Stem position and root infection influence heartwood formation in Douglas-fir plantations

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Abstract: Heartwood formation influences timber quality and utilization, yet the factors driving its variation remain poorly understood. Understanding these variations can guide management strategies to influence heartwood development and enhance timber value through adapted silvicultural practices. This study examined the relationships between heartwood area and various tree characteristics in Douglas-fir plantations aged 25–34 years, across four sites within their native range in the southern interior of British Columbia, Canada. Stem analysis was used to quantify heartwood area and its relationships with tree-level variables, including sapwood area, tree height, root infection, and competition. To account for vertical variation along the stem, discs were categorized into three height classes based on relative stem height: lower (0–30%), middle (31%–60%), and upper (61%–100%). Heartwood area was primarily influenced by sapwood area, with the strongest effect at the middle stem, followed by the upper and lower positions. Tree height showed a position-dependent effect: positive in the lower stem and negative in the middle and upper sections. Root infection significantly increased heartwood area in the lower stem, with its effect weakening at higher positions. Competition had statistically significant but minimal effects, ranging from slightly negative in the lower stem to slightly positive in the upper stem. Our findings suggest that promoting sapwood development, particularly in the mid-stem, can enhance heartwood formation. While practices like thinning may contribute to this, the positive association between competition and heartwood in the middle stem indicates that maintaining moderate stand density may be more beneficial than aggressive spacing. Although root infection may locally stimulate heartwood near the base, its longer-term effects can disrupt the sapwood-heartwood balance and reduce tree vigor. Therefore, silvicultural strategies should aim to promote heartwood primarily through stand density management while limiting reliance on root stressors, integrating disease control measures to sustain overall tree health.

Keywords: Tree structure; Douglas-fir; Heartwood; Sapwood; Root disease; Competition

Introduction

Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) is native to western North America, from southern British Columbia in Canada to central California in the United States (Hermann and Lavender 1990). In British Columbia (B.C.), it exists in two varieties: the coastal variety (var. *menziesii*), found along the southern mainland coast and Vancouver Island, and the interior variety (var. *glauca*), which occurs in the southern part of the province and extends north (Government of British Columbia 2024). Douglas-fir produces valuable commercial timber that has been introduced beyond its native range into European countries (Spiecker et al. 2019). It exhibits moderate hardness, stiffness, stability, and resistance to fungal and insect attacks (Nicolescu et al. 2023). The desirable wood properties have led to its continued high demand internationally (Spiecker et al. 2019). The wood's versatility extends to various applications, including building materials, furniture, lumber, veneer products, interior and exterior finishing, and pulp, suiting multiple industries (Nicolescu et al. 2023; Natural Resources Canada 2024).

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Wood consists of sapwood and heartwood, which are distinguished by their appearance, anatomical structure, and functions. In coniferous trees such as Douglas-fir, sapwood is the portion of the xylem located between the cambium and heartwood. While most cells in the xylem are dead at maturity, the sapwood contains parenchyma cells, which remain alive and play a role in storage and metabolic functions (Wiedenhoeft and Miller 2005). The contents of sapwood flow across connections with adjacent tracheids through pairs of intertracheary bordered pits (Kozlowski and Pallardy 1996; Gartner and Meinzer 2005). These connections facilitate the transfer of water from the soil to the leaves (Gartner and Meinzer 2005).

In contrast, heartwood constitutes the inner, physiologically inactive portion of wood that does not conduct sap. As the xylem ages, parenchymal cells produce secondary metabolites before they die, which are released to the surrounding cells, resulting in the formation of more colored (compared to sapwood) xylem tissues (Zink-Sharp 2004). This alteration in color is attributed to chemical extractives such as tannins, dyestuffs, oils, gums, resins, and salts of organic acids that accumulate in cell lumens and walls, along with the disappearance of living nuclei and a reduction in nitrogen, starch, and sugar content (Kozlowski and Pallardy 1996; Zink-Sharp 2004; Wiedenhoeft and Miller 2005; Luo et al. 2018).

Heartwood formation and its development are influenced by various factors, including growth rate, tree biometric traits, stand characteristics, and environmental conditions (Larson 1969; Larson et al. 2001; Taylor et al. 2002). For example, in coastal Douglas-fir trees in plantations in Portugal, heartwood forms around 8–9 years of cambial age and progresses at a rate of 0.7–0.9 rings per year, with heartwood comprising about half of the lower stem's cross-sectional area, tapering upwards (Cardoso and Pereira 2017). While sapwood has an average radial width of 75 mm at the stem base and tapers upwards, it is denser (595 kg/m^3) and mechanically stronger than heartwood (544 kg/m^3), although heartwood's durability and decay resistance are vital for the tree's long-term integrity and industrial value (Duriot et al. 2021). This variation in heartwood formation is largely determined by growth conditions, including silvicultural treatments such as planting density and thinning methods (Pollet et al. 2017; Boakye et al. 2023). For instance, in uneven-age Douglas-fir stands in interior B.C., thinning was found to increase basal area increment (Acquah et al. 2024).

