Received: 6 March 2025 | Accepted: 2 August 2025
DOI: 10.1111/1365-2745.70151

BRITISH ECOLOGICAL SOCIETY Journal of Ecology

RESEARCH ARTICLE

Resolving the effects of functional traits on tree growth rates: The influence of temporal dynamics and divergent strategies by leaf habit

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Funding information
University of Freiburg (Innovationsfonds Forschung); Natural Sciences and Engineering Research Council of Canada, Grant/Award Number: RGPIN-2018-05201; National Science Foundation, Grant/Award Number: NSF-DBI-2021898

Handling Editor: Sean McMahon

Abstract

1. Ensuring the sustainability of forest ecosystems requires understanding the mechanisms underlying tree growth and predicting their relative influence across taxa and environments.
2. Functional ecology posits that variation in tree growth is related to individual differences in functional traits, which serve as proxies for resource acquisition and investment strategies. However, studies of trait–growth relationships have produced inconsistent results, likely due to unaccounted factors like interspecific interactions, ontogeny, differing leaf habit strategies, and variation in resource acquisition and allocation.
3. We investigated the utility of key functional traits as predictors of tree height growth rates in common garden experiments in the absence of interspecific interactions. We posit that trait–growth relationships vary with age and between two groups relating to leaf habit: deciduous and evergreen species.
4. Using data from 38 tree species planted in monoculture plots across seven sites of the International Diversity Experiment Network with Trees (IDENT) in North America and Europe, we compiled height growth rates over 9 years post-germination. We modelled growth using a Bayesian hierarchical generalized linear model incorporating four above-ground functional traits related to resource acquisition and investment: specific leaf area (SLA), wood density (WD), leaf dry matter content (LDMC) and seed mass (SM). Improvements in predictive power due to the variation of trait effects with age and leaf habit were evaluated via alternative hypothesis-driven models, using the Expected Log Pointwise Predictive Density (ELPD) as a performance measure.

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5. Trait effects on growth varied with age and leaf habit, shifting between positive and negative effects, reflecting changes in resource acquisition and investment strategies. The relationships between traits and growth were strongest during the first three growing seasons for deciduous species and during the seventh to the ninth for evergreen species. Accounting for age and leaf habit substantially improved predictive power.

6. *Synthesis*. Traits are not consistently associated with tree growth rates but instead reflect dynamic resource acquisition and investment strategies over time and between deciduous and evergreen species. Despite this variability, our findings confirm the utility of functional traits to predict tree growth rates, especially when trait effects are considered to vary with age and leaf habit.

KEYWORDS
common-garden experiment, functional ecology, hierarchical models, IDENT, plant development and life-history traits, trait–growth relationships, tree age, tree growth

1 | INTRODUCTION

Functional traits are useful indicators of the fundamental differences in plant strategies related to resource acquisition and investment (Reich, 2014; Wright et al., 2004). These traits—whether morphological, physiological or phenological—serve as proxies for the underlying mechanisms driving plant growth and performance in specific environments (Violle et al., 2007). Thus, trait-based approaches have the power to shift community ecology from a descriptive to a mechanism-oriented perspective (Chalmandrier et al., 2021; Boulangeat et al., 2012). Leveraging functional traits to gain a mechanistic understanding of demographic rates could improve the predictive capabilities for plant performance across diverse spatial and temporal contexts (Funk et al., 2017).

Despite the promise of functional traits to predict demographic rates of trees, attempts to link traits to individual growth rates have produced mixed results (Swenson et al., 2020; Yang et al., 2018). For instance, a previous global study of juvenile trees found that a combination of commonly measured functional traits accounted for only 3% of the variation in growth, calling into question the utility of traits for prediction (Paine et al., 2015). In contrast, similar combinations of traits explained ~40% of the variation in tree growth within neotropical permanent forest plots (Poorter et al., 2008). There are several explanations for this lack of consistency among trait–growth relationships observed in previous studies. First, prior assessments of trait effects on growth were conducted in diverse environments, such as experimental plots of varying species richness, as well as unmanaged tropical forests, but failed to control for the influence of neighbouring tree diversity on trait expression and growth, a factor that could modulate trait–growth relationships in natural and managed forests (Liang et al., 2016; Paquette & Messier, 2011) as well as in diversity experiments where it is in fact expected (Williams et al., 2020). Furthermore, questions about the reliability of traits as predictors of growth often stem from the assumption that growth strategies remain unchanged throughout a tree's lifespan (Falster et al., 2018). Inconsistencies between findings are often interpreted as a limited predictive capacity of functional traits when, in fact, they may reflect differences in whether studies focus on seedlings or adult trees, which can exhibit distinct resource acquisition and investment strategies. In line with this, studies have shown that tree age, size and ontogenetic stage can introduce temporal variation in the strength and direction of trait–growth relationships. This variation can sometimes result in contrasting effects, where positive and negative associations between traits and growth at different life stages effectively cancel each other out, reducing the overall observed influence of traits (Gibert et al., 2016; Iida et al., 2014; Swenson, 2013; Visser et al., 2016; Yang et al., 2018). Similarly, trait–growth relationships are almost always assumed to be consistent across species, overlooking the role of leaf habit (whether deciduous or evergreen) in driving differences in resource acquisition and investment strategies (Kikuzawa, 1994; Lusk & Warton, 2007). Deciduous species are typically more resource-exploitative, have lower tissue construction costs, and have higher photosynthetic capacity and transpiration rates early in life, even when standardized for leaf lifespans (Reich et al., 1992). They typically grow faster than evergreen species, which tend to be more conservative, have lower photosynthetic capacity and greater water-use efficiency (Chabot & Hicks, 1982; Eamus, 1999). Given that deciduous and evergreen species (and most especially deciduous angiosperms and evergreen gymnosperms) are thought to use distinct mechanisms for resource acquisition and investment (Givnish, 2002), and that these mechanisms most likely change over different stages of their life cycles (Gibert et al., 2016), it is reasonable to expect that trait–growth relationships would also differ both between these two groups and over time.

This study aims to establish whether functional traits can be useful predictors of tree height growth in the absence of interspecific interactions. This analysis of trait–growth relationships focuses exclusively on monoculture plots within common garden experiments, minimizing the influence of external abiotic and biotic factors, such as competition and facilitation, that may introduce confounding variability in previous research. We consider traits whose importance for growth has been previously shown to mediate resource acquisition and investment and for which data is available for many species: specific leaf area (SLA), wood density (WD), leaf dry matter content (LDMC) and seed mass (SM). We assess the contribution of these traits in predicting variation in juvenile tree height growth rates using Bayesian hierarchical generalized linear models while examining how much predictive power can be gained by considering that trait–growth relationships vary with age and between deciduous and evergreen species. We pose one overarching hypothesis for each trait and further analyse how age and leaf habit influence their validity. (1) We expect trees with higher SLA to grow faster since they produce leaves with a larger light-capturing area per unit biomass, thus exhibiting higher photosynthetic rates per unit dry matter investment (Reich, 2014; Reich et al., 1997; Wright et al., 2004). (2) Conversely, higher WD implies greater stem carbon investment per unit wood volume, smaller cells with thick walls and lower hydraulic conductance, which should translate to slower height growth rates (Castro-Díez et al., 1998; Chave et al., 2009; Poorter et al., 2008). (3) Trees exhibiting higher LDMC (i.e. higher ratio of leaf dry mass to leaf saturated mass) have leaves with elevated carbon concentrations, primarily due to higher proportions of cell walls and secondary compounds. These characteristics result in higher tissue construction costs per unit volume, leading to slower growth rates (Polley et al., 2020; Poorter & De Jong, 2002; Ryser, 1996). (4) Finally, we hypothesize that larger SM may be associated with slower overall growth rates. Despite larger SM aiding in seedling establishment and survival by minimizing size-dependent mortality (Rose & Poorter, 2003), small-seeded species, often considered 'pioneer' species, need to compensate for their limited reserves by rapidly developing roots and leaves to achieve independent resource acquisition early on (Poorter et al., 2008; Turnbull et al., 2012). The above hypotheses are consistent with Reich (2014) for resource abundant conditions, such as weeded common garden tree experiments.

