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7. Insect Pests and Pathogens of Trees

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Because of the scope of this paper it has been written in two sections with the summaries and references combined.

Summary

- Evidence for current effects of climate change (CC) on forest insect pests in the UK is limited and largely anecdotal as appropriate long-term data sets are lacking. However, empirical or circumstantial evidence from North America (high confidence, H) and continental Europe (medium confidence, M) provide clear evidence for changes in abundance, damage or distribution related to CC.

- Increases in endemic levels of ‘feeding’ resulting from greater abundance, longer periods of seasonal activity or increased voltinism as a result of CC are not likely to have significant economic effects over a rotation (M). However, significant sublethal effects on tree growth in successive years, which may be likely under CC, would be economically significant (M). Increased impact from insects that can degrade valuable timber or kill mature trees provide the greatest risk to forestry and some of these insects are likely to benefit from CC (H).

- Predicting effects of CC on abundance and population dynamics from empirical studies of insects’ response to climatic variables is fraught with difficulties, but some generalisations can be made based on life history and other ecological characteristics of different insect groups. For those insects where one or a few factors have a dominating influence on abundance and damage, more specific and reliable predictions can be made.

- For the three insect groups discussed, the following responses to a warming and more unstable climate are projected. For aphids and related species, an extended period of activity and increased abundance is likely. Higher temperatures will increase the reproductive rate and those species that have multiple generations or can remain active throughout the year are likely to benefit most (H). Moderate drought stress of host trees as a result of changes in the spatial and seasonal distribution of rainfall will be favourable for some species.

- Many bark beetles and related species depend on damaged or moribund host trees for breeding success and increased damage by insects in this group is likely (H). Attacks on living trees over relatively large areas are possible for some species when population densities are high. Significant risk factors are therefore, more frequent and possibly larger windblows (M), drought stress on trees (M), and a possible increase in defoliator outbreaks (low confidence, L). Species with a southern distribution are likely to extend their range northward (M) and changes in silviculture such as the introduction of longer rotations as part of a carbon-capture strategy could increase vulnerability of trees to insects in this group (L).

- The abundance of Lepidoptera and sawflies can often be influenced by a range of factors and much remains to be discovered about the population dynamics of individual species. On balance, some species in this group are likely to become more abundant as a result of an increase in the number of generations per year (L-M), and an increase in tree susceptibility through changes in the seasonal timing and amount of rainfall on some sites (L-M). Some species with a predominantly southern distribution are likely to extend their range northwards.

- Adaptation measures adopted by the forestry sector to mitigate the effects of CC have the potential to influence pest abundance and damage (L-M). The main risk factors are afforestation, an increase in rotation length and the introduction of new tree species or provenances better adapted to a warmer climate.

- The severity of many tree disease epidemics are often weather related with temperature, rainfall and soil moisture acting as the main drivers and influencing sporulation, dispersal and survival (H). Episodes of climatic extremes such as periods of drought and windblow may also reduce host resistance to pathogen attack or cause wounds to trees that facilitate pathogen entry (H).

- Pathogens that infect foliage or have an aerial phase are likely to be especially responsive to the direct effects of CC. One example where this is already affecting production is Dothistroma needle blight (H). Other examples such as oak mildew or Swiss needle present an increasing disease risk in the future (L).

- In contrast, direct CC effects may have little impact on the growth and sporulation of ubiquitous root attacking and decay fungi such as *Armillaria* and *Heterobasidion* but drought stress is likely to predispose trees to attack by these pathogens and increase mortality (medium to high confidence, M-H). Likewise, latent pathogens which infect but can be asymptomatic for years are predicted to become more damaging as opportunities for activation and invasion increase with water stressed hosts (medium confidence, M).

- Milder winters are likely to enhance the over-wintering success of certain frost intolerant, root attacking Phytophthoras such as *P. cinnamomi* and *P. alni* leading to successive years of damage, particularly to broadleaved hosts (H) and may even extend periods of activity causing greater damage. The activity of some of the more recently arrived aerial *Phytophthora* species such as *P. ramorum* is likely to be favoured by mild springs with increased precipitation, whilst unusual weather events of rainfall associated with high winds could provide more opportunities for long-distance dispersal (M).

- Higher temperatures are likely to result in faster development rates and therefore rapid increases in the populations of insect vectors that disseminate pathogens, and also allow them to extend to tree populations at higher elevations (M).

- New threats such as chestnut blight and pitch canker, which have traditionally been viewed as southern European problems are extending their northern range (H). Trade pathways between EU countries inevitably provide more opportunities for such pathogens to arrive in the UK, and a changing climate is increasingly likely to favour establishment and secondary spread (M).

- Both horse chestnut and oak are now affected by significant bacteria-related disorders, that bacterial pathogens of trees may feature to a greater extent in future (L),

- Major forestry trees such as pine, oak, beech and sycamore, which together make up almost a third of forest cover in Britain, are at growing risk from known pathogens due to CC (M). The major forestry species Sitka spruce which comprises over half of the conifer resource is presently most exposed to pathogen threats driven by indirect CC effects such as drought stress, making it most vulnerable to root rot and latent pathogens (L).

- Provenance and species selection can counter the impacts of some climate-driven diseases, but introductions of new pests and pathogens in the UK over the last 20 years is also undermining CC adaptation efforts (H).

General Introduction

Fire, drought, windstorms, introduced species, as well as pests and pathogens are the most frequently mentioned agents of natural disturbance which bring about forest change. Climatic change is likely to influence all these drivers of disturbance, with fire and drought usually invoked as the agents most likely to increase and adversely affect ecosystems as climate warming occurs (Dale *et al*. 2001). For biotic disturbances, there has been some analysis of the impact of climate change on insect populations and the associated damage in forests, but generally less consideration of the potential impact of pathogens and diseases of trees and their subsequent influence on forests although this is now changing (Broadmeadow *et al.* 2009; Pautasso *et al*. 2012).

The most serious insect pests of commercial forestry can cause significant economic loss through the cumulative impact of sublethal effects on growth over a rotation (Straw 1996), and some can kill trees. Temperature is the predominant abiotic factor directly affecting insects, influencing growth, reproduction and development (Bale *et al.* 2002) and is the key climate variable projected to increase over the coming decades (Murphy *et al*. 2009). Together with likely changes in other climate variables, it has the potential to influence the distribution, abundance and impact of forest pests either directly or indirectly through effects on their natural enemies and the trees on which they feed.

For pathogens, two abiotic factors are most often cited in the development of plant disease epidemics - temperature and moisture. Just as with insect pests, climate change is also likely to have both direct and indirect effects on the activity of tree pathogens. Changes in temperature, precipitation, soil moisture and relative humidity have all been shown to have a direct influence on the sporulation, dispersal and survival success of many pathogens, whilst episodes of climatic extremes such as extended drought periods often reduce growth and affect the regulation of resistance mechanisms in trees. The indirect outcome of the latter is that trees may become more susceptible to disease outbreaks and plant pathosystems that already cause some damage are likely to become more difficult to manage, affecting the sustainability of commercial forest species under future climate scenarios.

As the UK climate changes, the new ‘bioclimatic envelope’ (Pearson & Dawson 2003) may support the establishment and spread of exotic agents not presently considered a threat to UK forestry. These may spread naturally but one of the most important routes of introduction is through the pathways of international trade in trees and timber. This subject, which comes largely within the remit of plant health legislation, is not addressed in this review in relation to insect pests, coverage of which is restricted to likely effects of CC on native or well established exotic pests, although some exotic pathogen threats are considered.

Overall, the prospect of climate change raises a number of important questions about likely effects on the vulnerability of UK forests to attack by pests and pathogens. As far as the management of native or long established forest insect pests or pathogens is concerned, the most important questions are:

- How will their distribution be affected by CC and will they alter their range or the area in which damage occurs?
- Will there be changes in the amount, frequency or duration of damage to trees?
- Will new pests or pathogens arise as the climate warms?

- Will any changes in forest management as an adaptive response to CC increase the risk of damage by pests and pathogens?

This technical paper reviews the information available on both insect pests (section A) and on forest pathogens (section B) either affecting British forests now, or at risk of doing so in the future.

Section A: Insect Pests

A.1 Background

Many factors affect the distribution, abundance and pest status of forest insects. The magnitude and significance of the effects of climate change (CC) will depend to a large extent on the life history characteristics of different kinds of pest and the relative importance of food resources, natural enemies, competitors and of climate itself in influencing population dynamics. For many insects, it is the complex interaction between these factors that determines insect population dynamics and, as a consequence, it is in general not possible to predict outbreaks or damage to trees with any precision. These difficulties increase in assessing how insect populations are likely to respond to a projected future climate.

