

Pathogen impacts and implications for species diversification in UK forestry

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Abstract

With global productive forestry subject to the pressures of climate change and pest/pathogen damage, there is considerable industry focus on building resilience into commercial plantations. Diversification is a key facet of resilience and entails identification of suitable forestry species to supplement or replace those already in use. An important attribute to consider when evaluating species for potential use in diversification efforts is resilience to local pathogens. This study assessed the impact of endemic pathogens on 17 tree host species and up to three provenances per species across four experimental trial sites by conducting health surveys and collecting sample material to identify causal agents. Significant variability was detected among the 12 conifer and five broadleaf species, and among provenances, with the pines being heavily impacted by the needle blight pathogen *Dothistroma septosporum*. When compared to Scots pine (*Pinus sylvestris* Linnaeus), the non-native radiata (*Pinus radiata* D. Don) and maritime (*Pinus pinaster* Aiton) pines fared worse in terms of disease impact, with the destructive shoot pathogen *Gremmeniella abietina* detected on both. Our foliage necrosis and shoot mortality data indicate that use of native Scots pine provenances is advisable over non-native alternatives. The needle cast pathogen *Nothophaeocryptopus gaeumannii* was detected on all provenances of Douglas fir (*Pseudotsuga menziesii* (Mirbel) Franco) at three of the sites, resulting in significant foliage necrosis. The range of detected pathogens and their impacts on key species of industry interest are discussed, alongside considerations as to how these results will inform future species and provenance choices.

Introduction

Tree pathogens are a major biotic pressure on productive forests globally. Notable examples include severe damage of lodgepole pine (*Pinus contorta* Douglas ex Loudon) plantations in Sweden by the shoot pathogen *Gremmeniella abietina* (Karlman *et al.*, 1994) and direct losses estimated at \$19.8 million per annum due to the impact of the needle blight pathogen *Dothistroma septosporum* on radiata pine (*Pinus radiata* D. Don) plantations in New Zealand (Watt *et al.*, 2011). The invasive oomycete pathogen *Phytophthora ramorum* has caused extensive damage to larch (*Larix* spp.) plantations in the UK, with millions of trees felled during subsequent efforts to contain the disease (Webber, 2017). Additionally, ash dieback, caused by the ascomycete *Hymenoscyphus fraxineus*, has drastically reduced European ash (*Fraxinus excelsior* Linnaeus) populations across most countries in Europe (Hultberg *et al.*, 2020). These occurrences indicate the potential for tree disease epidemics to inflict significant ecological and economic damage and provide diverse examples of pathogens which have impacted forests in recent decades.

The threat posed by these pathogens is exacerbated by expansion of the global plant trade and by climate change. Cross-border movement of live plant material, timber and seeds has facilitated entry of pathogens into new geographical areas far from their native ranges (Franić *et al.*, 2024; Liebhold *et al.*, 2012). This is reflected in the cumulative increase in novel pest and pathogen detections in the UK, with 19 incursions of new invasive

species associated with tree diseases since 2000 compared to just five in the previous 30-year period (Defra, 2023). In tandem, anthropogenic climate change will likely worsen the impact of forest disease epidemics, with extreme weather events weakening host trees, making them more susceptible to pathogen infection (Wainhouse *et al.*, 2016). Warming temperatures may also expand the distribution range of certain pathogenic species into previously unaffected areas (Ghelardini *et al.*, 2016).

In commercial forestry, managed for production of timber and other wood products, the increasing risk posed by pests and pathogens is heightened when considering the narrow range of tree species in operational use. Globally, there has been a strong trend toward monospecific plantations of fast-growing species suitable for a broad range of environmental conditions (Messier *et al.*, 2021). The resulting low species diversity is observed across major forest production regions; eucalyptus (*Eucalyptus* spp.) plantations in Brazil cover approximately 7.6 million hectares (IBÁ, 2019), whilst Sweden's forests are dominated by even-aged plantations of pine (*Pinus* spp.) and spruce (*Picea* spp.) (Hertog *et al.*, 2022). In New Zealand, radiata pine accounts for more than 90 per cent of production forestry (Hall, 2023) and in parts of France stands of maritime pine (*Pinus pinaster* Aiton) predominate (Layton *et al.*, 2021). In the UK, there is a heavy reliance on Sitka spruce (*Picea sitchensis* (Bongard) Carrière), which accounts for 53 per cent of commercial coniferous forest area (Stokes *et al.*, 2023). This lack of diversity allows for novel biotic aggressors to have an increased

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impact on productive forestry tree species. This is observed in spruces (e.g. Norway spruce (*Picea abies* (L.) H. Karst) and Sitka spruce) across Europe, for example with intensifying outbreaks of the spruce bark beetle *Ips typographus* (Inward, 2024).

One adaptive management response is species diversification. This entails identification of a wider range of forestry species with sufficient attributes to supplement or replace those already in use. The rationale for this is straightforward: by expanding the portfolio of tree species used in managed woodlands, the proportion of damage caused by species-specific pathogens will be lowered (Ennos et al., 2019). There is global interest in the diversification of planted forests to mitigate ongoing pressure from climate change and pest/pathogen damage (Messier et al., 2021) and a major facet of this is provenance selection. Provenance refers to the geographical origin of the genetic resource used to establish a plantation, with local adaptation across different regions resulting in the expression of variable traits between provenances (Risk et al., 2021). These traits can include differences in cold hardiness, drought tolerance, phenology, growth rate and, of particular relevance to this study, pest and disease resistance (Lu et al., 2016). Provenances therefore provide an important secondary level of diversification within alternative species.

Future species and provenance selections are made on the basis of evidence obtained from experimental trials. These are field experiments where replicated blocks of species/provenance plots are grown together to evaluate their performance over time. This allows for measurements of growth and health related variables to be compared across geographical regions (Whittet et al., 2019). In 2012, a new series of trials was established in the UK to complement the EU-funded REINFFORCE project (Orazio et al., 2013) and to assess a range of species and provenances of interest to the UK forestry industry. The species present ranged from those already in widespread usage to comparatively untested exotic species. Mean survival and height data, along with observations on biotic and abiotic factors influencing performance, were collected five and six years post-planting (Reynolds et al., 2021; Ovenden et al., 2024). Dothistroma needle blight (DNB) was identified as the main disease present and the trials included a DNB-resistant provenance of radiata pine. Reynolds et al. (2021) reported putative variation in susceptibility to DNB between pine species and among provenances of the same species. However, the DNB susceptibility levels were not quantified, providing an opportunity for future assessments to investigate disease responses across the range of pines present. The impact of *P. ramorum* was also discussed, with resultant statutory felling of a larch plot at one of the sites, alongside heavy infection of western red cedar (*Thuja plicata* D. Don) by Thuja blight, caused by the ascomycete *Didymascella thujina*, in the spring of 2017.

These observations from Reynolds et al. (2021) suggest the need for follow-up assessments to better understand the full range of pathogens present at the trials and their impacts on tree health. As disease susceptibility is a crucial determinant of the commercial utility of tree species, such assessments would provide a necessary supplement to the survival and height data previously collected. This study examined the impact of local endemic pathogens on the health of species and provenances present at the trials. This was achieved by: 1) Recording a number of health-related variables and identifying the primary causal agents of disease damage detected and 2) Determining the variability in susceptibility to pathogen pressure between species and provenances. The results will provide foundational data on pathogen threats to the species and provenances under assessment. Taken alongside survival and height data, this will provide

a more holistic assessment of likely performance in a commercial setting.

Methods

Species trials

Tree health assessments were conducted at four Forest Research species trials planted in the UK in 2012 and 2013 representing different geographical locations and site characteristics (Fig. 1, Table 1). The sites Glentress (Scotland) and Westonbirt (SW England) were surveyed in May and July of 2021 respectively; Bramshill (SE England) and Llandovery (Wales) were surveyed in July of 2022. A total of one to three provenances of 17 species were assessed across the four sites, after omitting cases of poor or failed establishment. The range of species planted across sites varied to a certain extent to reflect geographical suitability. Table 2 lists the full range of species and provenances planted at each site. The geographical origin for each provenance code is presented in Supplementary Table 1. For all sites, experimental units were planted in 49-tree plots (7 x 7 rows) at 2 x 2 metre spacing and were arranged in a randomised block design replicated three times.

Tree health assessments

Tree health assessments followed a standardised survey method with 13 trees assessed per plot by moving through each plot in a south-west to north-east direction (Fig. 2). Where tree density restricted access to the interior of a plot, an alternative survey method was used whereby 13 trees visible from the outer perimeter were assessed instead (Table 2). Tree health was assessed by assigning each survey tree a percentage score ranging from 0–100 per cent for the following health variables: foliage necrosis (bronzed, brown [necrotic] and chlorotic foliage), defoliation (premature loss of foliage), shoot mortality (withering and death of fine shoots extending from branches), branch mortality (death of branches connected to main central stem) and main stem mortality (proportion of main stem and associated branch systems dead). The percentage score was based on the extent of visible damage taken as a proportion of all visible foliage, shoots, branches or main stem. For example, a survey tree where half of all visible foliage displayed symptoms of browning or chlorosis would receive a score of 50 per cent for the foliage necrosis variable. When symptoms suggested infection by fungal or oomycete pathogens, foliar and shoot samples were collected for subsequent morphological and molecular identification of causal agents.

