



HAL
open science

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

Jose Climent, Ricardo Alía, Katri Karkkainen, Catherine Bastien, Marta Benito-Garzon, Laurent Bouffier, Giovanbatti de Dato, Sylvain Delzon, Arnaud Dowkiw, Margarita Elvira-Recueno, et al.

► To cite this version:

Jose Climent, Ricardo Alía, Katri Karkkainen, Catherine Bastien, Marta Benito-Garzon, et al.. Trade-offs and Trait Integration in Tree Phenotypes: Consequences for the Sustainable Use of Genetic Resources. *Current Forestry Reports*, 2024, 10.1007/s40725-024-00217-5 . hal-04512732

HAL Id: hal-04512732

<https://hal.inrae.fr/hal-04512732>

Submitted on 20 Mar 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution 4.0 International License



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

Jose Climent¹ · Ricardo Alía¹ · Katri Karkkainen² · Catherine Bastien³ · Marta Benito-Garzon⁴ · Laurent Bouffier⁴ · Giovanbattista De Dato⁵ · Sylvain Delzon⁴ · Arnaud Dowkiw³ · Margarita Elvira-Recuenco¹ · Delphine Grivet¹ · Santiago C. González-Martínez⁴ · Haleh Hayatgheibi⁶ · Sonja Kujala² · Jean-Charles Leplé⁴ · Ruth C. Martín-Sanz⁷ · Marina de Miguel⁴ · M. Cristina Monteverdi⁵ · Sven Mutke¹ · Christophe Plomion⁴ · José Alberto Ramírez-Valiente¹ · Leopoldo Sanchez³ · Aida Solé-Medina¹ · Jean-Paul Soularue⁴ · Arne Steffenrem⁸ · Angela Teani⁵ · Johan Westin⁶ · Richard Whittet⁹ · Harry Wu⁶ · Rafael Zas¹⁰ · Stephen Cavers¹¹

Accepted: 21 February 2024
© The Author(s) 2024

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.

Extended author information available on the last page of the article

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.

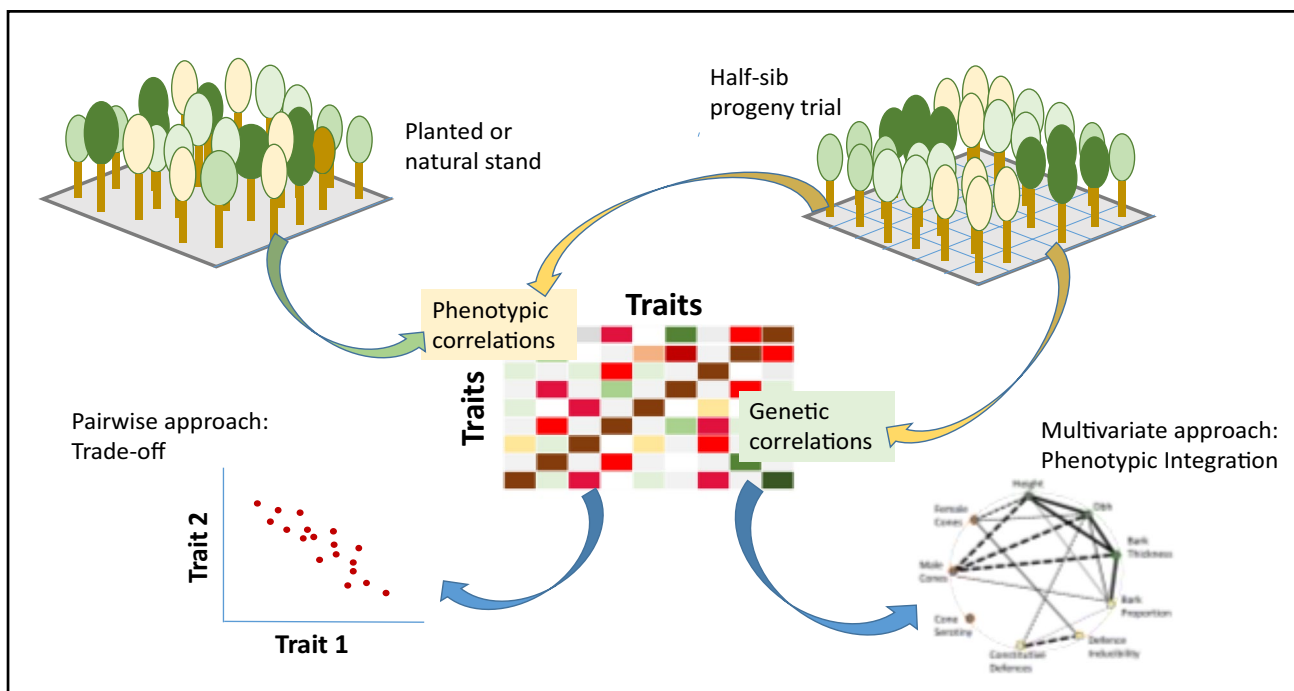
Another key point to take into account is the fact that genetic correlations between traits can differ depending on multiple factors such as population, environment, age, and selective pressure [15•, 16]. Genotype-by-environment interactions may influence the expression of trade-offs, as the magnitude 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 |
|---------------------------------------|----------|---------------------------|--|------------------|-----------------------------|
| <i>Hymenoscyphus fraxineus</i> | Fungus | Ash dieback, chalara | Ash (<i>F. excelsior</i> , <i>F. communis</i>) | East Asia | Europe |
| <i>Bursaphelenchus xylophilus</i> | Nematode | Pine wood nematode | Pines | North America | Japan, Portugal, Spain |
| <i>Fusarium circinatum</i> | Fungus | Pine pitch canker | Pines | Central America | Worldwide |
| <i>Agrilus planipennis</i> | Insect | Emerald ash borer | Ash | NE Asia | North America |
| <i>Dothistroma septosporum / pini</i> | Fungus | Dothistroma needle blight | Pine (<i>P. radiata</i>) | Himalayas, Andes | New Zealand, Asia, NE Spain |
| <i>Austropuccinia psidii</i> | Fungus | Myrtle rust | Eucalypt | South America | Brazil, Australia |
| <i>Leptoglossus occidentalis</i> | Insect | Western conifer seed bug | Stone pine (<i>P. pinea</i>) | 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 bark 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 (Δ TSDM, [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

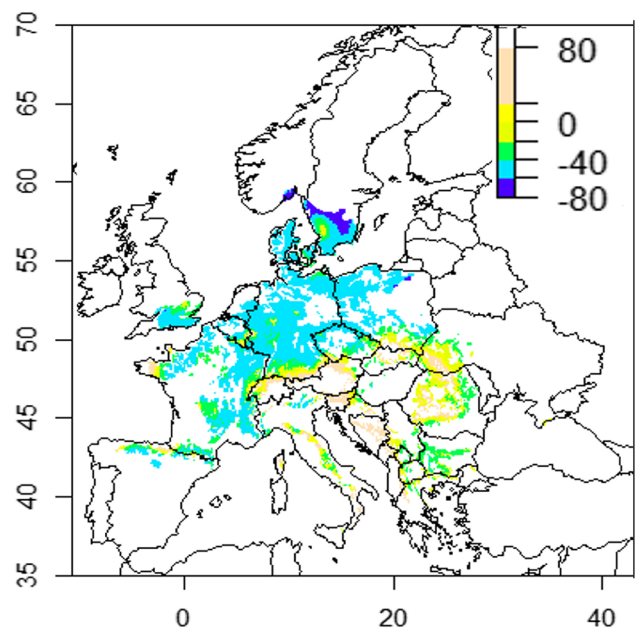


Fig. 2 Differences in predicted height (cm) between models considering only climate variables (precipitation of the warmest month of the trials) and considering leaf flushing as a covariate. Negative values (blue) indicate those regions where aboveground primary tree growth is limited by the timing of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

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.

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 die-back 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 CO₂ 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 CO₂ 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 <i>Pinus pinaster</i> , 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 <i>P. halepensis</i> 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 <i>Fagus sylvatica</i> . 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 <i>Picea abies</i> , while selected seedlings with delay in growth cessation resulted in a slightly greater cold injury in <i>Pinus contorta</i> | 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 <i>Pinus taeda</i> | 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

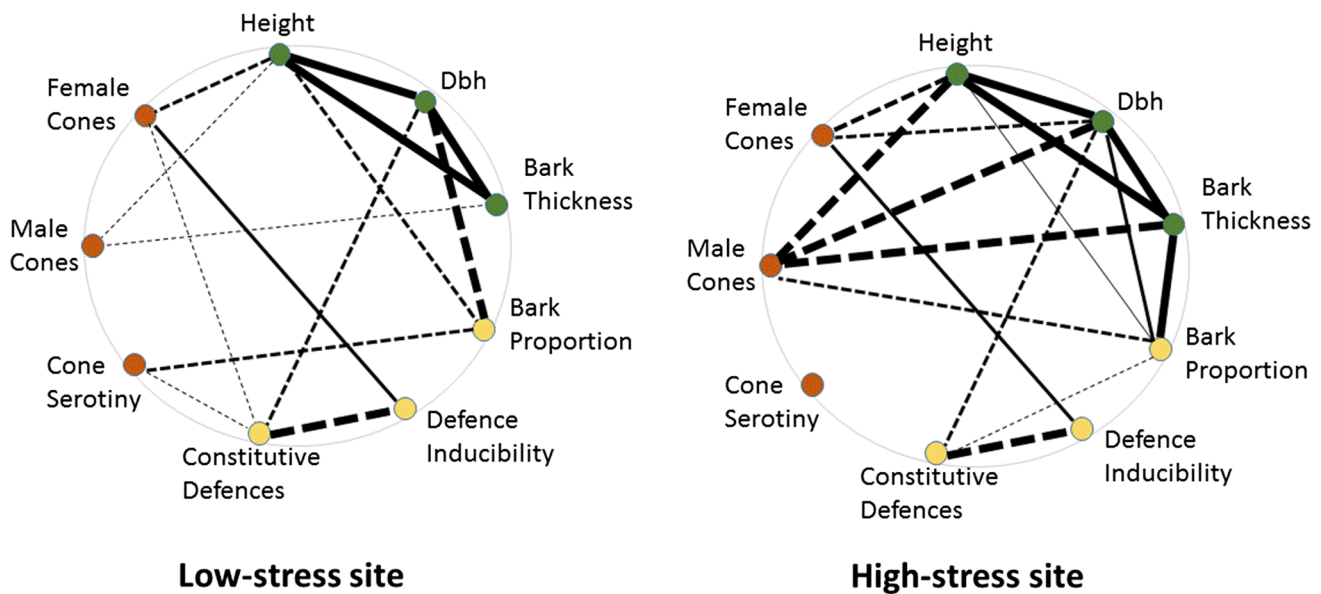


Fig. 3 Change in the coordination network among traits from a provenance trial of Aleppo pine (*P. halepensis*) replicated in two contrasted environments. Solid and dashed lines represent significant positive and negative correlations (based in population BLUPs), respectively, with line thickness proportional 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.

