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Species diversification – which species should we use?

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Summary

Species diversification can increase resilience of British forests if diversifying species are adapted to site, genetically variable, and do not harm existing forests. Immediate increase in resilience is best achieved using native or well-established exotic species, rather than 'alternative' species. 'Alternative' species currently lack adequate information on site requirements and appropriate seed sources, and there has been little assessment of their potential for damaging existing forests through pest/pathogen transfer and invasive behaviour. Future use of 'alternative' species for diversification should be contingent on rigorous biological risk assessment, results from forestry scale trials, and the establishment of sustainable British seed sources.

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Articles in recent editions of this journal are in agreement that future multi-purpose forest management in Britain should be aimed at creating resilient woodland systems (Wilson, 2016; Spencer, 2018; Willoughby and Peace, 2019). This is reflected in current policy documents from a range of organisations (DEFRA, 2018; Forestry Commission England, 2018; Scottish Government, 2019; Welsh Government, 2017; Woodland Trust, 2019). The overarching objective is for woodland systems to be capable of withstanding the combined threats posed by directional climate change, increasingly extreme weather events, and a continual influx of novel pests and pathogens brought in by global movement of people, plants and products.

It is widely recognised that present levels of tree species diversity are unacceptably low in British forests, leaving them with insufficient resilience to environmental challenges. This is true in the commercial conifer sector, where Sitka spruce dominates as large monoculture stands. It is also the case in semi-natural woodlands where native tree diversity has been dramatically reduced over the centuries through deliberate removal of less productive species, and unplanned loss of more palatable species through intensive herbivore pressure. In this situation increasing the number of tree species within British forests, species diversification, can potentially enhance resilience.

Diversification reduces the proportion of any one tree species in a forest, and therefore spreads the risk of damage to the forest as a whole from pressures that affect species differently, such as a discrete, extreme weather event, or the introduction of a novel pest or pathogen. For instance, Norway spruce is less tolerant of wind exposure than Sitka, but more tolerant of frost. Douglas fir is intolerant of exposure, but less susceptible than spruces to drought. Mixed crops are likely to recover more quickly in the event of extremes of wind, frost or drought than their pure stand counterparts. Likewise planting a mixed stand of Scots pine and larch will prevent complete crop failure in the event of infection by either *Dothistroma* or *Ramorum* disease. Furthermore diversification reduces the absolute density of any one tree species and consequently reduces the probability of highly damaging epidemics developing even in the presence of novel pests or diseases. Species diversification therefore has the potential to promote resilience to both short term and sustained environmental challenges. However, realising these benefits is contingent upon an appropriate choice of diversifying species.

<u>Criteria for species choice</u>

The addition of a tree species will increase the resilience of the forest only if certain conditions are met. The introduced species must possess a combination of traits that is different from those of existing species, must be well adapted to the planting site, and genetically variable. If the species is poorly adapted to the planting site or contains inadequate genetic variation it will be more vulnerable to extreme weather events, pests and diseases than the species which it augments. The result will be a forest system that is less resilient than the original.

An additional condition that must be met is that introduction of the species should not adversely affect other components of the existing forest systems, thereby reducing their overall resilience. Typically this could occur if the diversifying species; was more competitive than existing species and led to their displacement, if the diversifying species increased the likelihood of fire, pest or pathogen damage to existing tree species, or had a detrimental effect on other important components of forest biodiversity e.g. understorey species, epiphytes etc.

Species Available for Diversification

The tree species that can potentially be used for immediate diversification of British forests fall into three categories. The first comprises native British tree species. The second encompasses the well-established exotics that have undergone comprehensive species and provenance trials, and/or for which there is considerable experience in operational forestry. These include Douglas, grand and noble fir, Corsican and lodgepole pine, European and Japanese larch, Norway and Sitka spruce, western hemlock and western red cedar, sycamore and sweet chestnut. The final group available for diversification are often referred to as 'alternative' species (listed in Table 1). They have been identified as having potential in British forestry, but have so far only been deployed in small scale planting covering less than 100ha. (Forest Research, 2019; Silvifuture, 2019). 'Alternative' species are distinct from both native and well-established exotic species in that there is limited knowledge of their performance and degree of adaptation to British conditions. Some have only been grown within arboreta or forest gardens (Stage 1 testing). Others have been assessed in small stands located on a limited range of British sites (Stage 2 testing). Rather few 'alternative' species have been established in large plots at a forestry scale over a range of ecologically diverse conditions (Stage 3 testing). Furthermore only a third of 'alternative' species have published data from British provenance trials that is adequate for guiding seed collections from the wild, and less than a quarter are present as established stands in Britain that could act as sources of certified seed for sustained planting programmes (Table 1).

