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The ash resource and the response to ash dieback in Great Britain

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Abstract

In Great Britain, *Fraxinus excelsior* is important both environmentally and as a timber species with an estimated 126 million trees in woodlands and a further 27-60 million in non-woodland environments. The species is more common in Britain than elsewhere in much of continental Europe and forms a major component of several woodland types. It has also been at the centre of the most advanced breeding programme of any broadleaved tree in Britain, and is the only species with tested material available under Forest Reproductive Material Regulations. Inevitably therefore, the impacts of the ash dieback pathogen, *Hymenoscyphus fraxineus*, are likely to be far reaching for both forest economics and ecosystem function. Up until 2012 the ecology of ash was relatively understudied, but the confirmed arrival of *H. fraxineus* in Britain in that year stimulated funding for a study of the role of ash in woodlands. It also opened up new avenues of research to study the genomes of both pathogen and host and discover genetic markers in ash for tolerance to this novel pathogen. Here we report on the existing resource for *F. excelsior* in Britain and summarise the multiple areas of new research focussed around ash dieback, including the infection biology, population genetics, pathogen spread modelling and efforts at disease mitigation. As a first stage in breeding disease tolerant ash, the genome of a low heterozygosity *F. excelsior* individual has been sequenced and, in collaboration with Danish scientists, markers for tolerance identified in a tolerant tree (Clone 35) from Denmark. There have also been early steps in propagating and screening a wide range of *Fraxinus* species and selection of tolerant *F. excelsior* genotypes for a new breeding programme.

Introduction

Of the three *Fraxinus* species found in Europe only the common ash, *Fraxinus excelsior*, is native to Britain (Wallander 2008) where it is one of the most common and familiar broadleaved species. It is the foundation of many valued ecosystems, an important element in the British landscape, and produces valuable timber on relatively short rotations (Kerr and Evans 1993). The species has a broad distribution throughout Europe where it can occur in widely different climates of both maritime and continental character (Pliûra and Heuertz 2003). It can also be present in both the early and the mature stages of woodland succession (Peterken 1993; Pliûra and Heuertz 2003).

Fraxinus excelsior is considered an ecologically flexible species and grows naturally on many different site types throughout Great Britain except in the extreme north-west of Scotland. Wardle (1961) reports that the whole of lowland Britain falls within the range of temperature and rainfall tolerances for *F. excelsior*, with a combination of exposure and unsuitable soil probably responsible for its altitudinal limits. However, it is considered to be nutritionally demanding, growing best on deep, fertile well-drained soils where it can reach a yield class of 10 to 12 (Evans 1984). It rarely forms pure stands of any great extent, occurring more commonly as a component of mixed broadleaved woodland (Joyce 1998). Under the National Vegetation Classification (NVC) for Great Britain, ash is the dominant species of woodland types W8 (*Fraxinus excelsior – Acer campestre – Mercurialis perennis*) and W9 (*Fraxinus excelsior – Sorbus aucuparia – Mercurialis perennis*), is locally common in W7 (*Alnus glutinosa – Fraxinus excelsior – Lysimachia nemorum*) and W12 (*Fagus sylvatica – Mercurialis perennis*) and forms a component of several other woodland communities (Rodwell 1991). Drought tolerance and frost sensitivity also make *F. excelsior* a species likely to be favoured in the short term by climate change (Broadmeadow *et al.* 2005; Scherrer *et al.* 2011). The National Forest Inventory (NFI) for Great Britain surveys woodlands greater than 0.5 ha in area and trees with a diameter at breast height (dbh) greater than 4 cm (Forestry Commission 2013). In 2013, the NFI estimated there were 1.3 million hectares of broadleaves, of which 142 thousand hectares are ash corresponding to 11 % of all broadleaves and 5 % of all species (Figure 1). This is approximately 126 million trees. Furthermore, an estimated 4.2 billion seedlings and saplings were accounted for, of which about 30 % are ash. The greatest concentrations of ash are found in southern England, with a broad band running through the English midlands, but it also occurs at lower densities in Wales and eastern England, being less prevalent in the north of England and Scotland.

