

REVIEW ARTICLE

Effects of planting density on the performance of reforestation and afforestation plantings in temperate and boreal forests: a systematic review

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Introduction: Rising demand for forest products, climate mitigation, and ecosystem restoration has driven international pledges to expand forests, mostly on abandoned agricultural lands and areas of low conservation value. According to a recent survey among restoration practitioners across Europe, optimal planting designs and densities are key questions for reforestation efforts.

Objectives: We aimed to determine how planting density affects the performance of reforestation/afforestation plantings, how these effects vary by climate, species types, and stand age, and whether there are planting density thresholds triggering significant performance shifts.

Methods: Using both descriptive statistics and meta-analyses, we systematically reviewed 120 studies from temperate and boreal forests to analyze planting density effects on the performance of tree plantings.

Results: Higher planting densities increase overall yield but also mortality. Negative effects on individual stem growth occur mainly at early ages, while negative impacts on individual stem growth and survival intensify over time. Benefits on stand yield are observed at both young and old ages, and there are no clear differences in the density response of shade-tolerant and shade-intolerant species. On average, an increase in planting density of 71 and 118% is needed to cause significant impacts on performance at stand-level and individual-tree level, respectively, though effects vary across studies and variables.

Conclusions: Observed patterns aligned with expectations, as higher planting densities increased mortality and lowered individual growth while promoting overall yields. However, the timing and thresholds of positive and negative effects vary, presenting opportunities to optimize management through variable densities over time.

Implications for Practice: Higher planting densities can initially enhance stand yield and carbon sequestration while improving stem quality by limiting branchiness, but for longer-rotation plantations focused on timber quality, thinning is recommended. As plantations age, reduced individual-tree growth and quality, along with higher mortality, may require density reductions to meet management goals. Without better information, intermediate planting densities may help balance growth and stem quality without restricting individual performance. The strong demand for practical knowledge in Europe highlights the need for more local evidence, particularly on alternative performance indicators like physiological traits, tree health, and a range of biomass compartments.

Key words: planting design, restoration practices, silviculture, stand dynamics, tree growth, tree regeneration

Introduction

Forest restoration is considered crucial for meeting the gap in the supply of forest goods and services, conserving biodiversity, and mitigating the impacts of climate change through carbon sequestration (United Nations 2019). The global recognition of this role is reflected in multiple large-scale restoration initiatives (World Conservation Union 2020; Forest Declaration Assessment 2021; Trillion Trees 2024). In Europe, the recently adopted Nature Restoration Law (European Commission 2024) aims to restore 20% of the European Union's land and sea areas by 2030, while the European Green Deal sets a target of planting 3 billion additional trees by 2030 (European Commission 2021, 2022). A significant portion of the required large-scale afforestation and reforestation effort is expected to take place on

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abandoned agricultural or degraded lands, where natural tree regeneration may be insufficient (Holl & Aide 2011; Simonsen 2013; van Bijnsterveldt et al. 2022). Against this background, tree planting remains a primary strategy for achieving the successful restoration of forest ecosystems.

Despite the increasing number and scale of restoration initiatives, practical guidance on optimal planting designs remains limited, especially for highly degraded or historically non-forested landscapes (Bannister et al. 2018; Fargione et al. 2021). A survey conducted among restoration practitioners within the “SUPERB” project (Systemic Solutions for Upscaling of Urgent Ecosystem Restoration for Forest-related Biodiversity and Ecosystem Services) (SUPERB 2022) across 12 large-scale demonstration areas in Europe revealed that determining an appropriate planting design and density is one of the most common initial challenges. Tree density or the spacing of trees in a stand determines the amount of resources available to each tree, and thus, the way in which trees and forest stands develop. As such, it is a key attribute that can be manipulated to meet different management purposes, initially through the number and spatial arrangement of trees to establish, and later through thinning interventions (West 2006; Nyland 2016).

Although forest restoration and silviculture are often seen as separate fields, forest restoration practices can often be derived from silvicultural principles and practices, as their goals are often similar. This is particularly the case when promoting regeneration establishment, even if the long-term goal may differ. Whether it is for production or conservation purposes, reforestation or afforestation techniques aim at establishing tree species on non-forested lands to achieve certain ecosystem functions. In that sense, knowledge from silvicultural studies on planting patterns and techniques can also be applied in the context of forest restoration plantings (Guldin 2008; Lamb 2012; Bannister et al. 2016).

One important area where silvicultural knowledge can inform forest restoration practices is planting density. The influence of planting density on a range of attributes of individual trees and plantation stands is generally known. Typically, a decision has to be made between optimizing individual-tree growth through wider spacing versus maximizing overall stand growth through higher stand density (Forrester et al. 2013). However, these relationships are highly context-dependent, varying with species characteristics, site conditions, and stand development stages (Schönau & Coetzee 1989; West 2006). While numerous case studies have examined the influence of stand density on tree and stand development, a comprehensive synthesis of how planting density influences plantation performance (in terms of growth-related outcomes and functional attributes) across different environmental conditions and stand ages is still lacking.

Systematic reviews play a crucial role in synthesizing existing research to provide structured and reproducible insights into complex ecological questions, as well as identifying knowledge gaps. They facilitate evidence-based decision-making by consolidating and analyzing existing knowledge in a transparent manner and providing incentives for future research. We conducted a quantitative systematic review to evaluate the effects of planting density on the performance of reforestation and afforestation plantings across different climates, functional tree species groups (shade-tolerant vs. shade-intolerant), and stand development stages.

Our goal was to provide a rigorous synthesis of existing evidence, addressing the following key questions: (1) what are the effects of increased planting density on the overall performance of reforestation or afforestation plantings?; (2) how do these effects vary across different climates, species types, and stand ages?; and (3) are there identifiable thresholds of planting density variations that lead to significant shifts in the performance of planted stands?

Both modern silviculture and forest restoration initiatives increasingly pursue multiple objectives, driven by the rising demand for a wider variety of goods and services by societies (Chazdon 2008; Puettmann et al. 2012). The extent to which these objectives are achieved can be assessed through a variety of quantitative indicators, which, in studies on planting density effects often comprise growth-related and functional attributes that are mostly focused on the performance and development of the tree species established (e.g. growth, physiological activity, resource-use efficiency, structural complexity, etc.) (West 2014). Here, we refer to these as performance indicators. Although they capture only a subset of the broader array of ecosystem attributes recommended for evaluation in restoration initiatives, they nonetheless represent a key component of restoration assessment, as in the early stages the focus is often on successful tree establishment (Ruiz-Jaen & Aide 2005; Gann et al. 2019). Thus, for the purposes of this study, performance indicators were considered valid measures of early restoration success, based on the assumption that the products and functions measured align with the intended goals of the plantations.

A recent review by Moreno et al. (2023) partially addressed the effects of planting density on tree and plantation performance. However, it primarily focused on individual-tree species across various global regions, without describing general patterns. Moreover, it did not include a quantitative analysis of the trends reported across studies. In this study, we adopt a broader perspective, emphasizing general trends across studies in different ecological and silvicultural contexts, and apply a quantitative and meta-analytical approach to synthesize their results. Furthermore, with the purpose of maximizing both the representativeness and the accuracy of our analyses, we address our research questions through a dual approach: (1) a trend analysis based on the patterns informed by a larger number of studies and (2) meta-analyses based on a smaller sample of studies that provided more specific quantitative data.

With our results, we expect to provide a comprehensive overview on the effects of planting density within the spectrum of climate types occurring within Europe (temperate, continental, and dry), which mostly encompass temperate sensu Adams et al. (2019) and boreal forests sensu DeAngelis (2008). Adapted to specific contexts, needs, and site conditions through the integration with local data, these results can help formulating general recommendations for large-scale forest restoration initiatives.