Silvicultural practices can influence wood properties such as juvenile wood percentage and ring density, with lower stand densities correlating with decreased juvenile wood content and ring density (Kantavichai et al. 2020). In addition, factors like disease and insect presence can affect wood quality, as evidenced by the susceptibility of sapwood to decay compared to heartwood in the central Cascades of Oregon (Gartner et al. 1999). In coastal plantations, such as those studied by Cardoso and Pereira (2017), the general variation in heartwood properties, including its proportion and decay resistance, depends on tree characteristics, growth conditions, and management practices (Bamber and Fukazawa 1985; Hillis 1987; Taylor et al. 2002). For example, while wood strength loss due to fungi is linked to the degradation of lignin and cellulose in heartwood (Schmidt 2006), changes in tree density or thinning treatments do not always affect heartwood proportion but can impact other wood properties, such as decay resistance (Gartner et al. 1999).

Armillaria ostoyae occurs circumpolar in the northern hemisphere (Watling et al. 1991) and is the primary causal fungus responsible for Armillaria root disease causing white rot decay. All woody species in Canada are hosts, but Douglas-fir is rated as highly susceptible to Armillaria root disease in the interior of British Columbia (Cleary et al. 2008). This disease infects roots and can lead to tree death or the non-lethal infections that are associated with significant reduced productivity (Cruickshank et al. 2011). Root infection in stands of interior Douglas-fir from stump inoculum leads to mortality of individual trees, typically starting about 5–7 years after stand establishment, with tree deaths peaking at around age 13–15, and then increasing again at about age 55 (Cruickshank and Filipescu 2012; Cruickshank 2017). Although aboveground symptoms are initially minimal, mortality can persist throughout the rotation (Cleary et al. 2008). Lumber from diseased trees often has fewer boards compared to healthy trees of similar breast height diameter, suggesting potential effects on stem taper or form. Warp is the most common issue affecting lumber and quality from diseased trees, while knots are the predominant defect in lumber from healthy trees (Cleary et al. 2008; Cruickshank et al. 2006; 2009).

Building on this context, our study aims to evaluate the factors influencing the formation of heartwood within planted interior Douglas-fir stands in B.C., focusing on how diseases, competition, and other tree characteristics influence this process. Heartwood and sapwood are complementary parts of the wood structure, with their proportions changing as trees grow. Therefore, understanding heartwood formation is critical for linking growth conditions and wood quality. We hypothesize that (1) greater sapwood area and belowground root infection will increase heartwood formation and (2) increased competi-

tion will reduce heartwood formation. The hypothesis assumes that greater sapwood area provides more material to transition into heartwood as trees grow. Root infections, while depriving sapwood of resources for growth, accelerate the transition to heartwood by causing sapwood to lose its function or die. In contrast, competition-induced resource scarcity limits overall sapwood development, ultimately reducing heartwood formation. While previous studies have focused on plantations with specific tree origins in regions outside of British Columbia, their findings may not be directly applicable to all populations or environments. Our study, conducted in the interior of B.C., therefore, takes into account local ecological and environmental factors that may differ significantly from those in other regions.

Material and Methods

Study area

The study area comprised Douglas-fir plantations within the Interior Cedar Hemlock (ICH) biogeoclimatic zone in southern British Columbia of Canada. The ICH is sheltered from maritime influence by coastal mountains, creating a continental climate with moist summers, cold wet winters, and a snowpack that mitigates summer moisture deficits (Lloyd et al. 1990). The ICH zone ranks second in productivity after the Coastal Western Hemlock zone and boasts the highest tree species diversity in British Columbia. Douglas-fir commonly dominates mature seral stands and is a preferred species for regeneration on harvested sites. The ICH zone harbors approximately 71,000 ha of Douglas-fir plantations. *Armillaria ostoyae* (Romagn.) Herink is prevalent in the Interior Douglas-Fir, Montane Spruce, Engelmann Spruce, Subalpine Fir, and Cedar Hemlock zones, with its incidence and damage most pronounced in the ICH (Morrison et al. 1991).

Study sites and measurements

Douglas-fir plantations were selected for sampling in four sites at Chuck Creek (CC), East Barriere (EB), Kingfisher (KF), and Kuskanax (KX) near Nakusp (Table 1). The selection criteria included accessibility by roads capable of accommodating a lowbed trailer with a 20-ton excavator and sufficient space for the excavator to travel on-site. In addition to these logistical factors, sites were chosen to represent a range of ecological conditions relevant to the study, such as differences in elevation, precipitation, and temperature. Kingfisher, for example, has about 1.86 times the precipitation of Chuck Creek and 1.67 times that of East Barriere, about 59% of Chuck Creek's and 64% of East Barriere's summer heat index, and an elevation about 270 m lower than Chuck Creek. The Kuskanax site was specifically chosen because it was planted after a wildfire, adding variability to the study. All sites, except Kuskanax, had previously undergone clearcutting and were planted with Douglas-fir at a density of 1600 stems/ha. These sites represent the oldest plantations that could be accessed with an excavator, which was a limiting factor in site selection.