Our analysis is focused on juvenile trees of 38 species from monoculture plots among seven sites of the International Diversity Experiment Network with Trees (IDENT) across North America and Europe (Tobner et al., 2014). We limited our study to juvenile trees, drawing on a meta-analysis showing that shifts in trees' physiological and structural priorities generally make trait–growth relationships weaker at later ontogenetic stages (Gibert et al., 2016). Furthermore, we posit that the early years of establishment, whether following stand-replacing disturbances, gap dynamics or natural regeneration, are critical in shaping forest succession and future forest composition. During this period, traits should theoretically align with species' fundamental life-history strategies. We, therefore, focus on the first 9 years following germination, examining the temporal dynamics of trait–growth relationships across three distinct periods: from germination of the seed to the third growing season inclusively, from the fourth through the sixth and from the seventh through the ninth.

2 | MATERIALS AND METHODS

2.1 | Sites description and data selection

This study was undertaken as part of the IDENT, a collaborative initiative comprising common garden experiments aimed at evaluating the impact of tree diversity on ecosystem functioning across North America, Europe and Africa (Tobner et al., 2014). All experiments conducted within IDENT include plots that were planted to represent different levels of tree species richness and functional diversity. Here, we considered only monoculture plots to minimize the impact of interspecific interactions. We used data from the seven oldest experiments within IDENT, which had been established for at least 9 years. Plots within the IDENT experiments were planted at uniform density, with spacing between individuals ranging from 0.4 to 0.5 m. All sites were weeded at least until canopies were beginning to close. All experiments follow a hierarchical design: trees are planted within plots, nested within blocks. Blocks represent replicates of all tree community compositions, and the spatial arrangement of plots within each block is randomized. Across the seven IDENT experiments used here, three included resource amendment treatments in addition to controls. Specifically, a distinct sub-experiment in Freiburg, Germany, included plots with added nitrogen, phosphorous or both (Wein et al., 2016); in Macomer, Italy, and Sault-Ste-Marie, Canada, half of the blocks received supplementary water (Belluau, Vitali, et al., 2021b; Van de Peer et al., 2018). Since treatment and control plots within an experiment were exposed to different environmental conditions, we treated each combination of experiment and resource treatment (hereafter referred to as a site) as an independent entity in statistical analyses, resulting in 12 sites encompassing a total of 38 species. These included 18 deciduous species (16 angiosperms and 2 gymnosperms) and 20 evergreen species (6 angiosperms and 14 gymnosperms) (Table S1). Some species were assessed in multiple experiments (Table 1; Figures S1–S3).

2.2 | Growth calculations

We gathered height data of juvenile trees grown in monoculture plots from the 12 sites. Measurement frequency varied among sites, and in some cases, a few growing seasons elapsed between two consecutive measurements. For each height measurement, we recorded the number of growing seasons (i.e. number of summers passed) since seed germination. Trees that died, showed dieback, or were cut and resprouted were removed from the analysis. Individual height growth rates were determined by calculating the difference in height between two measurements and dividing it by the number of growing seasons that elapsed between the measurements. We compared three distinct time periods to assess the effect of age: (1) from germination to after the third growing season inclusively (referred to as 'period 0–3'; $n = 9450$), (2) from the fourth through the sixth growing season (referred to as 'period 4–6'; $n = 4615$) and (3) from the seventh through the ninth growing season (referred to as 'period 7–9'; $n = 5381$). As trees were not consistently measured

TABLE 1 Selected IDENT sites and their characteristics.

	FAB, USA	Cloquet, USA	Auclair, Canada	Sault-Ste-Marie, Canada	Montreal, Canada	Freiburg, Germany	Macomer, Italy
Reference	Grossman et al. (2017)	Tobner et al. (2014)	Tobner et al. (2014)	Belluau, Vitali, et al. (2021b)	Tobner et al. (2014)	Wein et al. (2016)	Van de Peer et al. (2018)
Latitude	45.40°	46.68°	47.70°	46.52°	45.42°	48.02°	40.24°
Longitude	−93.19°	−92.52°	−68.66°	−84.34°	−73.94°	7.83°	8.72°
Biome	Temperate	Temperate	Temperate	Temperate	Temperate	Temperate	Mediterranean
Planting date	2013	2010	2010	2013	2009	2013	2014
Soil type	Sandy	Sandy loam	Loam	Sandy loam	Sandy	Sandy loam	Slit loam
Elevation (m)	279	383	333	210	39	278	615
Species included in this study	*Acer rubrum* *Betula papyrifera* *Juniperus virginiana* *Pinus banksiana* *Pinus resinosa* *Pinus strobus* *Quercus alba* *Quercus ellipsoidalis* *Quercus macrocarpa* *Quercus rubra* *Tilia americana*	*Acer platanoides* *Acer saccharum* *Betula papyrifera* *Betula pendula* *Larix decidua* *Larix laricina* *Picea abies* *Picea glauca* *Pinus strobus* *Pinus sylvestris* *Quercus robur* *Quercus rubra*	*Acer platanoides* *Acer saccharum* *Betula papyrifera* *Betula pendula* *Larix decidua* *Larix laricina* *Picea abies* *Picea glauca* *Pinus strobus* *Pinus sylvestris* *Quercus robur* *Quercus rubra*	*Acer saccharum* *Betula papyrifera* *Larix laricina* *Picea glauca* *Pinus strobus* *Quercus rubra*	*Abies balsamea* *Acer platanoides* *Acer rubrum* *Acer saccharum* *Betula alleghaniensis* *Betula papyrifera* *Larix decidua* *Larix laricina* *Picea abies* *Picea glauca* *Picea omorika* *Picea rubens* *Pinus resinosa* *Pinus strobus* *Pinus sylvestris* *Quercus robur* *Quercus rubra* *Thuja occidentalis* *Tilia cordata*	*Acer platanoides* *Acer saccharum* *Betula papyrifera* *Betula pendula* *Larix decidua* *Larix laricina* *Picea abies* *Pinus strobus* *Pinus sylvestris* *Quercus robur* *Quercus rubra*	*Acer monspessulanum* *Arbutus unedo* *Fraxinus ornus* *Olea europea* *Phillyrea latifolia* *Pinus halepensis* *Pinus pinaster* *Pinus pinea* *Pistacia lentiscus* *Quercus ilex* *Quercus pubescens* *Quercus suber*

after every growing season, we selected these three periods to maximize both the number of individual trees for which height was recorded at both the beginning and end of the period. We also aimed to maximize the number of species, thereby capturing the greatest trait variability. These three periods also corresponded to key stages in terms of intraspecific competition intensity. Period 0–3 and period 4–6 represented growth under mostly competition-free conditions, reflecting nursery production and the initial post-planting open-canopy stage. Period 7–9 coincided with the early stages of canopy closure, where intraspecific competition emerged. Differences in sample sizes across periods reflect the fact that height measurements were not available for all years at all sites, as well as tree mortality between periods. Trees at different sites experienced varying conditions prior to plantation, either in nurseries or outside the experimental plots, with conditions kept constant within each site. This pre-plant period was included in the analysis to capture the entire seedling stage.