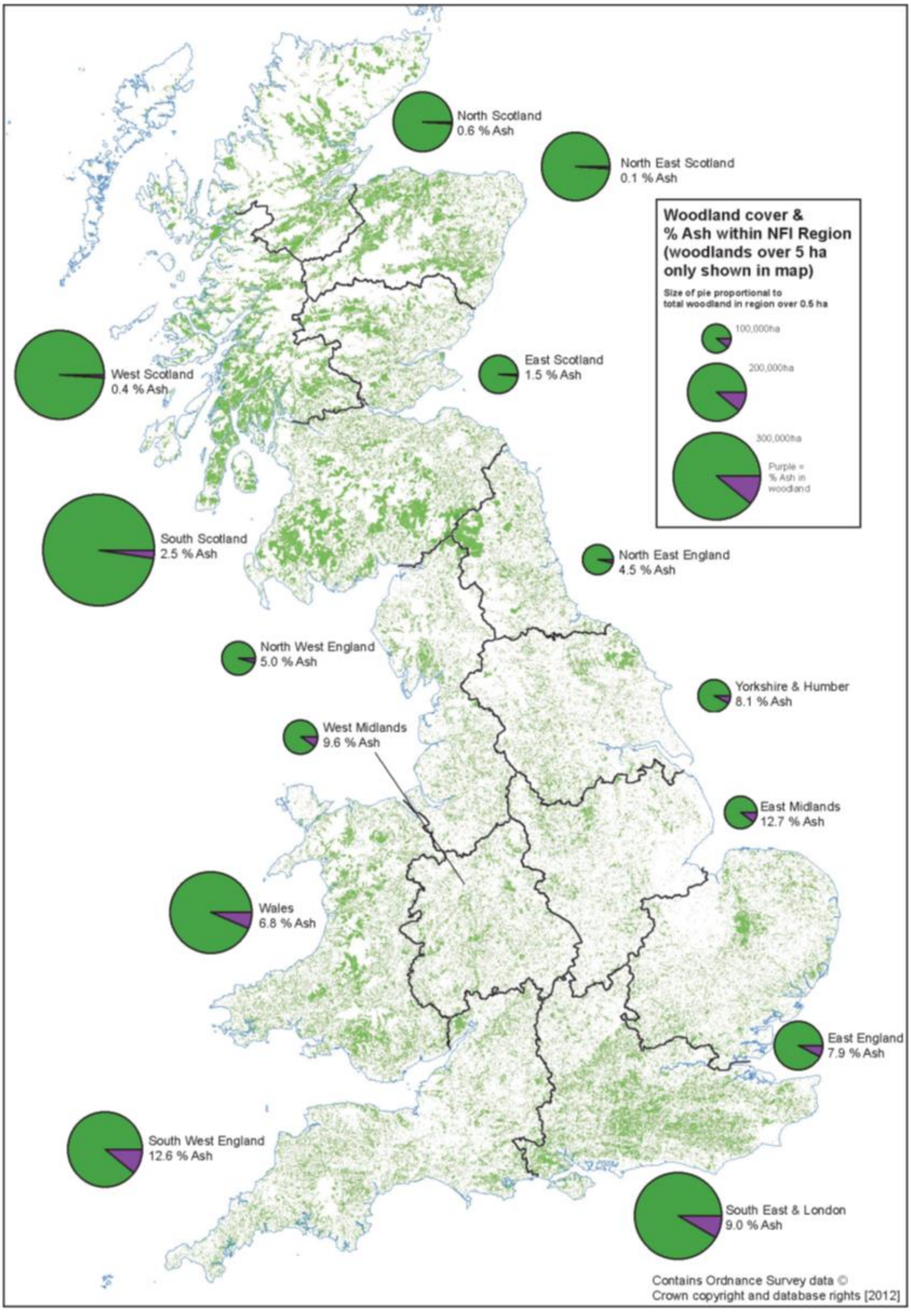

Figure 1 Total woodland cover in Great Britain with proportion of ash by National Forest Inventory region. Forestry Commission 2013. Reproduced from the National Forest Inventory Report (Forestry Commission 2013). Size of pie proportional to total woodland in region: smallest represent forest area up to 100 000 ha, medium up to 200 000 ha, large up to 300 000 ha. Proportion of ash in each of the areas shown in violet.

Ash is also common in non-woodland environments. In 2014, the Tree Council carried out a survey of ash in non-woodland situations on behalf of the Department of the Environment, Food and Rural Affairs (Defra) and estimated there were a further 27-60 million ash trees outside woodland areas with a dbh of more than 4 cm (Defra 2015). This includes 20 million as standards in ash dominated hedgerows (averaging one ash tree every 5 m); 3.6 – 4.0 million ash trees in urban situations; 17 – 34 million in woodlands of less than 0.5ha, and 4 - 4.4 million along the corridors of road and rail networks. In addition to this, the same survey estimated there were a further 400 million smaller ash trees in the form of seedlings and saplings (Defra 2015).

With ash playing such a dominant role in much of Great Britain, and with public fears of a repetition of Dutch elm disease, the UK government has been quick to resource new research into ash dieback following findings of the ash dieback pathogen *Hymenoscyphus fraxineus* in the country. Initially this focussed on providing an understanding of the likely rate of disease spread but with longer term aims of disease mitigation and re-calibration of the already established breeding programme of *F. excelsior.* The research has included an evaluation of the ecological role of ash and its associated species (Mitchell *et al.* 2014a, b, c) with ongoing studies into the genomics of the causal pathogen and host *Fraxinus*, a search for markers indicative of disease tolerance and mass screening of trees for tolerance with which to establish a new breeding programme for ash. As previous work on ash had built up a collection of material from across its natural range of around 40,000 individuals this is also a resource for the current and future research aimed at the creation of resilient ash populations.

Genetic structure of the ash resource in Great Britain

Several studies investigating patterns of genetic diversity within ash have compared variation within and among populations in Europe (Heuertz *et al.* 2004a 2004b; Fraxigen 2005; Sutherland *et al.* 2010 and the RAP project (Realising Ashes Potential, online at www.teagasc.ie/advisory/forestry/rap/) and looked at patterns of local adaptation (FRAXIGEN 2005; Clark 2013).

Heuertz *et al* (2004a) found high levels of genetic diversity with low differentiation between populations; populations from central and western Europe essentially formed a single deme. Work on the genetic variation within British populations by FRAXIGEN (2005), Sutherland *et al.* (2010) and Clark (2013) revealed that the majority of study populations originate from refugia in the Iberian Peninsula (Heuertz *et al* 2004b). Sutherland *et al* (2010) also reported rare and localized individuals identified from the Baltic region as well as three previously unreported haplotypes. Allelic richness differed between sites, decreasing from the east to the west (Sutherland *et al.* 2010) and in the north compared to the south (Heuertz *et al* 2004a). The RAP project also investigated gene diversity, gene flow patterns and hybridisation in ash (between *F. excelsior* and *F. angustifolia*) mostly using microsatellite as genetic markers. These studies indicate that ash in Britain is more genetically diverse than in continental Europe and as a consequence could potentially yield more highly tolerant individuals in response to ash dieback.

