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Research paper

How eco-evolutionary principles can guide tree breeding and tree biotechnology for enhanced productivity

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Tree breeding and biotechnology can enhance forest productivity and help alleviate the rising pressure on forests from climate change and human exploitation. While many physiological processes and genes are targeted in search of genetically improved tree productivity, an overarching principle to guide this search is missing. Here, we propose a method to identify the traits that can be modified to enhance productivity, based on the differences between trees shaped by natural selection and ‘improved’ trees with traits optimized for productivity. We developed a tractable model of plant growth and survival to explore such potential modifications under a range of environmental conditions, from non-water limited to severely drought-limited sites. We show how key traits are controlled by a trade-off between productivity and survival, and that productivity can be increased at the expense of long-term survival by reducing isohydric behavior (stomatal regulation of leaf water potential) and allocation to defense against pests compared with native trees. In contrast, at dry sites occupied by naturally drought-resistant trees, the model suggests a better strategy may be to select trees with slightly lower wood density than the native trees and to augment isohydric behavior and allocation to defense. Thus, which traits to modify, and in which direction, depend on the original tree species or genotype, the growth environment and wood-quality versus volume production preferences. In contrast to this need for customization of drought and pest resistances, consistent large gains in productivity for all genotypes can be obtained if root traits can be altered to reduce competition for water and nutrients. Our approach illustrates the potential of using eco-evolutionary theory and modeling to guide plant breeding and genetic technology in selecting target traits in the quest for higher forest productivity.

Keywords: adaptation, anisohydric, aridity, climate, ecology, evolution, forestry, functional traits, genetic modification, gmo, hydraulics, life history, mathematical model, mortality, risk management, selection, strategy, transpiration, wood.

Introduction

The potential benefits of genetically improved plants are huge, in particular, under progressing climate change (Fenning et al. 2008). Consequently, molecular biology and biotechnology for the purpose of improved productivity of agricultural plants and trees are rapidly developing fields of research (Nelson and Johnsen 2008, Harfouche et al. 2014). New promising ways to modify physiological processes via their associated genes

are constantly being developed, and there has already been significant progress in improving many factors linked to tree productivity, e.g., for *Salix*, *Populus* and *Eucalyptus* species (Girijashankar 2011, Ye et al. 2011, Hanley and Karp 2014). For trees, this progress has been based largely on a reductionist approach, targeting each promising physiological process or plant trait separately (Nelson and Johnsen 2008). However, because different processes are linked within the plant and also with the environment, the pure reductionist approach may

not readily tell us how different modifications will interact and function under variable environmental conditions. For example, the productivity effect of a molecular enhancement of the wood formation process (e.g., cambial activity, Nieminen et al. 2012) may not be independent of the carbon (C) supply to the wood-forming zone, which depends on photosynthetic rate and leaf area, which itself is dependent on C supply. Further, an enhanced growth of one tree may hamper the growth of neighboring trees via resource competition. In summary, trees are complex systems and forests are even more complex. In the face of this complexity, we argue that a holistic perspective based on the physiological, ecological and evolutionary principles that ultimately govern plant function can help select plant traits to target for genetic improvements.

Growth of both natural and managed forests tightly depends on the environmental conditions, such as resource availability. In particular, water availability and drought are often limiting for forest growth and may become even more so under future climatic conditions (Anderegg et al. 2012, Dai 2013). Thus, we will focus on how tree properties vary and how they can be modified to enhance growth and water-use efficiency (WUE) under different degrees of water limitation or drought severity. To account for wood quality and biomass we analyze the effects on productivity in relation to wood density (Zhang et al. 2003). However, before we can evaluate possible trait modifications, we must have a mechanistic understanding of how the relevant tree traits vary with environmental conditions, and how these traits are linked to productivity.

Plants respond to water limitation in a multitude of ways, and vast amounts of details are known and incorporated in models of root uptake, leaf conductance and transpiration (Landsberg and Sands 2010). However, to understand whole-plant drought effects and mortality risk, a holistic system perspective is necessary due to the multiple interacting plant responses (Anderegg et al. 2012). Furthermore, the drought responses need to be integrated within the full growth and survival (life-history) strategy of the plant. In comparison to relatively well understood trade-offs among the acquisition of different resources (Maire et al. 2013), the strong links between water limitation and life-history strategies, such as trade-offs between survival and growth (Poorter et al. 2010), are not well understood at a mechanistic level. Such a mechanistic understanding is, however, necessary for development of improved plant varieties that are robust under variable drought conditions (Tardieu 2012). Thus, to understand and predict the variability in drought-related plant traits a new mechanistic model is needed that merges physiology (photosynthesis, respiration and transpiration) and life-history strategy (risk management).

Here, we derive a mechanistic model of trait variation in response to drought, based on the principle that traits adapt to maximize fitness (Spencer 1896, Orr 2009), approximated

by lifetime reproductive output. This principle allows us to integrate the effects of growth and survival, which is fundamental for understanding the evolution of drought-related traits, such as wood density and hydro-sensitivity (the sensitivity of stomatal conductance to leaf water potential), which affect both mortality risk and potential growth rate. In addition, the overarching principle enables us to put the effects of drought into context with other limiting factors, such as light environment and disturbance frequency as well as competition. To facilitate understanding, the model includes only the most relevant ecophysiological and structural plant properties or functional traits (Violle et al. 2007) at the organ or plant level, such as photosynthetic capacity, conductive capacity, hydro-sensitivity, wood density, and allocation of C to defense and belowground (Figure 1). We do not address the underlying molecular processes and genetic controls nor the methods of modification, but explore which traits should be modified and how much. Because we focus on traits that are naturally variable, we assume that these traits can be altered. For some traits, such as hydro-sensitivity, the knowledge of its natural variability is limited (Klein 2014), but on the other hand, it has already been subject to successful alteration via aquaporins (Sade et al. 2009, Moshelion et al. 2014).

The ultimate purpose of our model is to illustrate how eco-evolutionary theory and modeling can be used to direct tree breeding and to evaluate options in a realistic context, which is not practical to do experimentally due to the long life span of trees and complexity of the forest environment. In a plant breeding program, our suggested method of identifying optimal traits and improvement potential would be the first step in development of an ideotype, that is, an ideal tree for a given purpose and environment (Nelson and Johnsen 2008), which can be followed by genetic mapping of the selected traits (Hanley and Karp 2014), genomic methods (Resende et al. 2012) and detailed species-specific modeling linking genes with physiological processes (Messina et al. 2011). We develop our approach in two stages: (i) we construct a simple model of plant fitness in terms of growth and survival under variable drought and light/disturbance conditions, which is representative of the natural variability of the traits. (ii) Using the natural trait values as a starting point, we explore the potential and limitations of tree (species) selection, and trait modifications to increase productivity in a managed forest environment.

A mechanistic model of trait variability

Overview

Many plant traits affect both growth and survival—two main aspects of plant fitness—in opposite ways. For example, defense against pests not only increases survival, but also uses up C that could have been used for growth (Figure 1). To handle such trade-offs and other interactions among plant

functions and traits, we model fitness. Fitness is a measure of a genotype's (represented by one or more individuals) success in propagating itself, which is a function of growth, survival and production of offspring (Orr 2009). Specifically, here we use fitness defined as population growth rate of a genotype, which we approximate by lifetime reproductive production (Franklin et al. 2012). The fitness equation integrates the effects of all modeled traits on growth and survival under the assumption that fitness is maximized. Below we describe how growth and survival respond to trait values and environmental conditions before we combine them in the fitness equation.

Importantly, the purpose of the model is not primarily to predict growth of any particular species or forest type, but to illustrate the benefits of a trait and fitness-based modeling approach in tree breeding for readers from various disciplines. Thus, to minimize model complexity and the number of uncertain parameters, we use the simplest possible mathematical representations (Appendix) that capture the relevant mechanisms.

The environment—drought and light

We represent water availability in terms of drought severity (D) and its effects on photosynthesis and mortality (see Growth model section below). Drought severity represents the mean total effect of water limitation on photosynthesis and mortality, regardless of the specific contributing factors, such as rainfall, temperature, soil type and feedback from water use by vegetation.

Light environment is a major determinant of plant strategies and growth, and it is linked to disturbances. Disturbance

frequency not determines only often maximum life span but also duration and size of gaps, when death of large trees creates high-light environments with limited duration. By defining the environment variable 'niche duration' we can account for both frequency of disturbances that limit stand life span (e.g., fire) and duration of gaps (duration of high light). Rather than referring only to fully sunlit gaps the niche duration refers to the generalized relationship between light level and duration of the environment (Figure 2). Because the stronger the light, the faster the plant growth, and the quicker a gap is filled, we assume a negative relationship between niche duration and mean light level. Furthermore, because the mean light level depends on the canopy cover and depth (leaf area index, LAI), which is limited by water availability, we assume a positive relationship between drought and light in natural environments.

