



Tree Physiology 34, 1141–1148  
doi:10.1093/treephys/tpu112



## Editorial

# Genetics of superior growth traits in trees are being mapped but will the faster-growing risk-takers make it in the wild?

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Received November 4, 2014; accepted November 20, 2014; handling Editor Michael Ryan

Increased biomass production of trees is a research field of great contemporary interest. Estimates of future needs for production of fibre, wood and biofuel suggest a need for significantly increased production in forests (Ragauskas et al. 2006). This demand can only be met through increased productivity and/or resource utilization efficiency of tree crops. That is, we must explore the potential to optimize the genetic makeup of trees to achieve greater productivity in their growing environments.

Since the introduction of molecular biology in plant sciences, the interest in genetic improvement of both agricultural and tree crops has been increasing and is currently one of the most intense areas of plant research. At the same time, tree and stand growth have been studied within (and across) the fields of ecophysiology, ecology, silviculture and forest management. This work has resulted in statistical and process-based models that relate tree growth to availability of various resources, and that thus can inform management (Landsberg and Waring 1997). Process-based growth models have been developed largely independent of the expanding knowledge base in molecular biology and the findings that tree growth can be directly improved through genetic alterations of specific processes such as lignin synthesis, frost hardiness and nitrogen (N) assimilation (Ragauskas et al. 2006, Ye et al. 2011). Similarly, we have underutilized the potential for ecological theories and growth models to guide breeding programmes by predicting the performance of genetically altered trees in

the field. This *Invited issue* is designed to stimulate research targeted at explicitly linking molecular understanding and tools and growth of forest stands.

## Molecular understanding of tree growth is ever expanding

Several recent reviews have dealt with the molecular genetics of tree growth, ranging from more method-oriented approaches (Groover 2007, Grattapaglia et al. 2009) to overviews of links between single genes and superior crop (Van Camp 2005) or tree phenotypes (Eriksson et al. 2000, Ye et al. 2011). Tree molecular biology has seen tremendous advancements, particularly since the publication of the first tree genome (Tuskan et al. 2006, Wullschlegel et al. 2013). We can now attribute the complex responses of trees to specific genetic (or epigenetic; Kvaalen and Johnsen 2008, Rohde and Junttila 2008) markers or even to single genes. For example, Garcés et al. (2014) propose candidate genes for forward genetic approaches that can help us discover naturally occurring nucleotide variations associated with productivity and wood quality. By uncovering some of the molecular machinery underlying phenotypic differences between juvenile and mature wood of *Pinus pinaster* (Ait.), Garcés et al. propose new ways to take advantage of superior growth of trees in their juvenile stage in production forests. Another example is provided by Yu et al. (2014), who report on a gene encoding *endo*-1,4- $\beta$ -glucanase in *Populus*

(KOR1). The KOR genes have functions in cellulose synthesis, and altered expression of such genes may result in phenotypes with altered wood composition, potentially of interest for various applications.

Growth is the result of many interconnected processes and as such a very complex trait. Hanley and Karp (2014) present a strategy for dissecting growth traits into defined components that could form a basis for molecular breeding and gene discovery. They discuss how modern genomic and genetic tools are best used for uncovering genes controlling traits that are well correlated with growth in *Salix* (stem number and height, leaf area and clumping indexes). Hybrids between the more targeted approaches, based on hypotheses of growth-determining traits and processes, and the unbiased approach described by Hanley and Karp may present the best opportunities to narrow down the search for genetic mechanisms underlying growth. To that end, the choice of tissue for studying the expression of genes is of critical importance. Cañas et al. (2014) describe a technique, a combination of laser capture microdissection and next-generation sequencing, enabling analyses of transcriptomes of specific cell types and tissues from root tips of *P. pinaster*. Applying this technique in studies of, for example, growth transition processes and shifts in resource availabilities could lead to significant advances in our understanding of the molecular processes underpinning growth.