Statistical analyses

All statistical analyses were performed in R v. 4.3.2 (R Core Team, 2023). Data were analysed using linear mixed models, so as to account for the random effect of repeated measurements within plots. All outcome variables were arcsine transformed to meet the assumptions of linear regression. Analysis of variance was used to assess the statistical significance of fixed effects: species and site, for species comparisons, and provenance, site and provenance-site interactions for provenance comparisons. Adjusted marginal means and pairwise comparisons, with a Tukey correction for multiple comparisons, were obtained using the emmeans package (Lenth, 2024).

Morphological identification of fungal species

Morphological identification of putative causal agents of observed damage was achieved initially via examination of samples in the field with a hand lens followed by more detailed examination



Figure 1. Locations of Forest research species trials assessed during this study

of collected material in the laboratory using a dissecting microscope. Individual fruiting bodies were squashed in 10 per cent glycerol or water on a microscope slide and examined using a light microscope at x100 and x400 magnifications to observe spores. Observed fruiting structures and spore type characteristics were compared to published species descriptions. When no diagnostic characteristics were evident, foliar samples were placed on

dampened paper towels and sealed in plastic bags for incubation at room temperature over seven days, with periodic checks for the development of fruiting bodies.

Isolations from shoot samples

Isolations were performed on all collected shoot samples. Using a sterile scalpel, the outer bark was removed from shoot

Table 1. Trial site characteristics (adapted from Reynolds et al., 2021)

Site Characteristics	Glentress	Westonbirt	Bramshill	Llandovery
OSGB Grid ref	NT303399	ST840891	SU852652	SN818371
Lat, Long	55.38°N: 3.06°W	51.36°N: 2.13°W	51.22°N: 0.46°W	52.01°N: 3.43°W
Elevation (m asl)	170–210	140	95	175
Aspect	SE	nil	nil	NW
Slope	Steep	Flat	Flat	Moderate
Rainfall (mean annual, mm)	892	824	665	1351
Exposure (DAMS score)	10	14	12	10
Soil nutrient regime	Rich	Carbonate	Poor	Medium
Soil moisture regime	Fresh	Moderately dry	Very moist	Very moist
Soil	Gala Unit 4—Wacke	Forest Marble Formation- Limestone	Camberley Sand	Triwdr Formation -Mudstone and Sandstone

Table 2. Tree species and provenances assessed at the four trial sites, including method used for plot assessment whereby standard refers to method outlined in Fig. 2 and outer refers to scoring of outer periphery trees only, and number of plots assessed using each method. Geographical information for each provenance code is provided in Supplementary Table 1

Species	Provenances present at each site				Survey method and number of plots scored		
	Glentress	Bramshill	Llandovery	Westonbirt	Standard	Outer	Total
Scots pine	POLA	POLA	POLA	POLA	11	1	12
	SCOT	SCOT	SCOT	SCOT	12	0	12
	VALS	VALS	VALS	VALS	12	0	12
Radiata pine	DOTH	DOTH	DOTH	DOTH	11	1	12
	WO	WO	WO	WO	12	0	12
Maritime pine	CORD	CORD			6	0	6
	LACO	LACO			6	0	6
	LAND	LAND			6	0	6
Weymouth pine	643	643			6	0	6
	CZRI	CZRI			6	0	6
Douglas fir	ORCO	ORCO	ORCO	ORCO	1	11	12
	ORSI	ORSI	ORSI	ORSI	12	0	12
	WASH	WASH	WASH	WASH	12	0	12
European larch	THEI	THEI	THEI	THEI	7	5	12
Hybrid larch	LAVE	LAVE	LAVE		5	4	9
		TRUU	TRUU		6	0	6
Sitka spruce	QSS		QSS	QSS	7	2	9
	USS		USS	USS	9	0	9
Western red-cedar	DARR		MONT	MONT	9	0	9
Atlantic cedar	VISF	MENE			6	0	6
Coast redwood			NOCA	NOCA	6	0	6
Japanese red cedar			P1	P1	6	0	6
			P2	P2	6	0	6
			P3	P3	6	0	6
Pedunculate oak			FRAN	FRAN	6	0	6
			UNIT	UNIT	9	0	9
Silver birch	UNIT	UNIT	UNIT	UNIT	12	0	12
		NORD	NORD	NORD	3	0	3
Red oak	FEST	FEST			6	0	6
Big leaf maple				232	3	0	3
Pyrenean oak			P1	P1	6	0	6

sections displaying visible lesions. Tissue pieces of approximately 5 mm² were removed from expanding lesion margins and plated onto Malt Extract Agar (MEA) or, in cases of suspected *Phytophthora* infection, *Phytophthora*-specific Synthetic Mucor Agar (SMA) amended with antibiotics (Elliot et al. 1966). Plates were then incubated in the dark at room temperature (approximately 20°C) for 7–14 days with periodic checks for hyphal growth. Growing colonies were subcultured onto MEA, or V8 in the case of suspected *Phytophthora* isolates, and incubated at 17°C for molecular identification.

Molecular identification of fungal species

Molecular identification was carried out by PCR amplification of the internal transcribed spacer region of the ribosomal DNA (ITS). This is a DNA barcode region commonly used for fungal identification (Tekpinar & Kalmer, 2019). All DNA samples were amplified using the ITS1F (5' CTTGGTCATTTAGAGGAAGTAA 3') and ITS4 (5' TCCTCCGCTTATTGATATGC 3') primers (White et al., 1990). For direct sequencing of lesion material and foliar samples which did not present any characteristic fruiting structures or spore types after incubation, samples were lyophilised overnight

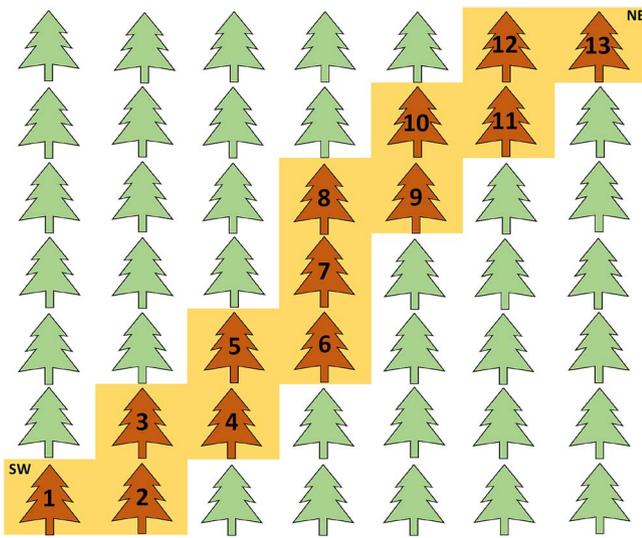


Figure 2. Standard survey method whereby thirteen trees in the order numbered were assessed per plot by moving from the south-west (SW) to the north-east (NE) corners of each plot

using an Alpha 1–2 LDplus freeze dryer (Martin Christ, Osterode). Homogenisation was then performed by adding three steel beads to each sample tube and grinding in a mixer mill (MM 400, Retsch, Haan) for 60 seconds. DNA extractions and PCR inhibitor removal was performed using the NucleoSpin® Plant II kit (Macherey-Nagel, Düren) and the OneStep™ PCR Inhibitor Removal Kit (Zymo Research, California), as per the manufacturer's instructions. PCR mixtures (50 μ L) contained: 10 μ L of 5x Colourless GoTaq® Flexi Buffer (Promega, Madison), 29.75 μ L of H₂O, 2 μ L of each primer, 3 μ L of MgCl₂, 1 μ L of dNTPs, 0.25 μ L of Taq polymerase and 2 μ L of DNA sample. Negative controls contained 2 μ L of H₂O in place of the DNA sample and positive controls contained 2 μ L of *Chalara fraxinea* gDNA. All samples were amplified using a Veriti™ 96 Well Thermal Cycler (Thermo Fisher Scientific, Waltham) programmed with the following cycling parameters: 95°C for 5 min followed by 30 cycles of 35 s at 95°C, 60 s at 55°C and 45 s at 72°C, with a final extension step of 5 min at 72°C and cooling at 4°C.

For sequencing of fungal cultures, a direct colony PCR method was used in place of DNA extraction. For each sample, a sterile pipette tip was used to scrape fragments of mycelium from the colony surface. These fragments were placed in a 0.2 mL tube with 20 μ L of 20 mM NaOH (pH 12) and incubated in a Veriti™ 96 Well Thermal Cycler (Thermo Fisher Scientific, Waltham) using the following cycling parameters: 100 °C for 15 min, followed by 4°C for 5 min. Post incubation, 20 μ L of 40 mM Tris-HCl (pH 5) was added to each tube, with the lysate used for PCR amplification. PCR mixtures (40 μ L) contained: 20 μ L Quick-Load Taq 2x Master Mix (New England Biolabs) 14 μ L of H₂O, 2 μ L of each primer and 2 μ L of DNA sample. Negative controls contained 2 μ L of H₂O in place of the DNA sample and positive controls contained 2 μ L of *Chalara fraxinea* gDNA. Amplification was performed using a Veriti™ 96 Well Thermal Cycler (Thermo Fisher Scientific, Waltham) programmed with the following cycling parameters: initial denaturation of 95°C for 2 min, followed by 30 cycles of 95°C (35 sec), 55°C (55 sec) and at 72°C (45 sec), and a final extension step at 72°C for 10 minutes.

