Key points

- *The European common ash (Fraxinus excelsior) is one of our most important native tree species.*
- *The species is now under threat from Ash Dieback Disease, caused by the invasive fungal pathogen Hymenoscyphus fraxineus.*
- *The disease is now fully established and has been identified in all counties in Ireland.*
- *A small proportion of ash trees show natural tolerance to the disease and this tolerance is heritable.*
- *An approach to generating sources of tolerant ash seeds and plants is proposed and an indicative timeline for producing and mobilising tolerant ash material for field planting outlined.*

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Breeding for tolerance to Ash Dieback Disease

COFORD Council Forest Genetic Resources Working Group

Introduction

The European common Ash (*Fraxinus excelsior*) is one of our most important native tree species, it comprises approximately 3.8% of the forest estate or 25,280 ha, 60% of which has been planted since 1990 (DAFM, 2017). It is the second most important component, after hawthorn, in large proportions of the hedgerow network. On the island of Ireland, it is estimated that there are over half a million kilometres of hedgerows (400,000+ km in the Republic of Ireland and 113,000+ in Northern Ireland) (McCraken et al. 2017). Ash is the second most frequent tree species in Irish native woodlands, being present within 90.2% of sites and comprising 18.5% of trees (Perrin et al. 2008). Woodlands dominated by ash have a rich shrub and herb flora as a result of their relatively open canopy and are one of the most species-rich of all Irish woodland types (Short, 2018). Ash is a key component of "Alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior*", a priority habitat which is protected under the EU Habitats Directive (92/43/EEC). Ash is commonly referred to in Ireland's cultural heritage and has often been associated with sacred wooded sites. The timber is also traditionally used for the production of hurleys, while the low moisture content of the wood make it a preferred firewood species.

The species is now under threat from Ash Dieback (ADB) Disease, caused by the invasive fungal pathogen *Hymenoscyphus fraxineus*. The disease is observed in most European countries, including Ireland. It results in massive tree mortality and threatens the existence of the species all over the continent. It originated in Far East Asia, spread to continental Europe in the mid-1990s, and detected in Ireland in 2012 on imported trees. The disease is now fully established and has been identified in all counties in Ireland. Figures 1 and 2 illustrate the distribution of the disease on the island on Ireland (DAFM, DAERA).

Hymenoscyphus fraxineus, also known as *Chalara*, has a complex life cycle. Infection first makes its way into a tree when the spores of the fungus are carried in the air and land on healthy leaves over the summer months. The fungus then grows into the leaves and down into the leaf petiole or rachis, and progressively into twigs, branches, and the stem, causing dieback. The infected leaves gradually wilt and blacken, but may remain on the tree for some time. These infected leaves then fall to the ground over the autumn and early winter months and the fungus produces

