Pollen Contamination and Pollination Management in Tree Seed Orchards

Report of a Literature Survey for the Future Trees Trust

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1. Executive Summary

A literature review was conducted into factors affecting pollination within tree seed orchards, with specific reference to the circumstances of the ongoing Future Trees Trust selective breeding programme for silver birch (*Betula pendula*) in the United Kingdom and Ireland. Particular emphases were placed on the management of potential contamination from external pollen sources and on the encouragement of pollen and seed production, representative of the full range of clones included within seed orchards. The work was intended to inform the future development of the birch breeding programme in terms of the selection of optimal seed production methods. Research and development work conducted to date by Forest Research has employed the Finnish 'indoor polyhouse' form of birch seed orchard, whereas commercial and operational seed production stakeholders may prefer field orchards on cost grounds.

Conventional tree seed orchard practice has favoured open-grown field orchards, although it has long been recognised that such open-grown orchards are vulnerable to contamination by external pollination. This has the deleterious effect of diluting or eroding the levels of genetic gain, realised from initial phenotypic field selections, by a fraction of one half of that proportion of orchard pollination that arises from external sources. Rates of external pollination are very variable and can be in the range of 20-80%. The silvicultural and economic costs inherent in such erosion of realised gain increase in significance with successive rounds of breeding, based on the outcomes of progeny testing and controlled crossing, as the embodied investment and latent gains are greater. Conventional methods for mitigating external pollen contamination in field tree seed orchards (e.g. geographical isolation, buffer zones, supplemental mass pollination etc.) are only partially effective in protecting gain, especially in situations where long-distance mass transportation of pollen during the flowering season occurs. This is known to be the case for birch in Scandinavia based on aerobiological studies.

The development of indoor polyhouse seed orchards for birch in Finland and Sweden largely addresses the issue of external pollen contamination by physical isolation, but introduces a number of other issues related to the artificial microenvironment within the polyhouse and the effects that this can have on quantity and pattern of flowering. British experience to date has been rather variable, with evidence for limited pollen production and asymmetric contribution by included clones. Finnish experience over four decades suggests that careful measures are required to ensure copious and genetically representative seed production and that these can include atomisation, ventilation, irrigation, fertilisation, CO_2 enrichment and fan-assisted pollination. These measures increase the costs of polyhouse orchard production and require more specialist skillsets, which in turn renders the approach less commercially attractive.

The results of the literature review support the original decision to adopt the Finnish indoor polyhouse seed orchard approach for birch breeding in UK/ Ireland but also recognise that, where operational production of improved birch seed is undertaken in an unsubsidised commercial context, it may prove difficult to sustain this approach. Recommendations are made for genetic researches into the patterns of external pollen contribution in open-grown field seed orchards and of internal pollen contribution in polyhouse seed orchards to provide better quantification and basis of scientific evidence for the management of such orchards of either type. Transparent description of basic material of birch produced is important, as is adequate state financial support.

2. Background

This literature review was commissioned as one part of the Future Trees Trust Silver Birch Group 2014-15 Work Plan (Project 1, Task 3). The primary aim of the review was to inform the future development of the FTT silver birch tree improvement programme and the subsequent production of tested birch material for operational deployment. Results are also likely to be relevant to FTT work on other tree species.

Since its inception during the mid-1990's, the FTT silver birch (*Betula pendula*) tree improvement programme (formerly operated by the BRC and BIHIP respectively) has employed a first generation selective breeding approach, closely based on that developed in Finland over the past 40-50 years. Selected superior individuals ('plus trees') of silver birch have been identified in each of four geographical regions (Great Glen, Tayside/Perthshire, Grampian/ Cairngorms and South Scotland/ North England). These trees have been clonally replicated by taking scion cuttings and commercially grafting these onto downy birch (*Betula pubescens*) rootstocks. Grafted stock plants have then been used to form four regional research seed orchards in polyhouses operated by Forest Research at their Northern Research Station. Small quantities of seed have been produced and used to propagate seedling transplants for inclusion in progeny trials at several sites across Scotland, also by Forest Research. Seed orchards have typically included 3-5 rametes of each of 40-50 selected clones. The rationale for selecting the 'Finnish polyhouse' approach for UK birch seed orchards has been to strictly control pollen contamination from wild birch of inferior phenotypes, by both physical isolation and seasonal desynchronisation of pollination. This approach is relevant for research, capturing maximum gain from field selections. Some challenges have been encountered with operation of these polyhouse orchards, including delayed and intermittent seed production and uneven clonal contributions.