Methods

This study was conducted following the PRISMA guidelines (Preferred Reporting Items for Systematic reviews and Meta-Analyses) for adequate reporting in systematic reviews (Page et al. 2021), and the extended guidelines of Synthesis Without Meta-Analysis (SWiM) to be used in systematic reviews when estimating effect sizes is either not possible or fully adequate (Campbell et al. 2020).

Literature Search

We organized the search on the basis of the main components of the review question (Table S1). Each of the column names represents a different component, and the terms within it are either a synonym or a related concept. Along the search string, the different components were linked with the Boolean operator “AND,” whereas the different terms within each component category were linked with “OR.”

Analog searches were conducted in Web of Sciences (WOS), Wiley Online Library, and Ovid, on the 8th of September 2023 (Table S2; see Table S3 for viewing the actual search strings). Unlike WOS and Ovid, Wiley Online Library did not offer the possibility to explicitly search based on subject, which normally helps limit the search outcomes to relevant studies. Thus, in this case, the subject-related terms had to be searched within the abstract. However, this would have had the disadvantage of excluding studies that did not explicitly include “silviculture” or “forestry” in their abstract, thereby limiting our results from this search engine considerably. To prevent this, we also included the term “tree” among the subject-related terms, which we considered more likely to appear in the abstract of studies involving tree plantations.

To verify the suitability of the search string, the outcomes of the review question were compared against a sample of four pre-selected relevant studies (Table S4).

Study Selection

After removing duplicates, we screened the complete list of studies by reviewing title and abstract, and discarded those studies that did not address the research questions or were not peer-reviewed articles from scientific journals. Subsequently, we conducted a full-text review of the remaining studies to evaluate the following inclusion criteria: (1) peer-reviewed article from a scientific journal; (2) full-text online availability; (3) written in English, Swedish, German, Spanish, French, Portuguese, or Italian (i.e. the languages that the group of authors could cover); (4) based on field experiments (either manipulative or observational); (5) conducted under one of the climate types occurring in Europe according to the Köppen classification (i.e. temperate, continental, and dry) (Peel et al. 2007); (6) addressing a relevant review population sensu Page et al. (2021) (i.e. mono-specific, unthinned forest plantations established on previously non-forested lands); (7) relevant comparison (stands of trees originating from different planting densities); (8) relevant outcome or variable reported (survival, growth or other indicator of seedling, tree, or stand performance); (9) means and standard deviations of the performance indicators, or results of statistical tests were provided. Given the heterogeneity among studies in the lower and upper limits of planting density of the plantations compared (e.g. 1000 vs. 3000 individuals/ha in study A and 800 vs. 20,000 individuals/ha in study B), the expected effects of an increase in planting density may have been too diverse to describe as the result of the same or similar processes. Thus, to limit the range of densities within studies, we selected studies with a maximum difference of 10,000 individuals/ha between the highest and lowest density levels. In addition, we excluded studies exclusively focused on short-rotation coppice plantations (i.e. studies exclusively involving planting densities above

5000 trees/ha). We also excluded studies that evaluated the effects of planting density exclusively on internal wood properties or other features of trees without an obvious ecological or economic implication.

Data Extraction

The selected studies used different response variables to evaluate the performance of tree plantations (i.e. either of seedlings, trees, or stands) in response to varying planting densities. The output for each response variable reported in a single study as a result of an increase in planting density was regarded as an individual observation. Based on the data provided, each observation was classified as reporting a significant ($p < 0.05$) or a null effect (i.e. no significant effects), and significant effects were classified as positive or negative. Several studies used multiple response variables as indicators of performance. Thus, a single study could report multiple observations, and as a consequence, the total number of observations was larger than the number of studies included. In general, a positive effect of increased planting density was defined as an increase in the reported response variables (e.g. basal area increment, height growth, diameter growth, and crown growth), based on the assumption that higher values indicated better performance. However, for most variables related to stem quality (e.g. slenderness, stem deviation, knot abundance, and branch density), the opposite was true, with increases in such variables being indicative of a decline in plantation performance and thus negative effects (see Table S5). It is important to recognize that these definitions are subject to the interpretation given by study authors, as some variables may reflect both positive and negative outcomes depending on the context. For instance, high crown biomass might suggest strong tree vitality while also indicating reduced stem quality.

Since several studies compared more than two levels of planting density, we looked in each case for significant effects between the maximum and lowest density levels compared. In addition, we registered the minimum range of densities between which the significant differences in the corresponding response variables occurred. We did not use the stand density index (SDI) for quantifying stand density, as a vast majority of the studies did not provide the diameter of the planted trees (Reineke 1933). For meta-analyses of the effects of planting density on the performance indicators, we extracted the means and standard deviations of the corresponding response variable for the lowest and highest level of planting density under comparison, as well as the sample sizes involved, whenever this information was available. When only available in graphical format, the means and standard deviations were obtained using WebPlotDigitizer (Rohatgi 2022). When standard error values were provided, these were transformed into standard deviation by multiplying them by the square root of the sample size.

In addition to including multiple response variables, studies often evaluated the effects of planting density on multiple species or species varieties, at different ages, under different additional treatments (e.g. fertilizing vs. no fertilizing), or on different experimental sites, and provided separate results for each of such subgroups (hereafter sub-factors). In order to

prevent biasing the results toward studies with a higher number of observations, the output for each subgroup was weighted by dividing it by the total number of sub-factors addressed in the corresponding study. Finally, in order to cover the variation in the effect of planting density across different plantation ages, we registered the effect of planting density at the oldest reported age within the following age classes: (1) ≤ 5 years; (2) greater than 5 and ≤ 10 years; (3) greater than 10 and ≤ 20 years; and (4) greater than 20 years.

Data Synthesis

Data for Trend Analyses. We recorded the frequency of null, positive, and negative effects of increased planting density on each of the response variables reported by the different studies, and calculated the proportion of each type of effect from the total number of observations obtained for each of those variables (Page et al. 2021). Owing to the large number of response variables, and in order to facilitate interpretation, they were grouped into categories according to the overall structural or functional attribute of a plantation that they accounted for (Table S5). Variables accounting for very specific attributes were left as single-variable categories. For each variable and category, and for all observations together, we also calculated the mean proportional increase in planting density at which significant changes in the response variables occurred.

We made comparisons of the overall frequency of positive, negative, and null effects on plantation performance between groups of observations stemming from plantations of different ages (≤ 5 ; > 5 and ≤ 10 ; > 10 and ≤ 20 ; > 20 years), climates (temperate, continental, and dry), and species types (shade-tolerant vs. shade-intolerant).

Meta-Analyses. When more than five studies in a given category reported means, standard deviations, and sample sizes, we performed meta-analyses to assess the impact of increased planting density on the corresponding attribute described by that category. With the “Metafor” R package (Viechtbauer 2010), we used the means, standard deviations, and sample sizes reported in each study to calculate Hedges’ d (Hedges & Olkin 2014) as an effect size metric to compare mean effect sizes between high- and low-density plantings. We used random effects models to estimate the mean effect sizes in order to account both for the within-study variance (i.e. the sampling error) and the between-study variance (Borenstein et al. 2021).

For studies reporting the response of a certain attribute to planting density in interaction with different sub-factors (e.g. for plantations of different species, under different fertilizing treatments, or at different locations), we aggregated the reported effect sizes into a single combined effect size per study with the “aggregate” function from the “Metafor” R package. In this case, the multiple outcomes from the corresponding study were assumed to be independent from one another (Viechtbauer 2010).

