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TITLE

Generalised slow growth of fast growing tree species

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ABSTRACT

Trees are an important carbon sink as they accumulate biomass via photosynthesis[1]. Identifying tree species that grow fast is commonly considered essential to effective climate change mitigation through forest planting. Although the functional traits that influence tree growth are well-understood[2], field studies often fail to detect clear growth-trait relationships at the global scale[3]. By consolidating three independent datasets and classifying the fast- and slow-growing species based on their functional traits values, we show that tree species which are supposedly fast-growing, due to their trait values, generally grow slowly in field conditions. This discrepancy between the theory and field observations is explained by the interactions with environmental conditions that influence growth. Fast-growing species appear to require both moist and mild climates and fertile soils, conditions that were generally not met in the field. Conversely, slow-growing species showed generally higher realised growth, due to their ability to tolerate unfavourable environmental conditions. In general, stress-tolerant and supposedly slow-growing tree species commonly grow more steadily than supposedly fast-growing tree species. We recommend encouraging fast-growing tree species only in areas that can really support their high potential growth. In most regions, characterised by stressful conditions, the supposedly slow-growing species appear to have a higher potential to fix carbon in their biomass.

MAIN TEXT

Our capability to mitigate current rates of climate change depends on the reduction of greenhouse gas emissions and greater carbon (C) sinks[4]. Along with oceans, forests constitute one of the two main carbon sinks on Earth[4], but the potential for enhancing forest carbon sinks differs among biomes[5]. Tropical forests are under high anthropogenic pressure with a continuous decline in surface area[6,7]. Therefore, maintaining their role in climate change mitigation firstly requires protection and restoration[1,8]. Conversely, despite being threatened by global changes[9–11], forested area in temperate and boreal forests is expanding and remains important for climate change mitigation through biophysical effects (evapotranspiration and albedo), and carbon storing in soils, standing biomass and wood products[1,5,6,12–16]. 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 is all the more an option as the functional traits that enable fast growth have already been identified in experiments under controlled conditions[2,17–24], making possible to identify *fast-growing* plant species[25] characterised by high values for several traits (such as maximum photosynthetic capacity [A_{max}], specific leaf area [SLA] and leaf content of nitrogen [N]). Nevertheless, although strong growth-trait relationships were observed for seedlings under controlled conditions, studies on adult trees in natural conditions display high variability. Even if local- to regional-scale studies identified some growth-trait relationships[21,26–30], some others found only weak relationships at best[31–35], and studies that compared tree growth in contrasting regions failed to find consistent patterns (excepted for wood density). This lack of clear pattern led some scientists to question whether trait-based studies are a good approach for predicting plant growth[3,36,37]. The aim of the present study was to question whether theoretically fast-growing 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 and mild climates, fertile soils)[21,38], but *(ii)* these conditions are more and more uncommon due to wide-spreading nutritive and climatic stresses[39–42]. Based on this, and because fast-growing species are also resource-demanding species and stress-sensitive species[17,19,25,43,44], we hypothesised that fast-growing species are often constrained by environmental limitations and consequently do not perform on average better than slow-growing species. 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 1,041 monospecific stands, distributed in 139 common gardens (hereafter referred to as "sites"), and representing 153 distinct tree species. The consolidated database was composed of three independent datasets that enabled us to test the reliability of results in different contexts and at different tree ages (see Methods): (i) the European Atlantic Network (hereafter referred to as EAN), (ii) the TreeDivNet network (TDN), and (iii) a global dataset of stand biomass (SBD). To avoid confusion, we put forth that the concept of fast- and slow-growing tree species refer here to their potential growth rate as predicted by their functional trait values, but not to their effective growth rate realised in field conditions. In other words, a tree species that is expected to grow fast based on its high trait values (hereafter referred to as *fast-growing*$_{\text{(TD)}}$ *species*; TD for "trait-defined") may actually have a slow effective growth in field conditions.