Once areas for safe extractor travel and work were identified, a grid was overlayed on each area, and coordinates were selected from each grid until the required number of plots was

Table 1. Descriptive statistics of Douglas-fir site details and average stem data.

Attribute	Chuck Creek	East Barriere	Kingfisher	Kuskanax	Overall sites
Lat. / Long.	51.6N / 119.7W	51.3N / 119.8W	50.7N / 118.8W	50.2N / 117.8W	NA / NA
Elevation (m)	690	700	420	480	NA
Mean summer heat-moisture index	70	64	41	55	NA
Mean annual summer precipitation (mm)	224	249	416	320	NA
Mean tree age	34	25	30	32	34
Mean heartwood area (cm^2)	67.15 ± 79.24	38.49 ± 51.56	52.37 ± 54.70	67.63 ± 78.57	57.62 ± 69.23
Mean heartwood area prop. (%)	36.78 ± 20.14	24.42 ± 15.17	33.25 ± 16.47	32.52 ± 15.92	32.05 ± 17.53
Mean sapwood area (cm^2)	148.42 ± 116.97	173.16 ± 108.97	150.66 ± 99.27	203.36 ± 129.14	83.96 ± 75.37
Mean sapwood area prop.	63.21 ± 20.14	75.57 ± 15.17	66.74 ± 16.47	67.47 ± 15.92	67.94 ± 17.53
Mean diameter (cm)	15.64 ± 5.34	13.67 ± 3.93	15.40 ± 4.52	17.53 ± 5.15	15.56 ± 4.95
Mean tree height (m)	12.35 ± 2.57	9.97 ± 1.46	13.39 ± 2.57	15.76 ± 2.16	12.86 ± 3.05
Mean crown length (cm)	893 ± 291	928 ± 149	948 ± 262	963 ± 262	934 ± 252
Mean crown volume (cm^3)	39.04 ± 33.40	104.43 ± 59.39	37.20 ± 29.23	35.57 ± 22.20	54.06 ± 48.35
Number of infected and healthy trees per site (12 trees each for 24 trees per site)	24	24	24	24	NA
Mean proportion of infected roots	26	25	26	27	NA

Lat.: latitude, Long.: longitude, Min: minimum, Max: maximum, Prop: proportion, mean and standard deviation (denoted as mean ± standard deviation).

established. At each site, 6 plots (10-m radius) were randomly located. In each plot, 4 trees were randomly sampled, resulting in a total of 24 trees per site and 96 trees across all sites. Tree coordinates were measured using a traditional survey transit mounted on a tripod at the plot center. The angle from north to each tree and the distance from the tree to the plot center were recorded. From these measurements, the x and y coordinates for each tree were calculated.

The diameter of each tree was measured at breast height (1.3 m, DBH) and crown width measured at cardinal points. Trees were extracted in the fall using a 20-ton Link Belt excavator equipped with a clamshell bucket attachment to minimize root, stem, and branch breakage. Soil was manually removed from the roots of all trees in the plots after the soil thawed in the following spring. Infection was determined by the presence of mycelial fans in the bark or cambium. Tree height (m), crown length (m), and height to live crown (m) were recorded for each tree after pulling. Crown length ratio was calculated as the ratio of crown length to total tree height. The basal area of individual trees was calculated and used for further analysis, with DBH measured in centimeters. A non-spatial competition index was calculated for each sampled tree using the sum of the plot's basal area of trees that were larger than the target tree (basal area of larger trees or BAL, cm^2).

Cross-sectional stem disks were cut at intervals of 0, 0.3, 1.3, and 2 m from the base of the stem, and then at every 2-m interval thereafter until the diameter of the stem was reduced to 2 cm. The sapwood-heartwood boundary was distinct in Douglas-fir, especially after wetting with water, if need be, and was assessed visually and marked before digitization for on-screen area measurements of heartwood area (HWA, cm^2) and total wood area (cm^2). Sapwood area (SWA, cm^2) was calculated from the difference between total wood area and HWA.

Distance from the apex (DFA; m) was calculated by subtracting the disc sampling height relative the soil line from the total tree height to evaluate heartwood area consistently along the stem. The position of the sample disc relative to the base of the live crown (distance to crown base, DCR, m) was calculated as the difference between disc height and live crown height. Positive values indicate that the disc is located within the crown, while negative values indicate that the disc is below the crown.

