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TREE GENETICS (M MENCUCCINI, SECTION EDITOR)

Trade-offs and Trait Integration in Tree Phenotypes: Consequences for the Sustainable Use of Genetic Resources

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Abstract

Purpose of Review In this review, we synthesise current knowledge on trade-offs among traits in key fitness dimensions and identify major research gaps with the intention of laying the groundwork for a rapid advance in tree breeding for multiple objectives as a key contribution to the sustainability of planted forests in the future.

Recent Findings Trade-offs among growth, reproduction, defence, stress tolerance and product quality predicted theoretically have been reported experimentally in many breeding programmes. Among these trade-offs, the genetic linkage between resistance against biotic threats and growth (or other relevant traits) is particularly critical for the current and future management of forest genetic resources. Maintaining tree growth and wood quality in the novel environments of the future requires the assessment of genetic correlations of target traits with phenology, closely linked to survival to temperature extremes. Improving our current knowledge on the genetic trade-offs of drought tolerance as a breeding objective in forest trees obligates a more precise definition of both the specific traits and the experimental conditions. Published evidence suggests that common target traits in breeding programmes may trade-off with reproductive success and fire-adaptation, and the simultaneous improvement of growth and wood quality traits still remains as a constraint in traditional tree breeding.

Summary Changing environments combined with pests and diseases are challenging plantation forestry worldwide, which implies an urgent need to develop new improvement strategies to build the resilience of forestry for our future environments. It is essential to have a better understanding of how traits interact, especially those important for production, climate and biotic threat resilience, but much of the information is still missing. Since many key trade-offs are affected by the environment, we need new studies under novel environments to forecast levels of multi-trait integration in breeding populations.

Keywords Trade-offs · Phenotypic integration · Breeding · Forest trees · Resilience · Global change

Introduction

When science-based silviculture started in Europe a few centuries ago, the main objective was optimising timber production, namely stem growth, in even-aged stands. Nowadays, the objectives of silviculture have broadened considerably to include multiple ecosystem services [1•] while the sustainability of plantation forestry faces a major challenge from climate-change driven abiotic stress combined with pests and diseases in many countries [2•].

Selection of improved genetic material has delivered important increases in wood production and quality, but shifts in the environments to which improved genetic materials have been adapted will disrupt the productivity relationships on which current plantation management models are based. Recently, tree breeding has broadened the suite of considered traits to resistance to abiotic or biotic factors in addition to those related to wood quality [3]. While most current breeding lines implicitly incorporate some tolerance to endemic pests and diseases (i.e.

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good productivity typically means having survived such challenges even if the trait is not explicitly selected for), the new biotic threats are driving a push for rapid discovery of tolerant genotypes (Table 1). Few of the existing advanced genetic improvement programmes for the main timber species address biotic stresses, and from now on, breeding populations will need to be monitored constantly for changes in abiotic-biotic interactions arising both due to climate change and emerging and invasive organisms [4••].

Trade-offs (i.e. balancing of goals all of which are not attainable at the same time) are a key concept in adaptive evolution because they occur at every level of biological organisation, from molecular and cellular processes to organismal and ecological functions. Since organisms are complex, integrated systems, trade-offs necessarily emerge due to the concomitance of multiple traits [5••]. Life history theory postulates the existence of trade-offs between fitness functions that are expressed as costs in survival, growth and reproduction [6]. Both individual tree and population fitness depend on a wide number of interacting traits, which are also highly dependent on the environment. Since natural selection acts on trait combinations [7•], both genetic correlations between traits and functional constraints may curtail the genetic variation for each individual trait [8, 9].

At the population level, trade-offs arise from the evolutionary history of the populations in response to different drivers [10]. At the individual level, limited resources and energy budget are thought to limit the investment in one function with respect to another, for example, higher investment in reproduction one year may reduce reproductive investment the next year or result in reduced survival [11]. Thus, direct selection on one trait can lead to indirect selection on covarying traits if they share a genetic, developmental or physical basis [12•]. These trade-offs with a genetic basis are the priority from an evolutionary and breeder perspective [13] (Fig. 1).

A genetic correlation measures the genetic effect shared between two traits in a given population. It can be estimated by phenotyping related individuals in common garden trials, although complementary studies must be carried out to understand the functional mechanisms underlying the focal traits. The correlation can arise from pleiotropy (where the effects of a gene can have fitness effects in more than one trait that could be of different signs) or linkage disequilibrium (LD, correlation between genes in different parts of the genome) [14]. This is of primary importance for managing genetic resources, as a negative correlation due to LD can be overcome, but a pleiotropic effect cannot.

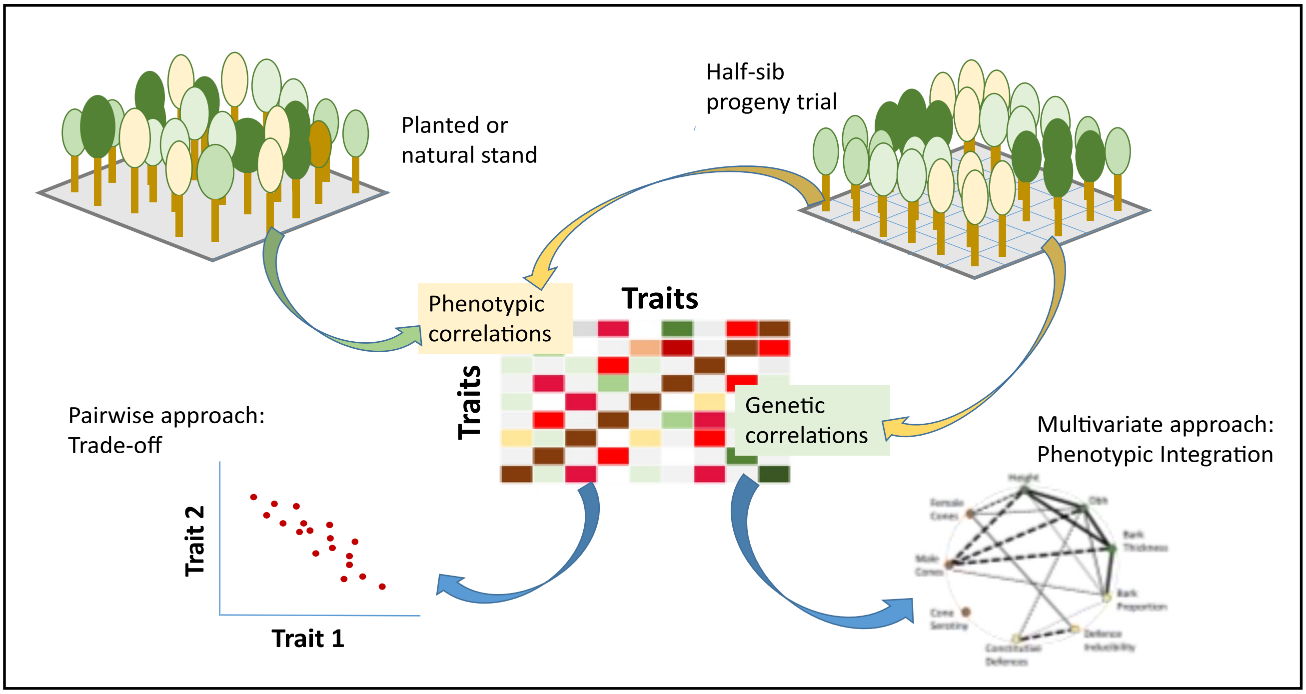
Another key point to take into account is the fact that genetic correlations between traits can differ depending on multiple factors such as population, environment, age, and selective pressure [15•, 16]. Genotype-by-environment interactions may influence the expression of trade-offs, as the magnitude of plasticity could be heterogeneous among different traits, and thus, correlations among traits could disappear or even change in sign depending on the specific context [17, 18••].

Therefore, genetic improvement has a role to play in managing genetic correlations that could result in different pair-wise trade-offs and different levels of phenotypic integration among traits. A recent trend in evolutionary ecology intends upscaling pair-wise phenotypic and genetic correlations to the multivariate integrated phenotype, i.e. the multivariate correlations of traits indicative of main evolutionary and functional processes [19, 20•]. This relatively recent approach is still largely unexplored in forest tree breeding, and indeed requires an important effort in phenotyping.