Acknowledgements Many thanks to Marie-Laure Desprez-Loustau for her contribution to the initial steps of the manuscript (the “Defence: Pests, Diseases and Multiple Resistance” section)

Author contributions J.C. and C.B. created the review draft. J.C. wrote section “Reproduction”, prepared Fig. 1, contributed to Table 2, coordinated the section authors and underwent successive revisions for coherence between sections. R.A. wrote section “Conclusion and Perspectives”, prepared Table 2, contributed to the Introduction and pruned and organised the bibliography. K.K. wrote section “Seasonality (Phenology)”, together with S.K. and M.B.G., underwent several revisions to the entire text and contributed also to section “Reproduction”. M.B.G. also prepared Fig. 2. L.B., L.S. and A.S. contributed to the Introduction. G.D.D. wrote section “Growth: the Key Breeding Objective” together with A.T. and commented in other sections. J.A.R.V. completed section “Survival Rate” from a first version by H.W. and J.W. and contributed to the Introduction. R.Z., J.P.S., M.E., wrote section “Defence: Pests, Diseases and Multiple Resistance”. J.P.S. also commented on other sections. M.M., A.D., S.D., C.M. and C.P. wrote section “Drought tolerance and WUE” and M.M. also coordinated changes after review in this section. S.C. and R.W. wrote section “Tolerance to Temperature Extremes”. RC.M.S. wrote section “Fire

Adaptive Syndromes". H.H. and A.S. wrote section "**Wood Quality**". S.M. wrote section "**Non-Wood Forest Products**". D.G., J.C.L. and S.C.G.M. 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

Funding Open Access funding provided thanks to the CRUE-CSIC agreement with Springer Nature. H2020 773383 (B4EST), RTI2018-094691-B-C32 and C33 (RESILPINE), University of Bordeaux's France 2030 programme 'GPR Bordeaux Plant Sciences'.

Data Availability No datasets were generated or analysed during the current study.

Compliance with Ethical Standards

Competing interests The authors declare no competing interests.

Human and Animal Rights and Informed Consent This article does not contain any studies with human or animal subjects performed by any of the authors.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

Papers of particular interest, published recently, have been highlighted as:

- Of importance
- Of major importance

- 1.● Sheppard JP, Chamberlain J, Agúndez D, Bhattacharya P, Chirwa PW, Gontcharov A, et al. Sustainable forest management beyond the timber-oriented status quo: transitioning to co-production of timber and non-wood forest products—a global perspective. *Curr For Reports*. 2020; 6:26–40. **This review provides perspectives and insights of worldwide forest research with examples from diverse and dynamic use of forest products that are undervalued and often misrepresented to provide a logical argument for transitioning to sustainable management of forests for timber and NWFP.**
- 2.● Jactel H, Desprez-Loustau M-L, Battisti A, Brockerhoff E, Santini A, Stenlid J, et al. Pathologists and entomologists must join forces against forest pest and pathogen invasions. *Neo-Biota*. 2020; 58:107–27. **This opinion paper reviews recent biotic invasions of exotic pests and pathogens and advocates increased collaboration between these two scientific communities to improve the long-term health of forests.**
3. Jansson G, Hansen JK, Haapanen M, Kvaalen H, Steffenrem A. The genetic and economic gains from forest tree breeding

programmes in Scandinavia and Finland. *Scand J For Res*. 2017;32:273–86.

- 4.●● Guégan J-F, De Thoisy B, Gomez-Gallego M, Jactel H. World forests, global change, and emerging pests and pathogens. *Current Opinion in Environmental Sustainability*. 2023; 61: 101266. **This review highlights that the subject of pathogens and plant pests, traditionally rooted in agronomic approaches, lacks work on macroecology and biogeography, and discusses the research orientations to better anticipate their ecological and economic impacts in order to better achieve environmental sustainability.**
- 5.●● Mauro A, Ghalambor CA. Trade-offs, pleiotropy, and shared molecular pathways: a unified view of constraints on adaptation. *Integr Comp Biol*. 2020; 60:332–47. **This paper reviews the classic paradigms in which physiologists and evolutionary biologists have studied trade-offs and highlights the ways in which network and molecular pathway approaches unify these paradigms. It also discusses how these approaches allow researchers to evaluate why trade-offs arise and how selection can act to overcome trait correlations and evolutionary constraints.**
6. Stearns SC, Roff DA. *The Evolution of Life Histories*. London: Oxford University Press; 1992.
- 7.● Damián X, Ochoa-López S, Gaxiola A, Fornoni J, Domínguez CA, Boege K. Natural selection acting on integrated phenotypes: covariance among functional leaf traits increases plant fitness. *New Phytol*. 2020; 225:546–57. **This paper gives experimental evidence to the adaptive value of phenotypic integration in leaf functional traits of a shrub species, by analysing whether natural selection favoured the expression of individual traits, particular combinations of traits or leaf phenotypic integration.**
8. Murren CJ. The integrated phenotype. *Integr Comp Biol*. 2012;52:64–76.
9. Murren CJ. Phenotypic integration in plants. *Plant Species Biol*. 2002;17:89–99.
10. Braendle C, Heyland A, Flatt T physiology of life, 2011 U. Integrating mechanistic and evolutionary analysis of life history variation. *Mech Life Hist Evol*. Oxford: Oxford University Press; 2013;3–10.
11. Stearns S. Trade-offs in life-history evolution. *Funct Ecol*. 1989;3:259–68.
- 12.● Morrissey MB. Selection and evolution of causally covarying traits. *Evolution*. 2014; 68:1748–61. **In this paper, the authors use path analysis to formally define “extended” selection gradients, which are the total effects of traits on fitness, as opposed to the existing definition of selection gradients, and thus obtaining a more intuitive scheme for characterizing multi-trait selection.**
13. Weih M. Trade-offs in plants and the prospects for breeding using modern biotechnology. *New Phytol*. 2003;158:7–9.
14. Sinervo B, Svensson E. Correlational selection and the evolution of genomic architecture. *Heredity*. 2002;89:329–38.
- 15.● Benavides R, Carvalho B, Matesanz S, Bastias CC, Cavers S, Escudero A, et al. Phenotypes of *Pinus sylvestris* are more coordinated under local harsher conditions across Europe. *J Ecol*. 2021; 109:2580–96. **In this work, the authors found that trait covariation varied at different spatial scales and increased under harsher conditions, and the robustness and repeatability of this pattern suggests its adaptive role for Scots pine responses to different environments.**
16. Stearns S, de Jong G, Newman B. The effects of phenotypic plasticity on genetic correlations. *Trends Ecol Evol*. 1991;6:122–6.
17. Sole-Medina A, Robledo-Arnuncio JJ, Ramirez-Valiente JA. Multi-trait genetic variation in resource-use strategies and phenotypic plasticity correlates with local climate across the

- range of a Mediterranean oak (*Quercus faginea*). *New Phytol.* 2022;234:462–78.
18. ●● Schneider HM. Characterization, costs, cues and future perspectives of phenotypic plasticity. *Ann Bot.* 2022; 130:131–48. **This key review discusses the characterization and costs of plasticity and promising research directions including trade-offs, costs and limits to the expression of plasticity in plants.**
 19. Pigliucci M. Phenotypic integration: studying the ecology and evolution of complex phenotypes. *Ecol Lett.* 2003;6:265–72.
 20. ● Santini F, Climent JM, Voltas J. Phenotypic integration and life history strategies among populations of *Pinus halepensis*: an insight through structural equation modelling. *Ann Bot.* 2019; 124:1161–71. **This seminal paper uses structural equation modelling to evaluate phenotypic integration between six latent variables related to water use, growth and reproduction in a provenance trial of Aleppo pine, revealing meaningful ecotypic trends of trait covariation.**
 21. ● Poorter H, Jagodzinski AM, Ruiz-Peinado R, Kuyah S, Luo Y, Oleksyn J, et al. How does biomass distribution change with size and differ among species? An analysis for 1200 plant species from five continents. *New Phytol.* 2015; 208:736–49. **Using a huge database, this paper changes the long-lasting theory of fixed allometric exponents across plant taxa. Rather, continuous shifts in allometric exponents with plant size during ontogeny and evolution are the norm. Across seed plants, variation in biomass distribution among species is related more to function than phylogeny.**
 22. Poorter H, et al. Interspecific variation in relative growth rate : on ecological causes and physiological consequences. In: Lambers H, et al., editors. *Causes and consequences of variation in growth rate and productivity of higher plants.* The Hague, The Netherlands: SPB Academic Publishing; 1989. p. 45–68.
 23. Lind BM, Menon M, Bolte CE, Fiske TM, Eckert AJ. The genomics of local adaptation in trees : are we out of the woods yet ? *Tree Genet Genomes.* 2018;14:29.
 24. Chmura DJ, Guzik M, Ro R. Allometry varies among related families of Norway spruce. *Ann For Sci.* 2017;74:36.
 25. Stovall JP, Fox TR, Seiler JR. Allometry varies among 6-year-old. *For Sci.* 2013;59:50–62.
 26. Stovall JP, Fox TR, Seiler JR. Short-term changes in biomass partitioning of two full-sib clones of *Pinus taeda* L . under differing fertilizer regimes over 4 months. *Trees.* 2012;26:951–61.
 27. Vizcaíno-Palomar N, Ibañez I, Gonzalez-Martinez SC, Zavala MA, Alía R. Adaptation and plasticity in aboveground allometry variation of four pine species. *Ecol Evol.* 2016;6:7561–73.
 28. McCarthy MC, Enquist BJ. Consistency between an allometric approach and optimal partitioning theory in global patterns of plant biomass allocation. *Funct Ecol.* 2007;21:713–20.
 29. Weiner J. Allocation, plasticity and allometry in plants. *Perspect Plant Ecol Evol Syst.* 2004;6:207–15.
 30. Tardieu F. Virtual plants: modelling as a tool for the genomics of tolerance to water deficit. *Trends Plant Sci.* 2003;8:9–14.
 31. Chambel MR, Climent J, Alía R. Divergence among species and populations of Mediterranean pines in biomass allocation of seedlings grown under two watering regimes. *Ann For Sci.* 2007;64:87–97.
 32. Aranda I, Alía R, Ortega U, Dantas ÂK, Majada J. Intra-specific variability in biomass partitioning and carbon isotopic discrimination under moderate drought stress in seedlings from four *Pinus pinaster* populations. *Tree Genet Genomes.* 2010;6:169–78.
 33. ● Martín-Sanz RC, San-Martín R, Poorter H, Vázquez A, Climent J. How does water availability affect the allocation to bark in a Mediterranean conifer? *Front Plant Sci.* 2019; 10:607. **This paper shows both ecotypic variation of bark allocation and a strong effect of site on the allometry between wood and bark in a replicated common garden of Aleppo pine, such that the stressful environment consistently reduced relative bark allocation in all provenances.**
 34. Santos-Del-Blanco L, Bonser SP, Valladares F, Chambel MR, Climent J. Plasticity in reproduction and growth among 52 range-wide populations of a Mediterranean conifer: adaptive responses to environmental stress. *J Evol Biol.* 2013;26:1912–24.
 35. Garland T. Trade-offs. *Curr Biol.* 2014;24:R60–1.
 36. Zotz G, Wilhelm K, Becker A. Heteroblasty—a review. *Bot Rev.* 2011;77:109–51.
 37. ● Das AJ, Stephenson NL, Davis KP. Why do trees die? Characterizing the drivers of background tree mortality. *Ecology.* 2016; 97:2616–27. **This paper analyses a large tree dataset, and found that, rather than being driven by abiotic factors such as lightning or windstorms, the “ambient” or “random” background mortality that many forest models presume to be independent of tree growth rate is instead dominated by biotic agents of tree mortality, with potentially critical implications for forecasting future mortality.**
 38. Reich PB, Walters MB, Ellsworth DS. From tropics to tundra: global convergence in plant functioning. *Proc Natl Acad Sci.* 1997;94:13730–4.
 39. ●● Reich PB. The world-wide “fast-slow” plant economics spectrum: a traits manifesto. *J Ecol.* 2014; 102:275–301. **This essential work develops the theory that a single ‘fast-slow’ plant economics spectrum that integrates across leaves, stems and roots is a key feature of the plant universe and helps to explain individual ecological strategies, community assembly processes and the functioning of ecosystems.**
 40. Martínez-Vilalta J, Piñol J. Drought-induced mortality and hydraulic architecture in pine populations of the NE Iberian Peninsula. *For Ecol Manage.* 2002;161:247–56.
 41. Harter DEV, Nagy L, Backhaus S, Beierkuhnlein C, Fussi B, Huber G, et al. A comparison of genetic diversity and phenotypic plasticity among European beech (*Fagus sylvatica* L.) populations from Bulgaria and Germany under drought and temperature manipulation. *Int J Plant Sci.* 2015;176:232–44.
 42. Philipson CD, Dent DH, O’Brien MJ, Chamagne J, Dzulkifli D, Nilus R, et al. A trait-based trade-off between growth and mortality: evidence from 15 tropical tree species using size-specific relative growth rates. *Ecol Evol.* 2014;4:3675–88.
 43. Thiel D, Kreyling J, Backhaus S, Beierkuhnlein C, Buhk C, Egen K, et al. Different reactions of central and marginal provenances of *Fagus sylvatica* to experimental drought. *Eur J For Res.* 2014;133:247–60.
 44. Wright SJ, Kitajima K, Kraft NJB, Reich PB, Wright IJ, Bunker DE, et al. Functional traits and the growth-mortality trade-off in tropical trees. *Ecology.* 2010;91:3664–74.
 45. Wu HX, Ying CC. Geographic pattern of local optimality in natural populations of lodgepole pine. *For Ecol Manage.* 2004;194:177–98.
 46. St Clair JB, Howe GT, Kling JG. The 1912 Douglas-fir heredity study: long-term effects of climatic transfer distance on growth and survival. *J For.* 2020;118:1–13.
 47. ● Younginger BS, Sirová D, Cruzan MB, Ballhorn DJ. Is biomass a reliable estimate of plant fitness? *Appl Plant Sci.* 2017;5:1600094. **Biomass or growth rate are frequently used and often positively associated with fecundity, which in turn suggests greater overall fitness. This paper confirmed the utility of biomass as an appropriate surrogate for fitness under many circumstances, but suggested that additional fitness measures should be reported along with biomass or growth rate whenever possible.**
 48. Olsson T, Ericsson T. Genetic parameter estimates of growth and survival of *Pinus sylvestris* with mixed model multiple-trait

