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Compensatory Growth in *Pinus ponderosa* (Dougl Ex Laws) Plantations Under Early Silvicultural Treatments

Crecimiento compensatorio en plantaciones de *Pinus ponderosa* (Dougl Ex Laws) bajo tratamientos silviculturales tempranos

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ABSTRACT

Early pruning and thinning in *Pinus ponderosa*, plantations in Andean Patagonia triggered compensatory growth, characterized by greater trunk growth and structural adjustments. We used a factorial design and mixed-effects models to evaluate stem growth, crown light dynamics, tracheid length (TL), foliar biomass (FB), wood density (WD), and Huber values (Hv) five years after treatment. Trees under combined pruning and thinning (PT) showed the greatest basal area increment, indicating resource reallocation to supportive structures despite early foliage loss. Pruned trees maintained higher Hv and achieved partial recovery of FB. Tracheid elongation was greatest in treated trees, suggesting accelerated xylem maturation, while WD remained unchanged. These results demonstrate the structural plasticity of *P. ponderosa*, which maintains hydraulic function and growth after canopy disturbance. Our findings provide useful guidance for silvicultural planning in temperate plantations.

Keywords
compensatory growth • hydraulic architecture • adaptive response

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RESUMEN

Los tratamientos tempranos de poda y raleo en plantaciones de *Pinus ponderosa* en la Patagonia Andina provocaron respuestas de crecimiento compensatorio, evidenciadas por un mayor desarrollo del fuste y ajustes estructurales. Mediante un diseño factorial y modelos de efectos mixtos, se evaluaron el crecimiento del tallo, la dinámica de luz en la copa, la longitud de traqueidas (TL), la biomasa foliar, la densidad de la madera y la razón de Huber (Hv) cinco años después del tratamiento. Los árboles sometidos al tratamiento combinado de poda y raleo (PT) mostraron el mayor incremento en el área basal, indicando una reasignación de recursos hacia estructuras de sostén a pesar de la pérdida foliar inicial. Los árboles podados mantuvieron valores elevados de Hv y lograron una recuperación intermedia de biomasa foliar, mientras que la elongación de traqueidas fue mayor en los árboles tratados, lo que sugiere una maduración acelerada del xilema. La densidad de la madera no se vio afectada. Estos resultados demuestran la plasticidad estructural de *P. ponderosa*, evidenciando su capacidad para mantener la funcionalidad hidráulica y sostener el crecimiento ante modificaciones en la copa. Los hallazgos aportan herramientas útiles para la planificación silvícola en plantaciones templadas.

Palabras clave
crecimiento compensatorio • arquitectura hidráulica • respuesta adaptativa

INTRODUCTION

Pinus ponderosa is the most widespread conifer species in forest plantations in Andean Patagonia, Argentina (24). Its cultivation in ecotone zones has government support for its establishment and silvicultural management. This species shows intermediate growth and numerous basal branches requiring pruning to reduce fire risk or improve wood quality. Forest managers must apply these cultural practices at an early, pre-commercial thinning stage for these cultural practices to be effective. However, researchers have not fully clarified how pruning and thinning affect early tree growth and development.

Previous studies have explored the influence of pruning and planting density on *Pinus ponderosa's* growth and physiological performance. For Gyenge *et al.* (2009, 2010) demonstrated that pruning temporarily reduces diameter growth, while planting density significantly affects resource availability and individual tree growth. Additionally, Gyenge *et al.* (2012) analyzed responses to water stress under different competition levels, showing short- and long-term physiological adjustments. Similarly, Martínez-Meier *et al.* (2015), highlighted that intraspecific competition alters the wood structure in high-density stands, increasing earlywood density and reducing the hydraulic efficiency of trees, affecting their ability to respond to water stress conditions.

Cambial maturation is a key process in woody plants. It produces secondary xylem composed of tracheids and other cellular elements. Tracheid size is a key indicator of this maturation, influencing both hydraulic and mechanical function (13). In *P. ponderosa* from this region, tracheid length (TL) increases during the transition from juvenile to mature wood (17, 34).

TL in conifers also correlates with tracheid diameter (30). Together, these traits determine water transport efficiency through the xylem. Therefore, TL provides valuable information on cambial maturation and its impact on wood function and quality.