### Tree production physiology and economics of survival

We use tree production physiology as a framework to identify traits and processes we may be able to modify with molecular tools and that would result in enhanced growth (Figure 1). Tree production physiology (or ecology) is focused on the basic processes governing tree growth and includes plant resource acquisition (carbon, water and mineral nutrients), resource utilization efficiencies (for example light, water and N-use efficiencies), resource allocation and abiotic and biotic stresses (including competition). Here we are broadening the more traditional view of production physiology to include 'risk management', and in the following sections we explore how tree and stand growth can be enhanced through increased resource capture and resource-use efficiencies, and through matching costs to risks through risk management.

Tree production physiology originated from agricultural crop production physiology, but the latter has come much further in using molecular tools to increase the yield (Van Camp 2005). One reason for this is the difference in life span of the plants in the two systems. While most agricultural crops are annuals or biennials, tree crops are obligate perennials making the breeding programmes more complex. Trees may also have developed a wider suite of risk management strategies than crops (Table 1). These strategies would arguably increase the chance

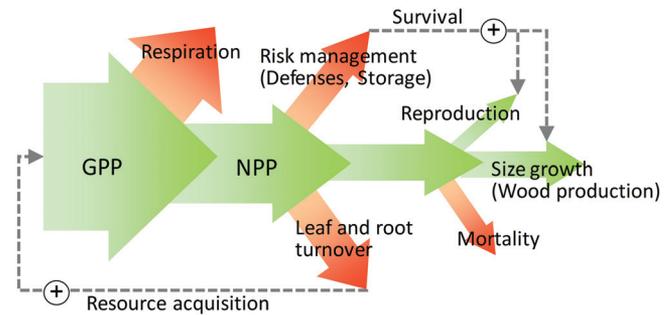


Figure 1. Tree growth modelling framework showing the carbon (C) flow from photosynthesis towards wood production and reproduction, which are key goals contributing to fitness. While some C fluxes contribute directly towards these goals (benefits, green arrows) others represent C losses (costs, red arrows) of which some have indirect benefits, such as root production for resource acquisition and risk management for survival under stress (grey dashed arrows). Artificially reducing risk management (e.g., defence against pests) or root production channels more C to wood growth under managed conditions but may increase vulnerability to drought and pests. In contrast, increased efficiency of a process, such as enhanced nutrient acquisition per root production, increases growth under all conditions.

of survival during harsh times that inevitably confront long-lived organisms, but at the same time incur costs, thus reducing their growth rates. Identifying such risk management strategies may therefore lead to suggestions for tree improvements. Because the trade-offs between survival and growth are not well understood at a mechanistic level, we need novel (holistic) approaches that merge physiology (basic processes) to fitness and life-history strategy (risk management; Franklin et al. 2014).

### Resource acquisition and use efficiencies

**Carbon** When other resources are not limiting, growth is related to the rate of carbon (C) acquisition, which in turn is a function of light absorption and the efficiency at which light energy is transformed to chemical energy (gross primary productivity, Figure 1). Following the analyses by Monteith (1977) and Long et al. (2006), the primary production ( $P_n$ ) is a function of the annual radiation at a specific site ( $S_t$ ) multiplied by three terms: the light interception efficiency ( $e_l$ ), the light conversion efficiency ( $e_c$ ) and the energy content of the produced biomass ( $k$ ):

$$P_n = S_t \times e_l \times e_c \times k^{-1} \quad (1)$$

Light interception is a function of leaf area integrated over time. How can trees intercept a maximum of incoming radiation? Rapid establishment, early increase of size, as well as altered crown architecture and leaf display (Hanley and Karp 2014) are obvious targets for optimization of this parameter. Increased wood production due to higher light interception has been demonstrated in irrigated (5% increase) and fertilized (10% increase) eucalypt plantations (Ryan et al. 2010, Forrester et al. 2013). However, in the same plantations, light conversion

Table 1. Risk management strategies and their potential importance to tree growth.