- restricted maximum likelihood analysis. *Scand J For Res.* 2002;17:103–10.
49. Persson T, Andersson B. Genetic variance and covariance patterns of growth and survival in Northern *Pinus sylvestris*. *Scand J For Res.* 2003;18:332–43.
 50. Kroon J, Ericsson T, Jansson G, Andersson B. Patterns of genetic parameters for height in field genetic tests of *Picea abies* and *Pinus sylvestris* in Sweden. *Tree Genet Genomes.* 2011;7:1099–111.
 51. Persson T, Andersson B, Ericsson T. Relationship between autumn cold hardiness and field performance in northern *Pinus sylvestris*. *Silva Fenn.* 2010;44:255–66.
 52. • Calleja-Rodriguez A, Andersson Gull B, Wu HX, Mullin TJ, Persson T. Genotype-by-environment interactions and the dynamic relationship between tree vitality and height in northern *Pinus sylvestris*. *Tree Genet Genomes.* 2019; 15, 36. **A particularly wide-scale work addressing the relationship between growth and survival/vitality in Scots pine, indicating stronger positive genetic correlation between survival and height in harsher (colder) than in milder environments.**
 53. Rousi M, Possen BJMH, Ruotsalainen S, Silfver T, Mikola J. Temperature and soil fertility as regulators of tree line Scots pine growth and survival—implications for the acclimation capacity of northern populations. *Glob Chang Biol.* 2018;24:e545–59.
 54. Russo SE, Brown P, Tan S, Davies SJ. Interspecific demographic trade-offs and soil-related habitat associations of tree species along resource gradients. *J Ecol.* 2008;96:192–203.
 55. Bigler C, Veblen TT. Increased early growth rates decrease longevity of conifers in subalpine forests. *Oikos.* 2009;118:1130–8.
 56. Negreiros D, Fernandes GW, Efremova AA, Le Stradic S, Neves ACO. Growth-survival trade-off in shrub saplings from Neotropical mountain grasslands. *South African J Bot.* 2016;106:17–22.
 57. Yang W, Liu F, Zhou L, Zhang S, An S. Trade-offs between growth and survival of non-pioneer light-demanding tree seedlings in tropical forest of Hainan Island. *China J Trop Ecol.* 2011;27:611–20.
 58. • Ramírez-Valiente JA, Santos del Blanco L, Alía R, Robledo-Arnuncio JJ, Climent J. Adaptation of Mediterranean forest species to climate: lessons from common garden experiments. *J Ecol.* 2021;1022–42. **A review and analysis of common garden data showing that no negative association between growth- and persistence-related traits at the intraspecific level, but marked adaptation to temperature and precipitation regimes.**
 59. Villar-Salvador P, Puértolas J, Cuesta B, Peñuelas JL, Uscola M, Heredia-Guerrero N, et al. Increase in size and nitrogen concentration enhances seedling survival in Mediterranean plantations. Insights from an ecophysiological conceptual model of plant survival. *New For.* 2012;43:755–70.
 60. Reekie E, Bazzaz FA. Reproductive allocation in plants. Elsevier Academic Press; 2005.
 61. Obeso JR. The costs of reproduction in plants. *New Phytol.* 2002;155:321–48.
 62. Karlsson PS, Méndez M. The resource economy of plant reproduction. *Reprod Alloc Plants.* 2005;1–49.
 63. Barringer BC, Koenig WD, Knops JMH. Interrelationships among life-history traits in three California oaks. *Oecologia.* 2013;171:129–39.
 64. Vilà-Cabrera A, Martínez-Vilalta J, Retana J. Variation in reproduction and growth in declining Scots pine populations. *Perspect Plant Ecol Evol Syst.* 2014;16:111–20.
 65. Leal DB, Thomas SC. Vertical gradients and tree-to-tree variation in shoot morphology and foliar nitrogen in an old-growth *Pinus strobus* stand. *Can J For Res.* 2003;33:1304–14.
 66. Reznick D. Costs of reproduction: an evaluation of the empirical evidence. *Oikos.* 1985;44:257.
 67. • Santos-del-Blanco L, Climent J. Costs of female reproduction in a conifer tree: a whole-tree level assessment. *J Ecol.* 2014; 102:1310–7. **This paper undertakes a singular cone-withdrawal manipulative experiment to unveil costs of reproduction in young Aleppo pines to demonstrate experimentally an effect in next female reproduction, while effect on vegetative growth was marginal.**
 68. Thomas SC. Age-related changes in tree growth and functional biology: the role of reproduction. 2011;33–64.
 69. Bonser SP, Ladd B. The evolution of competitive strategies in annual plants. *Plant Ecol.* 2011;212:1441–9.
 70. Sala A, Hopping K, McIntire EJB, Delzon S, Crone EE. Mast-ing in whitebark pine (*Pinus albicaulis*) depletes stored nutrients. *New Phytol.* 2012;196:189–99.
 71. Qiu T, Aravena MC, Andrus R, Ascoli D, Bergeron Y, Berretti R, et al. Is there tree senescence? The fecundity evidence. *Proc Natl Acad Sci USA.* 2021;118:1–10.
 72. McDowell SCL, McDowell NG, Marshall JD, Hultine K. Carbon and nitrogen allocation to male and female reproduction in Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca*, *Pinaceae*). *Am J Bot.* 2000;87:539–46.
 73. Verdú M, Spanos K, Čaňová I, Slobodník B, Paule L. Similar gender dimorphism in the costs of reproduction across the geographic range of *Fraxinus ornus*. *Ann Bot.* 2007;99:183–91.
 74. Savolainen O, Karkkainen K, Harju A, Nikkanen T, Rusanen M. Fertility variation in *Pinus sylvestris*: a test of sexual allocation theory. *Am J Bot.* 1993;80:1016–20.
 75. Santos-Del-Blanco L, Climent J, González-Martínez SC, Pannell JR. Genetic differentiation for size at first reproduction through male versus female functions in the widespread Mediterranean tree *Pinus pinaster*. *Ann Bot.* 2012;110:1449–60.
 76. Mutke S, Sievänen R, Nikinmaa E, Perttunen J, Gil L. Crown architecture of grafted Stone pine (*Pinus pinea* L.): shoot growth and bud differentiation. *Trees-Struct Funct.* 2005;19:15–25.
 77. Leslie AB. Branching habit and the allocation of reproductive resources in conifers. *Ann Bot.* 2012;110:915–21.
 78. Ne’eman G, Goubitz S, Werger MJA, Shmida A. Relationships between tree size, crown shape, gender segregation and sex allocation in *Pinus halepensis*, a Mediterranean pine tree. *Ann Bot.* 2011;108:197–206.
 79. • Santos-del-Blanco L, Alía R, González-Martínez SC, Sampedro L, Lario F, Climent J. Correlated genetic effects on reproduction define a domestication syndrome in a forest tree. *Evol Appl.* 2015; 403–10. **This work examined the genetic change and correlated responses of reproductive traits as a result of selection for timber yield in *Pinus pinaster* progenies, finding a strikingly high correlated effect after a single event of artificial selection, interpreted as evidence of an underlying genetic trade-off.**
 80. Bravo F, Maguire DA, González-Martínez SC. Factors affecting cone production in *Pinus pinaster* Ait.: lack of growth-reproduction trade-offs but significant effects of climate and tree and stand characteristics. *For Syst.* 2017;26 (2): e07S.
 81. Kelly D, Sork VL. Mast seeding in perennial plants: why, how, where? *Annu Rev Ecol Syst.* 2002;33:427–47.
 82. Shestakova TA, Mutke S, Gordo J, Camarero JJ, Sin E, Pemán J, et al. Weather as main driver for mast-ing and stem growth variation in stone pine supports compatible timber and nut co-production. *Agric For Meteorol.* 2021;298–299:108287.
 83. Sadras VO. Evolutionary aspects of the trade-off between seed size and number in crops. *F Crop Res.* 2007;100:125–38.
 84. • Qiu T, Andrus R, Aravena MC, Ascoli D, Bergeron Y, Berretti R, et al. Limits to reproduction and seed size-number trade-offs