2.3 | Trait data

We opted to use mean trait values derived from individual measurements in global trait databases and in the literature. This provided a 'universal' mean value for each species, aligning with the broader objective of advancing functional ecology by leveraging widely available trait data (Wright et al., 2004). Functional trait data for SLA, WD, LDMC and SM were primarily obtained from a comprehensive database that consolidates entries predominantly derived from the TRY database of plant traits (Kattge et al., 2011, 2020). This database was meticulously curated to remove duplicates and exclude measurements made on trees subjected to any specific treatment, grown in laboratory settings or in pots (Belluau, Bouchard, et al., 2021a). Missing trait data were provided by locally measured values from IDENT-Montréal (Belluau & Mordacq, 2023) and additional literature searches. For each trait, we initially calculated the mean value for each species within each dataset to ensure equal weighting across datasets and then computed the overall mean of these dataset-specific means for each species.

2.4 | Analyses

To assess the relationship between individual growth and the four functional traits, we fit a first Bayesian hierarchical model based on the hypothesis that trait effects vary with both time period and leaf habit (*Main model*; MH1). This *Main model* assumes that tree height growth follows a Gamma distribution, parameterized by mean (μ) and shape (α) (Bürkner, 2024; Faraway, 2006). This modelling framework allowed us to flexibly handle the complexities of our hierarchical model, which involved correlated trait predictors and the need to jointly model μ and α, while providing uncertainty intervals for estimates across hierarchical levels. We opted for a Gamma distribution because height-growth rates are strictly positive, exhibit variance that increases with the mean, and the Gamma distribution is well suited to modelling tree-size (and hence growth) data (e.g. Kelemen et al., 2024; Podlaski, 2017). In our *Main model*, each parameter is modelled with a linear predictor, using a logarithmic link function. For the mean parameter μ, we included population-level effects for the period in interaction with both leaf habit and each trait. To account for and control background variation in climate and site quality across different sites and within site replicates, we included group-level effects of the time period based on site identity and replicated blocks nested within the sites. These were meant to control for environmental differences specific to each site, which vary between geographic locations. For the shape parameter α, we included population-level effects for leaf habit and period in interaction, and group-level effects with the same structure as for the mean parameter. Correlations between the two linear predictors (μ and α) were assumed for group-level effects based on the same grouping factor. Each parameter was assigned weakly informative priors (Gelman et al., 2008): at the scale of the standardized predictors, we used student-*t* priors with 3 degrees of freedom, centred on 0, and with a standard deviation of 2.5. We used LKJ priors (Lewandowski et al., 2009) with hyperparameter η equal to 1 to model correlations between group-level effects. The structure of this *Main model* is presented below, where y_{ijkmn} is the height growth rate for observation *i*, with leaf habit *j*, over period *k*, originating from project site *m* and block *n*. The Iverson bracket is denoted by [], γ and δ represent population-level effects, ψ and ζ represent group-level effects.

(a) *Main model* (MH1)

$$
\begin{aligned}
& y_{ijkmn} \sim Gamma\left(\mu_{ijkmn}, \alpha_{jkmn}\right) \\
& \ln\left(\mu_{ijkmn}\right) = \gamma_0 + \\
& \quad \gamma_{001}\, SLA + \gamma_{002}\, WD + \gamma_{003}\, LDMC + \gamma_{004}\, SM + \\
& \quad [j \neq \mathrm{Deciduous}]\left(\gamma_{010} + \gamma_{011}\, SLA + \gamma_{012}\, WD + \gamma_{013}\, LDMC + \gamma_{014}\, SM\right) + \\
& \quad [k \neq \mathrm{Period}\ 0-3]\left(\gamma_{k00} + \gamma_{k01}\, SLA + \gamma_{k02}\, WD + \gamma_{k03}\, LDMC + \gamma_{k04}\, SM\right) + \\
& \quad [j \neq \mathrm{Deciduous} \wedge k \neq \mathrm{Period}\ 0-3]\left(\gamma_{k10} + \gamma_{k11}\, SLA + \gamma_{k12}\, WD + \gamma_{k13}\, LDMC + \gamma_{k14}\, SM\right) + \\
& \quad \psi_m + \psi_{mn} + [k \neq \mathrm{Period}\ 0-3]\left(\psi_{km} + \psi_{kmn}\right) \\
& \ln\left(\alpha_{jkmn}\right) = \delta_0 + \\
& \quad [j \neq \mathrm{Deciduous}]\,\delta_{01} + [k \neq \mathrm{Period}\ 0-3]\,\delta_{k0} + [j \neq \mathrm{Deciduous} \wedge k \neq \mathrm{Period}\ 0-3]\,\delta_{k1} + \\
& \quad \zeta_m + \zeta_{mn} + [k \neq \mathrm{Period}\ 0-3]\left(\zeta_{km} + \zeta_{kmn}\right)
\end{aligned}
$$

We used the 10,000 posterior samples drawn from this *Main model* to compute 90% equal-tailed uncertainty intervals (from 5% to 95%) for each coefficient estimate, with point estimates based on the mean. We regard the evidence for the existence of an effect as *weak* if the corresponding uncertainty interval includes zero. We also generated predictions for the differences in coefficient estimate values between all combinations of time period and leaf habit for each trait and their corresponding 90% uncertainty intervals. This analysis allowed us to assess hypotheses related to changes in the magnitude of every trait–growth relationship over time and between deciduous and evergreen species. Given the logarithmic link function for the mean, we calculated a multiplicative factor for every coefficient estimate to facilitate their interpretation and compare the strength of the trait–growth relationship at each period and for each leaf habit in each trait's original unit. This factor represents the value by which individual growth changes with each unit increase in one trait (akin to the slope of a regression) while the other traits are maintained at their mean value. These factors were obtained by back-transforming each standardized coefficient estimate into the target trait's unit, followed by computing its exponential. To visualize trait–growth relationships across age and leaf habit, we used the *Main model* to predict growth within the observed range for each trait, each period and each leaf habit, keeping other traits at their mean value and excluding group-level variation. Lastly, we conducted Bayesian hypothesis tests to assess differences in predicted growth rates from the *Main model* across time periods and between deciduous and evergreen species within the same period. Comparisons where the posterior probability exceeded 0.90 (equivalent to a 90% uncertainty interval that excludes zero) were considered to have strong evidence for a difference.