These complexities are illustrated by the outbreak history and population dynamics of the pine looper moth, *Bupalus piniaria* in the UK. This important defoliator has cyclic population dynamics in some forests, typically in northern England and Scotland, where insecticidal control of outbreaks may be necessary to prevent heavily defoliated trees from succumbing to bark beetle attack (Bevan 1974, Cedervind *et al.* 2003, Långström *et al*. 2001). In outbreak areas, affected forests are historically associated with growth on poor sandy soils, with outbreaks sometimes preceded by severe droughts (Barbour 1988). In other forests, smaller non-cyclic fluctuations in abundance prevail so that pine looper, as with many other insect pests, is characterised by differences in population dynamics in different parts of the UK (Barbour 1988, Kendall *et al.* 2005). Although climatic factors do not appear to be important in pine looper population dynamics (Barbour 1988, Kendall *et al.* 2005), they may increase the overall risk of outbreaks on particular sites.

For most UK forest pests the details of population dynamics and of potential interacting factors are not as well-known as those of pine looper. Nevertheless, useful generalisations can be made from more detailed studies of the same insect in different regions or of related species with similar ecological characteristics. In some cases, one or two factors may have a dominating influence on pest abundance so that more specific predictions about likely effects of CC may be possible. Examples include the association between drought or windblow and bark beetle outbreaks, the effect of silvicultural operations on pest abundance, or the link between particular site conditions and the occurrence of damage. The pests considered in this review are grouped according to similarities in their ecology and life history characteristics, allowing some general predictions to be made. Climate change also has the potential to influence the abundance of insects with no history of significant damage to trees, but these will be difficult to anticipate.

A.2 Climate variables and their direct and indirect effects on insects

Climate itself may have a direct effect on insect pests, by influencing survival or development rate for example, or an indirect one by affecting the host tree on which they feed or through effects on the abundance or efficacy of the natural enemies that attack them (Ayres & Lombardero 2000, Masters *et al*. 1998). As a direct cause of mortality, climatic factors are generally unrelated to population density and so have no direct regulatory role. They may, however, change the form of density-dependent feedbacks and so have more complex effects on population dynamics (Klapwijk *et al*. 2012). Levels of mortality may also be sufficiently high or frequent to maintain populations at a low level, for example near the latitudinal or altitudinal range limit. For many pests however, it is likely that interactions between direct and indirect effects will determine changes in abundance and impact on trees. The main climate-related variables discussed and their main effects on insects are shown in Table A.1.

Table A.1 Projected climate changes relative to 1961-1990 baseline under the medium emissions scenario (Murphy *et al*. 2009) and likely direct or simple indirect effects on insects. Predicted effects on the abundance and impact of forest insect pests are discussed in the following sections.

	Climate variables and projected change to 2080	**Main predicted effects**	**Insect groups most affected**
Temperature	Greatest increase in summer mean temperature in southern England - up to 4.2 °C (2.2-6.8°C). Warming greater in summer than winter	**Development rate.** Increase in insect development rate, no. of generations and frequency of ‘sister’ broods; range extension	Multi-voltine aphids; semi-voltine bark beetles, weevils and wood-boring Lepidoptera; sawflies
Precipitation	Reduction in summer precipitation by up to 40% in southern England. Little change over parts of northern Scotland. Up to 33% increase in winter precipitation in winter in west of UK.	**Drought stress.** Reduction in resin flow in conifers; change in nutritional quality of leaves **Fire.** Increase in fire damaged trees	Bark beetles, especially primary pests; longhorn and buprestid beetles; aphids Bark and ambrosia beetles
Climate variability & extreme events	Storms difficult to predict and projected changes vary with climate model	**Windblow,** An increase in area and/or frequency of windblown and uprooted trees	Bark and ambrosia beetles

A.2.1 Temperature

Temperate insects normally experience significant daily and seasonal variation in temperature as well as in other environmental factors, and have appropriate adaptations to survive them. Nevertheless, unseasonably hot or cold weather can cause significant mortality and temperature can set ultimate limits to geographical range. In the maritime climate of the UK, which does not experience the climatic extremes found in continental areas of Europe, many forest pests are widely distributed, with the obvious exceptions of recently introduced pests which have not yet colonised all suitable areas.

Over most of the temperature range to which particular species are adapted, there is a linear relationship between growth rate and temperature (Trudgill *et al.* 2005). Development of the different stages of an insect’s life cycle is usually quantified as the thermal sum, above a minimum developmental temperature, that is required for completion of the life cycle. At higher temperatures, this sum is accumulated earlier in the season allowing some species, including aphids and some bark beetles, to complete additional generations, extending the period over which feeding damage occurs and possibly resulting in an increase in population growth (Steinbauer *et al*. 2004, Altermatt 2010).

Insects that are uni-voltine (one generation per year) such as many defoliators adapted to feed on newly flushed leaves of broadleaved trees, cannot increase the number of generations. These insects adjust the timing of the life cycle to allow for faster development by extending the dormant overwintering stage (e.g. van Asch *et al.* 2013). Natural variation from year to year around optimal timing of insect emergence occurs because there are subtle differences in the way that environmental signals such as temperature, photoperiod or the requirement for winter chilling influence the time of budburst and insect development (Buse & Good 1996, van Asch & Visser 2007, Valtonen *et al*. 2011). Climate change therefore, has the potential to increase the mismatch between insect emergence and budburst (Dewar & Watt 1992), the significance of which will depend on the effect of asynchrony on insect population dynamics. In general, larvae that hatch too early can starve while late emerging larvae have to feed on leaves that are tougher, lower in nitrogen and with higher levels of secondary chemicals (Feeny 1970, Haukioja *et al*. 2002, Tikkanen & Julkunen-Tiitto 2003). An effect of phenological asynchrony on population dynamics has been demonstrated in some insects, such as western spruce budworm in Canada (Thomson *et al.* 1984) but not others (Watt & Woiwod 1999, van Asch & Visser 2007). Natural variation in egg hatch usually allows some overlap with budburst and given the strong selection pressure and the short generation time of insects relative to their host tree, they are likely to be able to track changes in the timing of budburst in their host trees at least in the medium term (van Asch & Visser 2007).

Insects that are capable of bi-voltine development (two generations per year) like some sawflies, can have a second generation under favourable conditions before entering diapause at the onset of the dormant season. As with Lepidoptera, an increase in the number of generations may increase population growth (Altermatt 2010). Insects that are multi-voltine, such as aphids, have the potential to be much more responsive to rising temperatures resulting in a significant increase in abundance and damage.

Natural enemies of pest insects such as parasitoids have similar adaptations to temperature changes as their hosts. However, they are constrained to some extent by the adaptations of their particular insect host, and synchrony in the timing with key host life stages may depend on a different thermal response (Hance *et al*. 2007). Yet elevated temperatures may influence parasitoids differently to their hosts in terms of altered distribution and phenology (Jeffs & Lewis 2013). Many factors affect tri-trophic interactions – between the host tree, herbivore and its natural enemies (Thomson *et al*. 2010, Jamieson *et al.* 2012), so that it is not possible to say, other than in very general terms, how the dynamics will be affected as temperature rises.

A.2.2 Precipitation

Precipitation can have both direct and indirect effects on insects. Small insects such as aphids or early instar larvae of defoliators feeding on the plant surface can be dislodged by intense and prolonged summer rainfall and larger instars can be prevented from feeding (Dixon 1998). In contrast insects in ‘protected’ microhabitats, in bark or woody stems or on roots will be buffered to a greater or lesser extent from environmental extremes, although heavy winter rains can cause flooding and increased mortality of overwintering stages in the soil. Prolonged periods of hot dry weather (Rebetez *et al*. 2006) on the other hand can be desiccating but may also indirectly benefit insects through changes in the nutritional quality of the host tree, or a reduction in the effectiveness of its defences (Rouault *et al*. 2006, Jactel *et al*. 2012).