Light strategy is often characterized in terms of 'shade tolerance', which can be defined in various ways, but ranges from a 'slow' low-light strategy with late reproduction and long lifespan to 'fast' with early reproduction and short lifespan (Reich 2014). In our model, shade tolerance is not defined a priori by any specific parameter but corresponds to the set of parameter values that are optimal under a given environment (quantified as environmental duration).

Growth model

Photosynthesis, or gross primary production (GPP in Figure 1), determines the gross input of C to the plant and is limited by light and photosynthetic capacity (A_{sat}), which is modeled as a function of canopy photosynthetic nitrogen (N, Franklin et al. 2012) and conductance. Part of the assimilated C is used to cover the costs for the essential maintenance of the current biomass (respiration, leaf and root turnover) and the remainder—net growth (G)—can be used for biomass growth, reproductive production and investment in defense. Costs of maintenance respiration and litter production are defined as a function of plant N (Franklin 2007). Costs of stem, roots and conductive capacity, such as sapwood and aquaporins (Chrispeels et al. 1999), are expressed in proportion to canopy N, reflecting the interdependence among the different organs (Franklin 2007). We account for shifts in below-ground C allocation by letting the ratio of root C costs: canopy N increase with drought severity (Poorter et al. 2012), which is the expected response to declining resource uptake per root biomass (Franklin 2007). The amount of canopy N and conductive capacity are determined by optimization (net growth maximization) with respect to their benefit for photosynthesis versus the C-costs for N uptake and maintenance respiration (Franklin 2007), which means that total canopy N (but not leaf N concentration) declines with drought severity due to the increased root C costs per N uptake. Whereas canopy N acclimates to changing conditions due to management, conductive capacity (e.g., sapwood: canopy N ratio) is genetically

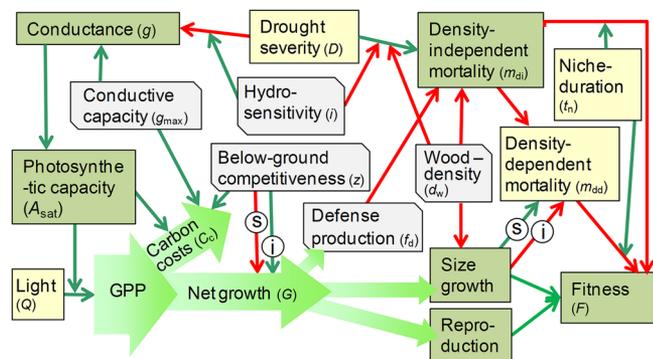


Figure 1. Model structure showing C fluxes (block arrows), environmental factors (light, yellow boxes), heritable traits analyzed for modification potential (gray diagonal-corner boxes) and other plant traits (darker green boxes). Symbols (in parentheses) are explained in Table A1. Arrows show positive effects (light, green arrows) or negative effects (dark, red arrows). For example, increased hydro-sensitivity aggravates the negative effect of drought on conductance while it alleviates drought-induced mortality. Some traits have opposite effects on an individual (arrows with encircled i) compared with the stand (arrows with encircled S), such as size growth, which reduces an individual's density-dependent mortality risk at the same time at it increases the stand level density-dependent mortality. Note that color versions of Figures 1, 2 and 4–9 are available in the online version of this paper.

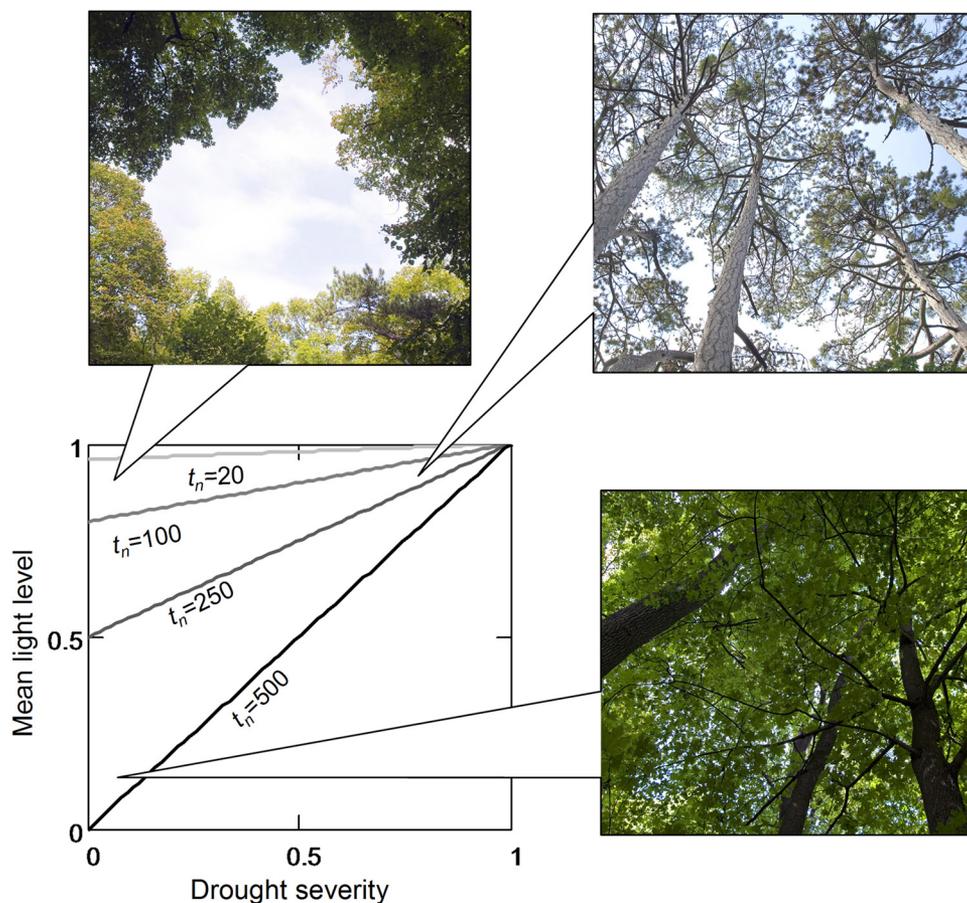


Figure 2. The light–drought environment in the model. Each line shows a different niche duration (t_n), that is, for how long a combination of drought and light conditions is likely to last (Eq. (A1)). Example figures show a forest gap where light is high but duration short as it will quickly close through re-growth and canopy expansion of surrounding trees (top left), forest understory with low light that may persist for long periods of time (bottom right) and a dry forest with sparse canopy and high-light penetration (top right), where duration may be long or short, and depend on frequency of catastrophic disturbances, such as fire.

determined (optimized) for the plant's native environment and does not change due to management of the environment.

To keep the analysis tractable we do not model age effects or ontogenetic development, but yearly mean growth and mortality per area. This implies that the growth and mortality predictions are representative for forest growth averaged over the lifetime of the trees, or for forests at approximately a steady-state age-distribution, but not necessarily for very young or very old trees.

Water limitation

To account for drought effects on plant mortality and photosynthesis, we use the environmental variable drought severity (D), which includes effects of both mean water availability and variability, in particular drought length (Parolari et al. 2014). Drought leads to reduced plant water potential to which the plants respond by reducing the conductance of water, which also reduces the conductance of CO_2 and therefore photosynthesis (A_{sat}). Conductance (g) is a function of conductive capacity (g_{max}) and stomatal regulation (Figure 1).

Conductive capacity determines the maximal flux rates of CO_2 into the plant and water out of the plant and is limited by factors such as sapwood cross-sectional area. We model conductance regulation based on a new concept, hydro-sensitivity (i). Hydro-sensitivity is a measure of how responsive stomatal conductance is to leaf water potential, that is, high and low hydro-sensitivity correspond to an isohydric and an anisohydric strategy, respectively (Sade et al. 2012, Klein 2014). However, instead of explicitly modeling stomatal response to water potential, we model its consequences in terms of how photosynthesis responds to D . The higher the hydro-sensitivity, the more the plant reduces conductance—therefore modeled photosynthesis (A_{sat})—in response to D Eq. ((1), Figure 1).

$$g = g_{\text{max}}(1 - i \times D \times 1.5) \quad (1)$$

The premise that hydro-sensitivity is a meaningful species-specific trait is supported by observations across multiple species and biomes, suggesting that the sensitivity of plant

conductance to drought is consistent within species (Martínez-Vilalta et al. 2014). The purpose of this functional model of plant water limitation is to bring out the essential time-averaged effects on photosynthesis and mortality risk without the need to model the underlying highly dynamic physical processes in terms of water potentials and gas flux balances. As we do not model water flux and transpiration we also use plant conductance as a proxy for water use.

Competition

In addition to the light and drought-dependent behavior, we also consider another important component of a plant's growth strategy: competitive behavior for soil resources (nutrients and water). Competition implies that a tree can gain shared resources at the expense of its competitors, and that the soil volume it can access (rooting volume) is larger than the actual mean soil volume available per tree. Each individual then optimizes investments in uptake of water and nutrients according to this 'overestimated' accessible soil volume. Consequently, the total investments in uptake of all the competitors at the stand level will be higher than what would be optimal if all the trees could collectively optimize uptake investments or if each tree had its own resource pool (King 1993, Franklin et al. 2012, 2014). Thus, we model the effect of increasing belowground competition implicitly as an increase in belowground C allocation (fine-roots, mycorrhiza or other C release) per canopy N.