- that shape forest dominance and future recovery. *Nat Commun.* 2022; 13:1–12. **This work showed that seed production is not constrained by a strict trade-off between seed size and numbers across plant phylogeny. In addition, gymnosperms showed lower seed production than angiosperms, potentially due to their extra investments in protective woody cones.**
85. Herms DH, Mattson WJ. Does reproduction compromise defense in woody plants? In: Baranchikov Y, Mattson WJ, Hain FP, Payne TL, editors. *For insect Guid patterns interactions with For trees.* USDA Forest Service; 1991. p. 35–46.
 86. Schiestl FP, Kirk H, Bigler L, Cozzolino S, Desurmont GA. Herbivory and floral signalling: phenotypic plasticity and tradeoffs between reproduction and indirect defense. *New Phytol.* 2014;203:257–66.
 87. Redmond MD, Davis TS, Ferrenberg S, Wion AP. Resource allocation trade-offs in a mast-seeding conifer: Piñon pine prioritizes reproduction over defence. *AoB Plants.* 2019;11:1–11.
 88. Larrinaga AR, Sampedro L, Zas R. Resource availability and herbivory alter defence-growth-reproduction trade-offs in a masting Mediterranean pine. *Environ Exp Bot.* 2024;217:105546.
 - 89.● Lauder JD, Moran E V., Hart SC. Fight or flight? Potential trade-offs between drought defense and reproduction in conifers. *Tree Physiol.* 2019; 39:1071–85. **This is an interesting theoretical and literature review postulating divergent life-history strategies among conifers in response to water stress: enhancing allocation to stress avoidance and tolerance, versus enhancing allocation to reproduction at the expenses of higher mortality risk due to drought.**
 90. Prada E, Climent J, Alía R, Díaz R. Life-history correlations with seasonal cold hardiness in maritime pine. *Am J Bot.* 2016;103:20126–2135.
 91. Schulman E. Longevity under adversity in conifers. *Science.* 1954;119:883–4.
 92. Paine TD, Lieutier F (eds). *Insects and diseases of Mediterranean forest systems.* Springer International Publishing Switzerland. 2016.
 93. Franceschi VR, Krokene P, Christiansen E, Krekling T. Anatomical and chemical defenses of conifer bark against bark beetles and other pests. *New Phytol.* 2005;167:353–76.
 94. Mumm R, Hilker M. Direct and indirect chemical defence of pine against folivorous insects. *Trends Plant Sci.* 2006;11:351–8.
 95. Pagán I, García-Arenal F. Tolerance to plant pathogens: theory and experimental evidence. *Int J Mol Sci.* 2018;19:810.
 96. Daniel A, Herms WJM. The dilemma of plants: to grow or defend. *Q Rev Biol.* 1992;67:283–335.
 97. Belsky AJ, Carson WP, Jensen CLL, Fox GA. Overcompensation by plants: herbivore optimization or red herring? *Evol Ecol.* 1993;7:109–21.
 98. Sampedro L, Moreira X, Zas R. Costs of constitutive and herbivore-induced chemical defences in pine trees emerge only under low nutrient availability. *J Ecol.* 2011;99:818–27.
 99. Koricheva J. Meta-analysis of sources of variation in fitness costs of plant antiherbivore defenses. *Ecology.* 2002;83:176.
 - 100.● Sampedro L. Physiological trade-offs in the complexity of pine tree defensive chemistry. *Tree Physiol.* 2014; 34:915–8. **This review deals with the paramount difference in defensive strategy between constitutive and induced defences in pines, and postulating that plant resistance based on inducible defences, although energy saving, is a risky strategy as its benefits are based on the reliable identification of biotic cues.**
 101. Villari C, Faccoli M, Battisti A, Bonello P, Marini L. Testing phenotypic trade-offs in the chemical defence strategy of Scots pine under growth-limiting field conditions. *Tree Physiol.* 2014;34:919–30.
 102. Coley PD, Bryant JB, Chapin FS. Resource availability and plant antiherbivore defense. *Adv Sci.* 1985;230:895–9.
 103. Rhoades DF, Cates RG. Toward a general theory of plant anti-herbivore chemistry. *Biochem Interact Between Plants Insects.* 1976;168–213.
 104. Eyles A, Bonello P, Ganley R, Mohammed C. Induced resistance to pests and pathogens in trees. *New Phytol.* 2010;185:893–908.
 105. Cipollini D, Heil M. Costs and benefits of induced resistance to herbivores and pathogens in plants. *CAB Rev Perspect Agric Vet Sci Nutr Nat Resour.* 2010;5:005.
 - 106.●● Agrawal AA. A scale-dependent framework for trade-offs, syndromes, and specialization in organismal biology. *Ecology.* 2020; 101:1–24. **This paper evaluates leaf economics spectrum traits and their associations with plant defense against herbivory. Scale-dependent predictions emerge for understanding plant ecology holistically, and this approach can be fruitfully applied more generally in evolutionary ecology. Adaptive specialization and community context are two of the primary drivers of trade-offs and syndromes across biological scales.**
 - 107 Zas R, Sampedro L, Prada E, Lombardero MJ, Fernández-López J. Fertilization increases *Hylobius abietis* L. damage in *Pinus pinaster* Ait. seedlings. *For Ecol Manage.* 2006;222:137–44.
 108. Hood S, Sala A. Ponderosa pine resin defenses and growth: metrics matter. *Tree Physiol.* 2015;35:1223–35.
 109. Endara MJ, Coley PD. The resource availability hypothesis revisited: a meta-analysis. *Funct Ecol.* 2011;25:389–98.
 110. Moreira X, Mooney KA, Rasmann S, Petry WK, Carrillo-Gavilán A, Zas R, et al. Trade-offs between constitutive and induced defences drive geographical and climatic clines in pine chemical defences. *Ecol Lett.* 2014;17:537–46.
 111. Pearse IS, Hipp AL. Global patterns of leaf defenses in oak species. *Evolution.* 2012;66:2272–86.
 - 112.● López-Goldar X, Villari C, Bonello P, Borg-Karlson AK, Grivet D, Sampedro L, et al. Genetic variation in the constitutive defensive metabolome and its inducibility are geographically structured and largely determined by demographic processes in maritime pine. *J Ecol.* 2019; 107:2464–77. **This papers check the neutral evolutionary hypothesis in the genetic differentiation in secondary metabolites in *Pinus pinaster*. Neutral differentiation was predominant, and evidence of local adaptation was only found for total constitutive sesquiterpenes and a few individual plant secondary metabolites.**
 113. Lorio PL. Growth-differentiation balance: a basis for understanding southern pine beetle-tree interactions. *For Ecol Manage.* 1986;14:259–73.
 114. Gershenson J. The cost of plant chemical defense against herbivory: a biochemical perspective. In: Bernays EA, editor. *Insect-Plant Interact.* Boca Raton: CRC Press; 1993. p. 73.
 115. Moreira X, Zas R, Solla A, Sampedro L. Differentiation of persistent anatomical defensive structures is costly and determined by nutrient availability and genetic growth-defence constraints. *Tree Physiol.* 2015;35:112–23.
 116. Fernandez C, Monnier Y, Santonja M, Gallet C, Weston LA, Prévosto B, et al. The impact of competition and allelopathy on the trade-off between plant defense and growth in two contrasting tree species. *Front Plant Sci.* 2016;7:1–14.
 117. Kovalchuk A, Keriö S, Oghenekaro AO, Jaber E, Raffaello T, Asiegbu FO. Antimicrobial defenses and resistance in forest trees: challenges and perspectives in a genomic era. *Annu Rev Phytopathol.* 2013;51:221–44.
 118. Koricheva J, Nykänen H, Gianoli E. Meta-analysis of trade-offs among plant antiherbivore defenses: are plants jacks-of-all-trades, masters of all? *Am Nat.* 2004;163:e64–75.
 119. Eichenberg D, Purschke O, Ristok C, Wessjohann L, Bruelheide H. Trade-offs between physical and chemical carbon-based leaf