A.2.3 Carbon dioxide

Much attention has been focussed on the concentration of atmospheric CO_2 as one of the main drivers of CC. A number of studies have investigated possible effects on insects resulting from changes in the growth or nutritional quality of their host plant induced by higher concentrations of CO_2 (Zavala *et al*. 2013). A ‘fertilisation effect’ on tree growth has been demonstrated in a number of studies (Bazzaz 1990, Townend 1993, Kuokkanen *et al*. 2001, 2003, Stiling & Cornelissen 2007) that could offset increases in endemic levels of insect feeding in a warmer climate (Worrell & Malcolm 1990, Straw 1995). Of particular interest is how CO_2 influences the concentration of nitrogen and defensive secondary chemicals that affect insects. Experimental increases in CO_2 concentration or temperature have produced different responses in conifers and broadleaves and between different parts of the tree (Zvereva & Kozlov 2006). Some of the observed responses to elevated CO_2 and temperature alone disappear when both are increased in a more realistic representation of future climate, emphasising that single factor experiments may not give realistic insights into the responses of insects to CC (Zvereva & Kozlov 2006, Lawton 1995). In general, studies on woody plants show that under elevated CO_2 and temperature, nitrogen concentration decreases while the C/N ratio increases, a response likely to have negative effects on those insects sensitive to concentrations of secondary chemicals. Some insects however, may be able to compensate for reduced nutritional quality by increasing consumption, emphasising the difficulty of making general predictions of how CO_2 will indirectly affect insects via the host tree. Although overall, the effects of CO_2 may be small (Watt *et al*. 1995, Whittaker 1999, Awmack *et al*. 2004), clear negative effects on abundance have been shown for leaf miners in a long-term study on oak (Stiling & Cornelisson 2007).

A.2.4 Climate variability and extreme events: storms, drought and fire

Predictions of future climate necessarily refer to average effects over relatively large areas but variability in the climate can have important effects. In severe storms, trees can be partially uprooted or blown down over large areas making them vulnerable to attack by bark beetles, and facilitating population build-up of pest species. Prolonged periods of dry weather can also ‘stress’ trees sufficiently to increase their susceptibility to these important pests and precipitate outbreaks that can spread over large areas (Bakke 1983, Wichmann & Ravn 2001). Hot dry spells are also likely to increase the risk of fires (Broadmeadow & Ray 2005) and in conifer forests, fire damaged trees can also be vulnerable to bark beetle attack (Fernandez 2006, Långström *et al*. 1999).

A.3 Evidence for current effects of climate change on forest insects

Possible impacts of CC on the abundance or distribution of forest pests in the UK are difficult to attribute directly to a warming climate. For example, the apparent range expansion and increased abundance of the thermophilic buprestid beetle *Agrilus biguttatus* in southern Britain may be due to temperature increases, but is also likely to have been influenced by increased availability of susceptible host oak trees associated with Oak Decline (Brown *et al*. 2015). There is some circumstantial and empirical evidence of effects of CC in continental Europe. Analysis of records over 200 years of pine forest defoliation shows a long-term trend of decreased outbreak activity in the defoliating moth *Dendrolimus pini* following periods of unusually warm weather. Conversely, high summer temperatures increased the likelihood of outbreaks of the sawfly *Diprion pini* (Haynes *et al*. 2014). An increase in winter temperatures has been an important driver of latitudinal and altitudinal range expasion of the pine processionary moth, *Thaumetopoea pityocampa,* (Battisti *et al* 2005, 2006). More dramatic examples come from North America where there has been an increase in the severity of bark beetle outbreaks (Bentz *et al* 2010). In western states, outbreaks of the mountain pine beetle, *Dendroctonus ponderosae*, have killed millions of hectares of pine. Empirical data show that in parts of its range, mountain pine beetle now has an earlier and longer flight season, attacks trees at higher elevations, and a proportion of the population now has a bi-voltine life cycle (Logan *et al* 2010; Mitton and Ferrenberg 2012).

A.4 Insect life history and the potential effects of CC on abundance and damage

In a changing climate, variation in the location, extent, frequency and severity of damage will very much depend on the ecological characteristics of different pests and, of course, the methods and objectives of forest management. In the following sections, insects are discussed in three natural groupings, aphids, scale insects and related species; bark beetles, weevils and related species, and defoliators. These groupings reflect differences in ecology, the nature of the threat to forests and differences in the relative importance of direct and indirect effects of CC on population dynamics. Predicted effects on some of the most important UK forest pests are given in Table 2.

A.4.1 Geographical and host range extension

One of the more general predictions of the effect of CC is that in temperate regions of the northern hemisphere, insects are likely to increase their range (Vanhanen *et al*. 2007, Jepson *et al*. 2008). Ranges may increase in elevation or extend northwards as the climate warms, but may also be displaced rather than extended as may occur if, for example, southern areas of the UK become unsuitable for some insects. Climatic suitability is only one aspect of geographical range extension. Other factors include the availability of hosts, the occurrence of physical barriers or the effects of competitors and natural enemies (Gaston 2003). The extent and rate of range extension will depend on the relative importance of biotic and abiotic factors that currently limit distribution and dispersal.

Although many endemic forest pests are widely distributed in the UK, insects with a predominantly southern distribution are likely to increase their range in a warmer climate. Examples include *Agrilus biguttatus*, associated with declining oak trees (Sallé *et al*. 2014, Gibbs & Greig 1997, Hartmann & Blank 1992, Moraal & Hilszczanski 2000), and the recently introduced gypsy moth, *Lymantria dispar* and oak processionary moth, *Thaumetopoea processionea* (Townsend 2013). An important question in range extension is whether ‘outbreak ranges’ – locations within the area of wider distribution where outbreaks tend to occur – also increase. Recent studies of *O. brumata* and autumnal moth, *Epirrita autumnata*, in Scandinavia provide evidence that they do (Jepsen *et al*. 2008).

Host range extension can also be an important cause of increased damage to trees. A number of insects have exploited the opportunities for host range expansion provided by afforestation of upland Britain. Some 2% of angiosperm-feeding moths, mostly from the Tortricidae, Geometridae and Noctuidae, have been recorded on introduced conifers (Fraser & Lawton 1994). Host shifting moths are most likely to be polyphagous on a wide range of woody trees and shrubs, to occur in habitats associated with afforestation, and to overwinter as eggs. ‘Ecological opportunity’ is therefore an important aspect of host range extension (Strong *et al*. 1984). A well-known example is that of winter moth, *Operophtera brumata*. This insect is predominantly a pest of oak but also occurs naturally on heather, *Calluna vulgaris*, and bilberry, *Vaccinium myrtillus*, in upland areas, sometimes at outbreak densities (Kerslake *et al*. 1996). In some parts of northern Britain, Sitka spruce has been defoliated by local populations of winter moth, causing significant damage (Stoakley 1985). Species with a more intimate association with the host such as miners, case-bearers or borers do not appear to host shift (Fraser & Lawton 1994).

A.4.2 Aphids, scale insects and related species

Within this group of sucking insects there are a number of significant pests that generally have sublethal, though significant, effects on trees (Straw *et al* 2005), and some may contribute to a more general decline involving other organisms. Some species such as Adelgids have complex life cycles (Carter 1971) involving host alternation. Gall production is characteristic and can be the cause of significant 'cosmetic' damage in high value plantations and this problem may well increase as the climate warms.

Many insects in this group are relatively small, sedentary and exposed on the surface of the plant and are vulnerable to weather-induced mortality factors such as heavy rainfall and unseasonable frosts. Natural enemies can be an important cause of mortality in some species, but the host tree and its nutritional quality often has a strong influence on population growth and development (Day *et al* 2004). This is especially true of some scale insects which tend to have life cycles that are closely synchronised with the annual cycle of host trees so that indirect effects of CC acting through the host are likely to be more important than direct effects. During dispersal flight, aphids can be transported long distances on air currents and are therefore often widespread pests. Aphids such as the green spruce aphid, *Elatobium abietinum*, which give birth to live young and have multiple generations per year are likely to respond strongly to a warming climate. This aphid can be active throughout the year, so both summer and winter temperatures influence the life cycle. In mild autumn weather there may be high overwintering populations, but sudden cold snaps can cause high mortality (Carter 1972, Powell & Parry 1976). Currently, severe defoliation can occur at intervals of 3-7 years (Day & Kidd 1998) but as the climate warms, the frequency of outbreaks may increase, with the risk that high populations will occur in successive years, resulting in tree mortality (Straw 1995). Drought has been demonstrated to benefit *E. abietinum*, maintaining higher populations on Sitka spruce and leading to increased needle loss from host trees (Banfield-Zanin & Leather 2014). Changes in the species or provenance of spruce planted as an adaptation response to CC has the potential to either increase or decrease aphid abundance and damage (Day 1984a).

Overall, the abundance and damage caused by aphids and related insects is likely to increase under CC. Higher temperatures will increase their reproductive rate and those species that have multiple generations or can remain active throughout the winter are likely to benefit most. Moderate drought stress of host trees through changes in seasonal and spatial rainfall distribution will be favourable for some species. Additionally, an increase in aphid abundance on conifers may increase vulnerability to bark beetle attack.

A.4.3 Bark beetles, weevils and wood-boring beetles.