Statistical analyses

We first conducted exploratory analyses in R software (R Core Team 2024) to examine relationships among predictor variables at the disc, tree, and plot levels (see Appendix Figure A1 for a full list of variables). At the disc level, we included sapwood area (SWA), disc height (m), distance from the apex (DFA), and disc crown radius (DCR, m). Tree-level variables included tree age (years), total height (m), crown length (CL, cm), height to the live crown (m), and the basal area of larger trees (BAL, cm^2). The binary variable for belowground root infection (BGRI; 0 = healthy, 1 = diseased) was excluded from correlation analysis because the Pearson correlation assumes continuous data.

To select candidate predictors for modeling, we evaluated multicollinearity using variance inflation factors (VIF). Variables with VIF < 5 and biological relevance, namely SWA, tree height, BAL, and BGRI were retained in the final model set.

To investigate the relationship between HWA and predictor variables, we fitted separate linear mixed-effects models (LME) for each relative stem height category using the *nlme* package in R (Pinheiro et al. 2024). Discs were grouped into three height classes based on their relative position along the stem: lower (0–30%), middle (31%–60%), and upper stem inside the crown (61%–100%). Preliminary analyses revealed height-specific variation in the effect of predictors on HWA, and interaction terms involving height were not readily interpretable in a unified model. Therefore, a stratified modeling approach was used to assess the relative importance of predictors within each stem position category.

The final model structure, applied separately to each stem height group, was:

$$\log(HWA_{ij} + 1) = \beta_0 + \beta_1 (SWA_{ij})^{0.1} + \beta_2 \, Height_j + \beta_3 \, BGRI_j + \beta_4 \, BAL_k + b_{0j} + \varepsilon_{ij} \quad [1]$$

Where:

- HWA_{ij} is the heartwood area of disc i within tree j; the response variable was log-transformed as $\log(HWA_{ij} + 1)$.
- $(SWA_{ij})^{0.1}$ is the 0.1-power-transformed sapwood area measured at the same disc level.
- $Height_j$ is the total height of tree j.
- $BGRI_j$ is a binary indicator of belowground root infection for tree j.
- BAL_k is the basal area of larger trees, calculated at the plot level k, where tree j is located.
- $b0_j$ is a random intercept for tree j, accounting for the clustering of disc samples within trees.
- ε_{ij} is the residual error term.

To account for repeated measurements at different disc heights within trees, the model included an exponential spatial correlation structure with a nugget effect (corExp), based on

vertical distance from the apex (DFA). Site and plot effects were tested, but did not significantly improve model fit and were therefore excluded.

Model diagnostics confirmed that residuals were normally distributed and exhibited no systematic patterns when plotted against model fixed effects (Appendix Figure A2). Because HWA was log-transformed, we applied a bias correction factor (Snowdon 1991) to back-transform model predictions for visualization on the original scale (cm^2).

Results and discussion

Stem position effects on heartwood area variability and model fit

Our results (Table 2) showed that the lower stem had negligible random effect variation (0.0001), the upper stem exhibited moderate variability (0.30), and the middle stem showed higher variability (0.49), indicating that unmodeled tree-level differences were most pronounced at mid-height. Given the financial and operational constraints, the sample size used in this study was considered appropriate for the scope of the research. However, larger sample sizes and a greater number of study sites would certainly provide more robust results and reduce the potential for bias due to limited sampling. Further research with expanded sample sizes and more diverse site conditions would improve the precision of the model, particularly in capturing between-tree variability in the middle stem. The residual variation ranged from 0.28 to 0.47, with the middle stem showing the lowest residual variance, suggesting better model precision at that position. Despite these considerations, overall model fit, as indicated by AIC, was best for the upper and lower stem sections (222.46 and 222.93, respectively), and poorest for the middle stem (279.81), likely due to greater between-tree variability that was not fully accounted for by the fixed effects. These results suggest that heartwood area was more consistently predictable across trees in the upper and lower stem sections, possibly due to more uniform structural traits and environmental exposure in those positions. Further studies with larger sample sizes would provide more insights into these dynamics.

Main Effects on heartwood formation

The effects of predictor variables on heartwood area varied by stem position (Table 2, Figure 1A), with SWA emerging as the strongest and most consistent driver of heartwood formation. Its influence was greatest in the middle stem (β_1 = 13.52), followed by the upper (β_1 = 8.63) and lower sections (β_1 = 4.74). The middle stem likely shows the strongest effect because it serves as a transitional zone for water transport and tree metabolism. Positioned near the crown, it sustains active water and nutrient flow, yet is old enough for inner sapwood layers to begin converting into heartwood. In contrast, the lower stem contains older, more stabilized heartwood, while the upper stem consists of younger tissue where this transition is not yet prominent. This intermediate position in the stem balances sapwood maintenance and heartwood formation, driving dynamic changes in wood structure. This pattern aligns with the role of sapwood as the active xylem responsible for water and nutrient transport (Kozlowski and Pallardy 1996). As trees age, older sapwood loses conductivity and transforms into heartwood through the accumulation of extractives and polyphenolic compounds that enhance decay resistance (Zink-Sharp 2004; Wiedenhoeft and Miller 2005; Luo et al. 2018). The strong SWA–heartwood relationship in the mid-stem reflects this transitional physiology, where expanding crowns demand sustained conductive capacity, while inner sapwood layers convert to heartwood to maintain functional sapwood volume (Bamber 1976; Zink-Sharp 2004).