Unlike governmental research and tree breeding institutions in Sweden and Finland, Forest Research are not currently mandated or resourced to operate production seed orchards. Polyhouse orchards are therefore discontinued after sufficient seed has been collected for progeny testing. Recently, commercial nurseries and seed producers have expressed an interest in establishing qualified production seed orchards with the selected silver birch material, pending the results of FR progeny testing at 6-10 years. Fresh grafted material has been produced for these orchards by striking cuttings from Forest Research clonal field archives. Private-sector preference has generally been to establish conventional open-grown field orchards, as with other tree species. Although vulnerable to external pollination, these retain 'qualified' status of clonal collections. Open-grown field seed orchards are considerably less expensive than polyhouse orchards and there are questions as to whether polyhouse orchards can form the basis of any commercial enterprise, as opposed to state/ charitably-funded R&D projects. The Finnish selected birch seed production programme enjoys up to 85% state funds.

The question of which type of orchard to operate for UK silver birch in the future will become of increasing significance with any subsequent rounds of clonal selection, increasing the theoretical gain that is potentially defended from 5-15% up to 25-30% that might be expected from any second round of advanced generation breeding. Decisions would have to be taken at that stage as to business models for production. If polyhouse orchards are used, proficiency in their management will need to improve, whereas if open-grown seed orchards are used, optimum design/ location is then vital.

3. Methods

The project was undertaken by a conventional online literature search, abstracting and selective review approach deploying four working days during February/ March 2015. Literature search and review resources at the Universities of Aberdeen and Edinburgh and at Harper Adams University were utilised. It is not considered that additional working time would significantly enhance the outputs and results from this review.

4. Scope of the literature

While there was some record of tree seed orchard establishment and management during the 1930's (especially in Scandinavia), scientific planning and systematic operation of research and production tree seed orchards only became more widespread from the 1950's onwards, and increasingly so from the 1970's. A good summary of international experience, accumulated by the mid 1970's, is provided by Forestry Commission Bulletin 54 (Faulkner, 1975), which remains a key source. This literature reviewed dates mainly from the period 1970 to the present, with earlier work concentrating on seed orchard design and operation and much recent work reporting studies deploying increasingly sophisticated genetic techniques for paternity analyses.

The vast majority of published activity in forest tree breeding and seed orchard establishment/ management has concentrated on a small number of plantation genera – mainly pines (*Pinus* spp), spruces (*Picea* spp), larches (*Larix* spp), birches (*Betula* spp), poplars (*Populus* spp), Douglas fir (*Pseudotsuga menziesii*) and *Eucalyptus* spp. There has been some work on other coniferous genera such as *Abies*, *Cryptomeria*, *Tsuga* and *Thuja* and also some on tropical hardwood species for development work. There has been limited sustained work relevant to major temperate hardwood genera, two main reasons being their longer improvement cycles and lower financial returns.

Geographically, activity and publication have been similarly rather concentrated – e.g. the Pacific Northwest (for Sitka spruce, Douglas fir, western hemlock), south-eastern Unites States (for slash and loblolly pines), Scandinavia (for Scots pine, Norway spruce, birch, aspen), Continental Europe (Norway spruce, larch, hardwood species), Australia (*Eucalyptus* and pine species), New Zealand/ South Africa (pine species), tropical countries (pine species, *Eucalyptus*, tropical hardwoods). British/ Irish tree breeding and seed orchard work has concentrated on Sitka spruce with some work on Scots pine, larch, Douglas fir and much less extensively for oak, beech and cherry.
The majority of work reported in the literature has formed part of large state-funded forestry research and development programmes in North America and Scandinavia, carried

out either by government research establishments or by state-funded academic bodies. Some tropical work has also been undertaken as part of overseas development programmes by the US, Germany, Denmark and Scandinavian countries. Since the 1980's, some reported work has been conducted by larger public-private research collaborations/ cooperatives in North America, mainly for Douglas fir and southern pine species – this especially since more powerful genetic technologies have held out the prospect of more rapid realisation of gains from breeding. With the exception of Finnish and Swedish birch polyhouse orchards, almost all orchards were open-grown.