The *Main model* was compared with three hypothesis-driven sub-models to assess the predictive performance gained by considering trait effects to vary with time period and/or leaf habit. These models were identical in structure to the *Main model* but excluded either the interaction between traits and period (MH2), the interaction between traits and leaf habit (MH3), or both interactions (MH4; Table S2). We also parameterized three baseline models of increasing complexity and without trait effects to evaluate the overall predictive power of the *Main model*. These baseline models ranged from a simple intercept-only model to one that included experimental structure and period (MB1 to MB3; Table S2). We quantified predictive accuracy using Leave-One-Out Cross-Validation (LOO-CV) and calculated the Expected Log Pointwise Predictive Density (ELPD) for each model, where higher ELPD values indicate better performance at predicting the response based on a new dataset (Bürkner et al., 2024; Vehtari et al., 2017). Pairwise comparisons of models were based on differences in ELPD relative to their standard errors. We calculated a Bayesian R-squared (Gelman et al., 2019) to assess the portion of height growth variance explained by our *Main model*.

All models were fit and analysed using the *brms* package in R version 4.3.0 (Bürkner et al., 2024; R Core Team, 2024; Stan Development Team, 2024). Prior to analysis, all trait data were centred and scaled, and SM was log-transformed. Four Markov chains were run for each model, with 7500 warmup and 2500 sampling iterations, resulting in a total of 10,000 retained posterior samples. Additional sampler settings are detailed in the code. Models were assessed for convergence and fit using trace plots, effective sample sizes, *R*-hat values and posterior predictive checks (PPC) plots implemented in the ShinyStan app (Gabry et al., 2022; Vehtari et al., 2021). Visual inspection of quantile residuals showed no sign of missing predictors. Dataset along with scripts are archived on Zenodo (https://doi.org/10.5281/zenodo.16799185).

3 | RESULTS

3.1 | Model comparison

The *Main model* (MH1) accounted for 55% of the variation in height growth ($R^2=0.55$) and exhibited the best predictive performance among all tested models, as indicated by its ELPD score (Figure 1, Table S3). By incorporating interactions between period, leaf habit and functional traits, the *Main model* clearly outperformed all other

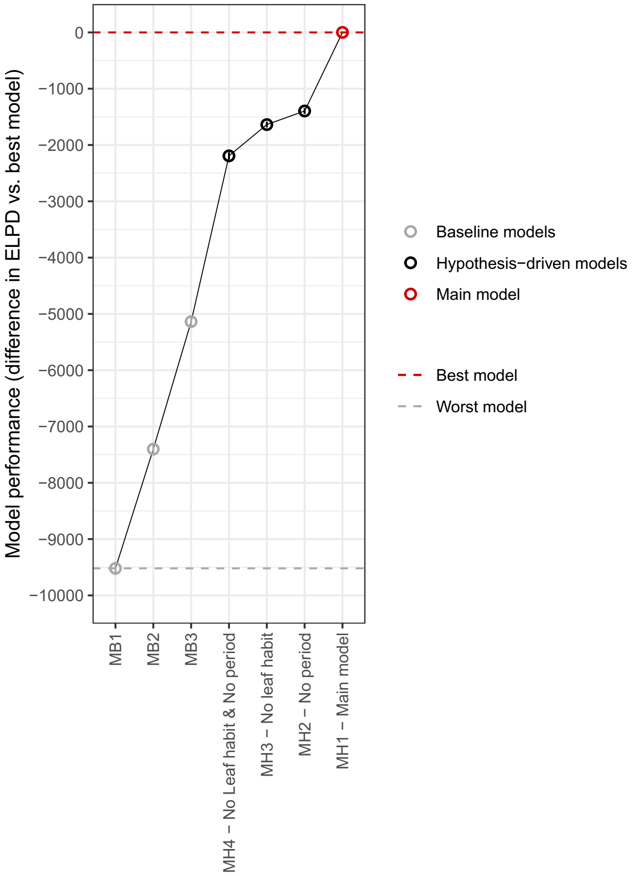

FIGURE 1 Model performance comparison based on differences in Expected Log Pointwise Predictive Density (ELPD). Models are evaluated relative to the best-performing model (*Main model*). Dashed lines indicate ELPD thresholds for the best and worst models, with vertical lines showing standard error of differences.

hypothesis-driven models in terms of predictive power, with ELPD differences of 1396.1 (SE = 52.4), 1637.4 (SE = 51.5) and 2192.7 (SE = 63.9) compared with MH2, MH3 and MH4. The *Main model* also outperformed all baseline models, with an ELPD improvement of 5137.3 (SE = 92.4) over the most complex baseline model, which included group-level effects for experimental structure and time period as independent population-level effects (MB3) (Figure 1, Table S3). Notably, a comparison of the simplest hypothesis-driven model (MH4) with the most complex baseline model (MB3) revealed an ELPD difference of 2944.6 (SE = 73.8), indicating that even when trait effects are not allowed to vary with period or leaf habit, traits hold substantial predictive power for growth under our experimental setting where interactions with other tree species are absent (Table S4). Based on the superior performance of the *Main model*, only its output was retained for further analyses.

3.2 | Trait effects on growth

Coefficient estimates were almost all different from 0 (Table 2). Growth was influenced by all combinations of trait, period and leaf habit except for four cases: SLA did not influence growth of deciduous species in period 7–9; WD did not influence growth of deciduous species in periods 4–6 and 7–9; and WD did not influence growth of evergreen species in period 7–9. Furthermore, the 90% uncertainty intervals of the differences in coefficient estimates revealed that almost all trait effects varied between every combination of period and leaf habit (Table S5). This shows that the relationship between functional traits and growth is sensitive to the age of the tree and leaf habit. The only exceptions were that there was no difference between the effect of SLA on growth of evergreen species between period 0–3 and period 7–9; the effect of WD on growth of deciduous species did not differ between the three periods; and the effect of WD did not differ between deciduous and evergreen species in period 7–9 (Table S5).

The multiplicative factors (Table 2) and model prediction plots (Figure 2) show that SLA had an early strong positive influence on the growth of deciduous species during period 0–3, which decreased over time, becoming slightly negative during period 4–6. By period 7–9, this effect was indistinguishable from zero, as the uncertainty intervals included zero. For evergreen species, SLA had a weak effect in all periods, fluctuating from positive to negative and then back to positive. WD had a subtle, positive effect on the growth of deciduous species during period 0–3 but had negligible effects in subsequent periods, with uncertainty intervals, including zero for both period 4–6 and period 7–9. For evergreen species, WD showed a strong negative effect during the first two periods, peaking at period 4–6 before becoming indistinguishable from zero in period 7–9. LDMC initially had a strong positive influence on initial growth of deciduous species, which weakened and became negative in period 4–6 and returned to positive in period 7–9. For evergreen species, LDMC followed the opposite trend, starting negative, then becoming slightly positive, before returning negative again by period 7–9. Finally, SM had a negative effect on the growth of deciduous species, which stayed relatively stable throughout the three periods. There was more temporal variation in the relationship for the evergreen species, with a strong positive effect of SM on growth in period 0–3, which then stabilized in period 4–6 and became highly positive again in period 7–9.

