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TITLE

Widespread slow growth of acquisitive tree species

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ABSTRACT

Trees are an important carbon sink as they accumulate biomass via photosynthesis[1], and hence identifying tree species that grow fast is commonly considered essential to effective climate change mitigation through forest planting. Although species characteristics are key information for plantation design and forest management, field studies often fail to detect clear relationships between species functional traits and tree growth[2]. By consolidating four independent datasets and classifying the acquisitive and conservative species based on their functional trait values, we show that acquisitive tree species, which are supposedly fast-growing species, generally grow slowly in field conditions. This discrepancy between the current paradigm and field observations is explained by the interactions with environmental conditions that influence growth. Acquisitive species require moist mild climates and fertile soils, conditions that are generally not met in the field. Conversely, conservative species, which are supposedly slow-growing species, show generally higher realised growth, due to their ability to tolerate unfavourable environmental conditions. In general, conservative tree species grow more steadily than acquisitive tree species in non-tropical forests. We recommend planting acquisitive tree species in areas where they can realise their fast-growing potential. In other regions, where environmental stress is higher, conservative tree species have a larger potential to fix carbon in their biomass.

MAIN TEXT

The potential to mitigate current rates of climate change depends on reducing greenhouse gas emissions and enhancing carbon (C) sinks[3]. Along with oceans, forests constitute one of the two main carbon sinks on Earth[3], but the potential for enhancing forest carbon sinks differs among biomes[4]. Tropical forests are under high anthropogenic pressure with a continuous decline in surface area[5]. Therefore, maintaining their role in climate change mitigation firstly requires protection and restoration[1]. Conversely, despite being threatened by global changes[6], the forested area in temperate and boreal regions is expanding and remains important for climate change mitigation through biophysical effects (evapotranspiration and albedo), carbon storage in soils, standing biomass and wood products[1,4,5,7]. In such a context, sequestering carbon in tree biomass and hence promoting tree species that grow fast may strengthen one of the pathways to increased mitigation. This leads to a key question for managing forests in a global change context: which tree species enable an efficient and sustainable mitigation?

Research in plant ecophysiology has shown in controlled conditions that species able to efficiently acquire resources (sunlight, water, nutrients) generally grow fast[8–10]. These *acquisitive* species are characterised by high values of functional traits involved in resource collection, such as specific leaf area (SLA; for sunlight) and specific root length (SRL; for water and nutrients). Acquisitive species also have high values of functional traits involved in transforming resources into biomass (maximum photosynthetic capacity [A_{max}], and leaf content of nitrogen [N]). Because of their ability to efficiently acquire and transform resources, acquisitive species are commonly considered as being *fast-growing* species in most environments[8,10]. Similarly, species that are more efficient at keeping their internal resources (*i.e.* nutrients, water and energy) than collecting external resources are defined as *conservative* species and are commonly assumed to be *slow-growing* species, except in particularly unfavourable environments. Current knowledge thus suggests that acquisitive tree species should be promoted for mitigating climate change through fast biomass growth, but this paradigm is only partly supported by the literature. We compiled data from 10 independent greenhouse experiments, involving a total of 212 tree species from all biomes, and confirmed the well-established result that seedlings of acquisitive species (*i.e.* with high SLA values) grow faster than conservative species (low SLA values) under favourable conditions of temperature and resource availability (Extended Data Fig. 1). Conversely, while robust growth-trait relationships are observed for seedlings under controlled conditions, studies on adult trees in natural conditions displayed high variability. Even if local- to regional-scale studies identified some growth-trait relationships[11,12], some others found only weak relationships at best[13,14], and studies that compared tree growth in contrasting regions failed to find consistent patterns[2]. This lack of a clear pattern has led some scientists to question whether trait-based studies are a good approach for predicting plant growth[2,15]. The aim of the present study was to evaluate whether acquisitive tree species do really grow fast in the field. The premises of our study are that *(i)* the observed growth-trait relationships are relevant only in environmental conditions favourable to biological activity (*i.e.* moist warm climates and fertile soils)[10,11,16], but *(ii)* these conditions are more and more uncommon due to widespread nutritive limitations and climatic stresses[17–20]. Based on this, and because acquisitive species are resource-demanding and also stress-sensitive[9,21–23], we hypothesised that acquisitive species are often constrained by environmental limitations and consequently do not perform on average better than conservative species (Extended Data Fig. 2). To test this hypothesis, and hence investigate the interactive effects of functional traits, climate and soil on tree growth, we compiled data describing tree growth, functional traits and environmental conditions for 1,262 monospecific stands, distributed in 160 common gardens (hereafter referred to as "sites"), and representing 223 distinct tree species. The consolidated database was composed of four independent datasets that enabled us to test the reliability of results in all forest biomes, all forested continents, and at different tree ages (see Methods): *(i)* the European Atlantic Network (hereafter referred to as EAN), *(ii)* the TreeDivNet network (TDN), *(iii)* a global dataset of stand biomass (SBD), and *(iv)* a dataset containing additional tropical data (TED).

First, we investigated growth-trait relationships without taking into account possible interactions with site conditions. We found that, in non-tropical forests, tree growth showed significant correlations with many functional traits (Extended Data Fig. 3 and 4) such as wood density (Extended Data Fig. 3C), a functional trait that is consistently and negatively associated with growth rate[15,24,25]. We notably found that tree growth was negatively associated with several important traits typically linked to fast growth (*e.g.* SLA, leaf N and P content; Extended Data Fig. 3AEF). This was particularly noticeable for the maximum photosynthetic capacity of tree species (A_{max}: Figure 1 and Extended Data Fig. 5), which is a key trait in plant growth as it integrates the effects of other traits[23,26]. In a second step, following our first premise and because there was large variability in growth-trait relationships (Figure 1 and Extended Data Fig. 5), we investigated the extent to which local conditions influence growth-trait relationships. For this purpose, we analysed the growth-trait-site interactions through random forest models, mixed linear models, and linear modelling of growth-trait correlation values. The analysis of the EAN data showed that drivers of forest growth such as atmospheric N deposition[27], climate[18,28] and soil properties[29] were all highly influential (random forest models; Extended Data Table 1). In these sites, three functional traits had consistent relationships with tree growth across sites, and consequently along environmental gradients (Extended Data Table 2; negative effect: wood density; positive effect: leaf carbon and root phosphorus [P]).

In contrast, some traits (*e.g.* SLA, SRL, leaf N, leaf photosynthetic capacity [A_{max}]) had inconsistent relationships with tree growth (Extended Data Table 2). We considered that these inconsistent relationships may be due growth-trait-site interactions, and investigated such interactions using mixed linear modelling. We found statistically significant growth-trait-site interactions for most functional traits, at worldwide scale and at different development stage of trees (Table 1). Finally, we explored these interactions by studying to which extent the growth-trait relationships depended on local conditions (as approximated by the site productivity, which integrates all environmental constraints on plants). It resulted that, for these traits, both the strength and the direction of the growth-trait relationships depended on the local environment. Notably, if some traits such as wood density had a consistent effect across different environments, as the site productivity increased, the strength of correlation between growth rate and trait value weakened (Figure 2A). This dependency on site conditions was particularly clear for several functional traits, such as A_{max}, SLA and SRL, which previously showed inconsistent effects over sites (Extended Data Table 2). For these traits, which are key for acquiring and using resources, the correlation with growth rate progressively switched from negative to positive with increasing site productivity (Figure 2BCD; Extended Data Fig. 6). We observed this pattern for most traits in the EAN sites (Extended Data Fig. 7) and it was confirmed in three common gardens of the TDN network and four tropical common gardens (Figure 2; Extended Data Fig. 6).

