A critical review of very early selection protocols in tree breeding for timber

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Introduction

Breeding of crops to maximize particular attributes is something humanity had done for generations. Examples such as corn or tomatoes are now very different from their wild ancestors, however, with forest trees used for wood products much smaller changes have been made. One of the reasons for the slower advance is the comparatively long breeding cycle time. In order to make significant advances in the manipulation of properties of forest trees to maximize their benefit for use in human products, breeding cycle time needs to be reduced.

Initially there are two problems which need to be solved in order for to reduce the breeding cycle. One, propagation before individuals reach an age of reproduction, and two, reliable selection of individuals for desired properties very early in their lifespan. The propagation problem is not of concern here and can be solved through various micro-propagation techniques, for background information see (Baker, 1992; Watt et al., 2003). The problem of predicting future attributes from very young trees has seen some attention over the last decade, for convenience this will be referred to as the early selection problem. In essence trees change a number of properties during their life time as their interaction with the environment evolves. Particular properties which exist at young ages will not necessarily exist at older ages and visa versa, because wood is preserved during growth those properties will exist in the wood laid down at that point in the trees' life, for example in the pith. Wood properties near the pith may degrade or be damaged later in life through various processes. The relationship between one or more wood properties at different positions in the stem may influence some macroscopic property of interest to breeders, for example deformation during sawing.

A major problem with very early selection was discussed in detail by (Apiolaza, 2009), essentially he argued that even with a high year to year autoregressive correlation for a trait, a 15 year lag between measurement and harvest makes the association between selection criterion and objective trait value virtually non-existent. A consequence is very early selection can not be reliably used for maximisation/minimisation selections. Apiolaza (2009) made it clear at the time very early selection is usable only when the aim is to reach a non-reversible threshold, ie a screening problem. The example given was stiffness where he argued because MFA is known to only reduce with age and density does not decrease with age (the two traits which govern stiffness), and grading of stiffness is a threshold problem it is advantageous to get wood to the threshold as early in life as possible, but only because once the threshold is met further gains do not increase value, and there is strong physiological evidence to show that the trait value will not dip back below the threshold later in growth. To further the argument Myszewski et al. (2004) found non-significant genetic correlations between rings 4-5 and 19-20 for MFA (and therefore likely stiffness and growth-strain as MFA is thought to be the a significant factor in both cases). As an example; two trees reach a threshold stiffness at age 5 of 2 GPa, and one has a stiffness of 3 GPa at age 10 and the other has a stiffness of 9 GPa at age 10. Both trees met the threshold stiffness at the same time so are worth the same amount, but the correlation between stiffness at age 5 and age 10 is non-existent.

Currently no trials have been set up specifically to investigate GxE with very early selection methods. As a result little is known about how early selection methods will perform outside of the environment in which they were selected even if only considering properties at the age of selection. GxE is an important part of a tree breeding cycle, as properties differ from one environment to the next, and the level of genetic control independent of the environment needs to be quantified in order to create a good selection. Which genetics perform well in which environmental conditions needs to be quantified and used during decision making processes to ensure the appropriate genetics are deployed at each unique site (White and Adams, 2007). In the future investigating how reliably GxE iterations can be predicted at young ages should be a high research priority. Currently no known experiments have been setup for this purposes and the available data does not have significant genetic overlap to obtain meaningful results for any traits. Even at older ages, large numbers of trials are needed to accurately separate genetic and environmental effects. Dieters et al. (1995) investigated 171 tests of slash pine consisting of over 2100 full sibling families from 170000 individuals. Heritabilities taken from one or a small number of sites can produce almost any heritability between 0 and 0.5, unbiased heritabilities (heritabilities taking into account site effects) ranged from 0.072 to 0.12 depending on age, showing the importance of having large GxE trails and ensuring appropriate age distributions (Dieters et al., 1995). Without significant GxE investigation, genetic parameters can be extremely misleading. Further, along with expressing consern about differing genes being responcable for growth at different ages, Hodge and White (1992) suggested large site index differences between progeny test sites and commercial production land will decrease the reliability of progeny test data in predicting breeding values.

