Juvenile-mature correlations in tree breeding programmes

Report of a Literature Survey for the Future Trees Trust

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1. Executive Summary

A literature review of juvenile-mature correlation in previous tree breeding programmes was carried out as a contribution to the technical planning and design of the Future Trees Trust silver birch breeding programme. Seed collected from three orchards (for Great Glen, Grampian/ Cairngorm and Tayside) was used by Forest Research to establish genetic gain trials to obtain measures of gain from the initial selections. These trials are now at or nearing the earliest age (5-6 years) at which assessments of gain and any second selection of superior individuals might be made. It is therefore important to make an appropriate decision as to the earliest age at which such assessments will be reliable.

Juvenile-mature correlation is an important parameter quantifying the reliability with which later (ideally intended rotational) performance can be inferred from juvenile performance in field progeny/ genetic gain trials. The tree breeder has an inherent dilemma in that he/she wishes to make assessments and selections as early as possible to shorten the breeding cycle and bring improved seed to the market, but he/she also wishes to ensure that the maximum gain is secured and later performance is reliable. A central problem in this area is that few progeny/ genetic gain trials are (or can viably be) pursued and observed until the intended rotation is approximated, as this can be several decades. Hence the tendency is to design and observe the trials only until the correlation in performance between successive assessments approaches unity.

Traditional tree breeding approaches emphasised the need to observe field trials until one-third to one-half of the intended rotation length - this typically implying a period of 15-30 years of observations. Attempts to select superior individuals and families within field progeny trials at the nursery or pre-4 year stages of growth have shown that this cannot be reliably pursued. These early selection approaches have generally been found to be unreliable (with correlations $r<0.4$), with a higher risk of misleading results where retrospective evaluations are made.

For birch, early indications in Scandinavia were that second generation selections could be made within progeny trials at 5 years. However more recent reports of the Finnish improvement programme, tend to suggest that selection at <u>10-12 years</u> is now the preferred approach. In the case of the FTT ash programme, the early indications were that juvenile-mature correlations were becoming useful by six years and stable and satisfactory by 10-15 years, allowing for relatively early selections to be made within breeding-seedling orchards.

Many modern conifer breeding programmes have satisfied themselves that selections at 6-12 years are feasible (with r-values the 0.6 to 0.8) and recommend selection (a) with caution from 6-8 years, (b) with confidence from 10-12 years.

Trial analyses age-age correlations in FTT provenances trials between the relative height measures taken at 2/3 years and at 10-12 years are satisfactory (r-values ranging from 0.74-0.86) for the Dunkeld, Moray, Glentrool and Ballinoe (Irish) trials, but weaker ($r=0.45$) for the Kintyre trial.

Conclusions:

a. It may be possible to start making initial assessments/ internal selections from the 5-6 year stage onwards, but these should not be regarded as definitive.

b. Assessments at 8-10, 10-12 and 15 years should be obtained to allow the calculation of age-age correlations between these measures and assessment to be made of stabilisation of juvenile-mature correlation towards mid-rotation.

c. The optimum age for selection of superior individuals and families within field progeny trials for birch in Scotland (with an intended rotation of 40-60 years) is realistically more likely to lie within the range 8-12 years than 6-8 years. This is particularly the case due to the emphasis on stem form as a selection criteria, for which age-age correlations appear to develop more slowly than those for height growth, based on the experience of the Swedish programme.

d. Hence assessments made at 10-12 years and 15 years should certainly be used to refine any selections attempted earlier at 6-8 years, deleting any inclusions whose performance disappoints later and adding in any coming good later.

e. Subsequent observation and follow-up assessment to 15-25 years is usually desirable.

This is likely to embody the most prudent recommendation for the FTT birch programme.

2. Background

Seed collected from three orchards (Great Glen, Grampian/ Cairngorm and Tayside/ Perthshire) was used by Forest Research to establish genetic gain trials to obtain measures of gain from the initial selection. These trials in Aberdeenshire, Perthshire and Fife, are now at 5-6 years old. For the South Scotland/ North England collection it is intended to establish genetic gain trials at a later date if sufficient additional seed is produced from recently-formed private polyhouse orchards.