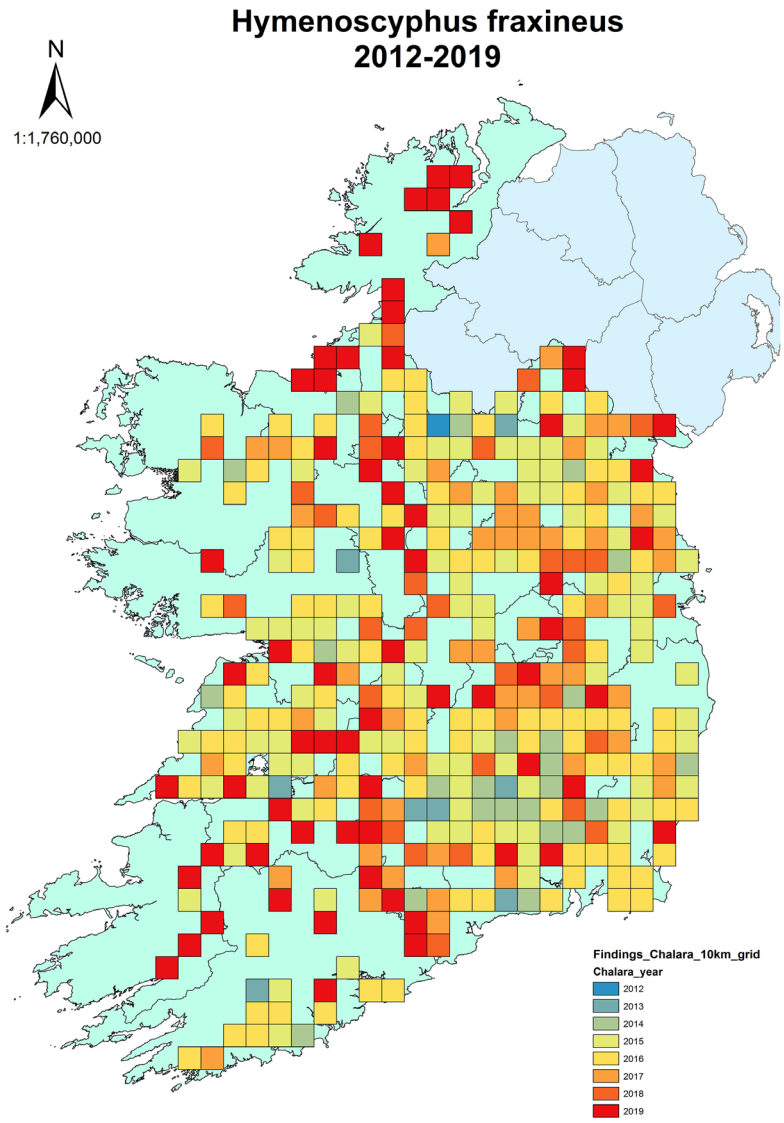

Figure 1: Recorded Occurrence of ash dieback disease 2012-2019 by year of first finding (DAFM)

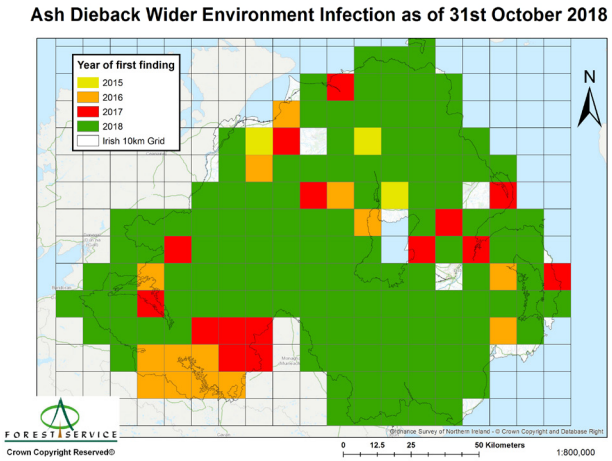

Figure 2: Wider infection of recorded ash dieback disease in Northern Ireland (DAERA)

characteristic blackened rachises. These blackened rachises harbour the disease over winter. In the sexual reproductive stage of the fungus, which takes place over the course of the summer and autumn months (June to October), very small white mushroom-like fruiting bodies develop on the blackened rachises and decaying leaf litter from the previous autumn and winter. When mature, these tiny fruiting bodies release large quantities of microscopic spores into the air, some of which will land on the leaves of ash trees to begin the cycle again, increasing the disease pressure. Where the disease is already present in a locality further local spread is likely to be caused by spores borne on the wind, each year travelling many kilometres from the original source.

Impact of Ash Dieback in Ireland

The impact of the disease is very much in evidence and has had a substantial negative impact on young privately-owned plantation forests. In March 2013 the Department of Agriculture, Food and Marine (DAFM) introduced a Reconstitution Scheme to restore forests planted under the afforestation scheme which had suffered from or which were associated with plants affected by disease. By the end of 2018, some €5.8 million has been paid out under the Scheme and over 1000 hectares of infected and associated ash plantations

have been cleared and replanted with alternative species. In 2018 DAFM commenced a review of its policy in relation to ADB in recognition of the latest scientific advice, namely that eradication of ADB was no longer feasible and that the DAFM policy response should reflect this position. The review process included a stakeholder and public consultation period and detailed field consideration of damage level evaluation together with a broader range of silvicultural and management options available to forest owners. The review was undertaken with the assistance of Teagasc and international experts. Current support schemes were reviewed to ensure the continued relevance of DAFM's response and value for money for both the taxpayer and the individual owners, and to ensure that the forest owner is provided with a broader range of silvicultural and management options. As part of the review process the practical management advice for forest owners and their forestry advisors is being developed in order to better inform them as to management options for ash plantations with the disease. It will also outline an enhanced suite of grant aid categories, and other options, depending on the age of the ash plantation and degree of infection, the purpose of which is to encourage a management-based focus to dealing with the disease, rather than simply clearing and replacing all infected ash forests. At the time of writing (December 2019) the proposed new support measures were out for consultation with industry stakeholders.