Tree height exhibited a position-dependent influence on heartwood area (Table 2, Figure 1B), showing a positive association

Table 2. Summary of the linear mixed-effects model coefficients for predicting heartwood area based on Equation [1].

Effect Type	Parameter	Lower (0–30%)	Middle (31%–60%)	Upper (61%–100%)
Fixed	Intercept	-4.3901*	-16.7305*	-10.1728*
	SWA	4.7402*	13.5231*	8.6335*
	Height	0.0750*	-0.0754*	-0.0419*
	BGRI	0.3618*	0.1936	0.0819
	BAL	-0.0000	0.0001*	0.0000
Random	Intercept (SD)	0.0001	0.4916	0.3029
	Residual (SD)	0.4717	0.2779	0.3739
AIC		222.9330	279.8137	222.4609

Definition of abbreviations: sapwood area (SWA), basal area of larger trees (competition index, BAL), belowground root infection (BGRI), SD (standard deviation).
* Significant at $p \leq 0.05$

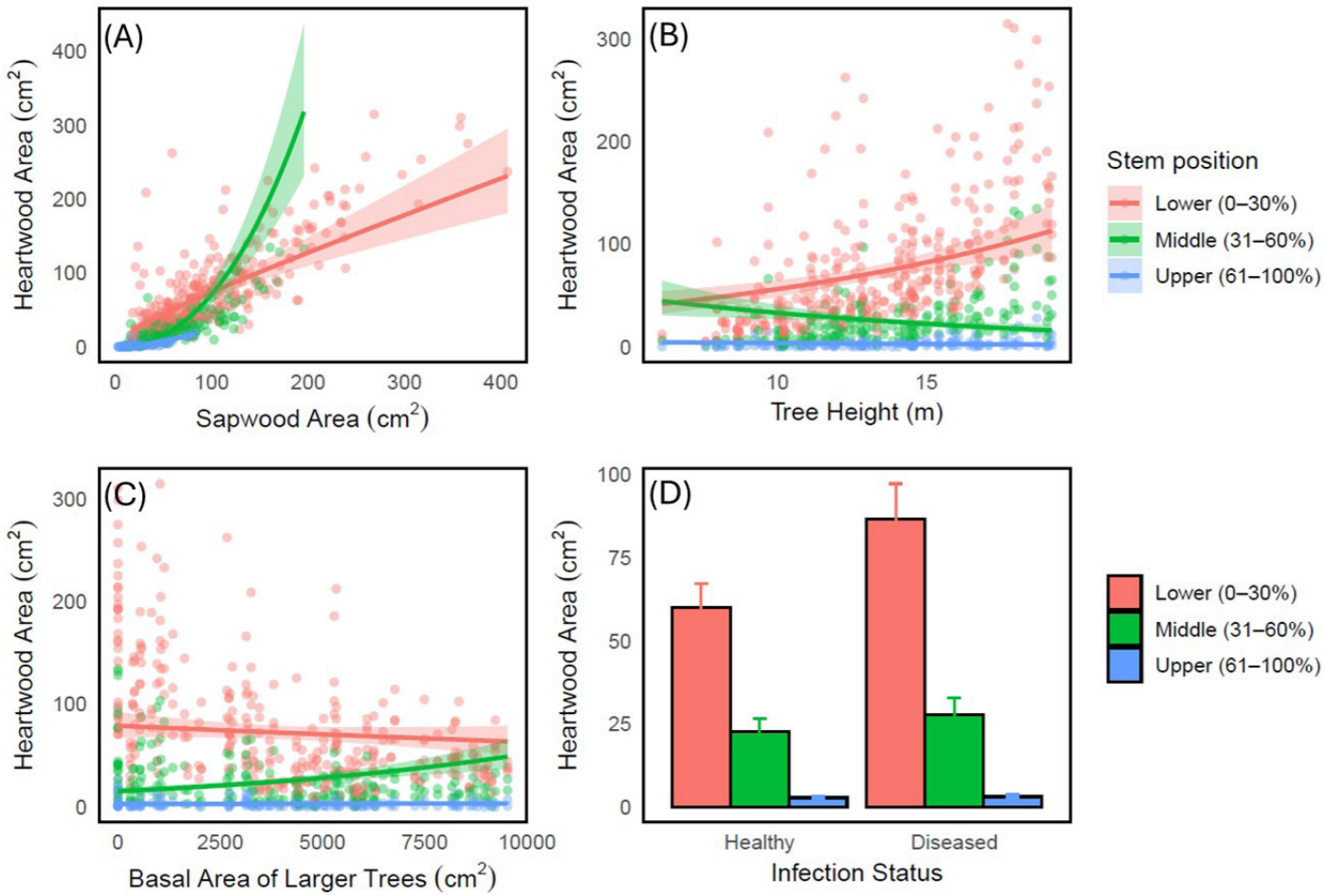

Figure 1. Effects of key predictors on heartwood area by stem position.
Relationships between heartwood area and (A) sapwood area, (B) tree height, (C) basal area of larger trees, and (D) infection status. All relationships are grouped by stem position (lower, middle, upper). Lines represent model predictions, shaded areas indicate 95% confidence intervals, and points show observed data.

at the lower stem ($\beta_2 = 0.08$), but negative associations in the middle ($\beta_2 = -0.08$) and upper ($\beta_2 = -0.04$) sections. However, we did not measure the age (i.e., ring number) at different stem heights in this study, and future studies should consider this as a critical factor in understanding heartwood development. While the age of the wood may play a significant role in heartwood formation, it is important to note that the transition from sapwood to heartwood does not occur uniformly at a given height. This variability could introduce a confounding effect when interpreting the results, as the timing and extent of the transition may differ between stem positions. At the base, taller trees may accumulate more heartwood because the older basal wood has had more time to undergo the sapwood-to-heartwood transition and may contribute to mechanical support (Cardoso and Pereira 2017). In contrast, the negative associations observed higher up the stem may reflect the prioritization of sapwood retention to sustain water transport to the crown. Additionally, upper stem sections generally exhibit slower basal growth than the base, particularly in mature trees, due to resource allocation toward height growth and crown development (Kozlowski and Pallardy 1996). This reduced secondary growth may limit the accumulation of heartwood in those sections.