Mortality risks and strategies for survival

Mortality can be described in terms of density-dependent mortality and density-independent mortality, which in our model includes three main causes: (i) pests—attacks by herbivores and pathogens, (ii) drought—drought-induced damage including cavitation, defoliation and other contributing factors (Anderegg et al. 2012) and (iii) mortality (other than drought-related) that is controlled by wood density, such as mechanical breakage (Chave et al. 2009). All other causes of density-independent mortality are included in a constant baseline mortality. All sources of mortality (defined below) are expressed in terms of probability of death during 1 year and are summed to obtain total mortality.

Density-independent mortality All the density-independent mortality risks decline exponentially with investments in risk management (defense), based on the rationale that (i) the severity of the worst event that the plant can survive is proportional to its investment in defense and (ii) minor adverse events are common while the probability of severe events declines rapidly (exponentially) with severity. This distribution of adverse events results if attack severity is a function of the total rate of individual attacks (attacks per time) by multiple independently attacking agents, such as insects. A mathematically similar exponential distribution of drought mortality

and the efficiency of drought management can be expected if drought severity (D) is linked to the number of days without precipitation, which is a main driver of drought mortality (Parolari et al. 2014).

Following the rationale described above, pest mortality declines exponentially as a function of the fraction of acquired resources invested in defense, while wood-density-related mortality declines exponentially with wood density. In a risk management perspective, these responses can be seen as risk resistance or loss control strategies (Näsholm et al. 2014). The plant response to drought is more complex as trees can use both risk resistance and avoidance strategies (Näsholm et al. 2014). A major danger of drought lies in the risk of hazardously low water potentials (negative pressure) in water conduits. This risk can be avoided by isohydric behavior, closing the stomata in response to declining water potential, or it can be controlled or resisted, by sufficiently high wood density (Chave et al. 2009, Poorter et al. 2010, Reich 2014) via its effect on xylem wall strength (Hacke et al. 2001). Thus, plant survival under drought depends on a combination of isohydric behavior–risk avoidance, which reduces the drought impact (negative water potential) and wood density, which controls resistance to the impact–loss control. Consequently, drought mortality declines exponentially with both isohydry (increasing hydro-sensitivity) and wood density in the model. In the absence of isohydry, drought mortality is proportional to the ratio of drought severity : wood density.

Density-dependent mortality Density-dependent mortality (m_{dd}) or self-thinning (Yoda et al. 1963) is a consequence of increasing competition for resources, most importantly light, with increasing individual size or number of individuals per area. Density-dependent mortality increases with growth rate and declines with increasing density-independent mortality (Franklin et al. 2009a). Assuming that stand biomass is at steady state, total mortality ($m_{dd} + m_{di}$) must match biomass increment, which results in m_{dd} equal to relative biomass growth rate minus density-independent mortality: $m_{dd} = (1/B)(dB/dt) - m_{di}$. Stand biomass (B) is assumed to be proportional to the amount of photosynthetic canopy N, which is linked not only to canopy size but also to the supporting stem and root structures (pipe model, Shinozaki et al. 1964) and thus to total biomass.

Because m_{dd} is linked to stand level growth rather than to the growth of the individual, or genotype, itself, it is only partly linked to the strategy and fitness of the individual. Specifically, the density-dependent mortality influences an individual's strategy only to the extent that the strategy affects its own environment (environmental feedback, Franklin et al. 2012). In our model, the parameter e determines the strength of this feedback on fitness, that is, how much density-dependent mortality m_{dd} an individual imposes on itself, adding to its total strategy-related mortality $m = m_{di} + e m_{dd}$. In a heterogeneous environment with

multiple coexisting strategies (many species), a strategy can evolve with minimal feedback from density-dependent mortality, that is $e \rightarrow 0$, while in a homogenous environment a single-dominant strategy may strongly influence density-dependent mortality, that is $e \rightarrow 1$. We used $e = 0.25$ but found that model predictions varied only marginally within a range of e values between 0 and 0.5.

The controlling principle—traits evolve to increase fitness

Plant traits evolve to increase fitness (population growth rate of a genotype, see Overview above) via their effects on both productivity and survival (Figure 1). In the model, fitness of a plant is approximated by its fecundity (F), or individual reproductive production (G_{RI}) integrated over the niche duration (t_n , Eq. (2)).

$$F = \int_0^{t_n} G_{\text{RI}}(1 - m)^t dt \quad (2)$$

For simplicity we assume that mortality (m , probability that a tree dies during 1 year), growth and reproduction do not vary over time. In reality a plant's strategy changes over its lifetime: from investing for the future by prioritizing size growth and resource acquisition at younger ages to reproductive production at mature ages. To account for these two different age-dependent goals in our age-independent model, we approximate integrative reproductive production (G_{RI}) with a combination of size (volume) growth and reproductive production (a constant fraction of net production, Appendix).

We assume that the native plant traits in a given environment (as defined by drought severity, light and niche duration) are evolutionary stable strategies and correspond to the trait values that maximize F (Franklin et al. 2012), that is, the set of traits that results in an optimal balance of individual growth and survival. Because the effect of individual growth on density-dependent mortality (environmental feedback) is 'diluted' among many individuals, the optimal individual strategy differs from a stand level optimum. Although evolution does not always lead to maximization of fitness, this is a reasonable approximate assumption for forests (Franklin et al. 2012). Due to environmental variability in light and niche duration (t_n in Eq. (2)), not only one but a range of optimal strategies can be modeled to coexist at the same site, e.g., light-demanding species in gaps and shade tolerants in shade as discussed above (The environment—drought and light).

Results for natural trees—does the model explain trait variability?

Because the model integrates well-known aspects of risk management, where reducing mortality risk implies costs in terms of reduced photosynthesis and growth, it is evident that the results will show trade-offs between productivity and survival (as governed by Eq. (2)). However, it is not self-evident how

different growth-related traits or risk management strategies will interact, e.g., if the trees increase hydro-sensitivity or wood density in response to drought, and how it depends on pest defense or niche duration. The question is whether the concerted action of all traits is reasonable in terms of predicted inter-trait relationships. In addition, we evaluated the sensitivity of the results to variation in parameter values and modeled the effect of a 10% change in the most sensitive parameter for each predicted trait.

The model predicts that increasing drought severity reduces growth and increases wood density (Figure 3), which is a means to counteract the increasing drought mortality. At the same time, density-dependent mortality declines while there is a slight increase in pest mortality (Figure 4) following a slight reduction in defense allocation (Figure 3). This means that the plant responses to different risks interact so that at increasing drought severity, investment in drought management is increased at the expense of pest resistance. This leads to higher pest mortality in drier environments and under drought stress, in agreement with observations (Preisler et al. 2012, Arango-Velez et al. 2014). Furthermore, plant conductance (Eq. (1)) per photosynthetic N declines with drought severity in the model (Figure 3f) in agreement with observations and leaf-scale optimization models (Prentice et al. 2014).

For each drought level, different temporal strategies are possible, corresponding to a gradient from adaptation to short duration high-light (disturbed) patches to long duration lower light environments (shade) (Loehle 2000). Along this gradient from high- to low-light environments, growth and density-independent mortality decline in agreement with observations (Condit et al. 1995), which is correlated with increasing wood density and investment in defense (Figure 4), in line with observations (Loehle 1988, Coley and Barone 1996). These adaptations to different light environments give rise to negative relations between wood density and both growth and mortality (Figure 5). These relationships correspond well with the observed wood economics spectrum (Chave et al. 2009) and the 'fast-slow' plant strategy spectrum (Reich 2014) where trees with low wood density live fast and die young and vice versa for trees with high wood density.