- defence: of intraspecific variation and trait evolution. *J Ecol.* 2015;103:1667–79.
- 120.● Howe M, Mason CJ, Gratton C, Keefover-Ring K, Wallin K, Yanchuk A, et al. Relationships between conifer constitutive and inducible defenses against bark beetles change across levels of biological and ecological scale. *Oikos.* 2020;129:1093–107. **This work postulated that biological and ecological scale may influence potential trade-offs. Experimentally, focused on one system, conifer phloem monoterpenes that resist bark beetle attack and analysed constitutive-induced relationships from genotypic to interspecific levels. This work provided a general model for understanding how underlying physiological trade-offs are variably manifested across scales.**
 121. Agrawal AA. Current trends in the evolutionary ecology of plant defence. *Funct Ecol.* 2011;25:420–32.
 - 122.● Hahn PG, Maron JL. A framework for predicting intraspecific variation in plant defense. *Trends Ecol Evol.* 2016;31:646–56. **This key work reviewed studies documenting intraspecific variation in plant defence across resource gradients and found little support for RAH (resource availability hypothesis), one of the most well-supported theories regarding the evolution of plant defences.**
 123. Zas R, Sampedro L, Prada E, Fernandez-Lopez J. Genetic variation of *Pinus pinaster* Ait. seedlings in susceptibility to the pine weevil *Hyllobius abietis* L. *Ann For Sci.* 2005;62:681–8.
 124. Di MG, Voltas J. Multienvironment evaluation of *Pinus pinaster* provenances: evidence of genetic trade-offs between adaptation to optimal conditions and resistance to the maritime pine bark scale (*Matsucoccus feytaudi*). *For Sci.* 2016;62:553–63.
 125. Simler-Williamson AB, Rizzo DM, Cobb RC. Interacting effects of global change on forest pest and pathogen dynamics. *Annu Rev Ecol Evol Syst.* 2019;50:381–403.
 126. Santini A, Ghelardini L, De Pace C, Desprez-Loustau ML, Capretti P, Chandelier A, et al. Biogeographical patterns and determinants of invasion by forest pathogens in Europe. *New Phytol.* 2013;197:238–50.
 127. Chuine I, Beaubien EG. Phenology is a major determinant of tree species range. *Ecol Lett.* 2001;4:500–10.
 128. Savolainen O, Pyhäjärvi T, Knürr T. Gene flow and local adaptation in trees. *Annu Rev Ecol Evol Syst.* 2007;38:595–619.
 129. Aitken SN, Yeaman S, Holliday JA, Wang T, Curtis-McLane S. Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evol Appl.* 2008;1:95–111.
 130. Petterle A, Karlberg A, Bhalerao RP. Daylength mediated control of seasonal growth patterns in perennial trees. *Curr Opin Plant Biol.* 2013;16:301–6.
 - 131.● Singh RK, Svystun T, Aldahmash B, Jönsson AM, Bhalerao RP. Photoperiod- and temperature-mediated control of phenology in trees – a molecular perspective. *New Phytol.* 2017;213:511–24. **This paper discuss current knowledge of the molecular-level regulation of the annual growth cycle of woody trees in temperate and boreal regions, and identify key questions that need to be addressed in the future, considering the striking similarities between key components mediating photoperiodic control of growth cessation and bud set in trees with signalling pathways controlling growth cessation and floral transition in Arabidopsis.**
 - 132.● Gárate-Escamilla H, Hampe A, Vizcaíno-Palomar N, Robson TM, Benito Garzón M. Range-wide variation in local adaptation and phenotypic plasticity of fitness-related traits in *Fagus sylvatica* and their implications under climate change. *Glob Ecol Biogeogr.* 2019;28:1336–50. **Using a huge database of *Fagus sylvatica* trees in Europe, this work assessed how local adaptation and phenotypic plasticity are trait-dependent (growth and phenology) and traits covary along climatic gradients, with differential consequences for fitness.**
 133. Benito Garzón M, Robson TM, Hampe A. Δ TraitSDMs: species distribution models that account for local adaptation and phenotypic plasticity. *New Phytol.* 2019;222:1757–65.
 - 134.● Cooper HF, Grady KC, Cowan JA, Best RJ, Allan GJ, Whitham TG. Genotypic variation in phenological plasticity: reciprocal common gardens reveal adaptive responses to warmer springs but not to fall frost. *Glob Chang Biol.* 2019;25:187–200. **In this paper, changes in two key phenology traits (fall bud set and spring bud flush) in a widespread riparian tree species were assessed in a reciprocal transplant experiment. They found different plastic responses on phenology due to transfer, depending on the climate of origin, with trees from hotter, southern populations exhibiting greater plasticity compared to the northern, frost-adapted populations.**
 135. Gárate-Escamilla H, Brelford CC, Hampe A, Robson TM, Garzón MB. Greater capacity to exploit warming temperatures in northern populations of European beech is partly driven by delayed leaf senescence. *Agric For Meteorol.* 2020;284:107908.
 136. Howe GT, Aitken SN, Neale DB, Jermstad KD, Wheeler NC, Chen THH. From genotype to phenotype : unraveling the complexities of cold adaptation in forest trees 1. *Can J Bot.* 2003;81:1247–66.
 137. Notivol E, Garcia-Gil MR, Alía R, Savolainen O. Genetic variation of growth rhythm traits in the limits of a latitudinal cline in Scots pine. *Can J For Res.* 2007;37:540–51.
 138. Aitken SN, Hannerz M. Geneecology and gene resource management strategies for conifer cold hardiness. In: Bigras, F.J., Colombo, S.J. (eds) *Conifer Cold Hardiness. Tree Physiology*, vol 1. Springer, Dordrecht. 2001;23–53.
 139. Westin J, Sundblad LG, Strand M, Hällgren JE. Phenotypic differences between natural and selected populations of *Picea abies*. I Frost Hardiness. *Scand J For Res.* 2010;15:5:489–99.
 - 140.● MacLachlan IR, Wang T, Hamann A, Smets P, Aitken SN. Selective breeding of lodgepole pine increases growth and maintains climatic adaptation. *For Ecol Manage.* 2017;391:404–16. **By comparing natural stand and selectively bred lodgepole pine seedlots in a common garden, this work assessed the effects of selection on phenotypic variation and climatic associations among breeding zones for growth, phenology and cold hardiness, to conclude that breeding has produced taller lodgepole pine seedlings that are not adaptively compromised relative to their natural seedling counterparts.**
 141. Larson PR. Wood formation and the concept of wood quality. *Bull. Ser. 74. Yale University, School of Forestry*; 1969.
 142. Jayawickrama KJS, McKeand SE, Jett JB, Wheeler EA. Date of earlywood-latewood transition in provenances and families of loblolly pine, and its relationship to growth phenology and juvenile wood specific gravity. *Can J For Res.* 1997;27:1245–53.
 143. Fukatsu E, Nakada R. The timing of latewood formation determines the genetic variation of wood density in *Larix kaempferi*. *Trees - Struct Funct.* 2018;32:1233–45.
 144. Nilsson JE. Seasonal changes in phenological traits and cold hardiness of F1-populations from plus-trees of *Pinus sylvestris* and *Pinus contorta* of various geographical origins. *Scand J For Res.* 2001;16:7–20.
 145. Sarris D, Christodoulakis D, Körner C. Recent decline in precipitation and tree growth in the eastern Mediterranean. *Glob Chang Biol.* 2007;13:1187–200.
 146. Van Asch M, Visser ME. Phenology of forest caterpillars and their host trees: the importance of synchrony. *Annu Rev Entomol.* 2007;52:37–55.
 147. Elzinga JA, Atlan A, Biere A, Gigord L, Weis AE, Bernasconi G. Time after time: flowering phenology and biotic interactions. *Trends Ecol Evol.* 2007;22:432–9.
 - 148.●● Hammond WM, Williams AP, Abatzoglou JT, Adams HD, Klein T, López R, et al. Global field observations of tree

- die-off reveal hotter-drought fingerprint for Earth's forests. *Nat Commun.* 2022;13:1761. **This meta-analysis of a geo-referenced global database documenting climate-induced mortality events spanning all tree-supporting biomes and continents, from 154 peer-reviewed studies since 1970, quantified a global “hotter-drought fingerprint”: a hotter and drier climate signal for tree mortality—across 675 locations encompassing 1,303 plots, and postulated that the frequency of mortality-year climate conditions strongly increases nonlinearly under projected warming.**
149. Brodrribb TJ, Bowman DJMS, Nichols S, Delzon S, Burrett R. Xylem function and growth rate interact to determine recovery rates after exposure to extreme water deficit. *New Phytol.* 2010;188:533–42.
 150. Urli M, Porté AJ, Cochard H, Guengant Y, Burrett R, Delzon S. Xylem embolism threshold for catastrophic hydraulic failure in angiosperm trees. *Tree Physiol.* 2013;33:672–83.
 151. Plomion C, Bartholomé J, Bouffier L, Brendel O, Cochard H, de Miguel M, et al. Understanding the genetic bases of adaptation to soil water deficit in trees through the examination of water use efficiency and cavitation resistance: maritime pine as a case study. *J Plant Hydraul.* 2016;3:23.
 152. Nardini A, Luglio J. Leaf hydraulic capacity and drought vulnerability possible trade-offs and correlations with climate across three major biomes. *Funct Ecol.* 2014;28:810–8.
 153. Martínez-Villalta J, Prat E, Oliveras I, Piñol J. Xylem hydraulic properties of roots and stems of nine Mediterranean woody species. *Oecologia.* 2002;133:19–29.
 154. Gleason SM, Westoby M, Jansen S, Choat B, Hacke UG, Pratt RB, et al. Weak tradeoff between xylem safety and xylem-specific hydraulic efficiency across the world's woody plant species. *New Phytol.* 2016;209:123–36.
 155. Pritzkow C, Szota C, Williamson VG, Arndt SK. Phenotypic plasticity of drought tolerance traits in a widespread eucalypt (*Eucalyptus obliqua*). *Forests.* 2020;11:1–14.
 - 156.● Song Y, Bouteiller XP, Larter M, Plomion C, Sin F, Delzon S. A safe breeding ground: genetically improved maritime pine for growth and stem form has more efficient but not more vulnerable xylem. *Tree Physiol.* 2023;43:366–78. **This paper compared the hydraulic efficiency and hydraulic safety in four varieties of *Pinus pinaster* over successive cycles of genetic improvement for shape and growth, and found that improved varieties presented higher hydraulic conductivity with larger tracheid lumen size and tracheid lumen fraction, and smaller wall thickness reinforcement and tracheid density, but not at the cost of reduced embolism resistance.**
 157. Sáenz-Romero C, Lamy JB, Loya-Rebollar E, Plaza-Aguilar A, Burrett R, Lobit P, et al. Genetic variation of drought-induced cavitation resistance among *Pinus hartwegii* populations from an altitudinal gradient. *Acta Physiol Plant.* 2013;35:2905–13.
 158. Lamy JB, Delzon S, Bouche PS, Alia R, Vendramin GG, Cochard H, et al. Limited genetic variability and phenotypic plasticity detected for cavitation resistance in a Mediterranean pine. *New Phytol.* 2014;201:874–86.
 - 159.● López R, Cano FJ, Choat B, Cochard H, Gil L. Plasticity in vulnerability to cavitation of *Pinus canariensis* occurs only at the driest end of an aridity gradient. *Front Plant Sci.* 2016;7:1–10. **This work assessed intraspecific variation and relative contribution of plasticity to adaptation of vulnerability to cavitation, efficiency of the xylem to conduct water and biomass allocation, in six populations of *Pinus canariensis* growing in three provenance trials (wet, dry, and xeric). They found that the variability for hydraulic traits was largely due to phenotypic plasticity, whereas, genetic variation was limited and almost restricted to hydraulic safety traits and survival.**
 160. Nguyen-Queyrens A, Bouchet-Lannat F. Osmotic adjustment in three-year-old seedlings of five provenances of maritime pine (*Pinus pinaster*) in response to drought. *Tree Physiol.* 2003;23:397–404.
 161. López R, Aranda I, Gil L, L G. Osmotic adjustment is a significant mechanism of drought resistance in *Pinus pinaster* and *Pinus canariensis*. *For Syst.* 2009;18:159–166.
 162. Bulfe NML, Fernández ME. Morpho-physiological response to drought of progenies of *Pinus taeda* L. contrasting in mean growth rate. *New For.* 2016;47:431–51.
 - 163.● Gray EF, Wright IJ, Falster DS, Eller ASD, Lehmann CER, Bradford MG, et al. Leaf-wood allometry and functional traits together explain substantial growth rate variation in rainforest trees. *AoB Plants.* 2019;11:1–11. **This paper is focused in the functional traits that drive interspecific variation in growth rate in adult plants of 41 woody species of an Australian rainforest. While it was widely assumed that the key trait drivers would be the same than in seedlings (e.g. specific leaf area, or SLA), the authors propose using cost-benefit approaches teamed with combinations of leaf, wood and allometric variables to attain a more complete understanding of growth rates under field conditions.**
 164. Corcuera L, Cochard H, Gil-Pelegrin E, Notivol E. Phenotypic plasticity in mesic populations of *Pinus pinaster* improves resistance to xylem embolism (P50) under severe drought. *Trees - Struct Funct.* 2011;25:1033–42.
 165. Fichot R, Barigah TS, Chamillard S, Le Thiec D, Laurans F, Cochard H, et al. Common trade-offs between xylem resistance to cavitation and other physiological. *Plant Cell Environ.* 2010;33:1553–68.
 166. Cochard H, Casella E, Mencuccini M. Xylem vulnerability to cavitation varies among poplar and willow clones and correlates with yield. *Tree Physiol.* 2007;27:1761–7.
 167. Ducrey M, Huc R, Ladjal M, Guehl JM. Variability in growth, carbon isotope composition, leaf gas exchange and hydraulic traits in the eastern Mediterranean cedars *Cedrus libani* and *C. brevifolia*. *Tree Physiol.* 2008;28:689–701.
 168. Ramírez-Valiente JA, Cavender-Bares J. Evolutionary trade-offs between drought resistance mechanisms across a precipitation gradient in a seasonally dry tropical oak (*Quercus oleoides*). *Tree Physiol.* 2017;37:889–901.
 - 169.● Valliere JM. Tradeoffs between growth rate and water-use efficiency in seedlings of native perennials but not invasive annuals. *Plant Ecol.* 2019;220:361–9. **This paper compared the growth-WUE trade-off among seedlings of native perennials in California and the invasive annuals displacing them in mesocosms under altered N and water availability. Native species suffered a trade-off between relative growth rate (RGR) and water-use efficiency (WUE), while non-natives exhibited both high RGR and high WUE, especially under high resource availability.**
 170. Lauteri M, Pliura A, Monteverdi MC, Brugnoli E, Villani F, Eriksson G. Genetic variation in carbon isotope discrimination in six European populations of *Castanea sativa* Mill. originating from contrasting localities. *J Evol Biol.* 2004;17:1286–96.
 171. Lamy J-BB, Bouffier L, Burrett R, Plomion C, Cochard H, Delzon S. Uniform selection as a primary force reducing population genetic differentiation of cavitation resistance across a species range. Ingvarsson PK, editor. *PLoS One.* 2011;6:e23476.
 - 172.● Dixit A, Kolb T, Burney O. Trade-off between growth rate and water use efficiency in southwestern ponderosa pine provenances. *For Ecol Manage.* 2022;515:120239. **In a common garden of *Pinus ponderosa*, seedlings with higher growth rate had greater $\Delta^{13}C$, suggesting a trade-off between growth rate and water use efficiency. Provenances from warmer**