Caution needs to be taken when breeding for traits in trees in general and even more so with very early selection. Breeding trees to obtain particular traits at very young ages may result in unforeseen problems associated with the selection later in life. For example, breeding stiff trees at very young ages may result in increased mortality from wind throw as the ability to bend in a young stem has been suggested to be a trait which has evolved due to the low second moment of area in the stem (Davies, 2014). By reducing the ability for a small stem to bend, it will be more likely break or topple in strong wind events or when animals walk over or push it. Another example may be the development of above ground growth at the expense of root system development resulting in increased uprooting during severe wind events. Unfortunately breeding trial failures such as these are rarely reported in literature and therefore quantifying them is difficult. There is further potential for problems such as these to develop with very early selection protocols, but without running both very early selection and full length breeding trials in parallel over different environments with the same genetics it will be very difficult to identify negative traits developing as a result of very early selection.

Discussion

There are a number of attributes tree breeders are now wanting to select for; growth, health, form, durability, density, stiffness, growth-strain and volumetric shrinkage. Broadly these can be separated into two categories, maximization/minimization selection and threshold selection. For example, usually growth is maximized, while if form reaches a specific criteria it is considered good enough. This is an important distinction when coupled with tree physiology as trees present general patterns with some wood properties (such as MFA) which rarely reverse with age (Meinzer et al., 2011). As a result, when a threshold selection can be coupled with a trait which is governed by physiological characteristics which are known to develop in a particular way and if an appropriate test can be developed for that trait they could be selected at a young age. An example is stiffness within *Pinus radiata* where MFA is known to decrease and density increase with age (Xu and Walker, 2004) , resulting in stiffness increasing with age (Sharma et al., 2015b). Because a premium is paid once a predefined stiffness is reached it is a threshold problem where once the threshold is reached all later growth can (reasonably) be assumed to be over the threshold . An example where this type of selection does not work is growth, as the individuals which are desired grow to the largest size possible in the shortest about of time, i.e. a maximization problem. As Apiolaza (2009) alluded to, in order for very early selection to be profitable a switch in thinking is needed to the screening/selection to be only for wood produced early in the trees lifespan (corewood), extrapolating that information to older (outerwood) wood properties is problematic and can only be done when there is sound physiological reason, otherwise the autoregressive nature of wood properties through time results in no gains being made.

Various wood property traits will be addressed individually and their appropriateness for very early selection (arbitrarily defined here as selection at less than 20% of their commercial lifespan or a grater than 10 year lag between selection age and commercial harvest age) discussed with reference to literature, unpublished pilot trials and thought experiments. Where possible root causes for (un)suitability will be linked back to physiological understanding, or lack there of and suggestions will be made as to future research directions in order to increase the effectiveness of the tools used.

Growth

Growth, height, diameter and volume are discussed together as are very intertwined in todays breeding trials with diameter often used to predict height and volumes estimated from the two. These all fall into a maximization class breeding problem; volume is maximized over a predefined time frame. Because growth can be measured non-destructively research has been conducted investigating the ability to predict a trees future growth performance at differing ages, and verified on the same tree later in time. Dieters et al. (1995) investigated genetic correlations between volume measurements at differing ages and found the correlations to vary between 0.56 and 0.97 for lag times of between 3 and 9 years, with young trees producing poorer correlations than older trees even when the lag time was the same, others have found similar results (Mihai and Mirancea, 2016; Greaves et al., 1997; Stackpole et al., 2009; Osorio et al., 2003).

There is an argument for very early selection of growth and mortality which states something akin to "nurseries pick the top performing individuals at the age of a few weeks, therefore it stands to reason that the same could be applied at any age" However nurseries are picking individuals which are the most likely to survive the process of transplanting from the nursery bed to the forest, which requires a much shorter time frame prediction (a few weeks, not decades) and is a threshold problem, either the trees survive transplant or die. Physiologically larger individuals likely have more nutrient storage, more developed root systems, and larger canopies, giving them a competitive advantage over smaller individuals in a transplanted situation where they must re-establish and compete with other plants for resources. Nursery selection in this way makes no assumptions regarding how well the tree will perform later inline, it merely takes the individuals which at the time of picking has the physical characteristics which will help them service transplanting.