Provenance trials

Prior to the arrival of ash dieback disease there has been a focussed breeding programme of *F. excelsior* for improved timber characteristics (form and vigour) in Great Britain. Provenance trials were initially established by Forest Research between 1993 and 1996 on six sites in England and Wales to investigate adaptive variation (Cundall *et al.* 2003). These trials investigated performance of 22 provenances from mostly central and western Europe, but included some from Romania, Yugoslavia, and two from the Czech Republic. The more eastern provenances grew well, but were mal adapted to the maritime climate of Great Britain and suffered from frost damage after early budburst in spring (Cundall *et al.* 2003; Clark 2013) resulting in a high degree of forking. Further trials were established across Europe by the RAP programme in 2003 comprising 45 populations across a range from Ireland to Russia, with 39 provenances represented in the British trial.

Great Britain is divided in to four regions of provenance and 24 native seed zones for all broadleaved species, largely based on climatic and geological variation, with elevation (above and below 300m) a further consideration. In 2007, Forest Research established three trials with two populations from each of 21 of the native seed zones (ash being extremely scare or absent in the three most northerly seed zones). Most recently in 2009, a series of reciprocal transplant experiments along a 2000 km latitudinal transect from Inverness in the north of Scotland to the Pyrenees in the south of France was also established to investigate patterns of local adaptation (Clark 2013). However, early results have not shown evidence of local adaptation; instead some populations have grown well at all sites and the local population never performed best.

Arrival of the disease in Britain

First findings of ash dieback disease

In October 2012, after the first identification of *H. fraxineus* in a nursery (March 2012) and then in a recent landscape planting (May 2012), a small number of affected ash trees were found at sites in the wider natural environment in England, including established woodland in Norfolk and Suffolk. As a result, a comprehensive survey of Britain was conducted based on a grid of 10 x 10 km grid squares. Each 10 km square where ash was known to be present was visited and surveyed for ash dieback disease at three locations. Between October and November 2012, 2500 sites were visited of which 184 (about 7%) were subsequently confirmed as infected. Confirmation of *H. fraxineus* infection at affected sites utilised PCR-based diagnosis using the EPPO protocol (EPPO 2013) and did not just rely on presence of symptoms. The data revealed that the disease was present at a number of infected recently planted sites (ie where young trees had been planted in the preceding 3-5 years and which were probably infected prior to establishment) as well as wider environment sites where large trees in woodlands or hedgerows were affected (Freer-Smith and Webber 2015). Continuing surveillance between 2012-2014 was extensive; it was also both proactive, with areas around the original sites being revisited, and reactive by tracing all sites recently planted with *F. excelsior* or following up of disease reports from forestry professionals and the public. Figure 2 (a, b and c) show the disease distribution of both the recently planted and wider environment sites on completion of the systematic survey in early November 2012, at the end of December 2014 and June 2016, respectively. The figure also illustrates the rapid development of the ash dieback epidemic in Britain, such that by June 2016, 28% of the 10 km squares across Britain with ash were confirmed to have one or more infections of *H. fraxineus*.