Pine productivity depends strongly on canopy structure, including crown shape, leaf area index, leaf distribution, and shoot architecture. Tree growth is directly related to the ability to intercept solar radiation (31, 32, 33). As trees grow, vertical foliage distribution generates self-shading and reduces light to lower branches. This loss of light often triggers crown recession, the shedding of shaded leaves, which strongly influences growth dynamics (7, 15).

These conditions alter biomass partitioning among foliage, branches, and trunk. After pruning, they also modify the relationship between conductive tissue and leaf biomass (14). The Huber value (Hv), defined as the ratio of xylem cross-sectional area (G) to total leaf biomass (FB), is a key indicator of hydraulic function (23). Because gas exchange occurs through the leaf surface, predicting biomass partitioning requires considering both G and FB.

Silvicultural practices modify this functional relationship. Pruning reduces active leaf area, temporarily increasing Hv. This may enhance the ability of conductive tissue to supply water to residual foliage but can cause short-term hydraulic imbalance during drought (9, 21). In contrast, thinning reduces competition and promotes both greater leaf area and conductive tissue, thereby enhancing growth efficiency (11).

These responses depend on treatment intensity, initial stand conditions, and resource availability. To analyze them, we used linear mixed-effects models (MEMs). MEMs decompose variability into components associated with treatments and site or individual differences (4, 19, 35). They also handle covariates effectively by adjusting for interactions and accounting for dependencies such as repeated or nested data. This approach provides more precise comparisons between treatments and controls, even in heterogeneous or unbalanced datasets.

This study evaluates the effects of pruning and thinning on aboveground biomass allocation in *Pinus ponderosa*. We focus on the relationship between foliar biomass and trunk growth, and how this relationship changes after treatment. By analyzing biomass partitioning, we aim to determine whether silvicultural practices alter the balance between foliage and conductive tissue, thereby influencing growth dynamics and hydraulic function.

We hypothesize that pruning reduces photosynthetic capacity by removing basal branches. This reduction may decrease trunk growth and alter basal taper due to changes in branch structure and radial growth. In contrast, thinning increases light availability for remaining trees and reduces intraspecific competition. This effect may compensate for foliage loss caused by pruning, favoring resource allocation to trunk growth and potentially modifying xylem structure.

Given tracheid size is a key determinant of hydraulic efficiency, we further hypothesize that pruning and thinning induce adjustments in TL. These changes may represent compensatory responses to altered canopy structure and resource availability.

If Hv values in pruned and thinned trees converge toward those of controls, this would indicate xylem adjustment to balance water transport and mechanical support. However, if Hv differences persist, this would suggest long-term changes in biomass allocation and a departure from the expected proportionality between conductive tissue and foliage biomass.

These hypotheses guide the assessment of whether pruned trees adjust hydraulic and mechanical structures to maintain functional integrity under different management regimes. Additionally, analyzing TL as an indicator of xylem plasticity, together with wood density (WD), offers insight into how structural adjustments help trees cope with changes in resource availability and canopy modification.

Materials and Methods

We conducted a completely randomized factorial design in a 12-year-old *P. ponderosa* plantation in northwestern Chubut Province, Argentina (latitude -42.300059°, longitude -71.296954°). The stand had a mean diameter at breast height (dbh) of 8.5 cm and a mean top height of 4.43 m, with 3 × 3 m spacing. The site quality index ranged from 13 to 15 m (1).

Four silvicultural treatments were applied: pruning (P), thinning (T), pruning plus thinning (PT), and a control (C). Each treatment was assigned to five experimental units (EUs), for 20 units.

Each EU was a 144 m^2 plot with 16 trees, separated by a buffer row. Before applying treatments, and again five years later, we measured all trees ($n = 215$). Measurements included dbh with dendrometric tape, crown base height (CrwH) with metric tape, and total height (TH) with a Haglöf Vertex III hypsometer. The dbh point was permanently marked for consistent re-measurement. The crown base was defined as the lowest whorl with at least three live branches, provided that all branches below were dead or pruned.

Pruning removed 50% of the basal crown. Thinning eliminated 50% of the trees, primarily smaller and less vigorous individuals.