Silvercultural practices can have large influences on growth and different genetics can respond in differently to silvicutural practices (Smith et al., 1997). Very early selection occurs before trees are large enough for pruning or thinning and are treated in very different ways to a typical commercial stands, for example they may be planted at very high stockings to save money and have irrigation on highly fertile soil to lower mortality. Any genetics which thrive under these ideal conditions will be selected above others which may be better suited to the real world. For example, an individual which is slower growing but has high drought tolerance is not selected in an irrigated trial, but the selected fast growing individual then dies when is planted out in a dry area.

Health

Early selection for health appears feasible as a threshold criteria, only select trees which are healthy at the end of the breeding cycle. Once a tree has become sick (or died) it will lag behind other individuals in its stand giving suboptimal growth. If trees die or are excluded from very early selections due to poor health they are not included in the next breeding cycle (even if not directly selecting for health). Any undesirable heath problem which occurs during the very early breeding cycle and from which resistance is heritable can be selected against. However health problems which are associated with older ages can not be predicted using this crude early selection method of “if its not healthy dont select it”. Establishment health is a good candidate for very early selection, although it should be kept in mind that differing environments will cause different health challenges. Health is used as a broad term, but the genetics required to withstand drought are different to those required to withstand frost, or beetle attack. Identifying genetics with resistance to particular environmental pressures at a young age should improve planting out success of future trials if genetics are chosen appropriately for the environment, reinforcing why GxE trials are of the utmost importance.

Form

Form is characterized by the repetition of particular stem and branching characteristics. Trees used in very early selection typically have not been growing for long enough to show any repetition of traits such as a tendency to double leader, have large branches, or small internodes. Because of the lack of repetition, form in the traditional sense is hard to utilise within very early selection programs. When domesticating a wild species extremely poor individuals may still be recognizable at young ages, although the concept of form selection needs to be slightly redefined for very early selection programs. If an individual is “bush like” as in “at a small size it does not prioritize vertical growth” (assuming no mechanical damage has occurred), it seams reasonable to remove the individual from the breeding population because in this state it will become sub-dominant and struggle to regain the growth required to produce a straight stem of suitable size under a typical single age single species commercial stand management strategy, and be removed during thinning (if thinning was part of the stand management strategy). It seams unlikely that any domesticated species (even if only one breeding cycle has been completed) would still have genetics which produced individuals with form this poor. The strategy also provides no guaranty that remaining trees will possess satisfactory form characteristics at older ages. Very early form selection at best will remove the genetic anomalies such as highly inbred individuals of undomesticated species which are prone to “bush like” growth at young ages as the information required to asses an individual for form in the traditional sense is simply not available until significant repetition of branching and stem traits is measurable at an older age.

Density

Density is probably the most used wood property in breeding, although possibly due to the low measurement cost and high speed compared to other wood properties (Apiolaza, 2008). When maxamising material is the main concern, for example breeding for carbon sequestration, pulp or biofuels, maximising density makes sense, and while no early selection programs are known to exist for this purpose, if the trait can be expressed as a threshold of density the potential exists for very early selection to be valuable as density does not generally reduce with cambial age (Meinzer et al., 2011). Initially density gained a lot of attention as it was easy to measure and originally thought to correlate well with wood properties such as stiffness. In young trees, both Eucalypt (Chapters 3 and 4) and Pine (Sharma et al., 2015a) the correlation between stiffness and density is low. It could potentially be the case that when creating engineered wood products, selecting for a specific density may be of importance (Marra, 1992) e.g. gluing may work best at a given density value. Density doesn't decrease with cambial age (Meinzer et al., 2011) and if keeping density above a lower threshold is desired it is a good candidate for very early selection methods. Given the TRP of density shows an increase (or at least no decrease) with age, very early selection is unlikely to be reliable even if low density individuals are selected at a young age. There is no evidence that the selected trees will not go though a more rapid density change than the individuals which were not selected after the very early selection time frame. As a result, the selection could be counter productive and provide a genetic base of inferior trees.