Interestingly, hydro-sensitivity is maximal at intermediate drought severity (Figure 3). The reasons for this model behavior are (i) in the absence of water limitation, isohdry and associated reduction in photosynthesis are not worthwhile as drought mortality is insignificant in relation to other causes of mortality (Figure 4), (ii) at low but increasing water limitation the benefits of isohdry increases and (iii) in drier environments plants cannot afford high hydro-sensitivity as, in combination with drought, this leads to strong reductions in photosynthesis and thus inefficient use of the photosynthetic machinery (canopy N). Instead, increasing wood density is a better strategy that allows the plants to maintain high efficiency

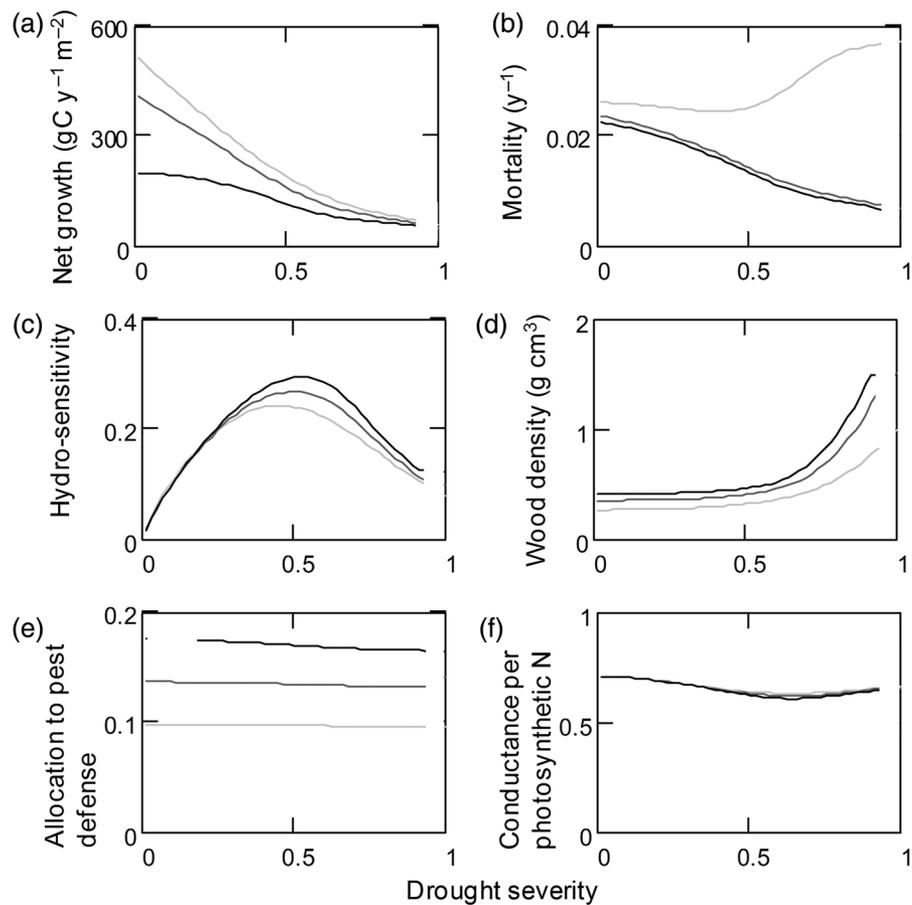


Figure 3. Modeled variation in native plant traits as a function of drought severity for trees adapted to different niche durations (t_n , see Figure 2). Each panel show results for $t_n = 20$ (light gray line), $t_n = 100$ (gray line), $t_n = 300$ (black line). Mortality is total mortality (Figure 4).

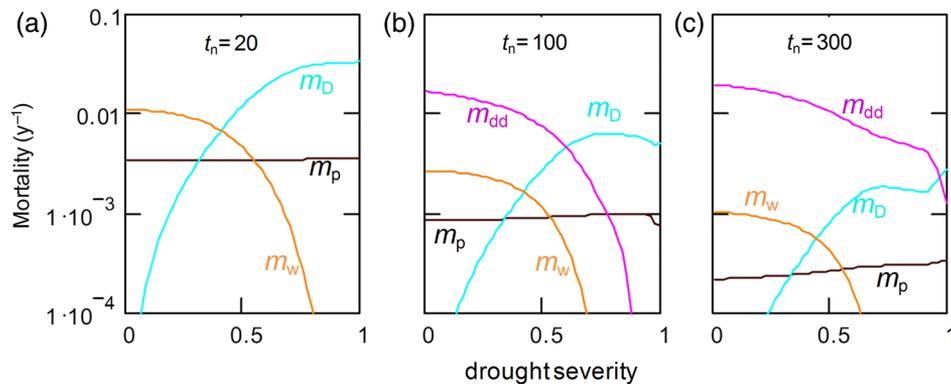


Figure 4. Different mortality risks as a function of drought severity for different niche durations (t_n , see Figure 2). The density-independent mortalities: pest mortality (m_p , black line), drought mortality (m_D , turquoise line) and non-drought wood-density-related mortality (m_w , orange line) all decline with niche duration, while density-dependent mortality (m_{dd} , magenta line) increases (it is too low to show in (a)). Increasing drought increases the relative importance of drought and pest mortality.

of the photosynthetic machinery under increasing drought, which more than compensates for the negative effect of wood density on fitness via reduced volume growth (Figure 1). This result may explain the seemingly contradicting observations of increased value of isohydry under low but increasing water stress (Kumagai and Porporato 2012, Sade et al. 2012) and

the prevalence of an anisohyric strategy in drought-adapted species (Sade et al. 2012, Klein 2014, Manzoni 2014).

In summary, despite its simplicity the model is able to capture major aspects of observed trait variability related to water and light availability. In addition, it suggests a novel, testable hypothesis for the relationship between hydro-sensitivity and

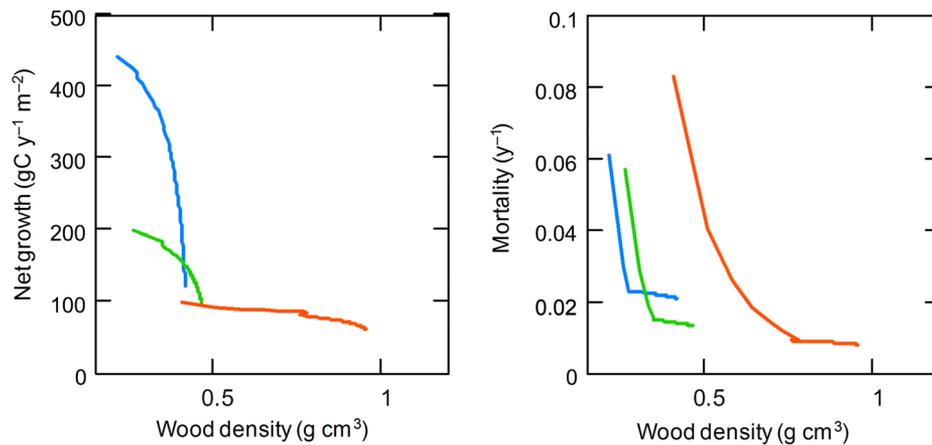


Figure 5. Modeled relationship between growth and total mortality versus wood density of trees in their native environment. The lines correspond to a wet site ($D = 0.13$, leftmost, blue line), an intermediate site ($D = 0.5$, middle, green line) and a dry site ($D = 0.8$, rightmost, red line). For each site, a range of niche durations (see Figure 1) from 10 to 400 years (corresponding to left and right endpoints of each colored line, respectively) were evaluated.

drought. A sensitivity analysis showed that net growth and total mortality are rather sensitive to photosynthetic N-use efficiency and C costs per N, but showed no indication that the sign or shape of any trait–drought or inter-trait relationship would be highly sensitive to parameter uncertainty (Table S1 and Figure S1 available as Supplementary Data at *Tree Physiology* Online). Although further testing would be necessary to thoroughly quantify the model's performance, we believe that it provides a sufficiently relevant mechanistic representation of our focal tree traits and their relation to productivity to support the further analysis of potential trait modifications.

Modifying trees for improved forest productivity

Modeling the managed forest

So far, the purpose of the model has been to establish the natural trait variability in trees, as shaped by evolution and growth in their natural environment. The next step is to identify possible ways to modify the trees to increase the productivity of a managed forest. For this, we must define the managed environment (how it differs from the natural, Figure 6) and the goal of the management. We can then replace the natural environment and the goal function (maximal fitness) of the trees in the model with the management goals. In this way, we can model trees adapted for maximal productivity or economic values instead of evolutionary success in nature.

While there are a multitude of different management methods to enhance tree growth, here we focus only on the most ubiquitous effect of management: limited stand density, limited life span and even-aged structure. Adaptation to limited life span is modeled simply by setting the niche duration to a hypothetical harvesting age of 40 years ($t_n = 40$). An even age structure means that most trees are about the same size, and we assume that they all have their tops exposed to full

light. Compared with natural forests, a managed forest often has a lower stand density if it is planted or subject to thinning, which results in reduced or eliminated self-thinning, or density-dependent mortality. Thus, we assume that there is no density-dependent mortality when modeling managed forest. In contrast, density-independent mortality remains a limiting factor for productivity also in managed forests, as we do not address alleviated density-independent mortality by pest control or irrigation.

A large range of costs and benefits related to both biological and economical factors influence the economic value of a forest. However, we limit our productivity perspective to wood volume production, while also acknowledging the importance of wood quality, which is closely associated with wood density (Zhang et al. 2003).

Based on the management goals and the environment, the model predicts the trait values that maximize productivity for each drought condition. In addition, we evaluate effects on WUE (modeled as wood volume production: plant conductance ratio). Changes in WUE that relate to changes in water use could lead to changes in water availability and drought severity over time, and alleviation or aggravation for increased and reduced WUE, respectively. Comparing the productivity and resulting traits of the trees optimized for maximal productivity with non-modified trees, we can identify potential trait modifications that could enhance productivity.