5. Development and types of tree seed orchard

Tree seed orchards have been developed over the past 80-100 years as an alterative to reliance on *in situ* natural regeneration or the use of transplants raised directly from field seed collections, which were the primary forestry methods prior to World War I. Natural forest regeneration was obviously constrained by the available seed sources within any given management area, which might not contain the desired tree species. Reliance on repeated seed collections from the field, although supporting a well-established international seed trade during the century following 1840, suffered from a number of inherent difficulties including inadequate availability of seed sources; logistical challenges due to geographical, political and economic factors; reliance on third-party agents and a tendency to collect from small numbers of fecund individuals. These made the costs of resulting nursery plants rather high and their quality variable. Seed orchards therefore emerged as a tool of convenience, later also allowing for the capture of inherent gain (mainly in vigour) from phenotypic selection of 'elite trees'.

During the first half of the period of use of tree seed orchards, the open-grown field type was exclusively used. Operational orchards consisted of collections of material onto accessible sites within the growing range of the species within which it was intended to form plantations or to restock clearfelled sites. Earliest areas of activity were Scandinavia and Germany, later North America, Australasia, tropics and the UK. Work was normally conducted by governmental agencies on behalf of the wider forestry sector. In the earlier phases of seed orchard operation and management, there was limited understanding of the significance of inward pollen flow from surrounding stands and any genotypic gain captured by orchard production was largely restricted to the maternal line. Even before the widespread deployment of genetic assay techniques, it began to be realised that pollination management (both internal and external) was a key component of effective tree seed orchard management. Basic techniques were developed to improve implied genetic integrity by means of physical isolation of orchards from external pollinators (isolation buffers of 200-500m and planted dilution buffers) and by locating them outside intended deployment regions, providing some degree of temporal isolation from local pollen by flower phenology.

From the 1970's onwards, a number of developments have led to increased attention to seed orchard internal design and pollination management. These included advent of genetic assay techniques for *post hoc* paternity analysis; increased gain to be defended resulting from multiple rounds of selection and controlled crossing and development of computerised statistical techniques for optimisation of internal layouts to achieve panmixis. Particularly for light-pollen boreal species such as pine, spruce and birch, it was realised that external (often distant) pollinators would always contribute a significant component of fertilisation in open-grown field orchards and that specific measures were required to enhance gain retention. In open-grown seed orchards these included increases in orchard size and deliberate 'supplemental mass pollination' to dilute or swamp the effect of external pollen sources. An alternative approach was to isolate seed orchards within glass-houses or polyhouses, which then allowed them to be operated safely within the intended regions of progeny deployment. This technique has largely been restricted to birch in Scandinavia (and to a lesser extent Canada), where production from a small number of intensively managed indoor orchards has the capacity to supply the whole regional forestry sector, justifying the higher expenditure. Use of enclosed orchards for most conifer species has been more limited.

6. Design and operation of tree seed orchards

Basic requirements for the effective operation of any type of seed orchard include:-

- Inclusion of the desirable material for the intended region of deployment, based on phenotypic field selections in the first instance, later on progeny testing and controlled crossing in advanced generation breeding work.

- Genetic diversity of included material such that progeny does not display inbreeding depression or adverse genetic drift effects. Usually it has been indicated that inclusion of 30-50 unrelated parent clones was necessary to achieve this, although it may be possible to operate with 20-30 clones where orchard design and pollination control are of a high standard. Until the advent of genetic assay techniques, unrelatedness in included material could only be inferred from geographical dispersal of the source material.

- Representation of the included material within the seed orchard collection, usually such that each accession has an equivalent chance of contribution to both the maternal and paternal lines in seed progeny. In some cases representation may be biased in favour of any known superior accessions, usually in more advanced generation breeding programmes where a first round of progeny testing has been undertaken. Initial representation needs to be maintained by replacement of any failed plants or grafts as necessary.