Considered individually, many functional traits showed a significant correlation with tree growth rate (Figure S1 and S2). Since these relationships were consistently observed among independent datasets, it suggests they are representative of a majority of forest areas. The negative relationship between growth rate and wood density (Figure S1C) was in line with current knowledge[26,35,37,45–48]. Conversely, we found that tree growth was negatively associated with several important traits typically linked to fast growth (*e.g.* leaf N content, SLA, and specific root length [SRL]; Figure S1ABE), contradicting the growth-trait theory and empirical observations in controlled environments. This is particularly noticeable for the maximum photosynthetic capacity of tree species (A_{max}: Figures 1 and S3), which is a key trait in plant growth as it integrates the effects of other traits[44,49].

Following our first premise, and because there was large variability in growth-trait relationships (Figures 1 and S3), we investigated further the extent to which local conditions influence growth-trait relationships. For this purpose, we classed the 139 sites based on soil properties, or on climatic conditions. These two classifications showed that the negative growth-trait relationships were strong under conditions unfavourable to biologic activity (*i.e.* soil high C:N or dry/cold climate) but did not exist under favourable conditions (Figure 2). A more in-depth investigation of these interactions was carried out using sites including at least 10 tree species and data about tree height growth (*i.e.* the complete EAN series). The analysis of the EAN data showed that drivers of forest growth such as atmospheric N deposition[50–52], climate[40,53–60], and soil properties[61–63] were all highly influential (Table S1). In this subset of sites, three functional traits had consistent relationships with tree growth across sites, and consequently along environmental gradients (Table S2; negative effect: wood density; positive effect: leaf carbon and root phosphorus [P]). By contrast, some traits had inconsistent (SLA, leaf P, and root N), or even contradictory relationships (tree max height, leaf photosynthetic capacity [A_{max}], leaf N, and SRL), with tree growth (Table S2). For these traits, both the strength and the direction of the growth-trait relationships depended on the local environment. To quantify local environment, we used site productivity as a proxy because it integrates all environmental constraints on plants. This confirmed that traits with a consistent effect across different environments, such as wood density or root P, maintained the same growth-trait relationship along the site productivity gradient. Nevertheless, as the site productivity increased, the strength of correlation between growth rate and trait value weakened (*e.g.* wood density in Figure 3A). This dependency on site conditions was also clear for several other key functional traits, such as A_{max}, SLA and SRL, which previously showed inconsistent effects over sites (Table S2). For these traits, the correlation with growth rate progressively switched from negative to positive with increasing site productivity (Figure 3BCD; Figure S4). We observed this pattern for most traits in the EAN sites (Figure S5) and it was confirmed in three common gardens of the TDN network (Figures 3 and S4). Using a categorical approach, we further investigated to what extent these interactions also existed in our other datasets (*i.e.* remaining TDN data and SBD, for which there was no direct estimation of site productivity): sites were grouped as "favourable" or "unfavourable" based on their soil and climate (*i.e.* soil C:N ratio and f_{climate} index, as in Figure 2). We found that these interactions were common and that the growth-trait relationships were generally stronger under unfavourable conditions (*i.e.* high soil C:N ratio or low f_{climate} value) than under favourable conditions (Figure S6).

All in all, our results supported our initial expectation that positive relationships between key functional traits (A_{max}, leaf N, SLA and SRL) 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, and observations in the field, can 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[21,37,64–66], 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. In such non-limiting conditions and resources, plant species that are able to acquire resources fast (due to high SLA and SRL) are favoured 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 acquire, to efficiently use nutrients and water from soils[49], and to endure stresses, conditions under which tree species with high trait values (SLA and leaf N) tend to be less efficient[43,44,67–69]. 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[70]. Consequently, the so-called slow-growing$_{\mathrm{(TD)}}$ species are stress-tolerant species[43,71,72] that are able to maintain substantial effective growth under conditions of ambient environmental stress despite trait values (such as low SLA[44,73]) 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[3,35,37].