Bark beetles and related species are among the most important pests of mature conifer forests in temperate regions. The most damaging species are primary pests that have eruptive population dynamics. They are characterised by their ability, when populations are sufficiently high, to precipitate a 'mass-attack' of individual trees through the release of aggregation pheromones, and once outbreaks are initiated they can be self-sustaining, spreading outside the initial outbreak area (Berryman 1987). Mass-attack species such as the European spruce bark beetle*, Ips typographus*, are currently absent from the UK, though this insect is frequently intercepted at ports (Gibbs & Evans 2000). The Eurasian spruce bark beetle, *Dendroctonus micans*, now widely established in the UK, is not a mass attack species but can nevertheless breed in living trees and cause significant mortality (Grégoire 1988, King & Fielding 1989). In common with a number of insects in this group, the life cycle is predominantly semi-voltine but this may become uni-voltine as the climate warms, increasing the potential for population growth. It is currently under effective biocontrol following the introduction and release of a specific predatory beetle (Fielding & Evans 1997), but changes in development rate may affect synchrony between predator and prey and the effectiveness of biocontrol in different parts of the UK.

All other UK bark beetles and most weevils of economic importance are ‘secondary’, only becoming pests under destabilised conditions, and typically breeding in logs, root-stumps or windblown or defoliated trees. These species, together with primary pests, are often associated with blue-stain fungi than can cause significant discoloration of timber. Following extensive windblows, there is usually a need for wet storage of timber to prevent degrade by pests and pathogens, and to prevent fallen trees acting as outbreak foci for bark beetles (Grayson 1989, Webber & Gibbs 1996). This requirement would increase in a more unstable climate.

A number of wood boring beetles cause technical degrade by attacking timber of dead or moribund trees, reducing its value by forming galleries (‘pinholes’) in the wood which are often stained by associated fungi. Bark and wood-boring insects are often associated with declining trees and the occurrence of complex decline syndromes in mature trees that may in part be a response to CC (Brasier & Scott 1994) is likely to result in increased abundance of these insects.

The impact of climate change on the abundance and damage cause by insects in this group will depend on changes in the frequency, timing or location of windblows, the occurrence of extended dry periods which compromise tree defences, and the influence of higher temperatures on voltinism. Species that are semi-voltine may complete a generation in a single year and uni-voltine species may increase the number of sister broods (Långström 1983, Sauvard 1993, Baier *et al*. 2007). The pine weevil, *Hylobius abietis*, is an example of a ‘silvicultural’ pest whose abundance and feeding damage to young transplants depends on the cycle of felling and replanting in managed forests (Eidmann 1985, Långström & Day 2004). Modelling the life cycle of this pest, under current and projected future climates (Inward *et al* 2012, Wainhouse *et al* 2014), indicates that the effect of CC on damage by this insect will vary across the UK. The current life cycle is predominantly semi-voltine so that transplants may be vulnerable to attack for several years after felling, particularly in the colder northern parts of the UK. As the climate warms, a shorter 2- year cycle is predicted to become increasingly common in these areas by the 2030s. Since most of the UK conifer plantations occur in the north and west of the UK, there could be a significant reduction in economic impact here, the shorter life cycle allowing either a reduced fallow period or an overall reduction in insecticide input. No reduction was predicted for southern parts of Britain.

Overall, damage by bark beetles and related species is likely to increase under CC. Key influences are likely to include a reduction in generation time, drought stress on trees resulting from changes in rainfall distribution, and a possible increase in defoliator attacks, windblow, and fire events making hosts more vulnerable to secondary insect pests. Additionally, some pest species may alter their distribution, whilst silvicultural changes may result in more mature (and more vulnerable) trees in longer rotations.

A.4.4 Defoliators – Lepidoptera and sawflies

Defoliators are a highly diverse group of insects, some of which can cause extensive outbreaks in both broadleaved and conifer forests. Their abundance is determined by complex interactions involving weather, natural enemies and site factors affecting both their survival and suitability of the host tree. Some species have cyclic population dynamics and for many, climate and site-related factors can contribute to the development of outbreaks. Many species are uni-voltine, but some sawflies have the potential for two or more generations per year. Conifers are particularly vulnerable to defoliators that can feed on more than one age class of needles and defoliated trees may be susceptible to attack by bark beetles.

Several species of Lepidoptera form a defoliating complex associated with broadleaved trees such as oak and birch. Winter moth, *Operophtera brumata* is one of the most important defoliators of oak where phenological synchrony of egg hatch with leaf flush in the spring is an important feature of population dynamics. This insect is highly polyphagous, with outbreaks even recorded on Sitka spruce in Scotland (Stoakley 1985), where synchrony does not appear to be important as young larvae can feed on spruce buds prior to budburst (Watt & McFarlane 1991). On oak however, asynchrony of winter moth egg hatch with leaf flush has been shown to affect initial larval survival, and due to rapidly accumulating leaf defences, to impact subsequent pupal survival and adult fecundity (reviewed by Singer & Parmesan 2010). Critically though, winter moth appears to be genetically adapting to climate change, by shifting its egg hatching date to better synchronise with bud burst (van Asch *et al*. 2013).

Some defoliators such as processionary moth, *Thaumetopoea processionea*, as well as causing significant defoliation (Pascual 1988, Roversi *et al*. 1997), can have an impact on human health because larvae are covered in urticating hairs that can cause skin and eye irritation or in some cases, severe allergic reactions (Lamy 1990, Maier *et al*. 2004, Gottschling & Meyer 2006). This and related species are a particular problem in urban and semi-urban areas where climate-related increases in abundance in these ‘heat islands’ are likely to be a significant problem.

The pine beauty moth, *Panolis flammea*, is an interesting example of a native defoliator that only became a significant pest in the UK following the widespread planting of the North American lodgepole pine in Scotland in the 1950s and 60s (Lines 1987, Stoakley 1977). Outbreaks may have been influenced by insect predators and parasitoids which are less abundant and diverse in lodgepole pine forests than native Scots pine (Hicks *et al*. 2001). The influence of climatic factors appears limited in the population dynamics and impact of this pest. Its rapid elevation from innocuous endemic on Scots pine to serious defoliator of an introduced pine is however important in the context of adaptation measures in UK forestry as a response to CC that involve the introduction and widespread planting of species better adapted to a warmer climate.

Within the sawflies, photoperiod and temperature play an important role in the timing of the life cycle and voltinism (Knerer 1993). Some species are widely distributed, with notable geographic variation in life history that may facilitate adaptation to changing climatic conditions. Outbreaks of pine sawfly, *Neodiprion sertifer*, have been associated with certain sites such as stands on dry, nutrient-poor soils, and in some countries outbreaks tend to follow unusually hot dry summers (Larsson & Tenow 1984); probably an important risk factor for some sawflies under CC. Outbreaks of the introduced European spruce sawfly, *Gilpinia hercyniae*, have been confined to the southern half of Britain where two generations may occur in favourable seasons (Billany *et al*. 1983, Billany & Brown 1977). Range expansion and changes in voltinism are likely responses to CC for this and some other sawflies.

Overall, climate change is likely to influence the abundance and impact of defoliators in a variety of ways. Some species may experience an increased number of generations each year, or an altered distribution. Their hosts may become more susceptible to attack through spatial and temporal changes to rainfall. Phenological asynchrony with host trees may however be countered by adaptation.

A.5 Genetic variation in insect populations and evolutionary responses to CC

Widely distributed forest insects may form distinct races in different parts of their range including genotypes that are adapted to local climate (Ayres & Scriber 1994, Parmesan 2006). Others may have different host races within the same local area, one of the best known examples of which is the larch budmoth, *Zeiraphera diniana*, which has larch and pine races (Day 1984b, Emelianov *et al*. 1995). Levels of genetic variability in insect populations may influence the ability to exploit ‘opportunities’ for host and/or range expansion provided by CC. For example, intraspecific variation in the freezing tolerance of eggs of populations of pine sawfly, *Neodiprion sertifer*, in southern Finland will allow adaptation to a changing climate and facilitate northward spread (Veteli *et al*. 2005).

A.6 General predicted effect of climate change on some UK forest pests

Based on the ecology and life history of representative UK forests pests, and assuming no significant changes in forest area and management, it is possible to make a general assessment of likely effects of climate change on pest status (Table A.2).

Table A.2 Risk of *increased* damage by UK forest insect pests to key host trees in the coming decades as the climate warms. Risk is rated as low, moderate, high or very high based on an assessment of life history characteristics, population dynamics, historical patterns of damage and likely changes in planting.