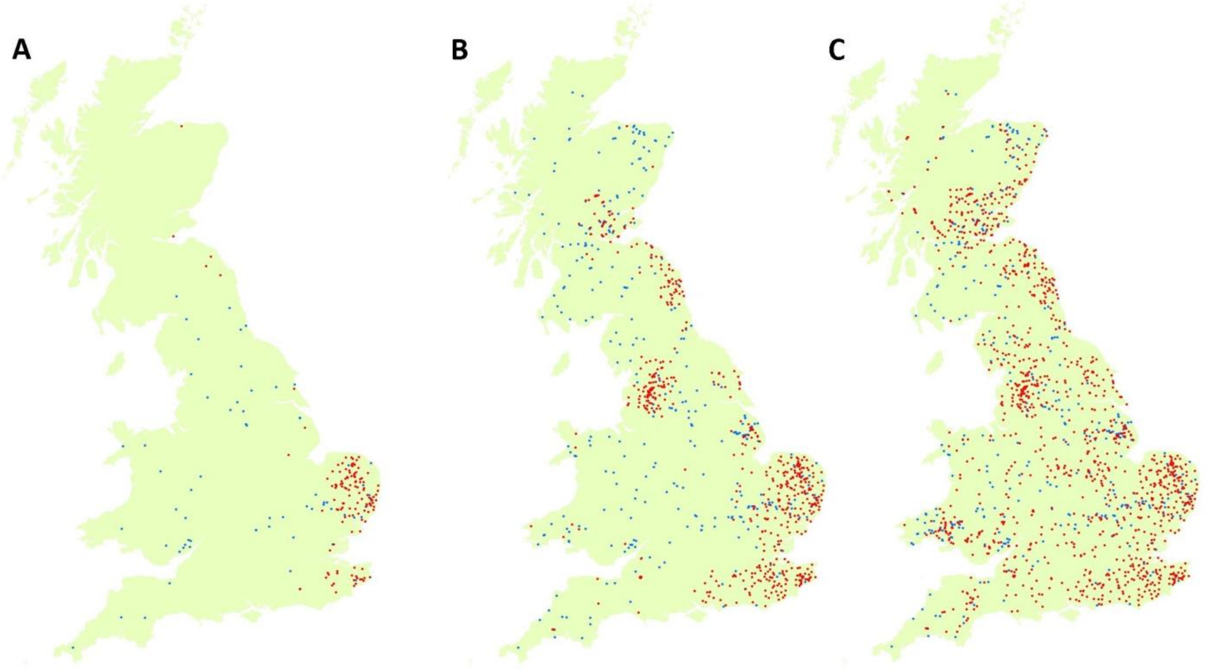

Figure 2 Number of confirmed infections of *Fraxinus excelsior* (European ash) with *Hymenoscyphus fraxineus* since November 2012. Two categories of infected sites are shown: those affecting young trees planted in the preceding 3-5 years in November 2012 (blue dots) and wider environmental sites where large trees in stands or hedgerows are infected (red dots). Map **(A)** shows findings up to November 2012; map **(B)** findings up to December 2014; map **(C)** findings up to June 2016 - *© Crown copyright and database right 2015. Ordnance Survey 100021242. © Crown Copyright 2015 – Land & Property Service No. 130036.*

Apart from formal surveillance, citizen science was harnessed to locate trees affected by ash dieback. In October 2012 soon after the first disease reports Britain, the ‘Adapt Low Carbon Group’ at the University of East Anglia launched AshTag, a smartphone app to enable the public to report trees they suspected of being infected with ash dieback. By submitting photographic evidence via the AshTag app, geo-tagging software provided information on the location of infected trees so that researchers and authorities could follow-up reports and build a picture of where the disease was present. Additionally, aluminium tags could be purchased to mark trees thereby enabling others to relocate trees easily for any follow-up visit. Between the launch in October and December 2012, over 12,000 people installed the app on their smartphones and around 1,000 geo-located photo reports were submitted and authenticated as consistent with ash dieback symptoms. AshTag quickly established that the disease focus was in south east England, particularly East Anglia, although disease reports covered a much wider area including 200 from Scotland.

Regulatory response

Hymenoscyphus fraxineus (or its anamorph *Chalara fraxinea*) has never been listed as a regulated organism in the EC Plant Health Directive which would require action to prevent spread. However, in response to the findings in the UK, emergency legislation at the national level was put in place at the end of 2012 in an attempt to limit any further introductions of *H. fraxineus* by essentially banning all imports of *Fraxinus* plants and seed from regions where the pathogen was known to be present (Anon 2012). This measure was based on evaluations of formal Pest Risk Analyses (Webber and Hendry 2012; Sansford 2013) that infected plants were the most likely entry pathway for *H. fraxineus*, whilst acknowledging that ash dieback was already present in at least some parts of the UK. In addition, during the early stages of the epidemic at least 50,000 ash trees on infected sites were destroyed in an attempt to prevent the disease spread, although the action was applied almost exclusively to recently planted stock.

Disease modelling

Although it was concluded that ash dieback outbreaks at recently established sites were due to use of asymptomatic but infected ash stock, the possibility of disease establishment as a result of spore inoculum wind-blown from continental Europe was also considered. Indeed, the concentration of wider environment infected sites along the eastern seaboard of England, mainly in Kent and East Anglia and sporadically in Lincolnshire and East Yorkshire northwards to Northumberland and Scotland in the early stages of the epidemic (Sansford 2013; Freer-Smith and Webber 2015) suggested that these could have been initiated from long-distance spore dispersal events from other parts of Europe.

To test this hypothesis, a model was developed by University of Cambridge, based on the UK Meterological Office's ‘Numerical Atmospheric-dispersion Modelling Environment’. This model strongly supported the likelihood of airborne incursion from Europe (M. Castle and R. Cox unpublished 2013). It concluded that between 2008 and 2011 there were at least 100 days on which environmental conditions including wind direction, rainfall and humidity, could have carried *H. fraxineus* spore masses from infected ash in mainland Europe across the English Channel or North Sea and caused infection of ash predominantly in east and south-east England (Downing 2012; Wentworth 2012). Epidemiological modelling of the likely progression of the ash dieback epidemic in Britain also indicated that the pathogen was likely to continue to spread in Great Britain although with potential for significant regional variation with areas in the south east, east and south west most likely to be affected in the early stages of the epidemic.

Research response – the host

Existing work on ash has resulted in a large, genetically diverse collection of material from across its natural range and for all categories of Forest Reproductive Material, amounting to approximately 40,000 individuals. This diverse resource has enabled several research bodies to tackle the impacts of ash dieback in Britain and will continue to contribute significantly to future research. Under an urgency grant from the Natural Environment Research Council in 2013, researchers from Queen Mary University, London sequenced the genome of a British *F. excelsior* tree of low heterozygosity produced by controlled self-pollination through the FRAXIGEN project. The results are published on the British Ash Genome Project website www.ashgenome.org.