Our initial aim was to investigate the extent to which the trait-defined fast-growing species really do grow fast outside of controlled experiments involving seedlings under non-limiting conditions. Our results indicate that fast-growing$_{\mathrm{(TD)}}$ tree species can indeed grow fast in field conditions, but this only occurs when environmental conditions support high biological activity[74–76]. Based on empirical observations, the current paradigm is that fast-growing$_{\mathrm{(TD)}}$ species generally outpace slow-growing$_{\mathrm{(TD)}}$ species, except in particularly resource-deficient in sites (Figure 4A). As a matter of fact, based on 139 sites, our data suggest that the optimal conditions needed by fast-growing$_{\mathrm{(TD)}}$ species are the exception rather than the rule (Figures 4BCD). Indeed, if fast-growing$_{\mathrm{(TD)}}$ species do perform well in particularly favourable environments, they are more sensitive to environmental harshness[77–80], whereas stress-tolerant tree species perform better in most environments, thus supporting our initial hypothesis that environmental conditions are generally disadvantageous to fast-growing$_{(TD)}$ species. In practice, fast-growing$_{(TD)}$ species grew on average more slowly in field conditions than other tree species (Figures 5). This difference was large in terms of height growth rate for young adult trees (Figure S7AB), and it remained significant in terms of biomass accumulation in mature stands (Figure S7C) despite higher wood density values of fast-growing$_{(TD)}$ species (Table S3). Such a persistent difference over time may be partly explained by similar survival rate at young stages ($P = 0.775$, $\chi^2 = 0.1$, $n = 571$ EAN stands), and longer lifespan values of slow-growing$_{(TD)}$ species (Table S3). As biomass of slow-growing$_{(TD)}$ tree species is more concentrated in carbon (Table S3), it indicates that these stress-tolerant tree species sequester on average even more biomass carbon than fast-growing$_{(TD)}$ tree species. Furthermore, because tree species having trait values typical of slow-growing$_{(TD)}$ species store more soil organic carbon[81], it suggests that this kind of tree species are highly efficient at sequestering carbon under unfavourable conditions at the ecosystem scale.

Forests provide many ecosystem services[82–85] such as microclimatic regulation, biodiversity preservation, air and water purification, soil protection and water regulation, improved social and mental well-being, and not only wood production and carbon sequestration. While our findings carry implications for carbon sequestration, it remains that the other ecosystem services require specific management practices and that sustainable forest management encompasses more than just selecting *the fastest growing tree species*. We consequently put forth that our results do not put into question general guidelines for sustainable forest management that are, among others, limiting physical disturbances, lengthening harvest rotations, maintaining a continuous vegetation cover, and favouring a high level of biodiversity. The latter recommendation is of particular importance since biodiversity is at the same time an issue for conservation and an efficient lever for increasing carbon sequestration[81,86] and forest resistance to disturbances and stresses[87,88]. On the other hand, taking into account the complexity of forest management does not mean that favouring certain tree species is not important. Indeed, the change of view regarding the so-called fast-growing$_{(TD)}$ species has implications for climate change mitigation through tree growth[15]. In order to enhance carbon sequestration in biomass, tree species should not be favoured on the basis of their absolute potential, but by matching them with local conditions, each tree species having its own ecological niche and specific requirements[60]. In a context of promotion for programs of massive tree planting, we stress that the choice of tree species should rely not on a priori expectations but on local forester knowledge and on local tree species. Furthermore, if low-risk strategies for mitigating climate change are a priority, then stress-tolerant tree species appear to be a better strategy for fixing carbon than trait-defined fast-growing species.

METHODS

Experimental networks and tree species.

Our study was based on three complementary sets of forest sites (EAN, TDN, SBD), their common features being: *(i)* spread across large-scale geographic regions, and *(ii)* composed of common gardens[89] with at least two different tree species compared. In each common garden, characterised by homogenous conditions, several monospecific stands were installed by planting one different tree species by stand. All stands within a given site were installed and managed identically. In total, tree growth was assessed in 1,041 monospecific stands distributed over 139 common gardens (hereafter referred to as "*sites*") located mainly in Europe, but also in all other forested continents (Figure S8; for more details, cf. section Data availability). Together, these sites encompass large ranges of climatic conditions and soil properties (Figure S9, Table S4). In total, our study comprised the growth data about 153 tree species representing 99 angiosperm species and 53 gymnosperm species, 61 genera, and 27 families (mainly, in decreasing order of abundance: *Pinaceae*, *Fagaceae*, *Fabaceae*, *Myrtaceae*, *Cupressaceae*, *Betulaceae*, *Sapindaceae* and *Meliaceae*). These tree species are representative of the main plant functional types (*i.e.* deciduous broadleaf = 37%; evergreen broadleaf = 28%; deciduous needleleaf = 3%; evergreen needleleaf = 32%), including nitrogen-fixing species (14%). The studied tree species are also representative of the main mycorrhizal symbioses (ectomycorrhizal = 30% and 79% in angiosperms and gymnosperms, respectively; arbuscular mycorrhizal = 48% and 21% in angiosperms and gymnosperms; mixed preference for mycorrhizae = 22% in angiosperms).