Following PCR, gel electrophoresis was carried out in 1 per cent agarose gels stained with GelRed® Prestain Plus 6X DNA Loading Dye (Biotium, Fremont). PCR products (approximately

650 bp) were viewed on a UVP 2UV Benchtop Transilluminator (Thermo Fisher Scientific, Waltham) under UV light. DNA samples were then cleaned up using an ExoSAP-IT™ PCR Product Cleanup Reagent (Thermo Fisher Scientific, Waltham) as per the manufacturer's instructions before Sanger sequencing. Raw sequences were aligned and edited using Sequencher® v. 5.4.6 for Windows (Gene Codes Corporation, Ann Arbor) and searched against published sequences in the Genbank NCBI nucleotide database using BLASTN+ (Altschul et al., 1990). Species identity was based on a 100 per cent or 99 per cent match across the entire sequence length to verifiable sequences derived from voucher specimens or published taxonomic papers.

Results

Key symptoms observed during health assessments

At all four sites, symptoms of foliage necrosis and shoot mortality were the primary indicators of pathogen damage detected. For the conifers, foliage necrosis was characterised by brown discoloration of needles (Fig. 3A, B), which in severe cases was prevalent throughout the crown (Fig. 3B), alongside foliar chlorosis and bronzing (Fig. 3C). Symptoms of foliage necrosis were also observed in association with shoot tip wilting (Fig. 3D), and shoot mortality was typified by the presence of bare, defoliated shoots in the crown (Fig. 3E). Another symptom observed most commonly on Weymouth pine (*Pinus strobus* Linnaeus) was swelling of stems at branch junctions, associated with bark cracking and resinosis (Fig. 3F). For the broadleaves, foliage necrosis and discoloration was characterised by necrotic leaf spots and coverings of white mycelium respectively, whilst shoot mortality was characterised by wilting or defoliation. As foliage necrosis and shoot mortality accounted for most observed pathogen damage, these two health variables were analysed statistically. Both variables were analysed first at the species level, with provenances and sites pooled due to inconsistent replication across sites, and second at the provenance level for Scots pine and Douglas fir, both of which were represented by three provenances present at all four sites.

Foliage necrosis and shoot mortality across all host species

For foliage necrosis, there was a highly significant effect of species and a non-significant effect of site (Tables 3A and 4A). Japanese red cedar (*Cryptomeria japonica* (Thunberg ex Linnaeus f.) D. Don) had the highest mean foliage necrosis score, which was significantly higher than all other conifers except for maritime pine, Douglas fir, radiata pine and coast redwood (*Sequoia sempervirens* (D. Don) Endlicher) (Fig. 4A). Douglas fir had a significantly higher mean foliage necrosis score than Sitka spruce (Fig. 4A). The four pine species also grouped in the upper range, with maritime pine having a significantly higher mean foliage necrosis score than Scots pine (Fig. 4A). Of the broadleaves, pedunculate oak (*Quercus robur* Linnaeus) and silver birch (*Betula pendula* Roth) had the highest mean foliage necrosis scores, which were significantly higher than Pyrenean oak (*Quercus pyrenaica* Willdenow) (Fig. 4A).

For shoot mortality, there was a highly significant effect of both species and site (Table 3B), with significantly higher shoot mortality across all species at Llandovery compared with Bramshill (Table 4B). As with foliage necrosis, the pine species grouped in the upper range, with maritime pine having a significantly higher mean shoot mortality score than Scots pine (Fig. 4B). Weymouth pine had a significantly lower mean shoot mortality score than

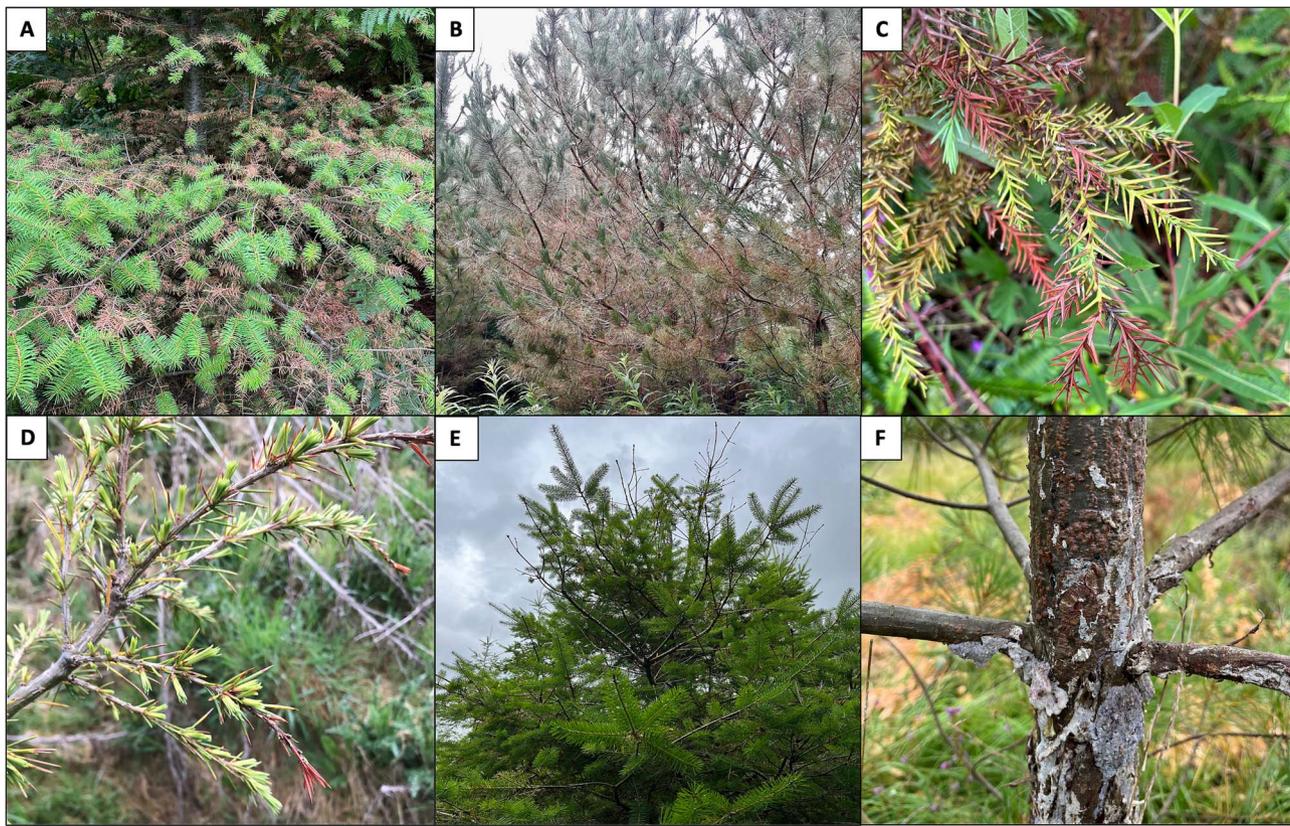


Figure 3. Selection of key symptoms observed during health assessments. A: *Nothophaeocryptopus gaeumannii* causing needle browning and loss on Douglas fir WASH at Bramshill, B: *Dothistroma septosporum* causing needle discoloration on radiata pine WO at Westonbirt, C: *Pestalotiopsis* sp. causing needle discoloration on Japanese red cedar P1 at Llandovery, D: Needle discoloration and loss due to *Sirococcus tsugae* on Atlantic cedar VISF at Glentress, E: Douglas fir ORCO shoot mortality at Llandovery with causal agent as yet unidentified, F: Stem bleeding on Weymouth pine 0643 at Bramshill, most likely due to rust infection