When the Nornex consortium (http://nornex.org/) started work on ash dieback in 2013, one of the aims was to identify genetic resistance in ash through genome sequencing and mapping (Downie 2016). Sequencing focussed on the genome of the ash-dieback-tolerant tree (Clone 35), identified as part of the Danish breeding programme (Kjear *et al.* 2011; McKinney *et al.* 2011) and which has been shown to be highly tolerant of *H. fraxineus.* Additional references for ash genome analysis also included the British *F. excelsior* tree of low heterozygosity (www.ashgenome.org). Genome annotation of *F. excelsior* was then carried out to differing degrees depending on the assemblies available and differential expression analysis revealed distinct expression patterns between resistant/tolerant and susceptible clones of *F. excelsior* to *H. fraxineus*. The next stage of research included the use of associative transcriptomics to identify markers associated with disease susceptibility in *F. excelsior* exploiting *H. fraxineus*-infected tissue from two different clones with extreme phenotypes (one highly susceptible and one of low susceptibility - namely Clone 35). A total of three genetic markers were identified, two GEM and one cSNP markers, associated with tolerance within Clone 35 but not present in the susceptible clone (Harper *et al.* 2016). The same markers were also found to occur in *Fraxinus* species that are considered to have very low susceptibility to ash dieback: *F. americana*, *F. ornus* and *F. mandshurica*. The markers were then tested as predictors of tolerance, using tissue from a panel of about 200 trees from Denmark with known levels of susceptibility and a further group of trees from Britain exposed to the disease for several years which had developed different levels of crown dieback, and successfully identified individuals with low levels of susceptibility (ie those with few crown symptoms of ash dieback). Building on this work, it is planned that ash populations from the Europe wide RAP trial, and individuals from a British wide clonal seed orchard of phenotypically superior parents will be assessed using these markers to predict tolerant individuals.

Two Defra funded projects are also looking directly for ‘field’ tolerance within ash population through mass screening of field resources. In 2012, when the UK ban on movement of ash came into force, forest nurseries were preparing for the field season with tens of thousands of ash seedlings ready for planting, most of which were then unsaleable due to the combined impact of the disease and the ban. The first project (Rapid screening for *Chalara* resistance using ash trees currently in commercial nurseries: TH0132) utilised some of this material and Forest Research established 14 field trials across East Anglia where *H. fraxineus* was already prevalent in the wider environment. Forty eight hectares were planted in the spring of 2013, with 155,000 seedlings from 15 seed sources (ten British native seed zones, two Irish, two from continental Europe and one improved British of qualified status). These plots have been monitored each year since planting. In 2014, all sites had some infected plants but overall survival was 91 %. However, by the end of 2015 in total over 50 % of trees were infected across all sites (Lee 2016). Ultimately the intention is to screen any individual trees that survive continuing exposure to the disease in anticipation that they are likely to prove tolerant to *H. fraxineus.*

The second Defra funded project (Selection and breeding of common ash for resistance to *Chalara fraxinea*: TH0133) is screening the existing resource already described (see Genetic structure of the ash resource). Called the Living Ash Project (http://livingashproject.org.uk), and using an estimate of 1% of screened trees showing a good degree of tolerance (>10 % crown dieback) to ash dieback (Kjear *et al.* 2011), the project aims to identify 400 putatively tolerance individuals from which to commence a new breeding programme. Additionally, trees in the wider environment, but of source identified status, are being screened using citizen science via AshTag. Since the use of AshTag to identify diseased trees in 2012, it has now been re-launched so that tagged trees can be monitored over time to follow disease progress and identify trees which potentially appear to be less susceptible to ash dieback because of their survival in highly infected areas; a 10,000 tags have been given away to encourage this initiative. In addition, a new series of ash progeny trials have been planted in spring 2016 using the tested seed from the original breeding programme. Paternity analysis is being undertaken, to enable both parents to be identified within any tolerant individuals arising from the trials. Finally, tissue culture and cryopreservation techniques are being developed to enable the rapid bulking up of tolerant genotypes. Any tree being put forward as putatively tolerant will be screened using the markers developed through the Nornex consortium.

Research response – the pathogen

In the early stages of the epidemic in Britain, findings in relation to the pathogen were consistent with those discovered elsewhere. Both idiomorphs or sexual mating types (MAT 1-1 and MAT 1-2) were found in populations of *H. fraxineus* regardless of whether these came from infected nursery stock or wider environment outbreaks (Open Ash Dieback hub http://oadb.tsl.ac.uk). Further work also showed that the pathogen has a somatic self–nonself recognition or vegetative compatibility ‘vc’ system that is readily expressed in culture. Moreover, in highly localised isolate samples almost all isolates are incompatible indicating high *vic* gene diversity and therefore an out-breeding life cycle (Brasier and Webber 2013). High levels of incompatibility between individuals also suggest that it might be difficult to deploy damaging fungal viruses against the pathogen as a disease control method, because viruses usually spread more readily in a fungal population with high levels of clonality which allow mycelium of different individuals to fuse and facilitate the transfer of deleterious agents such as viruses.

In depth genetic analyses by the Nornex consortium have also generated a reference genome for the ash dieback pathogen *H. fraxineus* using an isolate from Norfolk as the reference strain; transcriptome data for *H. fraxineus* have then been used to identify genes expressed during the fungal lifecycle (Downie 2016). When diversity in *H. fraxineus* was compared using historical accessions of *H. fraxineus* from across Europe, recently obtained isolates from Britain and isolates from Japan (Downie 2016), the genome sequence data were consistent with an extreme population genetic bottle-neck indicating just a few individuals of the pathogen have initiated the epidemic in Europe. Therefore, although *H. fraxineus* has high levels of outcrossing there is limited variation in the population structure, even at the epidemic front.

At the time that the Nornex project started there were no reproducible *in vitro* tests of pathogenicity in ash seedlings using either conidia (asexual spores) or ascospores (sexual spores) as a means of following infection by *H. fraxineus*. However, pursuing the idea that conidia could be involved, and through the use of confocal microscopy imaging, these asexual spores were shown to germinate on ash leaves *in vitro* and on artificial substrates, albeit with low efficiency. When similar conidial spore suspensions were applied to leaves of six week old ash seedlings symptoms were expressed which included browning of leaf veins and tips, progressing to leaf drop (Fones *et al.* 2016). Intriguingly this suggests that infection of ash leaves may not just caused by ascospores as previously thought, but may also be effected through asexual spores which had previously been though to act only as spermatia (Gross *et al.* 2012, 2014).