In this review, we collect and synthesise current knowledge on trade-offs in important tree fitness components such as growth, survival, reproduction and defence to biotic threats and their relevance for the management of genetic resources, with the main focus in temperate tree species with existing breeding programmes. In addition, we gathered state-of-the-art information on trade-offs related to relevant environmental cues for forest trees (seasonality, water availability, temperature extremes and fire), as well as others related to economically relevant yield (both wood and non-timber products). Finally, we also included the current knowledge about the molecular basis of trade-offs. Special emphasis is given to the environmental conditions affecting trade-offs and to identifying major knowledge gaps. This information will

Table 1 Worldwide examples of productive forest tree species with breeding populations affected by important biotic threats

Biotic agent	Type	Common name	Affected Tree species	Origin	Affected Region
Hymenoscyphus fraxineus	Fungus	Ash dieback, chalara	Ash (*F. excelsior, F. communis*)	East Asia	Europe
Bursaphelenchus xylophilus	Nematode	Pine wood nematode	Pines	North America	Japan, Portugal, Spain
Fusarium circinatum	Fungus	Pine pitch canker	Pines	Central America	Worldwide
Agrilus planipennis	Insect	Emerald ash borer	Ash	NE Asia	North America
Dothistroma septosporum / pini	Fungus	Dothistroma needle blight	Pine (*P. radiata*)	Himalayas, Andes	New Zealand, Asia, NE Spain
Austropuccinia psidii	Fungus	Myrtle rust	Eucalypt	South America	Brazil, Australia
Leptoglossus occidentalis	Insect	Western conifer seed bug	Stone pine (*P. pinea*)	North America	Spain, Portugal



		How we measure it	
Concept	What measures	Within populations	Among populations
Phenotypic correlation	Positive or negative relationship between two traits due to both genetic and environmental effects	Pearson’s correlations among individual phenotypic values	Pearson’s or Spearman’s correlations among population means
Genetic correlation	Positive or negative relationship between two traits due to additive genetic effects	Quotient between the genetic covariance and the product of additive genetic variances in half-sib progeny tests	Pearson’s correlations among population BLUPs
Trade-off	Balancing or antagonistic covariation between two traits	Pairwise regression of individual phenotypic values or genetic correlation	Pairwise regression among population means or BLUPs
Phenotypic integration	Level of relationship (positive or negative) among multiple traits of the phenotype	Phenotypic Integration indexes based on individual within-population values	Phenotypic Integration indexes based on population means or BLUPs

Fig. 1 Description of key concepts repeatedly mentioned in this review

be crucial for better management of standing genetic variation in breeding programmes and to assess whether genetic correlations could be broken down under specific environmental conditions. We aim to provide an important part of the knowledge base needed to advance wood production and quality and secure tree species adaptability under changing biotic and abiotic conditions.

Growth: the Key Breeding Objective

Growth is a key component of plant fitness, together with survival, reproduction and lifespan. Growth is a major criterion for most breeding programmes for many reasons, including that it is comparatively easy to measure (by means of single traits like total height, basal or breast-height stem diameter, seedling biomass, etc.) and it is the basis of most yield models. In fact, a sound comparison of genetic and environmental effects in any other trait should always consider size (cumulative growth) variability to control for ontogenetic allometric effects [21•]. Unsurprisingly, growth underlies many evolutionary trade-offs (both theoretical and experimental) and is the most frequent 'currency' for estimating costs in other key processes, such as reproduction and defence.

Plant growth and biomass allocation are the results of assimilation, water transport, metabolism cost, nutrient availability, soil type and plant age ([22] and references therein). Thus, the optimal biomass for the given resources is the outcome of several interrelated processes occurring at a finer scale. Plant growth is defined by plant size and by the amount of biomass allocated to the plant components. Height and diameter growth rates, above-ground and below-ground biomass, and leaf to wood ratio are usually the basic elements with which intra- and interspecific variability are measured. Height and stem diameter are linked to the ability of a tree to gain resources, thus measuring height development is an estimate of the capacity to capture light and indicates potential to secure carbon; similarly, stem diameter growth is related to water-absorption and transport capacity. These variables are also primary drivers for evaluating plasticity and selecting genotypes. Allocation strategies are, in fact, species- or genotype-specific [23], being genetically determined. Several authors [24–27] have noted the importance of applying different allometric analyses to mixtures of genetic groups since allometric equations vary among clones, half-sib or full-sib families.

According to the balanced-growth hypothesis [21•, 28], plants prioritise allocation to the organ that exploits the limiting resource. As a consequence, the same species or genotype can show different allocation patterns in different environments due to non-identical selective pressures [29]. The use of distinct allometric curves can account for the genetic variability of responses to environmental conditions [27, 30]. Relative allocation to above-ground and root biomass has been reported to change in seedlings of Mediterranean pines under contrasting water availability in controlled conditions, both between species and provenances within species [31, 32], with significant ecotypic variation patterns. Similarly, in multi-site common gardens testing *Pinus halepensis* provenances, both ecotypic variation and a strong effect of site water availability were found in the allocation between wood and bark [33•] and between reproductive and vegetative biomass [34]. In these studies, the more stressful the site, the lower the investment in bark and the higher the investment in reproductive organs.

These trade-offs in allocation, typical in biology when one trait is linked to a change in another, are also reflected into trade-offs between characteristics that enhance one aspect of individual performance but decrease that of another [35]. While ontogenetic allometric scaling is general in all plants [21•], the fact that many studies in forest trees are carried out in seedlings makes the interpretation of trade-offs related to differential allocation particularly problematic to be extrapolated to adult trees [36]. Moreover, size-related trends of many key functional traits of forest trees are still poorly known and often confounded with age-related trends [21•].

Trade-offs between growth and tolerance to abiotic stress in forest trees are highly expected, yet complex to dissect into precise anatomical and functional causes. Many avoidance (i.e. preventing the deleterious effects of adverse conditions) and tolerance (e.g. enduring such adverse conditions) mechanisms are costly in terms of allocation, and therefore, trade-offs are frequently reported in the literature. In a later section (trade-offs related to environmental cues), we present an extensive review of these aspects.

Trade-offs Between Basic Functions

Survival Rate

Individual survival is another key component of biological fitness. In the current context of widespread dieback events in forest tree populations [37•], understanding the underlying causes of tree mortality and how they are related to other fitness components is essential for forest conservation and breeding programmes.

Inter-specific studies have hypothesised the existence of a trade-off between survival and growth for a long time ([38] and more recently [39••]). These works suggested the existence of a functional variation between a conservative strategy of resource usage (water, nutrients, carbon) maximising survival, against an acquisitive strategy maximising growth. However, extensive evidence points out that global patterns of trait covariation do not reflect trade-offs at finer organisational levels such as within species. In fact, positive associations between survival and growth are rather common in forest tree species [58•].

Specifically, the relationship between stem diameter increment and mortality has been studied in different tree species and biomes [40–44], showing higher mortality related to growth reduction, i.e. a positive correlation between growth and survival. At population level using reciprocal transplant experiments, survival and growth are usually positively correlated, reflecting adaptation to different environments and that the best (adaptive) populations often have both higher survival and growth rate [45, 46]. The evolutionary significance of this positive relationship is evident particularly at early and juvenile life stages in the outcome that larger seedlings can have higher chance of survival in resource-limiting conditions. For instance, in drought-prone ecosystems, large seedlings have access to deeper underground water, which would increase their persistence probability during summer months. In addition, larger individuals can also have a higher competitive potential when other environmental factors such as light are limiting [59]. Positive additive genetic within-population correlations between survival and growth have been documented in Norway spruce and Scots pine provenance and progeny trials [48–50].

However, the size of the positive genetic correlation may change according to planting site and climate. In Scots pine, positive genetic correlation between survival and height was stronger in harsher environments (colder in this case) than in milder environments (assessed in 20 trials located in different climatic conditions in northern Sweden) [51, 52•]. Both temperature and soil characteristics were also found to affect the correlation between survival and growth at population level [53]. Among five sites in northern Finland, a positive correlation between survival and height was only found in one of them (with intermediate climate), while at four others (with milder or harsher environments), no significant correlation was observed. A fitness index combining survival and growth was proposed to deal with the uncertainty of the relationship.

While the number of genetic studies of the trade-off between survival and growth is very limited, there are many ecological studies testing it, especially in communities limited by light availability, such as tropical forests. The basis of these trade-offs varies depending on the multiple environmental factors behind the response of plant communities (e.g. nutrient, light, or water limitation, and recurrent perturbations such as fire) [54–56]. For example, light affects the relationship between growth and survival of tree seedlings of tropical tree species, with a significant effect of seed mass in low-light survival [57].

