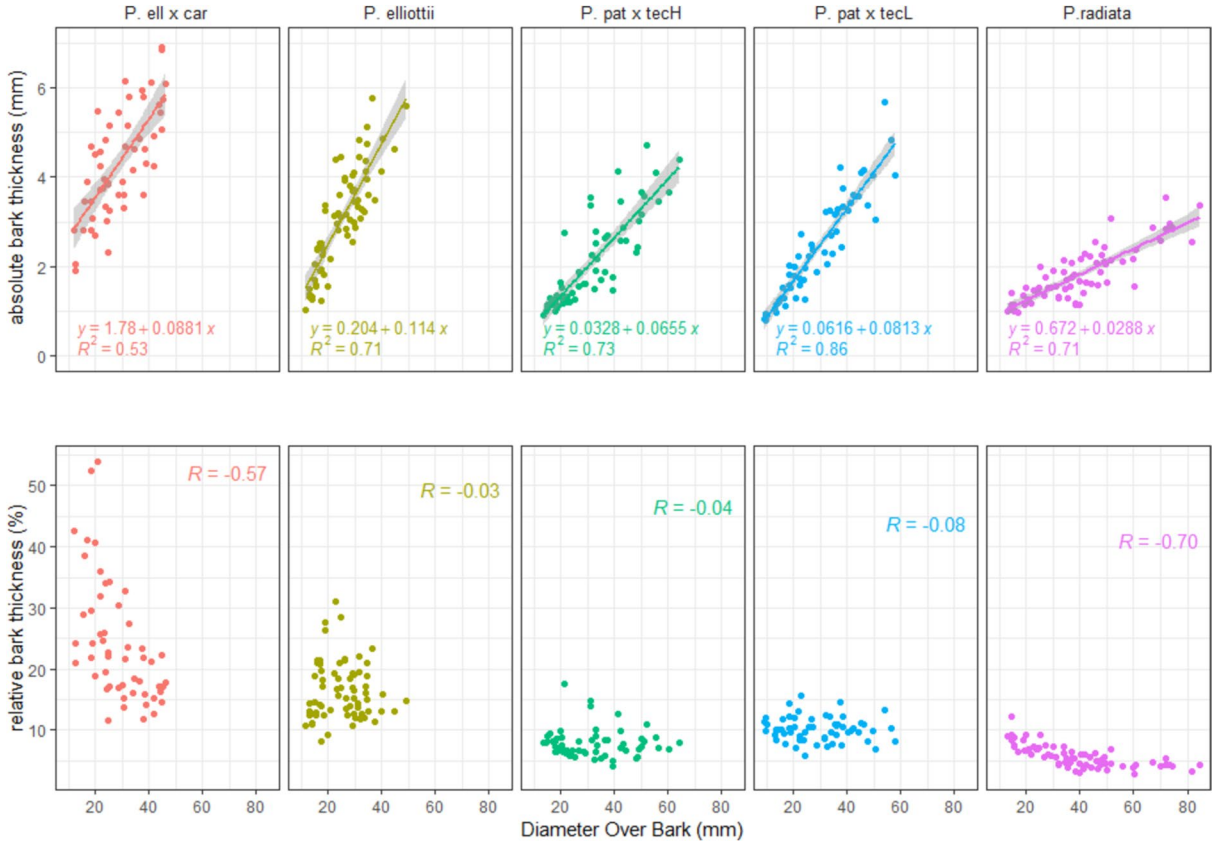


Fig. 5 Relationship between absolute and relative bark thickness with diameter over bark

P. elliottii and *P. ell*×*car* had much higher absolute and relative bark thickness along the stem than the other species studied (Fig. 6). Also, the difference between the *P. elliottii* and *P. ell*×*car* was only significant at 0% relative height (ANOVA: $p < 0.05$). At all relative heights, there was no significant difference between *P. pat*×*tecL* and *P. pat*×*tecH* (ANOVA: $p > 0.05$). The variation of *P. radiata* was similar to that of *P. pat*×*tecL* and *P. pat*×*tecH* at all relative heights except at 0% and 75% (ANOVA: $p < 0.05$). There was greater interspecies variability at the base of the stem (0%) than in higher portions.