This vertical trend aligns with the pipe model theory (Shinozaki et al. 1964), which suggests that the amount of sapwood in a stem segment is proportional to the foliage it supports, ensuring adequate water and nutrient transport from roots to canopy (Grier and Waring 1974; Waring et al. 1982). In the younger, upper sections of the tree, sapwood is actively produced and retained to meet these transport and storage demands. As xylem tissue ages, it loses conductivity and is transformed into heartwood, leading to greater heartwood accumulation in the lower stem where structural support becomes increasingly important (Rennolls 1994; Millers 2013). Similar verti-

cal patterns in heartwood distribution have been observed in Douglas-fir in Portugal (Cardoso and Pereira 2017) and western redcedar (*Thuja plicata*) in North America (DeBell and Lachenbruch 2009).

BGRI had a significant positive effect on heartwood area in the lower stem ($\beta_3 = 0.36$), but its influence weakened and became non-significant in the middle and upper sections, indicating a localized response near the tree base (Table 2, Figure 1D). This pattern suggests that the physiological and structural response to root infection is concentrated in the stem region closest to the infection source. The increased heartwood area in the lower stem likely reflects a defense mechanism, whereby trees deposit extractives and polyphenolic compounds to form reaction zones that limit the upward spread of root pathogens (Shigo 1984).

Root infections impair water and nutrient transport, reduce leader growth, and increase the shedding of lower foliage, diverting energy toward defense at the expense of overall growth (Cruickshank et al. 2011; Cruickshank and Filipescu 2012). In our study, the enhanced heartwood formation in the lower stem corresponds to reduced functionality of root vascular tissues and the tree's attempt to compartmentalize the infection. While we did not directly observe compartmentalization, this may reflect the tree's response to stressors, including both fungal and insect damage. This aligns with the progression of fungal lesions, which disrupt vascular transport over time (Cruickshank and Sattler 2020), forcing resource reallocation toward defense. For example, in conifers like Norway spruce infected with *Heterobasidion annosum*, trees form reaction zones to isolate pathogens, initially increasing heartwood in affected areas (Shigo 1979; Oliva et al. 2012; Mageroy et al. 2023).

This defensive strategy, while limiting pathogen spread, incurs significant costs. As root and lower stem vascular tissues become less functional, the tree's capacity to sustain growth diminishes, leading to reduced sapwood and heartwood volume and, in severe cases, mortality (Cruickshank et al. 2011; Westwood et al. 2012). Over time, the proportion of functional sapwood decreases, constraining the tree's ability to continue forming new heartwood (Oliva et al. 2012). Our results highlight that the most intense effects of root infection and the tree's defensive responses are concentrated near the stem base, where vascular disruption is greatest.