On the other hand, there is a general lack of empirical evidence on the growth-survival trade-off in climates where neither cold nor light are limiting factors, namely in Mediterranean climate zones. A meta-analysis of published results from common garden experiments showed no trade-off or even a positive correlation between previous growth and survival in field conditions [58•]. This trend is consistent with the higher survival rates of well-nurtured, bigger planting stock reported in various works under Mediterranean and even warm semi-arid conditions, both for broadleaves and conifers ([59] and references therein).

Reproduction

Reproduction is a third key component of biological fitness, and as such, trade-offs related to reproduction have been a classic field of research in evolutionary biology (see for example [60]). Trade-offs in reproduction are closely related to reproductive/vegetative differential allocation and the evolutionary concept of costs of reproduction in growth currency [61–64] or in other functional traits, like leaf nitrogen and chlorophyll content [65]. Costs of reproduction are a long-lasting research topic in evolution and ecology, with different approaches between both disciplines including phenotypic and genetic correlations, manipulative experiments and selection experiments [66].

Manipulative experiments are a preferred approach, as they allow confounding factors like size or genetic background to be controlled for. These methods (consisting of comparing functional responses of intact individuals with other genetic replicates whose flowers, fruits or cones had been removed) have been, however, seldom applied in forest trees (but see [67•]).

The differential investment in growth, maintenance and reproduction in trees and its changes along ontogeny makes their trade-offs quite more complex than those in short lived taxa [68–70]. Both the variation in thresholds of age and size for reproductive onset [60] and declining fecundity with age (senescence, see for example [71]) are key factors affecting trade-offs involved in reproduction in long-lived tree species.

The abundance of separate female and male flowers in many tree species makes the incorporation of sex allocation into the assessment of trade-offs related to reproduction highly relevant [67•]. Higher cost of reproduction in female (pistillate) individuals leads to a general lower growth within sexual dimorphism pattern in dioecious tree species [68]. Analyses of growth curves for some dioecious tree species also indicate sexual dimorphism in patterns of late-age growth decline, consistent with a different reproduction-growth trade-off [68]. While the higher cost of female reproduction associated with fruit and seed formation is widely backed by experimental data [61], the costs and trade-offs associated with huge pollen production in many wind-pollinating species are still largely unknown (but see [72]). Functional differences between males and females have been mostly studied in dioecious species (e.g. *Fraxinus*, *Juniperus*, *Taxus*) (see, for example [73]), but there is also evidence of trade-offs related to different sex allocation in monoecious species. For example, in *Pinus sylvestris*, a negative genetic correlation among female and male fertility (number of cones) was found among breeding progenies [74] while in *P. pinaster*, ecotypic population differentiation was found based on the different threshold size for female and male reproduction [75]. In many monoecious species, sex allocation is closely linked to crown architecture. For example, in most conifers, female reproductive organs occur in vigorous, orthotropic upper shoots, while male organs occur in secondary or tertiary shoots located in the lower crown [76]. These facts make trade-offs of reproductive and sex allocation highly likely to be related to tree architecture [77, 78].

Experimental evidence of genetic trade-offs with reproduction in forest trees based on selection experiments is almost absent in the literature. One of the few works, in *Pinus pinaster*, showed that a single artificial selection event for high allocation to straight stems as part of a breeding programme, significantly delayed female reproduction, consistent with an underlying trade-off among tree growth and architecture and reproductive allocation [79•]. This finding runs in parallel with many others related to the domestication process in different plants and animals, and contrasts with the positive phenotypic correlations between growth and reproduction (cone counts) often observed in field conditions (e.g., [80]).

The drivers of the extreme fluctuations among yearly seed crops (masting) in some species are still under scientific debate, but a complex combination of selection pressures from herbivores, climate effects and costs of reproduction is invoked [70, 81]. Therefore, masting should be considered as a potential key dimension in the study of reproductive trade-offs in forest trees, even when trade-offs among growth and reproductive effort in the same year do not always occur [82].

The potential trade-off between seed size and seed number is often mentioned in many works (see [83] for a review in crop plants). However, a recent meta-analysis has revealed that seed size and seed number are not strictly negatively correlated among taxa in forest trees, but investment in protective woody cones in gymnosperms was postulated to explain their general lower seed yield compared to angiosperms [84•].

Trade-offs among reproduction and defence are predicted by life-history theory [62], but so far, there is little empirical evidence in plants [85, 86]. Interestingly, two recent studies in conifer trees have confirmed that reproduction and defence are not maximised at the same time [87, 88]. The relationship between reproduction and other key functional traits such as water use efficiency and cold tolerance is similarly poorly known in forest trees [89•], but significant (positive or negative) correlations can be good evidence for micro-evolutionary trends in reproductive trade-offs [20•, 90].

Defence: Pests, Diseases and Multiple Resistance

Being sessile, long-lived and massive organisms, trees constitute an easy source of food for a wide array of organisms [91]. Insect herbivores, fungal pathogens and other infectious parasites may cause serious disorders, affecting growth, reproduction, survival and ultimately fitness [92]. To protect themselves, trees have evolved both resistance mechanisms to fight against the invader and reduce the damage it produces, and tolerance mechanisms aimed at minimising the impact of damage on tree fitness [93, 94].

Trees can be both tolerant and resistant to pests and pathogens [95]. Theoretical models have predicted conditions (amount of available resources, type of parasitism, probability of exposition to enemies, etc.) that would lead to the prevalence of either tolerance or resistance strategies in plant populations (e.g. [96, 97]). Prioritising one of the two strategies would negatively feedback on the selective pressure exerted to the other (e.g. lowering the impact of damage on fitness (tolerance) reduces the benefits of evolving enhanced resistance) which may exacerbate the trade-offs among both strategies. However, although some mechanisms underlying tolerance have been characterised in plants [95], tolerance has been overlooked in trees and remains quite elusive. As a consequence, most studies investigating defensive traits in trees are focused on resistance mechanisms.

In general, tree defensive mechanisms are energetically costly to produce [98] and require large amounts of carbon-based resources that, once employed for defence synthesis, are no longer available for other functions such as growth and reproduction [99]. Trade-offs between defensive investment and other life history traits are thus expected [100•, 101]. Indeed, trade-offs form the basis of current plant defence theories, on which a huge research effort has been expended to explain the extremely large variation in defence strategies, defence traits and defensive investment among and within plant species [96, 102, 103].

Costs of defences are key to understanding trade-offs related to defensive investment. Costs of defences have favoured the ability of trees to plastically regulate defensive investment according to the actual risk of being damaged [104]. As in other plant species, tree defensive mechanisms are produced constitutively, irrespective of the biotic context (constitutive defences) but can be also produced in response to an aggression (induced defences) [93]. Induced responses to biotic damage include the differentiation of new anatomical defences and the increased synthesis of chemical defences [104]. Induced defences are also costly to produce [98] but are considered a cost-saving strategy as, in absence of attack, the resources needed for their synthesis are available for other functions [105]. Associated with the long lifespan of trees and the heterogeneous environmental conditions and biotic risk that they face across time, induced defences are, at least theoretically, highly relevant in trees [104].

Trade-offs associated with defensive investment are variable in nature, can occur at different levels of genetic organisation and may have different practical and evolutionary implications [100•, 106••]. Probably the most noted trade off in the literature involving tree defences is the growth-defence trade-off for which a broad theoretical framework has been developed [96]. Compromises between growth and defence may arise at the phenotypic level but can also be genetically determined [106••]. At the phenotypic level, the growth–differentiation balance hypothesis (GDBH – [96]) states that under moderate resource limitation, growth may be more constrained than photosynthesis, so the excess of photoassimilates can be reallocated to defence production. Under moderate stress, trees may be thus better defended than under more favourable conditions (e.g. [107]). Severely stressful conditions may, however, deplete both growth and defences [108]. At the genetic level, the resource availability hypothesis (RAH—[102, 109]) predicts that habitats with high resource availability select for species with enhanced growth rates and low defensive capability, while impoverished conditions select for slow-growing but highly defended plants. These predictions have obtained ample support in empirical studies with forest trees [110, 111] even for explaining among-population variation within species [112•].

A paradigmatic example of how a tree needs to optimise the allocation of resources across life functions occurs in pines [113], whose main defensive mechanisms against biotic aggressions rely on oleoresin, a complex mixture of hydrocarbon molecules highly demanding on carbon resources [114, 115]. Compromises between growth and investment in resin production have been reported, for example, in *P. pinaster* seedlings [98, 115] and *P. halepensis* saplings [116], although in both studies, the emergence of such compromises appeared to be strongly context dependent, being only detectable under harsh conditions.