Relative bark thickness increased along the stem from base (0% relative height) to top (100% relative height) for *P. elliottii* (15 to 20.3), *P. ell*×*car* (17 to 21.1) and *P. radiata* (4.43–7.02) (Fig. 6). In *P. pat*×*tecL* and *P. pat*×*tecH*, the relative bark thickness decreased in the first half of the stem before increasing to a value higher than the relative thickness at 0%, although only very slightly for *P. pat*×*tecL* (10.2 to 11). At all relative heights except at 0%, *P. elliottii* and *P. ell*×*car* was similar to each other (ANOVA: $p > 0.05$) but were significantly different from the other species (ANOVA: $p < 0.001$). *P. pat*×*tecL* and *P. pat*×*tecH* was significantly different only at 0% and 25% relative height (ANOVA: $p < 0.05$). The variation of *P. radiata* was significantly different from that of *P. pat*×*tecL* and *P. pat*×*tecH* at all relative heights except at 75% (ANOVA: $p > 0.05$).

Discussion

The results showed that the differences in both absolute and relative bark thickness among the species were significant. Species-specific variation in bark thickness has been observed in many comparative studies (Crous et al. 2009; Eberhardt et al. 2017; Stängle and Dormann 2018; Shearman and Varner 2021; Singh et al. 2022). Several notable studies also indicate that relative bark thickness is a better parameter than absolute bark thickness when comparing species (Lawes et al. 2013; Hempson et al. 2014; Pausas 2015b; Midgley and Lawes 2016; Singh et al. 2022). This study showed that both absolute and relative bark thickness were significantly higher in *P. elliottii* and *P. ell*×*car* than the