For each category included in these analyses, we conducted separate meta-analyses with studies grouped according to climate type (temperate, continental, or dry), species type (shade-tolerant

vs. shade-intolerant), and age class (≤ 5 ; > 5 and ≤ 10 ; > 10 and ≤ 20 ; > 20 years), whenever the number of observations per performance category for these groups was ≥ 5 . In the case of age classes, however, we did not use the aggregated effect sizes, since single studies often assessed planting density effects on multiple age classes. Thus, to compare results among those categories, we required ungrouped observations. For this purpose, we treated observations as independent from one another, regardless of whether they stemmed from the same study or not.

Results

From the 1592 studies obtained from the different databases, 160 were discarded as duplicates. Furthermore, 941 were discarded after title and abstract screening. The remaining 491 studies were subjected to full-text reviewing. Following the inclusion criteria for this stage, 120 studies were finally considered relevant and used for data extraction (Table S6; Fig. S1).

Overview of the Evidence Base

While the studies finally included in this review span from 1965 to 2023, the majority of them were published between 1991 and 2023. Moreover, more than half of the studies included were published within the last decade of the time span covered (i.e. between 2014 and 2023) (Fig. S2). Geographically, most of the studies were conducted in the northern hemisphere, mainly in North America (41), eastern Asia (26), and Europe (14), whereas in the southern hemisphere they were concentrated in Latin America (19) (Fig. 1). Seventy-five percent of the studies were conducted in temperate regions, 13% in continental regions, and 12% in dry regions, according to the Köppen climate classification. Only a minority of the studies informed the land use prior to the establishment of the experiments (40%). Most studies (50%) were conducted on recently cleared forested lands, while the rest took place on former agricultural lands (28%) or other non-forested areas, including grasslands, pastures, and shrublands (23%).

Regarding the nature of the experiments, 12, 9, and 76% of the studies involved shade-tolerant, semi-shade-tolerant, and shade-intolerant species, respectively, while 3% involved a combination of different types. In relation to the experimental design, 10% of the studies compared two different planting density levels, whereas 73% of the studies addressed three to six different density levels. The remaining 17% of the studies addressed a gradient of planting density using a spoke or Nelder Wheel design, where seedlings are planted in concentric rings with exponentially increasing radii. The mean lowest and highest planting density per study were 891 ± 630 and 4015 ± 2667 , respectively. The experiments described in the studies were monitored three times on average. However, 51% of the studies involved a single evaluation. The oldest monitoring age per study ranged from 1 to 60 years, with an average of 14 ± 11 years. The observations were relatively evenly distributed among the pre-defined age classes described above, with studies focusing on the early stages showing the highest frequency (Fig. S3). Finally, most of the studies (85%) reported effects of planting density on plantations

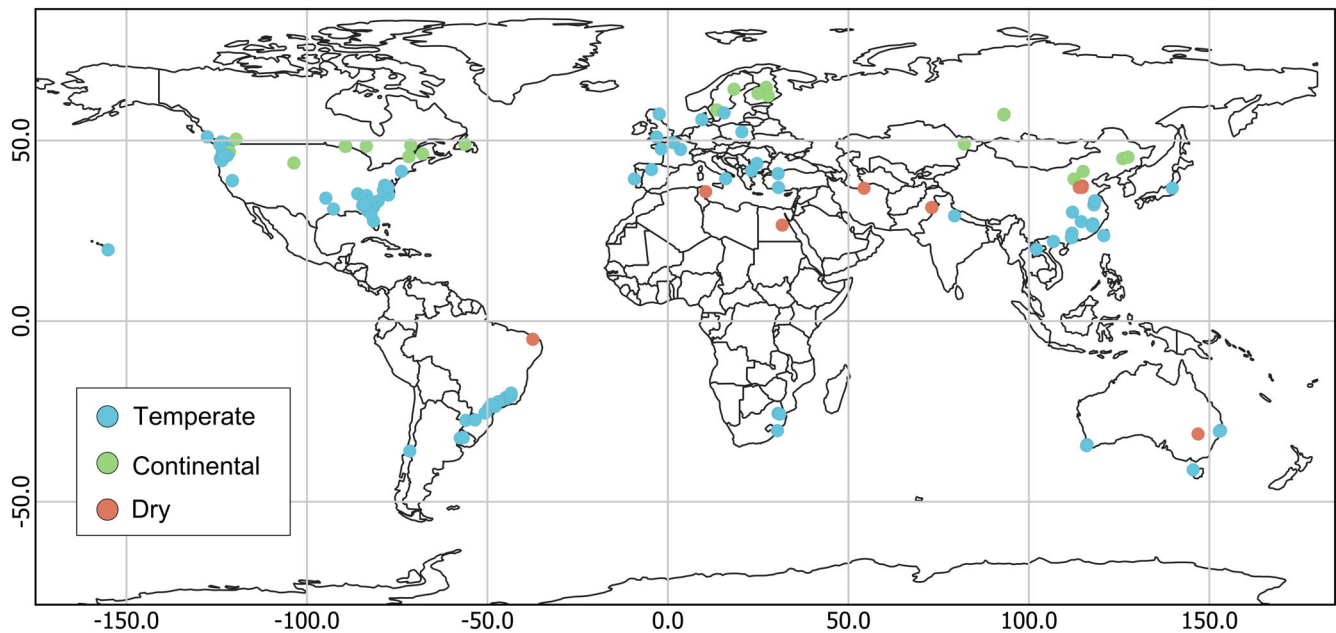


Figure 1. Location of the studies included, classified according to their Köppen climate type (Peel et al. 2007). This climate map was built based on observed climate data (i.e. precipitation and temperature), rather than strictly on geographic or biome boundaries. As a result, some sites that would typically be classified as subtropical or tropical may have instead been categorized as temperate or dry, due to localized climatic deviations driven by factors such as elevation gradients, slope orientation (aspect), proximity to coastlines, or other topographic and microclimatic influences.

of a single tree species, while 15% reported the effects on multiple plantations of different species.

Categories of Response Variables

From the 120 studies included, 68 variables indicative of performance were identified. Based on the structural or functional feature of the plantation that they accounted for, these variables were grouped into 26 categories (Table S5). The primary focus of the included studies was on aboveground biomass and growth variables, with “height growth” (87 observations), “diameter growth” (76 observations), and “stand volume” (45 observations) representing the variables most frequently analyzed. Conversely, there was limited evidence regarding the impacts of planting density on physiological attributes (e.g. water-use efficiency, light-use efficiency, and nutrient concentration), tree health, and belowground biomass, with none of the related categories counting more than seven observations (Fig. 2).

Effects of Planting Density on Performance

In total, 453 observations were reported. There was a high variability in the effect of increased planting density on performance, and while a majority of observations showed negative effects (41%), a large fraction (34%) did not show any significant effect. A smaller fraction of studies (25%) showed positive effects of a higher planting density. Comparisons among age classes revealed a growing effect of increased planting density with plantation age, with reported significant effects on performance gradually increasing from 55% in plantations up to 5 years old,

to 79% in plantations older than 20 years. While positive effects remain relatively constant, negative effects also show an increase with increasing age, from 32% of the total observations in plantations up to 5 years old, to 54% in plantations older than 20 years (Fig. 3).

The effect of higher planting density varied only slightly between plantations of shade-tolerant and shade-intolerant species, with no major differences observed among them. Across the different climate regions, the effects of increased planting density also seem relatively constant. Plantations in temperate regions show the lowest rate of significant negative effects of higher planting densities and the highest rate of significant positive effects, whereas negative effects are the most frequent in plantations in continental regions, and positive effects are the least frequent in plantations in dry regions (Fig. 3).