BAL had a negligible effect on heartwood area overall but exhibited a weak positive relationship at the middle stem section ($\beta_4 = 0.0001$; Table 2, Figure 1C). In this region, heartwood area tended to increase slightly with BAL, suggesting that trees may accelerate sapwood-to-heartwood conversion under resource-limited conditions such as reduced water or light availability (Sellin 1994). Because heartwood requires fewer metabolic resources to maintain than sapwood, this shift may provide a physiological advantage when competition restricts resource uptake (Moraes et al. 2023). In contrast, BAL had little influence at the lower and upper stem sections. At the base, heartwood is typically well-developed and less sensitive to competitive pressures. In the upper stem, the necessity of maintaining conductive sapwood for hydraulic function likely constrains heartwood formation, even under competition.

Conclusion

Heartwood formation in Douglas-fir plantations is strongly influenced by sapwood area, with the relationship being most pronounced in the middle stem section. Tree height increased heartwood area in the lower stem but reduced it in the middle and upper sections, likely due to structural needs, although these patterns may also be influenced by tree age, especially in younger stands. Root infection exhibited position-dependent effects, primarily increasing heartwood near the base as a defensive response. Competition had a positive effect on heartwood area in the middle stem section, suggesting that stand density influences heartwood development in a stem-position-specific manner. Forest managers aiming to enhance heartwood development and timber value may benefit from practices that promote sapwood expansion in the mid-stem region, where heartwood formation potential is highest. While wider spacing or selective thinning can encourage sapwood growth, stand density may also stimulate heartwood formation, suggesting that one or both factors might play a role in this process. Management strategies should therefore aim to strike a balance, avoiding both excessive crowding and over-thinning. Although root infection may initially stimulate heartwood formation near the base, it ultimately reduces overall growth and long-term heartwood potential if unmanaged. Reducing root disease inoculum prior to planting remains essential, or alternatively, heartwood should not be a management target on infected sites.