For the three existing regional field genetic gain trials, it is intended to pursue field assessments for growth and stem form at 6, 10 and potentially 15 years of age. The question at hand is how early it may be possible to make assessments of progeny performance (against selection criteria) that will allow reliable predictions to be made of the likely performance of birch at the intended rotation age for quality timber. The latter is difficult to assess under Scottish conditions - it might range from 30 years on a productive lowland site to 60-70 years under more challenging upland conditions. Superior individuals selected from within these trials could be used to found second generation clonal seed orchards, based on assessments of predicted gain. Stem form is considered equally important, if not more so, than vigour/ height growth in selection. The superior individuals selected from the trials might also be subjected to genetic studies in an attempt to retrospectively indentify their parents within the closed pollination environment inferred for the polyhouse.

An earlier breeding programme for silver birch at the University of Aberdeen (1970's and 1980's) made initial selections from progeny trials at 5-6 years of age, based on Finnish advice of that time. However more recent experience of breeding programmes for this species in Finland, Sweden and the Republic of Ireland has tended to recommend selection after 8-12 years of growth in trials, especially given the emphasis placed on stem form traits. Recent inspection of one of the FTT birch programme progeny trials in Fife has suggested that useful initial selections might be made after 6 years, but it is important to assess the published evidence from elsewhere to inform key decisions on this. That is the purpose of the current literature review task. It might be possible to consider adopting an approach where initial selections were made after 6-8 years but the field progeny/ genetic gain trials continue to be assessed until these reach 10 or 15 years, allowing for revision, refinement and augmentation of any earlier selections made.

3. Method

The project was undertaken by a conventional and online literature review. The project time available was 3 days and it is not consider that further resources would significant enhance the outputs and results.

4. Scope of the literature

This literature review attempted to encompass reported experiences from previous conventional tree breeding programmes throughout the world where juvenile-mature correlations had been predicted, estimated, determined and/ or analysed. Something of the order 60-70 relevant study reports were considered and these are detailed in the Bibliography at the foot of this literature summary report. Most studies reported works conducted during the half-century 1960-2010 when conventional systematic tree breeding activity was at its height internationally. The major regions yielding relevant literature were Fennoscandia (Finland and Sweden), Continental Europe (Germany, France etc.), Great Britain and North America. A small amount of work from sub-tropical countries, primarily dealing with Radiata pine and *Eucalyptus* was also included, with selections typically made at the seedbed stage. Recent work which involved improvement by biotechnological/ genetic modification was not examined.

Four major categories of studies were captured within the literature review:

a) generic methodological studies which attempted to explain the components of juvenile-mature correlation or to predict it from fundamental principles.

b) tree breeding programmes for principle production conifers in Fennoscandia, Continental Europe and North America (primarily spruces, firs and pines) where conventionally, selections would have been made at 15-25 years, but where valuable juvenile-mature correlations at 6, 8, 10 or 12 years have been cited and also used to justify earlier selection within ongoing programmes.

c) tree breeding programmes for hardwood species (birch, poplar, ash, cherry) in Fennoscandia, Continental Europe and North America where initial selections, based on strong juvenile-mature correlations, have typically been made at an age representing a lower fraction of the intended commercial rotation (e.g. 5-12 years in Scandinavian birch, 5-15 years in British ash and French cherry).

d) advanced tree breeding programmes where attempts have been made to infer juvenile-mature correlations from material (typically of shorter rotation crops such as sub-tropical pines, *Eucalyptus* etc.) studied at the nursery bed or growth chamber stage (1-4 years), often using multiple trait combinations.

The most common trait reported in studies reviewed was certainly height growth (particularly in young material < 5 years). As material under study became more mature, height remained an important variable, supplemented by girth and volume. A minority of studies, particularly in hardwood species, reported stem form assessments (either by single score or on multiple parameters, e.g. branch weight and angle), while some more sophisticated studies examined wood density and mechanical properties.