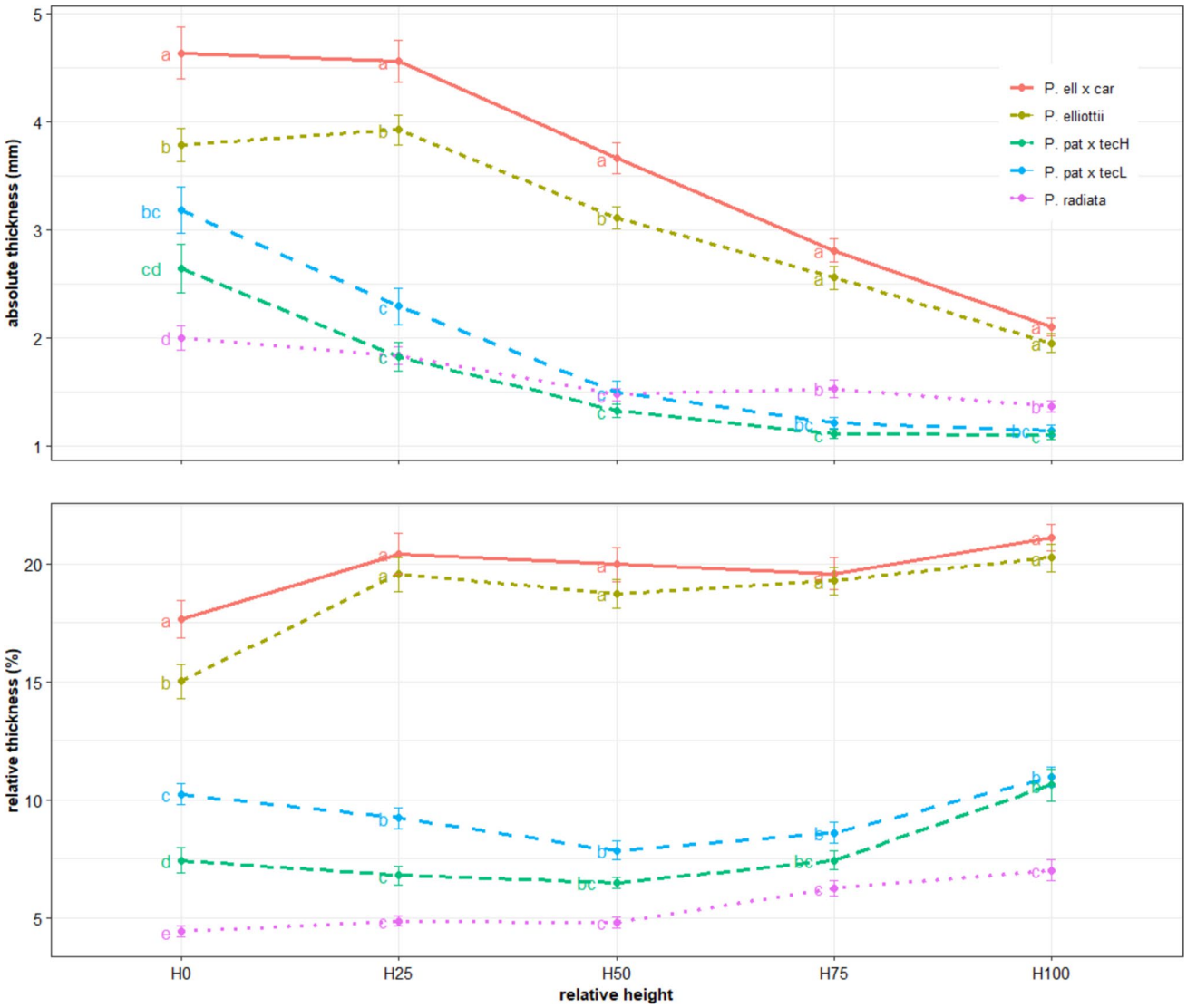


Fig. 6 Change in mean absolute (top) and relative (bottom) bark thickness along the stem from base to top with standard error bars

other three species investigated. Although no studies on the bark thickness of the hybrids were found, studies on much older species corroborate our findings. For instance, a study on 16-year-old pine species showed that *P. caribaea* had the highest relative bark thickness, followed by *P. elliottii* while *P. patula* and *P. tecunumanii* had much lower relative thickness (Crous et al. 2009). On the contrary, both absolute and relative bark thickness were the lowest in *P. radiata*. This result was also confirmed in studies comparing more mature pines. For example, bark volume, which is a function of bark thickness and diameter, was 17% in 24-year-old *P. elliottii* (Eberhardt et al. 2017). Also, Murphy and Cown (2015) reported 12–13% bark volume in 26-year-old *P. radiata* which was close to the 11.8% reported as the average for the species across the USA (Miles and Smith 2009). This study confirms the view that large variation in bark thickness between species is evident right from the early stages of plant development (Lehnebach et al. 2020; Rodriguez-Perez et al. 2022; Singh et al. 2022) also suggesting that species ranking of bark thickness remains relatively similar regardless of age.

Bark thickness and diameter

The results showed, as expected, an increase in bark thickness with increasing diameter and age. Many studies that

have examined the relationship between bark thickness and diameter in different species confirm this positive relationship (Kitikidou et al. 2014; Richardson et al. 2015; Stängle and Dormann 2018; Kidd and Varner 2019; Yilmaz, Ozdemir and Makineci 2021; Kurt, Calikoglu and Isik 2021; Magalhães 2021; Neumann and Lawes 2021; Yang and Radtke 2021; Singh et al. 2022; Hansen et al. 2023; Zhu et al. 2024). The increase in bark thickness has been reported to be linear in smaller diameters (Hempson et al. 2014; Midgley and Lawes 2016; Kurt, Calikoglu and Isik 2021) and plateau as the tree matures. In *P. brutia*, the linear relationship was observed up to 25 years (Kurt, Calikoglu and Isik 2021). Some studies suggest that assessment of bark thickness between species is more informative on trees in the linear range of variation (Poorter et al. 2014; Singh et al. 2022). In this study, a simple linear model was fitted, and diameter alone explained more than 70% of the variation in bark thickness for all but *P. ell*×*car* trees, where it accounted for 53%. This is in agreement with the results of most studies reporting that diameter explains most of the variation in bark thickness (Magalhães 2021; Zhu et al. 2024).