European Atlantic Network (hereafter referred to as EAN)

The EAN, also known as the REINFFORCE experimental network (https://reinfforce.iefc.net/en)[90], is composed of 38 common gardens displayed along the European Atlantic region. The EAN constitutes a gradient of latitude (38.7-56.5°N) and climatic conditions (Table S4), 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 36 common tree species (each having 3 geographical provenances) planted in an area (as flat and homogenous as possible) of around two hectares.

Among the 36 tree species of the EAN, we chose for our study 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 three selection criteria: *(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[91], 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*). We selected only one provenance per species based on several criteria (*e.g.* survival rate, data availability, etc.), 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 (hereafter referred to as TDN)

The TDN is a global network of forest diversity experiments (https://treedivnet.ugent.be)[92,93]. 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.[37]). Based on these criteria and the response we received from their principal investigators, we retained 14 sites in Europe and Northern America (Table S4). It is noticeable that the TDN sites are often (*i.e.* 10 sites among 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[81] 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 checks on data quality, we extracted data from this publication that contained biomass information for 76 sites. We complemented this dataset with biomass values from 16 sites, provided by some authors of the present study, giving 92 sites worldwide (Figure S8). In each site, there were 2-14 different tree species growing in monospecific stands (mean value: 3.6 ± 0.2 tree species per site), generally following a common garden design[81]. Stands that were described as unhealthy or containing important canopy gaps were not retained. In total, the SBD represented 334 site-species combinations. Unlike EAN and TDN data that were successive surveys of identified trees, the SBD contained only one survey of tree aboveground biomass at the stand scale. The SBD did not provide growth rate values because mortality rate was generally not known, but indicated the integrative response of tree species to local conditions in terms of growth and survival, that is standing biomass.

Data about tree growth and biomass.

Tree growth data in the EAN and TDN were similar, as these experimental networks are both based on successive surveys of young adult trees, enabling the quantification of growth rate in post-sapling stages. As such, these datasets were handled using a similar methodology. On the other hand, the SBD compiled comparisons of standing aboveground biomass of different mature tree species, and consequently this dataset was handled differently. The SBD gave information about biomass accumulation during adult tree ageing. Thus, the three independent datasets were complementary to each other, as it is well-established that the ontogenetic stage is an important factor driving trait-growth relationships[64,94].

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. When possible we excluded surveys that were carried out during the two years after planting, because this period just after planting 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 years 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.[37]), 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. 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 "*moribund*" trees might have biased our results, for instance by having a depressed growth rate before death. Comparing growth rate values with or without these moribund 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 absolute values (*i.e.* cm yr^{-1}), and that there was no difference at all when relative values were used. 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.)[95–98], we assumed that aboveground biomass was well-representative of stand total biomass. This dataset is based mainly on quite old common gardens (46 ± 2 years; 26-56 years between the first and third quartiles) for which it was not possible to calculate growth rate of tree individuals, as in the EAN and TDN data. Instead, growth rate was here estimated assuming that standing biomass was a good proxy of forest net growth[99,100], at least in forests that are not over-mature[101].

Trait data

The functional traits that were studied in our three datasets are known to be key traits in plant functioning[47,102,103]: plant maximal height (m), plant longevity (years), successional-stage (integer from 1 to 5, which is 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 and not area-based values because the former generally explain plant growth –and functioning in general– better than the latter[49,68,104].