Stiffness

Stiffness is generally a threshold problem, timber is graded using threshold stiffness values to define a particular price bracket. As a result, nothing is gained from maximizing stiffness above the desired threshold. Because stiffness is governed by acoustic velocity and density, both of which under normal circumstances follow a fairly universal pattern of decreasing MFA and increasing density with distance from the pith (Meinzer et al., 2011), if a desired stiffness is reached early in life it is reasonably assumed the stiffness of wood laid down later will not dip bellow the threshold. The combination of threshold selection and well established age-related physiological patterns make stiffness a good candidate for very early selection. Stiffness selection can also be formulated as a minimization problem; How early in life can a tree reach the desired stiffness. Due to testing constraints, measuring breeding populations in this manner is not feasible, however, harvesting at predetermined (early) age and selecting individuals which reach the threshold will likely result in a population reaching threshold stiffness earlier and hence provide stems with more wood usable in the higher value stiffness categories (for the given site, although the argument can be readily extended to GxE trials). A potential problem with very early selection of stiffness is by increasing stiffness of young (small) stems there will be a reduction in flexibility to resist toppling forces from animals and wind events. One of the most promising arguments for the evolution of the typical radial pattern of MFA and density is that trees experience differing mechanical loading depending on their size (Mattheck and Kubler, 1997), there is a biological advantage in having low stiffness when a stem has a low second moment of area, allowing for the stem to bend rather than break or topple when external forces are applied. As the second moment of area increases with diameter, the geometry of the stem plays a proportionally larger role than the stiffness of the stem than the material properties do. Once a stem reaches a significant diameter bending ability becomes compromised and hence the best defense strategy is to stand solid, making stiffer material more desirable. By breeding to have stiff material in small stems there may be an inadvertent increase in toppling or breakage at young ages, possibly outside of the age range of very early selection trials, or the trial may by chance not experience the required weather event due to its short cycle time.

Extractive Content

Extractive content could use similar selection type to stiffness, once trees start producing heartwood they (with the exception of some rear cases such as striping) don't stop. Therefore selection of individuals at an early age which have started producing extractives (assuming that the production of extractives is heritable) could lower the age at which the population starts producing heartwood. Further evidence exists that the worst heartwood exists in the pith and improves in resistance to decay with radius (Kokutse et al., 2006; Bhat and Florence, 2003) so it may be possible to set a threshold at a young age for the timbers durability as well. There are two conceivable reasons to select for the presents of particular extractives - one, the presents of extractives is required for natural durability, and two, the colour of the wood may fetch a premium. If extractives are present at a young age it does not guaranty that the individual will have superior durability, but the presence of extractives is required for durability and therefore assuming extractive content and durability are heritable, very early selection may have potential as a starting point for selection of this trait. However little is known about the relationship between durability and extractive content, which needs further investigation before its suitability for very early selection can be assessed. As heartwood tends to develop later in a trees life (compared to when very early selection takes place) it is unlikely any trees will be producing heartwood at the time of selection. Any proxy based selections should be treated with due caution, and a good understanding of the underlying physiologically between the proxy trait and later development of heartwood would be needed, currently no known research has identified or suggested a suitable proxy trait, backed by sound physiological theory.