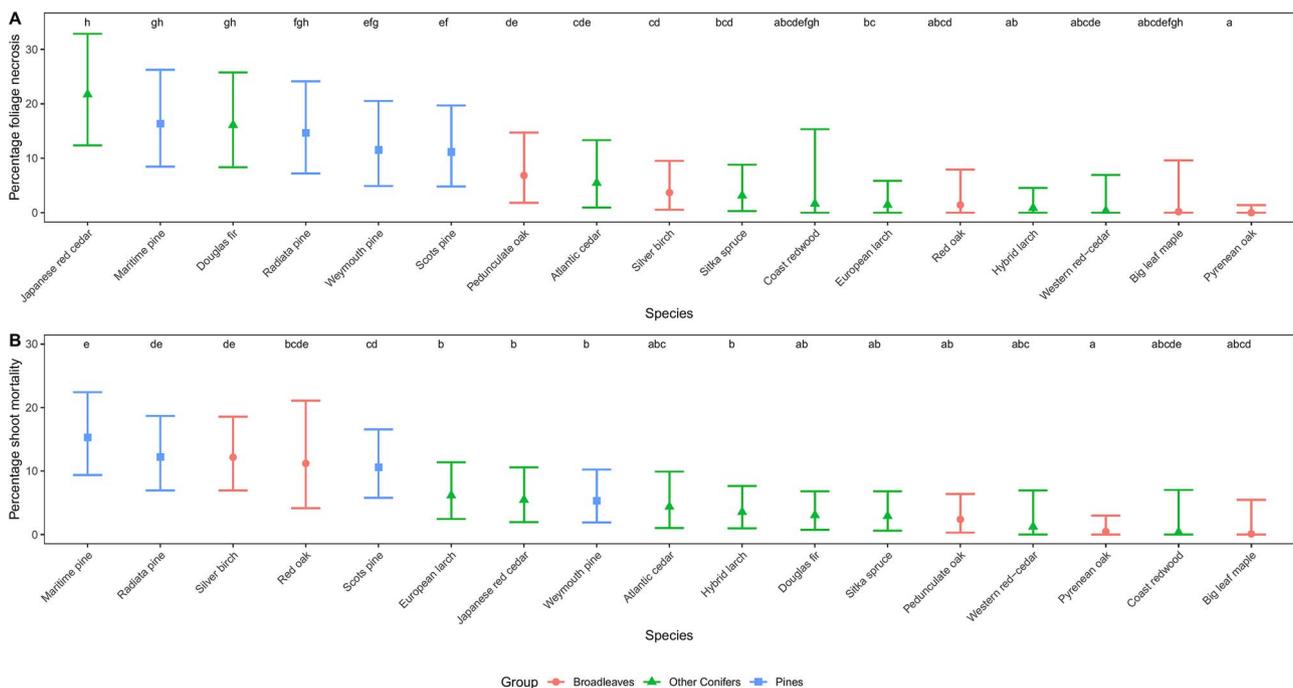


Figure 4. Mean foliage necrosis and shoot mortality scores for all species, provenances and sites pooled. Error bars represent 95 per cent confidence intervals. Letters denote honestly significant differences: Any species with shared letters are not significantly different from one another

Table 3. ANOVA output for all models

A. All Species: Foliage necrosis					
Variable	Sum Sq	Mean Sq	NumDF	DenDF	P. value
species	20.11	1.26	16	519.8554	<0.001
site	0.08	0.03	3	160.4975	0.4046
B. All Species: Shoot Mortality					
Variable	Sum Sq	Mean Sq	NumDF	DenDF	P. value
species	9.40	0.59	16	549.7391	<0.001
site	7.21	2.40	3	156.4463	<0.001
C. Scots Pine: Foliage necrosis					
Variable	Sum Sq	Mean Sq	NumDF	DenDF	P. value
prov	0.35	0.17	2	23.61630	0.0018
site	0.47	0.16	3	16.26065	0.0024
prov:site	0.73	0.12	6	30.07646	<0.001
D. Scots Pine: Shoot Mortality					
Variable	Sum Sq	Mean Sq	NumDF	DenDF	P. value
prov	0.60	0.30	2	17.27792	<0.001
site	0.68	0.23	3	16.92532	<0.001
prov:site	0.87	0.14	6	23.86093	<0.001
E. Douglas Fir: Foliage necrosis					
Variable	Sum Sq	Mean Sq	NumDF	DenDF	P. value
prov	0.14	0.07	2	34.04055	0.0606
site	3.83	1.28	3	19.71856	<0.001
prov:site	0.31	0.05	6	33.96745	0.0606
F. Douglas Fir: Shoot Mortality					
Variable	Sum Sq	Mean Sq	NumDF	DenDF	P. value
prov	0.10	0.05	2	113.18588	0.021
site	5.53	1.84	3	39.07236	<0.001
prov:site	0.27	0.05	6	81.75406	0.0037

Table 4. Collated mean foliage necrosis and short mortality scores by site for all models. Letters denote honestly significant differences: Any species with shared letters are not significantly different from one another

A. All species: foliage necrosis			B. All species: shoot mortality		
Site	Score (%)	HSD Group	Site	Score (%)	HSD Group
Glentress	6.1	a	Glentress	3.0	ab
Westonbirt	5.3	a	Westonbirt	3.8	ab
Bramshill	11.5	a	Bramshill	7.2	a
Llandovery	10.5	a	Llandovery	15.2	b
C. Scots pine: foliage necrosis			D. Scots pine: shoot mortality		
Site	Score (%)	HSD Group	Site	Score (%)	HSD Group
Glentress	17.8	ab	Glentress	12.1	ab
Westonbirt	21.9	ab	Westonbirt	16.8	ab
Bramshill	16.1	b	Bramshill	9.8	a
Llandovery	10.7	a	Llandovery	18.7	b
E. Douglas fir: foliage necrosis			F. Douglas fir: shoot mortality		
Site	Score (%)	HSD Group	Site	Score (%)	HSD Group
Glentress	0.7	a	Glentress	0.02	a
Westonbirt	0.6	a	Westonbirt	0.004	a
Bramshill	12.8	b	Bramshill	1.1	b
Llandovery	27.4	c	Llandovery	13.6	c

the other three pine species (Fig. 4B). No significant differences in mean shoot mortality score were detected among other conifer species (Fig. 4B). Of the broadleaves, silver birch and red oak (*Quercus rubra* Linnaeus) had the highest mean shoot mortality scores, with silver birch having a significantly higher score than pedunculate oak and Pyrenean oak, and red oak having a significantly higher score than Pyrenean oak (Fig. 4B).

Year of sampling had no significant effect on foliage necrosis ($P=0.412$) or shoot mortality ($P=0.181$).

Foliage necrosis and shoot mortality of scots pine at the provenance level

For Scots pine, there were significant effects of both provenance and site on foliage necrosis, and a highly significant

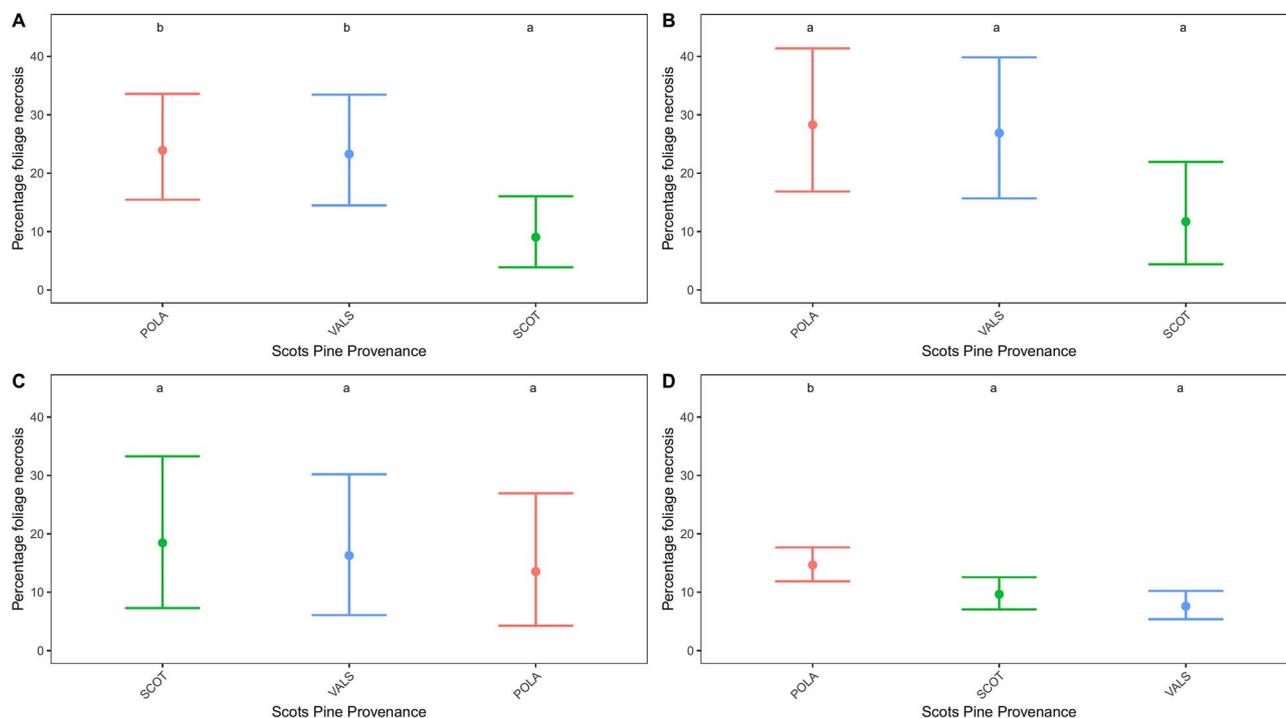


Figure 5. Mean foliage necrosis scores for scots pine provenances at each site. A: Glentress, B: Westonbirt, C: Bramshill and D: Llandovery. Error bars represent 95 per cent confidence intervals. Letters denote honestly significant differences: Any species with shared letters are not significantly different from one another

provenance-site interaction (Table 3C). Mean foliage necrosis scores across all provenances were significantly higher at Bramshill compared with Llandovery (Table 4C). At Glentress, provenances VALS (Spanish) and POLA (Polish) had significantly higher mean foliage necrosis scores than SCOT (Scottish) (Fig. 5A). The provenance POLA (Polish) also exhibited significantly higher foliage necrosis than the two other provenances at Llandovery (Fig. 5D), but no differences were observed among provenances at Westonbirt and Bramshill (Fig. 5B, C).