Risk management strategy	Subcategories	Examples	Effects on tree growth
Risk avoidance		Cessation of growth in response to anticipated stresses (low temperatures, drought, flooding, biotic stress)	Length of growing season shorter than what the climate allows
Loss control	Frequency control	Dimensioning of root and shoot areas to reduce the incidence of water stress	Optimizing biomass allocation for maximum survival at the expense of growth
	Severity reduction	Programmed cell death of tissues in response to pathogen attack	Optimizing response for survival at the expense of growth
	Diversification	Leaf age classes with differences in chemical defence; leaves with different sensitivities to abiotic stress	A fraction of acquired resources is channelled to produce tissues that are suboptimal in resource acquisition
Risk retention		Storage of resources, C and N	Acquired resources are not immediately re-invested in growth and thus the full potential is not realized

efficiency increased even more than light interception, by 11 and 13% under irrigation and fertilization, respectively.

The efficiency of converting solar energy into biomass depends on a range of processes from rates of photosynthesis and respiration to altered composition and quality of wood (Garcés et al. 2014, Yu et al. 2014). To what extent will increased photosynthesis (through  $e_c$ ) lead to increased tree growth? Long et al. (2006) concluded that when other factors are held constant in elevated atmospheric CO<sub>2</sub> experiments on agricultural crops, CO<sub>2</sub>-induced increases in photosynthesis are linked with increased yields. Elevated CO<sub>2</sub> may also increase tree biomass production (McCarthy et al. 2010), unless the availability of other resources is limiting growth (Oren et al. 2001, Norby et al. 2010, Marshall and Linder 2013, Sigurdsson et al. 2013). Long et al. (2006) argued that similar increases in net CO<sub>2</sub> uptake to those realized in elevated CO<sub>2</sub> experiments may be achieved by genetically engineering the theoretical maximum  $e_c$ . Plausible manipulations, i.e., where some success has been shown in agricultural crops, include increasing the rates of recovery from photoinhibition, replacement of current C<sub>3</sub> Rubisco with forms known to have higher catalytic rates, increasing the efficiency of RuBP regeneration and bypassing photorespiration (Flexas et al. 2013, Lin et al. 2014).

Yield ( $Y_p$ ) improvements in agricultural crops have to a large extent not targeted carbon acquisition but rather the harvestable fraction of biomass (harvest index,  $\eta$ ,  $Y_p = \eta \times P_n$ ). To what extent is altered allocation of biomass a realistic way forward to accomplish greater tree harvests? At first, harvest index improvements of agricultural crops may not seem to be applicable to trees, simply because we may consider that the former allocate a much smaller fraction of biomass to the harvested part than the latter. This is arguably not the case, because some crops may exhibit a harvest index of 60%, and for many trees, root biomass is a significant fraction of total tree biomass. The importance of allocation for wood production has been demonstrated in eucalypt plantations, where irrigation leads to an 8% increase in the fraction of net photosynthesis allocated to wood (Ryan et al. 2010). While it appears that tree

breeders would find biomass allocation as an important target, we also know that the relative allocation between aboveground and belowground may be difficult to manipulate genetically as it is plastic and varies along, for example, nutrient and water availability gradients (Hacke et al. 2000, Addington et al. 2006, Litton et al. 2007, Franklin et al. 2012). Nevertheless, potential modifications that reduce C partitioning to roots would likely enhance wood production (Franklin et al. 2014; Figure 2).

**Water** Analogously to the expression of yield based on the availability of solar energy, the determinants of yield under water-limited conditions can be based on the availability of water for transpiration ( $W$ ), water-use efficiency ( $WUE = P_n/W$ ) and harvest index ( $Y_p = W \times WUE \times \eta$ ; Passioura 1977, Morison et al. 2008). The determinants of water acquisition include the rate of transpiration and the hydraulic conductivity of the soil–plant–atmosphere continuum. Trees regulate transpiration through adjustments of total leaf area, the abundance and size of stomata, and at shorter time scales, the stomatal aperture. These adjustments are designed to reflect the hydraulic conductivity of liquid water to the leaves, determined by the structural properties of the xylem, relations between absorbing, transporting and transpiring tissues, and the ability of trees to refill embolized xylem elements.