Overall, deciduous species grew faster than evergreen species during the first two periods, peaking in period 4–6 and stabilizing through period 7–9. Evergreen species maintained constant average growth rates during the first two periods and started growing faster in period 7–9. By period 7–9, there was no difference between growth rates of deciduous and evergreen species (Figure 3; Table S6). Notably, stronger growth rates did not coincide with stronger trait–growth relationships. Trait–growth relationships were generally strongest in period 0–3 for deciduous species and in period 7–9 for evergreen species. For both leaf habits, trait–growth relationships weakened and approached zero during period 4–6 (Figure 2).

4 | DISCUSSION

Our study demonstrates that functional traits are highly predictive of the height growth rates of juvenile trees. However, trait–growth relationships differ markedly with age and between deciduous and evergreen species, with relationships often reversing over time from positive to negative, or vice versa. This observation is reinforced by the fact that including interactions with both leaf habit and period in our *Main model* greatly enhanced its predictive power compared with all other hypothesis-driven models, including MH4, the trait-based model that excluded these interactions. Trait–growth relationships in deciduous species are strongest during early development (period 0–3), with high SLA, high LDMC and low SM values leading to faster growth. These trait–growth relationships, however, lose strength as deciduous trees age. Therefore, for deciduous species, only our hypotheses for SLA and SM were confirmed, but only during period 0–3. In evergreen species, trait–growth relationships are even more variable in time but are strongest later in development (period 7–9). During this period, evergreen species exhibiting high SLA and high SM grow faster, whereas species with high WD and high LDMC grow slower. In evergreen species, our hypotheses were thus confirmed for all traits except SM during period 7–9, and for all traits except SLA and SM during period 0–3. This complex interplay between traits and growth underscores the importance of accounting for both time and leaf habit in studies of trait-driven growth patterns across species.

4.1 | Ontogeny of trait–growth relationships

For deciduous species, our model indicates that the relationship between SLA and growth is strongest during the first 3 years of development. During that period, high-SLA species exhibited rapid growth, likely due to lower marginal costs of leaf construction and

TABLE 2 *Main model* results showing multiplicative factors and standardized coefficients across periods for species with deciduous (D) and evergreen (E) leaf habits.

	Period 0–3		Period 4–6		Period 7–9		
Trait	**D**	**E**	**D**	**E**	**D**	**E**	**Unit**
SLA *mul. factor*	1.1114	1.0163	0.9700	0.9813	0.9954†	1.0239	mm^2/mg
std coef.	0.6835 5%: 0.6595 95%: 0.7079	0.1048 5%: 0.0737 95%: 0.1359	−0.1971 5%: −0.2410 95%: −0.1527	−0.1225 5%: −0.1505 95%: −0.0952	−0.0297† 5%: −0.0625 95%: 0.0033	0.1527 5%: 0.1085 95%: 0.1971	
WD *mul. factor*	1.1939	0.1064	1.3193†	0.0041	1.1334†	0.5832†	mg/mm^3
std coef.	0.1749 5%: 0.0638 95%: 0.2866	−0.3275 5%: −0.3452 95%: −0.3097	0.0378† 5%: −0.0081 95%: 0.0834	−0.8040 5%: −0.8463 95%: −0.7607	0.0155† 5%: −0.0310 95%: 0.0630	−0.0924† 5%: −0.1953 95%: 0.0112	
LDMC *mul. factor*	56.0330	0.0401	0.2344	21.2118	4.1119	0.0030	g/g
std coef.	0.2405 5%: 0.2197 95%: 0.2615	−0.1944 5%: −0.2146 95%: −0.1746	−0.0905 5%: −0.1233 95%: −0.0584	0.1829 5%: 0.1692 95%: 0.1966	0.0797 5%: 0.0386 95%: 0.1211	−0.3552 5%: −0.3978 95%: −0.3127	
SM[a] *mul. factor*	0.9268	1.1364	0.9689	1.0316	0.9103	1.3780	mg
std coef.	−0.1992 5%: −0.2162 95%: −0.1825	0.3349 5%: 0.3087 95%: 0.3610	−0.0828 5%: −0.1022 95%: −0.0641	0.0813 5%: 0.0355 95%: 0.1267	−0.2460 5%: −0.2664 95%: −0.2256	0.8390 5%: 0.7486 95%: 0.9319	

Note: Multiplicative factors (in grey) indicate the value by which individual growth is multiplied with each unit increase for a given trait while other traits are held constant at their mean value. Values <1 indicate a negative relationship, while values >1 indicate a positive relationship. Note that traits have different units and ranges, so comparison of multiplicative factors should only be made within the same trait and across periods and leaf habits. To facilitate comparisons across traits, standardized coefficients and their 90% uncertainty intervals are also presented. Combinations of trait, period and leaf habit where uncertainty intervals include zero (weak evidence) are marked with †.

[a] Values for SM reflect log-transformed data.