5. Prediction of juvenile-adult correlation by the equation of Lambeth (1980)

The juvenile-mature correlation (or more generally the age-age correlation) is normally expressed as the correlation coefficient "r-value" between two series of observations of any given breeding trait (usually height) taken at different ages. It also possible to express the correlation between different traits, as with juvenile height and mature breast-height diameter or volume. When making selections of superior individuals one would ideally like to obtain the r-value between the age of selection and the intended final rotation age as r > 0.80. However many tree breeders are willing to use weaker r-values in the range 0.5-0.8 to inform earlier selections in order to accelerate the improvement cycle on economic/ efficiency criteria.

Based on experiences from a number of progeny trial experiments, particularly in pine species, Lambeth (1980) proposed that the age-age correlation "r-value" between heights measured at two different ages can be reliably predicted using the formula:-

r = 1.02 + 0.308 ln Q [where Q is the quotient of the earlier and the later ages].

Many other authors in this field, such as Gill (1987) have accepted that this equation can potentially be applied with some caution to other tree species.

If one sets a threshold r-value of 0.5 for valuable selection, this implies that for birch with an intended rotation of 30 years, reliable assessments and selections can first be made at 6 years, for an intended rotation of 40 years, at 8 years, for an intended rotation of 50 years, at 10 years and for an intended rotation of 60 years, at 12 years.

If one sets a threshold r-value of 0.6 for valuable selection, this implies that for birch with an intended rotation of 30 years, selection can be made at 8 years, for an intended rotation of 40 years, at 12 years, for an intended rotation of 50 years, at 15 years and for an intended rotation of 60 years, just at 15 years (but for which r=0.59).

Given growing conditions for silver birch in Scotland, this formulaic approach would tend to suggest optimum selection should be undertaken between 8-12 years, which corresponds well with practices adopted in Irish, Finnish and Swedish programmes.

In the earlier stages of any progeny trial experiment, once initial establishment effects are overcome, genetic and family differences are likely to become the primary determinants of relative performance. However, as Gill (1987) has pointed out, there is a tendency for estimates of heritability and additive variance then to decline as progeny trials age, due to the inevitable fact that environmental factors of growth (competition between inclusions, weather and pest damage etc) have an increasingly significant impact on the performance observed. Only if some element of heritable genetic/ family variation between progenies survives through to full rotation age is conventional breeding feasible. Hence there are good arguments for making selections between progenies and families based on observations during the "window of opportunity" before competition between inclusions becomes severe. This typically tends to be the period when tree height is in the range 2-5m, although this is variable to some extent with species morphology. This is commented on by Namkoong *et al* (1972) and Namkoong and Conkle (1976). See also:- Dean et al (2006), Eriksson (1991), Haapanen (2001), Kang (1991), Lindgren (1984), Wakely (1971), Ying and Morgenstern (1979) for commentaries on time development of correlation values.

6. The experience of the University of Aberdeen birch breeding programme

The independent programme of trial improvement work on silver birch, conducted by the University of Aberdeen between 1977 and 1988, represented an earlier attempt at breeding this species in Britain, based on emerging Fenno-Scandinavian experiences.

This work has previously been reported in detail in the literature by Blackburn and Brown (1988), Richardson (1992) and more recently by Malcolm and Worrell (2001), the latter authors reporting their later assessment in 1997 of a progeny trial at Tilquhillie, surviving from the original programme, and by that time 12 years of age.