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Appendix – Figures

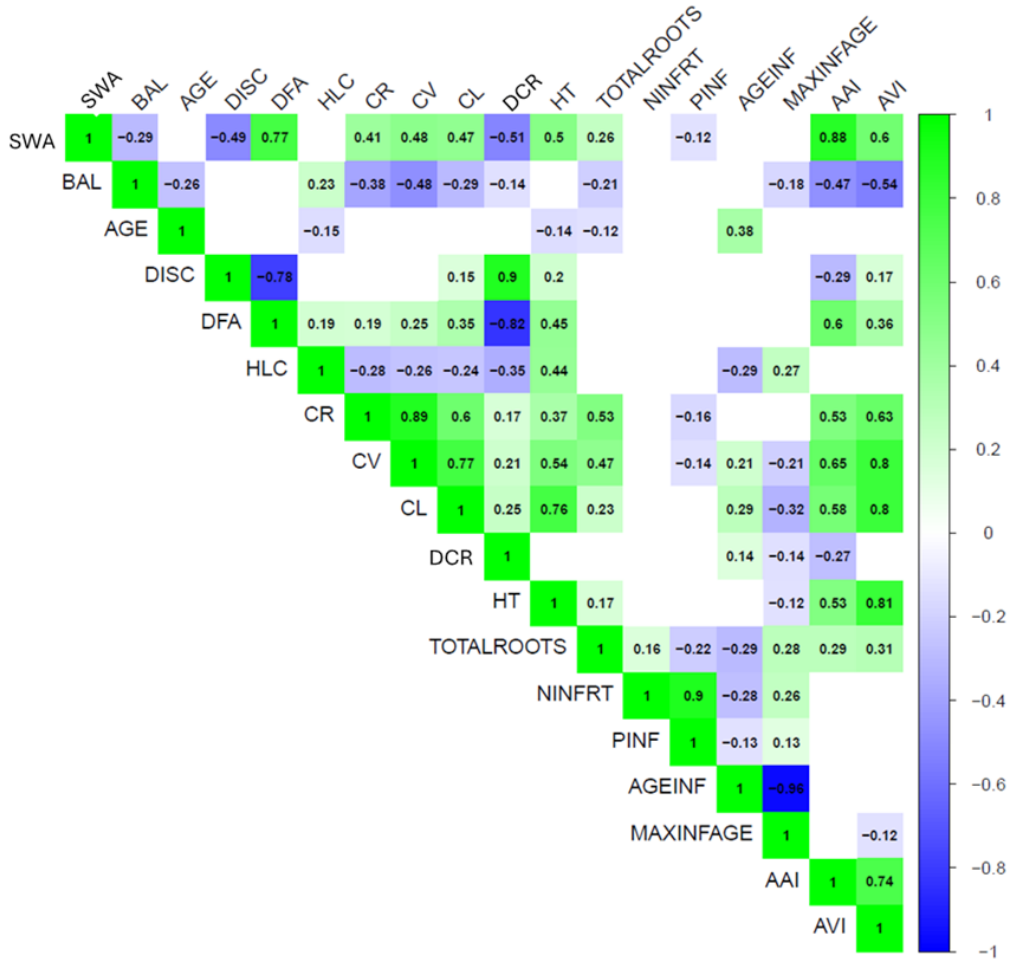

Figure A1. Pairwise correlation matrix between continuous tree variables. Only significant correlations (P<0.05) are shown. The blanks are not significant. **SWA** – Sapwood Area (cm²), **CL** – Crown Length (cm), **BAL** – Basal Area of Larger Trees (cm²), **MAXINFAGE** – Time Since Infection (years), **DFA** – Distance From Apex (m), **DISC** – Disc Height (m), **AGE** – Age of Tree (years), **HT** – Tree Height (m), **NINFRT** – Total number of infected primary roots at final age, **TOTALROOTS** – Total number of primary roots at final age, **PINF** – Percentage of primary roots infected at final age, **AGEINF** – Tree age at first infection, **HLC** – Height to Live Crown (cm), **CR** – Crown Radius (cm), **CV** – Crown Volume (m³), **AAI** – Average Yearly Area Increment for Last Years (cm²), **AVI** – Average Yearly Tree Volume Increment for Last Years (m³), **DCR** – Distance to Crown Base (m).

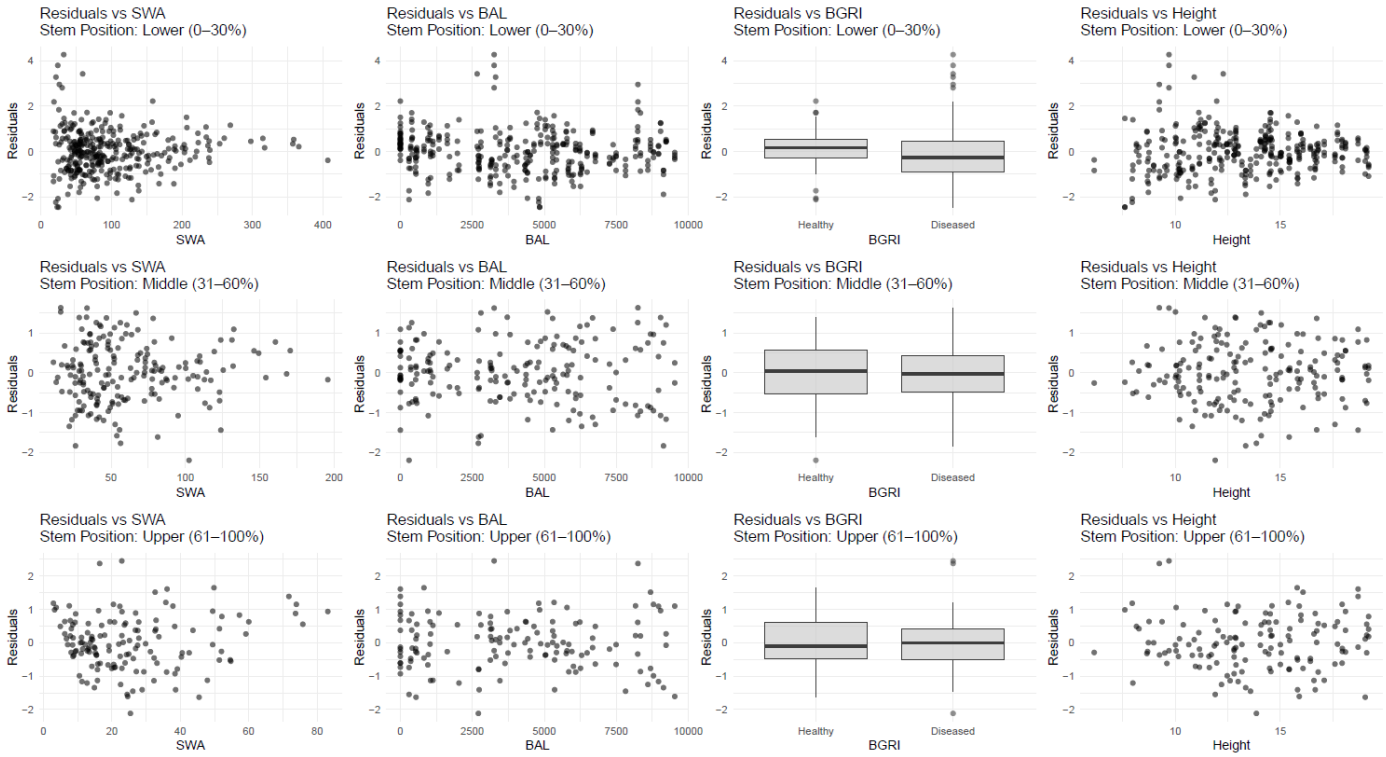

Figure A2. Residuals vs. Individual Predictors from the Linear Mixed-Effects Model. The model (Eq. 1) effectively predicts heartwood area in Douglas-fir, as evidenced by residual plots showing residuals centered around zero for all predictors, including sapwood area (SWA), basal area of larger trees (BAL), belowground root infection (BGRI), and tree height.