Higher yield may result from higher WUE as has been shown across productivity gradients among eucalypt plantations (Stape et al. 2004). Indeed, high ‘intrinsic’  $WUE_A (=A/g_s)$ , where  $g_s$  is stomatal conductance) is currently the main objective for breeding (Flexas et al. 2013). Increasing yield and WUE means that the  $A-g_s$  relationship must change;  $A$  must be enhanced at a given  $g_s$ . Such changes have been achieved in *Arabidopsis thaliana* (L.) Heynh. ERECTA mutants and in wheat (Flexas et al. 2013). Increased maximum  $e_c$  through manipulations discussed above may lead to simultaneous increases of  $A$  and  $A/g_s$ . Similarly, an enhancement of  $A$  can be achieved through increased mesophyll diffusion conductance to CO<sub>2</sub> ( $g_m$ ) from sub-stomatal cavities to the site of fixation. Genetic manipulation of  $g_m$  may be possible since specific genes (for example,

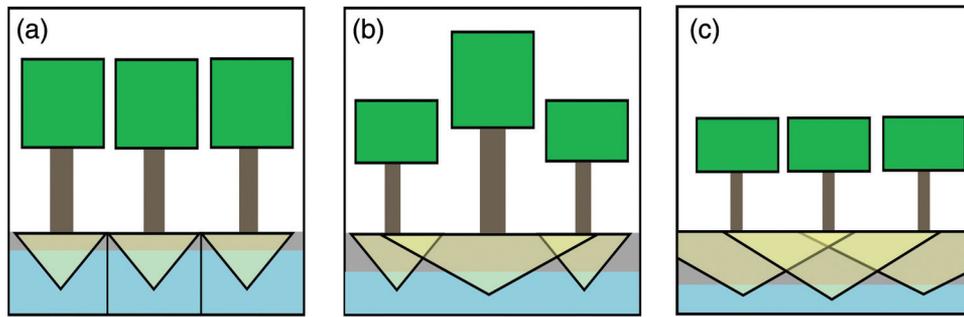


Figure 2. Belowground competition. (a) In a non-competitive setting, each tree manages its own belowground root resource pool (blue) to optimize root allocation (triangles) and aboveground growth. (b) When the trees share a common resource pool, one tree can take up more resources at the expense of its neighbours. (c) The other trees follow the same strategy, not to be out-competed, which leads to increased root production and resource uptake beyond the optimum for stand growth.

the aquaporin *NtAQP1*) have been shown to affect  $g_m$ . Only when the increase in  $g_m$  is not coupled with a comparable increase in  $g_s$ ,  $WUE_A$  is also enhanced. Therefore, the contribution of the underlying processes to increased WUE matters and must be considered when enhancements in productivity are evaluated against the costs of resources.

**Mineral nutrients** In many natural ecosystems, restricted availability of N and/or phosphorus (P) is the norm, and growth of trees is largely a function of their capacities to acquire these elements from soil and the associated costs for acquisition. Attempts to enhance plant uptake capacities for mineral N through increased expression of nitrate transporters have not been reported for trees. Such attempts have obviously not been successful for crop plants, possibly because the efflux of mineral N is upregulated concomitantly to the increased influx of N (Britto and Kronzucker 2004). Boosted uptake of organic N sources through overexpression of specific amino acid transporters was reported for the model plant *A. thaliana* (Forsum et al. 2008). However, the potential ramifications of such alterations for crop plants and for trees are not clear. Two outstanding examples of increased N-use efficiency (NUE) in response to single gene alterations exist. In the first example, overexpression of a pine glutamine synthetase (GS) gene leads to significant increases in NUE and also to significant increases in the growth of *Populus* trees (Gallardo et al. 1999, Fuentes et al. 2001, Fu et al. 2003, Jing et al. 2004). Potential mechanisms underpinning the observed growth effects include a higher rate of both primary assimilation of  $NH_4^+$  and re-assimilation of  $NH_4^+$  ( $NH_3$ ) produced during different endogenous processes such as photorespiration and N remobilization. In the second example, increased NUE resulted from a single gene alteration of alanine amino transferase (AlaAT; Good et al. 2004, 2007, McAllister et al. 2012). Although there are no studies on potential effects of overexpressing this gene in trees, several reported superior growth of agricultural crops overexpressing AlaAT. For both GS and AlaAT overexpression, the hypothesized explanation for the

increased NUE and growth is enhanced rates of assimilation of absorbed N leading to increased capacities for internal N remobilization, in turn allowing for a more rapid uptake of external (mineral) N.