	Host	**Risk of increased damage**	**Likely effects on populations and damage in a warmer more unstable climate**
Bark beetles, weevils and related species			
Dendroctonus micans Spruce bark beetle	Spruce	High	Reduced generation time may increase abundance. Drought stress of host trees decreases resistance to attack. Range extension resulting in more widespread damage
	Pine	Low	
Hylobius abietis Pine weevil	Spruce	Moderate	Reduced generation time increasing population size but reducing period of risk, especially in northern forests.
	Pine	Moderate	
Tomicus piniperda Pine shoot beetle	Pine	High	Windblow in stormy weather increases breeding material. Sister broods increase abundance. Host stress through drought or defoliation reduces resistance of living trees to attack.
Agrilus biguttatus Two-spotted oak buprestid	Oak	Moderate	Availability of declining oaks and warmer weather likely to increase abundance. Northward range extension as climate warms.
Platypus cylindrus Oak pinhole borer	Oak	Moderate	Availability of declining oaks and warmer weather likely to increase abundance and damage to timber.
Ips cembrae Larch bark beetle	Larch	Moderate	Windblow in stormy weather increases breeding material. Sister broods increase abundance. Host stress through drought or defoliation by sawflies reduces resistance of living trees to attack. Range extension likely to increase area of damage.
Aphids, scale insects and related species			
Elatobium abietinum Green spruce aphid	Spruce	Very high	Multiple generations in warm weather result in rapid population increase, exacerbated by increased winter survival. Drought stress of host trees favourable to population growth.
Cryptococcus fagisuga Beech scale	Beech	Low	Reduced importance of beech in a warmer more drought prone climate likely to reduce importance of beech scale.
Lepidoptera			
Thaumetopoea processionea Oak processionary moth	Oak	High	Range extension likely to increase significance of this pest.
Bupalus piniaria Pine looper moth	Pine	Moderate	Reduced rainfall on vulnerable sites has potential to trigger outbreaks
Operophtera brumata Winter moth	Spruce	Moderate	Phenological synchrony with oak may be disrupted as the climate warms, reducing likelihood of outbreaks in the short-medium term. Exposure to novel hosts during afforestation can result in local outbreaks.
	Oak	Moderate	
Lymantria dispar Gypsy moth	Oak	Low	A newly established pest may increase its range as the climate warms resulting in localised defoliation.
Panolis flammea Pine beauty moth	Pine	Low	Has potential to cause outbreaks on exotic pines introduced as an adaptation to climate change.
Zeiraphera diniana Larch budmoth	Spruce	Low	Disruption of phenological synchrony with host tree likely to reduce risk of outbreaks in short-medium term.
	Pine	Low	
	Larch	Low	
Sawflies			
Gilpinia hercyniae European spruce sawfly	Spruce	Moderate	Increased number of generations extends seasonal occurrence of damage and may increase abundance. Range extension may result in local damage.
Neodiprion sertifer Lesser pine sawfly	Pine	Low	Possible increased risk of damage on dry nutrient-poor sites.
Cephalcia lariciphila Web-spinning larch sawfly	Larch	Low	Range extension may result in localised defoliation, depending on the future importance of larch.

A.7 Effects of adapting forestry to climate change

The introduction of measures to increase the resilience of UK forests to climate change has the potential to influence the distribution and abundance insect pests. Changes in climatic suitability for broadleaves and conifers and implications for management are discussed by Broadmeadow *et al*. (2005), Broadmeadow & Ray (2005) and Ray *et al*. (2002), and a wider European perspective is given by Kolström *et al*. (2011) and Lindner *et al*. (2010). Some changes in forest management considered by Rollinson (2002) include increasing forest area, extending rotation length and increasing stocking density as a means of increasing carbon storage. Other possible changes are the introduction of new species or provenances, planting of previously unforested areas, establishing species mixtures instead of monocultures and the wider use of short rotation coppice.

Lengthening the rotation of plantation trees could increase the risk of attack from bark beetles because overmature trees are, in general, more susceptible. In addition, forests of older, less vigorous trees are likely to be more favourable for the establishment of accidentally introduced species. Lengthening rotations will also expose trees to a longer period of climatic change, which is likely to affect their growth and vigour. One possible consequence is an increased incidence of decline syndromes such as that of Oak Decline (Denman and Webber 2009, Denman *et al.* 2014), symptoms of which can develop over many years and may vary with location (Manion 1981, Manion and Lachance 1992).

In previous decades, afforestation programmes have resulted in the emergence of new pest problems and a number of insects have exploited the opportunities for host range expansion. The introduction of new provenances or species better adapted to a warmer climate may also lead to the emergence of new native pests, though the use of Pest Risk Analysis methods (Anon 2001) should identify the main risks. The pest problems resulting from the widespread planting of lodgepole pine emphasises the importance of trial plantings on a range of sites to assess likely susceptibility. The introduction of new species and provenances would of course also be susceptible to the introduction of pests that attack them within their natural range, increasing the likelihood of the establishment of these exotic pests if they were accidentally introduced.

There is some evidence that, at least for some pests, forest monocultures are more susceptible to insect pests than more ‘natural’ mixed forests (Jactel & Brockerhoff 2007). While forests of mixed species composition are likely to support a more diverse flora and fauna than monocultures, and this may be an important objective of forest management, overall there is no strong evidence that less diverse forests are inherently more likely to suffer outbreaks of insect pests. However, the risk will depend to some extent on the ecological characteristics of particular pests.

Section B: Pathogens

B.1 Background

Fungi and Oomycetes are recognised as the most common pathogens of trees, although advances in molecular diagnostics have highlighted a growing number of damaging bacterial pathogens. In general, all fungi and bacteria have an optimum temperature range for activity, and this largely determines their potential for survival, growth and their range, thus defining their geographical distribution in relation to their hosts.

Climatic extremes such as drought periods and flooding have been shown to increase the risk of damage by certain pathogen groups. For example, using a GIS-based modelling approach Green and Ray (2009) generated maps for Scotland which identified areas and tree species most at risk to future climate change and were able to predict that a number of diseases are likely to increase in frequency and severity due to drought stress in eastern Scotland. In addition, the frequent storm events predicted for the UK are likely to increase levels of physical injury on trees, and thereby indirectly create wounds that facilitate the entry of pathogens. Increasing levels of root damage by root-rot pathogens also have the potential to make trees more vulnerable to windthrow during storm events.

For many of the forest pathogens that are found in the UK distribution data and the influence of environmental factors are often poorly known. However, case studies provide evidence for how some of the major pathogen groups such as foliar, root rot and canker causing agent are currently behaving in response to climate change (CC) and how this could change in the future.

B.2 Foliar pathogens

Unlike root and wood infecting fungi, foliar pathogens are directly exposed to fluctuations in air temperatures and UV radiation without the environmental buffering supplied by surrounding soil or woody tissue. Thus foliar disease fungi are probably more immediately responsive to CC than most other pathogens, with sporulation and the infection process linked strongly to changes in temperature and precipitation (Peterson 1967). Even in the absence of CC, it has long been observed that rainfall patterns usually affect the frequency and severity of foliar diseases from year to year. Consequently foliar pathogens which require free moisture for host infection, sporulation and spore dissemination are likely to become more damaging in parts of the UK with projected increased spring and summer rainfall.

B.2.1 Broadleaf foliar pathogens

Foliar pathogens most likely to impact on broadleaved species include *Marssonina* species which cause leaf spots and blights on a number of tree hosts, including species of poplar, birch and willow, for which they are regarded as important forest diseases (Sinclair *et al.* 1987). In general, lesions caused by *Marssonina* spp. develop predominantly on leaves and very young shoots, leading to premature defoliation during epidemics (Phillips & Burdekin 1982, Sinclair *et al.* 1987). *Marssonina betulae* can also cause damaging branch and stem cankers on silver birch resulting in crown dieback, with debilitating infections recorded on young birch at numerous new native woodland plantings in Scotland (Green & MacAskill 2007; DeSilva *et al*. 2008).

Fungal diseases caused by *Venturia* spp. which result in blackening and death of leaves and shoots on willow and poplar species are favoured by wet but usually cool weather (Peace 1962). Wet springs usually elicit many reports of these disorders and in recent years this disease has caused severe damage to young, regenerating aspen on the west coast of Scotland, possibly due to particularly wet conditions during spring and early summer.

Foliage rusts caused by *Melampsora* species are some of the most damaging diseases of commercially grown willow and poplar in the UK (Phillips and Burdekin, 1982). Some warm-temperature *Melampsora* species, such as *M. allii-populina* which currently has a geographical range in southern and central Europe, are predicted to become more problematic in the south of the UK due to climate change (Lonsdale & Gibbs 2002). Threats posed by northward shifts of existing rust species, together with evolution of new pathogenic races of these diseases, have potentially serious implications for willow and poplar grown in short rotation coppice for biofuels.