All in all, our results supported our initial expectation that positive relationships between key functional traits and tree growth occur only in field conditions with favourable environments but are uncommon in stressful environments. The discrepancy between an abundant literature based on experiments under controlled conditions (Extended Data Fig. 1) and observations in the field, can thus be explained by ontogenetic effects, functional ecology, and changes in resource allocation. Indeed, for obvious technical constraints, experiments under controlled conditions (often greenhouse experiments) used seedlings as model plants whereas *in situ* studies often focused on saplings or adult trees. Seedlings, saplings and adult trees respond differently to environmental constraints[11,15], which may explain why our results did not align with expectations derived from theory and greenhouse experiments. In addition, greenhouse seedlings were generally grown under conditions with optimal temperature, light intensity, water and nutrient supplies, and with no herbivory pressure. In such non-limiting conditions, acquisitive species are by definition able to acquire resources fast (due to high SLA and SRL) and can in turn produce new biomass quickly (A_{max}, leaf N), defining the concept of *fast-growing species*. Conversely, under unfavourable conditions, plant growth is not limited by C assimilation (as under optimal conditions) but is constrained by the capacity to efficiently use nutrients and water from soils[26] and to endure stress, conditions under which tree species with high trait values (SLA and leaf N) tend to be less efficient[10,22,23,30]. Furthermore, allocation of resources to processes and organs that promote stress tolerance (*e.g.* for defence) and reproduction rather than growth changes the relationship between functional traits and growth[31]. Consequently, conservative species are generally stress-tolerant[10,22,32] that are, on average, able to maintain substantial effective growth under conditions of ambient environmental stress despite trait values (such as low SLA[23,33]) that reduce maximum growth rate. In the field, along gradients of environmental conditions from favourable to stressful, functional traits involved in plant growth shift progressively from beneficial to deleterious. This observed change explains the inconsistency in the literature between greenhouse experiments and field studies[2,15,34].

Based on empirical observations, the current paradigm is that acquisitive species are fast-growing species because they generally outpace conservative species, except in particularly resource-deficient sites (Figure 3A). However, based on common gardens worldwide, our data suggest that the optimal conditions required by acquisitive species are the exception rather than the rule (Figure 3BCD). Indeed, if acquisitive species do perform well in particularly favourable environments[35,36], they are more sensitive to environmental harshness[37,38], whereas conservative, stress-tolerant, tree species perform better in most environments, thus supporting our initial hypothesis that environmental conditions are generally disadvantageous to acquisitive species. In practice, acquisitive species grew on average more slowly in field conditions than conservative tree species (Figure 4ABC), except in tropical regions (Figure 4D). This difference was large in terms of height growth rate for young adult trees (Supplementary Fig. S2AB), and it remained significant in terms of biomass growth and accumulation in mature stands (Supplementary Fig. S2C and S3). Such a persistent difference over time may be partly explained by a similar survival rate at young stages ($P = 0.775$, $\chi^2 = 0.1$, n = 571 EAN stands), and longer lifespan values of conservative species[39] (Extended Data Table 3). Despite this step forward, further research is still needed as several questions remain open (*i.e.* growth-trait interactions with other important processes such as growth-survival-reproduction trade-offs, competition along gradients of productivity, intra-specific variability, inter-specific effects in mixed forests or multi-strata forests). This is particularly the case for tropical forests for which functional traits and ecological strategies have on average less importance than in non-tropical forests (Figure 1; Extended Data Fig. 3), confirming previous studies that found non-significant or minor effect of functional traits –except wood density[40]– on growth rate of tropical trees[12,34,41,42]. This average weak effect is consistent with our main findings since tropical forests generally present favourable climatic conditions and high net primary production (Supplementary Fig. S4). In wet tropical regions, a general positive growth-trait relationship might even have been expected, but tropical forests are often locally limited by water supply or nutrient availability[17,18,43,44], resulting in complex growth-trait-site interactions[35,45]. As such, and based on our tropical data, we posit that local conditions are probably favourable from site to site for acquisitive species or conservative species[35,37,46].

Forests provide many ecosystem services[47] and not only wood production and carbon sequestration. While our findings have implications for carbon sequestration, there remain the other ecosystem services and sustainable silviculture encompass more than just selecting *the fastest growing tree species*. We consequently put forth that our results do not question the general guidelines for sustainable forest management that include, amongst many others, favouring a high level of biodiversity that is an issue for conservation. Biodiversity is an even more important issue because mixing tree species in forests is an efficient lever for increasing carbon sequestration[48] and for improving forest resistance to disturbances and stressors[49]. On the other hand, taking into account the complexity of forest management, this does not mean that favouring certain tree species is not important. Indeed, the change of view regarding the so-called fast-growing species has implications for climate change mitigation through tree growth[7,50]. In tropical regions, where functional traits seem to have a limited influence on tree growth, we posit that protecting forests from degradation[5] remains the priority. Conversely, in non-tropical regions, in order to enhance carbon sequestration in biomass, tree species should not be favoured based on their absolute potential, but by matching them with local conditions, each tree species having its own ecological niche and specific requirements[28]. In a context of promotion for programs of massive tree planting, we stress that the choice of tree species should not rely on a priori expectations but on local forester knowledge. Furthermore, if low-risk strategies for mitigating climate change are a priority, then dedicated approaches should always consider choosing tree species with caution, regardless the other silvicultural options employed. As such, conservative tree species –which are stress-tolerant and long-lived– appear to be a better strategy for fixing carbon than the so-called "*fast-growing*" acquisitive tree species, which generally grow slowly.

METHODS

Experimental networks and tree species.

Our study was based on complementary sets of forest sites (EAN, TDN, SBD, TED), their common features being: *(i)* spread across large-scale geographic regions, and *(ii)* composed of common gardens[51] with at least two different tree species compared. In each common garden, characterised by homogenous conditions, several monospecific stands were installed by planting only one tree species by stand. All stands within a given site were installed and managed identically. In total, tree growth was assessed in 1,262 monospecific stands distributed over 160 common gardens (hereafter referred to as "*sites*") located mainly in Europe, but also in all other forested continents (Supplementary Fig. S5). Together, these sites encompass large ranges of climatic conditions and soil properties (Supplementary Fig. S6 and Table S1). In total, our study comprised the growth data about 223 tree species representing 166 angiosperm species and 57 gymnosperm species, 114 genera, and 42 families (mainly, in decreasing order of abundance: *Pinaceae*, *Fabaceae*, *Fagaceae*, *Myrtaceae*, *Cupressaceae*, *Betulaceae*, *Malvaceae*, *Meliaceae*, and *Sapindaceae*). These tree species are representative of the main plant functional types (*i.e.* broadleaf species: 59% deciduous and 41% evergreen; needleleaf species: 10% deciduous and 90% evergreen). The studied tree species are also representative of the main mycorrhizal symbioses (ectomycorrhizal = 20% and 75% in angiosperms and gymnosperms, respectively; arbuscular mycorrhizal = 65% and 25% in angiosperms and gymnosperms; mixed preference for mycorrhizae = 15% in angiosperms), and included tree species with N-fixing symbioses (20%).