- Spatial arrangement of the included material to optimise the chances of desirable 'panmixis' (equivalent likelihood of each male x female combination in seed progeny). This is usually not optimised by simple row or repeat block arrangements of rametes of included clones and some form of randomised intimate or randomised block design is typically preferred. A range of computerised techniques are available for seed orchard design.

- Management of the included material such that each accession contributes equally to the seed progeny in terms of both maternal and paternal lines. This can be very difficult to achieve due to inherent differences in the fecundity of clones (permanent or annually varying) and issues affecting the physical dispersal of pollen within the orchard (especially if enclosed). Supplemental mass pollination, fan-forced circulation, simulated droughting and other artificial techniques may be required for panmixis.

- Location and design of the orchard such as to reduce chances of external pollination and associated gain losses. If not physically enclosed, orchards should be located away from massed sources of external pollination (e.g. forest stands of the species concerned) and occasional external individuals felled within an 'isolation buffer zone'. Required widths of isolation buffer zones are typically estimated to be in the range 200-500m but there is significant uncertainty that this is effective. 'Dilution buffer zones' of trees from which seed is not collected may also be used. Location of the orchard outside the source zone of the included material can also improve isolation by introducing a phenological shift in flowering date, but this can be undermined where long-distance pollen transport events occur, especially earlier in the season, as in boreal species such as pine, spruce and birch.

7. Contamination in open-pollinated field tree seed orchards

Overall significance

Contamination by pollination from external sources is recognised as a very significant challenge in the operation of any open-grown field seed orchards of wind-pollinated species. External pollination is regarded as undesirable as it dilutes or erodes the genetic gains to be expected from selection of included material on field phenotypic criteria, or based on the results from previous rounds of progeny testing. It is usually assumed that the external trees contributing to such pollination will not display the desirable genetic characters sought – in some cases this might not be the case where surrounding stands are of superior phenotype for some reason. Also, there are often concerns that, where seed orchards are operated in regions distant from the source of the accessions and intended deployment zone for progeny, external pollinators may be less well adapted to anticipated growing conditions. This can lead to the progeny from the seed orchard being variable and unstable in quality and potentially inferior to material from seed stands located within the intended deployment zone for progeny. Where the number of external pollinators is small, but their contribution to progeny is large, there may also be risks of inbreeding depression despite a diverse orchard set.

Impact on genotypic gain

The impact on genotypic gain of pollen contamination in seed orchards is traditionally evaluated on the assumption that half of the genotypic gain is matrilineal and half patrilineal. Hence if any given fraction of seed arises from external pollination, half of that fraction of expected gain is forfeit, as only the patrilineal contribution is affected. This may of course be an invalid assumption if realised genotypic gain is not equally due to the matrilineal and patrilineal lines, which can now be genetically investigated. The silvicultural and economic consequences of these losses in genotypic gain become more severe as genotypic gain being defended increases with more intensive selection, particularly in second and subsequent rounds of tree improvement. Gains attributable to any first round selection of superior phenotypes in the field may only be 5-15%, but this can rise to 25-30% for later rounds of family selection and crossing. The embodied investment is also likely to be greater for subsequent rounds.

Proportion

Numerous studies have been published which attempt to assess the proportion of fertilisation events in tree seed orchards that may arise from external pollen sources. Earlier studies had to rely on simple methods such as pollen trapping at the perimeter, whereas more recent approaches have used allozyme or DNA marker techniques. Almost all reported examples relate to orchards of productive conifers such as Scots pine, Monterey pine, southern pines, Norway spruce and Douglas fir. Very few relevant studies cover hardwood seed orchards. Young *et al* (2000) review those studies reported prior to that date, while Bilgen and Kaya (2014) and Torimaru *et al* (2009) present more recent data. Reported contamination rates vary very widely from a few percent up to 80% (see Table 1), reflecting very heterogeneous conditions in the sample population (e.g. size, age, buffering, management, location and species). For a boreal species such as birch, it seems not unreasonable to assume typical contamination rates in the range 40-50%, implying 20-25% losses of genotypic gain.