At the end of the experiment, we randomly selected 32 trees for destructive sampling. Each treatment contributed eight trees, with at least two per EU.

Vertical light profiles were measured immediately after treatment and again five years later. Eight HOBO sensors were mounted horizontally on a rod at 1 m intervals, from 0.3 m above ground to the apex. The top sensor served as the reference. The rod was positioned at the crown periphery in four cardinal directions per tree for at least one minute each time. Mean light intensity was then calculated per tree, and integrated light intensity (ILI) along the crown was obtained using Simpson's rule (3).

Five years after treatment, we felled the sampled trees and collected stem disks at stump height (0.1 m) and at breast height (1.3 m). Polished and digitized discs were analyzed with Map Maker v3.5 to measure total cross-sectional area (including bark) and under-bark area. The latter represented woody tissues without separating xylem and phloem. Bark proportion was also compared among treatments and excluded from further analyses. Annual ring areas corresponding to the experimental period were extracted to calculate cross-sectional area increment at both heights, incGdbh and incGstump, respectively.

Tracheid length (TL) was assessed in two annual rings per tree-one formed before and four years after treatment. Wood samples corresponding to each ring were macerated following the Franklin (1937) technique. Tracheids were measured under an optical microscope at 40× magnification equipped with an ocular micrometer, following the anatomical measurement standards of the IAWA (2004) and the recommendations of Muñiz and Coradin (1991). A total of 1,920 tracheids were measured (30 tracheids × 2 rings × 32 trees).

In addition, oven-dried wood samples were used to determine anhydrous density at breast height (2 annual rings × 32 trees; n = 64 samples). For this purpose, samples were first saturated in water to determine their saturated weight, then air-dried for 24 h, and subsequently oven-dried at 103°C to obtain anhydrous weight. Between drying and weighing, samples were kept in a desiccator with silica gel to prevent moisture absorption. Basic density was then calculated using saturated and anhydrous weights, applying the maximum moisture content formula described by Smith (1954).

We estimated total tree foliar biomass (FBtree) in two steps. First, we developed an allometric model predicting needle biomass from branch diameter (FBbranch), using 59 trees from 15 regional plots.

These trees represented a wide range of sizes (dbh: 5-38 cm; height: 3-21 m; crown length: 1.5-15.5 m; age: 9-34 years). One branch per tree was sampled. Twigs and needles were separated, oven-dried at 60 °C, and weighed. The branch diameter was measured 5 cm from the insertion using a digital caliper. In a second step branch model was then applied to all branches of the sample trees to estimate FBtree. Then we fitted a mixed-effects model (MEM) to predict FBtree using "crown length × dbh^2" as the main predictor. The model was validated with a jackknife resampling procedure (5, 8).

We also tested whether site quality (intercept growth, 1) was a significant covariate. The allometric equation for branch biomass was: FBbranch [g] = 0.299 × dbh [mm]^2.186. Following Nakagawa and Schielzeth (2013), this model explained 84% of the variance (marginal $R^2 = 0.84$). For FBtree, the marginal R^2 was 0.859, with no significant effect of site quality. We therefore applied the following equation to the factorial experiment: FBtree [kg] = 91.20 × crown length [m] × dbh^2 [m^2].

Statistical analyses addressed the following variables: 1) incGdbh, 2) the relationship of incGdbh vs Hv and FBtree, 3) the relationship of incGdbh vs incGstump, 4) TL, 5) WD, and 6) Hv.

We fitted MEMs for variables 1), 2), 3), and 4) (table 1, page 38), and assessed fixed effects with likelihood ratio tests (LRT).

For all variables, treatment differences were tested with Tukey-adjusted pairwise comparisons using estimated marginal means (EMMs) (16). MEMs were adjusted according to Bates *et al.* (2015). All analyses were performed in R (2021).

The general model structure was:

$$y \sim \text{Fixed factors} + \text{Covariates} + (1 \mid \text{Grouping factor}).$$

Specific cases for variables 1)- 3) are detailed in table 1 (page 38).

Table 1. Full MEMs formulations to perform tests. incGdbh: the dependent cross-sectional area increments under bark at breast height.