European Atlantic Network (hereafter referred to as EAN)

The EAN, also known as the REINFFORCE experimental network (https://reinfforce.iefc.net/en)[52], is composed of 38 common gardens found across the European Atlantic region. The EAN constitutes a gradient of latitude (38.7-56.5°N) and climatic conditions (Supplementary Table S1), from Portugal to Scotland. The common gardens were installed in 2011-2013 and monitored afterwards with common protocols. Each common garden had ~2000 trees and 37 common tree species (each having several geographical provenances) planted in an area (as flat and homogenous as possible) of about two hectares. All the seedlings were produced in the same nursery at the same time, and their vigour and homogeneity were checked by the coordinators of the network before being sent to the different common gardens. Among the tree species of the EAN, for our study we chose 23 tree species (*Acer pseudoplatanus*, *Betula pendula*, *Calocedrus decurrens*, *Castanea sativa*, *Cedrus atlantica*, *Cupressus sempervirens*, *Eucalyptus nitens*, *Fagus orientalis*, *Fagus sylvatica*, *Larix decidua*, *Liquidambar styraciflua*, *Pinus nigra*, *Pinus pinaster*, *Pinus sylvestris*, *Pinus taeda*, *Pseudotsuga menziesii*, *Quercus ilex*, *Quercus petraea*, *Quercus robur*, *Quercus rubra*, *Robinia pseudoacacia*, *Sequoia sempervirens*, *Thuja plicata*) based on several selection criteria, including: *(i)* species that have enough trait values reported in the literature (*e.g.* leaf nutrient content and photosynthetic capacity), *(ii)* having a diversity of plant functional types (*i.e.* broadleaf species versus needleleaf species, deciduous versus evergreen, early- and late-successional species[53], N-fixing species or not and different mycorrhizal symbioses) and taxonomic families, and *(iii)* species with a good survival rate in the network, implying that species that were planted outside their ecological niche were not retained (*e.g. Ceratonia siliqua* and *Pinus caribaea*; see Appendix 2). We selected only one provenance per species based on several criteria (*e.g.* survival rate, data availability, etc.; Appendix 3), one criterion being that we chose preferably a provenance that was within or close to the European Atlantic region, or (for non-European species) having a climate similar to those of the European Atlantic region. A provenance of a given tree species was not replicated, except for four species (*Betula pendula*, *Cedrus atlantica*, *Pinus pinaster* and *Quercus robur*) that were replicated three times in each common garden. We used these replicates to exclude the common gardens that showed spatial heterogeneity, as quantified by the coefficient of variation of tree growth among replicates of a given provenance (in the retained sites, CV = 26.6 ± 2.7%). We also excluded a few common gardens where catastrophic events (disease problems, exceptional drought just after tree planting, or destruction of most seedlings by dense populations of herbivores), caused very low survival and made it difficult to obtain reliable growth data. Finally, data from three common gardens were merged and considered as one single common garden because these sites were located next to each other (distance < 1 km). All in all, we retained 32 sites. The dataset comprised 139,049 values of total tree height from 18,576 different trees.

TreeDivNet (or Tree Diversity Network, but hereafter referred to as TDN)

The TDN is a global network of forest diversity experiments (https://treedivnet.ugent.be)[54,55]. We selected sites from this network with the following criteria: *(i)* a limited number of sites that were located in the same areas as the EAN to avoid giving a high statistical weight to the European Atlantic region, *(ii)* the tree species included in the experimental design are species for which trait data are available in the literature, and *(iii)* stands were planted before 2010 in order to have growth data on young adult trees (*sensu* ref.[15]). Based on these criteria and the response we received from their principal investigators, we retained 14 sites in Europe and Northern America (Supplementary Table S1). It is noticeable that the TDN sites are often (*i.e.* 10 sites out of 14) located on land that was previously dedicated to agriculture (*i.e.* fertilised croplands or grasslands). In each site, there were 3-12 different tree species, growing in monospecific stands, resulting in 88 site-species combinations. The choice of the planted tree species was made by each site principal investigator, based on knowledge of the ecological niche of tree species, and their suitability to local environmental conditions. Tree species were replicated at least twice in each site (except in one site where there was no replication). The dataset comprised 81,932 tree height measurements from 19,778 different trees.

Stand Biomass Dataset (hereafter referred to as SBD)

The SBD originated from a study[56] that investigated the influence of tree functional traits on soil organic carbon, but which also used stand biomass values when available, as an explanatory variable. After assessing the data suitability, we extracted data from this publication that contained biomass information for 76 sites. We complemented this dataset with biomass values from 28 sites, provided by some authors of the present study or found in recent publications (Appendix 4), giving 104 sites worldwide (Supplementary Fig. S5). In each site, there were 2-14 different tree species growing in monospecific stands (mean value: 3.5 ± 0.2 tree species per site), generally following a common garden design[56]. Stands that were described as unhealthy or containing important canopy gaps were not retained. In total, the SBD represented 359 site-species combinations. Unlike EAN and TDN data that were successive surveys of identified trees, the SBD contained only one survey of aboveground tree biomass at the stand scale. For the SBD, growth rate was estimated as the stand biomass divided by the stand age, and was consequently the mean rate of net biomass accumulation (see below).

Tropical Extra Data (hereafter referred to as TED)

Because the EAN-TDN-SBD data were more representative of Mediterranean forests, temperate forests and boreal forests than of tropical forests, we complemented our study with data about this latter biome through an investigation of the literature. Because field experiments having a common garden design with mature monospecific stands are rare in tropical studies, we used inclusion/exclusion criteria that were more flexible than for our other datasets (*i.e.* growth metric, tree age). We retained six publications (Appendix 4) that contained usable growth data about 10 sites. After having checked that functional trait values existed in the literature (see below), we retained 71 distinct tree species and 196 site-species combinations (Supplementary Table S1). In each TED site, there were 4-37 different tree species (19.6 ± 4.8 species per site) growing in monospecific stands.

Data about tree growth.

Tree growth data in the EAN and TDN were based on surveys of young adult trees, enabling the quantification of growth rate in post-sapling stages. On the other hand, the SBD compiled information about aboveground net biomass accumulation during adult tree ageing. Finally, the TED were informative of growth dynamics of tropical tree species at different tree development stages (from saplings to adult trees). Thus, these independent datasets were complementary to each other, as it is well-established that the ontogenetic stage is an important factor driving trait-growth relationships[57,58].

Tree growth values were calculated based on the difference between two surveys at the tree scale for EAN and TDN data, on one survey at the stand scale for SBD data (by dividing the stand biomass value by the stand age), and on the available metric for TED.