The obvious attraction of using 'alternative' species in diversification is that it widens the choice available to foresters at a time when disease problems (ash dieback, *Dothistroma*, *Phytophthora ramorum*) have reduced the number of both native and well-established exotic tree species that can be planted. However before promoting the use of 'alternative' species for diversification we must establish whether their deployment is likely to enhance the resilience of British forests relative to the use of native or well-established exotics.

Choosing species adapted to site

There is already extensive experience with sourcing, planting and managing native timber tree species whose ecological characteristics and site suitability are well understood. Moreover, nursery managers are currently active in developing sustainable seed sources for a wider range of native tree species (including minor species) to ensure that a diversity of provenances are available for planting in different regions of Britain (Woodland Trust, 2015). There is therefore the opportunity to choose appropriate provenances of native species for diversification programmes that will be well adapted to site and lead to an increase in forest resilience.

For long established exotic species, the large scale species and provenance trials conducted across a range of site types over many years by Forest Research, combined with commercial planting experience, provide reliable information for selecting an appropriately adapted species and seed source (Lines, 1987).

For 'alternative' species far less evidence is available for matching species to site and choosing appropriate seed sources. The degree of risk associated with 'alternative' species will depend on the stage of testing that has been reached; the more advanced the stage of testing, the lower the risk. Forest Research's own experience with exotic introductions bears this out as less than 1 in 5 species showing promise in small scale plots (stage 1) have ultimately found a place in British forestry after more extensive testing (stages 2 and 3) (MacDonald et al., 1957). Planting in the absence of reliable information has led to costly failures in the past. For example, planting of Corsican pine on sites with insufficient winter sunshine led to complete elimination of stands by Bruchorstia disease (*Gremmeniella abietina*) (Read, 1968), while inappropriate choice of the south coastal provenance of lodgepole pine based on year 6 data resulted in catastrophic damage caused by wet snow (Lines, 1966). Initial successes have often been followed by problems apparent only after widespread planting, especially when newly arrived diseases prove to have a disproportionate effect on commercial species. Recent examples include damage by *Phytophthora ramorum* on larch and *Dothistroma* on Corsican pine (Brasier and Webber, 2010; Brown and Webber, 2008). These experiences suggest that diversification using 'alternative' species which have not been evaluated in both operational species and mature provenance trials (stage 3) may fail to achieve the desired increase in forest resilience.

Establishing a genetically variable stand

Forest resilience is founded not only on species diversity, but also on the presence of adequate genetic variation within individual tree species. This confers population level resistance to pests and pathogens in the present generation of a given species and the potential for its future adaptation (Cavers and Cottrell, 2015; Ennos, 2015). A number of 'alternative' species advocated for diversification e.g. hybrid poplars are clonally propagated and typically planted as monoclonal blocks, so lack any of the genetic diversity needed to confer resilience. This is demonstrated by repeated breakdown of disease resistance in such stands, necessitating regular planting of new clones (Pinon and Frey, 2005). Thus planting of these species as single genotype stands will reduce rather than enhance forest resilience.

For 'alternative' species propagated by seed, collections need to be made from base populations with high genetic diversity. For practical convenience, and to capitalise on the gains that can be made from a single round of natural selection under British conditions, seed sources of 'alternative' species should ideally comprise British stands of at least 1-2 ha derived from seed of 30 or more parents that have been sampled in an appropriately adapted native stand. If large scale provenance trials have been established, they could ultimately be managed to serve as seed sources. However for many 'alternative' species appropriate British seed sources do not yet exist. For instance only one of the 'alternative' species newly added to the voluntary

FRM scheme (coast redwood) has had stands certified, and in both cases the seed source from which the stand has been derived is unknown. Seed collection from British stands of unknown origin, even when certified under FRM regulations, may be unsuitable because they may be the product of seed collected from only a handful of parents in the wild. Such stands will contain inadequate genetic diversity upon which to found a resilient population. Moreover the planting stock obtained from such stands will suffer from inbreeding depression, which in trees may reduce survival by 80% (Stoehr et al., 2015). As an example Lines and Aldhous (1961) cite the case of a British plantation of Douglas fir derived from seed of two parents which produced inbred offspring with a high number of deformities. Lack of genetically appropriate seed sources for 'alternative' species can therefore compromise their utility in diversification programmes.