Tabla 1. Descripción del modelo lineal completo de efectos mixtos utilizados para los análisis. incGdbh: variable dependiente, incremento del área transversal del tronco bajo la corteza a la altura del pecho.

Test	Full model formulation
1)	incGdbh ~ intercept + Treatment + FBtree-f + (1|plot:tree)
2)	incGdbh ~ intercept + Hv-f + FBtree-f + (1|plot:tree)
3)	incGdbh ~ intercept + Treatment + incGstump + (1|plot:tree)
4)	TL ~ intercept + Treatment + age + (1|plot:tree)

The fixed effects factor was silvicultural treatment with levels C, P, PT, and T as Treatment. Covariates FBtree-f: Tree foliar biomass at the end of the experiment, Hv-f: Huber value at the end of the experiment, incGstump: cross–sectional area increments under bark at stump height. Random effects: grouping the individual tree nested in the EU, experimental unit, or plot.

El factor de efectos fijos fue el tratamiento silvícola con niveles C, P, PT y T. Covariables: FBtree-f: biomasa foliar del árbol al final del experimento; Hv-f: valor de Huber al final del experimento; incGstump: incremento del área transversal del tronco bajo la corteza a la altura del tocón. Efectos aleatorios: agrupamiento del árbol individual anidado en la unidad experimental (EU), o parcela.

RESULTS

Bark proportion at breast height did not differ among treatments (LRT; F = 0.582, df = 3, p = 0.633). Bark represented 19.7 ± 3.1% of trunk cross-sectional area. It was excluded from all subsequent analyses.

At the beginning of the experiment, integrated light intensity (ILI-i) (table 2) was higher in pruned treatments P (90.4 ± 2%) and PT (90.1 ± 1%) than in control C (70.8 ± 2%) and thinning T (84.2 ± 1%). The similarity between P and PT indicates that pruning was the main factor increasing crown light exposure, primarily by raising crown base height (CrwH) (table 2).

By the end of the experiment, integrated light intensity (ILI-f) decreased in all treatments: - 9.9% C,

-18.6% P, - 20.9% PT , - 7.5% T. Despite this reduction, pruned treatments retained the highest final values-P (73.6%) and PT (71.3%)-showing a lasting structural effect on canopy light penetration.

Table 2. Tree biometric values in the factorial experiment.

Tabla 2. Valores biométricos observados de los árboles en el experimento factorial.

Treatment	Dbh$_i$ [mm]	Dbh$_f$ [mm]	CrwH$_i$ [m]	CrwH$_f$ [m]	TH$_i$ [m]	TH$_f$ [m]	ILI$_i$ [%]	ILI$_f$[%]	incG$_{dbh}$[mm^2]
C	88 ± 16 a	151 ± 20	0.10 ± 0.1	1.1 ± 0.4	3.8 ± 0.4 a	6.1 ± 0.6 a	71 ± 2 c	64 ± 2 a	9,659.0 ± 2.263
P	86 ± 22 a	142 ± 21	2.08 ± 0.4	2.03 ± 0.3	3.7 ± 0.6 a	5.7 ± 0.5 a	90 ± 2 a	74 ± 4 d	8,123.0 ± 2.089
PT	88 ± 19 a	150 ± 22	2.28 ± 0.2	2.16 ± 0.3	3.8 ± 0.5 a	5.8 ± 0.6 a	90 ± 1 a	72 ± 2 b	9,445.0 ± 2.592
T	88 ± 20 a	160 ± 27	0.11 ± 0.1	0.92 ± 0.4	3.8 ± 0.5 a	6.1 ± 0.6 a	84 ± 1 b	78 ± 3 c	11,406.0 ± 3.543

Mean ± standard deviation for each treatment. Dbh: diameter at 1.3 m height, CrwH: live crown base height, TH: total height, ILI: integrated light intensity, incGdbh: increment in cross-sectional area of woody tissues at breast height. Suffixes “-i” and “-f” denote the initial and final moments of the experiment. Different letters show significant statistical differences.

Media ± desviación estándar para cada tratamiento. Dbh: diámetro a 1,3 m de altura, CrwH: altura de la base de la copa viva, TH: altura total, ILI: intensidad lumínica integrada, incGdbh: incremento del área seccional de tejidos leñosos a la altura del pecho. Los sufijos “i” y “f” indican los momentos inicial y final del experimento. Letras distintas indican diferencias estadísticas significativas.