Powdery mildew caused by the fungus *Erysiphe alphitoides* is the most important leaf disease of oak in Britain (Peace 1962, Morris & Perring 1974), although the disease is now known to be caused by not one but a number of novel fungal species that recently have been described (Braun 1987, Takamatsu *et al*. 2007) and are present in Europe (Mougou *et al*. 2008, Marçais & Desprez-Loustau 2014). Owing to the rapid spread of airborne conidia they may also be present and widespread in the UK (Lonsdale 2015) although this has yet to be established.

Overall, powdery mildew affects native oak in Britain in all situations from nurseries, to gardens and woodlands. The most susceptible oak species are *Quercus robur* and, to a lesser degree, *Q. petraea*; but mildew has also been recorded on less susceptible species (Woodward *et al*. 1929). The stage of host physiological development is critical to disease development. Both *E. alphitoides* and *E. quercicola* colonise only young leaves (Marçais & Desprez-Loustau 2014, Lonsdale 2015) and require relatively warm temperatures for growth. Thus as a rule only a short window of opportunity is available for spring infection unless early warm temperatures occur, but second and third lammas growth is vulnerable in the summer. The damaging effects can be amplified if attacks are in tandem with defoliation events, especially spring defoliation (Marçais & Breda 2006, Hajji *et al*. 2009). As a consequence powdery mildew on mature trees can be a serious disease, reducing the health and vigour of oak although it is usually not lethal under the current climate. The effect on seedlings and saplings however, is more serious, rendering them uncompetitive to surrounding vegetation and affecting the succession of oak in woodlands (Marçais & Desprez-Loustau 2014, Soutrenon 1998).

Epidemiological information on oak mildew is complex and sometimes contradictory because of the different types of inoculum. The main mildew pathogen (*E. alphitoides*) survives as mycelia in overwintering buds and ascospores which are produced in fruiting structures called chasmothecia. The incidence of chasmothecia recorded in the UK was very low but since the 1990s has increased (Lonsdale 2015) which could be climate change induced or due to a genetic shift in populations resulting in variants with greater capacity for forming the chasmothecia sexual stage (Tollenaere & Laine 2013). Studies on effects of relative humidity and temperature on conidia (asexual spores) of *E. alphitoides* show that dry conditions are required for release and free moisture inhibits germination. Warm temperatures are required, with high levels of germination even occurring at 30°C (Hewitt 1974, Glawe 2008). In contrast, the ejection of ascospores requires free water and takes place after rain events (Glawe 2008). Disease incidence is therefore affected by prevailing weather conditions (Glawe 2008, Tollenaere & Laine 2013, Lonsdale 2015), but altered host-pathogen phenological synchronicity is also likely to play an important role. Higher mean winter temperatures are probably a precursor to raised disease peaks in spring, possibly because of earlier ascospore release thus coinciding with susceptible spring leaf growth (Marçais *et al*. 2009). However, mycelial overwintering in buds is also favoured by these conditions and early warmer springs lead to earlier infections.

Overall, in a changing climate predicted to have warmer, wetter winters and drier summers the intensity of powdery mildew attacks could increase and start earlier, provided there were sufficient dry days for germination. Both early and late foliage could succumb, and outbreaks could be more damaging if conditions remain mild and dry through the summer months. Heavy infestations over successive years would also contribute to oak decline through reduced productivity and decreased growth of infected trees.

B.2.2 Conifer foliar pathogens

Conifer needles and shoots can also be affected by foliar pathogens and in some instances these are likely to be favoured by climate change. The most striking example is Dothistroma needle blight caused by the fungus *Dothistroma septosporum*. Apart from causing premature needle loss thereby affecting growth and productivity, at epidemic levels it is also a potentially lethal disease of pine trees. Woods *et al.* (2005) report that in British Columbia, Canada, there has been a marked increase in the frequency of weather conditions favourable to the disease which in turn has significantly aided the current *D. septosporum* epidemic in that country.

The same process appears to be taking place in Britain. From the late 1990's onwards there has been a dramatic increase in the extent and severity of this disease particularly in East Anglia. It is now causing widespread damage on *Pinus nigra* ssp. *laricio* (Corsican pine) which is around 4% of conifer cover in Britain, and in consequence a moratorium on planting Corsican pine on the public forest estate was introduced in 2007 (Brown and Webber 2008). Since then, the disease has been found to have a major impact on lodgepole pine (*Pinus contorta* ssp. *latifolia*) in areas such as the Moray Forest District of Scotland (Brown 2007), and most recently is affecting Scots pine (*P. sylvestris*) in the native Caledonian pine forests of Scotland (Anon 2013). In Britain the main infection period for *D. septosporum* is thought to be May – September with moisture required for spore release. Sporulation can occur at temperatures as low as 5^{o}C, with temperatures of 15 - 20^{o}C and ten hours or more of wetness on the needle surface usually required for infection (Peterson 1967; Gadgil 1974). Analysis of meteorological data from East Anglia where the disease was initially the most severe in the UK has shown that the frequency of climatic events favourable for infection, namely consecutive days (3 to 5+ days) with rain and maximum daily temperatures of 18 – 22^{o}C, have increased significantly during the spring and summer period over tht last 40 years. Since the 1970s, these events have doubled in frequency and if sustained as future climate change scenarios suggest, they could become very significant in the long term for Dothistroma needle blight even for pine species often considered as less susceptible to this disease (Archibald & Brown 2007).

Diplodia pini (formerly *Sphaeropsis sapinea*) causes a disease known as Diplodia blight. It affects many species of pine worldwide causing a variety of symptoms such as shoot blight, top dieback, and cankers on stem and branches (Paoletti *et al*. 2001). The fungus can exist in shoots and cones as latent or asymptomatic infections and drought stress then predisposes pine trees to damaging disease episodes (Johnson *et al*. 1997, Paoletti *et al*. 2001). Currently, *S. sapinea* causes most damage to pine in southern Europe consistent with its optimum growth temperature of 30°C (Milijasevic 2006). It has however, become an increasing disease problem in France (Piou *et al*. 1991) and has been reported with growing frequency on Austrian pine (*Pinus nigra*) and Scots pine (*P. sylvestris*) in the UK, mainly in the south, affecting both young crops and mature trees (Brown & MacAskill 2005). The projected warmer temperatures and more frequent droughts are likely to result in *S. sapinea* becoming more problematic on pine in the UK. Desprez-Loustau *et al*. (2007) highlighted the potential of this pathogen to become more damaging with future climates but also remarked that the major impacts of climate change might be indirect, i.e. be expressed because of effects on host physiology such as drought stress rather than directly on the fungus.

Swiss needle cast, caused by the fungus *Phaeocryptopus gaumannii*, is an introduced disease of Douglas fir (*Pseudotsuga menziesiii)* found throughout much of the planted range of Douglas fir in Europe although in Britain it is largely limited to the west and north. Until recently damage was minimal and findings a rarity, but increasing reports of the disease to the Forest Research Tree Health Diagnostic Advisory Service (THDAS) suggest it may be on the rise. This may be similar to the climate driven change in disease levels that has emerged since the early 1990s in western USA, where a severe epidemic of Swiss needle cast has affected Douglas fir in the coastal fog belt zone of the Pacific Northwest (Klienjunas 2011). The epidemic is considered to be driven by increased winter temperatures and spring rainfall, with the incidence positively correlated with degree-day accumulation during winter and leaf wetness hours from spring through to autumn. With every decade since 1970, Oregon winter temperatures have increased by 0.2 to 0.4 °C and spring precipitation by 0.7 to 1.5 cm, resulting in an upsurge in disease (Stone *et al.* 2008). A similar process may now also be taking place in Britain, particularly in westerly regions, and Swiss needle cast may well become more frequent in future affecting the productivity of high value Douglas fir grown in this region.

Overall, milder winters are likely to affect the over-wintering strategies of most foliar fungal pathogens, particularly those on evergreen species, increasing the rates of survival and activity of those diseases for which low winter temperatures are currently a limiting factor (Desprez-Loustau *et al*. 2007). However, more empirical information is needed on the specific environmental requirements of many of these diseases in order to predict with accuracy likely changes in pathogen behaviour and range.

B.3 Root pathogens

It has long been recognised that interactions exist between drought stress and fungal diseases of forest trees, causing drought-stressed trees to be more susceptible to disease (Bier 1959, Hepting 1963, Schoeneweiss 1975). With projections of increased frequency and severity of drought in parts of the UK, trees growing on drought-prone sites are likely to suffer increased attacks by root infecting fungi. The widespread wood and root rotting pathogens (Basidiomycetes) such as *Heterobasidion annosum* and *Armillaria* spp. are already recognised as capable of causing commercially significant levels of damage.