For shoot mortality, there were highly significant effects of provenance and site and a highly significant provenance-site interaction (Table 3D). Significantly higher shoot mortality was observed for Scots pine at Llandovery compared with Bramshill across all provenances (Table 4D). No significant differences in mean shoot mortality score were detected between provenances at Glentress, Westonbirt and Bramshill (Fig. 6A, B, C). At Llandovery, all three provenances had significantly different scores, with POLA (Polish) having the highest shoot mortality, and SCOT (Scottish) the lowest (Fig. 6D).

Foliage necrosis and shoot mortality of radiata pine at the provenance level

Due to poor survival (44 per cent mean survival across the trial sites, as per Reynolds et al., 2021) full results for radiata pine have not been included. However, due to the inclusion of a *Dothistroma* resistant provenance (DOTH) and the fact that both provenances were replicated at all four sites, a brief summary of findings is presented here.

For foliage necrosis, there was a non-significant effect of provenance ($P = 0.434$), a highly significant effect of site ($P = 0.003$) and a non-significant provenance-site interaction ($P = 0.485$). Mean foliage necrosis scores across all provenances were significantly higher at Westonbirt when compared to Glentress and Llandovery. At Bramshill, the provenance DOTH had a significantly higher

mean foliage necrosis score than WO. No significant differences between provenances were detected at the other sites.

For shoot mortality, a non-significant effect of provenance ($P = 0.800$), significant effect of site ($P = 0.029$) and significant provenance-site interaction were detected ($P = 0.028$). Mean shoot mortality across all provenances was significantly higher at Llandovery when compared to Glentress. At Bramshill, the provenance DOTH had a significantly higher mean shoot mortality score than WO. No significant differences between provenances were detected at the other sites.

Foliage necrosis and shoot mortality of Douglas fir at the provenance level

For foliage necrosis of Douglas fir, there was a non-significant effect of provenance, a highly significant effect of site and a non-significant provenance-site interaction (Table 3E). Foliage necrosis in all provenances was significantly higher at Llandovery than for all other sites and lowest at both Glentress and Westonbirt (Table 4E). The only difference among provenances was found at Bramshill, with WASH (Washington cascade, USA) significantly higher than ORSI (Oregon, Siskiyou, USA) (Fig. 7C).

For shoot mortality of Douglas fir, there was a significant effect of provenance, highly significant effect of site and significant provenance-site interaction (Table 3F). Mean shoot mortality scores across all provenances at each site followed the same trend as for foliage necrosis, with Llandovery having a significantly higher score than Bramshill, and significantly lower scores at Glentress and Westonbirt (Table 4F). No significant differences in mean shoot mortality scores were detected among provenances at Glentress and Westonbirt, with all scores near zero (Fig. 8A, B). Whilst shoot mortality scores for all three provenances were marginally higher at Bramshill, no significant differences were detected (Fig. 8C). At Llandovery, ORSI (Oregon, Siskiyou, USA) had a significantly higher mean shoot mortality

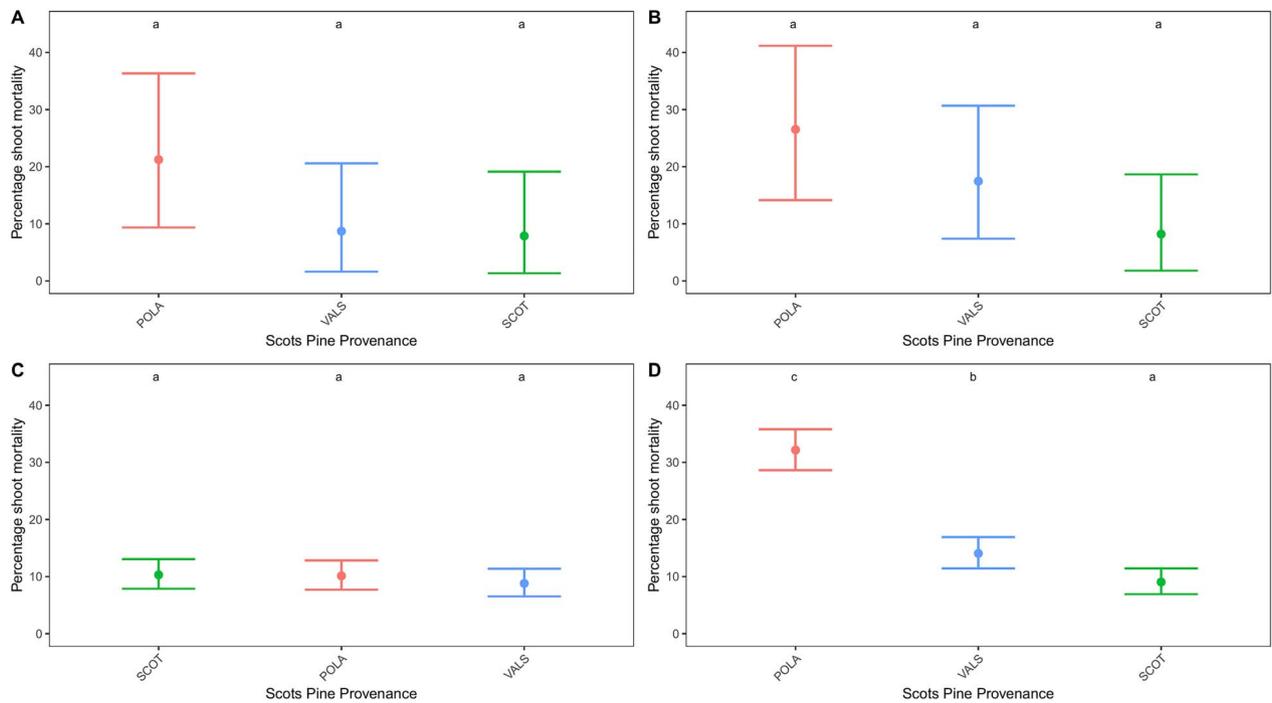


Figure 6. Mean shoot mortality scores for scots pine provenances at each site. A: Glentress, B: Westonbirt, C: Bramshill and D: Llandovery. Error bars represent 95 per cent confidence intervals. Letters denote honestly significant differences: Any species with shared letters are not significantly different from one another

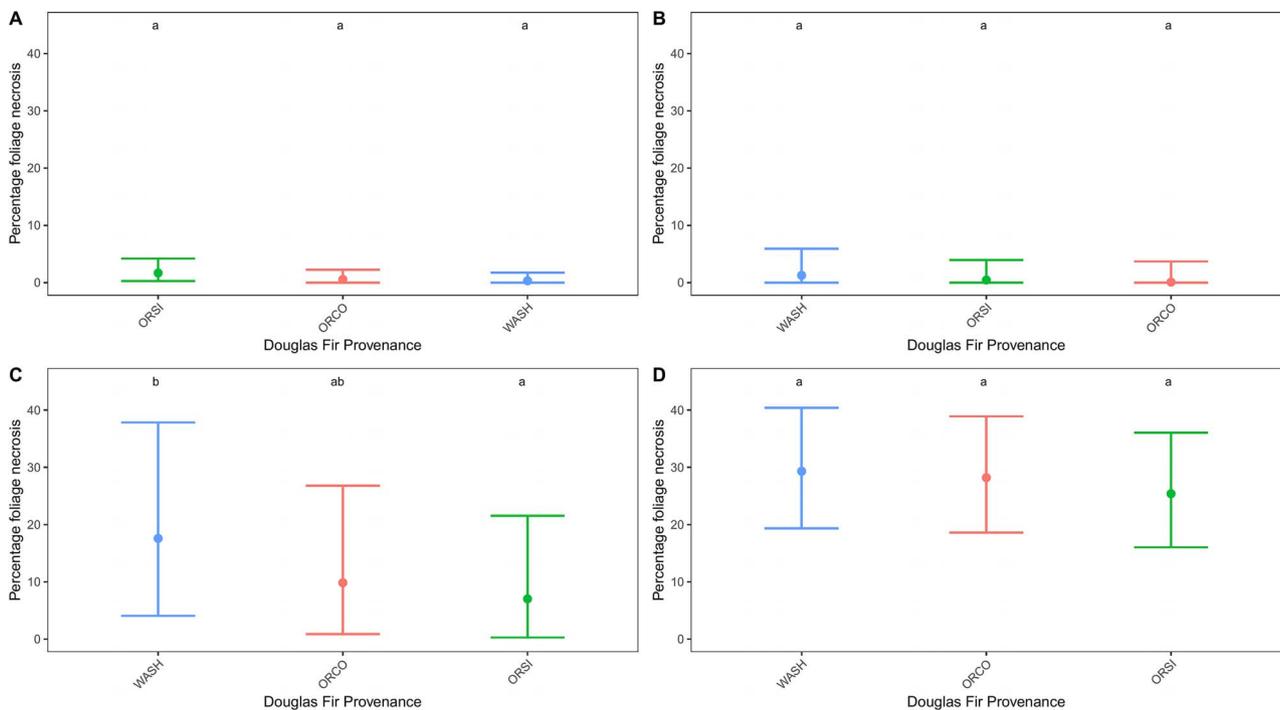


Figure 7. Mean foliage necrosis scores for Douglas fir provenances at each site. A: Glentress, B: Westonbirt, C: Bramshill and D: Llandovery. Error bars represent 95 per cent confidence intervals. Letters denote honestly significant differences: Any species with shared letters are not significantly different from one another

score than WASH (Washington cascade, USA) and ORCO (Oregon Coast, USA) (Fig. 8D).