Leaf biomass (FBtree) increased in all treatments during the experiment (table 3). The magnitude of change, however, differed among treatments. Control (C) and thinning (T) reached the highest final values, 10.8 ± 3.8 kg and 12.6 ± 5.2 kg, respectively. Both started from similar baselines, 2.8 ± 1.3 kg and 2.9 ± 1.7 kg, corresponding to increases of 287% and 331%.

Table 3. Functional and structural values of tree traits in the factorial experiment.

Tabla 3. Valores funcionales y estructurales observados de los atributos del árbol en el experimento factorial.

Treatment	FBtree -i [kg]	FBtree -f [kg]	Hv-i [mm^2 / kg]	Hv-f [mm^2 / kg]	TL-i [µm]	TL-f [µm]
C	2.79 ± 1.3 a	10.81± 3.8 a	1,901.0 ± 243 a	1,412.0 ± 197 a	1,690.0 ± 212 ac	1,752.0 ± 145 ad
P	1.23 ± 0.8 b	7.03 ± 2.7b	4,709.0 ± 1,715 b	1,920.0 ± 203 b	1,614.0 ± 145 ac	1,763.0 ± 129 ad
PT	1.27 ± 0.8 b	7.97 ± 3.3 b	4,803.0 ± 1,424 b	1,940.0 ± 341 b	1,403.0 ± 292 ac	1,546.0 ± 263 ad
T	2.93 ±1.7 a	12.64 ± 5.2 a	1,896.0 ± 331 a	1,359.0 ± 165 a	1,680.0 ± 267 ac	1,893.0 ± 277 ad

Treatment	WD-i [g/cm^3]	WD-f [g/cm^3]
C	0.384 ± 0.01 a	0.373 ± 0.02 a
P	0.385 ± 0.03 a	0.373 ± 0.02 a
PT	0.375 ± 0.05 a	0.379 ± 0.04 a
T	0.393 ± 0.05 a	0.381 ± 0.04 a

FBtree: tree foliar biomass, Hv: Huber value, TL: tracheid length, and WD: wood density. Mean ± standard deviation. Different letters show significant statistical differences. For TL-i and TL-f, the first letter compares treatment, and the second letter compares experimental moment - initial *vs* final- for the same treatment. Suffixes "i" and "f" denote the initial and final moments of the experiment.

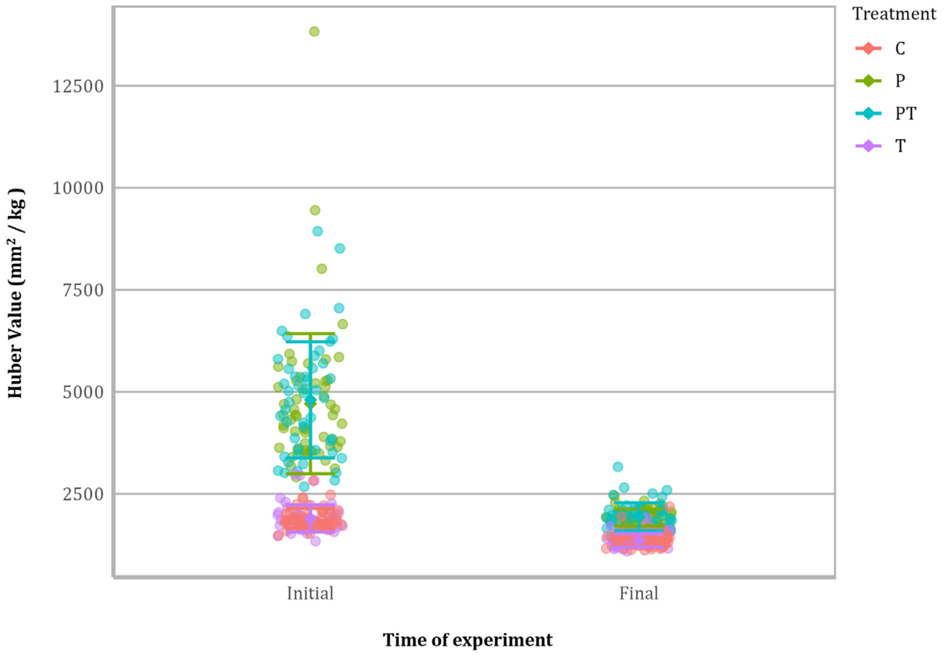
FBtree: biomasa foliar del árbol, Hv: valor de Huber, TL: longitud de traqueidas y WD: densidad de la madera. Media ± desviación estándar. Letras distintas indican diferencias estadísticas significativas. Para TL-i y TL-f, la primera letra corresponde a la comparación entre tratamientos y la segunda al momento del experimento -inicial *vs* final- para el mismo tratamiento. Los sufijos "i" y "f" indican los momentos inicial y final del experimento.