As detailed by Richardson (1992), the approach adopted was fundamentally similar to that of the current FTT birch improvement programme and the earlier systematic tree improvement work on birch, undertaken in Finland from 1960 onwards. In 1977, 100 superior birch individuals were selected in the field, with 80 of these deriving from north-east Scotland and the other 20 from a diverse range of locations across England, Scandinavia, East Germany and Poland. Seed was collected from these individuals (hence this was a half-sib field selection as opposed to the full-sib scion collection method employed in the FTT programme). Seed collections were used to raise plants in a polyhouse nursery, with half-sib families then being tested in a field progeny trial, established in 1979 at Craibstone Estate near Aberdeen. Throughout the period up to 1987, several further field selections of some 180-200 silver birch plus trees from across Scotland and the North of England were made. Seed collected was used to produce nursery transplants in a similar way, leading to establishment of field progeny trials at five Scottish locations. Although these latter trials were abandoned relatively early, following environmental damage, early height growth and resistance assessments had suggested strong genetic differences (Blackburn and Brown, 1988).

In the case of the earlier Craibstone progeny trial, and following the model from previous Finnish birch breeding (as explained by Lepisto, 1973), selections were made of superior performing individuals within the trial after five growing seasons (1979-1984). From these, 14 full-sib families were produced by controlled crossings. These were to be compared with 6 half-sib families from trees of good form and 4 half-sib families from trees of inferior form, within a small second generation progeny trial, established at Tilquhillie on south Deeside in 1986. The Tilquhillie trial was assessed after two growing seasons in late 1987 for height, annual height increment and estimated stem form. Malcolm and Worrell (2001) report their 1997/1998 (hence 12 year) reassessments of this only surviving trial from the Aberdeen programme. Again height and stem form were re-assessed, this time with the addition of breast-height diameter. There was a poor reported age-age correlation between the 2 and 12 year height measures ($r = 0.21$), with significant re-ordering of the performance ranking between 2 and 12 years. For comparison, application of Lambeth's equation would lead one to expect $r=0.47$. Malcolm and Worrell (2001) suggest that competition and climatic leader damage may well have compromised these results to some extent. However they do give cause for concern that second generation selection at 5 years may be premature. There was, however, evidence that the original basis of selection in terms of stem form had been preserved up to 12 years, with the controlled crosses showing superior form to the open-pollinated half-sib inclusions. Further attempts to establish second generation progeny trials of full-sib selections from the first generation University of Aberdeen progeny trials were sadly later abandoned.

7. Experience from Finnish, Swedish and Irish birch breeding programmes

Relevant experience in the conventional breeding of silver birch, directly comparable to the FTT programme is available from Finland, Sweden and the Republic or Ireland.

Tree breeding work on silver birch has been under way in Finland since 1960 and is fully reported by Hagqvist and Hahl (1998), Koski (1991), Koski and Rousi (2005), Lepisto (1973), Poykko (2008, 2013), Velling *et al* (2002), Vihera-Aarnio (1991), Vihera-Aarnio and Ryynanen (1995) and Vihera-Aarnio and Velling (1999). The programme has proceeded by a similar approach to that adopted to date by the Future Trees Trust, with field selection of plus trees, establishment of polyhouse seed orchards and progeny testing of first generation selections to produce subsequent generations of seed orchards with enhanced gain. Koski and Rousi (2005) mention that age-age correlations on volume yield between 13 and 32 years of growth had r-value of 0.833 (where Lambeth's equation would estimate $r=0.74$). Vihera-Aarnio and Velling (1999) suggest that observed differences in performance at 8-12 years are expected to be retained at least until 30 years growth. Stem form appears to show weaker age-age correlations within the Finnish birch breeding programme and hence selections should be delayed where form is a priority.

Tree breeding work in Sweden has followed a similar model and is reported by Erken (1972), Stener (2002) and Stener and Jansson (2005) who report work where progeny trials of silver birch were assessed annually up to 10 years of growth. Age-age correlations were typically valuable from 4 years ($r>0.6$) and secure by 6 years ($r>0.9$) in terms of height growth, but Stener (2016, pers comm) clearly recommended waiting until 10 years to make selections where stem form was a key determinant of superiority. These findings confirm impressions obtained from the Finnish references.