Fungal species detected during health assessments

A total of 19 fungal pathogen species were detected during health assessments across the four trial sites. Table 5 details the full

list, along with the identification method used and the site, host species, provenance and tissue of origin for each fungal species detected. These species were identified based on morphological or molecular identification and can be linked to the damage observed. Particularly prevalent was the needle blight pathogen *Dothistroma septosporum*, detected on all provenances of both radiata pine (e.g. Figure 3B) and Scots pine at all four sites and on two

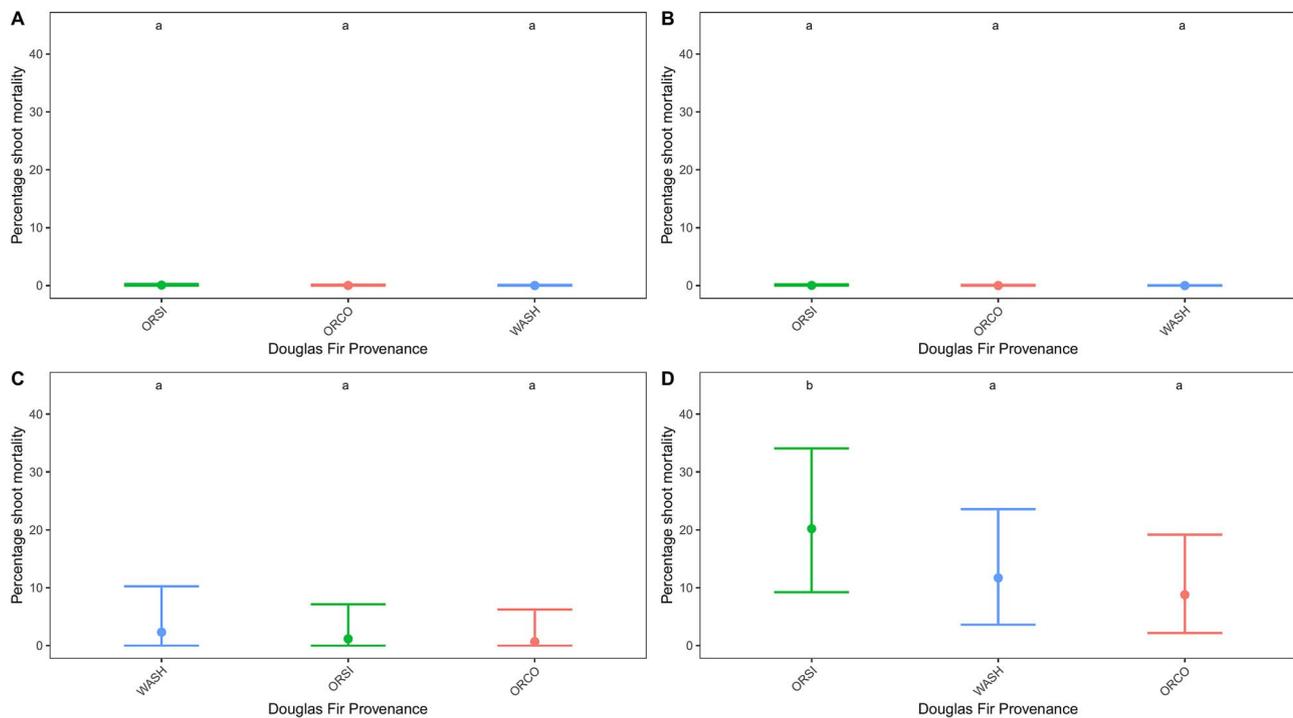


Figure 8. Mean shoot mortality scores for Douglas fir provenances at each site. A: Glentress, B: Westonbirt, C: Bramshill and D: Llandovery. Error bars represent 95 per cent confidence intervals. Letters denote honestly significant differences: Any species with shared letters are not significantly different from one another

provenances of maritime pine at Glentress (Fig. 9A) and Bramshill (Table 5). A notable needle cast pathogen, *Nothophaeocryptopus gaeumannii*, was detected on all provenances of Douglas fir at three sites (Table 5, Figs. 3A and 9B). Other needle cast pathogens detected included *Rhizosphaera kalkhoffii*, on a provenance of Sitka spruce at Westonbirt (Table 5), and *Cyclaneusma minus*, on a provenance of radiata pine at Glentress (Table 5).

Known shoot pathogens of conifers included *Sirococcus tsugae*, detected on a provenance of Atlantic cedar (*Cedrus atlantica* (Endl.) Manetti ex Carrière) at Glentress (Table 5, Fig. 3D), *Gremmeniella abietina*, detected on provenances of maritime and radiata pine at Glentress (Table 5), *Cenangium ferruginosum*, detected on a provenance of maritime pine at Glentress (Table 5), *Pestalotiopsis* sp., detected on all provenances of Japanese red cedar at Westonbirt and Llandovery (Table 5, Figs. 3C, 9C) and *Didymascella thujina*, detected on a provenance of western red-cedar at Westonbirt (Table 5). Significant shoot mortality was observed on a provenance of Douglas fir at Llandovery (Fig. 3E), with the causal agent as yet unidentified although a fungus identified as *Diaporthe rudis* was isolated from this material.

Symptoms of stem swelling, bark cracking and resinosis were observed on both provenances of Weymouth pine at Bramshill (Fig. 3F). These symptoms are consistent with infection by the white pine blister rust pathogen *Cronartium ribicola* although the causal agent was not confirmed.

Known foliar pathogens of broadleaves included the powdery mildew fungus *Erysiphe alphitoides*, detected on provenances of pedunculate and Pyrenean oak at Westonbirt and Llandovery (Table 5). Known shoot pathogens of broadleaves included *Apiognomonia errabunda*, detected on a provenance of red oak at Glentress (Table 5), and *Marssonina betulae*, detected on provenances of silver birch at Glentress, Westonbirt and Llandovery (Table 5).

The remaining seven fungal species or species groups detected have reported instances of pathogenic capacity but could not

be linked to known tree diseases of their respective hosts. This included *Phacidiopycnis washingtonensis*, associated with rot of pome fruits and leaf blight of Pacific madrone (*Arbutus menziesii* Pursh), which was isolated from dying foliage of coast redwood at Westonbirt (Table 5; Fig. 9D). An additional six species (*Coniothyrium lignorum*, *Cosmospora berkeleyana*, *Cryptosporiopsis diploidoides*, *Pezicula neocinnamomea*, *Pezicula neosporulosa* and *Pezicula pseudocinnamomea*) were also detected and have no reported associations with disease symptoms. They are therefore most likely endophytes, which are non-pathogenic members of fungal communities within trees. These are presented in Supplementary Table 2.

Discussion

This study provides a quantitative assessment of key pathogen impacts on a new generation of forestry species trials in the UK. Our findings clearly show that significant variability exists in foliage necrosis and shoot mortality at both the species and provenance level. The results highlight significant health impacts due to pathogens on several species of commercial potential across the trial sites, in particular the non-native pines. This work aligns with the considerable industry focus on identification of species to aid diversification efforts in commercial plantations. We discuss the most prevalent pathogens detected, their impact on forestry species of immediate industry interest and the implications for future species selection.

Pathogen impacts on the pines

The ascomycete needle blight pathogen *D. septosporum* was particularly impactful. It was detected consistently across all provenances of Scots, radiata and maritime pines, with significant levels of foliage necrosis observed. Since the late 1990s, *D. septosporum*

Table 5. All fungal pathogen species identified, identification method (Mor: Morphological, Mol: Molecular), host species, origin tissue, sites (G: Glentress, W: Westonbirt, B: Bramshill, L: Llandoverly) and provenances