In this study, the change in bark thickness at both ages was linear for all the species. Like diameter, bark thickness has also been reported to increase linearly with tree age before plateauing (Sonmez et al. 2007; Stängle and Dormann 2018; Kurt, Calikoglu and Isik 2021; Mosaffaei and Jahani 2021; Yilmaz, Ozdemir and Makineci 2021). Within this linear range, it is reasonable to assume that only changes in slope will occur. An aspect of bark growth that has received little attention is the role it plays in dendrochronology and the dating of wood formation. Especially since bark growth needs to be accounted for to accurately determine the time of wood formation (Drew and Downes 2009). Diameters are most often measured over bark, but the wood formed is assessed inside bark. Also, growth in diameter is due to addition of both wood and bark, such model can be used to isolate and minimize the influence of bark. A clear understanding of the change in bark thickness over time translates into more accurate predictions of how the prevailing growth factors influence specific wood properties. Growth measured outside bark can thus be disaggregated into wood and bark growth for fine-scale inferences. With the growing interest of tree breeders in the screening of wood properties as early as 2 years (Apiolaza and Sharma 2023), it is of additional importance if the properties can be related to environmental changes.

The rate of increase in bark thickness varied from *P. elliottii, P. ell*×*car, P. pat*×*tecL, P. pat x tecH* and *P. radiata* in descending order. Previous studies report that the threshold for safety from low-intensity fires is a bark thickness of about 10 mm (Hoffmann et al. 2012; Hempson et al. 2014; Poorter et al. 2014; Pile et al. 2017). Considering the bark thickness threshold of 10 mm and using the species equations generated in this study, they would achieve fire protection at diameters of 86 mm (*P. elliottii*), 93 mm (*P. ell*×*car*), 152 mm (*P. pat*×*tecL)*, 122 mm (*P. pat*×*tecH*) and 324 mm (*P. radiata*) respectively. *P. radiata* would attain fire safety much later in the rotation than the other species considered, under the assumption that the rate of change of bark allocation remains constant and linear. Regardless, the results suggest that *P. elliottii* and the hybrids are more fire-resistant than *P. radiata,* which is generally accepted as a fact by commercial forestry practitioners in South Africa. In addition to other traits, such as rapid growth and investment in below-ground attributes, early investment in thick bark is a fire adaptation strategy adopted by many species including pines (Hempson et al. 2014; Poorter et al. 2014; Pile et al. 2017; Kidd and Varner 2019). Our results confirm trends observed previously in some of these species in both juvenile and mature trees. A prescribed fire experiment with different pine species including *P. elliottii* and *P. patula* showed that at 3 years, *P. elliottii* was the most fire-resistant (de Rhonde 2002). Similarly, a study comparing the protective role of bark in fire found that *P. radiata* was more fire-sensitive, while *P. elliottii* was more fire-resistant (Odhiambo et al. 2014).

Along the stem

The variation in bark properties along the stem is a function of both absolute thickness and stem diameter (Cellini et al. 2012; Liepinš and Liepinš, 2015). The results of this study showed that absolute bark thickness decreased from the stem base upwards in all species studied—although different patterns were evident between species. Many previous studies have reported a decrease in absolute bark thickness along the stem (Laasasenaho et al. 2005; Eberhardt 2015; Hammond et al. 2015; Murphy and Cown 2015; Kidd and Varner 2019; Ramalho et al. 2019; Magalhães 2021). This indicates that bark at the bottom or lower parts of the stems is thicker than further up. The decrease in bark thickness was the lowest in *P. radiata* indicating that bark thickness remains fairly uniform along the stem. This pattern of variation of bark along the stem is reported to be one of the reasons for the fire susceptibility of *P. radiata* (Odhiambo et al. 2014) since the lower part of the stem is usually exposed to higher temperatures in low-intensity fires (flame height ≤ 2 m) (Graves, Rifai & Putz 2014; Wolfe et al. 2014).