In contrast, pruning treatments began with significantly lower FBtree due to foliage removal. Initial values were 1.2 ± 0.8 kg in P and 1.3 ± 0.8 kg in PT. By the end, both reached intermediate levels: 7.0 ± 2.8 kg in P and 8.0 ± 3.3 kg in PT. These increases of 472% and 528% indicate compensatory foliage regrowth in pruned trees, while unpruned treatments followed steady canopy expansion.

Initial Hv-i (figure 1, page 40; table 3) was substantially higher in P (4,709 ± 1,715 mm^2/kg) and PT (4,803 ± 1,424 mm^2/kg) than in C (1,901 ± 243 mm^2/kg) and T (1,896 ± 331 mm^2/kg). This pattern reflected the immediate pruning-induced reduction in leaf biomass. Over time, Hv declined in all treatments, showing a rebalancing between conductive tissue and foliage. The greatest declines occurred in P (-59.2%) and PT (-59.6%). Yet, both treatments retained higher final Hv values than controls, indicating a persistent structural effect of pruning.

Tracheid length varied widely but increased in all treatments (figure 2, page 40), consistent with age-related xylem maturation (Test 4 in table 1, page 38; AIC = 864.9, model p = 0.0001, Age coefficient = 28.35, p = 0.003). Increases were largest in T (+12.7%) and PT (+10.2%), followed by P (+9.2%) and C (+3.7%). These results suggest that silvicultural treatments may accelerate tracheid elongation. Although differences were not statistically significant, treatment effects revealed biologically relevant trends.

Wood density remained stable across treatments during the five years (table 3). Initial values ranged from 0.375 to 0.393 g/cm^3. Final values showed only slight variation (0.373-0.381 g/cm^3). No significant differences were detected, indicating that treatments did not markedly affect wood density.



Dots jittered to provide a more comprehensive understanding.

Los puntos están desplazados (jitter) para facilitar su visualización.

Figure 1. Huber values (Hv) for initial and final treatment moments.

Figura 1. Valores observados de la razón de Huber (Hv) al inicio y al final de los tratamientos.