Results for improved trees—potential for increased productivity in drier environments

After modeling non-modified trees in a managed environment to obtain a baseline for comparison (Figure 7), we evaluated the potential of optimizing drought and defense traits to maximize productivity. Of these traits, wood density, hydro-sensitivity and defense allocation have important effects, whereas the

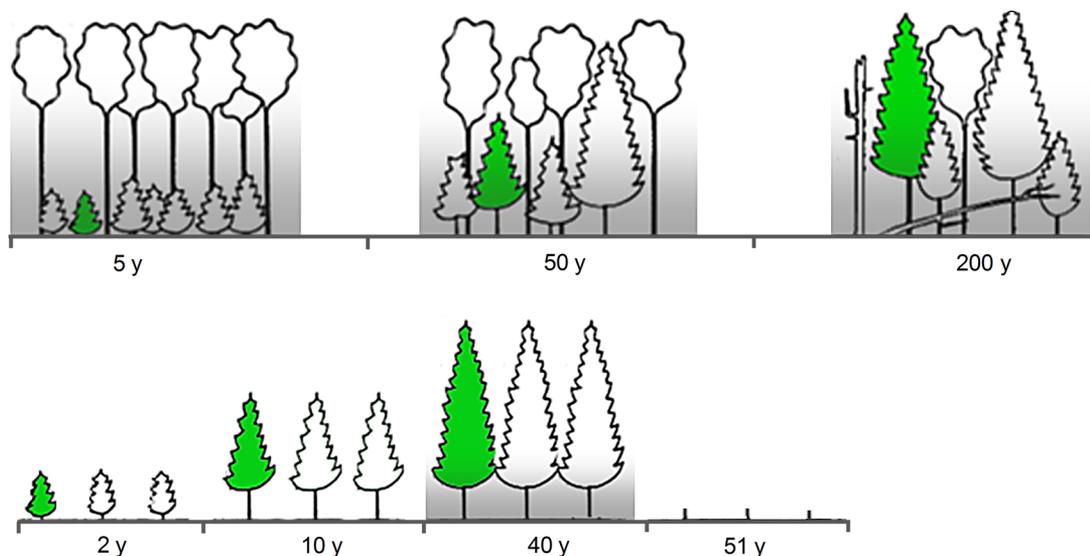


Figure 6. Tree life in a natural forest (upper panel) and a managed forest (lower panel). In a natural forest the life span is potentially very long, but uncertain due to both disturbances (density-independent mortality) and density-dependent mortality mainly caused by shading from larger trees. In a managed forest, density-dependent mortality and shading is largely avoided, but the life span is short. Due to the different conditions, maximal growth in managed forest requires different trees than those that have evolved to maximize fitness in nature.

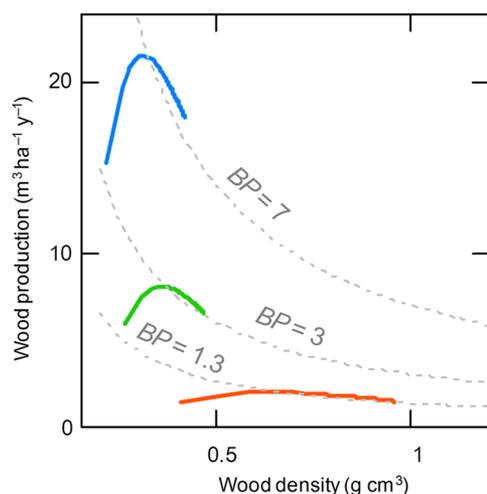


Figure 7. Modeled wood production versus wood density of genetically non-modified trees. The same trees that were modeled in Figure 5 under natural conditions are here modeled under management conditions, assuming harvest age = 40 years and no density-dependent mortality. Dotted gray lines show isoconlines for wood biomass production (BP, $\text{Mg ha}^{-1} \text{ year}^{-1}$). The lines correspond to a wet site ($D = 0.13$, leftmost, blue line), an intermediate site ($D = 0.5$, middle, green line) and a dry site ($D = 0.8$, rightmost, red line).

improvement potential of plant conductive capacity (maximal conductance per photosynthetic N) was negligible. Whereas only very minor increases in biomass or volume production can be achieved at the wet site, larger increases in production can be obtained in the intermediate and dry sites (Figure 8). In the intermediate site, the maximal volume production is obtained by trees with low wood density and cannot be significantly

increased by tuning hydro-sensitivity or defense allocation (Figure 8c). However, by selecting trees with higher wood density, wood quality may be improved, while the biomass production of those trees can be increased (Figure 8c, arrow) by reducing hydro-sensitivity and allocation to pest defenses (Figure 9c, arrow). According to the model results, there are no significant reductions in WUE associated with the trait modifications suggested above. On the contrary, in the dry site, WUE can be significantly increased while volume productivity is maintained by selecting trees with lower wood density than the most productive native trees and increasing their hydro-sensitivity and allocation to defense (Figures 8f and 9f).

In comparison to the potential effects of modifying the drought and defense traits, the effect of reduced belowground competitive behavior is more consistent: it increases productivity in all trees at a site regardless of wood density (Figure 8). This is due to an alleviation of the plants' tendency to acquire resources at the expense of their neighbors and the resulting over-investment in resource uptake at the stand level. The strongest benefit of reduced competition is predicted for the dry site (Figure 8), due to the increasing share of the C budget used belowground for water and nutrient uptake under drier conditions, which amplifies the importance of the costs of over-investments in belowground resource capture. Maximum optimized productivity is obtained at slightly lower wood density than the rather high wood density of the native trees at this site. Thus, under dry conditions, trees with slightly lower wood density than the dominant native trees should be used to maximize productivity (Figure 8e, arrow) if their belowground competition can be reduced. For maximum productivity these

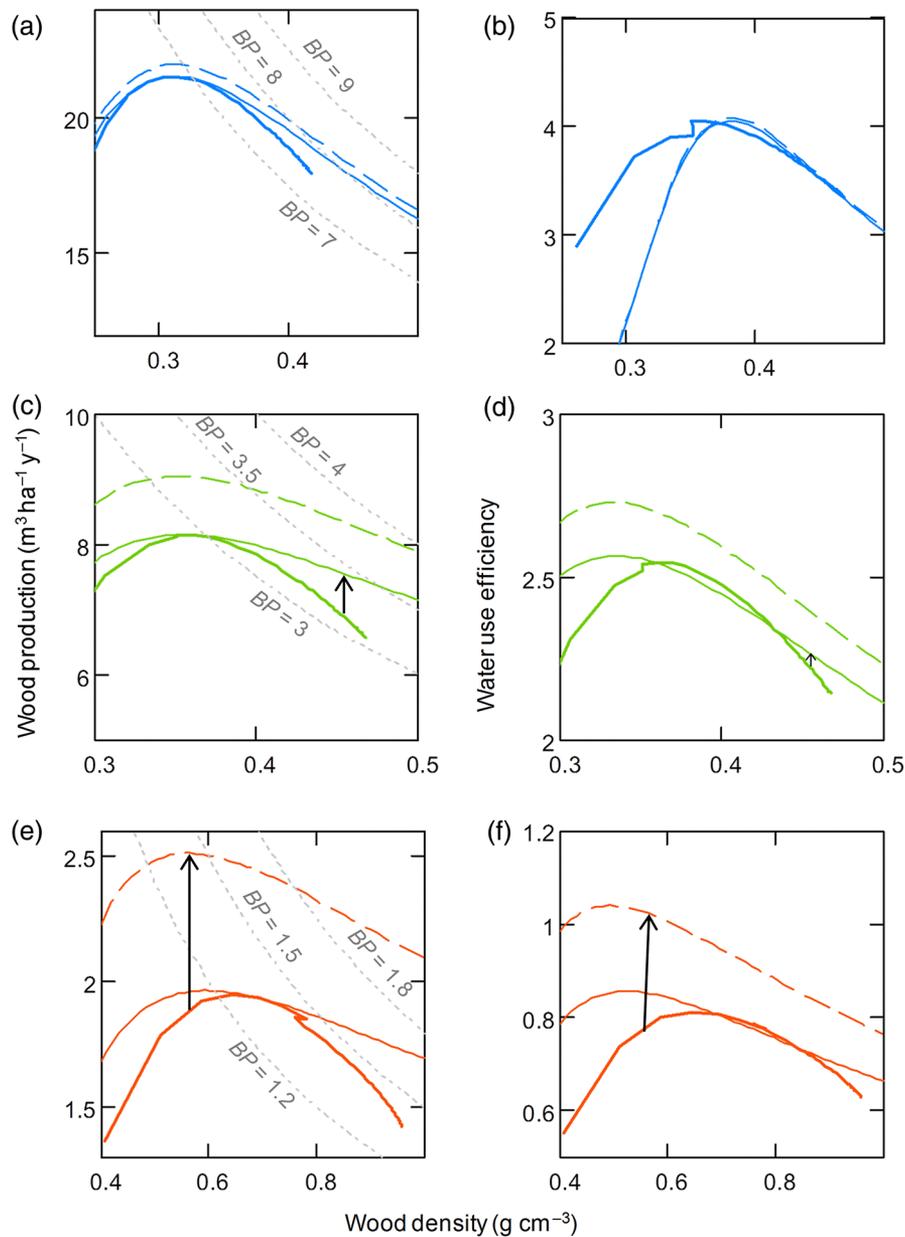


Figure 8. Modeled potential increases in productivity and associated changes in WUE (wood volume production : conductance ratio). Results are shown for a wet site (a, b), an intermediate site (c, d) and a dry site (e, f), for non-modified trees (thick lines), trees with optimized hydro-sensitivity and defense allocation (thin lines) and for optimized trees with reduced competitive behavior (10% reduced belowground C cost per canopy N, dashed lines). Dashed gray lines show isoconlines for wood biomass production (BP, $\text{Mg ha}^{-1} \text{ year}^{-1}$). In the intermediate site (c, d), the arrows show potential productivity increase by reducing hydro-sensitivity and defense allocation (Figure 9c and d) at a fixed wood density. In the dry site (e, f), the arrows show the effect of modifications to maximize productivity via increased hydro-sensitivity and defense allocation (Figure 9d and e) and reduced belowground competition.