With regards to specific categories of performance indicators, planting density has a significant effect on survival in 58% of the cases, all of which are negative. Moreover, higher planting densities exert considerable influence on variables related to stem biomass increase, with most related factors (“diameter growth,” “stem volume/biomass,” “stand volume,” and “stand basal area”) showing significant effects in over 75% of the cases. For individual seedling or tree biomass, these effects are mostly negative, with all significant effects being negative for “diameter growth,” and 85% for “stem volume/biomass.” Although significant effects on “height growth” are less frequent (50%), the majority of these (66%) are also negative. In contrast, at the stand-level, higher planting densities exhibit predominantly positive effects, as shown by “stand volume,” “stand basal area,” and “stand-level aboveground biomass.” These show significant responses to

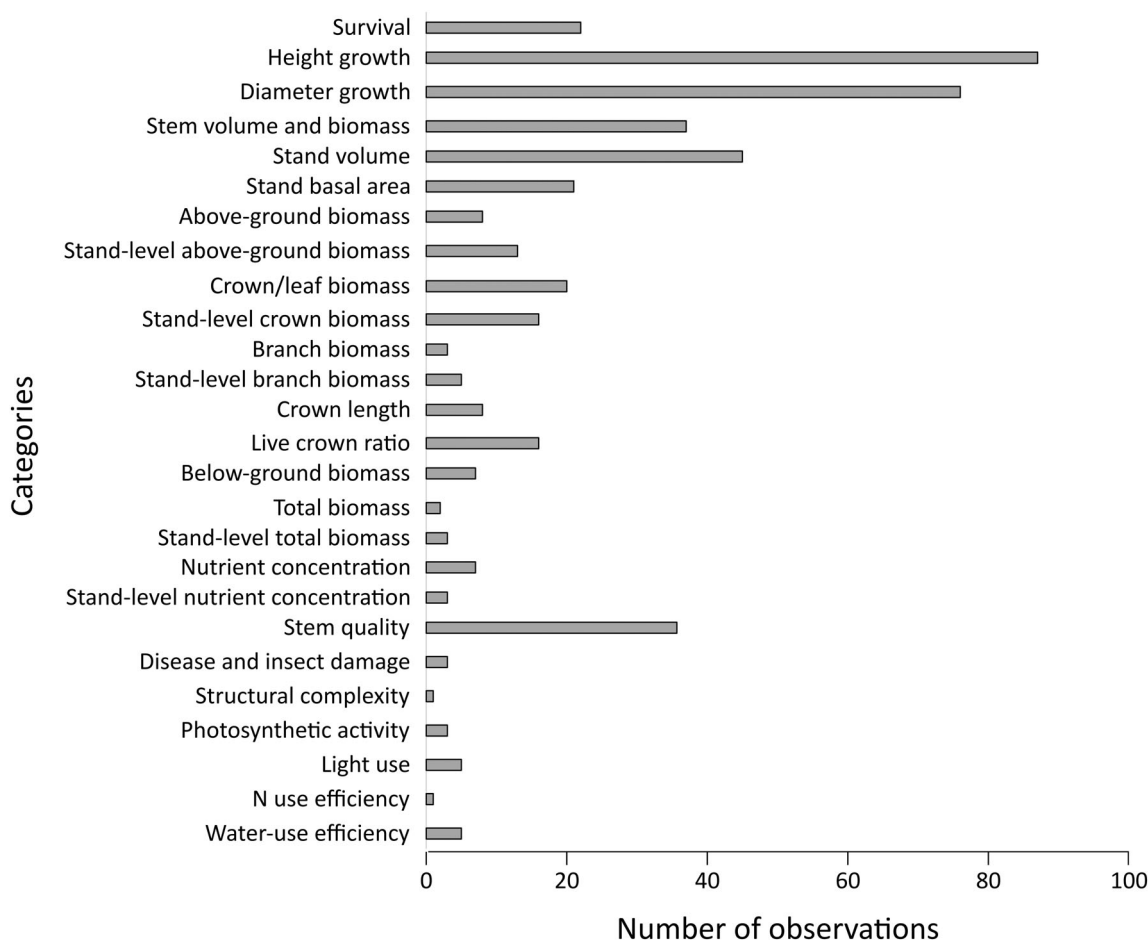


Figure 2. Number of observations per category of response variables. The complete list of variables and categories can be found in Table S5.

increased planting density in more than 69% of the cases, out of which 94% are positive for “stand volume,” and 89% for both “stand basal area” and for “stand-level aboveground biomass” (Fig. 4).

Variables associated with crown biomass increase show a similar pattern, with significant effects on individual-tree “crown/leaf biomass” being mostly negative (74%), while significant effects on “stand-level crown/leaf biomass” are mostly positive (85%) (Fig. 4).

The variables included in “live crown ratio” show significant effects of higher planting densities in 75% of the cases, all of which are negative. Finally, the impacts on “stem quality” are significant in only 49% of cases, out of which 63 and 37% indicate an improvement and a decline in quality, respectively (Fig. 4).

The negative effects on “survival,” “height growth,” “diameter growth,” and “stem volume/biomass” are already relevant at an early plantation age and tend to become more pronounced with time. This is especially the case for survival and “diameter growth,” which at ages greater than 20 show almost exclusively negative effects of higher planting density. For “height growth,” however, positive effects also show a gradual increase with age, whereas for “stem volume/biomass,” they show a gradual decrease. The variables grouped under “stand volume” show a

consistent dominance of positive effects across age classes, with frequencies ranging between 52 and 86%, and with negative effects permanently less frequent than 14%. At early ages, “Stem quality” is hardly influenced by increasing planting density. However, an increase of positive effects occurs at ages 5–10, to be followed by an increase in negative effects at ages 10–20 years (Fig. 5).

Critical Thresholds

As mentioned above, the mean lowest planting density per study was $891 \pm 630 \text{ ha}^{-1}$. According to our results, an average increase of 118% in planting density is required to cause significant changes—either positive or negative—in individual-tree performance. In contrast, a 71% increase is sufficient to cause significant differences in stand-level performance parameters. Among the attributes or indicators of performance with at least five observations, most are affected by relatively low increases in planting density (up to 58%). Especially for individual-tree crown biomass and for stem quality, slight increases of approximately 30% in planting density seem to cause significant changes. However, indicators related to stem growth tend to exhibit higher thresholds, with “stand volume,” “diameter growth,” and “height