There have also been other research initiatives. Another major Defra funded project (Mitigation of the impacts of ash dieback in the UK – TH0119) which is still ongoing includes studies to identify the durations of spore release in UK outbreaks and measure the volumes of spores released into the air to provide core data for modelling of pathogen spread. Additionally, experiments in the laboratory and natural outbreaks are examining the susceptibility of ash species commonly grown in the UK and aim to determine how seasonal factors and inoculum levels affect infection rates. The work is also evaluating the safe disposal of infected tree material such as fallen leaves and twigs through processes such as composting and how readily this can eradicate *H. fraxineus*. In October 2014, the first details of the laboratory and field work on testing the efficacy of currently available fungicides against ash dieback were published (Anon 2014). The most effective compounds were either triazoles or carboxamides which were found to reduce both foliar symptoms and stem lesions induced on young trees in field trials. Although it is recognised that chemical treatments are unlikely to be economic when applied to trees in woodlands they could have a useful role in protecting specific high value trees, although repeated treatments would probably be required. Any successful treatments would also need to be integrated into good practice guidelines for management of ash dieback.

Management options and conclusions

Britain's broadleaved woodlands are dominated by relatively few species, which can limit management options when deciding what to do in ash dieback infected woodlands. While Scotland still has a thriving timber industry mainly based on conifers, many woodlands, particularly in England, are managed for conservation and amenity objectives, with public access often playing a key role. Early outbreaks of ash dieback were originally contained, with new plantations being removed and burnt on site. However, as the disease spread to the wider environment, management objectives for older woodlands have aimed to slow the spread and lessen the impacts of the disease. Now, the principle aims of management are to:

- Maintain the values and benefits associated with ash woodlands and iconic trees;
- Secure an economic return where timber production is an important objective;
- Reduce the presence and rate of spread of *Chalara* ash dieback;
- Maintain as much genetic diversity in ash trees as possible with the aim of ensuring the presence of ash in the long term;
- Minimise impacts on associated species and wider biodiversity.

In some regions especially where *F. excelsior* forms pure stands, the disease has also been viewed as an opportunity to increase species diversity and build resilience into ecosystems such as the ash woods of the Peak District in northern England.

Across Britain, disease levels are still patchy with only 28% of the 10 km squares across the country with one or more infections of *H. fraxineus* in 2016 Ash dieback has been found in all counties in England to varying extent, but some ash dominated areas of Wales and the south west and southern Scotland are still relatively disease free. However, the south east of England, where the disease was first encountered, is heavily infected with many young ash stands suffering very high mortality. Although this suggests very rapid disease progression based on the first reports of *H. fraxineus* in Britain in 2012, a more complex picture is also emerging. A recent study has provided evidence that some ash stock apparently infected with *H. fraxineus* was planted in England as early as the 1990s, with affected trees dying of the disease in the mid-2000s (Wylder et al. 2016). This places *H. fraxineus* in England much earlier than previously thought, and suggests there can be a lag phase of more than a decade before outbreaks start to have an impact on the landscape.

As the disease progresses different strategies are required to allow land managers time to intervene and adapt woodland management prescriptions in the expectation of high losses to come. Maintaining the structure and value of any woodland should be the primary aim of management, while avoiding accelerating any decline in condition. In heavily infected areas, it is now advised that woodlands should be thinned as usual to promote canopy development while focusing on retaining species other than ash. It can be difficult to ensure that the ecological role realised by ash trees is maintained as no one species encompasses all the functions of ash. Those trees showing the most extreme dieback symptoms should be favoured for removal and the lop and top burnt on site where possible. Although some landowners are felling ash to realise the economic benefits before ash dieback has established, the most common end use for ash in the current market is for firewood. This means that the rush to fell ash before it becomes infected is lessened, and tolerant trees are therefore likely to remain, potentially allowing for natural regeneration with some degree of tolerance.

Where infection is absent or at low levels, a ‘business as usual approach’ has been recommended in high forest situations to maintain tree vigour and retain a full canopy. Trees to be selected for thinning which show symptoms of ash dieback are most easily assessed in the summer when symptoms are most visible. If only small numbers of recently planted or naturally regenerated ash show symptoms, it may be beneficial to remove the entire planting to slow the wider spread of disease and allowing time to establish new trees of other species. No one species will fulfil the ecological niche of ash. However, work by Mitchell *et al.* (2014 a, b, c) has attempted to quantify the role of ash. Out of 955 species that utilise ash trees in some way, 45 species (largely invertebrates) are reported to be obligate ash users, with a further 62 species being highly associated, rarely using other species. Planting beech (*Fagus sylvatica*) and oak (*Quercus*) species (where appropriate) will facilitate a large number of these highly associated species, as will sycamore (*Acer pseudoplatanus*) and hazel (*Corylus avellana*). However, the ecosystem function of ash, in terms of both levels of light within a woodland and rate of decay of leaf litter, is better served by supplementing ash with small leaved lime (*Tilia cordata*) and common alder (*Alnus glutinosa*).