Trait values were obtained from a previous global scale study of 178 different tree species[81]. To fill the data gaps, we first complemented this database with values found in 46 publications and a few specialised websites (Appendix 1). Content values were extracted from an open database[105]. 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 root) and measured (WD, SLA, SRL) following standard methods[106,107]. Data obtained from field samplings showed satisfactory consistency with the initial database[81] (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 (https://www.anaee-france.fr/en/infrastructure-services/in-natura-experimentation/foret/xylosylve)). 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 gap-filling 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 (Figure S10), which is a common pattern in functional ecology[21,81,108,109] as plant functions are dependent on each other, implying trade-offs and high levels of correlation among traits[71,102,103,110–113]. Due to this strong interplay among functional traits[44,114], and because data about nutrient content of fine roots were scarce for tree species of TDN and SBD, we restrained the use of root traits to EAN results. Trait value distribution was comparable among datasets (Table S5).

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 three 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 sites were extracted from publications[81], with the same availability limitation. This process of data acquisition implied that site data were homogeneous in the EAN dataset whereas they contained a various proportion of missing values and there were some heterogeneities in the methods used (*e.g.* for soil phosphorus analyses) for TDN and SBD.

Due to missing auxiliary data in the TDN and SBD 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[115]; soil properties[116,117]) 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 consistent with previous large-scale studies[39,118]. 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 ($r = -0.82$). We retained only a few variables to describe climatic conditions: MAT and MAP (which are commonly used in ecology[53–56]), and the "*climate factor*" index (hereafter referred to as f_{climate})[119] because highly-correlated variables can bias methods of model selection[120]. 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 temperature (Figure S11), conditions that favour biological activity[121]. This f_{climate} index is normalised between 0 (harsh conditions) to 1 (optimal conditions)[39]. We applied the same parsimonious approach for soil data, retaining clay content, SOC content, P content, C:N ratio and pH as explanatory variables.

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:

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

The three approaches for data analysis were: *(i)* mixed linear models (*lme4* package[122]; assigning the site identity as a random effect), *(ii)* predictive linear models with iterations, based on AIC for the selection of the best model (*ols_step_forward_aic* function of the *olsrr* package[123]), and *(iii)* non-linear "*random forest*" analyses (*randomForest* package[124]). For the latter, we followed a backward elimination method[125] to select by iterations the best random forest model, which consists of eliminating 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[126,127] 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 influencing factors of site productivity (Table S1).

TDN data had the same metric of tree growth as EAN data (*i.e.* tree height growth, in cm yr^{-1}), that is why we quantified productivity of TDN sites using the same method as for EAN sites (Equation 1). This approach was less reliable for TDN data as the tree species were not the same in all sites (as it was the case in EAN sites). We assumed however that this possible bias had a small impact on results because the number of tree species in each TDN site was reasonably high (Table S4).

Contrary to EAN and TDN data, we could not calculate site productivity in SBD data because the growth metric was different (*i.e.* stand aboveground biomass, in $Mg_{\text{-dry weight}}\ ha^{-1}$). We consequently used a surrogate by calculating a site suitability index based on soil C:N and f_{climate}, which were identified as the main drivers of EAN sites productivity (see equations in § *investigating site-trait interactive effects on tree growth*).

Defining relative growth rate

Tree growth rate obviously does not depend only on functional traits but also strongly on site properties (*i.e.* local climate and soil fertility)[40,57,59,61–63]. Indeed, when we investigated the main factors influencing tree growth, all our results confirmed foresters' knowledge that site productivity was the main factor controlling tree 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 second variable 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 transformed the absolute values of tree species growth (cm yr^{-1}) to relative values of growth. This was done by dividing the absolute values of tree species growth by the site productivity value. This ratio was then log-transformed (natural logarithm):

$$\text{Eq. (2):} \qquad relative\ species\ growth = log\left(\frac{absolute\ value\ of\ species\ mean\ growth\ rate}{site\ productivity}\right)$$

Positive relative growth rates indicate that these species had a higher growth rate than the average growth of the site, and negative relative values indicate a lower growth rate than average for the site. Nevertheless, 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 relative growth, with skewness problems of data distribution. Consequently, we corrected extreme values of relative growth to -2.0 based on assessments of data distribution (histograms; Shapiro-Wilk tests). An example of a data subset is presented in Figure S12 that shows how the transformation of growth values removed the relationship between tree species growth and site productivity (Figure S12AB). An example of relationships between a functional trait and growth is also presented (Figure S12CD).