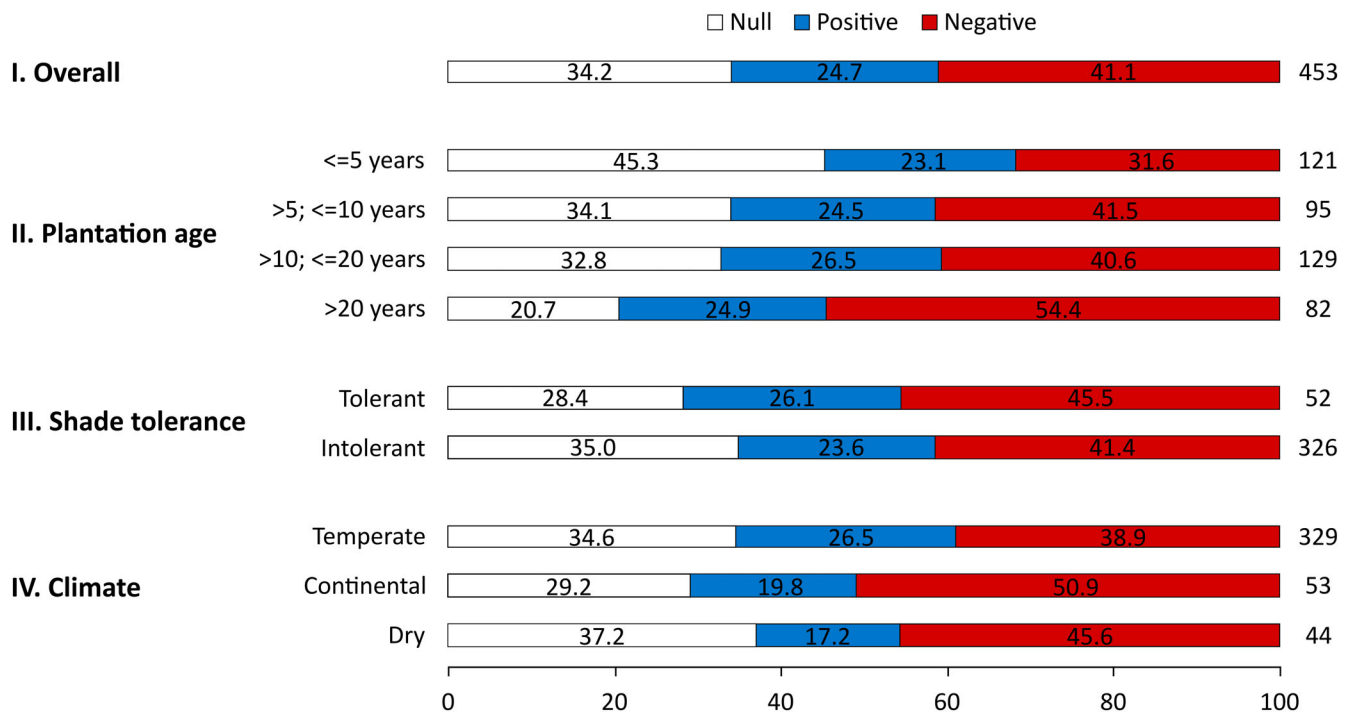


Figure 3. Frequency of observations indicating positive, negative, and null effects of increasing planting density on the performance of plantings or planted individuals. Values within the bars indicate the frequency (%) of each effect type. Values outside the bars indicate the number of observations of each class.

growth” requiring increases of over 100% in planting density (104, 158, and 250%, respectively) (Fig. 6).

Meta-Analyses

According to the meta-analyses, higher planting densities show a tendency for a negative impact on survival. However, this effect does not prove significant, neither overall, nor for the single age classes for which the number of observations allowed grouped analyses. Further subgroup analyses were not possible for this category due to the lack of observations and studies (<5). While categories accounting for individual-tree growth variables (i.e. “height growth,” “diameter growth,” “stem volume/biomass,” and “crown or leaf biomass”) also show a negative trend in their responses to higher planting density, in these cases the overall effects are significant, with consistent results for most age classes, except for height growth at ages greater than 10 years, and for crown growth. The negative effect on individual growth variables is also consistent across climatic zones and levels of shade tolerance in tree species, but it is not always statistically significant, and in some cases could not be evaluated due to lack of observations, especially in the case of the variables grouped under “crown or leaf biomass” (Fig. 7).

For stand-level variables of stem growth (i.e. “stand volume” and “stand basal area”), a higher planting density shows an overall significant positive effect. For the variables grouped under “stand volume,” this effect is strongest for young plantations (up to 5 years), but loses strength with increasing age, with no significant effects in the age classes 5–10 and greater than

20 years. For plantations in temperate regions the significant effect is also stronger than the average, although a comparison with other climate types was not possible. For plantations composed of shade-intolerant species, the positive trend is not significant, whereas for shade-tolerant species there were not enough observations. For “stand basal area,” there were only enough studies for grouped analyses for plantations under the temperate climate type, which showed significant positive effects of a higher planting density. Stand-level aboveground biomass showed a positive but non-significant effect, and subgroup analyses were only possible for plantations from temperate regions, with all related observations coming from this climate type (Fig. 8).

The meta-analyses did not show significant effects of increased planting density on either “stand-level crown or leaf biomass” or “stem quality.” This lack of effect holds true both overall and within specific age groups, climate types, and species types for which there were enough observations for meta-analyses. The only exception was plantations up to 5 years of age, which show a significant negative response to increased planting density on stem quality (Fig. 8).

Discussion

Overall Patterns

According to our results, the probabilities of higher planting density having negative, positive, or null effects on the performance of reforestation or afforestation plantings are equally distributed, and thus, decisions on whether to increase or decrease

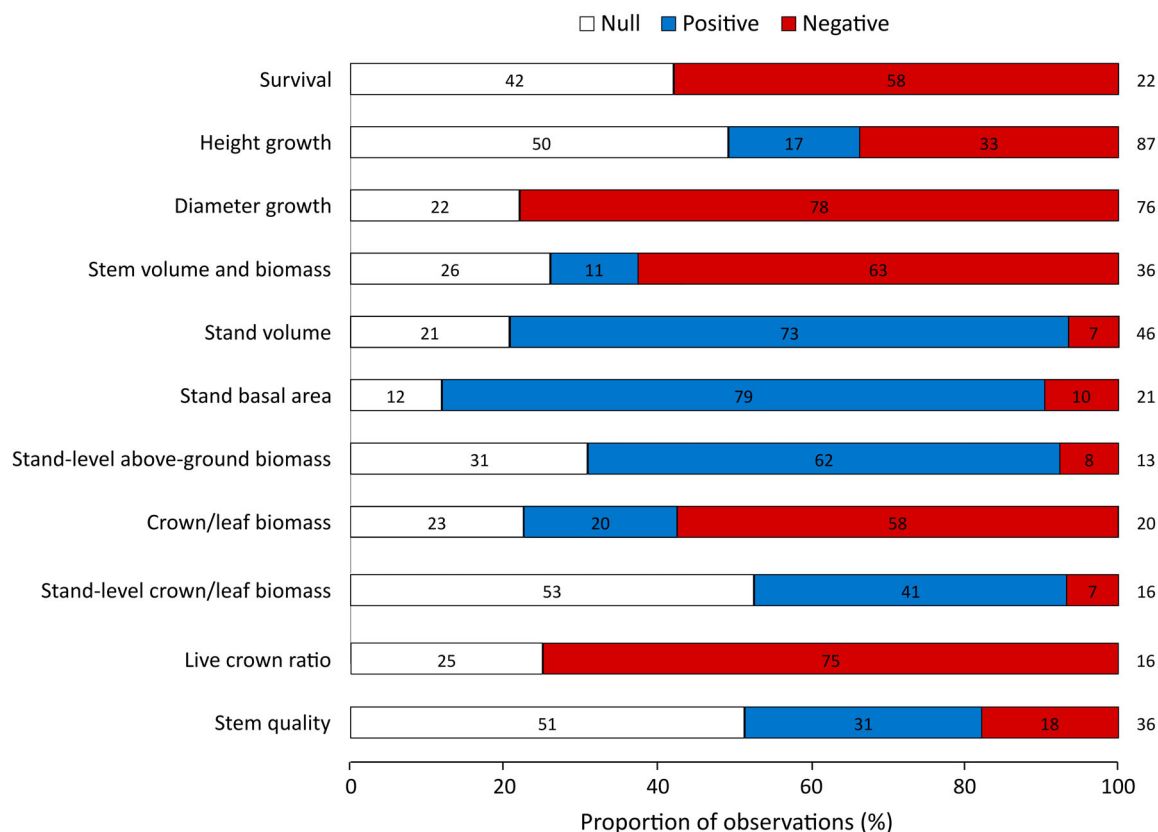


Figure 4. Frequency of observations indicating positive, negative, and null effects of increased planting density on the performance of stands or individual trees, by category of response variables. All categories represent individual-tree variables unless explicitly stated as stand-level. Values within the bars indicate the frequency (%) of each effect type (approximate to unit), whereas values outside the bars indicate the number of observations of each category. Only categories with at least 10 observations are shown.

plantation density should be largely context-dependent and guided by the specific response variable of interest. Furthermore, our general assumption is that positive effects are associated with a higher performance of tree plantings. However, the interpretation of these trends ultimately depends on the context and management objectives, since what is considered a desirable outcome may vary depending on the goals of a given restoration project.