The UK has historically imported a large proportion of its planting stock from Europe, even when the seed may have been of UK origin. With the confirmation of the ash dieback pathogen in a nursery in 2012, the risks associated with disease introductions via imported nursery stock were highlighted. This has led to much wider questioning within the industry about seed sourcing, the history of material as it is grown and moves through the supply chain, and been the launchpad of initiatives such as the Grown in Britain Campaign (http://www.growninbritain.org). Government guidance now routinely recommends using UK grown planting stock, and UK origin, but suggests diversifying in terms of species and provenances choice to include near continental material, whilst still promoting use of British grown stock. Looking forward, the foundations are already in place to predict some of the factors associated with disease tolerance, to identify trees with low disease susceptibility and thereby rebuild the ash population in Britain in the future.

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References

Anon. 2012. The Plant Health (Forestry) (Amendment) Order 2012. Statutory Instrument 2012, No. 2707. In force 29 October 2012. 6pp.

Anon. 2013. Results from preliminary screening of approved fungicides for efficacy against *Hymenoscyphus fraxineus* (*Chalara fraxinea*), the cause of ash dieback file:///C:/Users/OWNER/Downloads/12430_ Shortreportonresultsfromfungicideefficacytestingforchalarav2.pdf

Brasier, C. and Webber, J., Vegetative incompatibility in the ash dieback pathogen *Hymenoscyphus pseudoalbidus* and its ecological implications. *Fungal Ecology* 6(6) 501-512. http://dx.doi.org/10.1016/j.funeco.2013.09.006

Broadmeadow, M.J.S., Ray, D. and Samuel, C.J.A. 2005. Climate change and the future for broadleaved tree species in Britain. *Forestry* 78: 145-161.

British Ash Genome Project 2013. http://www.ashgenome.org (accessed on 5 February 2016).

Clark, J.R. 2013. Adaptation of ash (*Fraxinus excelsior* L.) to climate change. Ph.D. Thesis, Bangor University, UK.

Cundall, E.P., Cahalan, C.M. and Connolly, T. 2003. Early results of ash (*Fraxinus excelsior* L.) provenance trials at sites in England and Wales. *Forestry* 76: 385-399.

Downie, A. 2016. Nornex Final Report: An open consortium (Nornex) for molecular understanding of ash dieback disease. http://oadb.tsl.ac.uk/wp-content/uploads/2016/04/Nornex_Final_Report_April_2016.pdf (accessed on 15 May 2016).

Defra 2015. Chalara in Non-Woodland Situations. http://randd.defra.gov.uk/Default.aspx?Menu=Menu&Module=More&Location=None&ProjectID=19770&FromSearch=Y&Publisher=1&SearchText=ash dieback &SortString=ProjectCode&SortOrder=Asc&Paging=10#Description (accessed on 15th May 2016).

Downing, E. 2014 *House of Commons Library - Ash dieback disease: Chalara fraxinea.* http://www.parliament.uk/business/publications/research/briefing-papers/SN06498/ash-dieback-disease-chalara-fraxinea (accessed on 7 January 2016).

EPPO. 2013 PM 7/117 (1) *Hymenoscyphus pseudoalbidus*. *EPPO Bull*. 43: 449–461.

Evans J. 1984. *Silviculture of Broadleaved Woodland*. Forestry Commission Bulletin 62. HMSO London.

Fones, H.N., Mardon, C. and Gurr, S.J. 2016. A role for the asexual spores in infection of *Fraxinus excelsior* by the ash-dieback fungus *Hymenoscyphus fraxineus*. Submitted to journal.

Freer-Smith, P.H. and Webber, J.F. 2015. Tree pests and diseases: the threat to biodiversity and ecosystem services. *Biodivers. Conserv.* 24 DOI: 10.1007/s10531-015-1019-0.

Forestry Commission, 2013. National Forest Inventory estimates of quantities of broadleaved species in British woodlands, with special focus on ash. HMSO, Edinburgh.

FRAXIGEN, 2005. Ash species in Europe: biological characteristics and practical guidelines for sustainable use. Oxford Forestry institute, University of Oxford, UK. 128 pp.

Gross, A., Zaffarano, P.L., Duo, A. and Grünig, C.R. 2012. Reproductive mode and life cycle of the ash dieback pathogen *Hymenoscyphus pseudoalbidus*. *Fungal Genetics and Biology* 49(12): 977-986.

Gross, A., Holdenrieder, O., Pautasso, M., Queloz, V. and Sieber, T.N. 2014. *Hymenoscyphus pseudoalbidus*, the causal agent of European ash dieback. *Molecular Plant Pathology* 15(1): 5-21.

Harper, A.L., McKinney, L.V., Nielsen, L.R., Havlickova, L., Li, Y., Trick, M., Fraser, F., Want, L., Fellgett, A., Sollars, E.S.A., Janacek, S.H., Downie, J.A., Buggs, R.J.A., Kjear., E.D. and Bancroft, I. 2016. Molecular markers for tolerance of European ash (*Fraxinus excelsior*) to dieback disease identified using associative transcriptomics. *Scientific Reports* 6: 1-7.

Heuertz, M., Hausman, J.F., Hardy, O.J., Vendramin, G.G., Frascaria-Lacoste, N. and Vekemans, X. 2004a. Nuclear Microsatellites reveal contrasting patterns of genetic structure between western and southeastern European populations of the common ash (*Fraxinus excelsior* L.). Evolution 58 (5): 976-988.

Heuertz, M., Fineschi, S., Anzidei, M., Pastorelli, R., Salvini, D., Paule, L., Frascaria-Lacoste, N., Hardy, O.J., Veksemans, X. and Vendramin, G.G. 2004b. Chloroplast DNA variation and postglacial recolonization of common ash (*Fraxinus excelsior* L.) in Europe. *Molecular Ecology* 13: 3437-3452.