Tree height growth (EAN, TDN)

The quantification of tree growth rate was based on tree height, a variable that was monitored in all common gardens (contrary to other metrics such as biomass, volume, or stem diameter). Growth rate values (cm yr^{-1}) were calculated as the difference in tree height between two surveys (each carried out during the dormant season for vegetation), taking into account the number of growing seasons between the two surveys. This method was compared with a method that estimates tree growth simply as the height:age ratio and found good consistency ($r = +0.97$). Nevertheless, we preferred to quantify tree growth based on two surveys because it enables excluding the period after plantation (*i.e.* 1-2 years), which is often problematic for seedlings (the so-called "*transplant shock*"). We chose the final survey based on available data for each site, trying to find a trade-off between the quantity of available data and the duration of growth (*i.e.* the time difference between the two surveys). The measurement period was generally between 3 and 9 years (41 sites) but was shortened to 1-2 years when necessary (5 sites). Taking into account the start of monitoring, growth data were mainly representative of young adult individuals (37 sites where age > 5 yrs; ontogenetic stage defined by ref.[15]), with a small proportion of saplings (9 sites; 1 yr < age ≤ 5 yrs), but no seedlings (0 site; age ≤ 1 yr).

Before analysis, data were curated with several quality controls. Notably a few negative values of tree growth were observed so we removed these trees, which apparently "*shrank*" probably due to dieback of their top (~4% of trees). In the case of multi-stemmed trees (~2% of trees), we selected the height value of the tallest stem as the tree height value. We also removed a few site-species combinations for which not enough surviving trees remained (*i.e.* n < 5). In the EAN dataset, we observed that some trees (~12%) died after the second survey retained in our study. For each site, we tested the extent to which these nearly dying trees might have biased our results, for instance due to a depressed growth rate before death. Comparing growth rate values with or without these nearly dying trees showed that there was a significant difference (Dunnett test on ratio values, and linear regression analysis testing for both zero intercept and unit slope) for only one common garden when growth rate was assessed in original values (*i.e.* cm yr^{-1}), and that there was no difference at all when standardised values were used (see § Data analyses). Based on these tests, we decided to not remove trees that died after the second survey, except for the common garden mentioned above. After all these quality checks, growth rate was estimated for each site-species combination as the arithmetic mean height growth value of all trees.

Stand Biomass Dataset (SBD)

The SBD contained data of standing aboveground biomass (in $Mg_{\text{-dry weight}}$ ha^{-1}). Considering the tight allometric relationships that exist among tree structural components (stem, stump, branches, roots etc.)[59–62], we assumed that aboveground biomass was well-representative of stand total biomass. This dataset is based mainly on quite old common gardens (46 ± 3 years; 25-63 years between the first and third quartiles) for which generally only one survey of biomass measurements was available. When needed, stand aboveground biomass was estimated using –specific or generic[63]– allometric relationships. The estimated values were evaluated using an independent dataset[64] and showed satisfactory consistency (Supplementary Fig. S7). Growth rate was calculated by dividing standing aboveground biomass by stand age. Because there was no information about tree mortality, SBD growth rate (in Mg ha^{-1} yr^{-1}) was the mean rate of net biomass accumulation.

Tropical Extra Data (TED)

While growth data were homogeneous in other datasets (*i.e.* $cm_{\text{-height}}$ yr^{-1} for EAN+TDN, Mg ha^{-1} yr^{-1} for SBD), growth data for TED used several metrics (relative growth rate, $cm_{\text{-height}}$ yr^{-1}, $cm_{\text{-diameter}}$ yr^{-1}, kg $tree^{-1}$ yr^{-1}). This limitation implied that, contrary to other datasets (which could be used with original values and mixed linear modelling to explore growth-trait-site interactions; see below § Data analyses), TED data were used mainly for growth-trait relationships.

Trait data

The functional traits that were studied in our four datasets are known to be key traits in plant functioning[65–67]: plant maximal height (m), plant longevity (years), successional-stage (integer from 1 to 5; from pioneer species to climax species), seed mass (mg; log-transformed to avoid data skewness), wood density (mg cm^3), foliage and root element content (C, N, P, Ca; mg g^{-1}), specific leaf area (SLA; mm^2 mg^{-1}), maximum photosynthetic capacity (A_{max}; µmol g^{-1} s^{-1}) and specific root length (SRL; m g^{-1}). We used mass-based values of A_{max} and foliage composition but not area-based values because the former generally explain plant growth –and functioning in general– better than the latter[26,68–70].

Trait values were obtained from a previous global scale study of 178 different tree species[56]. To fill the data gaps, we first complemented this database with trait values (if any) found in the publications containing our growth data, and in 76 publications and a few specialised websites (Appendix 5). Wood carbon values were extracted from an open database[71]. When several values existed for a trait-species combination, we retained the mean value. In a second step, we measured traits for the 23 tree species of the EAN. To do this, we sampled one common garden (in south-western France) for mature foliage (n=36 per species), living branches (n=3 per species) and living fine roots (n=6 soil cores; roots of < 2 mm in diameter). Samples were analysed (C, N, P, Ca; for foliage and roots) and measured (WD, SLA, SRL) following standard methods[72,73]. Data obtained from field samplings showed satisfactory consistency with the initial database[56] (r=+0.55 to +0.95 for WD, SLA and element contents in leaves; regression slope values were close to 1) and we kept the measured values for our study. For four tree species of the EAN (*Calocedrus decurrens*, *Cedrus atlantica*, *Eucalyptus nitens*, *Fagus orientalis*) we had no A_{max} value, so in the field we also measured their maximum photosynthetic capacity under good conditions (cumulated precipitation in the week before sampling = 34.5 mm; soil water content during measurements ~ 60-70% of the soil water holding capacity; vapour pressure deficit = 0.64-1.38 kPa; air temperature = 16-25°C; photosynthetically active radiation > 1500 µmol m^{-2} s^{-1}; data from the XyloSylve monitoring platform, 1.5 km from the common garden). Finally, for genera with several tree species, we complemented trait values by replacing missing values by the mean value of their genus, provided that at least two values were available and that they had a similar magnitude. This latter gapfilling represented a small proportion of trait values (proportion of estimated values for a given tree species: median = 0%; mean = 5%).

Trait values were generally highly interrelated (Supplementary Fig. S8), which is a common pattern in functional ecology[11,56,74,75] as plant functions are dependent on each other, implying trade-offs and high levels of correlation among traits[32,65,67,76–79]. Due to this strong interplay among functional traits[23,80], and because data about nutrient content of fine roots were scarce for tree species of TDN and SBD, we restrained the use of most root traits to EAN results. Trait value distribution was comparable among datasets (Supplementary Table S2).