The birch breeding programme pursued in the Republic of Ireland, dealing with both silver and downy birches is of much more recent origin and has adopted lessons from the Scandinavian breeding programmes. O'Connor (2015) reports that progeny trials have been established containing 94 families of downy birch, 47 families of silver birch, and 37 controlled crosses of downy birch have been assessed repeatedly over 10 years of growth. Juvenile-mature correlation data have not yet been calculated or published and it is understood that Ellen O'Connor will work these up in due course, but second generation progeny selections to found subsequent seed orchards are apparently being pursued at 10 years in the case of downy birch, along the lines of the previously described work in Finland and Scandinavia.

8. Experience from international conifer breeding programmes

Although less directly relevant to the birch breeding effort, copious information on juvenile-mature correlation has become available from various conifer breeding programmes. The key literature examined for principle conifer species includes:-

Sitka spruce (UK) - Gill (1987), Lee (1999), Lee and Matthews (2004), Forest Research (2016, online).

Douglas fir (US, Canada) - Namkoong (1972), Ye and Jayawickrama (2014) and Zas *et al* (2004)

Scots pine (Europe) - Eriksson *et al* (1993), Giertych (1974), Haapanen (2001), Jansson *et al* (1998) and Jonsson *et al* (1990).

Norway spruce (Europe) - Jansson *et al* (2005), Karlsson *et al* (1998, 2002).

White spruce (Canada) - Alberta TISC (2008), Newton (2003), Rweyongeza (2013) and Ying and Morgenstern (1979)

Radiata pine (various) - Burdon et al (1993), Codesido *et al* (2012), Dean *et al* (2006)

Other pines (various) - Namkoong and Conkle (1976), Squillace and Gansel (1974), Steinhoff (1974) and Van Havereke (1972).

The overall picture for juvenile-mature correlations from work on conifers is that:-

- assessments are almost always for height, dbh and volume traits with rather little work on stem quality in conifers but some on inherent timber properties.
- some studies have attempted to retrospectively assess inherent juvenile-mature correlations based on purposive mature selections made at or near rotation.
- early selection/ correlation approaches (seedbed and prior to 4 years growth) have generally been found to be unreliable ($r<0.4$), with a higher risk of misleading results where retrospective evaluations (based on purposive selections) are made (Lascoux and Kremer, 1994).

- more traditional/ conservative approaches favoured conifer selections after 15-20 years to obtain secure juvenile-mature r-values in the range 0.80 to 1.00. This applies especially to more slow-grown conifer species such as Scots pine.

- many modern conifer breeding programmes have satisfied themselves that selection at 6-12 years (with r-values into the range 0.6 to 0.8) captures most gain achievable by waiting to 15 years - for example Gill (1987) suggests that initial selections in Sitka spruce progeny trials can be undertaken from 6 years.

- shorter-rotation species such as radiata pine may be more suitable for early-selection at 3-6 years and some authors have suggested that juvenile trait combinations rather than single traits can be used as predictive variables.

As the anticipated rotation length for silver birch grown in Scotland is likely to be comparable to that for productive conifers such as spruce and fir, the information on juvenile-mature correlations available from conifer breeding programmes might tend to recommend selection (a) with caution from 6-8 years, (b) with confidence from 10-12 years. This appears consistent with the Lambeth equation and Finnish birch work.

9. Experience from other temperate hardwood breeding programmes

Rather few studies have been reported in which longer-rotation temperate hardwood species (other than relatively faster-grown birch, poplar and aspen) in field progeny/ genetic gain trials have been followed through to rotation/ near rotation. The reasons for this are (a) the very long timescales/ high costs inherent in such work and (b) the fact that it is very difficult to maintain the initial stocking in the trial beyond 20-30 years in most cases, and any selective thinning regime in favour of better performing progeny will impair the opportunity to make neutral assessments of juvenile-mature correlations. Most reported studies in hardwoods derive “interim assessments” of juvenile correlations between measures taken at, for example 6, 10 and 15 years. Studies in hardwoods typically assess both height growth and some form of stem quality index (which can be a simple 1-5 “wow factor” or more sophisticated indices). Where performance is seen to be “settling down”, with r-values into the range 0.8-1.0, tree breeders may be willing to accept selections made from gain trials, or roguing of breeding-seedling orchards (BSOs) as from 12-15 years of growth. Where rank ordering remains volatile, observation may need to continue on to 20-30 years of age.