Growth Strain

There are a number of issues associated with trying to select for growth strain at any age. First growth strain, in the sense of a breeding trait needs to be defined. The breeders' desire with this trait is to capture genetics which produce little or no movement during sawing. Minimization of movement during sawing (or reducing movement below a threshold), which breeders have been calling growth strain is not necessarily the same as what physiologists call growth strain (derived from growth stress). Growth strain in the strict sense is a contraction which happens in the secondary cell wall during formation (see Chapter 1), when combined with numerous other geometric and material properties it produces movement at the macroscopic scale when boundary conditions are relaxed (for example during sawing, or a typical strain gauge test), giving what breeders have been referring to as growth strain. If selection was to take place only considering cellular level growth strain, it is related to MFA, however MFA and growth strain are correlated, making an inverse threshold problem, i.e. MFA must not go below a value associated with undesirable growth strain. In order to accomplish this the whole lifespan is needed as the MFA TRP decreases with time (Meinzer et al., 2011), and consequently growth strain increases. Growth strain is expected to increase to some unknown maximum occurring at some unknown time, which cant be known to be reached until the desired age of felling. Biechele et al. (2009b) found experimental evidence of an increase in surface strain with age and concluded that a multivariate approach is needed in trees of saw log dimensions as all growth parameters (crown width, crown area, crown eccentricity, crown length, tree height, DBH and slenderness in their case) have low correlations with growth strain. Biechele et al. (2009a) suggests interactions among parameters may also be useful but warns due to the large number of interactions growth strain its self may not be a useful breeding property.

Timber movement during cutting is influenced by a number of material and geometric properties such as MFA, reaction wood production, grain angle, crown shape and stem lean. Crown formation, soil conditions, prevailing and extreme wind events could all cause stem lean or an asymmetric crown which would result in an increase in growth strain within certain areas of the stem along with asymmetric stem formations, and as a result could cause more, less predictable deformation during sawing. More complicated as movement in mill (or during testing) is dependent on multiple inner wood properties such as spiral grain and crown habit (form) changes in time. It may be that genetic selection for low movement timber at milling is not possible due to the large number of genes responsible for so many properties which effect local GS production, which in turn creates a complicated three dimensional strain field within the stem. There are a lot of properties which would need to be simultaneously either maximised or minimised within an individual, and their correlations may not be favourable. For example, low base growth strain, low tendency to produce reaction wood, poor performance of reaction wood produced, symmetric crown and stem properties. Further complications arise as the traits which influence the magnitude of strain at a given point of development change with time, as a result different traits would need to be maximised/minimised at different stages of development in order to manipulate the production of the three dimensional strain field to produce the least amount of movement at the time of milling. It seams very unlikely this is achievable though breeding even over multiple sites and using full length breeding cycles due to the large numbers of traits which would need to be manipulated, some of which may not have a significant level of heritability, may have strong environmental interactions or are negatively correlated with other required traits. The most promising rebuttal to this argument is the mechanisum of growth strain production is under high genetic control and for some reason does not just lay down more reaction wood to get a given force, i.e. the amount of reaction wood will be consistent for a given influence, however the stress that reaction wood is capable of could be under simple genetic control.

An argument could be made that because growth strain is so heavily effected by verious micro-environmental aspects site level characteristics such as rain fall, aspect, soil type etc. will have less of an effect than on other properties, although no evidence exists for this. If it is the case that so many different properties influence the production of growth strain the variation between individuals within a site compared to the variation between sites would be much smaller than other traits which are controlled by less complex generation mechanisms. Growth can be significantly hindered by a lack of water, and that will effect all (say cloned) individuals more-or-less equally on a given uniform site. However with growth-strain, a broken branch, being pushed over by an animal, a wind tunnel effect etc. could all alter the growth strain from tree to tree even though the site level environment is essentially uniform and the genetics are identical. Whether this argument is valid should be investigated in the future as it may have a profound effect on the way genetic-environment interactions are considered within breeding programs as technology advances and individual tree monitoring becomes more realistic. Further, if it is the case silvicultural techniques will likely be better suited to growth strain manipulation than breeding.

Currently there is a significant knowledge gap regarding what material and geometric properties result in timber movement during (green) sawing. Further there is a lack of understanding of the strain field within a given stem, and how the field relates to the deformation of timber during milling. Before very early assessment of tree level growth strain can be considered for incorporation into a breeding program, an understanding of what causes timber deformation during green sawing is needed. Once an understanding of how the field relates to deformation, work is needed to investigate the influences which create the strain field, only then can those properties be investigated and tools developed to determine if selection for low growth strain as a means of reducing sawing deformation is feasible.