Lack of adaptation to site, and seed sourcing problems thus argue against the immediate widespread use of 'alternative' species for increasing resilience. However these are not the only considerations to be borne in mind. Introducing an 'alternative' species into an existing forest, be it a native woodland or a commercial plantation, has the potential to damage that forest. We now consider the risks involved.

<u>Species choice and pest and pathogen damage</u>

Diversification with native and well-established exotic species should pose no additional pest and pathogen risk to the forests into which they are introduced so long as they are; based on seed of appropriate provenance which contains adequate genetic diversity, sourced from stands in Britain or known to perform well in Britain, and raised from seed in British nurseries which adopt comprehensive biosecurity measures. However 'alternative' species represent novel exotics. Evidence from across the globe demonstrates that after an initial enemy free period, introductions of exotic trees are eventually colonised by pests and pathogens from their native range as a result of long distance transport (Wingfield et al., 2015). These may have a more damaging effect on the introduced species in Britain than in the tree's native range, especially if the species is growing under stress in an inappropriate site. However of greater concern is that introduced pests and pathogens may transfer onto native or well established exotic species which are highly susceptible to this novel threat. Such transfers will take place most readily and have most devastating effect when the introduced 'alternative' species is closely related to a species present in the existing forest.

Historical examples of pathogen damage to native trees caused by introduction of related 'alternative' species are well documented. In the nineteenth century Japanese chestnut was introduced into the US to improve chestnut production. The chestnut blight fungus carried by resistant Japanese chestnut transferred to the highly susceptible American chestnut and led to the latter's elimination from the native forest ecosystem (Anagnostakis, 1987). More recently Manchurian ash resistant to the ash dieback fungus was transferred from eastern to western USSR to diversify forestry in that region (Drenkhan et al., 2014). Transfer of the ash dieback fungus onto susceptible European ash native to western USSR has ultimately led to the pandemic of ash dieback that has swept across Europe and could kill up to 70%

of ash trees in Britain. Finally the introduction of Corsican and lodgepole pine to increase the productivity of British forests is associated with the introduction of two novel races of *Dothistroma septosporum* now present in native Scots pinewoods (Piotrowska et al., 2018). Exotic pine species are now being removed from the vicinity of native Scots pine to reduce inoculum load and minimise disease damage.

Measures to prevent entry of exotic pests and pathogens with introduction of 'alternative' species include strict biosecurity checks on imported planting stock and seed. However establishment of oak processionary moth and the recent introduction of chestnut blight into Britain, despite its notifiable pathogen status, evidence the fallibility of biosecurity measures. Furthermore seed import has been responsible for introduction of the lodgepole pine race of *D. septosporum*, and there are at least two other examples where seed exchange has led to transfer of important pine pathogens between North America and Europe (Piotrowska et al., 2018). Even if biosecurity measures are successful, the presence of stands of 'alternative' species may provide a bridgehead for entry of exotic pathogens via long distance transport of spores.

Apart from increasing the chance of incursion of exotic pests and pathogens, the use of susceptible 'alternative' species can create reservoirs of infection for pests and pathogens able to attack native or well-established exotic species. This is currently the case in western Russia where highly susceptible green ash (*Fraxinus pennsylvanica*) introduced from North America acts as a reservoir for emerald ash borer. Native European ash suffers significant damage from emerald ash borer in the vicinity of planted green ash, but not elsewhere (Orlova-Bienkowskaja et al., 2019). A similar situation could arise in Britain where stands of introduced oriental spruce, highly susceptible to *Dendroctonus micans*, could act as sources of elevated infestation of the established exotic Sitka spruce despite the control exerted by *Rhizophagus grandis*.