Another important set of trade-offs associated with tree defences are those occurring among different types of defences or between different defensive strategies. As any single tree species has a wide array of potential enemies, trees have multiple physical and chemical defences that may be effective in deterring specific or general aggressors [117]. This battery of defences also compete for the same resources, which may favour the emergence of trade-offs in the expression of different types of defences [118]. Empirical support of this kind of trade-offs is, however, limited [119], and in the case of trees, chemical and physical defences tend to be more positively rather than negatively correlated [101]. A special case is the trade-off between constitutive and induced defences. Both defensive strategies appear to be negatively correlated among each other both across [110] and within species [120•], although the strength and direction of this relationship depend on the biotic and scale context [120•]. Besides the aforementioned conflicts that may exist in the allocation of resources to both constitutive and induced defences, both strategies also tend to be negatively related from an evolutionary perspective. Species or lineages that are well defended constitutively should be less attacked by parasites so they are expected to be exposed to a lower selection pressure to evolve induced defences [121]. Because the relationships between growth (or other vital functions) and constitutive and induced defences may be opposite [122•], the negative genetic correlations between constitutive and induced defences open an interesting field of applied research aimed at simultaneously maximising growth and defensive status that would require further attention.

There is empirical evidence that intraspecific variation in resistance to specific pests and pathogens may negatively covary with growth in a number of tree species. For example, resistance of *Pinus pinaster* families to the pine weevil *Hylobius abietis* has been shown to be negatively correlated with their growth potential, with the genetic material selected for growth being significantly more susceptible than the unimproved control [123]. Similarly, *P. pinaster* populations adapted to more favourable conditions and with higher growth potential were shown to be more susceptible to the bast scale *Matsucoccus feytaudi* than their counterparts originating from harsher conditions [124]. Counterexamples of no relationship or even positive relation between growth and resistance to specific parasites exist in other pathosystems [101]. Given the relevance that growth-resistance trade-offs may have in the context of tree breeding programmes, we urgently need to understand the extent and conditions under which we should expect these constraints.

Of particular relevance is whether genetically based variation in resistance to one specific parasite might confer resistance to another. Most, if not all, studies exploring variation (and covariation) in tree resistance are focused on a single pathogen or pest species that is currently threatening tree populations. However, the number and severity of biotic threats to trees continues to grow, especially in the context of global change [125]. New exotic pathogens, constrained in the past within their natural ranges by biogeographic barriers, are expanding to new regions, causing alarming sanitary problems for the native flora, and particularly to forests [126]. To what extent, genetic resistance to current threats that will also provide protection to future biotic risks remains largely unknown. Similarly, we still lack specific studies in forest trees testing whether there are trade-offs or instead coordination between resistance to biotic attacks and to abiotic stressful conditions. Theoretically, resource-limiting conditions should simultaneously favour both resistance to biotic threats and tolerance to abiotic stress and no trade-off should be expected. However, allocation conflicts between both types of mechanisms, which may be indeed more pronounced in harsher environments, might counterbalance this trend.

Trade-offs Related to Environmental Cues

Seasonality (Phenology)

Genetic correlations between phenology, timing of events and many important characteristics of trees as aboveground primary growth make phenology a crucial trait for tree breeding and for optimal deployment of forest reproductive material. Phenological traits have been observed to show substantial clinal differentiation in populations of temperate and boreal trees, suggesting the importance of local adaptation in shaping the patterns of genetic variation in phenology-related traits [127]. Beyond the importance for breeding, phenology plays a major role in adaptation to climate change [128], and it can be even the major determinant of tree species range [129]. Aboveground primary growth (i.e. shoot elongation) is controlled by two environmental cues: photoperiod plays a major role in the regulation of growth cessation and bud set phenology in various tree species, while release of dormancy and bud burst are mainly regulated by temperature [130].

Climate change challenges populations to alter patterns of timing in traits related to annual aboveground primary growth rhythm which include the regulation of growth cessation, bud set, dormancy and bud break. Ample within-population variation suggests that natural selection or artificial selection via breeding can produce new combinations even with some degree of genetic correlation between traits. In the timing of bud-burst, where variation has a genetic component with temperature as the major environmental cue, very early phenotypes are selected against due to spring frost damage. On the other hand, variation in timing of cessation of growth also has a strong genetic component and is strongly controlled by photoperiod. Warming climate would conduce towards an adaptive later timing of growth cessation and onset of endodormancy (i.e. internally controlled growth inhibition), to achieve a longer growing season and minimise the risk that dormancy breaks in the ecodormancy (i.e. environmentally driven growth inhibition) period that follows endodormancy [129, 131•]. Primary aboveground growth-phenology trade-off indeed depends on the environment. Species distribution models based on fitness-trait reaction norms allow a clear view of this (ΔTSDM, [133]). For example, in the case of European beech (*Fagus sylvatica*), phenology was found to constrain maximum growth in the northern and western parts of its range but not in south-eastern regions (Fig. 2). Adaptive changes in phenology driven by warmer springs [134•], or warmer springs and autumns, may result in a modified growing season length [135].

Trade-offs between phenology, aboveground primary growth and cold hardiness are well documented between populations but within-population correlated responses to selection between these traits are not so clear. For instance, genetic correlations between timing of onset of growth and cessation of growth are mostly minor (e.g., [136, 137]). The length of growing period is clearly correlated with shoot elongation at population level; however, the situation within breeding populations needs to be addressed. Genetic gain in primary growth by breeding can be attained following two alternative methods: selecting fast-growing genotypes, or selecting genotypes with longer growing period, at the risk of increasing mortality from cold damage [136, 138]. Advancing breeding makes the question increasingly important, but only a few studies have compared natural and selected populations so far. In *Picea abies*, no clear differences in frost hardiness were found, [139], but in *Pinus contorta*, there were large differences in growth traits, with selected seedlings showing a slightly delay in growth cessation and no effect on timing of growth initiation, resulting in a slightly greater cold injury [140•]. More studies will be needed to assess the effects of selection for growth on phenology traits.

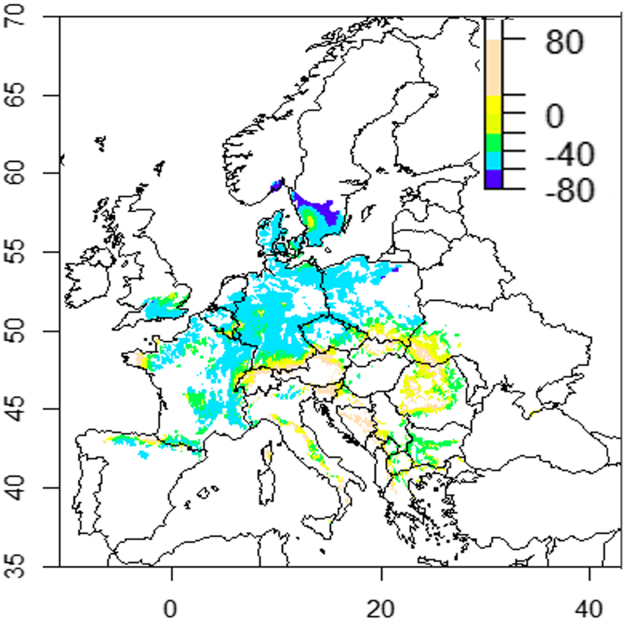


Fig. 2 Differences in predicted height (cm) between models considering only climate variables (precipitation of the warmest month of the trials) and considering leaf flushing as a covariate. Negative values (blue) indicate those regions where aboveground primary tree growth is limited by the timing of leaf phenology. Adapted from [132•]

Even if the direct effect is uncertain, it is likely that growth phenology has pronounced effects on the properties of wood. The density of softwood species is related to the relative proportion of earlywood and latewood; the latter probably mainly formed after apical growth cessation when the auxin levels decrease [141]. The effect of a later cessation of apical growth causing a later transition to latewood and lower specific gravity has been observed among populations of *Pinus taeda* [142]. Furthermore, it was suggested that the genetic variation of wood density was mainly determined by the timing of latewood formation in *Larix kaempferi* [143].

In the boreal and temperate region, the cold winter period determines timing of onset and cessation of growth, and variation in these traits correlates with growth and survival.