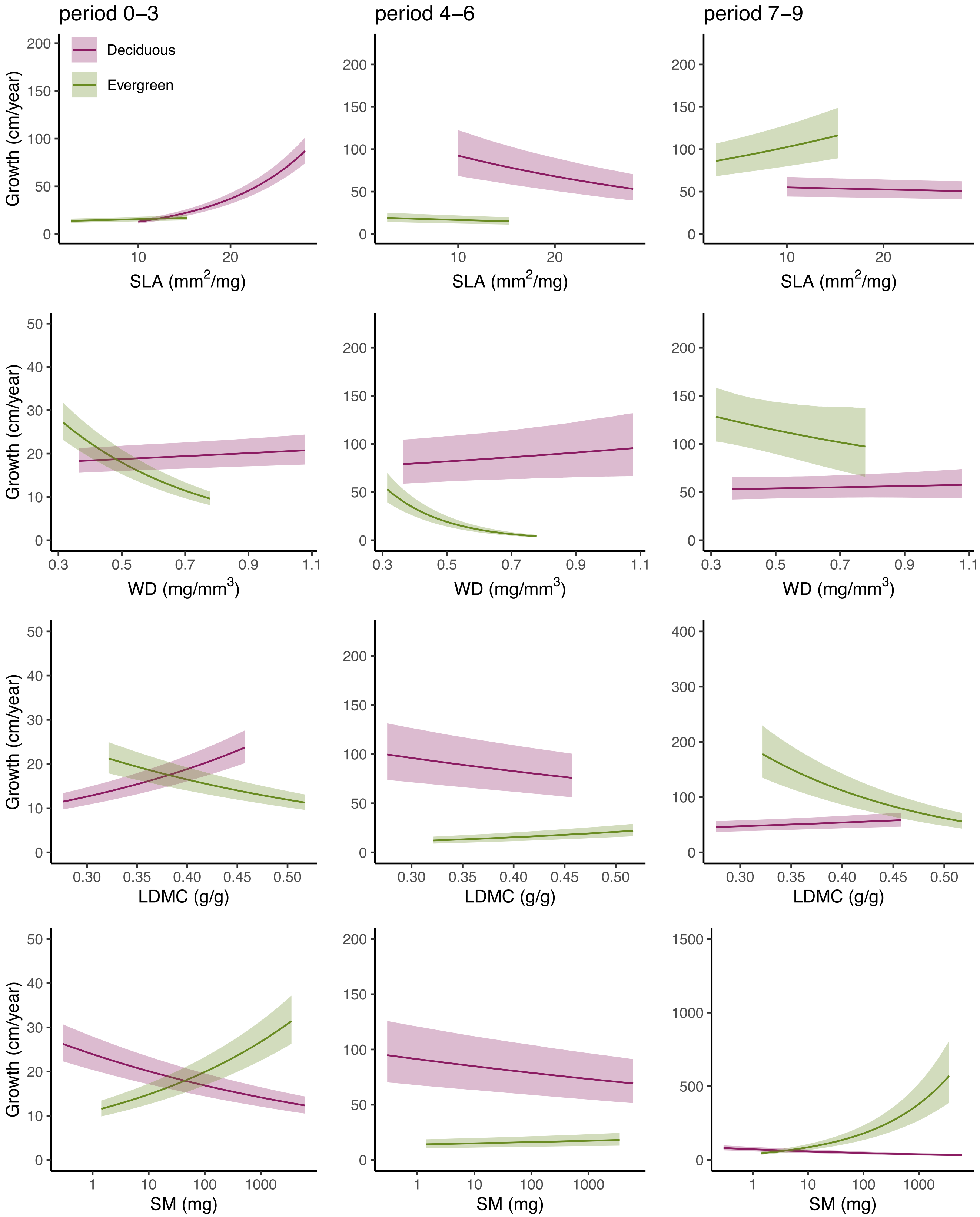

FIGURE 2 Predicted relationships between trait values and height growth rate (cm/year) for deciduous (purple) and evergreen (green) tree species across the three time periods. Predictions for each trait were obtained from the *Main model*, with non-target traits held constant at their mean values. Shaded areas correspond to 90% uncertainty intervals, and solid lines correspond to the mean point estimates. Predictions were made on observed trait value ranges for either deciduous or evergreen species. The *x*-axis for SM is presented on a natural log scale to reflect the transformation used in the model while improving interpretability.

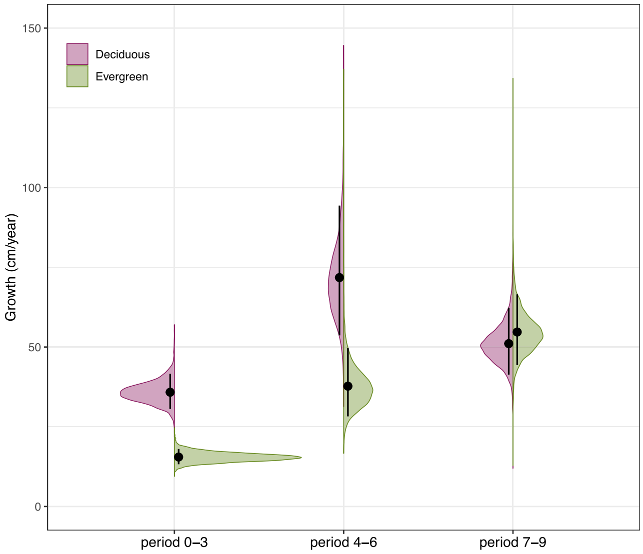

FIGURE 3 Predicted height growth rate (cm/year) across the three time periods (0–3 years, 4–6 years and 7–9 years) for deciduous and evergreen species. Points represent mean height growth rate predictions from the *Main model* based on population-level effects, with vertical lines indicating 90% uncertainty intervals for the average growth per period. Violin plots display the distribution of predicted mean growth rates, with the width of each shape reflecting the proportion of predictions at a given value. Results from Bayesian hypothesis tests comparing growth across time periods and between leaf habits are summarized in Table S6.

minimal investment in support structures (Cornelissen et al., 1996). However, as trees age and increase in size, the benefit of reduced leaf construction costs diminishes, as leaves represent a smaller fraction of the total biomass. Simultaneously, the cost of wood construction increases and the higher leaf turnover rate in high-SLA species imposes additional energy demands (Falster et al., 2018). These factors combined ultimately reduce the early growth advantage of species exhibiting high SLA, weakening the relationship between SLA and growth and causing it to become negative in later stages (Gibert et al., 2016). Inversely, among evergreen species, height growth is only very slightly related to SLA across the first 9 years of age, which may in part be due to the narrower range of SLA values in evergreen species (2.7–15 mm^2/mg) compared with deciduous species (10–28 mm^2/mg) (Figure S4). The weak relationships may also reflect SLA measurement errors, which are particularly common in narrow- or needle-leaved species like most evergreens included in this study, due to the lack of a standardized protocol for these specific leaf morphologies (Cornelissen et al., 2003; Wilson et al., 1999). More generally, SLA is also a highly plastic trait both at the population and individual level (Smart et al., 2017), which makes it prone to intraspecific variation. Thus, using mean trait values from individuals growing in different environments may have had a stronger impact on the observed relationship between SLA and growth compared with other traits.

The effects of WD differed markedly between deciduous and evergreen species. In deciduous species, WD effects remained weak throughout and became indistinguishable from zero after the third growing season. In contrast, stronger relationships were found for evergreen species, which remained negative across all periods. This observation agrees with Falster et al. (2018), who predicted a consistently negative relationship between WD and growth based on the fact that trees allocate new biomass to their stems throughout their lifespans. However, the fact that this was prominent only in evergreen species suggests that WD may play a limited role in explaining growth variations in deciduous species, which likely rely more on resource acquisition strategies tied to other traits linked to hydraulic properties or photosynthetic capacity, such as stem hydraulic conductivity and vessel diameter. Support for this comes from the observations that SLA had a substantial effect on the growth of deciduous species, especially in the first period, while the influence of SLA on the growth of evergreen species was much weaker. Similarly, Qi et al. (2021) reported a strong relationship between WD and height growth rates in broadleaved evergreen species in a subtropical forest, whereas WD showed no significant relationship with growth in broadleaved deciduous species. They proposed that the growth of evergreen species might be more closely associated with traits related to leaf carbon assimilation and the construction costs of leaves and stems, such as WD, while the growth of deciduous species appears to be more strongly influenced by stem hydraulic conductivity and vessel diameter. These hydraulic traits are strongly linked to photosynthetic capacity by maintaining the leaf water supply needed to support high rates of leaf gas exchange during a shorter growing season (Brodribb & Feild, 2000; Kaproth et al., 2023). While not explicitly addressed here, given that these traits are considered 'hard' traits and are thus underrepresented in global databases, future research focusing on these relationships could provide valuable insights into the mechanisms driving growth differences across leaf habits.