If we assume low age-age correlation of surface growth strain (or even a moderate one, which there is currently little evidence either way), it could be argued that selection for high surface growth strain of young trees which slowly reduce with growth may be the optimal profile. High surface strain in small stems (the wood on the surface is under tension) provides a flatter profile over the majority of the stem when the tree is much larger, so the gradient from one side to the other of a board is lower potentially resulting in less deformation. While there is no evidence that strain at a young age is a poor predictor of strain at an old age, the reverse does not have any evidence either (but it is much more common in other traits for young cambium properties to be poor predictors of older traits (Apiolaza, 2009)), it is worth considering that a potential result of selecting for low surface strain at a young age may have the unintended consequence of increase saw board deformation at commercial harvest age. This argument reaffirms the need to have significant physiological understanding of how a trait is produced before proxy tests (whether they are proxies in time or property or both) are used for selection.

Conclusions

? presented a list of requirements for a successful tree breeding program.

1) clear program and product objectives

2) sound knowledge of biology, silviculture and genetics

3) sound breeding strategie, well trained personal supported by a stable budget

4) efficient mass propagation nursery and plantation management systems to optimize yield and product quality

5) maintenance of broad genetic base

6) supportive research program

These points become even more crucial when considering very early selection as additional errors are added in order to reduce breeding cycle time. Due to the unknown relationships between various properties at different ages and how they will effect each other at commercial rotation age, having clearly defined program and product objectives is strongly linked to having sound understanding of the biology, silviculture and genetics of the species, both of which can only be achieved with a supportive research program which focuses on fundamental understanding of how the trees grow and why. Without this knowledge it will be nearly imposable to develop reliable testing procedures for very early selection.

There are two ways to develop very early selection methods once a suitable level of understanding of tree development is achieved. One is to have sufficient fundamental understanding that given properties at one age guaranty given properties at another (stiffness from MFA and density for example). The second option is a statistical approach, either using periodic non-destructive testing on the same individuals to obtain age-age correlations (DHB or height through time for example) or specifically designing trials to test how well destructive tests at one age predict properties at another ideally using clones. For this to be successful environmental factors need to be considered, one option is to clone trees at full rotation age from multiple (significantly different) sites which share genetics and test the clones under the intended very early selection procedures, typically high stocking within a nursery site. If a sufficient number of individuals, families and environments are represented a relationship between how well the given very early selection procedure (for that trial) can estimate outcomes on the different sites at different ages can be obtained and hence the site and procedures could be used to accelerate breeding cycles provided none of the above change significantly and the age-age correlations for the traits are sufficiently high.

The above discussion leads to the conclusion that for a trait to be a viable candidate for very early selection (in addition to significant levels of heritability, genetic variation, environmental variability etc. which are required for success for all breeding programs) at least one of the following three is required:

1) Extremely high age-age correlations. No known evidence exists stating that any of the properties discussed here poses significantly high age-age correlations. Truthing at full rotation age would be required to estimate age-age correlations over multiple environments.

2) A non-reversible threshold problem governed by physiology eg stiffness and possibly heartwood quality.

3) A trait which is defined within the very early selection breeding cycle life span, for example planting survival at one year.

If the following can be met, full rotation age trials are still continually required to ensure inadvertent traits are not being selected for.

Very early selection may provide some substantial gains in breeding efficiency for a limited number of wood properties, however development of the procedures needs to come from thorough understanding of the biology, physics and genetics of both the trait and the testing procedures, further it needs to be truthed with full rotation age trials from multiple environments. Full rotation age individuals need to be tested and the population characterised across multiple significantly different sites with sheared genetics first, and then a very early selection test could be developed and the results compared across sites and properties of the full rotation age trees. While commercially it is tempting reverse this procedure and complete very early selection first, there is no evidence of any positive or negative gain being made and will likely waste substantial amounts of time and money.

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