On the other hand, the absolute bark thickness of *P. elliottii* and the hybrids decreased fairly uniformly from the stem base to the tip. There was more bark allocated in the lower half of the stem, resulting in more dramatic bark taper as was observed in their pattern of variation. This pattern is similar to what is generally observed in fire-resistant species as they invest more bark in the parts of the stem most vulnerable to fire (Hoffmann et al. 2012; Graves, Rifai and Putz 2014; Hempson et al. 2014; Odhiambo et al. 2014; Poorter et al. 2014; Murphy and Cown 2015; Pile et al. 2017; Shearman et al. 2018; Kidd and Varner 2019).

Regarding the relative bark thickness, an increase along the stem was observed in *P. radiata*, *P. elliottii* and *P. ell*×*car*. Comparing this result with the pattern observed for absolute bark thickness, it shows that the decrease in wood diameter is more pronounced than the decrease in bark thickness. It is possible that the thicker bark in the upper half of the stem contributes significantly to supporting the upright position of the tree. The role bark plays in keeping an uprightness position in especially young plants has been reported in some studies (Pausas 2015b; Clair et al. 2019). A variation similar to that in this study was observed along the stem of different juvenile hardwoods (Kidd and Varner 2019). In contrast to our results, a decrease in relative bark thickness along the stem was observed in 16 year *P. caribaea*, *P. elliottii* and *P. tecunumanii* (Crous et al. 2009) and in saplings of hardwood species (Hammond et al. 2015).

Unlike the others, an interesting pattern of variation was observed in *P. pat*×*tec* hybrids. The relative thickness decreased from the stem base up to 50% of the stem length, where it was the lowest, and then increased in the upper half. This suggests that in *P. pat*×*tec* hybrids, the most productive parts of the tree stem contain significantly less bark which is especially advantageous for sawlog production at the end of the rotation because of the low bark proportion. This decline and subsequent increase in bark has also been observed in Scots pine, Norway spruce, silver birch and aspen (Liepinš and Liepinš, 2015). In that study, they reported that the pattern was identical across all trees in the study, which were between 5 and 141 years old. Another study also observed a similar pattern in 5-year-old clonal *Eucalyptus* (Ramalho et al. 2019).

Research highlighted in the sections above demonstrates that bark traits observed in juvenile trees will most likely remain consistent throughout the tree's lifespan. This insight enables critical silvicultural decisions to be made as early as the nursery stage. Plantation managers can strategically allocate species with thicker bark to fire-prone or environmentally harsh sites, enhancing their survival potential. Additionally, in breeding programs where bark thickness is a key selection criterion, decisions can be implemented earlier in the breeding process, streamlining efforts to improve resilience and adaptability in commercial forestry species.