- sites had lower growth rate and $\Delta^{13}C$ (higher water use efficiency) than provenances from cooler sites during the driest year.**
173. Nguyen-Queyrens A, Ferhi A, Loustau D, Guehl J-M. Within-ring $\delta^{13}C$ spatial variability and interannual variations in wood cellulose of two contrasting provenances of *Pinus pinaster*. *Can J For Res.* 1998;28:766–73.
 174. Marguerit E, Bouffier L, Chancerel E, Costa P, Lagane F, Guehl JM, et al. The genetics of water-use efficiency and its relation to growth in maritime pine. *J Exp Bot.* 2014;65:4757–68.
 175. Bacon M. (ed) *Water use efficiency in plant biology.* Blackwell Publishing Ltd. Oxford. 2009;344.
 176. De Miguel M, Sánchez-Gómez D, Cervera MT, Aranda I. Functional and genetic characterization of gas exchange and intrinsic water use efficiency in a full-sib family of *Pinus pinaster* Ait. in response to drought. *Tree Physiol.* 2012;32:94–103.
 177. Moran E, Lauder J, Musser C, Stathos A, Shu M. The genetics of drought tolerance in conifers. *New Phytol.* 2017;216:1034–48.
 178. Brendel O, Pot D, Plomion C, Rozenberg P, Guehl JM. Genetic parameters and QTL analysis of $\delta^{13}C$ and ring width in maritime pine. *Plant Cell Environ.* 2002;25:945–53.
 179. Martínez-Villalta J, Cochard H, Mencuccini M, Sterck F, Herrero A, Korhonen JFJ, et al. Hydraulic adjustment of Scots pine across Europe. *New Phytol.* 2009;184:353–64.
 180. Fichot R, Chamaillard S, Depardieu C, Le Thiec D, Cochard H, Barigah TS, et al. Hydraulic efficiency and coordination with xylem resistance to cavitation, leaf function, and growth performance among eight unrelated *Populus deltoides* × *Populus nigra* hybrids. *J Exp Bot.* 2011;62:2093–106.
 181. Guet J, Fichot R, Lédée C, Laurans F, Cochard H, Delzon S, et al. Stem xylem resistance to cavitation is related to xylem structure but not to growth and water-use efficiency at the within-population level in *Populus nigra* L. *J Exp Bot.* 2015;66:4643–52.
 182. Gutschick VP, BassiriRad H. Extreme events as shaping physiology, ecology, and evolution of plants: toward a unified definition and evaluation of their consequences. *New Phytol.* 2003;160:21–42.
 183. Zimmermann NE, Yoccoz NG, Edwards TC, Meier ES, Thuiller W, Guisan A, et al. Climatic extremes improve predictions of spatial patterns of tree species. *Proc Natl Acad Sci.* 2009;106:19723–8.
 184. Korner C, Basler D, Hoch G, Kollas C, Lenz A, Randin CF, et al. Where, why and how? Explaining the low-temperature range limits of temperate tree species. *J Ecol.* 2016;104:1076–88.
 185. Neumann M, Mues V, Moreno A, Hasenauer H, Seidl R. Climate variability drives recent tree mortality in Europe. *Glob Chang Biol.* 2017;23:4788–97. **This work describes continental-scale patterns of recent tree mortality from the only consistent pan-European forest monitoring network, identifying recent mortality hotspots in southern and northern Europe, finding that warm summers as well as high seasonal variability in precipitation increased the likelihood of tree mortality.**
 186. Bi H, Parekh J, Li Y, Murphy S, Lei Y. Adverse influences of drought and temperature extremes on survival of potential tree species for commercial environmental forestry in the dryland areas on the western slopes of New South Wales. *Australia Agric For Meteorol.* 2014;197:188–205.
 187. Crockett JL, Westerling AL. Greater temperature and precipitation extremes intensify Western U.S. droughts, wildfire severity, and Sierra Nevada tree mortality. *J Clim.* 2018;31:341–54.
 188. McDowell NG, Williams AP, Xu C, Pockman WT, Dickman LT, Sevanto S, et al. Multi-scale predictions of massive conifer mortality due to chronic temperature rise. *Nat Clim Chang.* 2016;6:295–300.
 189. Anderegg WRL, Kane JM, Anderegg LDL. Consequences of widespread tree mortality triggered by drought and temperature stress. *Nat Clim Chang.* 2013;3:30–6.
 190. Allen CD, Breshears DD, McDowell NG. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere.* 2015;6:129.
 191. Matusick G, Ruthrof KX, Brouwers NC, Dell B, Hardy GSJ. Sudden forest canopy collapse corresponding with extreme drought and heat in a Mediterranean-type eucalypt forest in southwestern Australia. *Eur J For Res.* 2013;132:497–510.
 192. Leuzinger S, Vogt R, Körner C. Tree surface temperature in an urban environment. *Agric For Meteorol.* 2010;150:56–62.
 193. Haggmann RK, Hessburg PF, Prichard SJ, Povak NA, Brown PM, Fulé PZ, et al. Evidence for widespread changes in the structure, composition, and fire regimes of western North American forests. *Ecol Appl.* 2021;31. **The cumulative results document a substantial fire deficit and widespread alterations to ecological structures and functions. The loss of the once abundant influence of low- and moderate-severity fires suggests that even the least fire-prone ecosystems may be affected by alteration of the surrounding landscape and, consequently, ecosystem functions.**
 194. Chakraborty D, Matulla C, Andre K, Weissenbacher L, Schueler S. Survival of Douglas-fir provenances in Austria: site-specific late and early frost events are more important than provenance origin. *Ann For Sci.* 2019;76.
 195. Hänninen H. Does climatic warming increase the risk of frost damage in northern trees? *Plant Cell Environ.* 1991;14:449–54.
 196. Zohner CM, Mo L, Renner SS, Svenning JC, Vitasse Y, Benito BM, et al. Late-spring frost risk between 1959 and 2017 decreased in North America but increased in Europe and Asia. *Proc Natl Acad Sci.* 2020; 117: 12192–12200. **Starting from observations in many species at botanical gardens, this work modelled the change in frost damage across temperate and boreal regions of the world. The greatest increase in leaf-damaging spring frost has occurred in Europe and East Asia, where species are more vulnerable to spring frost than in North America.**
 197. Teskey R, Wertin T, Bauweraerts I, Ameye M, McGuire MA, Steppe K. Responses of tree species to heat waves and extreme heat events. *Plant Cell Environ.* 2015;38:1699–712.
 198. Smith W. *Tree pathology: a short introduction.* New York, London: Academic Press; 1970. p. 308.
 199. Martinez-Meier A, Sanchez L, Dalla-Salda G, Pastorino MJM, Gautry J-Y, Gallo LA, et al. Genetic control of the tree-ring response of Douglas-fir (*Pseudotsuga menziesii* Mirb. Franco) to the 2003 drought and heat-wave in France. *Ann For Sci.* 2008;65:102–10.
 200. Christiansen MN. The physiology of plant tolerance to temperature extremes. In: Jung GA, editor. *Crop Toler to Suboptimal L Cond.* ASA Special Publications. Madison, WI, USA: American Society of Agronomy, Crop Science Society of America, and Soil Science Society of America; 1978;173–91.
 201. Bassow SL, McConnaughay KDM, Bazzaz FA. The response of temperate tree seedlings grown in elevated CO_2 to extreme temperature events. *Ecol Appl.* 1994;4:593–603.
 202. Warren JM, Norby RJ, Wullschlegel SD, Oren R. Elevated CO_2 enhances leaf senescence during extreme drought in a temperate forest. *Tree Physiol.* 2011;31:117–30.
 203. Pausas JG, Bradstock RA, Keith DA, Keeley JE, Network GF. Plant functional traits in relation to fire in crown-fire ecosystems. pdf. *Ecology.* 2004;85:1085–100.
 204. Keeley JE, Pausas JG. Evolutionary ecology of fire. *Annu Rev Ecol Evol Syst.* 2022; 53:203–25. **This work reviews the different traits and syndromes providing fitness benefits following fires, depending on the fire regime. Some of these traits**