The negative correlations between freeze damage and height in 1-year-old seedlings suggest that selection for early cold acclimation (less freezing damage) may adversely affect later field performance [144]. The estimates of negative additive genetic correlations between cold hardiness at early stage and growth at late stage in mild environments indicated that early selection for cold hardiness can improve seedling survival but it may also reduce growth [51]. In warmer regions, growth can be continuous throughout the year, and other environmental cues determine the phenology of growth [145]. Phenology also affects other important fitness factors, for example, timing of bud burst may affect resistance to herbivory [146], and timing of flowering may affect resistance to many biotic stresses [147].

Drought Tolerance and WUE

Drought is one of the most important drivers of forest dieback worldwide with increasing negative effects as a consequence of climate change, including both higher vapour pressure deficit (VPD) in the atmosphere and lower soil moisture [148••]. Xylem cavitation resistance (resistance to desiccation under high negative water potentials) has been shown to be tightly linked to survival under severe drought, both in conifers [149] and angiosperms [150]. Another trait usually evaluated as an indicator of drought tolerance is water use efficiency (WUE, the ratio of net CO_2 assimilation to loss of water by transpiration). WUE rather influences the maintenance of photosynthesis under moderate drought conditions (reviewed by [151]).

Several studies supported the existence of a trade-off between xylem cavitation resistance and xylem transport efficiency [152, 153] suggesting that the improvement of water transport would imply a risk regarding drought resistance. Nevertheless, this trade-off is far from being universal [154], as exemplified by the varied results found in different species (e.g. [155]). For example, higher hydraulic conductivity (associated to larger tracheid lumen size and tracheid lumen fraction, and smaller wall thickness reinforcement and tracheid density) has been recently found in improved varieties of *Pinus pinaster*, but those features did not occur at the expenses of resistance to embolism [156•].

Resistance to cavitation presents poor genetic variation [157, 158]. In very few cases, significant genetic variation in resistance to cavitation has been estimated (e.g. *Pinus canariensis*, [159•]). For these species, other factors beyond the xylem properties may be important for drought tolerance. In this sense, it has been observed that populations from drier sites present a greater tolerance to drought through traits related to osmotic adjustment such as the 'water potential at the turgor loss point' (e.g. [160, 161]).

The existence of a trade-off between the ability to tolerate drought and growth is not clear. On one hand, faster growth rates may imply larger leaf area, which is disadvantageous in the presence of water stress due to increased transpiration surface [162]. Diameter growth rate has been negatively related to wood density [42], because producing denser wood is a costly strategy that may cause slow growth rates [163•]. However, the question of whether wood density, which may be explained by thicker vessel walls and smaller lumen diameter, results in higher resistance to embolism is yielding contrasting results [156•, 164, 165]. There is empirical evidence supporting a possible trade-off between accumulated growth and xylem safety (usually estimated as the xylem pressure causing 50% loss of conductance -P50) in hybrid poplar genotypes [166] and conifer species [167] (i.e. biomass accumulation is positively correlated with P50). On the other hand, a negative correlation between P50 and growth (i.e. higher resistance to cavitation associated with higher growth) has been also identified [165]. Moreover, drought tolerance through osmotic adjustment did not occur at the expenses of growth rates across populations of *Quercus oleoides* [168]. These contrasting results highlight the importance of considering different genetic backgrounds to establish the existence of a trade-off between drought resistance and growth.

Carbon fixation through photosynthesis occurs at the expense of losing water through transpiration. This physiological constraint is particularly important in water-limited environments, which may result in a trade-off between growth and WUE. At the inter-specific level, the trade-off between growth and WUE has been identified as a determinant of community assemblies in perennials [169•]. At the intra-specific level, genetic correlations in *Castanea sativa* [170] and phenotypic correlation across populations of *Pinus pinaster* [171] and *Pinus ponderosa* [172•] pointed to the existence of a trade-off between WUE and growth, while other studies did not find evidence supporting this trade-off in *P. pinaster* [32, 173, 174] or Mediterranean cedars [167]. WUE, as the result of various structural and physiological features influencing the ability to overcome drought periods, can be modulated by leaf area, root depth and density, hydraulic properties, photosynthetic capacity and stomatal control [175]. In this sense, a significant negative genetic correlation has been found between SLA (Specific Leaf Area) and intrinsic WUE in a *Pinus pinaster* inter-provenance cross [176]. The lack of generality on the relationship between growth and WUE can be explained by the influence of the intensity of water stress experienced [177]. In addition, we still need a better understanding of the extent to which WUE and drought tolerant phenotypes are determined by the environment and genetics [178].

A potential trade-off between xylem cavitation resistance and WUE, which may be explained if increased cavitation resistance co-varies with other plant hydraulic parameters that constrain gas exchange, has been highlighted [167, 171]. However, evidence for this trade-off is scarce [165, 179–181]. In addition, the complex interplay between xylem cavitation resistance, WUE and biomass growth in contrasted environments still deserves further study, to unravel the evolutionary constraints that determine the different strategies that trees use to face drought events.

Tolerance to Temperature Extremes

In plants, physiological function naturally varies with temperature and continues, even if inhibited, towards both the upper and lower temperature range limits. However, extreme temperature events are likely to induce abnormal physiological responses or tissue damage sufficient to cause severe growth limitation or mortality [182]. In tree species, as it is often the extreme rather than mean values that are critical, temperature extremes are an important factor determining range limits [183, 184] and governing demographic turnover. As the climate changes, the interaction of the frequency of temperature extremes and the timing and duration of normal growing conditions is likely to play a key role in the performance and persistence of tree species across their ranges [185•, 186–188]. In particular, an increasing frequency of extreme high temperature associated with hotter droughts is likely to be a major cause of mortality in tree populations [188–191], which will have extensive negative impacts in both natural [189] and urban [192] tree populations. Of course, extreme high temperatures associated with fire, even sub-lethal events, will also be a threat [193•]. At high northern and southern latitudes, or at high elevation, where extreme low temperatures are important, climate change–driven shifts in the timing and duration of the growing season may expose trees to tissue damage if late frosts persist [184, 194], or indeed increase in frequency under climate change [195, 196•].

Physiologically, the consequences of temperature extremes for trees may manifest themselves in multiple ways. The risks and outcomes also vary substantially with age, proportionately affecting young seedlings more severely than mature trees, although seeds may be more tolerant [197, 198]. High temperature extremes (beyond the increase in atmospheric water vapour deficit already mentioned in the "Drought Tolerance and WUE" section) may cause direct injury, such as bark or leaf tissue scorch, canopy necrosis [199] or may facilitate indirect impacts such as reduced vigour or infection. High temperature induces hydraulic [199] and chemical shifts that can alter metabolic processes, denature proteins and change the respiration-photosynthesis balance [198, 200]. Low temperature impacts, while less clearly defined, are typically associated with sub-0 °C effects, particularly in young tissue, where freezing causes cell destruction and wider cold injury [200]. Low winter temperatures have been observed to cause trunk damage in some hardwoods due to uneven freezing between heart- and sapwood [198] and may be a risk where future phenological mismatch develops due to climate change. It is likely that interactions between the ongoing increase in CO_2 levels, associated growth responses and extreme temperature are also likely to cause impacts, such as reduced seedling growth and competitive ability [201] and early senescence [202].

Given the direct and indirect effects of extreme temperature on trees, it is likely that trade-offs will exist between extreme heat and cold tolerance and traits such as leaf area, vessel dimensions, budburst and senescence phenology and bark thickness. Heat and cold tolerance differ substantially, with the former characterised by an ability to maintain hydraulic capacity, resist direct biochemical impacts and recover from damage while the latter may be more aligned with phenological traits such as spring growth initiation and winter hardiness. If freezing temperatures occur in the early or late stages of active annual growth, frost damage and serious stem defects such as forking of the apical shoot can result.

Fire Adaptive Syndromes

Fire is indeed a key natural selective factor in plants [203]. In recent years, there has been an increasing interest in the role of wildfires shaping plant life histories and the divergence in fire-adaptive traits as part of local adaptation under specific fire regimes (see for example [204•] for a recent review). In tree species, traits assumed to increase fitness under particular fire regimes include self-pruning of dead branches, early female flowering, serotiny, thick bark or resprouting ability [203]. Different studies have shown that these traits vary not only between species, but also within species under different fire regimes [205, 206]. Genetic variation within populations with moderate heritability has been found in the case of serotiny (in *Pinus halepensis*, [206]), but studies on additive genetic correlations involving fire adaptive traits are still missing.