Within the Future Trees Trust programme only work on ash, cherry and birch have been pursued to the point where second generation selections might be considered. In the case of the ash programme (now redirected to resistance breeding due to *Chalara*), the early indications were that juvenile-mature correlations were becoming useful by six years and stable and satisfactory by 10-15 years, allowing for relatively early selections to be made within breeding-seedling orchards (Clark, 2016, pers comm). However in the case of the oak programme, correlations were still unstable after 15 years of growth in trials and orchards, with observations likely to have to continue on to 20-25 years before sensible selections could be undertaken. The position for “intermediate” species such as sycamore and sweet chestnut is as yet unknown.

Selected relevant references for interim juvenile-mature correlations in temperate hardwoods include:- Cundall *et al* (2003) reporting on British ash provenance trials; Savill *et al* (1999) reporting on British ash breeding seedling orchards; Hall *et al* (1983) reporting black alder breeding work in North America; Nocetti *et al* (2014) and Santi *et al* (1998) reporting on cherry; Savill *et al* (2005) for a subject overview.

10. Indications of juvenile-adult correlations from FTT birch provenance trials

The Future Trees Trust birch provenance trial series (as reported by Lee *et al*, 2015) offers a useful opportunity to explore inherent correlations between height growth at the provenance (not family) level as measured after 1 year (Worrell *et al*, 2000), 2/3 years (Malcolm, 2011, pers comm) and 10-12 years (Lee *et al*, 2015) respectively (for Series 1). Trial analyses suggest that indicative age-age correlations between the relative height measures taken at 2/3 years and at 10-12 years are satisfactory (r-values ranging from 0.74-0.86) for the Dunkeld, Moray, Glentrool and Ballinoe (Irish) trials, but weaker (r=0.45) for the Kintyre trial. Age-age correlations between the absolute measures taken at 1 years and relative height measures at 10-12 years are only available for the Dunkeld and Moray trials for which r-values are 0.23 and 0.70 respectively. Similar analyses could be pursed for the Series 2 trials (3 and 8 years). Clearly these data cannot be directly equated with assessments of age-age correlation in progeny trials measured for individual progeny or half-sib families, but they do suggest that genetically-controlled growth performance traits are emerging by the three year point and that relatively early selections in silver birch may be feasible.

11. Conclusions and recommendations

Although the literature evidence available to address this question is rather diverse in terms of methods of original study, subject species, length of observation and observed correlations, there appears to be a persuasive overall case for the following recommendations in respect of the future development of the FTT birch breeding:-

a) selection of superior individuals and families within field progeny trials cannot be reliably pursued at the nursery or pre-4 year of age.

b) it may be possible to start making initial assessments/ internal selections from the 5-6 year stage onwards, but these should not be regarded as definitive.

c) assessments at 8-10, 10-12 and 15 years should be obtained to allow the calculation of age-age correlations between these measures and assessment to be made of stabilisation of juvenile-mature correlation towards mid-rotation.

d) the optimum age for selection of superior individuals and families within field progeny trials for birch in Scotland (with an intended rotation of 40-60 years) is realistically more likely to lie within the range 8-12 years than 6-8 years. This is particularly the case due to the emphasis on stem form as a selection criteria, for which age-age correlations appear to develop more slowly than those for height growth, based on the experience of the Swedish programme.

f. hence assessments made at 10-12 years and 15 years should certainly be used to refine any selections attempted earlier at 6-8 years, deleting any inclusions whose performance disappoints later and adding in any coming good later.

g. it is rather questionable whether any seed orchards established using second generation material selected at 5-6 years should be awarded "tested status" - this accolade should probably be reserved until confirmation at 10-15 years. It should be clear what criteria the assessment of superiority is based upon - for example the balance between height, volume and stem form

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