The length of time that it will take for the full impact of the disease to manifest itself in our hedgerows and mature forest is also starting to become clear. The disease has caused widespread damage in continental Europe, where experiences indicates that it can kill young ash trees quite quickly, while older trees can resist for some time. However, prolonged exposure, or another pest or pathogen attacking the tree in its weakened state, will eventually cause it to succumb. An analysis of surveys from across Europe was carried out by British researchers (Coker et .al, 2019). From this they estimated that from year 5 to year 15 after arrival of the pathogen, tree mortality will go up to 60%, and likely stay around those values.

Figure 3: stem infection of an ash tree *(image courtesy of Dr. Miguel Nemesio-Gorriz*)

The long-term prognosis is therefore one of significant tree mortality. There is nevertheless a degree of hope for the future. Work has continued on the development of appropriate silvicultural strategies to minimise its impact (Skovsgaard et al., 2017; Short, 2018), and also on potential replacement species (Mitchell et al., 2016; Hill et al., 2019). However, it is tree improvement: selection, breeding and deployment of ash trees tolerant to the disease which offers the opportunity to restore the species to our forests and hedgerows.

Combating ADB through tree breeding

In an attempt to reduce the impact of ADB, researchers from 35 countries, including Ireland, joined forces in an EU-funded COST Action FRAXBACK. The Action produced several documents on the consequences of ADB and guidelines for sustainable management of ash (Enderle et. al. 2017). Efforts have continued amongst the international research community, on the origin and biology of the fungus, and in understanding how the disease functions, how the tree can defend itself from it, and how tolerance to the disease is passed on to the seed offspring from ash trees and onto trees which have been propagated vegetatively.

Tolerance vs. resistance

Tolerance and resistance are terms that are often used interchangeably, when discussing ADB disease, therefore for clarity some definitions may be useful.

Tolerance: The tree can be infected to a very small extent and show very mild disease symptoms without stem infections and without any significant loss of leaf canopy or tree vigour: such trees are regarded as disease tolerant, under conditions of heavy disease pressure. Approximately 1 - 3 % of a given population of the common European ash (*F. excelsior*) will be naturally tolerant to the disease and this tolerance is heritable and is stable in trees that are propagated vegetatively (Kjaer et al. 2017; Enderle et al. 2017; Stener 2013, 2018).

Resistance: The tree is immune to the fungus meaning that it does not get infected under any circumstances. Resistance has not been found in any population of common ash, *F. excelsior*.

Tolerant trees in affected stands will produce tolerant progeny that can disperse naturally in the forest environments. Therefore, by natural evolution, equilibrium with the disease may occur. However, this would likely be the case over many decades or even centuries. Scientists have focused on selection and breeding to, in effect, speed up this process. By carrying out a selection programme, identifying individual ash trees that can withstand the disease, and implementing breeding and deployment strategies, tolerant material, may be deployed to our forests and hedgerows over a much shorter time frame.

Numerous studies have indicated that breeding for tolerance is feasible (Piliura et al., 2011; Mckinney et al. 2011; Kjaer et al. 2012, Kjaer et al. 2017, Plumb et al. 2019). A number of European countries have initiated breeding programmes, including Austria, Denmark, France, Poland, Sweden, Switzerland and the UK based on the phenotypic selection of tolerant healthy trees in environments with a high disease pressure. In Ireland we have been limited by a relatively low disease pressure as a high disease pressure is needed in order to identify tolerant trees (although this is changing). In 2013 DAFM organised for 14,000 plants from two distinct seed lots from Ireland, to be included in the UK mass screening trials. This programme involved 48 hectares of trial plantings over fourteen sites in the east of England and the mass screening of some 155,000 ash trees with fifteen different provenances. In addition, Teagasc has selected circa 1,000 genotypes on the island of Ireland and is screening this material under high disease pressure in Lithuania and resulting tolerant genotypes are expected to be brought back to Ireland in the next years. Teagasc has further focused on collaborating with six different European research agencies and has acquired and propagated approximately 200 ash genotypes which have been selected as putatively tolerant to ADB disease, having been observed as healthy over several years in infected locations with high tree mortality.