- enhance fire survival, while others promote recruitment in the postfire environment. Demonstrating that these traits are fire adaptations is challenging, since many arose early in the paleontological record, although increasingly better fossil records and phylogenetic analysis make timing of these trait origins to fire more certain.**
205. Tapias R, Climent J, Pardos JA, Gil LA. Life histories of Mediterranean pines. *Plant Ecol.* 2004;171:53–68.
 206. Hernández-Serrano A, Verdú M, Santos-Del-Blanco L, Climent J, González-Martínez SC, Pausas JG. Heritability and quantitative genetic divergence of serotiny, a fire-persistence plant trait. *Ann Bot.* 2014;114:571–7.
 207. Pausas JG, Keeley JE. Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. *New Phytol.* 2014;204:55–65.
 208. Schwilk DW, Ackerly DD. Flammability and serotiny as strategies: correlated evolution in pines. *Oikos.* 2001;94:326–36.
 209. Martín-Sanz RC, Santos-Del-Blanco L, Notivol E, Chambel MR, San-Martín R, Climent J. Disentangling plasticity of serotiny, a key adaptive trait in a Mediterranean conifer. *Am J Bot.* 2016;103:1582–91.
 210. Van Gelder HA, Poorter L, Sterck FJ. Wood mechanics, allometry, and life-history variation in a tropical rain forest tree community. *New Phytol.* 2006;171:367–78.
 211. Poorter L, McDonald I, Alarcón A, Fichtler E, Licona JC, Peña-Claros M, et al. The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. *New Phytol.* 2010;185:481–92.
 212. Zobel BJ, van Buijtenen JP. Wood variation and wood properties. In: *Wood variation*. Springer Series in Wood Science. Springer, Berlin, Heidelberg. 1989;1–32.
 213. Zobel BJ, Jett JB. The importance of wood density (specific gravity) and its component parts. In: *Genetics of wood production*. Springer Series in Wood Science. Springer, Berlin, Heidelberg. 1995.
 214. Dungey HS, Matheson AC, Kain D, Evans R. Genetics of wood stiffness and its component traits in *Pinus radiata*. *Can J For Res.* 2006;36:1165–78.
 215. Saranpää P. Wood density and growth. In: Barnett JR, Jeronimidis G, editors. *Wood quality: its biological basis*. Blackwell Publishing Ltd; 2003;226.
 216. Mork F. Die qualitaat des fichtenholzes unter besonderer ruc-sichtnahme auf schleif-und papierholz. *Papier Fabrikant.* 1928;26:741–7.
 217. Bendtsen BA, Senft J. Mechanical and anatomical properties in individual growth rings of plantation-grown eastern cottonwood and loblolly pine. *Wood Fiber Sci.* 2007;18:23–38.
 218. Cave ID, Walker JCF. Stiffness of wood in fast-grown plantation softwoods - the influence of microfibril angle. *For Prod J.* 1994;44:43–8.
 219. Gjerdrum P, Säll H, Storø HM. Spiral grain in Norway spruce: constant change rate in grain angle in Scandinavian sawlogs. *Forestry.* 2002;75:163–70.
 220. Chen ZQ, Gil MRG, Karlsson B, Lundqvist SO, Olsson L, Wu HX. Inheritance of growth and solid wood quality traits in a large Norway spruce population tested at two locations in southern Sweden. *Tree Genet Genomes.* 2014;10:1291–303.
 221. Hayatgheibi H, Fries A, Kroon J, Wu HX. Genetic analysis of lodgepole pine (*Pinus contorta*) solid-wood quality traits. *Can J For Res.* 2017;47:1303–13.
 222. Hong Z, Fries A, Wu HX. Age trend of heritability, genetic correlation, and efficiency of early selection for wood quality traits in Scots pine. *Can J For Res.* 2015;45:817–25.
 223. Lenz P, Cloutier A, MacKay J, Beaulieu J. Genetic control of wood properties in *Picea glauca* - an analysis of trends with cambial age. *Can J For Res.* 2010;40:703–15.
 224. Kucera B. A hypothesis relating current annual height increment to juvenile wood formation in Norway spruce. *Wood Fiber Sci.* 1994;26:152–67.
 225. Larson P, Kretschmann DE, Clark A, Isebrants JG. Formation and properties of juvenile wood in southern pines: a synopsis. Madison, WI: USDA Forest Service, Forest Products Laboratory 2001;42.
 226. Mellerowicz EJ, Baucher M, Sundberg B, Boerjan W. Unravelling cell wall formation in the woody dicot stem. *Plant Mol Biol.* 2001;47:239–74.
 227. Steffenrem A, Kvaalen H, Hoibo OA, Edvardsen OM, Skroppa T, Høibø OA, et al. Genetic variation of wood quality traits and relationships with growth in *Picea abies*. *Scand J For Res.* 2009;24:15–27.
 228. Merrill REMC. Heritability and genetic correlations for stem diameter and branch characteristics in white spruce. *Can J For Res.* 1985;15:494–7.
 229. Vestøl GI, Høibø OA. Prediction of knot diameter in *Picea abies* (L.) Karst. *Holz als Roh - und Werkst.* 2001;59:129–36.
 230. Høibø OA. The quality of wood of Norway spruce (*Picea abies* (L.) Karst.) planted with different spacing. Agricultural University of Norway; 1991.
 231. Johansson K. Effect of initial spacing on the stem and branch properties and graded quality of *Picea abies* (L.) Karst. *Scand J For Res.* 1992;7:503–14.
 232. Vestøl GI, Colin F, Loubere M, Loubère M. Influence of progeny and initial stand density on the relationship between diameter at breast height and knot diameter of *Picea abies*. *Scand J For Res.* 1999;14:470–80.
 233. Karlsson B, Hogberg K-A. Genotypic parameters and clone x site interaction in clone tests of Norway spruce (*Picea abies* (L.) Karst.). *For Genet.* 1998;5:21–30.
 234. Magnussen SYC. Early testing of jack pine.: II Variance and repeatability of stem and branch characters. *Can J For Res.* 1987;17:460–5.
 235. Magnussen SYC. Early testing of jack pine. I. Phenotypic response to spacing. *Can J For Res.* 1987;17:453–9.
 236. Gräns D, Hannrup B, Isik F, Lundqvist SO, McKeand S. Genetic variation and relationships to growth traits for microfibril angle, wood density and modulus of elasticity in a *Picea abies* clonal trial in southern Sweden. *Scand J For Res.* 2009;24:494–503.
 237. Wang X-R, Torimaru T, Lindgren D, Fries A. Marker-based parentage analysis facilitates low input ‘breeding without breeding’ strategies for forest trees. *Tree Genet Genomes.* 2009;6:227–35.
 238. Hong Z, Fries A, Wu HX. High negative genetic correlations between growth traits and wood properties suggest incorporating multiple traits selection including economic weights for the future Scots pine breeding programs. *Ann For Sci.* 2014;71:463–72.
 239. Fundova I, Funda T, Wu HX. Non-destructive wood density assessment of Scots pine (*Pinus sylvestris* L.) using Resistograph and Pilodyn. *PLoS One.* 2018;13:1–16.
 240. Baltunis BS, Wu HX, Powell MB. Inheritance of density, microfibril angle, and modulus of elasticity in juvenile wood of *Pinus radiata* at two locations in Australia. *Can J For Res.* 2007;37:2164–74.
 241. Wu HX, Ivkovic M, Gaspare WJ, Matheson AC, Baltunis BS, Powell MB, et al. Breeding for wood quality and profit in radiata pine: a review of genetic parameters. *New Zeal J For Res.* 2008;38:56–87.
 242. Fries A, Ulvcrone T, Wu HX, Kroon J. Stem damage of lodgepole pine clonal cuttings in relation to wood and fiber traits, acoustic velocity, and spiral grain. *Scand J For Res.* 2014;29:764–76.

243. Bridgwater FE, Talbert JT, Jahromi S. Index selection for increased dry weight in a young loblolly pine populations. *Silvae Genet.* 1983;32.
244. Pot D, Chantre G, Rozenberg P, Rodrigues JC, Jones GL, Pereira H, et al. Genetic control of pulp and timber properties in maritime pine (*Pinus pinaster* Ait.). *Ann For Sci.* 2002;59:563–75.
245. Bouffier L, Raffin A, Rozenberg P, Meredieu C, Kremer A. What are the consequences of growth selection on wood density in the French maritime pine breeding programme? *Tree Genet Genomes.* 2008;5:11–25.
246. Hasegawa M, Savard M, Lenz PRN, Duchateau E, Gélinas N, Bousquet J, et al. White spruce wood quality for lumber products: priority traits and their enhancement through tree improvement. *Forestry.* 2020;93:16–37.
247. Lenz P, MacKay J, Rainville A, Cloutier A, Beaulieu J. The influence of cambial age on breeding for wood properties in *Picea glauca*. *Tree Genet Genomes.* 2011;7:641–53.
248. Lenz P, Auty D, Achim A, Beaulieu J, Mackay J. Genetic improvement of white spruce mechanical wood traits—early screening by means of acoustic velocity. *Forests.* 2013;4:575–94.
249. Kennedy SG, Cameron AD, Lee SJ. Genetic relationships between wood quality traits and diameter growth of juvenile core wood in Sitka spruce. *Can J For Res.* 2013;43:1–6.
250. Lindstrom H, Evans R, Reale M. Implications of selecting tree clones with high modulus of elasticity. *New Zeal J For Res.* 2005;35:50–71.
251. Hayatgheibi H, Forsberg NEG, Lundqvist SO, Mörling T, Mellerowicz EJ, Karlsson B, et al. Genetic control of transition from juvenile to mature wood with respect to microfibril angle in Norway spruce (*Picea abies*) and lodgepole pine (*Pinus contorta*). *Can J For Res.* 2018;48:1358–65.
252. Gapare WJ, Wu HX, Abarquez A. Genetic control of the time of transition from juvenile to mature wood in *Pinus radiata* D. Don. *Ann For Sci.* 2006;63:871–8.
253. Abdel-Gadir AY, Krahmer L. Genetic variation in the age of demarcation between juvenile and mature wood in Douglas fir. *Wood Fiber Sci.* 1993;25:384–94.
254. Pérez-Moreno J, Guerin-Laguette A, Rinaldi AC, Yu F, Verbeke A, Hernández-Santiago F, et al. Edible mycorrhizal fungi of the world: what is their role in forest sustainability, food security, biocultural conservation and climate change? *Plants People Planet.* 2021;3:471–90.
255. Rodríguez-García A, López R, Martín JA, Pinillos F, Gil L. Resin yield in *Pinus pinaster* is related to tree dendrometry, stand density and tapping-induced systemic changes in xylem anatomy. *For Ecol Manage.* 2014;313:47–54.
256. Calama R, Gordo J, Madrigal G, Mutke S, Conde M, Montero G, et al. Enhanced tools for predicting annual stone pine (*Pinus pinea* L.) cone production at tree and forest scale in Inner Spain. *For Syst.* 2016;25.
257. Tadesse W, Nanos N, Auñón FJ, Alía R, Gil LA. Evaluation of high resin yielders of *Pinus pinaster* Ait. *For Genet.* 2001;8:271–7.
258. Mutke S, Iglesias S, Gil L. Selección de clones de pino piñonero sobresalientes en la producción de piña. *Investig Agrar Sist y Recur For.* 2007;16:39–51.
259. Liu Q, Zhou Z, Fan H, Liu Y. Genetic variation and correlation among resin yield, growth, and morphologic traits of *Pinus massoniana*. *Silvae Genet.* 2013;62:38–44.
260. Lai M, Dong L, Yi M, Sun S, Zhang Y, Fu L, et al. Genetic variation, heritability and genotype × environment interactions of resin yield, growth traits and morphologic traits for *Pinus elliottii* at three progeny trials. *Forests.* 2017;8:409.
261. Luo J, Xia W, Cao P, Xiao Z, Zhang Y, Liu M, et al. Integrated transcriptome analysis reveals plant hormones jasmonic acid and salicylic acid coordinate growth and defense responses upon fungal infection in poplar. *Biomolecules.* 2019;9:12.
262. Eichmann R, Schäfer P. Growth versus immunity—a redirection of the cell cycle? *Curr Opin Plant Biol.* 2015;26:106–12.
263. Berens ML, Berry HM, Mine A, Argueso CT, Tsuda K. Evolution of hormone signalling networks in plant defense. *Annu Rev Phytopathol.* 2017;55:401–25.
264. • Züst T, Agrawal AA. Trade-offs between plant growth and defense against insect herbivory: an emerging mechanistic synthesis. *Annu Rev Plant Biol.* 2017; 68:534. **They provide a working model of the plant defence signalling network for regulation of growth–defence trade-offs and propose a unifying framework for growth–defence trade-offs as a means to study the plant allocation of limiting resources.**
265. Li Y, Yang Y, Hu Y, Liu H, He M, Yang Z, et al. DELLA and EDS1 form a feedback regulatory module to fine-tune plant growth–defense tradeoff in Arabidopsis. *Mol Plant.* 2019;12:1485–98.
266. Neuser J, Metzen CC, Dreyer BH, Feulner C, van Dongen JT, Schmidt RR, et al. HBI1 mediates the trade-off between growth and immunity through its impact on apoplastic ROS homeostasis. *Cell Rep.* 2019;28:1670–1678.e3.
267. Smakowska E, Kong J, Busch W, Belkhadir Y. Organ-specific regulation of growth–defense tradeoffs by plants. *Curr Opin Plant Biol.* 2016;29:129–37.
268. Berens ML, Wolinska KW, Spaepen S, Ziegler J, Nobori T, Nair A, et al. Balancing trade-offs between biotic and abiotic stress responses through leaf age-dependent variation in stress hormone cross-talk. *Proc Natl Acad Sci USA.* 2019;116:2364–73.
269. •• Nguyen HC, Cao PB, San Clemente H, Ployet R, Mounet F, Ladouce N, et al. Special trends in CBF and DREB2 groups in *Eucalyptus gunnii* vs *Eucalyptus grandis* suggest that CBF are master players in the trade-off between growth and stress resistance. *Physiol Plant.* 2017;159:445–67. **This comprehensive transcriptional analysis performed on leaves, stems and roots from two Eucalyptus species after cold, heat or drought treatment suggest that factors which promote both stress protection and growth limitation, participate in the trade-off between growth and resistance in this woody species.**
270. • Porth I, White R, Jaquish B, Ritland K. Partial correlation analysis of transcriptomes helps detangle the growth and defense network in spruce. *New Phytol.* 2018;218:1349–59. **This paper use partial correlation analysis to identify gene networks underlying growth and susceptibility to weevil in spruce. In particular, transcripts that strongly modify the trade-off between growth and defense, and allow identification of networks more central to the trade-off.**
271. • Yu D, Wildhagen H, Tylewicz S, Miskolczi PC, Bhalerao RP, Polle A. Abscisic acid signalling mediates biomass trade-off and allocation in poplar. *New Phytol.* 2019;223:1192–203. **This study analyse genes involved in ABA stress signalling and photoperiodic regulation that affect drought resistance by trade-off with biomass production in poplar trees. The results suggest a critical role for ABA-mediated processes in balancing biomass production and climate adaptation.**
272. • Estravis-Barcala M, Mattera MG, Soliani C, Bellora N, Opge-noorth L, Heer K, et al. Molecular bases of responses to abiotic stress in trees. *J Exp Bot.* 2020;71:3765–79. **This review aims the understanding of the molecular bases of drought and temperature stresses in trees, with a focus on functional, transcriptomic, epigenetic, and population genomic studies. The importance of the review is that long-living trees have evolved a wide spectrum of molecular mechanisms to coordinate growth and development under stressful conditions, thus minimizing fitness costs.**