Based on post-fire strategy, woody plants can be classified into obligate resprouters, obligate seeders, facultative seeders and fire avoiders (see for example [203, 207]). Each strategy implies specific trait combinations (syndromes) that increase fitness under different fire regimes. Within these syndromes, some main trade-offs have been identified. One highly consistent among species is the negative correlation between degree of serotiny and bark thickness, since the first is associated to forming a precocious aerial seed bank that will be released after intense crown fires (and leading to abundant post-fire recruitment in the burned ground), while thick bark is associated to enhanced adult survival facing low-intensity understory fires. Moreover, highly serotinous species show low auto-pruning and lower life expectancy, frequently associated with less straight stems and low apical dominance, all of them traits increasing crown flammability [208]. However, the consistency of these trade-offs at the intraspecific level in forest trees is still largely unexplored.

Early and abundant female reproduction frequently associated with high serotiny is known to have a cost in vegetative growth (following the general life-history trade-off mentioned in "Reproduction" section). Moreover, resprouting ability ensuring adult persistence has been shown to trade-off with other traits enhancing post-fire recruitment [207, 208].

Beside trade-offs among traits within each fire adaptation syndrome, some key fire adaptive traits have been recently shown to be environmentally (and physiologically) dependent. Low water availability has been shown to decrease both the degree of serotiny and allocation to bark and absolute bark thickness in *Pinus halepensis* common gardens [33•, 209]. Meaningfully, in both cases, the environmental effect was shown to change the allometric relationships with tree or xylem size, and therefore, this is one fine example of climate change exacerbating negative trade-offs between competing functions, with fitness implications in future climate scenarios.

Trade-Offs Related to Forest Outcomes

Wood Quality

Studies in evolutionary ecology have identified relevant covariation between basic wood traits (density, structural stiffness) and contrasting life-histories in rainforest trees [210], still largely unexplored at the intraspecific level. Among species, high wood density and structural stiffness are related to long lifespan [210], typical of late succession, shade tolerant trees, also with a significant role of xylem hydraulic properties [211].

Under a commercial perspective, wood quality traits have indeed a major impact on the quality of end-use products. For structural purposes, defects caused by branch knots, crooked stems and spike branches are the most significant factors for downgrading sawn wood to less valuable products.

In defect-free softwood, density is the single best predictor of wood quality [212, 213], due to its strong correlation with clear-wood stiffness in mature trees [214]. Since the cell wall density is nearly constant within the stem and independent of growth rate [215], the cell-wall to void-volume ratio is the main driving density factor. The ratio is higher in the tracheids formed in late summer (latewood, [216]), resulting in two to three times higher density compared to those formed in early summer (earlywood). Along with density, microfibril angle (MFA; the angle at which the cellulose microfibrils in the secondary cell wall deviate from the long axis of the cell) also has a significant influence on the strength and stiffness of the wood-based products [217, 218]. The smaller the MFA in the S2 layer, the higher the stiffness of the tracheid and of the wood. A third important trait for the application of softwood is the spiral grain, the alignment of the longitudinal cells when viewed on the surface of a stem, log or the tangential surface of a board [219]. Spiral grain has important implications particularly in the formation of twists in boards from the juvenile core. High grain angles are also known to reduce wood stiffness.

Most wood properties and their genetic control change with cambial age and stabilise when cambium becomes mature. The general trend for conifers is that wood density and stiffness are lower, while MFA and grain angle are higher in the juvenile wood [212]. In contrast, MFA and grain angle decrease whereas wood density and stiffness increase as trees become mature [220–223]. Many juvenile wood features are undesirable for production, due to its low density, high grain angles, higher content of compression wood, high MFA, low crystallinity resulting in lower strength, stiffness, shape stability of lumber, and high variability compared with mature wood [224–226].

The trade-off between growth and wood quality is clearly evident in a sawn board, as knots and defects. Increased growth is usually due to a larger photosynthetic biomass/foliage, on a higher size and number of branches. In softwood, there is a strong positive genetic correlation between stem growth and branch/knot size [227, 228] but not frequency. Knots and grain distortions determine structural wood quality and are the main cause of downgrading to lower strength classes (reference). As branch diameter is known to be strongly affected by environment (e.g. [227, 229]) and competition (e.g. [230–232]), it may vary with age, site and spacing. Significant site by clone interactions for branch diameter, number of branches and stem straightness were found in *Picea abies* [233], and significant genotype by spacing interactions and poor age correlations for the branch diameter were observed in young *Pinus banksiana* [234, 235]. Nearly all estimated genetic correlations of wood density and stiffness with growth traits were unfavourable in major coniferous species: Norway spruce [3, 220, 227, 236], Scots pine [237–239], radiata pine [240, 241], lodgepole pine [221, 242], loblolly pine [243], maritime pine [244, 245], white spruce [246–248], and Sitka spruce [249].

The move of forest industries towards fast-growing plantations, which contain more juvenile wood due to the reduction in their rotation age, will result in inferior wood quality [245]. However, genetic control of wood properties makes it possible to select trees with low differentiation between juvenile and mature wood [236, 250] or to select trees with an earlier transition from juvenile to mature wood [251–253].

Non-wood Forest Products

Non-Wood Forest Products (NWFPs) are not another biological sink for resource allocation, but a heterogeneous, utilitarian category of any ‘biological resources other than wood that can be obtained from trees’. In many cases, NWFPs are related with the biological functions discussed before: resins and secondary metabolites are defence mechanisms that can be tapped by cutting and/or promoted with chemical stimulants, and obviously, fruits, nuts or cones are reproductive structures. Tree fungi, either parasitic or mycorrhizal, conform a different kind of NWFPs involving complex biotic and abiotic interactions [254].

Co-production usually entails both synergies and trade-offs between quantities and qualities for each product, also depending on specific silvicultural treatments. Frequently, positive phenotypic correlations based on ontogenetic allometry are reported for the amount of NWFPs and tree size, i.e. accumulated growth [255, 256]. On the other hand, selection for straight stems, high apical dominance and low branchiness, typical of many breeding programmes targeting timber production, is expected to decrease fruit or nut productivity (see, for example [79•]). However, so far, few studies have tested for genetic correlations or trade-offs in multipurpose trees between timber and non-timber production. When studied, generally positive genetic correlations have been found between NWFP productivity and growth/tree size, following the above-mentioned principle of ontogenetic allometry, whereas competing resource-sinks are complexly correlated, only evident when many traits are evaluated in the same individuals [257–261].

Molecular Basis of Trade-offs: Plant Growth and Stress Responses

The molecular basis of the trade-offs discussed above have not been thoroughly studied, with the notable exception of the molecular interactions between growth and stress responses. These have been mainly addressed in model species such as *Arabidopsis thaliana* (L.) Heynh, which we focus upon in this section.

Given sufficient selective pressure, one would expect plants to set up an impenetrable arsenal for their aggressors. However, immune responses have fitness costs and so trade-offs exist between growth and immunity, a mechanism that is regulated by phytohormones [262]. These small signalling molecules, such as auxins (AUX), gibberellins (GAs), cytokinins (CKs), abscisic acid (ABA), ethylene (ET), brassinosteroids (BRs), salicylic acid (SA) and jasmonic acid (JA), allow plants to rapidly adjust their development and growth to external cues such as biotic and abiotic stresses and thus play critical roles in stress responses and prioritisation [263]. Hormone signalling components are at least partly phylogenetically conserved, and some interactions have been identified between growth hormones (AUX, GA, BR, CK) affecting immune signalling, and typical stress hormones (SA, JA, ET, ABA) influencing growth and development. JA is known as a positive regulator of immunity against necrotrophic pathogens whereas SA positively regulates immunity against biotrophic/hemibiotrophic pathogens. Other phytohormones, such as ABA, AUX, BRs, ET, GAs, and CKs, modulate immunity in hormone signalling networks mainly through interactions with SA and JA [263].

In the particular case of herbivory, a working model of the plant defence signalling network for regulation of growth-defence trade-offs [264•] involves DAMPs, mitogen-activated protein kinases (MAPKs), specific wound-induced protein kinases (WIPKs), JA, GA, and transcription factors among others. Some actors are ubiquitous across species; others are specific (e.g. the transcription factor WRKY70 appears to have different roles in rice and Arabidopsis). Although the actors of such regulation networks are becoming known, how one process (growth or defence) is prioritised over another remains unclear.