Source

Most papers discussing sources of contaminant pollen in tree seed orchards emphasise profuse sources within a short distance of the orchard boundary, suggesting that pollen deposition falls off fairly rapidly with distance on an 'inverse power law' basis. This provided the scientific underpinning for the concept of 'isolation buffers' around tree seed orchards, typically measuring from 200-500m, which were held to reduce the proportion of contaminant pollen reaching the orchard boundary to an acceptable level, which could be further reduced by planted 'dilution buffers' around the orchard. This model informed much earlier tree seed orchard design from the 1950's to 1970's, particularly in North America and Scandinavia. However very significant critiques have emerged to this paradigm over more recent years, with recognition of mass transport of buoyant pollens in the upper atmospheric layers over 10^2-10^3km scales. Birch is one species that is recognised to display this tendency very significantly, and has been widely studied due to its major role in seasonal allergenic disease in human populations (e.g. Hilaire, 2007; Hjelmroos, 1991; Jato *et al*, 2007; Linkosalo *et al*, 2010; Siljamo, 2013; Skjoth *et al*, 2009; Sofiev *et al*, 2006; Yli-Panula *et al*, 2009). A particular concern for orchard contamination is large-scale wind-borne mass transport of pollen from distant regions (usually northward) during the earlier part of the flowering season, if female parts of the flower become receptive before local pollens. Given appropriate climatic conditions for local deposition, this could result in mass fertilisation of seed orchards by ill-adapted contaminant pollen from further south. It should be stated that such an effect is more likely within a continental landmass such as North America or eastern Scandinavia with birch-bearing territories to the south. Conditions in the British Isles with a prevailing southwesterly will generally provide "clean air" to orchards, especially in the west. However specific seasonal weather conditions with a Scandinavian 'blocking high' and prevailing easterlies could result in invalidation of the seed production from open-pollinated birch orchards in Britain. Conventional 'side protection' by isolation and dilution buffers might be ineffectual.

8. Pollination management in open-grown tree seed orchards

If the decision is taken to operate open-grown field seed orchards, certain measures can be taken to mitigate, not eliminate, the identified contamination risks. These are: -

- Regional isolation – location of the seed orchard outside the region of occurrence of the tree species involved, or, where this is impractical, at a sufficient latitudinal separation that phenological differences can reduce the likelihood of local pollen fertilising orchard trees due to asynchronous fecundity. This approach may have limited effects in situations of long-distance mass transport of pollen (see above) and may also increase risks that any local contamination will result in mal-adaptation for deployment.

- Local isolation – creation of an 'isolation buffer zone' of several hundreds of metres around the orchard either by careful prior selection of its location or by removal of potential contaminant sources from its vicinity, especially on the windward side. Under many conditions this approach may well result in significant levels of gain protection, but again there may be little benefit in situations of long-distance mass transport of pollen. A variety of studies have suggested optimum buffer widths in the range 200-1000m.

- Internal isolation – creation of a dilution buffer zone within the orchard but from which seed is not collected, operation on a 'blotting paper' principle. This assumes that contaminant pollen is primarily arriving horizontal to the ground, or approximately so, from local sources. Again, effectiveness against long-distance mass transport of pollen may be limited, especially if there is a vertical deposition component due to rainfall or downdraught.

- Orchard size/age –a larger, older seed orchard should have a lower percentage of contaminant pollination for a given level of external pollen incidence due both to the existence of a 'protected interior' and to the mass balance effect, such that opportunities for internal pollination predominate.

- Internal orchard design – some features of orchard layout may assist in promoting internal pollination percentage through pollen supply/ retention.

- Assisted or supplemental mass pollination – techniques designed to increase the production and delivery of desired pollination from within the orchard through promotion of earlier/ more copious male flowering, pollen collection and manual/ fan-forced pollen delivery to female flowers. Some approaches have used mass pollen collected from a known, phenotypically desirable source outwith the seed orchard, such as a selected seed stand, to swamp the effects of any suspected external pollen contamination. Such an approach may be valuable where contaminant pollen is arriving early in the season while female flowers are receptive and local pollen unavailable. Such approaches can only be expected to protect part of the 'at risk gain'.

- Physical isolation – techniques stopping short of full enclosure of the seed orchard within a glass-house or polyhouse, such as cuvette protection of flowering heads, tent protection during critical pollination periods etc.