Defining slow-growing species and fast-growing species

In order to compare the effective growth rates of the so-called fast-growing (or slow-growing) species, we classified tree species, not based on the observed growth rate, but based on their trait values (hereafter referred to as "*trait-defined*" classes of tree species; TD = trait-defined). Tree species were considered as fast-growing$_{(TD)}$ species if they have high values of photosynthetic capacity (A_{max}), SLA, and leaf N content[44,49]. We prioritised A_{max} to class tree species because this trait is integrative of plant functioning[44,49,128]. For tree species without an A_{max} value, we used the SLA value, or leaf N value instead. The procedure enabled to class 142 tree species, representing ~99% of growth data (~93%, ~5% and ~1% of data based on A_{max}, SLA and leaf N, respectively). In practice, however, there is no functional threshold value between slow-growing$_{(TD)}$ species and fast-growing$_{(TD)}$ species as species are distributed along trait gradients[44,129,130]. Following previous studies[25], we defined our species classes based on value distributions of our global database of functional traits. We defined fast-growing$_{(TD)}$ species and slow-growing$_{(TD)}$ species, with limit values equal to rounded 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}). These threshold values are consistent with the distributions reported in other studies carried out at the global scale (Figures 2 in ref.[129,130]).

With this trait-based classification, fast-growing$_{(TD)}$ species tended to be represented more in broadleaf deciduous species than in needleleaf evergreen species, whereas slow-growing$_{(TD)}$ species included both broadleaf species and needleleaf species (Table S3; Appendix 2). Similarly, both groups contained arbuscular mycorrhizal species and ectomycorrhizal species. Although there was no significant difference of shade tolerance and both groups contained early-successional species (*e.g. Pinus* species and *Betula* species), fast-growing$_{(TD)}$ species were on average characteristic of earlier successional stages than slow-growing$_{(\mathrm{TD})}$ species. Finally, fast-growing$_{(\mathrm{TD})}$ species live shorter and have more dense wood than slow-growing$_{(\mathrm{TD})}$ species.

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 depends on environmental conditions[29,36,64,74]. To test these possible site-trait interactions, we used two approaches, depending on data structure:

(1) 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 investigated the extent to which the influence of trait values depended on site productivity, and this was done by regressing a linear relationship between site productivity and the [species growth-trait value] correlation value of the same site:

Eq. (3): $$corr\{growth_{species} - trait\} = f(site\ productivity)$$

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

This case corresponded to all EAN sites and three sites from TDN. Nevertheless, it was not possible to compare r values from EAN directly with TDN because the probability of having by-random high r values tends to increase with decreasing size of data[131], implying that correlations obtained from TDN (10-12 species per site) were less reliable than those from EAN (23 tree species per site). Nevertheless, even if TDN r values were not used along with EAN r values to statistically test the interactions between site properties and growth$_{.\mathrm{species}}$-trait relationships, in the graphs we added the results from the three TDN sites that contained at least 10 tree species.

(2) For the common gardens that did not fulfil the conditions described above (which corresponded to all SBD data and the TDN sites with only 3-8 tree species), we assessed the site-trait interactive effect on tree growth using two approaches: a categorical analysis (2a), and a continuous analysis(2b). In the categorical approach (2a), we grouped sites into two classes of site productivity (hereafter referred to as "*favourable*" and "*unfavourable*"). Site productivity values were not available for most sites, so we considered site properties that are known to commonly influence plant growth: past land-use[50], soil properties such as soil phosphorus content[132] and climate. We retained neither past land-use nor soil phosphorus content as factors defining site productivity because this information was unfortunately not available for many sites. Instead, the soil C:N ratio is known for most of our sites, and has been identified as a reliable predictor of forest productivity[63]. In addition, soil C:N ratio appeared to be a good predictor of site productivity in the EAN (Table S1 and significant correlation: $r = -0.44$, $t = -2.67$, $P = 0.012$), probably because of its influence on soil N cycling and bioavailability[133,134]. Therefore, we retained this variable as a reliable proxy of productivity in TDN data and SBD data. For clarity and concision, we restrained the site properties to only one soil descriptor (*i.e.* soil C:N ratio) and one climatic descriptor (*i.e.* f_{climate}), which is also consistent with the interactive effects of soil properties and climate on