Additional challenges to ash

While outside the scope of this document it is important to note that *Agrilus planipennis*, also known as Emerald Ash Borer (EAB), is an invasive insect from Far East Asia that infests ash trees causing them to collapse within 2-5 years. EAB was introduced in North America in 2002 with devastating effects. It has brought five different American ash species to a decimation point where they have been reclassified from least concern to critically endangered. EAB has also been identified in western Russia and Ukraine and is progressing westwards. EAB is absent from the EU but poses a very serious threat and is listed as a priority pest under the EU Plant Health Regulation (2016/2031). Studies have found that even though the common European ash is not as susceptible as some American ash species, it is moderately susceptible to the insect with approximately 50% of the ash trees showing no symptoms in heavily infested areas (Straw et. al. 2013.). Several ash species are tolerant to ADB and EAB in their native range. One of these species, *Fraxinus mandshurica*, is very closely related to *F. excelsior*. Even though there are no studies on the correlation between resistance to ADB and EAB, it is likely that resistance to EAB may be found in the ash gene bank if genetic diversity is kept as an objective of an ash breeding programme.

Proposed strategy to restore the planting of ash trees in Ireland

There exists now an opportunity to implement a strategy that links together initiatives that are already underway, with additional measures recommended in this document, as well as the various actors in the sector, to establish a selection and deployment programme for ADB disease tolerance. It is recommended that such a strategy comprises two key elements:

1. Establish a population of tolerant material, suitably adapted to Irish growing conditions; and,

2. Ensure that tolerant planting material is available in sufficient quantities in the medium and long term.

Element 1: Establishing a population of tolerant material to ADB disease for Ireland

Efforts to date have focused on screening material abroad. This was necessary as disease pressure was too low to carry out an effective screening programme at home. Irish ash material is being screened while growing under heavy disease pressure in different points of Europe including the 1,000 ash genotypes in Lithuania and the 14,000 plants in the UK. Additionally, Irish ash is growing in different RAP trials across Europe, which were established around 15 years ago and are now ideal sources of tolerant ash genotypes. An effort should be put into monitoring this material and repatriate genotypes that show consistent tolerance to ash dieback disease.

> ***Recommendation 1:*** *Continue monitoring of Irish material included in screening programmes abroad and repatriate material as appropriate*

Disease pressure has built since the disease was first detected in Ireland in 2012 (Figure 1, Figure 2). This offers the opportunity for the survey of indigenous stands for trees tolerant to the disease, with the aim of retaining local genetic variation. Other sources of tolerant material may include thinned stands which have been heavily infected in which some individual trees produce healthy stump sprouts among the majority which are heavily diseased. The long-term effects of dieback may be to diminish the total genetic diversity in Irish populations of ash. To safeguard the genetic diversity in populations and compliment future breeding work, it would be desirable to collect and store seeds which are currently available from healthy seed producing trees.

Recommendation 2: *Undertake assessments of trees within indigenous stands to identify putatively tolerant trees of Irish origin for seed and scion wood collection*

Screening programmes have been initiated in a number of European countries. It would be desirable to work together, to share knowledge and material, and with it improve cost effectiveness, increase genetic diversity of the tolerant ash collections and speed up the availability of tolerant material.

Recommendation 3: *Continue collaboration between European programmes with a view to sharing scion and reproductive material from available European sources*

Movement of forest reproductive material (FRM) brings with it concerns over the adaptability of imported FRM to local conditions. Fortunately, prior to the outbreak of the disease, European provenance trials (Realising Ash Potential (RAP)) were set up to compare the performance of up to 47 European provenances under Irish conditions (Douglas et al. 2013). These trials have the potential to yield knowledge on the adaptability of European provenances to Irish conditions and may provide useful material for breeding (Figure 4).