Armillaria (honey fungus) is ubiquitous throughout the UK and attacks various conifer as well as many broadleaved tree species. In general, the optimum temperature for growth is around 25^{o}C under laboratory conditions. However, it is now recognised that there are several *Armillaria* species, and they all invade roots, causing a progressive white rot. Some, such as *A. gallica* and *A. cepistipes*, are weak pathogens and only able to invade trees which are debilitated by other factors. In contrast, *A. ostoyae* and *A. mellea* are considered to be aggressive with the ability to infect and even kill otherwise healthy trees (Gregory & Redfern 1998). *Armillaria mellea* is considered to be mainly a pathogen of broadleaved trees in ornamental parklands, natural woodlands and fruit orchards, but it can kill young coniferous trees (mainly pines and spruce) planted in sites where the broadleaved species have grown previously. In contrast, *A. ostoyae* is significant as a pathogen of coniferous trees, causing major damage in even second- and third-rotation stands of conifers but has also recently been detected on oak where its role is yet to be determined (S. Denman, unpublished data). Drought stress in trees is generally considered to be a predisposing factor to infection by *Armillaria*, especially for the less pathogenic species (Gregory & Redfern 1998, Desprez-Loustau *et al*. 2006). Since the likelihood of invasion of woodland by *Armillaria* spp. also increases with successive rotations, this process combined with the impact of CC is likely to make these pathogens more damaging in the future to UK forests. The effects could come from group killing in young re-stock sites as well as infections in older plantations and semi-natural woodlands.

Heterobasidion annosum (Fomes) is an important disease in plantation forestry, causing root and butt rot in stands of spruce, pine and other conifer species throughout the UK. It infects coniferous crops by colonising recently cut stumps and growing down through the stump roots and into roots of nearby living trees which happen to be in contact. This results in killing of young pines on vulnerable sites, and decay in the lower stems of many other coniferous species. The risks of inoculum build-up and infection by this fungus are considered to be greatest on well drained mineral soils in low rainfall areas in the east and south of the country (Redfern *et al.* 2001, Pratt 2003) with the highest risk on alkaline soils. *Heterobasidion* has also been found to show enhanced infection and growth in young spruce trees suffering moderate drought stress, although infection rates decreased under severe drought stress (Lindberg & Johansson 1992). As it is more common and damaging on drier sandy soils than in heavier soils with poor drainage or high water tables (Kuhlman *et al*. 1976, Puddu *et al*. 2003) climate change is likely to provide more favourable environmental conditions for *Heterobasidion* to spread in soils with reducing water potential, resulting in increased damage and greater economic loss. Like *Armillaria*, *H. annosum* has an optimum temperature for growth of *c.* 25^{o}C, so increased ambient temperatures could also enhance the process of stump colonisation and lead to higher rates of infection.

Climatic changes may also alter the interactions between some of these root attacking pathogens and the mycorrhizal fungi that are symbiotically associated with tree roots. Gange *et al.* (2007) concluded that over the last 50+ years, the fruiting patterns of mycorrhizal species have altered apparently in response to climate change (specifically increased late summer temperatures and autumnal rainfall). Mycorrhizal species associated with both conifers and deciduous trees tended to have their fruiting delayed, particularly in deciduous forests. Many species also now fruit twice a year and other researchers have confirmed this (Kauserud *et al.* 2013), suggesting increased mycelial activity and possibly greater decay rates in ecosystems. However, mycorrhizal relationships with host trees can be affected by drought allowing one fungal species to be out-competed and replaced by another. In an overview, Lonsdale and Gibbs (1996) concluded that root disease can be reduced in trees with mycorrhizal associates, but increased summer drought may encourage the spread of root disease due to changing mycorrhizal relationships and drought-induced decreases in host resistance.

B.4 Phytophthora pathogens

Phytophthoras are a mainly introduced group of pathogens that have proved to be highly damaging to host tree populations. More than 120 species have now been described (Kroon *et al.* 2012), many only recently, with some species attacking a wide host range. Around fifteen *Phytophthora* species are widespread in the UK including at least 4-5 recent arrivals. Most can be highly destructive and cause episodes of tree mortality under conducive conditions, by killing roots and girdling the root collar or lower stems. However, several of the more newly discovered *Phytophthora* species are aerial pathogens, adapted to infect above ground plant tissue and therefore potentially highly responsive to climatic change.

B.4.1 Root infecting Phytophthoras

Broadly, there are two groups of root infecting Phytophthoras, those that infect primary roots and tree collars, even extending into stems, and those that mainly attack fine feeder roots. Both types require moist soil conditions (even periods of flooding) for infection and spread, but the damage they cause tends to be most visible in the summer especially if trees are drought stressed with a reduced capacity to transport water to other parts of the tree. A build up of *Phytophthora* results in the death of fine feeder roots, even root and stem girdling, so trees may die suddenly when under water stress or show signs of marked decline. Evidence suggests that episodes of chronic oak decline are correlated with *Phytophthora* activity (Brasier & Jung 2003, Jung *et al*., 2000) and this also predisposes trees to attack by secondary organisms such as several species of *Armillaria* or bark beetles. Moreover, many species of *Phytophthora* can over-winter in soil and even persist for decades in the form of resistant propagules, becoming active again under favourable conditions. The predicted warmer climate will result in milder winters in the UK, and so may provide more suitable conditions for many of these root-attacking Phytophthoras.

In Britain there are several Phytophthoras causing root and collar rot and bleeding stem cankers of trees but *P. cambivora* and *P. plurivora* are probably the most frequently isolated. Most of the species have optimal growth temperatures around 22−25ºC and maximum temperature thresholds around 30−32ºC. Since 2000, there has been a significant upsurge in *Phytophthora* attacks on roots and stems of trees (particularly beech) by both these Phytophthoras in Britain and continental Europe and it is suggested that this increase is associated with climatic change (Brasier & Jung 2004, 2006, Bergot *et al.* 2004) and specifically warmer temperatures. Undoubtedly, soil environment plays an integral role in Phytophthora diseases; many attacks are associated with heavy soils with high clay content and physical changes due to soil compaction. Waterlogged conditions are also frequent precursors of disease, particularly in relation to attacks by *P. plurivora* and *P. megasperma* (Brasier, 2000). Thus, in a changing climate where more frequent events of periodic flooding and waterlogging are expected, increased severe root and collar attack by Phytophthoras are anticipated but empirical data are lacking.

One of the most destructive species of *Phytophthora*, *P. cinnamomi*, has been associated with the decline of several forestry, ornamental and fruit industries, as well as over 900 woody perennial plant species. It is most damaging at temperatures of 25^{o}C or above and its activity and distribution in the UK is therefore constrained by climatic conditions although this is changing. It is likely that the combination of heavy rainfall leading to occasional waterlogging and summer drought, predispose oak and other broadleaf genera to infection by *P. cinnamomi.* As *P. cinnamomi* is most pathogenic at temperatures of 25°C and above and does not survive freezing conditions in the soil, CLIMEX models were used more than 20 years ago to assess how its activity in Europe could alter as a result of climate change (Brasier and Scott, 1994). The model suggested that activity of *P. cinnamomi* is likely to increase significantly in the Mediterranean region and in maritime climates such as coastal western Britain, but not in central Europe. Since then more sophisticated models have tested various rainfall and temperature scenarios to predict future risk from *P. cinnamomi* (Thompson *et al.* 2014). Key factors are milder winters and unchanged or slightly increased spring rainfall and temperatures. Increased mortality by *P.*

cinnamomi is linked to mild wet springs which would enhance activity coupled with periods of drought stress (Desprez-Loustau *et al.*, 2006; Thompson *et al.*, 2014).

The extent of *P. cinnamomi* activity will also depend upon availability of suitable hosts and other ecological factors. Currently, tree species native or important in Britain and susceptible to *P. cinnamomi* include *Taxus*, *Fagus*, *Crataegus* and *Quercus* spp. (cf Brasier 2000), and *P. cinnamomi* is responsible for the large scale death of *Castanea sativa* throughout southern Europe and sporadic mortality in south-east England (Brasier 1999). Its prevalence in nurseries means that there is also potential to export the disease into the wider environment when infected but often symptom free plants are used in vegetation plantings.

Discovered in the 1990s in Europe, *P. alni* (which infects native alder), is also likely to show an increase in activity in response to climate change. This pathogen has now spread throughout river systems in much of England and Wales, and is found in Scottish river systems particularly in the east (Webber *et al*. 2004). There is evidence to suggest that it infects trees following flooding episodes, and warmer water temperatures during winter are strongly related to disease prevalence. Thus it has been suggested that the rapid rate of disease increase that has been seen in the south of England is a response by *P. alni* to higher water temperatures (Thoirain *et al.* 2007). In a modelling study to assess how climate change might influence alder disease, Aguayo *et al.* (2014) found that the most unfavourable conditions for the disease were colder than average daily winter temperatures of <3.5^{o}C and average daily temperatures in the preceding summer of >21-22 ^{o}C during July and August. Winter warming of river waters and reduced river flow during drought periods, including standing water after flooding events, are therefore all likely to contribute to more frequent episodes of infection by *P. alni* in Britain as our climate changes.