Site data

We collected auxiliary data related to factors (hereafter referred to as "*site properties*") that may affect tree growth, notably climate, atmospheric nitrogen (N) deposition, past land-use and soil properties. At the site scale, the collected information was: site name and location (longitude and latitude), elevation, mean annual values of temperature and precipitation (MAT, MAP), past land-use and fertilisation history (information provided by the principal investigator of each site), soil name and soil parent material, topsoil clay or sand content, and other topsoil properties (*e.g.*, pH, cation exchange capacity and its "base" saturation value, total content of phosphorus, soil organic carbon content [SOC] and its ratio with total nitrogen [C/N], and soil water holding capacity). Original site data were obtained differently for our four networks of common gardens: EAN site data were obtained using a shared protocol and soil analyses were carried out at a single laboratory. Data about TDN sites (and the few SBD sites that complemented the original dataset) were provided by the principal investigator of each site, when requested data were available. Data of most SBD-TED sites were extracted from publications[56], with the same availability limitation. This process of data acquisition implied that site data were homogeneous in the EAN dataset whereas they contained a varying proportion of missing values and there were some heterogeneities in the methods used (*e.g.* for soil phosphorus analyses) for TDN, SBD and TED.

Due to missing auxiliary data in the TDN-SBD-TED datasets (climate, elevation and soil properties), we complemented them from external sources using the latitude-longitude coordinates of the sites.

Similarly, we used global datasets to include variables that were never measured in the field (*e.g.* atmospheric N deposition). The data sources used were taken from the literature (N deposition[81]; soil properties[82,83]) or from large scale databases. Elevation values were obtained from the Enhanced Shuttle Land Elevation Data (https://www2.jpl.nasa.gov/srtm). For climatic variables, we collected data for mean annual values of precipitation or temperature (MAP, MAT; http://worldclim.org), potential evapotranspiration and aridity index (https://cgiarcsi.community). For sites in Europe, we also collected climate data from the Climate Downscaling Tool (https://www.ibbr.cnr.it/climate-dt), from the B4EST European project (https://b4est.eu), which enables one to work with scale-free queries, customised periods (for this study: the period of tree growth in our datasets) and many other variables (*e.g.* sum of degree-days above 5°C). The B4EST climate values were consistent with those obtained from other sources and were also consistent with data from the XyloSylve monitoring platform. The quality of the external sources was checked by comparing them with the measured values (when they existed) and showed acceptable consistency for most variables ($r = +0.67$ to $+0.90$ for MAT, MAP, soil pH and soil clay or sand content; regression slope values were close to 1) but not for some soil properties (*e.g.* P content or cation exchange capacity), which was in line with previous large-scale studies[17,84]. We observed a high level of covariation among several collected site variables. For instance, MAT was highly correlated with potential evapotranspiration (PET; $r = +0.84$), sum of degree-days above 5°C ($r = +0.85$) and mean temperature during the growing season ($r = +0.90$). Similarly, the soil water holding capacity was strongly controlled by soil clay content ($r = +0.86$) and sand content ($r = -0.82$). Because highly-correlated variables can bias methods of model selection[85], we retained only a few variables to describe climatic conditions: MAT and MAP (which are commonly used in ecology[86–89]) and the "*climate factor*" index (hereafter referred to as f_{climate})[90]. The climate factor index is based on monthly climatic conditions of a given site, and increases with concomitant water availability (*i.e.* precipitation:PET ratio) and warm temperatures (Supplementary Fig. S9), conditions that favour biological activity[91] and tree growth[17]. This f_{climate} index is normalised between 0 (harsh conditions) to 1 (optimal conditions)[17] and has already been tested at national or global scales[17,91,92]. We applied the same parsimonious approach for soil data, retaining clay content, SOC content, P content, C:N ratio and pH as explanatory variables. In addition to continuous climatic variables, we used a categorical approach to assess the influence of biomes on growth-trait relationships. In practice, we grouped all sites into three classes based on their latitude absolute value: *tropical sites* (|latitude| ≤ 23°), *high-latitude sites* (|latitude| ≥ 45°; ≈ cold sites[93]) and *intermediate sites* (≈ warm temperate sites).

With the scope of discussing our results in a global perspective, we finally collected data for all forests worldwide. Net primary production (NPP) of terrestrial ecosystems was retained using TERRA/MODIS data (https://neo.gsfc.nasa.gov/view.php?datasetId=MOD17A3H_Y_NPP). We averaged the annual NPP of all grid cells based on the 2010s decade. We also calculated the f_{climate} index at the global scale. To enable relevant comparisons with our results about forests, we kept in global data only cell grids having at least 90% of their surface area covered by forest ecosystems (land-use data: ref.[94]).

Data analyses

Identifying the factors influencing site productivity

We first explored the drivers of tree growth with data from the EAN, because these are derived from common gardens sharing the same studied tree species and protocols (29 sites with enough data). The influence of functional traits (*e.g.* leaf N content), site properties (*e.g.* MAT, soil pH) and site productivity were assessed using three independent approaches (see below). We defined site productivity as the arithmetic mean value of the mean growth rate (cm yr^{-1}) of the n tree species studied in this site:

$$\text{Eq. (1):} \qquad site\ productivity = \sum_{i=1}^{i=n} species_i\ mean\ growth\ rate/n$$

The three approaches for data analysis were: *(i)* mixed linear models (*lme4* R package[95]; assigning the site identity as a random effect), *(ii)* linear models based on AIC for the selection of the best model (*ols_step_forward_aic* function of the *olsrr* package[96]) and *(iii)* non-linear "*random forest*" analyses (*randomForest* package[97]). For the latter, we followed a backward elimination method[98] to select by iterations the best random forest model, which consists of eliminating the least important variables until out-of-bag prediction accuracy drops. The importance of each variable in the retained model is assessed based on the percentage increase of Mean Squared Error (%IncMSE). The threshold value above which a variable is considered as important is not consistent among studies using the random forest approach[99,100] and consequently we defined four levels of confidence to interpret our results: *low* (2% ≤ %IncMSE < 5%), *moderate* (5% ≤ %IncMSE < 10%), *high* (10% ≤ %IncMSE < 20%) and *very high* (%IncMSE ≥ 20%). Considering all tree species of the EAN together, soil C:N ratio and f_{climate} were the most influential factors of site productivity (Extended Data Table 1).

We quantified site productivity of TDN and SBD using the same method as EAN (equation 1). Because TDN data (and data from a few TED sites) had the same metric of tree growth as EAN data (*i.e.* tree height growth, in cm yr^{-1}), we were able to present merged results (*i.e.* EAN+TDN+TED). Because the growth metric of SBD was different (in Mg ha^{-1} yr^{-1}) these results were consequently presented separately. Contrary to other datasets, we could not calculate site productivity in all TED sites because the growth metric varied from site to site. Therefore, for some TED sites, only growth-trait relationships were investigated and no growth-trait-site interaction was tested.