Fungal Species	Identification Method	Host Species	Origin Tissue	Sites and Provenances
<i>Apiognomonia errabunda</i>	Mol	Red oak	Shoot	G (FEST)
<i>Cenangium ferruginosum</i>	Mol	Maritime pine	Shoot	G (LAND)
<i>Cyclaneusma minus</i>	Mor + Mol	Radiata pine	Foliage	G (WO)
<i>Diaporthe rudis</i>	Mol	Douglas fir	Shoot	L (WASH)
<i>Diaporthe</i> sp.	Mol	Atlantic cedar	Shoot	G (VISF)
	Mol	Maritime pine	Shoot	G (CORD)
	Mol	Douglas fir	Shoot	G (ORSI) L (ORCO)
	Mol	Pedunculate oak	Shoot	G (FRAN)
<i>Didymascella thujina</i>	Mor	Western red-cedar	Foliage	W (MONT)
<i>Dothistroma septosporum</i>	Mor + Mol	Radiata pine	Foliage	G, W, B, L (DOTH, WO)
	Mor	Maritime pine	Foliage	G, B (CORD, LACO)
	Mor	Scots pine	Foliage	G (LAND)
	Mor	Scots pine	Foliage	G, W, B, L (POLA, SCOT, VALS)
<i>Erysiphe alphitoides</i>	Mor	Pedunculate oak	Foliage	W (FRAN, UNIT)
	Mor	Pyrenean oak	Foliage	L (FRAN)
<i>Fusarium avenaceum</i>	Mol	Pedunculate oak	Shoot	W, L (P1)
<i>Fusarium</i> sp.	Mol	Scots pine	Shoot	L (FRAN)
<i>Gremmeniella abietina</i>	Mol	Maritime pine	Shoot	G (SCOT)
	Mol	Radiata pine	Shoot	G (CORD, LACO)
	Mol	Radiata pine	Shoot	G (DOTH, WO)
<i>Marssonina betulae</i>	Mor	Silver birch	Foliage + Shoot	G, W, L (UNIT)
				W, L (NORD)
<i>Nectria nigrescens/Nectria cinnabarina</i> (equal matches)	Mol	European larch	Shoot	G (THEI)
<i>Nothophaeocryptopus gaeumannii</i>	Mor	Douglas fir	Foliage	W, B, L (ORCO, ORSI, WASH)
<i>Pestalotiopsis</i> sp.	Mor	Japanese red cedar	Foliage	W, L (P1, P2, P3)
<i>Phacidiopycnis washingtonensis</i>	Mor	Coast redwood	Foliage	W (NOCA)
<i>Phacidium</i> sp.	Mol	Atlantic cedar	Shoot	G (VISF)
<i>Rhizosphaera kalkhoffii</i>	Mor	Sitka spruce	Foliage	W (QSS, USS)
<i>Sirococcus tsugae</i>	Mol	Atlantic cedar	Shoot	G (VISF)
	Mor	Douglas fir	Foliage	G (ORSI)

has caused considerable damage to pines in the UK, with Corsican (*Pinus nigra* J.F. Arnold subsp. *laricio* (Poir.)) found to be so badly affected that a moratorium on planting of the species was implemented in 2007 (Brown and Webber, 2008). Symptoms include the formation of distinctive red bands on needles and premature defoliation, reducing the overall photosynthetic capacity of the host (Forest Research, 2012). This inhibits growth and reduces yield from timber plantations: in stands suffering from 70 per cent mean crown infection, a 68 per cent decrease in mean annual volume increment has been observed (Brown and Webber, 2008). In addition to yield losses, at epidemic levels *D. septosporum* may also cause mortality of pine hosts (Wainhouse et al., 2016).

Dothistroma septosporum is clearly a pathogen of commercial significance, and one which this study indicates is of continued concern. There is recent evidence to suggest that planting of exotic pines has facilitated entry of novel *D. septosporum* races into the UK. Piotrowska et al. (2018) used microsatellite markers to identify three distinct strains of *D. septosporum* in Scotland: one of moderate genetic diversity and assumed to be endemic on native Caledonian Scots pine, a second exhibiting high levels of genetic variation and linked to the *D. septosporum* epidemic on Corsican pine and a third characterised by low genetic diversity and associated with introduced lodgepole pine. The implications of this are that the introductions of Corsican and lodgepole pine

have resulted in the co-introduction of exotic strains of *D. septosporum* from continental Europe and North America respectively. The lodgepole pine race has caused sufficient damage to plantations to necessitate extensive salvage felling and placement of a moratorium on planting of the species (Edwards, 2017), whilst the Corsican pine race appears to be causing more severe damage to Scots pine than the endemic *D. septosporum* race (Ennos et al., 2019).

Expanding exotic radiata and maritime pine plantings, shown by this study to be heavily impacted by *D. septosporum*, may inadvertently introduce or increase the abundance of exotic strains of *D. septosporum* and place more disease pressure on native Scots pine. There also appears to be no advantage to using the *Dothistroma*-resistant provenance of radiata pine, which had a significantly higher foliage necrosis score at Bramshill. This fact, coupled with the poor survival observed across the trial sites, further suggests that radiata pine may not be a suitable candidate for diversification.

Weymouth pine was notably less affected by *D. septosporum*. Whilst this may appear promising, the symptoms observed on Weymouth pine at Bramshill closely align with those described by Geils et al. (2010) for *C. ribicola*, the causal agent of white pine blister rust. With no aecia (the fruiting body of rust fungi) present, visual identification of the pathogen could not be made



Figure 9. Selection of fruiting bodies used for identification of fungal pathogens in this study. A: *Dothistroma septosporum* stromata rupturing through needle epidermis on maritime pine LACO at Glentress, B: Rows of black pseudothecia characteristic of *Nothophaeocryptopus gaeumannii* on Douglas fir WASH at Bramshill, C: Black spore tendrils characteristic of *Pestalotiopsis* sp. on Japanese red cedar C1 at Westonbirt D: Clear spore tendrils associated with *Phacidiopycnis washingtonensis* on coast redwood NOCA at Westonbirt

with confidence. In environmentally favourable conditions and in the presence of its alternate host (*Ribes* spp.), this pathogen has caused widespread and significant damage to Weymouth pine in North America (Kinloch, 2003). In the UK, Weymouth pine was discontinued as a forestry species in the late 1800s due to damage caused by *C. ribicola* (Forest Research, 2024a), with subsequent attempts to grow the species commercially in Europe resulting in failure (Ennos et al., 2019).

A further notable pathogen detection was *Grammaria abietina* on radiata and maritime pines. *Gremmeniella abietina* is the causal agent of Brunchorstia dieback (referred to in North America as Scleroderris canker), a disease associated with shoot dieback and cankers on a broad range of conifer species but most impactful on pines (Brown and MacAskill, 2005). The pathogen has proven particularly damaging on lodgepole pine and Scots pine in Sweden, with affected stands of Scots pine displaying a 64–85 per cent reduction in height growth (Karlman et al., 1994; Wang et al., 2017). In the UK, *G. abietina* has caused severe dieback on Scots pine leading to mortality (Brown and MacAskill, 2005) and was responsible for damage of Corsican pine plantations suffering from lack of winter sunlight due to inappropriate planting locations (Read, 1968). This pathogen was detected on multiple provenances of both radiata and maritime pine in our study, raising the question as to whether expansion of highly susceptible exotic pines in commercial plantations would result in significant build-up of *G. abietina* inoculum. This would pose a further disease risk not only to the exotic pines but also to native Scots pine.

Two other fungal pathogens were detected on the exotic pines: *C. ferruginosum* and *C. minus*, on maritime and radiata pine respectively. *Cenangium ferruginosum* is a shoot and canker pathogen found on many species of pine, normally affecting the lower branches (Mullet et al., 2017). In conditions of drought stress, however, *C. ferruginosum* has been observed to cause needle necrosis and subsequent mortality of shoots, branches and the main stem of Korean pine (*Pinus koraiensis* Siebold & Zucc.) (Ryu et al., 2018). *Cyclaneusma minus* is a needle cast pathogen which has proven to be very damaging on radiata pine plantations in New Zealand, with premature shedding of needles resulting in reduced growth over time (Hunter et al., 2016). With warmer winter air temperatures identified as a key climatic variable determining the severity of *C. minus* on radiata pine stands (Watt et al., 2012), it may be that the UK's warming climate will exacerbate this pathogen's impact.

One recommendation arising from this study is that pine diversification efforts should focus on the expansion of UK provenances within Scots pine. This is due to the elevated pathogen impacts found to be associated with exotic pines, reflected in their higher foliage necrosis and shoot mortality scores compared with Scots pine, and the potential risks of introducing novel *D. septosporum* strains and build-up of *G. abietina* inoculum. At three of the trial sites, the native provenance of Scots pine had significantly less foliage necrosis and shoot mortality than Polish and Spanish provenances. This is possibly due to coevolution of the native Scottish provenance with *D. septosporum* pathotypes

endemic to the UK, aligning with observations made by Perry *et al.* (2016). Scots pine is a species of considerable commercial interest, being the second most widely planted coniferous tree in Great Britain (Forest Research, 2023) and is classed as a principal forestry species. Priority should therefore be given to ensuring the continued viability of this species in a commercial setting, with the expansion of exotic pines potentially undermining resilience efforts.

Pathogen impacts on Douglas fir

Douglas fir was heavily impacted by the needle cast pathogen *N. gaeumannii*, detected on all provenances at three of the trial sites. *N. gaeumannii*, the causal agent of Swiss needle cast disease, has been responsible for a severe epidemic on Douglas fir in the Western United States which has persisted since the early 1990s (Hansen *et al.*, 2000). The pathogen causes damage to its host by physically blocking needle stomata with its fruiting bodies, known as pseudothecia, limiting CO₂ assimilation (Manter *et al.*, 2000). In heavily infected stands, this can result in annual growth losses of 20–50 per cent, with the economic impact in epidemic areas estimated to exceed \$200 million per annum (Maguire *et al.*, 2002). In the UK, *N. gaeumannii* is known to be ubiquitous on Douglas fir but is currently regarded as having limited impact (Forest Research, 2024b). However, changing climatic conditions in the UK, particularly warmer and wetter springs, may be increasing the prevalence and severity of this pathogen, with a noted increase in the number of *N. gaeumannii* cases reported to the Forest Research Tree Health Diagnostic and Advisory Service in 2019 (Blake and Perez-Sierra, 2020).