9. Pollination management in enclosed/ polyhouse tree seed orchards

Operation of tree seed orchards enclosed within glass-houses or polyhouses is not without its own challenges in terms of pollen management. These arise in the main from the artificial nature of the microenvironment within the polyhouse that may restrict rates of pollen production and dispersal and lead to uneven clonal fecundity. If not managed well, polyhouse seed orchards can produce very little seed of uncertain quality. Considerable expertise has been developed by the Finnish birch breeding programme since the early 1970's as presented by Annala (2003), Hagqvist (1992), Hagqvist and Hahl (1998), Koski (1982), Lepisto (1973), Poykko (2008), Tyssrjarvi and Pirttila (1984) and Vihera-Aarnio and Rynnanen (1994, 1995). Key points are:-

- Grafts must be thoroughly prepared and, in particular, use scion material which is fully dormant at the time of collection from field or stock plants. Delay of scion material into the start of the growing season on climatic or logistical grounds can diminish grafting success and later performance. Scions should be transported in cool boxes and protected from desiccation.

- Layout – Finnish recommendations are for the use of larger polyhouses with stock plants separated by 3 x 4m to allow sufficient space and light. This differs from the approach adopted to date in the GB research orchards which have been much smaller, with plants much less widely separated.

- Irrigation – suitable arrangements are required for automated irrigation from below to avoid mould impacts from leaf and flower wetting. Irrigation on a "seldom and thorough" basis is advised to retain a substrate moisture content in the target range 40-50% during the growing season.

- Atomisation **–** an automated atomisation system is required which will be used to regulate air temperature during hot weather and to maintain air humidity. Fine atomisation is preferable. Atomisation is most important in the younger phases of the orchard before leaf area builds up significantly.

- Ventilation **–** a suitable arrangement for ventilation is required to control the temperature range within the polyhouse orchard to 23-25^{O}C and to ensure that photosynthesis does not draw down CO_2 below external levels. Even on cooler days, a period of ventilation is required for the latter purpose. Permanent ventilation may be allowed from mid summer onward.

- CO_2-fertilisation – by means of compressed CO_2 release or propane combustion during the early summer to promote seed production. The aim is to raise the CO_2 concentration from the atmospheric background at ~330ppm to as much as 1000ppm. Ventilation is stopped during early morning CO_2 enrichment periods but resumed once levels fall to normal.

- Fertilisation of the growing medium two to three times during the growing season, preferably based on foliar nutrient analyses.

- Assisted pollination – by means of combined forced air movement (fans) and manual agitation/ blowing of the trees at the optimum time for pollen production. Ventilation must be carefully regulated during such activity.

- Seed collection – must be optimally timed based on regular sampling and germination testing to establish the optimum (usually July into August).

10. Comparative advantages and disadvantages of tree seed orchard types

Based on the literature review results, these two main types of seed orchard have the following advantages and disadvantages in the context of tree breeding programmes:

Outdoor open-grown field orchards

Advantages

- Familiar, relatively simple approach within the forestry context.
- Lower establishment and management costs.
- Lower specialist skill requirements.
- Higher volume of seed production (under many circumstances).
- Better pollen distribution/ more even clonal contribution (possible).

Disadvantages

- Much higher risk of external pollen contamination/ uncertainty as to paternity.
- Forfeit of a proportion of the genetic gain achieved by phenotypic selections.
- Less controlled environment with greater risks from climatic/ pest damage.

Indoor polyhouse orchards

Advantages

- Generally achieve near-complete exclusion of pollen contamination.
- Protects full genetic gain achieved from phenotypic selection investment.
- Provides a controlled environment within which to regulate seed production.

Disadvantages

- Considerably higher establishment and management costs.
- Requires higher-level skills and more specialist equipment.
- Withdraws seed production from the field forestry mainstream.
- May produce more limited amounts of seed of lower viability.
- May raise issues with uneven clonal contribution to seed production.