Standardising growth rate

Tree growth rate obviously does not depend on functional traits alone, but is also strongly dependant on site properties (*i.e.* local climate and soil fertility)[18,29,101–104]. Indeed, when we investigated the main factors influencing tree growth, all our results confirmed foresters' knowledge that site productivity was the main factor controlling species growth: site productivity was selected first by a mixed linear model ($\chi^2 = 63.2$), a predictive linear model (contribution to explained variance = 29.1 %) and a non-linear random forest model (%IncMSE = 55.3%). In addition, site productivity was much more predictive than the other variables (e.g. leaf C:N, leaf C, wood density) selected by these three models ($\chi^2 = 22.0$; explained variance = 10.4 %; %IncMSE = 34.2%). To remove the prominent influence of site productivity and hence to enable comparisons among species across all sites, we standardised the original values of tree species growth. To do so, we tested two different approaches: the z-score[105] and a log growth ratio (see equation 2). The two metrics were highly correlated to each other (r = +0.86), but the log growth ratio metric was more suitable for our data because *(i)* the z-score cannot be calculated for sites with only two tree species (Appendix 6) and *(ii)* the values transformed as log growth ratios showed better distributions as evaluated by normality tests (Lilliefors and Shapiro-Wilk tests[106]) and QQ plots. We consequently standardised the original values using the log growth ratio metric, which consisted in dividing the absolute values of tree species growth by the site productivity value. This ratio was then log-transformed (natural logarithm)[107]:

Eq. (2): $$log\ growth\ ratio = log\left(\frac{individual_{value}}{population_{arithmetic.mean}}\right) = log\left(\frac{species\ growth\ rate}{site\ productivity}\right)$$

The log growth ratio metric is very similar to the centered log-ratio metric[108], the later using the geometric mean instead of the arithmetic mean. We preferred to use the arithmetic mean because *(i)* the geometric mean might be biased if one single value of the studied population is nil or very close to zero (which happens sometimes when comparing the growth rate of different plant species), and *(ii)* the arithmetic mean is consistent with the site productivity metric (equation 1).

Positive standardised growth rates (*i.e.* log growth ratio values) indicate that these species had a higher growth rate than the average growth of the site, and negative standardised values indicate a lower growth rate than average for the site. For a few tree species that grew extremely slowly compared with the other species within the same site, this formula led to very negative values of standardised growth, with skewness problems of data distribution. Consequently, we corrected extreme values of standardised growth to -2.0 based on assessments of data distribution (histograms; Shapiro-Wilk tests).

An example of a data subset is presented, showing how the transformation of growth values removed the relationship between tree species growth and site productivity (Supplementary Fig. S10AC). An example of relationships between a functional trait and growth is also presented (Supplementary Fig. S10BD). It should be noted that standardisation of values was done for subsets of data with no missing value implying that, when there was a missing trait value for a tree species of a given site, the growth values of this site were standardised without taking into account this tree species (see an example in Supplementary Table S3). It is also noticeable that the method used for data standardisation, while improving statistical power, enabled the study of interactions with possible confounding factors[109] (see below).

Defining acquisitive species and conservative species

Because trait values constitute ecological gradients[23,110,111], continuous data analyses are adequate to test our hypothesis (see next section). Nevertheless, in order to test our hypothesis, we used in addition categorical analyses by classifying tree species into *acquisitive species* or *conservative species* based on their trait values. Tree species were considered as acquisitive species if they have high values of photosynthetic capacity (A_{max}), SLA and leaf N content[10,23,26]. We prioritised A_{max} to class tree species because this trait is integrative of plant functioning[23,26,112]. For tree species without an A_{max} value, we used the SLA value or the leaf N value instead. The procedure enabled the classification of 212 tree species, representing 98.3% of growth data (~87%, ~10% and ~1% of data based on A_{max}, SLA and leaf N, respectively). In practice, however, there is no functional threshold value between acquisitive species and conservative species as they are distributed along trait gradients[23,110,111]. Following previous studies[113], we defined our species classes based on value distributions of our global database of functional traits. We defined acquisitive species and conservative species, with limit values close to median values (A_{max} = 0.1 μmol g^{-1} s^{-1}; SLA = 13.3 mm^2 mg^{-1}; leaf N content = 19.3 mg g^{-1}). Although these threshold values are consistent with the distributions reported in other studies carried out at the global scale (Figures 2 in ref.[110,111]), we performed a sensitivity analysis to assess to which extent changing the chosen values may affect our results (see below).

With this trait-based classification, acquisitive species tended to be represented more in broadleaf deciduous species than in needleleaf evergreen species, whereas conservative species included both broadleaf species and needleleaf species (Extended Data Table 3; Appendix 7). Similarly, both groups contained arbuscular mycorrhizal species and ectomycorrhizal species. Although there was no significant difference in shade tolerance and both groups contained early-successional species (*e.g. Pinus* species and *Betula* species), acquisitive species were on average characteristic of earlier successional stages than conservative species. Finally, acquisitive species were shorter-lived than conservative species, which is consistent with how different ecological functions (*i.e.* growth, survival, reproduction) are coordinated in woody plants[39].

Investigating site-trait interactive effects on tree growth

We expected that the role of functional traits in tree growth was neither unidirectional (*i.e.* always positive or negative) nor systematic (*i.e.* the traits correlated with tree growth were not systematically the same across different regions), but that it depended on environmental conditions[12,35,58,114]. To investigate these possible site-trait interactions, we used three complementary approaches: *(1)* interactions were statistically tested using mixed models[45], *(2)* interactions were visually illustrated by regressing linear models between site productivity and growth-trait correlation values, and *(3)* the slope values of the regression between site productivity and standardised growth were compared for acquisitive species and conservative species.

(1) Mixed models were fitted on standardised values to remove the prominent effect of site productivity (see equation 2) and hence enable comparisons among sites. The mixed models were built with site identity and tree species identity as random factors, as follows:

Eq. (3): $$growth \sim trait + \left(trait \times site_{prod.}\right) + (1|site_{id.}) + (1|species_{id.})$$

with $site_{prod.}$ = site productivity (eq. 1); $site_{id.}$ = site identity; $species_{id.}$ = species identity.

(2) For common gardens where it was possible to quantify a site productivity metric (in cm yr^{-1}) and that included at least 10 different tree species, we graphically illustrated the extent to which the influence of trait values depended on site productivity by regressing a linear relationship between site productivity and the [species growth-trait value] correlation value of the same site:

Eq. (4): $$corr\{growth_{species} - trait\} = f(site\ productivity)$$

with $corr\{growth_{.species}\text{-}trait\}$ = correlation value (Pearson method) between species growth rate and species trait value; correlations being performed site by site.

This case corresponded to all EAN sites and a few sites from TDN and TED. Nevertheless, it was not possible to include TDN and TED r values to fit the linear regression because the probability of having by-random high r values tends to increase with decreasing size of data[115,116], implying that correlations obtained from TDN (10-12 species per site) or from TED (up to 34 species per site) were not directly comparable to correlations obtained from EAN (23 tree species per site). Nevertheless, even if TDN and TED r values were not used along with EAN r values to statistically test the interactions between site properties and growth$_{.species}$-trait relationships, in the graphs we added the results from the TDN-TED sites that contained at least 10 tree species.

(3) We tested whether the functional traits and site properties interactively influenced tree growth by comparing the slope value of the relationship between site productivity and tree growth (in standardised values), taking into account our two tree species classes (*i.e.* acquisitive versus conservative, with

respectively high and low values of A_{max}, SLA and leaf N). To do so, we built one linear regression model with interaction with site productivity, and a second model without interaction (using *aov* function). Then, the two regression models were compared using covariance analysis (using *anova* function). We concluded that a site-trait interaction existed if the slope of the regression was significantly different between the acquisitive tree species and the conservative tree species. For this approach, sites that included only acquisitive species, or only conservative species, we not taken into account in data analyses.