Plant growth-defence trade-offs have also been assessed regarding plant response to biotrophic bacterial infection [265]. In this study, the existence of a central module formed by two proteins (DELLA proteins and EDS1) modulating growth-defence trade-offs via direct interactions has been demonstrated, with a hypothetical model of negative regulatory loop modulating the balance between growth and defence against pathogen attack. The incompatibility between growth and immunity programmes have been attributed, at least partly, to the way apoplastic ROS homeostasis is modulated during both processes [266]. The authors showed that the growth-related transcription factor HOMOLOG OF BEE2 INTERACTING WITH IBH 1 (HBI1) controls the trade-off between growth and defence responses through a transcriptional regulatory network of reactive oxygen species (ROS) homeostasis and changes in the expression of NADPH oxidases (NOXs: RbohA & RbohC) and apoplastic peroxidases (POXs: POX17, POX57 & POX45). In the model proposed here, ROS derived from RbohC are spatially controlled and used to promote growth. In contrast, RbohA-derived ROS are needed for defence responses, inhibiting growth processes. Thus, ROS demands within the apoplast during plant growth and defence responses are incompatible.

Regulation of growth-defence trade-offs should also be conceptualised at the organ level [267] and take multiple stresses into consideration. In this regard, a genetically controlled mechanism by which plants balance trade-offs between conflicting responses to biotic and abiotic stresses by integrating them differently in young and old leaves has been unveiled [268]: abiotic stresses, such as high salinity and drought, blunted immune responses in older rosette leaves through ABA signalling, whereas this antagonistic effect was blocked in younger rosette leaves by PBS3, a signalling component of the salicylic acid (SA) defence phytohormone. This leaf-age dependent crosstalk could determine plant performance during combined stresses.

While most information on the molecular bases of trade-offs comes from annual plant model organisms, different studies have been carried out on tree species. For instance, a transcriptional analysis performed on different tissues from two Eucalyptus species after cold, heat or drought treatments showed the implication of CBF (C-repeat binding factor) and DREB2 (dehydration-responsive element binding) groups in trade-offs between growth and stress resistance [269••]. Another transcriptomic analysis undertaken in segregating progenies of *Picea glauca* subject to weevil attack identified important gene networks underlying growth and susceptibility [270•]. In particular, several transcripts were found to strongly modify trade-offs between growth and defence. The most significant variation in gene expression at the population level was in a terpenoid ABC transporter gene: expression of the putative PDR type ABC transporter ATPDR12/PDR12 was positively correlated with height but negatively correlated with weevil susceptibility. In addition, a functional analysis conducted in transgenic poplar investigated the role of some components of the ABA signalling network in drought resistance and biomass production [271•]. ABA plays a central role in plant acclimation to drought, being part of a conserved signalling network in land plants. This network involves ABA receptor proteins, i.e. Regulatory Component of ABA Receptors (RCARs)/Pyrabactin Resistance 1 (PYR1)/PYR1-like (PYL), phosphatases (PP2Cs) and SnRK2 kinases (sucrose nonfermenting 1-related protein kinase 2). Under normal conditions, PP2Cs suppress SnRK2 activity by dephosphorylation. Once ABA accumulates under stress, PYR/PYL/RCARs bind ABA and interact with PP2Cs to inhibit phosphatase activity. Consequently, SnRK2 is kept in its active, phosphorylated form, regulating downstream responses such as ion channels and AREB (ABA-Responsive Element Binding protein) transcription factors to induce stomatal closure and osmotic adjustment. The authors found that AREB3 overexpression resulted in enhanced drought resistance but a massive biomass loss. In poplar also, a transcriptome analysis generated a set of responsive genes for JA, SA and *Melampsora larici-populina* (poplar rust) treatments and proposed possible roles of JA/SA in regulating the balance between growth and defence responses by integrating multiple hormone signalling pathways [261].

These studies are the first of a potential long series concerning perennial forest trees. As knowledge on tree genomes and physiology increases, the large amount of molecular data collected on different kind of stress in trees pave the way for studies on the molecular bases of trade-offs between growth and stress responses [272•], as well as open the way to the study of other main trade-offs at the molecular interaction level.

Conclusions and Perspectives

Trade-offs among growth, reproduction, defence, stress tolerance and product quality predicted theoretically have been reported experimentally in many breeding programmes, reviewed in this work (Table 2).

Breeding for resilience demands considering new or neglected traits among the selection criteria. Particularly, reproduction as a major objective is directly related to the establishment of new forests that will reproduce naturally. Therefore, we need a better understanding of the interactions between reproduction and other processes that limit growth [273]. Also, plant breeders have selected alleles which maximise the benefits and minimise the costs of resistance to biotic attacks [274], but we will need to search for general defensive mechanisms to a wide range of pests and pathogens, even to those that may arise due to the ongoing global change [4••]. Given the altered wildfire regimes already occurring in temperate regions around the world [193•], inclusion of fire adaptation in breeding programmes now deserves some focussed attention.

All these challenges, and the inclusion of new breeding objectives related to wood and NTWP, would require exploring new solutions and designing novel breeding strategies, like subdivided populations [275], using restricted index selection [276], or by index selection with optimal economical weights to deal with trade-offs [277].

The fact that many key trade-offs may be affected by the environment deserves further attention in the deployment of forest reproductive materials. Entirely novel environments imply hidden reaction norms [278] that could exacerbate negative trade-offs with undesirable effects for the resilience of forest tree populations. In the same sense, ecologically marginal populations, even those relevant as genetic conservation units, may be particularly threatened due to worsening of trade-offs in an increasingly harsh environment [279••].

Beyond pairwise trade-offs, a challenging multivariate approach is steadily rising in recent basic and applied biological science: phenotypic integration, i.e. the multivariate correlations of traits indicative of main evolutionary and functional processes [19, 20•]. This multivariate approach will be particularly informative for the future adaptation of forest genetic resources (including breeding for resilience) if

Table 2 Summary of the trade-offs considered in this review, the direction of the theoretical expectations and the strength and direction of the empirical evidence. The reference number is ordered according to the citation in the text