trees should be modified further to enhance both hydro-sensitivity and defense allocation (Figure 9e, arrow), which can be seen as a means to compensate for the increase in mortality risk caused by their lower wood density compared with the native trees. Moreover, under intermediate and dry site conditions, reduced belowground competition increases WUE significantly (Figure 8) due to enhanced C allocation to wood (benefit) relative to roots (cost), which increases the C benefit : cost ratio.

Discussion

The benefit of an eco-evolutionary perspective in the search for ideal trees

The underlying force driving the trait variability and its effect on productivity in our model, and presumably in reality, is natural selection for increased fitness (approximated by lifetime reproductive production, Eq. (2)), which is constrained by trade-offs between investments in growth and reproduction

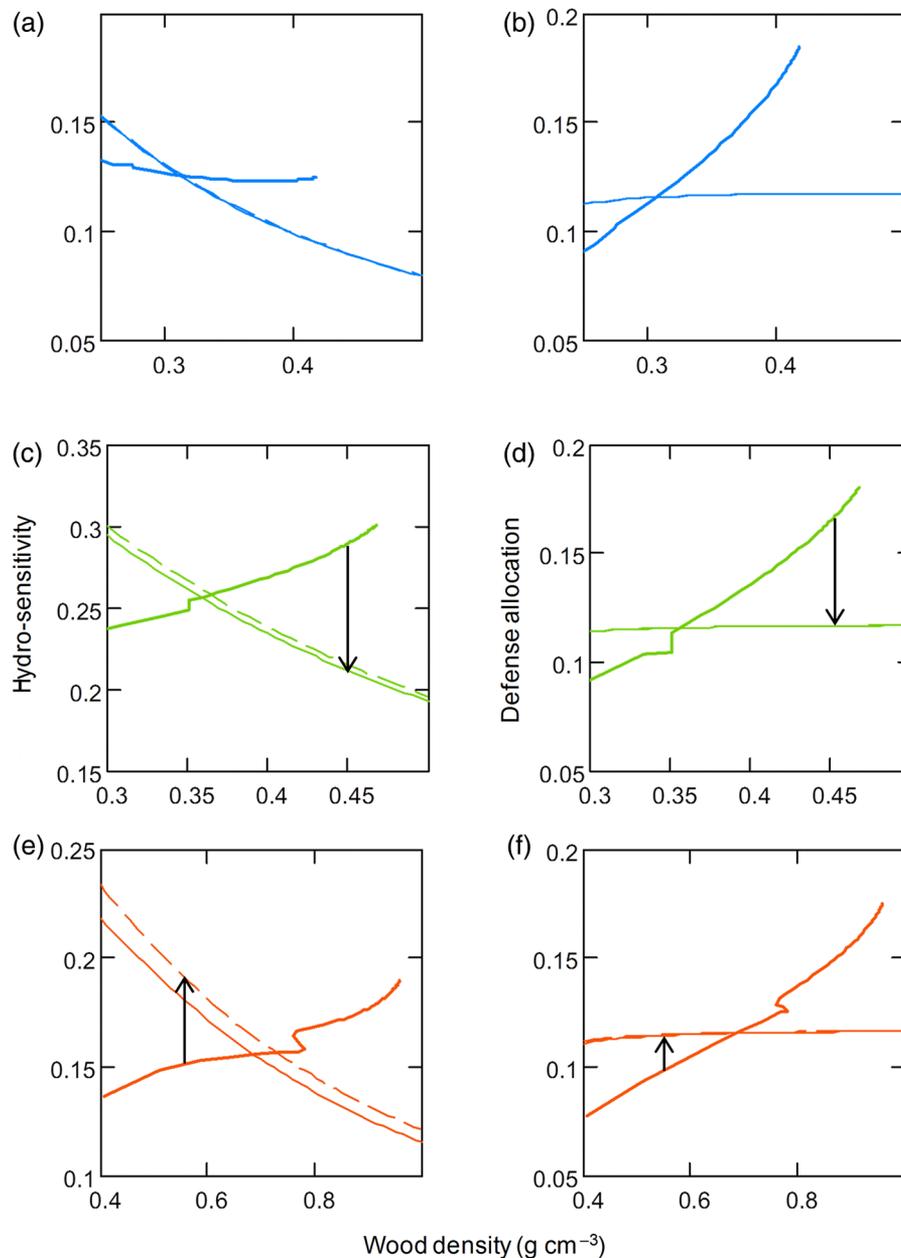


Figure 9. Hydro-sensitivity (a, c, e) and allocation to pest defense (b, d, f) corresponding to the productivity and WUE shown in Figure 8. In the intermediate site (c, d), the arrows show the reduction in hydro-sensitivity and defense allocation necessary for the productivity effects shown by the black arrow in Figure 8c. In the dry site (e, f), the arrows show the increased hydro-sensitivity and defense allocation required for enhanced productivity and WUE shown by the arrows in Figure 8.

versus investments to increase survival via risk management. This principle forms the backbone of the model, integrating the different contributing mechanisms in a holistic perspective on plant strategies in response to drought. Modeling of the physiological drought response is greatly simplified by our concept of hydro-sensitivity, which represents the aggregated effects on photosynthesis and mortality of the underlying physiological and physical mechanisms represented explicitly in more detailed models (Dewar 2002, Tuzet et al. 2003). Whereas this model is inadequate for resolving short-term dynamics in

water limitation, it facilitates understanding of drought effects in a larger context, where drought interacts with other risks and environmental factors over time.

While the focus on only a few key processes and traits helps us understand the key mechanisms, the absence of other drought-related trait variability in the model, such as leaf N content per area, may constrain the predicted productivity responses to drought and result in over-estimation of the role of the traits included. However, although we do not model conductance variability at the leaf level, our model predicts

that conductance (Eq. (1)) per photosynthetic N declines with drought severity (Figure 3f), qualitatively in agreement with observations and more detailed leaf-scale optimization models (Wright et al. 2003, Prentice et al. 2014). Importantly, our framework can readily be expanded with additional traits and details, as long as their respective effects on C gain, C costs and survival can be specified.

As expected, the model predicts strategies to change with environment so that more stable (longer niche duration in the model) and harsher environments (drier or more prone to pest attacks) lead to more investments in risk management at the expense of productivity. Interestingly however, there are shifts between different risk management strategies, from risk avoidance to loss control, for the same risk factor. This is illustrated by the transient increase in hydro-sensitivity in response to mild drought (risk avoidance) followed by increasing wood density (loss control) at more severe drought (Figure 3). Further research is necessary to elucidate the interaction of these and other drought strategies, such as deep roots (Lindh et al. 2014), osmotic regulation (Barchet et al. 2014) and leaf shedding (Waring 1987). In addition, refined representation of drought by separating duration and severity may reveal further drought-strategic diversity (McDowell et al. 2008). Nevertheless, our model's prediction of shifting drought strategies illustrates the power of the eco-evolutionary perspective in generating hypotheses for complex plant responses that are not understandable based on a single mechanism.

To help select or design the ideal trees for a particular purpose and environment the concept of 'ideotype' has been proposed, which essentially is a list of desirable features, or traits, which should be subsequently mapped and targeted for selection or modification (Nelson and Johnsen 2008). These traits, such as high nutrient-use efficiency, can be dissected into component (underlying) traits, such as high stem : leaf ratio (Nelson and Johnsen 2008). However, as illustrated by our analysis, not all wishes are possible to fulfill and different desirable traits may not be easily combined due to physiological and ecological trade-offs. Based on our approach, optimal combinations of traits and modifications can be identified and less-promising options avoided. For example, attempting to increase nutrient-use efficiency via an imposed increase in stem : leaf ratio may be counterproductive because most forest trees are likely to have evolved a strategy that optimizes the stem : leaf ratio to maximize stem growth in order to avoid being over-topped in the ubiquitous competition for light. Thus, although modification of the stem : leaf ratio may enhance nutrient-use efficiency it is likely to reduce growth. In addition, to be genetically improvable, traits should be heritable (have a genetically determined component), whereas leaf : stem : root allocation ratios are highly plastic in response to resource availabilities (Franklin et al. 2012) and may thus be difficult to control genetically. This underlines the need for better understanding of two aspects of plant traits: cost versus benefits and heritability. For example, our method to

identify and quantify improvement potential could be extended to include additional traits of importance for forest production, such as lignin concentration, if ecological and physiological costs and benefits were better known.