The balance between these factors has to be assessed in the context of individual tree breeding projects, research institutes and commercial enterprises. In the case of birch seed production, which can be seen as a rather specialist activity, the balance would appear to remain fairly firmly on the side of indoor polyhouse seed production at a restricted number of locations. This is reflected in practices adopted in Finland and Sweden since the early 1970's For those tree species where seed production from orchards is typically more limited in volume (e.g. oak), outdoor open-grown orchards may continue to be preferred. Many coniferous seed orchards continue to be open-grown. Generally as any tree breeding programme progresses to successive rounds of selection and controlled crossing, the level of implied genotypic gain will increase and the scientific value of measures to protect that gain during the seed production process likewise. Where seed orchards form part of commercial enterprises, it may be more difficult to support the additional expenditure associated with using polyhouses.

11. Implications for the FTT silver birch breeding programme

In the specific context of the ongoing Future Trees Trust silver birch breeding programme, the results of the present literature review appear to imply the following:-

- Good overall support for the original FR/BRC decision to adopt the Finnish polyhouse indoor orchard system for research and development purposes. This is the method of seed production that stands the best chance of capturing the maximum possible fraction of any realised genotypic gain.

- That the advantages of the indoor polyhouse orchard approach for birch seed production are likely to be accentuated in any second and subsequent rounds of advanced breeding, using the results of progeny testing to select superior clones and to implement controlled crosses for enhanced gain.

- That operation of open-grown seed orchards is sub-optimal in this instance due to the specific pollen dispersal characteristics of the *Betula* species, in particular their propensity to long-distance mass transportation of pollen. While isolation buffer zones have been proposed as a means of protecting such orchards in the past, their validity for birch appears highly uncertain.

- That operation of open-grown seed orchards should only be regarded as an expedient method of 'partial capture' of genotypic gain established by ongoing progeny testing to have been realised by phenotypic selection. The extent of the retained gain cannot currently be quantified with any certainty but is likely to lie within the range 60-80% of 'polyhouse gain'.

- That there would be distinct benefits in detailed scientific investigation of the pollen contributions within any open-grown birch seed orchards that are established, using suitable allozyme, micro-satellite and DNA marker techniques. Such work could usefully form part of an MSc or PhD research study. A key objective would be to quantify the 'retained gain'.

- That careful consideration needs to be given to the geographical location of any open-grown field birch orchards so as to minimise the likelihood of confounding pollen contamination from both local and distant (mass transported) sources. Sites on the western side of the British Isles may have lower associated risks of mass transported pollen deposition from Scandinavian/ Continental sources. By contrast sites in the north and east of the British Isles may experience local pollen supply from natural birch populations of better average phenotypic form. Northward pollen transport within the British Isles is likely to confer greater adaptation to future climates but possibly reduced phenotypic stem quality in some situations.

- Recognition that in a situation where seed production is to be conducted as part of a commercial enterprise as opposed to a state-funded development programme on the Finnish model, methods adopted may be sub-optimal. This must in practice be a decision for enterprises and also for regulators.

- That there should be transparent distinction of basic material produced from 'qualified' or 'tested' field orchards from that produced from indoor polyhouse orchards whenever it is presented to operational users of stock.

- That any future establishment and operation of polyhouse seed orchards for birch in Britain should be more fully informed by the experience of the Finnish programme, perhaps by inviting relevant Finnish advisers to UK.

- In particular, that main procedures for atomisation, ventilation, irrigation, fertilisation, CO_2 enrichment and pollen forced circulation within birch polyhouse seed orchards might need to be markedly more sophisticated.

- That any future establishment and operation of polyhouse seed orchards for birch in Britain would require considerably greater financial and staff resources than previously deployed and should form part of long-term continuous programmes along the same lines as the Finnish programme. The role for subvention funding from state or charitable sources is clear.

- That restrictions currently in place on Forest Research acting as a 'scientific seed producer' for the UK forestry sector under polyhouse conditions might need to be reviewed if it were decided that effective operation of indoor polyhouse orchards is an intrinsically non-commercial activity, as in Finland. Alternatively private producers could be subvented.

- That there would be distinct benefits in detailed scientific investigation of the pollen contributions within any polyhouse birch seed orchards that are res-established, using suitable allozyme, micro-satellite and DNA techniques. Such work could usefully form part of an MSc or PhD research study. A key objective would be to quantify relative clonal contributions/ fecundity.

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