<u>Species choice and invasive spread</u>

When species are introduced to a forest to increase resilience, the general assumption is that the diversifying species will remain restricted to the sites in which they have been planted. However, if a diversifying species proves to be adapted to the conditions, it may regenerate and subsequently invade other forest communities where its ecological effects can be highly undesirable. This is evidenced by the fact that in Europe, four of the eighteen most invasive introduced plant species are trees (DAISIE, 2018).

In the British landscape the intimate mixture of woodland types managed for different purposes means that the potential for damage by spread of invasive tree species from one forest type to another is especially high. Another feature of native woodlands in the north and west of Britain that makes them particularly vulnerable to invasive species is their low tree species diversity and, in particular, their lack of shade tolerant tree species. Thus many native woodlands in Scotland have few understorey tree species and support a very diverse ground flora with particularly rich fern, moss, liverwort and lichen assemblages. Invasion of such woodlands by shade tolerant shrub and tree species has devastating effects on the biodiversity for which they are prized (Broome & Mitchell, 2017).

When making decisions about introducing tree species to increase resilience, it is therefore imperative to take into account their potential for invasion of other forest communities in the area of introduction and the possible detrimental consequences this may have. In terms of British native and well-established exotic trees, particular care is needed with diversification involving shade tolerant beech and western hemlock which are known to be highly invasive in Scottish native woodland situations. Invasive non-native species are the second greatest cause of unfavourable condition in designated forest sites (Scottish Natural Heritage, 2011). With respect to 'alternative' species, the invasive potential of many tree species in temperate areas outside their natural ranges is already known. For instance the 'alternative' species red oak is known to act as an invasive on certain site types in other parts of Europe, displacing native pedunculate oak (Thomas, 2010; Nicolescu et al., 2018; Woziwoda et al., 2019). It is essential that information of this kind is taken into account whenever decisions about forest species diversification are made.

Conclusions

A number of important conclusions can be drawn concerning the choice of species for immediate species diversification of British forests.

- Diversifying with native or well-established exotic species is more likely to increase the resilience of existing forests than diversifying with 'alternative' species.
- Diversifying with 'alternative' exotic species that are closely related to native or well-established exotic species increases the risk of serious pest and pathogen damage to existing forests.
- Diversification with either native, well established exotics or 'alternative' species must consider their invasive potential, taking into account the range of woodland types to which they could spread from their planting site.

While it may not currently be prudent to utilise 'alternative' species in diversification programmes, their use may be highly desirable in commercial settings under the altered climatic, pest and pathogen environments of the future, and to facilitate the adoption of continuous cover forestry (Kerr, 1999; Ennos et al., 2018). At that time it will be essential to have data available from stage 3 species and provenance trials, and seed stands that have been established from an adequate number of parents of known provenance. These trials and seed stands need to be planted soon, then maintained, assessed regularly for a range of traits, and the results securely documented, if we are to be armed with sufficient information to decide which of the candidate species we should include in our future plantings.

Given the substantial resources needed to achieve these objectives for any one species, it would now seem timely to narrow down the existing long list of 'alternative' species to a short list comprising those with the most ecological and economic promise and the least likelihood of causing damage to existing forests. The groundwork for such an exercise has already been laid by publication in this journal of many ‘alternative’ species accounts (see references in Table 1). The results from this exercise are essential for focussing scarce research resources onto those ‘alternative’ species that can contribute to diverse and resilient commercial forests of the future.