Trait 1	Trait 2 or trade-off	Theoretical prediction	Empirical support in forest trees	References
Survival	Growth	Trade-off expected following divergent evolutionary trajectories between conservative and acquisitive strategies	Results among species generally confirming such trade-off. Environment-specific results within-species, generally non supporting a widespread trade-off, or showing positive correlation	40-46, 58
Reproduction	Growth	Key trade-off predicted by life-history theory based on differential allocation	Evidence in manipulative experiments, selection experiments	67
Reproduction	Growth	More pronounced trade-off in female vs male reproduction due to different costs between genders	Broad evidence in dioecious species, and intraspecific differences in monoecious species	73-75
Reproduction	Allocation to the main stem	Higher allocation to the main stem associated to high apical dominance would decrease reproductive allocation due to physical limitation	Confirmed in a single experiment in *Pinus pinaster*, within-pop selection experiment	79
Reproduction	Seed number vs seed size	A negative correlation predicted based in differential allocation: fewer bigger seeds or more smaller seeds	Lack of evidence in forest trees, except difference between conifers and broadleaves	84
Reproduction	Inter-annual reproductive trade-off	High reproductive output in mast years will cause lower reproduction in following years due to carbon storage depletion	Broad evidence in masting species and one manipulative experiment in *P. halepensis* confirming this trade-off	70, 81, 82
Reproduction	Defences	Resource allocation compromises predict the emergence of trade-offs among these functions	Reproduction and defences are not maximised at the same time in pines	87, 88
Defences	Tolerance vs resistance	A trade-off is expected between both complementary strategies, which follow opposite evolutionary trajectories	No previous studies on trees	
Defences	Constitutive vs Induced defences	Both limitation in resource allocation and contrasting evolutionary trajectories should favour the emergence of a trade-off	Negative relationships both within and among species	110, 120
Defences	Physical vs Chemical defences	Competition for resources should favour trade-off among both types of defences but integration of multiple defences may be beneficial for efficient resistance	Positive phenotypic relationships have been reported but results are highly variable depending on the specific defences tested	101, 119
Defences	Resistance to different biotic threats	Quantitative general defences may confer multiple resistance but specific resistance mechanisms may be needed facing different aggressors	No previous studies on trees	
Defences	Resistance to biotic and abiotic stress	Resource limiting conditions may favour both, but allocation compromises point in the opposite direction	No previous studies on trees	
Defences	Growth	Resource allocation compromises predict the emergence of trade-offs among these functions	Evidences of negative relationships are frequent but counterexamples do also exist	98, 100, 101, 110, 111, 123, 124
Phenology	Growth	Longer vegetative period is expected to increase growth	Primary growth is limited by budburst timing in *Fagus sylvatica*. Genetic gain in growth attained by selecting extended-growth genotypes in conifer breeding programs.	132•, 136, 137
Phenology	Cold damage	Earlier budburst or later bud set are expected to increase frost damage	Contrasting results among species, mostly conifers. No effect in *Picea abies*, while selected seedlings with delay in growth cessation resulted in a slightly greater cold injury in *Pinus contorta*	139, 140•
Phenology	Wood density	Secondary growth is related to apical growth, and in turn affecting early- latewood transition with effect in wood properties	Later cessation of apical growth related to later transition to latewood and lower specific gravity in *Pinus taeda*	142
Drought tolerance	Growth	Resource allocation compromises may limit growth in drought tolerant genotypes	Contrasting results	156, 163-168
Drought tolerance	Xylem cavitation resistance vs xylem efficiency	Anatomic xylem features improving water transport compromise xylem cavitation resistance	Contrasting results	152-156
Drought tolerance	Growth	Resource allocation compromises may limit growth in drought tolerant genotypes	Contrasting results	156, 161-168
Water use efficiency	Growth	Reduction of water loss through stomatal closure reduce carbon fixation through photosynthesis	Evidence at the interspecific level. At the intra-specific level some studies support this trade-off according to genetic correlations	32, 169-174, 176
Water use efficiency	Xylem cavitation resistance	Covariation of xylem cavitation resistance with other hydraulic traits may compromise WUE	Contrasting results across populations within a species. No significant trend detected at the intra-population level	167, 171
Tolerance to temperature extremes	Other functional traits	Trade-offs between extreme heat and cold tolerance are expected with leaf area, vessel dimensions, budburst and senescence phenology, bark thickness, etc	No previous studies on trees	
Fire adaptation	Serotiny vs bark thickness	Negative correlation predicted due to differential allocation and contrasting evolutionary trajectories of fire tolerant vs fire embracer species	Widely confirmed between species but lack of evidence within species	207, 208
Fire adaptation	Resprouting ability vs seed production	Negative correlation predicted due to differential allocation and contrasting evolutionary trajectories between fire tolerant and fire embracer species	Widely confirmed between species but lack of evidence within species	207, 208
Wood quality	Wood density vs lifespan	High stem stiffness due to higher density is predicted to relate positively to lifespan and vice versa, following the conservative/acquisitive life history divergence	Confirmed among species in tropical broadleaves. No information in conifers and/or within species.	210,211
Wood quality	Growth	Faster secondary growth is expected to decrease wood quality from multiple criteria: density, knots, percentage of juvenile wood, etc	Unfavourable estimated genetic correlations of wood density and stiffness with growth traits were in major conifers	3,220,221,227,236–249
NWFPs	Growth, other	Different trends can be expected, depending on the specific nature of the product (defensive compound, reproductive structure, bark, etc.) and the genetic level	No specific studies, but indirect relevant information	79, 255-261

fitness-related traits are regularly included in the phenotypic databases in addition to those considered as the main breeding objectives (Fig. 3). This is not easily attainable for the large experiments commonly used in breeding programmes, but, at least initially, can be tackled in a subsample of genotypes assessed in at least two contrasting environments.

Society is demanding that a wider portfolio of ecosystem services should be provided by forests [280]. Rather than focus on productivity traits alone, breeders will now have to consider searching for broad general defence ability or tolerance to abiotic stressors, balanced carefully against losses of potential gain (e.g. [20•, 100•]). Such a strategy

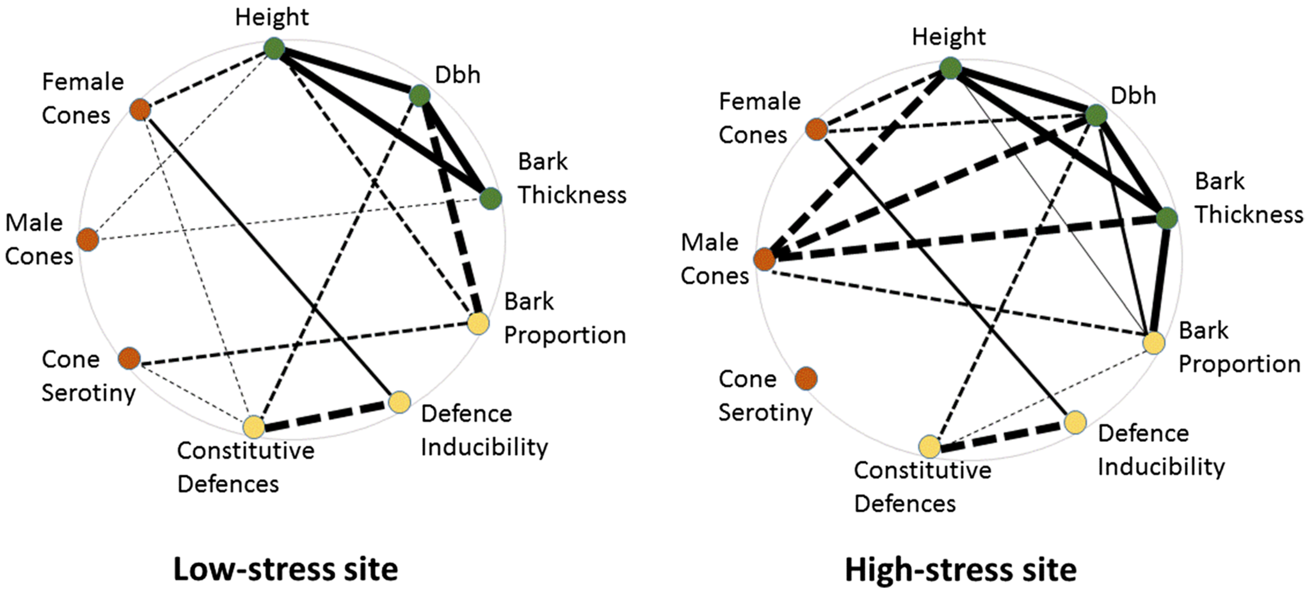


Fig. 3 Change in the coordination network among traits from a provenance trial of Aleppo pine (*P. halepensis*) replicated in two contrasted environments. Solid and dashed lines represent significant positive and negative correlations (based in population BLUPs), respectively, with line thickness proportional to correlation coefficient values. Climent et al. (unpublished). Low stress site corresponds to the one assessed in [20•]

would produce trees more likely to be resilient to a range of pressures over the lifetime of the plantation. Moreover, the growing prospect of advances in breeding efficiency through use of new genomic resources and models provides a major incentive to build the knowledge base on trait trade-offs. The primary concern is to know whether economically valued traits can be decoupled from deleterious effects and so unwanted correlated genetic changes in the breeding process can be avoided [281]. These questions are not exclusive to tree breeding. Genetic improvement of crop plants faces similar challenges, despite their far more uniform cultivation environments and typically annual turnover (see, for example [282•]). Trade-offs also have deep implications for the conservation of forest genetic resources, since natural selection in the wild cannot overcome constraints as easily as in breeding programmes. The goal of conserving adaptive potential, the ultimate aim of the European Forest Genetic Resource conservation programme, EUFORGEN [283, 284], for example, could be limited by trade-offs, especially in relation to resistance to both biotic and abiotic stressors and reproduction.

Much of the information for managing trade-offs in breeding and conservation activities is still missing. We urgently need new studies, under novel environments, to forecast levels of integration in improved populations. Comparisons between improved and natural populations and the effects of future environments on the expression of these trade-offs are also key topics for future study. Particularly, assisted migration is under discussion due to the accelerated rate of climate change [see, for example [285••] and references therein]. In recent years, the conscious movement of provenances and/or genotypes adapted to future projected conditions according to climate change scenarios constitutes a hot point of debate that has permeated society [286]. However, we still lack a scientifically defined position concerning different evolutionary, economical and ethical aspects of its application, particularly with regard to the practical importance of the coordinated responses of multivariate phenotypes under new environments, including the trade-offs described in this review.

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Adaptive Syndromes". H.H. and A.S. wrote section "Wood Quality". S.M. wrote section "Non-Wood Forest Products". D.G., JC.L. and SC.GM. wrote section "Molecular Basis of Trade-Offs: Plant Growth and Stress Responses". Finally, S.C. underwent several critical readings of the manuscript and overall style edits

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- •• Of major importance

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