Whereas some of the traits modeled are not directly measurable, they can be calculated from more readily measured sub-traits. For example, hydro-sensitivity can be expressed in terms of leaf water potential response to drought, stomatal response to leaf water potential, stomatal effect on internal CO₂ concentration and the effect of CO₂ on photosynthetic rate. However, the value of aggregating these traits is evident from the fact that the C-costs that (together with benefits of reduced mortality) control their regulation can only be quantified based on their concerted effect—the hydro-sensitivity of photosynthesis.

Implications for the modeled traits—where is the genetic gain?

Although our quantitative results should be interpreted as illustrations of possible effects rather than as a quantitative estimate of real potential, the model elucidates some opportunities and pitfalls worth consideration in the search for improved trees.

The model suggests that it is possible to enhance volume and biomass production in drier sites by changing hydro-sensitivity, allocation to pest defense, and wood density. Interestingly, changes in different directions may be necessary to increase productivity under different site conditions and depending on which trees species are targeted. While reduced defense allocation and hydro-sensitivity can enhance the productivity of trees adapted to moderately water-limited sites, changes in these traits in the opposite direction are required to enhance the productivity and WUE of trees with similar wood density in dry sites (Figure 9 at wood density ~0.5). This means that whether a modification, such as reduced hydro-sensitivity or allocation to defense, will enhance productivity depends on both the original properties of the trees in their natural environment and the expected managed site conditions. It also supports the suggestions that different tree genotypes are necessary for optimal productivity across environmental gradients (Nelson and Johnsen 2008, Harding et al. 2014). The model also illustrates the potential for increased fiber and biofuel production by combining enhanced biomass production with increased wood density in low wood-density trees (Figure 8c and d), as suggested by Dinus et al. (2001) for *Populus* species.

Although expected productivity can often be increased by shifting the trees' strategies towards higher risk behavior, as illustrated above, the trees also become less robust if risk factors, such as insect attacks and drought severity, increase significantly above expected levels. Following earlier studies (Loehle and Namkoong 1987), our model underlines the importance of this growth–survival trade-off, which means that selection or modifications for improved biomass growth rate

without increased resource access should lead to lower investments in risk management and therefore higher mortality. In principle, a 10% increase in growth rate should reduce survival by 10% under natural conditions, all other things being equal (Eq. (2)). Although at least one important aspect of the 'natural conditions', density-dependent mortality, can be avoided to a large extent by management, before declaring the success of a growth enhancement it may be advisable to look for potential reductions in survival investments (Loehle and Namkoong 1987). The effect of such reductions can be evaluated based on a model of the kind presented here, which may require less effort than measuring their results in terms of actual mortality due to its high variability caused by environmental variability.

Our results suggest that modification of plant conductive capacity per photosynthetic N cannot significantly enhance plant productivity under fixed water availability. The reason for this is that there is a respiration and turnover cost of conductive capacity for maintaining aquaporins and conductive tissues, which balances the potential gain in photosynthesis. This balance of gain and costs does not change much with drought severity in our model. Generally, relative distribution of resource use among component processes of the same function (such as N used for conductive capacity and photosynthetic machinery, which both are necessary for photosynthesis) should be expected to be rather invariant, unless the intrinsic efficiency of one of the processes or the interaction between them changes. Thus, changes should be expected if there is an interaction between conductance and nutrient availability, for example, if transpiration and the associated water flow enhance nutrient flux into the plant, as shown for phosphorus uptake (Cernusak et al. 2011). If nutrient uptake increases with transpiration, increased conductance, obtainable via over expression of aquaporins (Aharon et al. 2003), can enhance productivity via nutrient uptake under non-water-limited or irrigated conditions. Clearly, more research would be valuable on the interaction between nutrient and water uptake.

In contrast to shifts in growth–survival trade-offs, potential reduction of belowground competition does not carry any obvious negative side effects. Competitive strategies have evolved (as all strategies) to the benefit of the individual genotype, even if it occurs at the expense of collective forest growth. In theoretical models, it has been shown why belowground competition leads to excessive C investments in roots (King 1993, Franklin et al. 2012, Fariori et al. 2013) or mycorrhiza (Franklin et al. 2014) and excessive nutrient or water use compared with what would maximize collective productivity. Negative effects of competition have been observed for soy beans (Gersani et al. 2001), and production of coffee (Montagnon et al. 2001) and cocoa (Lachenaud and Montagnon 2002). However, for forests the empirical evidence appears to be mixed, with contrasting relationships between competition and productivity among sites and species (David Coates et al. 2013) or no effect (Litton

et al. 2004). Furthermore, whereas competition is augmented by genetic similarity (Boyden et al. 2008), similarity among individuals increases rather than reduces production of forest plantations (Stape et al. 2010). However, rather than challenging our model predictions these variable empirical results likely reflect the use of too simplistic measures of competition, which underlines the need for more detailed understanding of competition. Specifically, it is necessary to separate aboveground competition (for light), which increases stem growth, and belowground competition, which reduces stem growth (Franklin et al. 2012). While belowground competition is not readily measured in forests, the theoretically predicted negative effect on growth and its link to limited spatial resource distribution (e.g., shallow soil or patchiness, Franklin et al. 2012) has been confirmed for small plants (Gersani et al. 2001, Roiloa et al. 2014). Moreover, our predicted increase in WUE in response to reduced belowground competition (Figure 8) agrees with observed effects of alleviated competition obtained by reducing stand density in eucalypts (White et al. 2009). In summary, our model suggests that plant modifications that reduce belowground competition could lead to large gains in productivity and WUE, especially when belowground competition is expected to be strong, such as in shallow soils. Because root competition increases with the degree of overlap between the root systems of neighboring plant individuals, we suggest that genetic modifications that reduce the lateral range of the root system can reduce competition and thus enhance wood production.

Conclusions

Many plant growth processes can be enhanced by genetic alteration through breeding and biotechnology without necessarily improving forest productivity. For example, enhancing photosynthesis by reducing the hydro-sensitivity of a species may lead to higher wood production in one environment, but which may be overshadowed by excessive mortality in a drier environment. Enhanced root production may improve growth of seedlings in pots, but ultimately hamper forest productivity in the field due to belowground competition. Our eco-evolutionary model shows how such pitfalls can be avoided by evaluating traits through their effects on fitness (as approximated by lifetime reproductive production), balancing costs versus benefits and growth versus survival. The results suggest that different plant traits and the associated genetic gain potentials, such as shifting drought strategies from isohydric behavior to high wood density, interact in ways that can only be understood from a holistic fitness perspective. In conclusion, eco-evolutionary modeling may be useful as the initial step in selecting target traits for genetic enhancements. To facilitate such modeling, broader understanding is needed of both the fitness benefits and costs of key traits, such as wood density, hydro-sensitivity and competitive strategies.

Supplementary data

Supplementary data for this article are available at *Tree Physiology* Online.

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Conflict of interest

None declared.

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Appendix - Mathematical model description

The environment

As described in the text we assume a negative relationship between niche duration (t_n) and mean light level and a positive relationship between drought severity (D) and light (Figure 2). For simplicity we use the following linear equation:

$$f_Q = 1 - \frac{t_n}{t_{n\max}}(1 - D) \quad (A1)$$

Growth model

Gross primary productivity (Eq. (A2)) is modeled as done in Franklin et al. (2014) based on co-limitation of light-saturated photosynthetic capacity of the canopy (A_{sat}), and the product of above canopy photosynthetically active radiation and photosynthetic quantum efficiency (Q), times fraction radiation remaining (f_Q ; Eq. (A1))

$$\text{GPP} = t_d \frac{A_{\text{sat}} Q f_Q}{A_{\text{sat}} + Q f_Q} \quad (\text{A2})$$

where t_d is day length in hours.

Canopy light-saturated photosynthetic capacity (A_{sat} ; Eq. (A3)) is limited by N in photosynthetic machinery (N_p) and the relative conductance of CO_2 to this machinery (g). Maximal conductance, in turn, is determined by conductive capacity per N_p (g_{max}) while realized conductance is limited by hydro-sensitivity (i , sensitivity to drought, see the text) in proportion to the prevalence and severity of drought (D). To avoid the complexity of modeling water fluxes explicitly, we model only the effect of water limitation on photosynthesis and mortality and use dimensionless variables for water-related traits (g , g_h , g_{max} , i and D).

$$A_{\text{sat}} = a N_p \frac{g}{g + g_h}, \quad \text{where } g = g_{\text{max}} - i \times D \times 1.5 \quad (\text{A3})$$

where a is the maximal photosynthetic N-use efficiency and g_h is the half-saturating conductive capacity. As we do not explicitly model water cycling and transpiration we use whole-plant conductance, $g_p = g N_p$, as a proxy for water use.