Joyce, P.M. 1998. *Growing Broadleaves. Silvicultural Guidelines for Ash, Sycamore, Wild Cherry, Beech and Oak in Ireland.* COFORD, Dublin.

Kerr, G. and Evans, J. 1993. *Growing Broadleaves for Timber*. Forestry Commission Handbook 9. HMSO, London.

Kjear, E.D., McKinney, L.V., Nielsen, L.R., Hansen, L.N. and Hansen, J.K. 2011. Adaptive potential of ash (*Fraxinus excelsior*) populations against the novel emerging pathogen *Hymenoscyphus pseudoalbidus*. *Evolutionary Applications* 5: 219-228.

Lee, S. 2016. Screening ash for Chalara. Ash Newsletter April 2016. Forest Research, Northern Research Station, Edinburgh. 4pp.

McKinney, L.V., Nielsen, L.R., Hansen, J.K. and Kjear E.D. 2011. Presence of natural genetic resistance in *Fraxinus excelsior* (Oleraceae) to *Chalara fraxinea* (Ascomycota): an emerging infectious disease. *Heredity* 106: 788-797.

Mitchell, R.J., Beaton, J.K., Bellamy, P.E., Broome, A., Chetcuti, J., Eaton, S., Ellis, C.J., Gimona, A., Harmer, R., Hester, A.J., Hewison, R.L., Hodgetts, N.G., Iason, G.R., Kerr, G., Littlewood, N.A., Newey, S., Potts, J.M., Pozsgai, G., Ray, D., Sim, D.A., Stockan, J.A., Taylor, A.F.S. and Woodward, S. (2014a). Ash dieback in the UK: a review of the ecological and conservation implications and potential management options. *Biological Conservation* 175: 95-109.

Mitchell, R.J., Beaton, J.K., Bellamy, P.E., Broome, A., Chetcuti, J., Eaton, S., Ellis, C.J., Gimona, A., Harmer, R., Hester, A.J., Hewison, R.L., Hodgetts, N.G., Iason, G.R., Kerr, G., Littlewood, N.A., Newey, S., Potts J.M., Pozsga,i G., Ray, D., Sim, D.A., Stockan, J.A., Taylor, A.F.S. and Woodward, S. (2014b). *Assessing and addressing the impacts of ash dieback on UK woodlands and trees of conservation importance (Phase 2)*. Natural England Commissioned Reports, Number 151.

Mitchell, R.J., Bailey, S., Beaton, J.K., Bellamy, P.E., Brooker, R.W., Broome, A., Chetcuti, J., Eaton, S., Ellis, C.J., Farren, J., Gimona, A., Goldberg, E., Hall, J., Harmer, R., Hester, A.J., Hewison, R.L., Hodgetts, N.G., Hooper, R.J., Howe, L., Iason, G.R., Kerr, G., Littlewood, N.A., Morgan, V., Newey, S., Potts, J.M., Pozsgai, G., Ray, D., Sim, D.A., Stockan, J.A., Taylor, A.F.S. and Woodward, S. 2014c. *The potential ecological impact of ash dieback in the UK.* Joint Nature Conservation Committee Report (JNCC) 483. JNCC Peterborough. 222 pp.

Peterken, G.F. 1993. *Woodland Conservation and Management*. Chapman and Hall, London.

Pliûra, A. and Heuertz, M. 2003. EUFORGEN Technical Guidelines for genetic conservation and use for common ash (*Fraxinus excelsior*). International Plant Genetic Resources Institute, Rome, Italy. 6 pages.

Rodwell, J. 1991 *British Plant Communities. Volume 1, Woodlands and Scrub.* Cambridge, Cambridge University Press.

Sansford C.E. 2013. *Pest Risk Analysis for Hymenoscyphus pseudoalbidus (anamorph Chalara fraxinea) for the UK and the Republic of Ireland.* http://www.fera.defra.gov.uk/plants/plantHealth/pestsDiseases/documents/hymenoscyphusPseudoalbidusPRA.pdf (accessed on 7 January 2016).

Scherrer, D, Bader, M.K.F. and Körner, C. 2011. Drought-sensitivity ranking of deciduous tree species based on thermal imaging of forest canopies. *Agricultural and Forest Meteorology* 151: 1632-1640.

Sutherland, B.G., Belaj, A., Nier, S., Cottrell, J.E., Vaughan. S.P., Hubert, J. and Russell, K. 2010. Molecular biodiversity and population structure in common ash (*Fraxinus excelsior* L.) in Britain: implications for conservation. *Molecular Ecology* 19: 2196-2211.

Wallander E. 2008. Systematics of *Fraxinus* (Oleaceae) and evolution of dioecy. *Plant Systematics and Evolution* 273: 25-49.

Wardle P. 1961. Biological flora of the British Isles *Fraxinus excelsior* L. *Journal of Ecology* 49: 739-751.

Wentworth J. 2012. Transmission of ash dieback. POSTbox, December 2012. Houses of Parliament, Parliamentary Office of Science and Technology. http://www.parliament.uk/documents/post/Ashdieback_POSTbox.pdf (accessed on 7 January 2016).

Webber, J. and Hendry, S. 2012. Rapid assessment of the need for a detailed Pest Risk Analysis for *Chalara fraxinea*. Version 1.2, 9th August 2012, 15pp.

Wylder, B., Biddle, M., King, K., Baden R. and Webber, J. 2016. Mortality dating of *Fraxinus excelsior* to demonstrate the early presence of ash dieback (*Hymenoscyphus fraxineus*) in England. *Forestry* (submitted).