The comparisons among age classes indicate an increasing influence of planting density on performance with increasing plantation age, with negative effects of narrower spacing becoming increasingly frequent over time. This pattern can be interpreted as a consequence of increased competition among individuals at older ages, mainly due to their larger sizes and increasing growth rates (West 2006; Moreno et al. 2023).

The comparisons among species types (shade-tolerant/shade-intolerant) and climate types show little deviation from the overall trend. The biggest differences occur between categories, rather than within the overall trend. In that sense, the observed higher frequency of negative effects under continental than under temperate climates may be a sign of a higher competition for resources. Similarly, the lower proportion of positive effects in dry regions compared to temperate regions may be explained by intensified competition for water under an overall limited

availability (Crous et al. 2013; Bradford et al. 2022). However, neither climate types nor shade tolerance seem to play a decisive role in moderating planting density effects.

Responses by Category

In terms of specific categories indicative of plantation performance, both the trend analyses and the meta-analyses consistently indicate negative effects of higher planting densities on survival. The lack of significance in the meta-analyses may be attributable to the lower sample size for this category (eight studies and 24 observations), and the fact that 75% of the observations stemmed from plantations less than 10 years old, which may have only recently achieved canopy closure and where growing space may thus not yet have been limiting to the extent of causing significant tree mortality (Pretzsch et al. 2023).

The negative trend in the response of individual-tree growth variables (i.e. “height growth,” “diameter growth,” “stem volume/biomass,” and “crown/leaf biomass”) is also consistent between the trend analyses and the meta-analyses. However, in this case, the meta-analyses indicate significant negative effects, both overall and for most of the different age classes, excepting crown/leaf biomass, for which only overall significant effects arise. Moreover, according to the trend analyses, both for

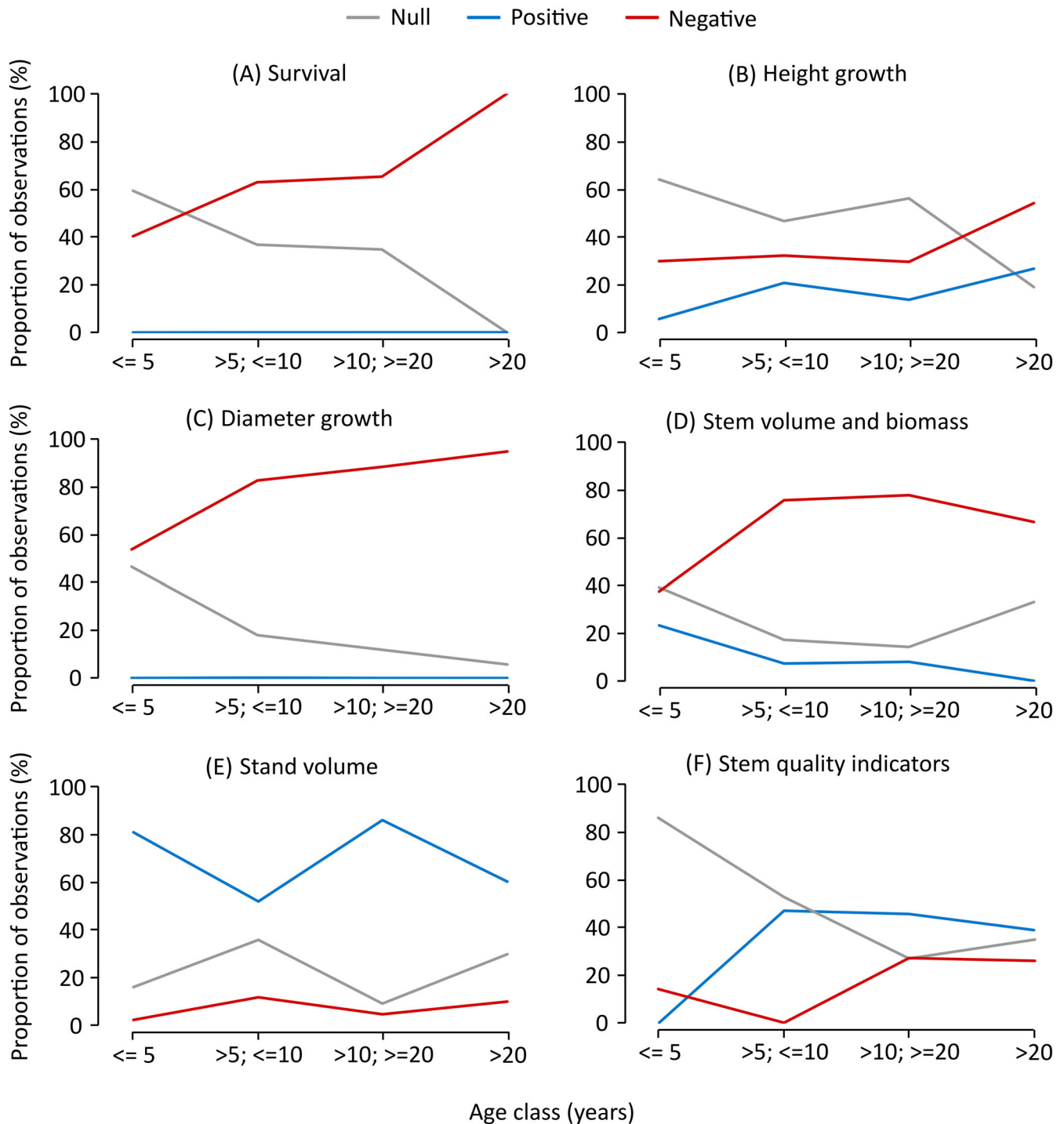


Figure 5. Frequency of observations indicating positive, negative, and null effects of increasing planting density for the different age classes. Only categories with at least five observations for each age class are shown.

survival and for individual stem growth variables, the overall trend suggests a growing proportion of negative effects with increasing plantation age. This is likely explained by increasing competition for resources with larger individual sizes in closed-canopy stands, ultimately triggering self-

thinning and density-dependent mortality (Zeide 2005; West 2006; Moreno et al. 2023).