The effects of LDMC on the growth of deciduous species were similar, although slightly weaker, to those of SLA, especially during the first 6 years of growth. LDMC is calculated by dividing the dry mass of a leaf by its water-saturated fresh mass, whereas SLA is the ratio of a leaf's one-sided area to its dry mass (Cornelissen et al., 2003). LDMC is, as suggested in our hypothesis, typically inversely related to SLA. Thus, the similar effects of SLA and LDMC on the growth of deciduous species during the first 6 years contradict our expectations. Upon further examination, these unexpected results can be largely attributed to *Betula papyrifera*, which exhibited much greater variability in growth rate compared with all other species, particularly during period 0–3 (Figure S5). To further explore this result, we conducted a supplementary analysis by parameterizing an alternative model identical in structure to the *Main model* but excluding *Betula papyrifera*. In this new model, results for period 0–3 aligned with expectations, showing a positive relationship between SLA and growth, and a negative relationship between LDMC and growth. However, the expected contrast between these traits was still not observed during the last two periods (Figure S6). A possible explanation is that *Betula papyrifera*, a fast-growing, early successional species, may simultaneously maximize resource acquisition (high SLA) and resource conservation (high LDMC) in the short term. This dual strategy likely results in exceptionally high growth rates that favour rapid establishment and maximizes early competitive advantage, thus showing atypical responses that do not align with the expected inverse SLA-LDMC relationship. When considering this, the effects of LDMC were much more important for evergreen species. This again supports Qi et al. (2021), that the growth of evergreen species depends more on leaf carbon assimilation and investment in the production of leaves and stems.

The contrasting observations between SM and growth in deciduous versus evergreen species could be interpreted through the lens of the well-established *r-K* continuum. The negative relationship observed in deciduous species across all three periods is consistent with an r-strategy, where small-seeded species exhibit higher initial growth rates. This aligns with our initial hypothesis that small-seeded species need to grow rapidly and become photosynthetically competent before seed reserves are exhausted. The predicted trend also parallels observations by Turnbull et al. (2012), who showed that this relationship tends to weaken over time as smaller trees, by virtue of their size, exhibit rapid early growth. In contrast, evergreen species align more closely with a K-strategy, where larger seeds are associated with faster growth, likely due to the greater reserves that enhance seedling establishment and promote subsequent growth. In our study, the two evergreen oaks (*Quercus suber* and *Quercus ilex*) also exhibited this trend with high SM values (Figure S4) and relatively high early growth rates compared with the other evergreen species. This pattern aligns with broader findings in oaks, where SM generally predicts absolute growth rates but not relative growth rates in juveniles (Cavender-Bares et al., 2004).

4.2 | Investigating leaf habit trends along the fast–slow continuum

The deciduous and evergreen species considered in our analysis appear to follow a fast–slow continuum of resource acquisition and investment, as described in prior studies (Chave et al., 2009; Diaz et al., 2016; Reich, 2014; Wright et al., 2004). Deciduous species displayed faster growth than evergreen species during the first two periods. This faster growth is consistent with deciduous species' typical categorization at the fast-growing end of the continuum, with high photosynthesis rates, rapid resource acquisition and low tissue construction costs. In contrast, evergreen species grew at a slower rate during the first two periods, and started growing faster after the seventh growing season, which aligns with a resource-conserving, slow-growth strategy. Over time, the growth advantage linked to the deciduous leaf habit declined, suggesting that the rapid growth of deciduous species during the seedling stage is not sustained as trees age. After the seventh growing season, growth rates of deciduous and evergreen species appeared to converge, possibly due to ontogenetic patterns of foliage age structure within the canopy or increasing intraspecific competition, which may have been stronger in deciduous species after their initially faster growth. During the seedling stage, the productivity per leaf (i.e. photosynthesis) and the proportion of total plant biomass in leaves are higher in deciduous than evergreen species, which tend to exhibit lower photosynthetic capacity and lower biomass allocation to leaves. However, as evergreen species grow, the accumulation of multiple-year foliage cohorts compensates for lower annual investment in leaf biomass, and growth rates increase. This makes the differences in growth rates between deciduous and evergreen species gradually diminish over the trees' lifespans. Ultimately, large mature trees, regardless of their leaf habit, should grow at similar rates, since deciduous species have much higher productivity per leaf but have less proportional biomass in leaves, while evergreen species have lower productivity per leaf but by that time have accumulated a higher proportional biomass in leaves (Reich, 1998; Reich et al., 1992, 1995). This aligns with findings by Archambault et al. (2019), who observed that seedling-stage evergreen gymnosperms at the IDENT Montreal site allocated a relatively greater proportion of biomass to roots rather than to above-ground structures.

Not only do differences in growth rates of species of both leaf habits diminish as trees age, but we can also expect that overall growth rates of all trees will decline with time, independently of leaf habit. Height growth rates generally slow down continuously as trees get taller, due to a decreasing proportion of total biomass allocated to foliage relative to reproductive structures (Falster et al., 2018). We therefore expect that height growth rates of evergreen species will also decline as trees become taller, following the same hump-shaped relationship with age as in deciduous species, first increasing then decreasing. Thus, while species likely retain their relative positions along the fast–slow continuum regardless of time or size, as observed by Zhu et al. (2018), our expectation that growth rates slow down over time and converge between deciduous and evergreen species necessarily implies a reduction in growth rate variation between these species over time. Consequently, we anticipate that trait–growth relationships will weaken over time, with decreasing variation in their direction as height growth rates level off near maximum height. Nevertheless, a comparison of species' maximum height estimates from the TRY database (Kattge et al., 2011, 2020) with the observed mean height after the ninth growing season shows that trees in our study are still far from reaching their potential maximum, so these predictions have yet to be confirmed.

It is also important to consider that leaf habit conveys information on contrasting life strategies linked to entire syndromes of traits (Reich et al., 1992). In this study, where almost all species belong to temperate biomes (except for species from the Mediterranean IDENT Macomer site), this information can be captured by a binary leaf habit variable. Indeed, there was no overlap in leaf longevity between the two phenological groups for the species considered here (Figure S7). This is consistent with the generalization that species with short-lived leaves are mostly deciduous, while species with relatively long leaf longevity are mostly evergreen (Hikosaka et al., 2021; Reich, 1998). Although this dichotomy should be applied with caution, as links between phenology and leaf structure are not always consistent (Reich, 1995; Reich et al., 1995), the deciduous species considered here all had a leaf longevity shorter than 12 months, and evergreen species all had a leaf longevity of 14 months or more (Figure S7; Kattge et al., 2011, 2020). While using the leaf habit dichotomy was sufficient to capture the contrasting strategies of the species considered here, future studies, including a larger gradient of growing conditions (where leaf longevity values may overlap between deciduous and evergreen species), might benefit from grouping species by functional groups based on differing leaf longevities. In such contexts, leaf longevity could offer a more nuanced and informative gradient of strategies compared with the simplified dichotomy of leaf habit (Reich et al., 1995).

At a broader level, it is worth reiterating that the trait values used in this study were sourced from global databases and represent species-level means. We show that these values remain highly relevant and offer strong predictive power for growth in managed field settings, where interspecific competition is absent. This contributes to a clearer picture of intrinsic trait–growth relationships, establishing a baseline understanding that is not confounded by environmental filtering. However, we could not directly account for intraspecific trait variation, which could play a key role in determining individual and population performance across environmental gradients and developmental stages (Westerband et al., 2021; Williams et al., 2021). Future work incorporating in-situ trait measurements would help refine these patterns and improve our understanding of how functional traits influence tree growth rates in more variable ecological contexts.