Analysing possible misleading effects or confounding effects in data analyses

Assessment of the datasets

The first three datasets that were built (EAN, TDN, SBD) are complementary in terms of tree age and climatic conditions. Because the collected data lacked tropical data, a fourth dataset (TED) was built to supplement the three others, and the final data were representative of all climates (Supplementary Fig. 11). Nevertheless, although the TED dataset was useful as complementary data, it is less homogeneous as it is based on several growth metrics (see above) and it includes sites having very different number of tree species (Supplementary Fig. 12). The TED results, when presented independently from other data, should consequently be interpreted with caution.

In addition, even as a data supplement, we combined cautiously TED data with other data. In most cases, we found no risk of biasing the results. An exception was the study of the interaction between site productivity and growth-trait relationships in young sites. Indeed, two sites showed being much more productive than the rest of the studied population (Supplementary Fig. 13). Because outliers of a predictor variable may induce spurious correlations[116,117], these two sites were not used during data analyses implying possible interactions with site productivity.

Interactions with tree age

It is well-established that tree growth rate varies as a function of tree age (*e.g.* ref.[118]) and we consequently tested this possible effect. For the young stands (EAN and TDN datasets; age at tree measurement = 3-24 yrs), we found no significant effect ($P > 0.1$), neither considering site productivity (mixed model: $P = 0.555$, $t = +0.60$, $df = 21.5$) nor considering tree growth at the stand scale ($P = 0.788$, $t = -0.27$, $df = 31.0$). We also checked if an interaction with tree species might exist by plotting the growth-age curve for each of them, and found no clear trend. We finally concluded that there was no substantial age effect in our data about young trees.

In contrast, data about mature stands showed a clear age effect on tree growth (Supplementary Fig. S14A). This effect had no influence on results when data were standardised because the standardised values are species growth rate (or species trait value) that are relative to the site productivity (eq. 2). Conversely, the age effect may affect the results when the site productivity is used as a predictor (eq. 3; see also Table 1 and Figure 3D), and we corrected growth values in these cases. To do so, we first fitted a non-linear regression between forest age and productivity (Supplementary Fig. S14A). The Modelling Efficiency value of the fitted regression was 0.46 (ref.[119]). Then, we calculated a standardised growth rate, using 40 years-old as a reference (which was close to the mean age value of SBD stands = 41.8 yrs):

Eq. (5): $$growth_{.40} = growth_{fitted.40} \times \left(\frac{growth_{original}}{growth_{fitted}}\right)$$

With $growth_{.40}$ = growth estimated at 40 years-old; $growth_{fitted.40}$ = value of the regression at age 40 yrs ($growth_{fitted.40}$ = 4.446 Mg ha^{-1} yr^{-1}); $growth_{original}$ = growth original value; $growth_{fitted}$ = value of the regression at the actual age of the stand.

The distribution of the corrected values is presented in the Supplementary Fig. S14B.

Intra-specific differences

Different populations of a given tree species may differ in terms of trait values and growth rate because of genetic differences and plasticity to local conditions[120]. In the present study, the effect of intra-specific variability was not quantified, as the inter-specific influence on growth was the main topic. Although it is well-established that intra-specific variability exists, it is also observed that inter-specific variation can be much larger than the intra-specific variation[121,122]. As such, retaining only the mean trait value of each plant species is considered as a relevant and reliable approach in large scale studies[2,110,111,122–124], even with partly imputed data[74,125]. In the present study dedicated to inter-specific variation, the coefficient of variation (CV) of trait values was 25% for wood density and ranged from 42% to 78% for the acquisitive-conservative traits (A_{max}, SLA, SRL, leaf N and P). Conversely, intra-specific variation of traits was found to range from 9% to only 22% of CV for wood density, SLA, leaf N and leaf P[126–128], confirming that inter-specific variability is larger than intra-specific variability in multi-species studies. Another possible problem is the variability of trait values over plant development[129] because some trait values found in the literature or trait databases were determined using seedlings and not adult trees[130]. However, it was also shown that trait values at seedling stage are well-correlated with trait values at adult stage[131], implying that inter-specific rankings are maintained over ontogenic development[132].

We used EAN data to evaluate the possible effect of intra-specific variability on tree growth. Indeed, each EAN site contains for each tree species up to eight different provenances. We found that intra-specific variability of tree growth was ~4-fold lower than inter-specific variability (CV = 17% and 66%, respectively), indicating that the inter-specific effect on tree growth was much more important than intra-specific variations. This result is in line with a recent study[133] showing that provenance is generally a second-order driver of tree growth.

Based on these results, the literature results and on published guidelines[134], we concluded the intra-specific variability of trait values (or of growth rate values) likely had a minor effect on our results.

Ecological niches

One possible pitfall in studies based on common gardens is that some tree species might be planted outside their ecological niche (*i.e.* unfavourable climatic/edaphic conditions), biasing the species growth dynamics. This possible bias was taken into account *(i)* during the design definition of most common gardens, *(ii)* during data acquisition, and *(iii)* after data acquisition:

At least for the common gardens of the EAN and TDN networks, the principal investigators (who are co-authors of the present study) chose tree species not at random but based on their ecological requirements, implying that the planted tree species were expected to be adapted to local conditions.

During data acquisition, we excluded a few tree species with low survival rate (EAN-TDN common gardens) or described as unhealthy (SBD-TED; see above § Experimental networks and tree species).

Finally, we tested a possible niche effect using our data and quantitative information about ecological niches. To do so, we studied the 23 tree species of the EAN network, which is a network with a factorial design (*i.e.* all tree species are present in all sites). For each tree species, we collected the surface area of the natural niche of the species and (for MAT, MAP and soil pH) the ranges of the species in natural conditions. This data collection was made based on information found in dedicated websites and publications (Appendix 8). Then, for each species-site combination, we evaluated if the trees were within or outside their niche by checking if the site conditions (MAT, MAP, soil pH) were within or outside the range of values reported for the species in natural conditions. We also tested if the ecological range of the tree species (as defined as $\{MAT_{max} - MAT_{min}\}$, and so on for MAP, soil pH) might explain tree growth. We found that: (1) in a majority of cases, tree species were planted in sites where environmental conditions were suitable for them (see percentage values in panels A-D of Supplementary Fig. S15), (2) trees planted in sites where conditions did not comply to the expected species requirements did not growth differently as compared with trees planted in suitable conditions (Supplementary Fig. S15A-D), (3) tree species with large ranges of ecological niche did not growth faster than tree species with narrow niches (Supplementary Fig. S15E-G), (4) tree species with large spatial niche did not perform better than tree species from small regions (Supplementary Fig. S15H), and (5) there was a slight, but significant negative effect of the MAP range value on standardised tree growth (Supplementary Fig. S15F). The latter result is mainly due to three tree species with large MAP range (caused by very high MAP_{max} values; > 2000 mm yr^{-1}) but, having on average, lower standardised growth rate than the other tree species. Although this MAP range effect was significant, it explained less than 1% of the growth variance ($R^2 = 0.7\%$) and became not significant when considering tree species with $MAP_{max} \leq 2000$ mm/yr (cf. red line in panel F), which is the most common case for temperate-boreal tree species. As a whole, we concluded that the ecological requirements of the studied tree species were fairly well-respected and we consequently assumed that the results of the study were not severely biased.