The causal agent of the significant shoot dieback observed across Douglas fir provenances at Llandovery could not be confirmed in the current study. However, *Diaporthe* sp. is a genus containing a wide range of known plant pathogens (Gomes *et al.*, 2013), with *Diaporthe rudis*, isolated from the symptomatic Douglas fir in this study, being known to infect conifer tree hosts such as maritime pine (Lopes *et al.*, 2021) and a number of broadleaf genera, including maple (*Acer* spp.), chestnut (*Castanea* spp.), hazel (*Corylus* spp.), beech, ash, gum, oak and willow (*Salix* spp.) (Udayanga *et al.*, 2014). More work is needed to investigate whether *D. rudis* is also pathogenic to Douglas fir.

Douglas fir is a major species of interest for commercial expansion in the UK, with industry delegates from a recent workshop held by Scottish Forestry and Forest Research identifying it as one of the top candidates for future productive application (Scottish Forestry, 2023). Douglas fir has previously been highlighted as a candidate species for diversification of Sitka spruce plantations (Cameron, 2015) and was found to have a General Yield Class (maximum mean annual increment in m³ ha⁻¹ year⁻¹) which was not significantly lower than Sitka spruce (Stokes *et al.*, 2023). Additionally, Ovenden *et al.* (2024) found that no significant differences in mean tree height were apparent between Douglas fir and Sitka spruce six years post-planting, with similar rates of survival depending on the provenance compared. Present as a UK forestry species since 1872, the classification of Douglas fir as a 'well-established' exotic suggests reduced (or more predictable) pathogen risks when compared to untested 'alternative' exotics, such as radiata and maritime pines (Ennos *et al.*, 2020).

Compared with Sitka spruce, the current primary forestry species in the UK, Douglas fir exhibited significantly higher foliage necrosis scores, due to the impact of *N. gaeumannii*. Whilst the needle cast pathogen *R. kalkhoffii* was detected on Sitka spruce, it is not considered to be a major pathogen (Tuffen and Grogan, 2019) as Sitka spruce displays only moderate susceptibility (Thrush *et al.*, 2021a). Selection of tolerant Douglas

fir provenances has previously been shown to mitigate damage caused by *N. gaeumannii* (Samek *et al.*, 2019; Wilhelmi *et al.*, 2017). Further efforts should focus on expanded provenance testing of Douglas fir for susceptibility to *N. gaeumannii* under UK conditions. It is notable that *N. gaeumannii* was not detected on Douglas fir at Glentress, possibly due to the comparatively open and cool aspect of the site, suggesting that site selection will also play a role in mitigating *N. gaeumannii* damage on Douglas fir.

Phytophthora pluvialis, an oomycete pathogen recently detected in the UK for the first time, was not detected on Douglas fir in this study. All confirmed infections of Douglas fir by *P. pluvialis* in the UK to date have been in the presence of infected western hemlock (*Tsuga heterophylla* (Raf.) Sarg) (Biddle, M, personal communication). Western hemlock therefore appears to be the primary host in the UK and was not included in the trials surveyed here. *Phytophthora ramorum* was not detected on any larch species surveyed. This may be due in part to statutory felling of larch plots with confirmed *P. ramorum* infections, as was the case at Glentress (Reynolds *et al.*, 2021).

Pathogen impacts on other conifers

In 2021, a multi-criteria analysis was used to identify the top five alternative conifer forestry species for commercial application in the UK (Peters *et al.*, 2021). The five highest ranked species included three of the conifers present in the Forest Research species trials, making them of particular interest for the pathogen impact survey. This includes coast redwood ranked in top position, Japanese red cedar ranked second, and western red cedar ranked third.

The fungal pathogen *P. washingtonensis* was detected on a provenance of coast redwood present at Westonbirt. This is the first reported instance of *P. washingtonensis* detected in association with foliage necrosis on coast redwood. The fungus was first described as the cause of post-harvest rot of apple (*Malus domestica* Borkh.), and canker and twig dieback disease on crabapple (*Malus sylvestris* (L.) Mill.) in the western United States (Xiao *et al.*, 2005). It was subsequently found to cause leaf blight disease on Pacific madrone in Washington and Oregon (Elliot *et al.*, 2014) and was detected in association with shoot dieback of giant redwood (*Sequoiadendron giganteum* (Lindl.) J. Buchholz.) in Germany (Langer *et al.*, 2024). The pathogen has been recently detected on coast redwood displaying foliage necrosis symptoms at a Forest Research operational species trial on the west coast of Scotland, and was also isolated from giant redwood with severe foliar and shoot dieback located at a plantation forestry site, also on the west coast of Scotland (Green, S, unpublished). Giant redwood was ranked fourth as a potential UK forestry species by Peters *et al.* (2021) but was not planted in the trials assessed in this study. Work is currently underway to confirm the pathogenicity of *P. washingtonensis* on both hosts and to better understand its potential impact on these two species of future commercial interest.

The fungal pathogen *Pestalotiopsis* sp. was detected on all provenances of Japanese red cedar present at both Westonbirt and Llandovery and could not be identified to the species level in this study. Whilst literature detailing the impacts of *Pestalotiopsis* sp. on Japanese red cedar is sparse, Thrush *et al.* (2021b) note that in conducive conditions *Pestalotiopsis funerea* can girdle stems, leading to death of the host. The damage caused by *Pestalotiopsis* sp. in the present study appears to be considerable, with Japanese red cedar having the highest levels of foliage necrosis across all host species. Further investigation of this pathogen's impact on Japanese red cedar and its potential to limit the future viability of the species in commercial forestry is warranted.

Didymascella thujina, causal agent of cedar leaf blight, was detected on a provenance of western red cedar at Westonbirt. Whilst host mortality due to this pathogen is rare, significant loss of incremental growth and branch mortality has been observed in heavily infected stands (Gray et al., 2013). The presence of *D. thujina* at Westonbirt had previously been noted and remedied through removal of heavy weed growth associated with humid conditions conducive to the pathogen (Reynolds et al., 2021). This provides an example of how management practices such as thinning can influence levels of disease damage. The symptoms detected during this study may be the remnants of this previous outbreak, reflected in the low levels of foliage necrosis and shoot mortality observed.

Pathogen impacts on broadleaves

Silver birch and oak are the first and second most widely stocked broadleaf species in UK forestry (Forest Research, 2023). They form part of the future scenario of a more diverse and resilient UK forest industry, although they are not as commercially important as conifer species at present. The fungal pathogen *Mycterothrips betulae* was detected on both provenances of silver birch across all four trial sites. *Marssonina betulae* is an aggressive, primary pathogen which causes leaf necrosis, shoot dieback and sunken stem cankers leading to progressive crown dieback in infected stands (Green and MacAskill, 2007). The impact of this pathogen was significant, with silver birch having the highest shoot mortality scores across all host species in the trials. For the oaks, *E. alphitoides* and *A. errabunda* were detected on pedunculate and red oak respectively. Classed as a major foliar pathogen of pedunculate oak, *E. alphitoides*, causal agent of oak powdery mildew, can significantly reduce growth and trigger tree decline (Copolovici et al., 2014). *Apiognomonina errabunda*, confirmed here by culture morphology which matched previously published descriptions (Vainio et al., 2017), has been linked to twig dieback on red oak with associated minor growth losses (Braze, 2018).

Abiotic factors

Abiotic factors will have influenced the health and performance of the species and provenances assessed during this study. For example, Reynolds et al. (2021) noted that differences in soil type between the trial sites resulted in heather check at Bramshill and rampant bramble and willow-herb growth at Westonbirt. With regard to pathogen impacts specifically: temperature, precipitation and humidity are all climatic variables which can significantly affect the level of damage observed (Sturrock et al., 2011) and result in fluctuations from year to year (Dun et al., 2023). As the four trial sites were located in different geographical regions of the UK, their individual climatic profiles will have played a role in the severity of damage recorded. A detailed assessment of this, particularly temporal trends in the three climatic variables specified above, was outside the scope of this work. However, the health variables measured reflect cumulative damage in the crown and are thus indicative of multi-year changes. As it is, the study provides a thorough account of pathogen impacts on the species trials ten years post-planting.

Conclusion

This study has provided insight into the main pathogen impacts on a range of species under consideration by the UK forestry industry for use in diversification efforts. This information can be used alongside other measures of performance to guide shortlisting of species for expanded provenance testing moving forward.

Significant health impacts associated with fungal pathogens were highlighted, with particular attention given to the risk posed by untested exotics which are closely related to native species. Such a practice may in fact undermine the desired resilience. For this reason, the key recommendation is that future diversification efforts focus on expanded provenance testing within Scots pine and the well-established exotic Douglas fir. Further work is also required to better understand the impact of *P. washingtonensis* and *Pestalotiopsis* sp. on coast redwood and Japanese red cedar respectively, both of which are ranked highly in terms of future commercial potential (Peters et al., 2021).

Supplementary data

Supplementary data are available at Forestry online.

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Data availability

The data underlying this article will be shared on reasonable request to the corresponding author.

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