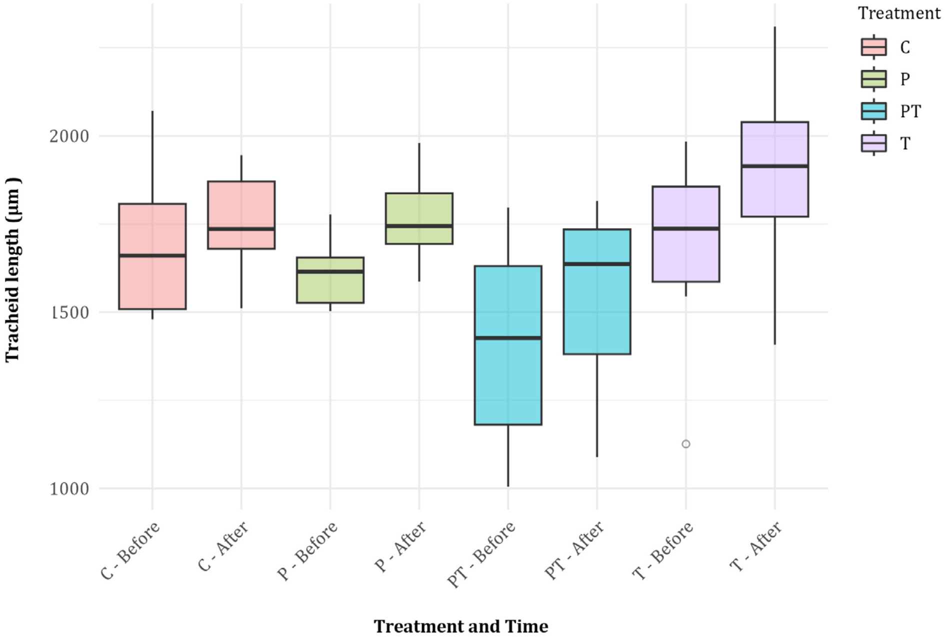
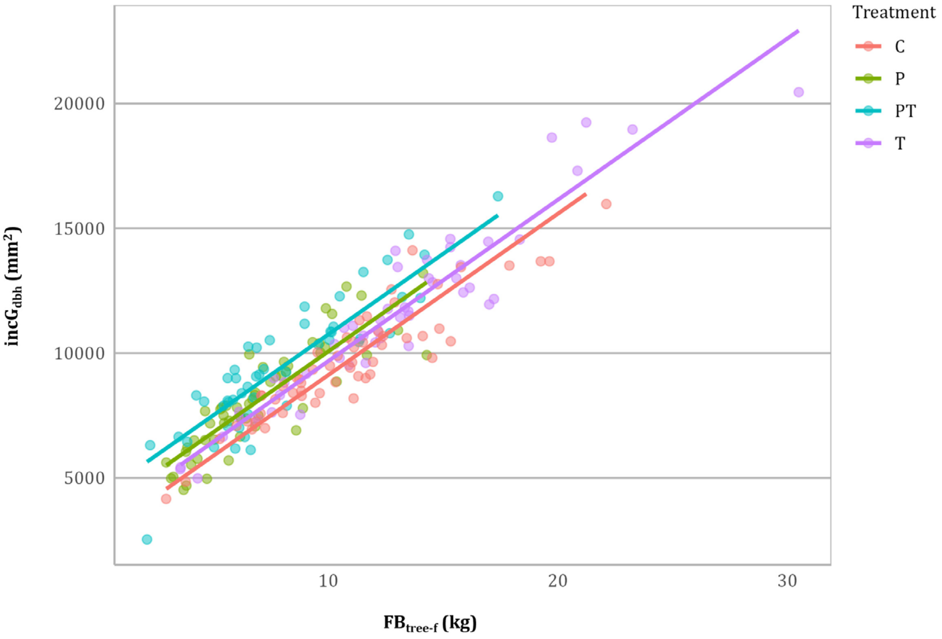


Figure 2. Tracheid length distribution, before and after treatment (C control, P Pruning, PT Pruning plus thinning, T thinning).

Figura 2. Distribución de la longitud de traqueida, antes y después del tratamiento (C testigo, P poda, PT poda y raleo, T raleo).

In Test 1 (table 1, page 38; figure 3), the full model with treatments and FBtree-f explained trunk growth variation (LRT: $\chi^2 = 422$, df = 7, $p < 2.2e\text{-}16$). Predicted intercepts were highest for PT (5,341.0 mm^2), followed by P (4,492.0 mm^2), T (4,013.0 mm^2), and C (3,315.0 mm^2). PT differed significantly from C ($\Delta = 1{,}626.0 \pm 454$ mm^2, p = 0.007). The PT-T contrast approached significance (p = 0.076), suggesting a trend. A complementary model using Hv-f and FBtree-f (Test 2) had similar explanatory power (AIC = 3,556.5 *vs.* 3,547.8). This supports the hypothesis that hydraulic adjustments mediate post-treatment growth.



Predictions according to the full model of test 1.

Predicciones según el modelo completo del test 1.

Figure 3. Observed (dots) and predicted (lines) values of increment of cross-sectional trunk area (incGdbh) for treatments along tree foliar biomass at the end of the experiment (FBtree-f).

Figura 3. Valores observados (puntos) y predichos (líneas) del crecimiento del área transversal del tronco (incGdbh) para los tratamientos, en función de la biomasa foliar final del árbol (FBtree-f).