Possible phylogenetic effect

Two tree species may be functionally very different because their most recent common ancestor existed in a far past, enabling its descendants to evolve differently for long times. As such, phylogeny may be a powerful predictor of plant species functioning[123,135] and, in our case, may have explained tree growth better than functional traits. We tested this possible effect for the EAN dataset because this network has a factorial design. We built a phylogenetic tree for the 23 species of the dataset, which included closely related species (*e.g.* species of the same genus) and evolutionary distant species (*e.g.* angiosperms and gymnosperms). The phylogenetic distance between two species was estimated based on the approach of the *most recent common ancestor*. The distance between angiosperms and gymnosperms was fixed as 350 Myr and the distance between *Cupressales* and *Pinales* was set at 273Myr[136]. Within the gymnosperms, the distances among clades down to genera were estimated based on a dedicated study[137]. Similarly, within the angiosperms, we used first the phylogenetic distances among families[138]. For shorter phylogenetic distances (*e.g.* between genera of the same family or between two species of the same genus), we used the Angiosperm Phylogeny Website and relevant references[137,139–141]. We calculated the phylogenetic distance of all possible pairs of tree species ($n = \sum_{i=1}^{i=23}(i-1)$), and then we tested to which extent this distance might explain tree growth and trait values. Using a linear plateau regression (R package *nlraa*), we found that the phylogenetic distance had an effect for tree species that were close to each other in the phylogenetic tree (*i.e.* distance < 98-137 Myr). However, this effect was weak and explained only a very small proportion of the variance, from 1% (for leaf Amax, wood density, or SRL; data not shown) to 5-11% (for SLA or leaf N-P; Supplementary Fig. S16). These results are consistent with previous studies showing that phylogeny often poorly explains functional traits, site properties or ecosystem functioning[56,142,143]. Based on these results and on the literature we concluded that, in our study, there was a significant but minor effect of the phylogeny on tree growth.

Possible spermatophyte effect

Our datasets comprise both angiosperm species and gymnosperm species. These two groups are evolutionary and functionally quite different[144–148], which might have induced apparent growth-trait correlations without any true functional relationships. We tested this possible effect by investigating to which extent the growth-trait relationships were observable within a spermatophyte group (*i.e.* only angiosperms or only gymnosperms). We found that growth-trait relationships were generally still significant for most traits (Supplementary Fig. S17ABD). Similarly, within the angiosperm group, acquisitive species and conservative showed the same growth trends as for the complete dataset, which was a significantly higher growth rate of the conservative species (Supplementary Fig. S17F; not tested within the gymnosperm group due to an insufficient number of acquisitive species). Conversely, the growth trait relationships were no longer significant, or significant only for angiosperms, for some other traits (Supplementary Fig. S17CE). These results are consistent with studies that explored plant functioning across plant functional types and found weaker or absent relationships for gymnosperms[149–151]. This pattern can be explained by the level of functional diversity within each group: for six major traits (A_{max}, SLA, SRL, wood density, leaf N and P), the range of values was between 59% and 215% higher for angiosperm species than for gymnosperm species (see also Figure S3 in ref.[149] and Figure 1 in ref.[150]). These ranges of values in the gymnosperm group were probably too narrow for some functional traits to enable isolating a significant growth-trait relationship. Besides, this explanation may also apply to leaf nitrogen (Supplementary Fig. S17C) as the data dispersion showed that the overlap between angiosperm data and gymnosperm data was small (38% of the full range, as compared with 53-63% for SLA or leaf P), suggesting that the general effect observed for leaf nitrogen was induced by the comparison of two functionally different clades. As a whole we conclude that, in agreement with the literature[124,149,150], whereas the angiosperm-gymnosperm dichotomy strengthens existing function-trait relationships by enlarging the ranges of trait values, these relationships generally remain relevant within a spermatophyte group.

Sensitivity of results to the retained threshold values

We tested the extent to which changing the threshold values retained for classifying tree species (acquisitive species versus conservative species, based on A_{max}, SLA or leaf N content) would change our results. First, for each of these three traits, we quantified the difference between the percentile 40% and the percentile 60%, which represents the part of a normal distribution where values change most (hereafter referred to as "*max change range*", MCR). In a second step, we defined the ranges of sensitivity analyses by adding or subtracting the MCR value to the threshold value initially retained. This resulted in large changes to the population size of the species classes (up to 3.0-fold; n = 250-747 stands of conservative tree species). These results explain why we did not use larger ranges of sensitivity analyses because the compared classes would have been extremely unbalanced in size, with deleterious effects on the stability of the results. The large changes to the population size of the species classes also highlight that the acquisitive-conservative status of the tree species of the present study should not be used alone for management decisions. Indeed, if a dichotomous classification was useful for data analyses, tree species are distributed along ecological and functional gradients, with many species having intermediate positions.

We finally performed the sensitivity analyses by testing the difference between tree species (acquisitive species versus conservative species) with varying threshold values (n = 5, including the value initially retained as median value). The results showed that the results were satisfactory, with quite stable slope values (Supplementary Table S4A) and a constant difference of growth rate between acquisitive species and conservative species (Supplementary Table S4B).

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DATA AVAILABILITY

The data generated in this study have been deposited in the https://entrepot.recherche.data.gouv.fr database under accession link https://doi.org/10.57745/3OIGHB (Etalab Open License 2.0, compatible CC-BY 2.0).

CODE AVAILBILITY

The main R procedures that were used have been deposited in the https://entrepot.recherche.data.gouv.fr database under accession link https://doi.org/10.57745/3OIGHB. Complementary information can be provided by authors on request.

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AUTHOR CONTRIBUTIONS

L.A. initiated the study and L.A. & M.C. designed it. L.A., M.C. and L.B. collected and curated data, with a particular support from R.B, C.O. and N.GB. (EAN data) and A.B. (SBD data). Trait data were collected and consolidated by L.A., R.B., M.C. and MR.B. N.G-B., and A.A-G. provided soil data from the EAN. All other authors provided data about tree growth from their respective common gardens.

L.A., M.C. and R.B. made the first analysis and interpretation of data. L.A. wrote the first version of the manuscript, with the contribution of M.C. and R.B. Then L.A. revised the successive following versions of the manuscript with contributions from all authors, particularly M.C., R.B., MR.B., MJ.G., B.M., C.M. and C.O.

COMPETING INTERESTS

R.B. is employed by a company that works with landowners to implement projects of reforestation or afforestation worldwide. F.J.S-P. and M.J.R-L. occasionally advise foresters or landowners. All other authors declare that they have no competing interests.

ADDITIONAL INFORMATION

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