273. Thomas CD. Translocation of species, climate change, and the end of trying to recreate past ecological communities. *Trends Ecol Evol.* 2011;26:216–21.
274. Brown JKM, Rant JC. Fitness costs and trade-offs of disease resistance and their consequences for breeding arable crops. *Plant Pathol.* 2013;62:83–95.
275. Hallingbäck HR, Sánchez L, Wu HX. Single versus subdivided population strategies in breeding against an adverse genetic correlation. *Tree Genet Genomes.* 2014;10:605–17.
276. Gapare WJ, Baltunis BS, Ivković M, Wu HX. Genetic correlations among juvenile wood quality and growth traits and implications for selection strategy in *Pinus radiata* D. Don. *Ann For Sci.* 2009;66:606.
277. Ivković M, Wu HX, McRae TA, Matheson CA. Developing breeding objectives for radiata pine structural wood production. II. Sensitivity analyses. *Can J For Res.* 2006;36:2932–42.
278. Schlichting CD. Hidden reaction norms, cryptic genetic variation, and evolvability. *Ann N Y Acad Sci.* 2008;1133:187–203.
- 279.●● Willi Y, Buskirk J Van. A review on trade-offs at the warm and cold ends of geographical distributions. *Phil Trans R Soc B Biol Sci.* 2022;377: 20210022. **This review is focused on the evolution of the ecological niche at the edges of distributions and demonstrates that trade-offs overlapped with some of the classic trade-offs reported in life-history evolution or thermal adaptation.**
280. Freer-Smith P, Muys B, Bozzano M, Drössler L, Farrelly N, Jactel H et al. Plantation forests in Europe: challenges and opportunities. *From Science to Policy* 9. *Eur For Inst.* 2019;50
281. Brotherstone S, Goddard M. Artificial selection and maintenance of genetic variance in the global dairy cow population. *Philos Trans R Soc B Biol Sci.* 2005;360:1479–88.
- 282.● Dwivedi SL, Reynolds MP, Ortiz R. Mitigating trade-offs in plant breeding. *iScience.* 2021;24:102965. **This study shows that regulating genes in grain crops deploy diverse functions to overcome trade-offs and therefore, mitigating trade-offs through breeding may expose new ones, which pose some caution in breeding for resistance.**
283. Lefèvre F, Koskela J, Hubert J, Kraigher H, Longauer R, Olrik DC, et al. Dynamic conservation of forest genetic resources in 33 european countries. *Conserv Biol.* 2012;27:1–12.
284. Koskela J, Lefèvre F, Schueler S, Kraigher H, Olrik DC, Hubert J, et al. Translating conservation genetics into management : Pan-European minimum requirements for dynamic conservation units of forest tree genetic diversity. *Biol Conserv.* 2013;157:39–49.
- 285.●● Aitken SN, Bemmels JB. Time to get moving: assisted gene flow of forest trees. *Evol Appl.* 2016;9:271–90. **This is a particularly comprehensive work addressing the current knowledge on the basis and perspectives of assisted migration (gene flow) in forest trees, with emphasis in N. America.**
286. Pelai R, Hagerman SM, Kozak R. Whose expertise counts? Assisted migration and the politics of knowledge in British Columbia's public forests. *Land Use Policy.* 2021;103:105296.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Authors and Affiliations

Jose Climent¹  · Ricardo Alía¹  · Katri Karkkainen²  · Catherine Bastien³  · Marta Benito-Garzon⁴  · Laurent Bouffier⁴  · Giovanbattista De Dato⁵  · Sylvain Delzon⁴  · Arnaud Dowkiw³  · Margarita Elvira-Recuenco¹  · Delphine Grivet¹  · Santiago C. González-Martínez⁴  · Haleh Hayatgheibi⁶  · Sonja Kujala²  · Jean-Charles Leplé⁴  · Ruth C. Martín-Sanz⁷  · Marina de Miguel⁴  · M. Cristina Monteverdi⁵  · Sven Mutke¹  · Christophe Plomion⁴  · José Alberto Ramírez-Valiente¹  · Leopoldo Sanchez³  · Aida Solé-Medina¹  · Jean-Paul Soularue⁴  · Arne Steffenrem⁸  · Angela Teani⁵  · Johan Westin⁶  · Richard Whittet⁹  · Harry Wu⁶  · Rafael Zas¹⁰  · Stephen Cavers¹¹ 

✉ Jose Climent
climent@inia.csic.es

Ricardo Alía
alia@inia.csic.es

Katri Karkkainen
katri.karkkainen@luke.fi

Catherine Bastien
catherine.bastien@inrae.fr

Marta Benito-Garzon
marta.benito-garzon@inrae.fr

Laurent Bouffier
laurent.bouffier@inrae.fr

Giovanbattista De Dato
giovanbattista.dedato@crea.gov.it

Sylvain Delzon
sylvain.delzon@u-bordeaux.fr

Arnaud Dowkiw
arnaud.dowkiw@inrae.fr

Margarita Elvira-Recuenco
margarita.elvira@csic.es

Delphine Grivet
dgrivet@inia.csic.es

Santiago C. González-Martínez
santiago.gonzalez-martinez@inrae.fr

Haleh Hayatgheibi
haleh.hayatgheibi@slu.se

Sonja Kujala
sonja.kujala@luke.fi

Jean-Charles Leplé
jean-charles.leple@inrae.fr

Ruth C. Martín-Sanz
ruthcristina.martin@uva.es

Marina de Miguel
marina.de-miguel@inrae.fr

M. Cristina Monteverdi
mcristina.monteverdi@crea.gov.it

Sven Mutke
sven.mutke@csic.es

Christophe Plomion
christophe.plomion@inrae.fr

José Alberto Ramírez-Valiente
jose.ramirez@inia.csic.es

Leopoldo Sanchez
leopoldo.sanchez-rodriguez@inrae.fr

Aida Solé-Medina
aidasome@gmail.com

Jean-Paul Soularue
jean-paul.soularue@inrae.fr

Arne Steffenrem
Arne.Steffenrem@nibio.no

Angela Teani
angela.teani@crea.gov.it

Johan Westin
johan.westin@slu.se

Richard Whittet
richard.whittet@forestresearch.gov.uk

Harry Wu
harry.wu@slu.se

Rafael Zas
rzas@mbg.csic.es

Stephen Cavers
scav@ceh.ac.uk

- 1 ICIFOR-INIA, CSIC, Ctra. A Coruña Km 7.5, 28040 Madrid, Spain
- 2 Natural Resources Institute Finland (LUKE), Latokartanonkaari 9, FI-00790 Helsinki, Finland
- 3 UMR 0588 BioForA, INRAE, 2163 Avenue de La Pomme de Pin, 45000 Orléans, France
- 4 INRAE, BIOGECO, Univ. Bordeaux, 33400 Pessac, France
- 5 Council for Agricultural Research and Economics, Research Centre for Forestry and Wood, Viale Santa Margherita, 80, 52100 Arezzo, Italy

- ⁶ Department of Forest Genetics and Plant Physiology, Umeå Plant Science Centre (UPSC), Swedish University of Agricultural Sciences, 901 87 Umeå, Sweden
- ⁷ iuFOR, University of Valladolid, Campus de Palencia, Avda. Madrid s/n, Palencia, Spain
- ⁸ Division of Forestry and Forest Resources, Norwegian Institute of Bioeconomy Research (NIBIO), Skolegata 22, 7713 Steinkjer, Norway

- ⁹ Forest Research, Northern Research Station, Roslin, Midlothian EH25 9SY, UK
- ¹⁰ Misión Biológica de Galicia, CSIC, A Carballeira, 8, 36143 Salcedo, Pontevedra, Spain
- ¹¹ UK Centre for Ecology & Hydrology (UKCEH), Bush Estate, Penicuik, Midlothian, Scotland, UK