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BROADLEAF SPECIES	Current Stage Species Trials	Provenance trials	Seed source	Known problems	Conspecifics present and at risk in Britain	Ref.
Big-leaf maple *Acer macrophyllum *, #*	2	-	N	D; *Phytophthora ramorum*	*Acer pseudoplatanus* *Acer campestris* *Acer platanoides*	4
Silver maple *Acer saccharinum **	2	-	N	D; *Ceratocystis virescens*	*Acer pseudoplatanus* *Acer campestris* *Acer platanoides*	6, 12
Green alder *Alnus viridis **	2	-	N	D; *Phytophthora alni*	*Alnus glutinosa*	27
Grey alder *Alnus incana *,#*	2	-	N/B	D; *Phytophthora alni*	*Alnus glutinosa*	27
Italian alder *Alnus cordata*,#*	2	-	N	D; *Phytophthora alni*	*Alnus glutinosa*	27
Red alder *Alnus rubra *,#*	2	+	N/B	*D; Phytophthora alni*	*Alnus glutinosa*	10
Cider gum *Eucalyptus gunnii *,#*	2	+	N	F		3,15
Tingiringi gum *Eucalyptus glaucescens*	2	+	N	F		3,15
Shining Gum *Eucalyptus nitens *,#*	2	+	N	F		3,15
Black walnut *Juglans nigra*	2	+	N	F	*Juglans regia*	1
Tulip tree *Liriodendron tulipifera **	2	-	N	D; *Phytophthora ramorum*		24
Lenga *Nothofagus pumilio **	2	-	N	D; *Phytophthora pseudosyringae*		11
Rauli *Nothofagus alpina *,#*	3	+	N/B	D; *Phytophthora pseudosyringae*		11
Roble *Nothofagus obliqua *,#*	3	+	N/B	D; *Phytophthora pseudosyringae*		11

Princess tree *Paulownia tomentosa* *	1	-	N	Invasive in North America		7
Poplar hybrids *Populus trichocarpa, P. deltoides and hybrids* *,#	3	Clonal	Clonal	D; *Melampsora larici-populina*	*Populus nigra*	21
Hybrid aspen *Populus x wettsteinii* *,#	2	Clonal	Clonal	D; *Melampsora larici-populina*	*Populus tremula*	21
Red oak *Quercus rubra* *,#	2-3	+	N	Invasive in Europe D; *Phytophthora ramorum*	*Quercus robur* *Quercus petraea*	26,23

CONIFER SPECIES	Current Stage Species trials	Provenance trials	Seed source	Known problems	Conspecifics present and at risk in Britain	Ref.
Caucasian silver fir *Abies nordmanniana* *,#	2	-	N	P; *Dreyfusi nusslini*		19
European silver fir *Abies alba* *,#	3	+	N	P; *Dreyfusi nusslini*		5
Pacific silver fir *Abies amabilis* *,#	3	+	N	D; *Heterobasidion annosum*		9
Atlantic cedar *Cedrus atlantica* *	2	-	N	D; *Sirococcus tsugae*	*Tsuga heterophylla*	12,14
Cedar of Lebanon *Cedrus libani* *	2	-	N	D; *Sirococcus tsugae*	*Tsuga heterophylla*	12,14
Japanese red cedar *Cryptomeria japonica* *,#	2-3	+/-	N			12,13, 14
Dawn redwood *Metasequoia glyptostroboides* *	1	-	N			
Sitka x White spruce hybrid *Picea glauca x Picea sitchensis* *	3	+	B		*Picea sitchensis*	22
Oriental spruce *Picea orientalis* *,#	2	-	N	P; *Dendroctonus micans*	*Picea sitchensis*	12,20
Serbian spruce *Picea omorika* *,#	2	-	N/B			12,20
Macedonian pine *Pinus peuce* *,#	2-3	+/-	N/B			18,8
Maritime pine *Pinus pinaster* *	2	-	N	D; *Dothistroma septosporum*	*Pinus sylvestris*	16
Radiata pine *Pinus radiata* *,#	2-3	+/-	N/B	D; *Dothistroma septosporum*	*Pinus sylvestris*	
Western white pine *Pinus monticola* *,#	2	-	N	D; *Cronartium ribicola*		12

Weymouth pine *Pinus strobus* *,#	2	-	N	D; *Cronartium ribicola*		2
Coast redwood *Sequoia sempervirens* *,#	2-3	+/-	N/B			12,25
Giant redwood *Sequoiadendron giganteum* *	2	-	N			12,25

Table 1. Attributes of 'alternative' broadleaved and conifer species proposed for diversifying British forests modified from Table 1 in Ennos *et al.* (2018). Presence in Silvifuture* and Forest Research# databases is indicated. **Current stages of species trials**: 1 (arboreta or forest gardens); 2 (small stands); 3 (forestry scale plots). **Provenance Trials:** + (Present with published data); +/- (Present but limited/no published data); - (Absent). **Seed source**: N (natural range); B (stand in Britain). **Known problem**: D (disease); P (pest); F (frost).

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