5 | CONCLUSIONS

Our analysis is to our knowledge the first to examine trait–growth relationships of trees across both age and leaf habit while controlling for interspecific competition. A central goal of functional ecology is to reliably predict life history, demographic rates and ecosystem functioning using a few easily measurable traits. Using widely available trait data, we observed that the strength and direction of trait–growth relationships vary with tree age and leaf habit, providing evidence against the idea that species follow fixed growth strategies throughout development. Our findings contribute to a growing body of research showing that resource acquisition and investment strategies change with ontogeny and leaf habit, influencing trait–growth relationships. We show that accounting for simple, easily measurable variables, such as age and leaf habit allows functional trait data from global databases to capture these dynamics, highly increasing their capacity to predict demographic rates, such as growth.

AUTHOR CONTRIBUTIONS

Mégane Déziel, Alain Paquette and Rita Sousa-Silva conceptualized the study. Mégane Déziel and Daniel Schoenig designed the methodology. Mégane Déziel curated the data, conducted all analyses with support from Daniel Schoenig, and wrote the initial draft of the manuscript. Alain Paquette, Dominique Gravel, Eric B. Searle, William C. Parker, Jeannine Cavender-Bares, Simone Mereu, Michael Scherer-Lorenzen, Charles A. Nock, Christian Messier, Peter Reich, Artur Stefanski, Ning Dong and Peter Hajek contributed data. Eric B. Searle, William C. Parker and Rita Sousa-Silva provided valuable feedback on the first version of the manuscript, which helped improve its clarity and impact. All authors contributed significantly to revising the following versions of the manuscript.

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ACKNOWLEDGEMENTS

We thank the many individuals who helped with the establishment and upkeep of the experimental sites within the IDENT network, as well as yearly measurements, but we are especially thankful for the important contributions of Cornelia Garbe (Tobner), Simon Bilodeau-Gauthier, Zoé Doucet, Wolf Wildpret, Tobias Gebauer, Leonarda Fadda, Pierpaolo Zara and Elyssa Cameron, as well as Daniel Lesieur and the Centre for Forest Research for maintaining the IDENT database. We also extend special thanks to Michael Belluau, Orane Mordacq and Charlotte Langlois for their help in curating trait data, which was obtained to a large part from the TRY plant trait database. We thank McGill University for access to the Montreal site. The Sault Ste. Marie site is funded by the Ontario Ministry of Natural Resources. The establishment of the Freiburg site was supported by a grant from the University of Freiburg (Innovationsfonds Forschung) to MS-L, in cooperation with Jürgen Bauhus. We also acknowledge an NSERC Discovery fund to AP that made this work possible. JC-B, AS and PBR acknowledge support by the National Science Foundation (NSF-DBI-2021898). We thank the Sardinian Forest authority 'FORESTAS' for hosting and supporting the management of the Macomer site. Data analyses were possible thanks to Calcul Québec and Compute Canada.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.70151.

DATA AVAILABILITY STATEMENT

Code and data used to produce the results are archived on Zenodo (https://doi.org/10.5281/zenodo.16799185) (Déziel et al., 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Upset plot representing the distribution and overlapping of tree species present among the different IDENT experiments considered for period 0–3. Numbers in parentheses next to each species indicate the number of individuals (*n*) sampled across sites. Each intersection on the horizontal axis represents a unique combination of sites where specific species are present, as indicated by filled circles. The number on top of each bar reflects the number of species shared across these site combinations, with species code names displayed on each bar. Species are categorized as deciduous or evergreens.

Figure S2. Upset plot representing the distribution and overlapping of tree species present among the different IDENT experiments considered for period 4–6. (Interpretation as in Figure S1).

Figure S3. Upset plot representing the distribution and overlapping of tree species present among the different IDENT experiments considered for period 7–9. (Interpretation as in Figure S1).

Figure S4. Trait values used to model growth for all species considered, ordered by value and identified as belonging to a deciduous or evergreen species.

Figure S5. Influence of *Betula papyrifera* on the relationship between height growth rate and functional traits (SLA and LDMC) for deciduous trees in period 0–3. Panels (a) and (b) show the relationships between height growth and SLA and when *Betula papyrifera* is included and excluded, respectively. Linear regression lines illustrate that including *Betula papyrifera* shifts the direction of the relationship between growth and LDMC. In the absence of *Betula papyrifera*, the relationship between growth and SLA shows an inverse pattern to that between growth and LDMC, consistent with theoretical expectations.

Figure S6. Predictions from the supplementary model parameterized without the inclusion of *Betula papyrifera* in the data. This figure focuses on the relationships between height growth rate, SLA and LDMC, as the associations with WD and SM were consistent with those observed in the original trait-based model. The primary finding here is the inverse relationship between SLA and LDMC for deciduous tree growth during period 0–3, which aligns with the discussion in the paper. This model helps to clarify the influence of *Betula papyrifera* on the trait–growth dynamics observed in the primary analysis.

Figure S7. Leaf longevity values for all species considered, ordered.

Table S1. Species included in analysis and their associated code.

Table S2. Description and formulas of alternative models. Models are divided into Hypothesis-driven and Baseline categories. Null hypotheses for Hypothesis-driven models are tested by comparing ELPD. Group-level effects are represented in grey.

Table S3. Model performance compared to the *Main model* based on ELPD differences and their standard error.

Table S4. Model performance compared to MH4 based on ELPD differences and their standard error.

Table S5. Prediction intervals of the differences between every combination of period and leaf habit, 5% and 95% percentiles. Absences of substantial differences are marked with †. Focal comparisons indicate the compared effects considered. For example, 'LDMC, Period 0–3, Deciduous vs. Evergreen' can be read as the difference between the LDMC trait effect on deciduous growth and the LDMC trait effect on evergreen growth for period 0–3; 'LDMC, Evergreen, Period 0–3 vs. Period 4–6' can be read as the difference between the LDMC trait effect on evergreen growth at period 0–3 and the LDMC trait effect on evergreen growth at period 4–6.

Table S6. Bayesian hypothesis testing of growth differences across time periods and leaf Habits: Hypotheses were tested using the posterior distribution of regression coefficients from the *Main model*. A hypothesis was considered supported if the posterior probability exceeded 0.95 (equivalent to a 90% uncertainty interval that excludes zero).

How to cite this article: Déziel, M., Schoenig, D., Sousa-Silva, R., Searle, E. B., Parker, W. C., Cavender-Bares, J., Mereu, S., Scherer-Lorenzen, M., Nock, C. A., Messier, C., Reich, P., Stefanski, A., Dong, N., Hajek, P., Gravel, D., & Paquette, A. (2025). Resolving the effects of functional traits on tree growth rates: The influence of temporal dynamics and divergent strategies by leaf habit. *Journal of Ecology*, *113*, 3191–3209. https://doi.org/10.1111/1365-2745.70151