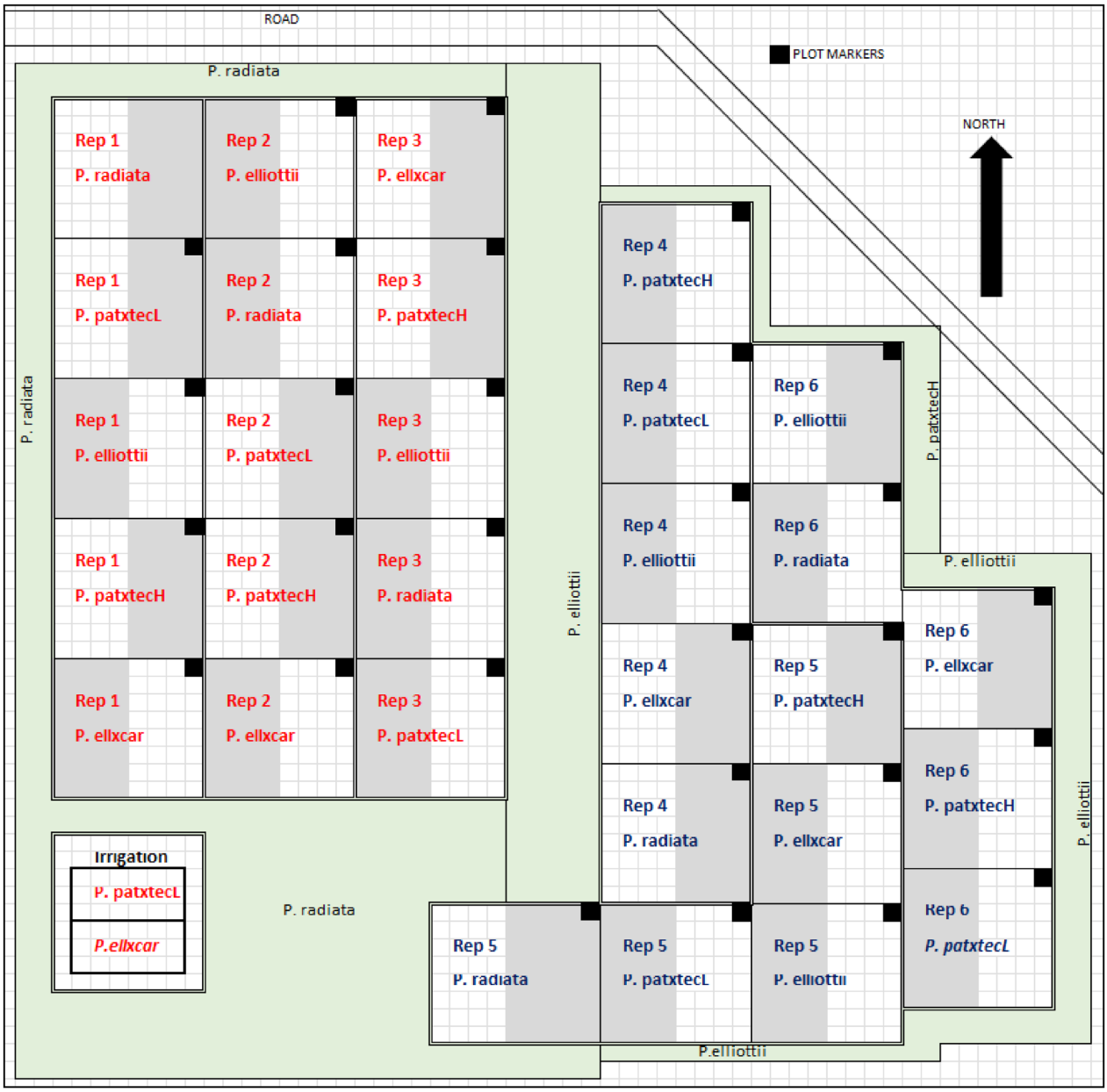
Conclusion

Using 2-year-old pine species, this study confirms that variation in bark properties is significantly different between species. Species known to have better fire tolerance, namely P. *elliottii* and *P. ell*×*car,* had thicker bark as well as a faster bark thickness increase with diameter. Even this early in their ontogeny, the studied species showed characteristics that are comparable to more mature trees of the same species (Hammond et al. 2015; Rodriguez-Perez et al. 2022). Because the ranking of the species is unlikely to change with size (Lehnebach et al. 2020), those with thick bark in the juvenile stage will remain with thick bark as the stems grow larger.

This means that bark thickness and proportions can be selected for early in development depending on the desired objectives of plantation management. Understanding the change in bark thickness over time will also improve the accuracy of dating when wood formation occurred. This will ensure that wood properties are correlated with spatial and temporal variation in environmental factors during the growth seasons. Furthermore, plantation managers interested in bark as a raw material can better predict which parts of the stem will produce better yields. Although this study provides important insights into bark allocation, future studies should examine bark from a broader age and diameter range for different commercial pine varieties to expand the knowledge base on bark allocation. More accurate and timely bark assessments will also ensure growth yield models are updated appropriately.

Appendix

Experimental layout with white and gray subplots corresponding to low N:K (1.6) and high N:K (2.8) respectively. The plots on the left, indicated with red text, are wind exposed plots, while the ones on the right, indicated with blue text, are wind sheltered trees. The irrigation treatment section of the trial is shown in the left bottom corner of the map. Light green represents buffer strips on the borders of the two experiments.



Declarations

Author contributions SA, DMD, and CBW contributed to the conception and design of the study. SA performed the data collection, and all authors contributed to the analysis. The first draft was prepared by SA and all authors contributed to previous versions of the manuscript. All authors approved the final manuscript.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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