### Stress and competition

Trees are commonly grown on lands not suitable for agricultural production and hence tree production often occurs under severe, suboptimal edaphic and climatic conditions. In this issue, Harfouche et al. review the molecular and physiological responses of trees to abiotic stress and suggest that new sequencing technologies will aid efforts to more rapidly decipher genetic diversity in stress responses present within plant communities, particularly woody perennials (Harfouche et al. 2014). As is the case for agriculture (Boyer 1982), water stress is likely the most common limiting factor for tree growth but saline soils and low or high temperatures will also hamper tree growth. There have been a number of successful attempts to increase tolerance to abiotic stresses such as cold (Benedict et al. 2006), salt (Lawson and Michler 2014), osmotic/drought stress (Wang et al. 2010, Han et al. 2013) and a combination of abiotic stresses (Gleeson et al. 2005). These studies have utilized transgenes ranging from stress-induced transcription factors (Benedict et al. 2006) to the introduction of enzymes to enhance the accumulation of compatible solutes (Gleeson et al. 2005). However, the long-term yield benefits of such transgenic manipulations for field-grown trees are yet to be shown (Polle et al. 2006, Minocha et al. 2014).

Barchet et al. (2014) used metabolic profiling of hybrid *Populus* clones subjected to water stress to investigate drought responses of different genotypes. For most clones, the synthesis of phenolic compounds and metabolites involved in osmotic adjustment increased and primary metabolism such as citric acid cycle and photorespiration decreased. Interestingly, the results suggest a dichotomy in the response of these clones to drought stress; some adjust the osmotic potentials of cells to stay active during water deprivation and others react by closing the stomata to avoid water loss. The advantage of the

former reaction is that growth may continue at restricted water availability but this may come at a price of increased mortality rates under very low soil moisture conditions (Moshelion et al. 2014). The advantage of the latter is a lower risk of detrimentally low soil water conditions but at a price of decreased competitive abilities under conditions of chronic mild water stress. Elucidating the mechanisms regulating these different clonal responses will be one of the keys to developing molecular and/or breeding approaches for fine tuning the stress tolerance of long-rotation plants such as trees to specific sites.

Abiotic and biotic stresses cause reductions in tree growth both through directly interfering with growth processes and causing structural damage, and indirectly through the resources set aside by trees to meet the anticipated stress. Harding et al. (2014) look at the C partitioning between growth and defence (condensed tannins, CT, and phenolic glycosides) in fast- and slow-growing genotypes of *Populus*. Accumulation of CTs may be a passive outcome of within-plant N distribution that leads to high C/N ratios in expanding leaves of slow-growing plants that eventually led to sequestration of C into CTs. Alternatively, accumulation of CTs may be an autonomous and active process that affects C and N distribution in plants and thereby weakens N-sink strength of developing leaves. Of these two possible mechanisms, Harding et al.'s study suggests an active partitioning of resources into defence compounds and, thus, direct competition between growth and defence processes.

Both constitutive and induced defence mechanisms incur costs in terms of energy and the availability of building blocks for growth (Figure 1). Increased carbohydrate availability under elevated atmospheric CO<sub>2</sub> enhanced resin flow in *Pinus taeda* trees, but only where growth was not enhanced through N amendment, thus allowing the extra carbohydrates to be used in defence (Novick et al. 2012). Conversely, abiotic stresses that limit photosynthesis, such as water stress, may lead to a reduced defence capacity against biotic stresses such as fungal pathogens. Arango-Velez et al. (2014) investigated the molecular responses of *Pinus contorta* × *Pinus banksiana* to water stress and to attack by *Grosmannia clavigera* (mountain beetle fungal associate). They show that water deficit results in enhanced expression of some defence-associated genes while other genes that are involved in defence against the fungal pathogen displayed reduced expression. The study highlights the complexity of plant responses to multiple stresses and suggests that the defence potential of a tree will depend on the balance between resource acquisition (photosynthesis), resource allocation to defence vs growth and the priming of induced defence by different stressors. Predictions from the model described by Franklin et al. (2014) suggest that the potential or optimal growth rate of trees may be negatively correlated with the degree of stress resistance while the realized growth rate, depending on the actual occurrence of stress, may be positively correlated to the degree of stress resistance.