Recommendation 4: *Assess ash provenance trials and determine acceptable zones of provenance for use in Ireland*

Having acquired and propagated tolerant plant material, it is essential to conserve the collection of tolerant ash trees as living gene banks (conservation collections). These conservation collections will be a significant and valuable genetic repository as well as a resource which will enable the scaling up of the production of tolerant plant material for deployment in the longer run. To safeguard the collections for the long term, at least three should be established in diverse locations.

Recommendation 5: *Establish gene bank conservation collections consisting of trees selected for tolerance to ash dieback*

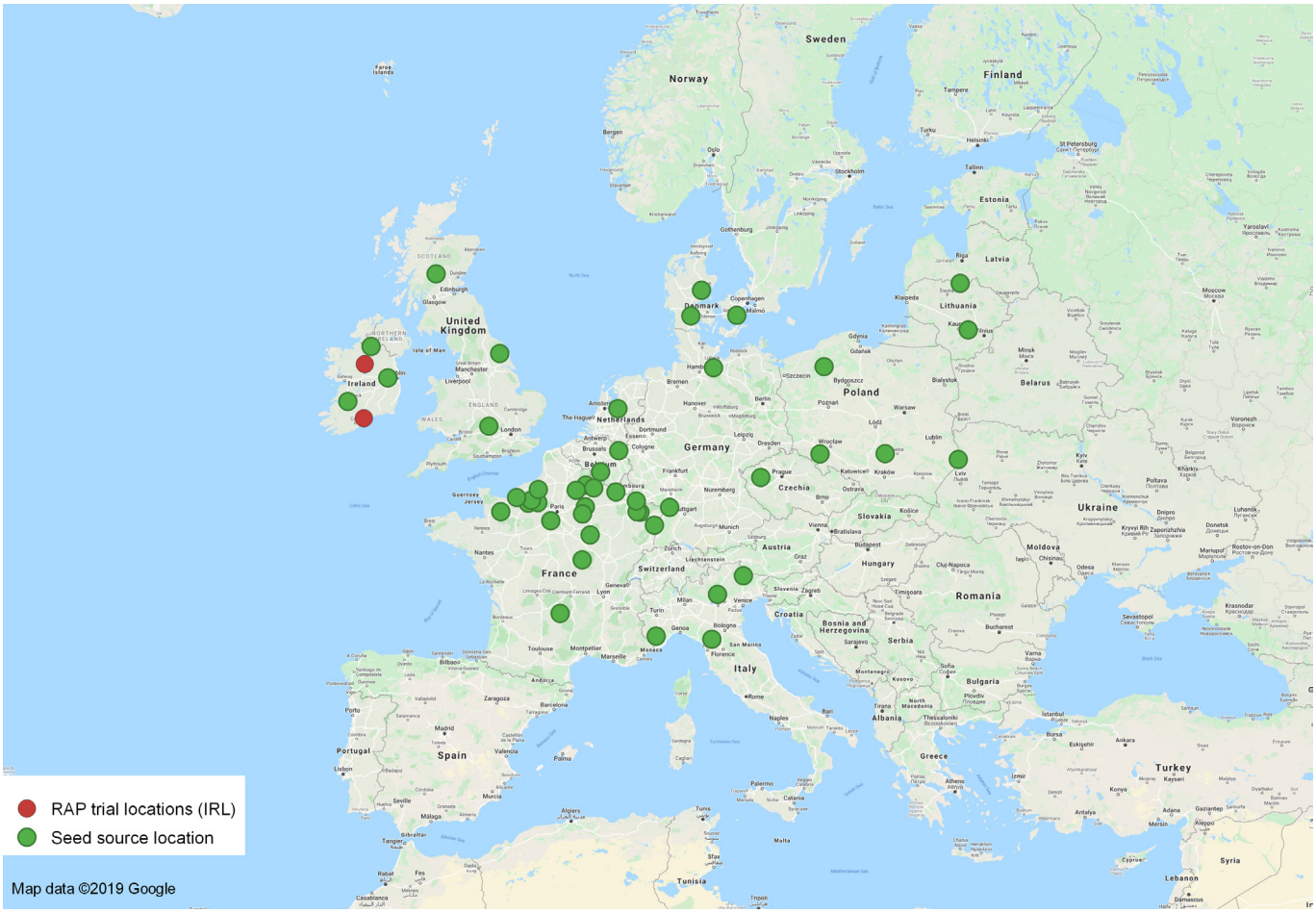

Figure 4: location of European provenances contained in RAP trials in Ireland. Red indicates the trial locations, green the provenance location.