Finally, the proportionality incGdbh *vs* incGstump, was not significantly affected by treatments (Test 3, $\chi^2 = 1.6198$, df = 3, p-value = 0.6549). Stem allocation patterns, therefore, remained consistent despite pruning.

DISCUSSION

Early silvicultural treatments in *Pinus ponderosa* plantations produced clear changes in growth and crown structure. Pruning and thinning, especially when combined, enhanced trunk growth rates despite the initial reduction in foliar biomass. Pruning increased crown light penetration, stabilized crown architecture, and promoted compensatory foliage development.

These treatments also triggered structural and functional adjustments. Pruned trees maintained higher Huber values (Hv) than controls during the study period. Tracheid length increased across all treatments, with greater elongation in treated trees. These anatomical shifts, although not always linked to higher trunk growth, indicate xylem maturation adjustments that may improve hydraulic efficiency.

The increased trunk growth in the pruning plus thinning treatment (PT) supports the hypothesis that *P. ponderosa* shows compensatory responses to early canopy interventions. Despite foliage loss from pruning, treated trees -particularly under PT- displayed greater xylem area increments, likely reallocating resources to supportive structures. These dynamics align with compensatory growth theory, which describes adaptive responses to sudden reductions in foliage (21, 22).

Our findings also indicate that *P. ponderosa* adjusts hydraulic architecture without compromising wood density. The separation between enhanced structural growth and stable density suggests anatomical plasticity via tracheid elongation and crown reconfiguration, not faster or lower-quality wood formation.. This result agrees with previous studies (9, 10, 11), which reported morphological and physiological adjustments under pruning, thinning, and drought, including crown restructuring and improved water-use efficiency, without changes in wood density. Likewise, Martínez-Meier *et al.* (2015) detected fine-scale density variations with microdensitometry, while our ring-level estimates revealed no significant effects, reinforcing the idea of macro-anatomical rather than biochemical adaptation.

Although this study focused on structural traits, the compensatory responses in trunk growth, foliage regrowth, and xylem anatomy likely reflect ecophysiological adjustments. Canopy opening in pruned treatments increased light exposure, possibly enhancing stomatal conductance and photosynthetic rates. These changes likely promoted carbon assimilation and foliage regeneration (20, 31).

Tracheid elongation and shifts in Huber values further suggest adjustments in stem hydraulic architecture. Such changes may improve specific hydraulic conductivity and support water transport to the regenerating canopy (10, 13, 30). Reduced competition in thinned plots likely improved water availability, favoring higher leaf water potential and maintaining stomatal function (9, 11). Although not directly measured, these responses match known mechanisms of resource reallocation and water–carbon coupling in conifers under stress (15, 18).

These findings refine the broader hypothesis by Fernández *et al.* (2011), who proposed that Pinus species show lower physiological plasticity than Eucalyptus. While this may hold at the biochemical level, our results highlight structural adaptability in *P. ponderosa*. This species compensates for canopy changes by adjusting conduit dimensions and crown structure to maintain hydraulic function while keeping wood density stable. Such capacity has important implications for resilience and productivity under silvicultural management and environmental variability.

This study has several limitations: a small sample size, a five-year monitoring period, and the absence of direct physiological measurements. Another limitation is that our design does not explicitly account for soil or landform heterogeneity, which can modulate radial growth patterns in arid environments (27). Future work should extend monitoring, include direct evaluations of stomatal conductance, photosynthesis, and hydraulic conductivity, assess vascular reuse after pruning, and incorporate spatial variation in site conditions. These efforts will help clarify the functional mechanisms driving compensatory responses in *P. ponderosa*.

Conclusions

This study confirms that early pruning and thinning in *Pinus ponderosa* plantations trigger compensatory growth, especially when both treatments are combined. The main effects included greater conductive tissue area, partial recovery of foliar biomass, and tracheid elongation, while wood density remained unchanged.

These structural adjustments support the hypothesis that hydraulic and anatomical plasticity drive the observed responses. The findings highlight the value of early silvicultural interventions to enhance growth and maintain hydraulic function, providing guidance for management in temperate conifer plantations. A deeper understanding of physiological and structural adjustments will further inform strategies to optimize productivity and resilience in *P. ponderosa*, especially in the early stages.

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