functional traits[135]. The rationale of f_{climate} selection is that, contrary to MAP or MAT, it combines information about both water availability and warmth, and has already been tested at national or global scales[39,121,136]. The values of these site properties used to separate the low- and high-productivity sites were defined as follows. The topsoil C:N threshold value was fixed as 12, which corresponds to a value that well separates typical forest soils (with high C:N values) from croplands, afforested croplands, and fertile sites (with low C:N values)[137–140]. The f_{climate} threshold value was fixed as 0.40, which separates dry or cold climates from milder climates[39]. Based on these threshold values, it appeared that a majority of our studied sites were unfavourable to tree growth (Figure S13). We then tested whether the slope of the growth-trait relationship (in relative values) was influenced by the site productivity class by building a regression model with interaction with the studied site descriptor, and a second model without interaction (using *aov* function). Then, the two regression models were compared using ANCOVA (using *anova* function). We concluded that a site-trait interaction existed if the slope of the regression was significantly different between the low-productivity class and the high-productivity class.

In the continuous approach (2b), we calculated an index of site suitability to biological activity. This way done by normalising and combining values of soil C:N ratio and f_{climate}:

Eq. (4): $$CN_{index} = min\left(1;\left({}^{12}\!/_{soil\ C:N}\right)\right)$$

Eq. (5): $$Climate_{index} = min\left(1;\left({}^{f_{climate}}\!/_{0.40}\right)\right)$$

with 12 and 0.40 being the threshold values in the categorical approach for soil C:N and f_{climate}.

Eq. (6): $$Site\ suitability = CN_{index} \times Climate_{index}$$

The site suitability index is a proxy of site productivity as it quantifies the site capacity to support a high biological activity. The site suitability index is normalised and ranges from 0 (extremely unfavourable conditions) to 1 (particularly favourable conditions). In the EAN dataset, site suitability is highly correlated to site productivity ($r = +0.53$, $t = 4.0$, df = 30, $P = 0.002$).

Analysing the sensitivity of results to the retained threshold values

We tested to what extent changing the threshold values retained for classing sites (favourable versus unfavourable, based on soil C:N ratio and f_{climate}), or for classing tree species (slow-growing$_{\text{(TD)}}$ versus fast-growing$_{\text{(TD)}}$, based on A_{max}, SLA or leaf N content) would change our results. We first quantified for each of these five factors 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; *e.g.* for soil C:N ratio, MCR ≈ 2). In a second step, we defined the ranges of sensitivity analyses by adding or subtracting the MCR value to the threshold value initially retained (*e.g.* for soil C:N ratio, range of analysis = 12 ± 2 = 10-14; Table S6A). Doing so led to make varying to a large extent the population size of site classes (up to 2.9-fold; n = 159-466 stands in unfavourable sites, based on soil C:N ratio) and species classes (up to 2.7-fold; n = 242-663 stands of slow-growing$_{\text{(TD)}}$

species). These results explain why we did not use larger ranges of sensitivity analyses because it would have implied comparing classes with extremely unbalanced size, with deleterious effects on results stability.

We finally performed the sensitivity analyses by testing the difference between site classes (favourable versus unfavourable) and between tree species (slow-growing$_{(TD)}$ versus fast-growing$_{(TD)}$) with varying threshold values (n = 5, including the value initially retained as median value; *e.g.* for soil C:N ratio: 10, 11, 12 {retained}, 13, 14). The results showed that the comparison between sites was stable despite varying values of soil C:N ratio (Table S6A). Although the lower part of the tested range for f_{climate} showed non-significant slope difference, the results were stable in term of slope values and the slope difference remained significant in the upper part of the range (Table S6B). Regarding tree species, the results were also satisfactory, with quite stable slope values (Table S6C) and a constant difference of growth rate between slow-growing$_{(TD)}$ species and fast-growing$_{(TD)}$ species (Table S6D).

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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. analysed data and interpreted results. 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 the contributions of all authors.

COMPETING INTERESTS

R.B. is employed by a company that works together 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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