Element 2: Providing tolerant planting material in sufficient quantities

Key to any tree breeding programme is to ensure that enough planting material is made available for deployment to justify the initial investment in selection and breeding.

Planting material can be generated through vegetative propagation and through seed production.

Vegetative propagation

Vegetative propagation is the fastest route for producing dieback tolerant ash trees. It offers the advantage that the propagated trees will be genetically identical to the original trees selected with regard to tolerance to all of the forms of dieback attack including stem and root collar infections.

A Swedish study over a period of 10 years has proven that field resistance to dieback disease has remained stable in trees which have been selected and propagated vegetatively (Stener 2013, 2018). Large scale vegetative propagation of tolerant ash trees involves significant nursery resources, initially to propagate trees by grafting and also for the production of cuttings which must have a high capacity for rooting. Cuttings derived from saplings have a juvenile physiology and a high capacity for rooting unlike cuttings derived from grafted trees. Sources of tolerant saplings would be obtainable from controlled crossings of tolerant parent trees. Grafted trees can also be a source of cuttings however, they must be firstly cultivated into a state of physiological juvenility. This state ensures that cuttings will produce roots at an efficient rate of over 80%. Restoring juvenility to tolerant grafted trees involves the technology of micropropagation and / or using a process of intensive pruning as developed and published by Teagasc (Douglas, et .al. 2017).

The system of vegetative propagation is flexible in the way that production of plants can be scaled up or down at the nursery level depending on plant demand.

> ***Recommendation 6:*** *Establishment of a vegetative propagation systems for deployment of tolerant material on pilot scales with a potential for scaling up to large scale deployment.*

Seed production

The second route to generating tolerant planting stocks of ash is the production of seeds which have genetic factors conferring tolerance to ADB. This is accomplished by facilitating the pollination of tolerant mother trees with pollen from tolerant father trees. The highest levels of tolerance can be obtained by the controlled pollination of tolerant mother trees with pollen from tolerant father trees in protected structures such as tunnels or glasshouses in which extraneous pollen can be excluded / minimised. In field conditions, it involves the establishment of dedicated seed producing orchards. Trees which will constitute the seed producing orchards will be propagated by grafting shoots which will be collected from the gene bank trees.

A period of 12 to 20 years will be required to pass before the trees in the seed orchards reach flowering stage. Natural cross pollination will result in the production of seed progeny that will have tolerant father and mother trees as the parents. This natural crossing of the tolerant trees is uncontrolled in the field and some level of contamination by pollen from non-tolerant local trees can be expected. However, despite such pollen contamination, it has been shown that progeny from tolerant trees have an increased level of tolerance. In addition, they have been shown to be sufficiently fit to become established as healthy trees in forests under conditions of natural regeneration (Semizer-Cuming, et al. 2019). One caveat regarding outdoor seed orchards pertains to the fact that the plants which constitute the orchards will consist of composite trees, i.e. a tolerant shoot grafted onto a rootstock plant. The level of rootstock tolerance will be unknown in advance but likely to be low as natural tolerance is only found in 1 – 3% of the trees. If the disease pressure is extremely high within the seed orchard some trees may be susceptible to infection at the root / stem junction and may succumb. This potential threat can be mitigated by establishing seed orchards on multiple sites since disease pressure varies from site to site. Furthermore, the wide spacing of trees in seed orchards will mitigate the build-up of disease pressure, furthermore as rooted cuttings are produced, grafted plants will be replaced. Efficiency in seed production is also affected by site conditions during pollination and during the period of seed development. Establishing multiple seed orchards in diverse geographic locations will improve the overall prospects for obtaining consistent quantities of seeds on an annual basis.