In contrast, Harfouche et al. (2014) provide several examples of transgenic plants that exhibit increased stress resistance but at the same time display increased growth rates even when not exposed to stress. Large-scale, long-term field tests combined with new technologies for phenotyping are needed to enable performance tests of trees with altered genetic makeup.

Tree growth may not be directly scalable to stand growth, a fact that is often overlooked in research dealing with superior genotypes of trees. This is because trees in a stand are exposed to different stresses and challenges (also relative to each other, dominant vs suppressed trees) than trees growing without competition. Competition for light, water and nutrients is more severe in stands while stressors such as wind, excess light and desiccation may be less severe. This means that genotypic changes that alter the growth rate of single trees may not manifest at the stand level; likewise, the phenotype of a specific tree in a stand may be different from its open-grown appearance. Model results as well as those from large-scale experiments suggest competition for belowground resources between trees in a stand may lead to increased allocation of resources to roots (Franklin et al. 2014), a response that is more intense than that expected based on reduction of resource availabilities. The concept of the tragedy of the commons—an individual gain in fitness and productivity at the expense of the collective—was introduced to explain this presumed suboptimal response of plants in communities to resource limitations (Figure 2). Model calculations suggest that this response is of evolutionary value for forest trees (King 1993, Franklin et al. 2012). Thus, predicting stand growth requires better understanding of such tree–tree interactions at both molecular and physiological levels.

### Trees as risk managers

Originating from economics, the theory of risk management has been introduced to ecological research (Wagner 2003, Martincorena et al. 2012). We may perceive trees as long-lived organisms that maximize fitness through reproduction and dispersal of seeds over years, decades or even centuries and must therefore manage risks through various strategies. Risk management is defined in economics as ‘... the identification, assessment, and prioritization of risks by coordinated and economical application of resources to minimize, monitor, and control the probability and/or impact of unfortunate events or to maximize the realization of opportunities’ (Hubbard 2009). Notably, this definition includes a statement relating to the costs of risk management. Risk management should hence be of central importance for tree fitness but also incur costs that necessarily would affect maximum growth rates in the short term (Figure 1).

We may consider that such risk management terminology is applicable to plant water relations, plant nutrient capture, plant growth initiation, and cessation and allocation of C and N to

different plant parts (roots vs shoots) and allocation to storage and defence compounds (Table 1; Franklin et al. 2014). Growth of trees may also be less than that of the potential because of conflicts between stress tolerance and active growth (Harding et al. 2014). Such conflicts are apparent for trees in temperate and boreal regions because the length of the season of active growth is positively related to growth but attempting to grow for the entire growing season would increase risks of damage by low temperatures. Similarly, Barchet et al. (2014) show how the transpiration–photosynthesis compromise may reduce risks at the expense of growth. Biotic stresses, pests and pathogens, may also have substantial effects on tree and stand performances. The allocation of resources to constitutive defence mechanisms such as production of secondary metabolites would arguably also incur a cost (Arango-Velez et al. 2014, Franklin et al. 2014).

Individual trees vary in how they face risks accompanied with potential gains and losses. An individual that exposes itself to a risk may do so (in an evolutionary sense) either because the potential gain is large in relation to the perceived risk or because the likelihood of survival in its growing environment is low. Low likelihood of survival may be due to competition and thus taking a risk, although potentially detrimental, may present a better alternative. An example of differences in risk behaviour is that of juvenile and adult trees of the same species. Augspruger and Bartlett (2003) compared the phenology of juvenile and adult individuals of 13 different deciduous species and found that budburst of juveniles was significantly earlier than that of conspecific adults in 10 species and none of the species displayed an opposite pattern. Taking the risk of an early season frost in exchange for capturing incoming radiation before the canopy of adult individuals has emerged may present a more favourable alternative than avoiding the risk but missing the opportunity.