As done in Franklin (2007), C costs (C_C ; Eq. (A4)) includes maintenance respiration and litter production and is proportional (with a factor c_N) to the amount of N in photosynthetic machinery (N_p) and in conductive tissues, which in turn is proportional (with a factor f_g) to N_p . In addition, for each amount of photosynthetic and conductive N there are associated root costs for water and nutrient uptake, which are proportional (with a factor f_r) to drought severity (D) and a belowground competition factor (z).

$$C_C = c_N N_p (1 + f_g g_{\text{max}}) (1 + f_r D z) \quad (\text{A4})$$

The C costs (C_C) do not include growth respiration, which is equal to $(\text{GPP} - \text{maintenance respiration}) \cdot (1 - y)$, where y is biomass growth efficiency, which is constant (Choudhury 2001). Assuming that litter production and maintenance respiration each contributes half of the C costs, C_C , net growth of biomass, G , can be expressed according to Eq. (A5), where t_y is growing season days per year.

$$G = t_y \left(\text{GPP} y - C_C \left(\frac{y + 1}{2} \right) \right) \quad (\text{A5})$$

Net growth (G) can be used for reproduction $G_R = f_R G$ or biomass growth $G_B = f_B G$, where f_R and f_B are constant fractions in the model.

Wood volume production (P_V ; Eq. (A6)) under managed conditions is calculated as mean yearly volume production up to the harvesting age $t_n = 40$ years, assuming that density-dependent mortality is avoided by management.

$$P_V = G_B \frac{1}{d_w t_n} \int_0^{t_n} (1 - m_{di})^t dt \quad (\text{A6})$$

We use the ratio $P_V / (g N_p)$ as a proxy for forest WUE.

Parameter values for the growth model (Table A1) were chosen to be representative of a temperate deciduous forest (Franklin et al. 2009b).

Mortality and survival

Following the rationale described in the main text, pest mortality (m_p) declines exponentially with the fraction of net growth invested in defense (f_d) according to Eq. (A7).

$$m_p = m_{p0} e^{-k_p f_d} \quad (\text{A7})$$

Drought mortality declines with hydro-sensitivity (i) and wood density (d_w) and increases with D according to Eq. (A8).

$$m_D = m_{D0} \frac{D}{d_w} e^{-k_D (i d_w / D)} \quad (\text{A8})$$

Drought-independent but wood-density-related mortality (e.g., risk of mechanical breakage) decline exponentially with wood density according to Eq. (A9).

$$m_w = m_{w0} e^{-k_w d_w} \quad (\text{A9})$$

As described in the main text, density-dependent mortality (m_{dd} , Eq. (A10)) is a function of relative biomass increment and m_{di} , where biomass (B) is assumed to be proportional to canopy N, that is, $B = k_B N_p$.

$$m_{dd} = \frac{G_B}{k_B N_p} - m_{di} \quad (\text{A10})$$

The total mortality that an individual can influence by its strategy (m) is the sum of m_{di} and the fraction of m_{dd} that is affected by the individual or genotype (Eq. (A11)). We assume that a genotype controls 25% of its own m_{dd} , that is, $e = 0.25$ in Eq. (A10).

$$m = m_{di} + e m_{dd} \quad (\text{A11})$$

Parameters for the mortality models (Table A1) were chosen to result in realistic modeled values of wood density (0.1–1.5,

Table A1. Model variables and parameters.

Symbol	Value	Unit	Description
<i>Dependent variables</i>			
A_{sat}		$\text{gC m}^{-2} \text{h}^{-1}$	Light-saturated canopy photosynthesis
BP		$\text{Mg ha}^{-2} \text{year}^{-1}$	Wood biomass productivity
C_{C}		$\text{gC m}^{-2} \text{day}^{-1}$	C costs, i.e., C used for maintenance respiration, litter production and for resource acquisition
d_{w}		g cm^{-3}	Wood density
F		$\text{gC m}^{-2} \text{year}^{-1}$	Fitness proxy Eq. (2)
f_{d}		–	Fraction of net growth allocated to defense against pests
f_{Q}		–	Fraction radiation remaining of above canopy radiation
g		–	Plant conductance for water and CO_2
$G, G_{\text{B}}, G_{\text{R}}$		$\text{gC m}^{-2} \text{year}^{-1}$	Total net, biomass, and reproductive growth, respectively
g_{max}		–	Plant conductive capacity
GPP		$\text{gC m}^{-2} \text{day}^{-1}$	Gross canopy C uptake (photosynthesis)
i		–	Hydro-sensitivity, i.e., sensitivity of stomatal conductance to plant water potential
$m, m_{\text{tot}}, m_{\text{di}}, m_{\text{dd}}$		–	Fitness influencing, total stand, density-independent, and density-dependent mortality, respectively
N_{p}		gN m^{-2}	Canopy photosynthetic nitrogen
P_{V}		$\text{m}^{-3} \text{year}^{-1} \text{ha}^{-1}$	Wood volume productivity
<i>Independent variables and parameters</i>			
A	0.5 ¹	$\text{gC gN}^{-1} \text{h}^{-1}$	Light-saturated photosynthesis per photosynthetic N
c_{N}	0.6 ¹	$\text{gC gN}^{-1} \text{day}^{-1}$	C costs per N in biomass
D	[0, 1]	–	Drought severity
e	0.25	–	Influence of a plant's (genotype) own impact on its density-dependent mortality
f_{g}	1 ²	–	N in conductive capacity per N_{p}
f_{r}	0.38 ¹	–	N in fine-roots per N_{p}
f_{R}	0.25 ¹	–	Fraction of G allocated to reproduction
g_{h}	0.5 ²	–	A_{sat} -half saturation value of g
k_{D}	20 ²	$\text{cm}^3 \text{g}^{-1}$	Drought mortality parameter
k_{p}	35 ²	–	Pest mortality parameter
k_{w}	17 ²	$\text{cm}^3 \text{g}^{-1}$	Non-drought wood-density-related mortality parameter
$m_{\text{O}}, m_{\text{wO}}, m_{\text{pO}}$	0.001, 2, 0.1 ²	year^{-1}	Baseline mortality, and maximum non-drought wood-density-related and pest mortality, respectively
m_{DO}	0.15 ²	g cm^{-3}	Drought mortality parameter
Q	3 ¹	gC h^{-1}	Photosynthetic quantum efficiency times photosynthetically active radiation above the canopy
t_{d}	12	h day^{-1}	Hours of photosynthesis per day
t_{n}		year	Niche duration, duration of a certain light–drought environment
t_{y}	200 ¹	day year^{-1}	Growing days per year
x	1	gC m^3	Future reproductive production per current volume growth
y	0.7 ³	–	Plant growth C conversion efficiency
z	1 (baseline)	–	Effect of belowground competition on C costs

¹Estimated for a temperate deciduous forest (Franklin 2007, Franklin et al. 2009b).

²Adjusted to result in realistic modeled values of productivity, wood density, defense allocation and total mortality (Condit et al. 1995, Chave et al. 2009).

³Choudhury (2001).

Chave et al. 2009), defense allocation and total mortality (Condit et al. 1995).

Fitness and strategy optimization

Fitness of a plant is approximated by its fecundity, or reproductive production integrated over its reproductive time (Eq.(2)). In Eq. (2), we approximate integrated reproductive production (G_{Ri}) with a combination of size (volume) growth and reproductive production (Eq. (A12)), where G is the net

growth of biomass (see Growth model above) and f_{R} is the fraction allocated to reproduction.

$$G_{\text{Ri}} = G(1 - f_{\text{R}})(1 - f_{\text{d}}) x/d_{\text{w}} + G f_{\text{R}} \quad (\text{A12})$$

An implicit assumption behind Eq. (A12) is that current volume growth will contribute to later reproductive production by a factor x that, in the absence of quantitative data on this relationship, is set to 1. However, our results are not very sensitive

to this factor; doubling or reducing this factor by half only had minor quantitative effects.

In the calculation of trait values of natural forests, the amount of canopy photosynthetic N (N_p) and the associated conductive capacity (g_{\max}) are assumed to be optimal so that net growth (G , Eq. (A5)), that is, photosynthesis minus C costs, is maximized (Eq. (A13)).

$$\frac{\partial G}{\partial g_{\max}} = 0, \quad \frac{\partial G}{\partial N_p} = 0 \quad (\text{A13})$$

The traits that are related to both mortality and growth, that is, fraction allocation to defense (f_d), wood density (d_w) and

hydro-sensitivity (i), are optimized with respect to fitness, F (Eq. (A14)).

$$\frac{\partial F}{\partial f_d} = 0, \quad \frac{\partial F}{\partial d_w} = 0, \quad \frac{\partial F}{\partial i} = 0 \quad (\text{A14})$$

In the calculation of forest productivity in the managed forest with native trees, only N_p was assumed to acclimate to the managed environment and therefore was re-optimized, whereas the other traits kept their values as estimated for their native environment. In the calculation of optimally modified trees all traits were re-optimized for maximum productivity in the managed environment.