> ***Recommendation 7:*** *Establishment of seed producing orchards for deployment of tolerant material.*

Timeline

An outline of the timescale for producing and mobilising tolerant ash material for field planting is given below.

Short term 1-3 year

- Acquisition of shoots from tolerant trees from abroad, identify and monitor putatively tolerant trees in Ireland
- Establishment of tolerant trees in gene banks outdoors, some of which should be in areas with a high disease pressure
- Bulking up of all tolerant material by grafting for field screening tests in areas with high disease pressure
- Designation of secure sites for hosting conservation collections and for confirmation screenings of all material selected as having a high tolerance to dieback disease

Medium term 2-6 years

- Micropropagation of tolerant individual trees for rejuvenation purposes

- Establishment of 'hedges' of tolerant trees using grafted plants and micropropagated plants to facilitate mass vegetative propagation on pilot / commercial scales

- Establishment of seed producing orchards using tolerant parent trees (indoors) with controlled crossings to produce small quantities of seeds which can be bulked up vegetatively

- Evaluation of the level of disease resistance in all material propagated by seeds

Long term 6-20 years

- Mass propagation of multiple genotypes of tolerant trees vegetatively using tolerant trees and saplings from controlled crossings as the propagation sources

- Establishment of seed producing orchards using tolerant parent trees (outdoors)

Conclusion

Tolerance to ADB disease is found in natural populations and this tolerance is heritable. Therefore, breeding for tolerance is feasible. This has been supported by numerous studies (McKinney et al. 2011; Kjaer et al. 2012, Kjaer et al. 2017, Pliura et al., 2017, Plumb et al. 2019). Tolerance to ADB is also stable in trees that are propagated vegetatively (Stener 2013, 2018).

An approach to generating sources of tolerant ash seeds and plants has been proposed and an indicative timeline outlined.

There are however significant challenges in realising such a strategy. These include providing resources for: acquiring and propagating tolerant material, its ongoing field assessment for disease tolerance over several years and the bulking up of this material by seed and vegetative means, for pilot scale field plantings and evaluation in forests.

In addition, the development of robust molecular markers and physiological tests are highly desirable to accelerate the selection of tolerant genotypes in the field and among progeny produced from breeding work, and also to provide a better understanding of the interaction of the pathogen with host ash trees. The potential for tolerance breakdown by mutations in the pathogen may be possible but has not been detected in over 20 years its presence in Europe. The genetic structure of the pathogen *Hymenoscyphus fraxineus* is stable across Europe (Gross et al 2014; Burokiene et al 2015). The introduction of new strains of the pathogen from Asia is the most likely route which would lead to a breakdown in the tolerance of those trees that are being selected for breeding and vegetative propagation (Mc Mullan et al. 2018).

Of particular relevance however is that we in Ireland have the capacity to deliver on such a strategy. Selection, breeding, progeny testing, orchard establishment, these require a long-term vision, and structures to ensure continuity. The challenges associated with long term research have been highlighted by a recent COFORD Report (COFORD, 2018). These challenges are of relevance to the FGR community and will need to be addressed in order for a strategy such as the one outlined above is to succeed.

Acknowledgements

The Forest Genetic Resources Working Group is a working group of the COFORD Council. The aim of the group is to develop a strategy for the development, conservation, and deployment of forest genetic resource material. The group is comprised of a range of experts and stakeholders from the forest sector, including: Fergus Moore (Chair, Forest Sector Development, DAFM), Brian Clifford (Forest Sector Development, DAFM), Gerry Douglas (Forest Genetic Resources Trust), Seamus Dunne (Forest Service, DAFM), Niall Farrelly (Teagasc), John Kavanagh (None-So-Hardy Forestry (LTD), Colin Kelleher (National Botanic Gardens (OPW)), Dermot O'Leary (Coillte CGA), Miguel Nemesio-Gorriz (Teagasc), Declan Little (Woodlands of Ireland), Conor O'Reilly (UCD), Jim McNamara (Laois Sawmills), Jenni Roche (NPWS), Richard Schaible (Forest Service Northern Ireland (DAERA-NI)), Luke Sweetman (Forest Service, DAFM), Brian Tobin (UCD).

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