Can we identify genetic differences in risk behaviour? Brereton et al. (2014) studied NUE in 14 genotypes of *Salix* sp. and found that canopy establishment after cutting was entirely driven by stored N. Yet, their analysis indicated that genotypes that displayed early transfer from dependency on stored N to uptake of new N had higher biomass production. Nitrogen-use efficiency in (temperate) trees is a complex trait involving not only uptake and utilization processes of N but also seasonal storage and retranslocation (Cooke and Weih 2005, Millard and Grelet 2010). In the study by Brereton et al. (2014), this complexity was shown through both positive and negative impacts of N storage on growth; stored N drove canopy establishment and thus storage enabled a longer growth season for plants. However, early onset of storage, long before leaf senescence, may have restricted growth of trees. Thus, late but rapid accumulation of N in storage organs would logically promote growth and genotype variation in onset and rate of this process may thus be a target for breeding for increased NUE.

Resistance to water movements is regulated through the abundance and activity of aquaporins at various positions in the tree, including roots, petioles and stems (Harfouche et al. 2014). Thus, aquaporin physiology may be a target for genetic improvements, aiming at, for example, transforming plants from isohydric (risk-avoiding or drought-sensitive) to anisohydric (risk-taking or drought-tolerant) water stress strategies. This may result in increased growth under well-watered conditions but also imposes higher risks for plants (Sade et al. 2012, Sade and Moshelion 2014). For anisohydric plants, higher water use, C uptake and yield come with a risk of hydraulic failure because they operate with narrower hydraulic safety margins during drought. Ultimately, the realized growth enhancement depends on the site conditions (water availability) and the properties of the trees (for example, wood density) that may compensate the increased risk for hydraulic failure of anisohydric plants (Franklin et al. 2014).

### Concluding remarks: towards an integrative framework

As shown by the range of studies in this issue, many organizational levels must be taken into account for the successful development of genetically enhanced trees, from the molecular and genetic basis of physiological processes to the long-term performance of a new genotype in a forest stand. In addition, growth performance usually depends on several factors that covary, including light interception, light conversion efficiency, C allocation to wood and stand structure (Ryan et al. 2010). Because multiple interacting processes and traits influence performance, a holistic model of their interactions may help select target traits for modification. Based on the premise that traits are adapted to maximize fitness in the trees' native environment, we can make informed assessments on how native traits depend on environmental conditions, such as water availability, and predict how they can be altered to maximize wood production in tree stands. Such model predictions suggest that under drier conditions, there is the potential to enhance production by modifications that increase growth at the expense of risk management (for example, reduced allocation to defences), or that shift the risk strategy from hydraulic loss control (high wood density) to risk avoidance (isohydric behaviour) (Franklin et al. 2014). Even larger effects on production could be obtained by trait alterations that reduce belowground competition.

The fitness-based framework also points to limitations of factorial approach to tree enhancement. As an example we may think of enhancement of foliage production to intercept more light, which also costs carbon that could have been used for wood growth, and may therefore reduce light-use efficiency (Figure 1). This illustrates the need to understand both the gains and the costs associated with potential trait modifications. The fitness framework (Franklin et al. 2014) can then be used

to balance carbon gains versus costs and risk management versus growth to find the optimal trait modifications in the quest for genetically enhanced forest production. Yet, the trade-offs between risk management and productivity discussed here raise the question stated in the title: will the faster-growing risk-takers make it in the wild? The simple answer is: probably not in the 'wild', but in the 'managed'. Similar to agricultural crops, the risk-takers' production may be superior under managed conditions with limited competition and short life. But such trees will potentially suffer from high mortality in the wild and would not be able to compete with native trees. This may however be an advantage, as it limits any potential risks of uncontrolled proliferation of genetically altered trees in the wild.

### Conflict of interest

None declared.

### Funding

Grants to T.N. from Kempe Foundation, The Swedish University of Agricultural Sciences (TC4F and Bio4E) and the research councils such as The Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning, The Swedish Research Council and The Swedish Governmental Agency for Innovation Systems are acknowledged. M.M. was supported by grants from the Israeli Forest Administration (JNF- KKL; Grant #0390140).

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