The occurrence of positive effects on height growth may be a result of lateral shading among individuals, which in some cases, particularly in productive stands, may actually stimulate

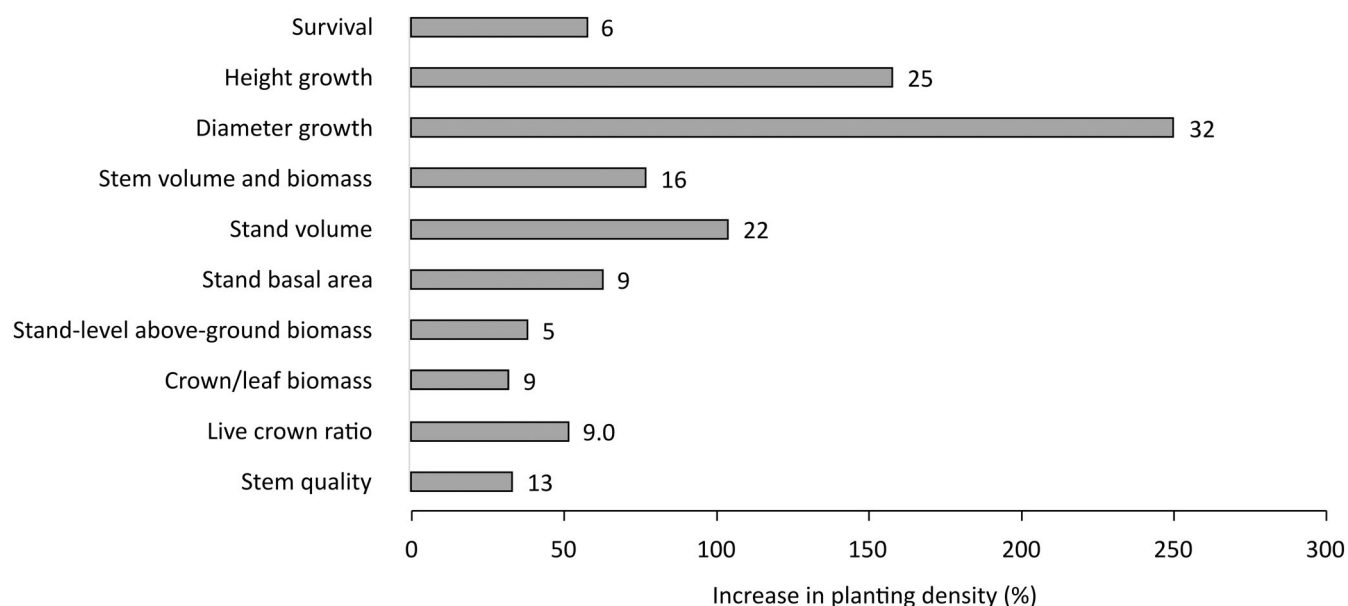


Figure 6. Mean increase of planting density causing a significant effect on plantings or planted individuals, by category of response variables. Values next to bars indicate the number of observations available for each category. Only categories with at least five observations are shown.

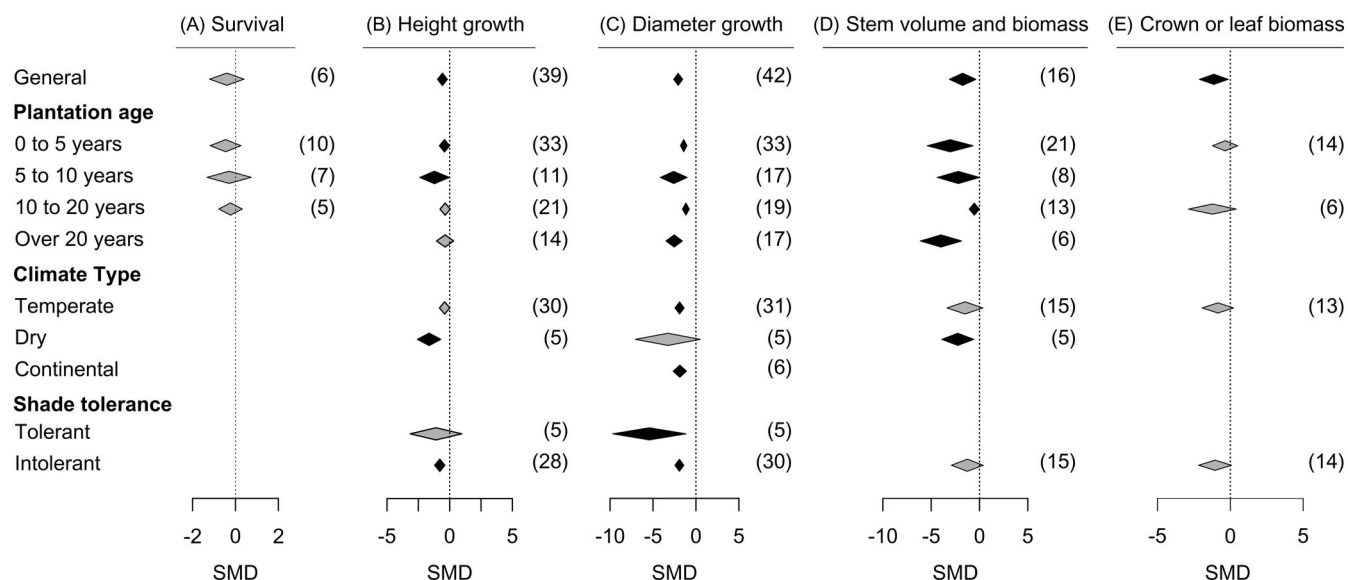


Figure 7. Forest plots of the meta-analyses on the effect of planting density on (A) survival, (B) height growth, (C) diameter growth, and (D) stem volume and biomass of individual trees. All categories refer to individual-tree variables. The figure shows the effect of low versus high density planting with corresponding 95% CIs of the individual studies, based on a random effects model, and expressed as standardized mean difference (SMD) (i.e. the difference between low vs. high density means in standard deviation units). The centroids of the polygons indicate the point estimate of the combined SMD for each group of studies or observations, while their outer edges indicate the 95% CIs limits. Polygons not intersecting the null effect axis (depicted in black) indicate an overall significant difference between groups (Viechtbauer 2010). Subgroups with fewer than five studies or observations were excluded. Numbers in brackets indicate the number of studies or observations in each case. Details on the studies employed in these analyses are provided in Table S6.

shoot elongation over other forms of growth (Hébert et al. 2016; Tymińska-Czabańska et al. 2022; Moreno et al. 2023). However, according to both the trend analyses and the meta-analyses, negative effects on height growth and other parameters of individual growth are dominant even at early ages, suggesting that

high planting densities are generally unsuitable for strategies aimed at maximizing individual-tree growth.

In contrast to individual-tree growth variables, stand-level growth variables (“stand volume,” “stand basal area,” “stand-level aboveground biomass,” and “stand-level crown/leaf biomass”) are

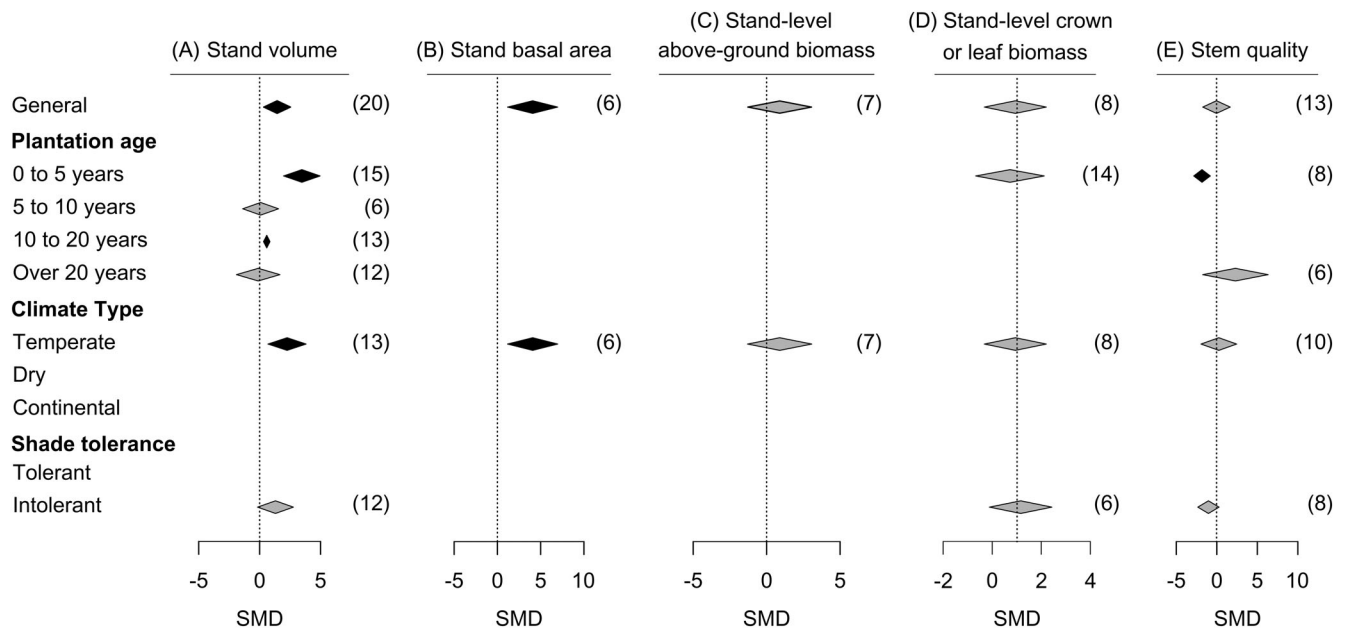


Figure 8. Forest plots of the meta-analyses on the effect of planting density on (A) stand volume, (B) stand basal area, (C) crown or leaf biomass, and (D) stem quality indicators. All categories refer to individual-tree variables, unless they are referred explicitly to as stand-level categories. For interpretation, see Figure 7.

show positive responses to higher planting densities. According to the meta-analyses, this trend was significant for stand volume and stand basal area. The higher overall yields of densely planted stands at the cost of lower individual performance over time is a pattern commonly observed in studies experimenting with tree density (West 2006). According to this trade-off, approaches aimed at optimizing individual-tree diameter and wood quality maintain wider spacings to reduce competition, whereas those aimed at higher overall biomass production (e.g. pulp or bioenergy plantations) apply narrow initial spacing, even at the expense of lower individual-tree performance (Forrester et al. 2013; Moreno et al. 2023). However, the positive effects of higher planting densities on total volume growth are already evident at early stand ages, whereas the negative effects on survival and individual diameter and volume growth, according to trend analyses, become most pronounced after 5–10 years, which is likely the time after canopy closure. Accordingly, the early years of a plantation (until 5–10 years after establishment) represent a window of opportunity during which higher planting densities can favor higher overall yields without significantly compromising survival and individual performance (Erkan & Aydın 2016). This may prove particularly useful under restoration approaches aimed at maximizing carbon sequestration (Erkan & Aydın 2016), accelerating canopy closure on highly exposed sites (Cunningham et al. 2015), or simply maximizing total biomass production in the short term (Cañellas et al. 2012).

The initial prevalence of null effects of planting density on stem quality, primarily observed at younger plantation ages, may be attributed to the small individual sizes. At these stages, interactions among individuals may be of little relevance for quality indicators of most species despite higher planting densities (Wang et al. 2018; West & Smith 2020). Surprisingly, the

only significant effects informed by the meta-analyses for this category were registered for plantations of 0–5 years of age. However, it is worth noticing that almost all observations used in the meta-analysis for this age class were derived from a single study, in which exceptionally high planting densities were employed as an upper limit (6600 trees/ha compared to an average of 4520 trees/ha for stem quality), which may have biased the corresponding results (Resquin et al. 2018).

Most of the observations describing the effects of planting density on stem quality (61%) addressed the impacts on branchiness (i.e. branch diameter and abundance). Thus, the emergence of positive effects at the age class 5–10 years and beyond, according to the trend analyses, may indicate the onset of competition for light as the stands approach canopy closure, under which side-shading starts limiting branch development (Egbäck et al. 2012; Isaac-Renton et al. 2020).

However, stem quality also depends on other factors such as straightness, absence of defects, and overall dimension (e.g. Benneter et al. 2018), meaning that increasing competition may have mixed effects. This is reflected in the rise of negative impacts at 10–20 years, which were largely driven by studies linking higher planting densities to increased slenderness. These contrasting effects on stem quality are typically managed by initially planting at high densities to control branching, followed by thinning to promote tree growth and vitality (West 2006).

Critical Thresholds of Planting Density

The wide range of planting densities in the different studies included here, and the lack of a unique reference level of planting density, make it difficult to determine a meaningful general

rate of increase in planting density that would cause significant changes in performance. Thus, the associated results described here should be interpreted cautiously. On average, a two-fold increase in planting density is required to cause significant changes in overall performance. However, this value exhibits a high variability among studies, and most importantly, among the specific attributes and functions addressed. This variability highlights the importance of making context-specific decisions when determining planting density that are based on the specific attributes or functions to optimize. If the goal is to enhance individual-tree crown biomass or stem quality, slight increases in planting density may be sufficient. However, promoting stand-level stem growth may require more substantial increases in planting density, and even higher increases would be required to trigger the observed negative effects on individual stem growth. Eventually, the slight density increments required to enhance individual crown biomass or stem quality at an earlier age may not be sufficient to simultaneously trigger the negative impacts observed on individual stem growth. Thus, identifying an optimal rate of increase specific to each case, which maximizes benefits while minimizing drawbacks, appears to be a key consideration.

Final Considerations and Further Research

In this review, we have summarized and synthesized quantitative empirical evidence on the effects of planting density on the performance of tree plantations. Our results indicate that adjustments to planting density, focused on specific performance goals and site conditions, can be a valuable tool for enhancing forest management and restoration outcomes. Yet, it is crucial to note that these results should be understood as general trends rather than strict prescriptions. On the one hand, they describe overall trends informed by a wide range of studies, each of them reflecting potentially different, unrelated dynamics. On the other hand, they are expressed in general terms, given the lack of uniform standard planting densities against which different levels can be compared. Moreover, beyond the patterns described here, optimal density is influenced by factors such as soil quality, species choice, climate, and associated costs. Thus, rather than describing universal patterns and identifying specific optimal planting densities, our aim in this study was to provide a comprehensive overview of general trends resulting from variations in planting density, and the associated trade-offs between different attributes and functions. In consequence, these findings should not be understood as a universal rule, but instead, as a reference of potential trends to expect as a result of varying planting densities.

In some cases, the sample sizes were insufficient to statistically verify the trends described here. However, the little variation across climates and species types suggests that the patterns observed here may be applicable across varying contexts. In order to translate them into concrete management schemes for specific goals, further evaluations and validations with site- and species-specific data are essential. It is also important to note that the studies analyzed here happened to be predominantly focused on early-stage impacts of planting density (i.e. 20 years of age). Therefore, identifying potentially diverging dynamics at later

stages seems relevant if no thinning is to be carried out. In addition, the focus of most studies on traditional performance variables such as survival and stem growth limits the strength and potential implications of this review. Alternative indicators of performance such as physiological attributes (e.g. water-use efficiency, light-use efficiency, and nutrient concentration), tree health, and biomass of structures other than the stem may be similarly important for management, especially from the perspective of forest restoration (Moreno et al. 2023). Consequently, research focusing on such indicators would allow us to provide broader results and more specific guidance.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Components of the research question and their corresponding synonyms or related terms.

Table S2. Search fields in which each of the string components were searched for each database, and the corresponding number of records retrieved.

Table S3. Search strings used in each of the different search engines.

Table S4. List of pre-selected studies against which the search results were compared to verify the inclusion of relevant articles.

Table S5. Response variables reported by the included studies and the corresponding categories in which they were classified.

Figure S1. Flow diagram of the study selection process.

Figure S2. Number of included studies per year addressing the effects of planting density on the performance of plantings or of planted individuals.

Figure S3. Distribution of the observations across age classes.

Table S6. List of included studies and associated data.

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