Two other recently arrived root infecting Phytophthoras that are now established in the UK are *Phytophthora lateralis* and *P. austrocedri* (previously *P. austrocedrae*) (see Green *et al.* 2013, Green *et al.* 2014). As a relatively low temperature species, *P. austrocedri* has a optimum temperature of around 17^{o}C for growth and a maximum of around 20 ^{o}C, so is likely to be disadvantaged by warmer summer temperatures and indeed its current distribution in Britain is so far limited to the north of England and Scotland (Green *et al.* 2014). However, the majority of sites affected by this pathogen both in Britain and in Argentina (where it was first described, Greslebin *et al.* 2007) are typified by areas of standing or moving water or soil water-logging. Weather extremes could make these conditions more prevalent in future and therefore increase the likelihood of disease caused by *P. austrocedri*.

B.4.2 Aerial Phytophthoras

Traditionally, aerial Phytophthoras have not been regarded as problematic in forests but more so on tree species in commercial fruit production or other cultivated crops. However, the arrival of *P. ramorum* in the USA (causal agent of ‘Sudden oak death’ in the west coast states California and Oregon) and its appearance in Europe, as well as the discovery of *P. kernoviae* in Britain, suggests that aerial Phytophthoras are probably much more common than previously thought. Like foliar pathogens, their activity is strongly tied to climatic patterns; both apparently thrive under the mild, moist conditions of western Britain, and sporulate and infect most abundantly in late spring and autumn (Webber 2008).

Another recent unexpected finding is that some of the Phytophthoras not adapted to aerial dispersal (i.e. non-caducous) and considered only as soil-dwelling and root infecting, are now being observed to cause aerial bark lesions on a range of tree species. It is hypothesised that this change in behaviour is most likely to be associated with climatic disturbance (Brasier and Jung, 2006).

First found in the UK in 2002, the risk posed by *P. ramorum* has increased significantly following its jump to a major new host, Japanese larch (*Larix kaempferi*) in 2009*.* Japanese larch not only suffers from lethal stem cankers caused by this pathogen, but infected needles also support massive sporulation events (Brasier & Webber 2010, Webber *et al*., 2010). Above average rainfall in the UK in 2012 led to a huge increase in the infection of larch in 2013, demonstrating that climate can have a major influence on *P. ramorum*. Vennette (2009) has also suggested that climate change could make forests on the west coast of the USA even more susceptible to this pathogen because of warmer temperatures during spring precipitation. Similar climate changes are also expected in western Britain where *P. ramorum* predominately occurs (Forestry Commission 2014) suggesting it will continue to be highly damaging. Unusual weather events of rainfall associated with high winds could also provide the opportunity for long-distance dispersal of *P. ramorum* similar to those in southern Oregon, USA (Peterson *et al.* 2014).

Only limited information is available on any of these aerial pathogens to allow judgements to be made in relation to how their geographic range and ecological behaviour may alter with climate change. As recently introduced Phytophthoras, they are now being exposed to native or local vegetation that has little resistance, as these host plants have not co-evolved with these pathogens. Therefore, predicting the impact of CC on the behaviour of these pathogens is very uncertain.

B.5 Declines

The concept of a tree decline is one characterised by a slow progressive deterioration in tree health or vigour, reduced tree growth accompanied by branch dieback (Manion 1991). It primarily affects mature trees and has a complex etiology often involving both biotic and abiotic factors. Decline diseases often have a strong association between climate extremes and disease severity (see Manion & Lachance 1992). Climate change projections suggest increases in intensity and frequency of in storms, heavy precipitation events and extremes of temperature including late frosts. In succession these events could place significant stress on trees increasing their susceptibility to weak fungal pathogens and initiating or progressing decline (Bendixsen *et al*. 2015). Similarly, successive wet and dry periods could negatively affect trees through altered carbon balance and water relations, allowing weak or secondary pathogens to take advantage (Haavik *et al*. 2015). A strong relationship has been demonstrated between climate warming and the onset of crown die back in selected species of hardwoods in eastern Canada (Auclair *et al*. 1992). Climate change is therefore likely to bring about a notable increase in long term (chronic) ‘declines’ of mature beech, oak and ash in the UK, conditions thought to be exacerbated by drought (Gregory & Redfern 1998). In addition to root-infecting pathogens, one of the most common species being *Armillaria* (see section 3), there are a number of stem and branch canker diseases which have the potential to cause greater damage on these broadleaved species in the UK due to a combination of more frequent episodes of higher temperatures and drought stress (see section 6). Probably the most cited example of tree decline in the UK is oak dieback or oak decline (Gibbs 1999).

B.5.1 Oak decline and root infecting fungi

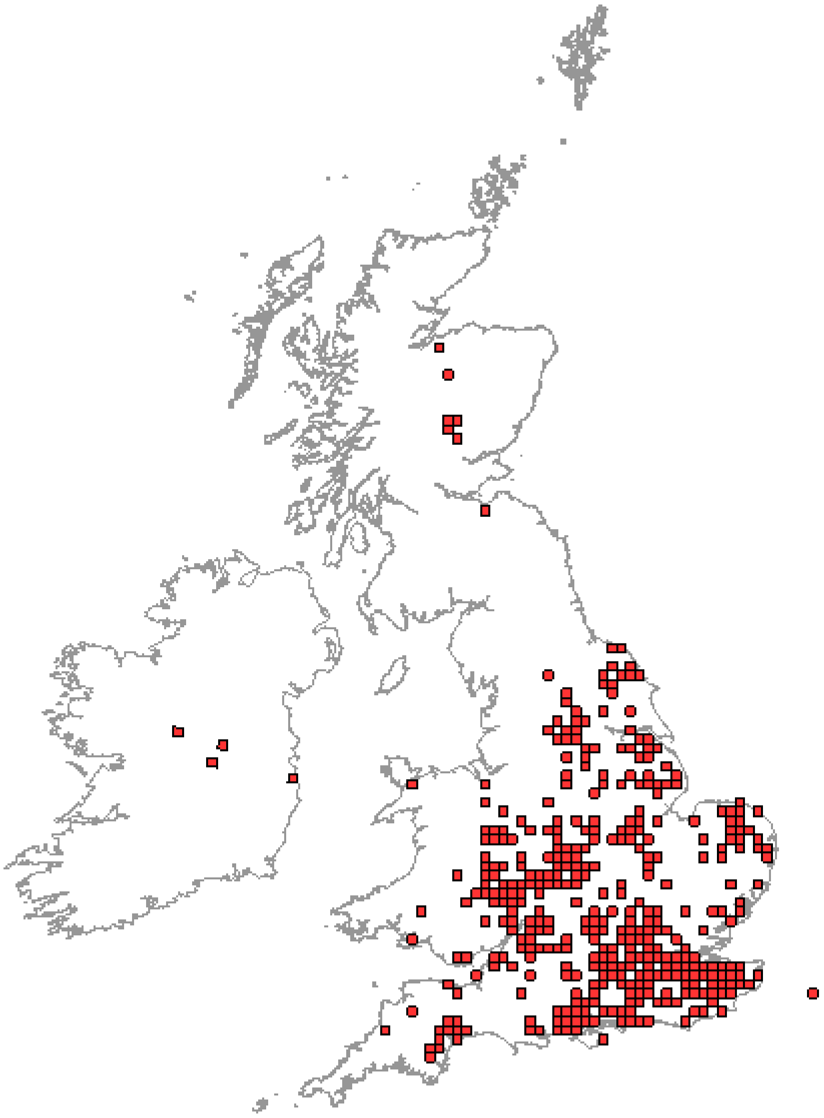
Damaging episodes of oak decline and dieback in England have been identified over the past century. Both severe wind events and drought have been identified as the primary cause. Generally, common or pedunculate oak (*Quercus robur*) is considered to be more susceptible to oak decline than sessile oak (*Q. petraea*) in Britain (Gibbs & Grieg 1997, Gibbs 1999) in part because it is adapted to grow on moist, fertile soils, so lack of soil water impacts on it adversely. Elsewhere in Europe, particularly in Germany and Sweden, it has been recognised that species of *Phytophthora* (especially *P. quercina*) which attack the fine feeder roots also play a key role in oak decline.

Another key organism implicated in the process of oak decline in parts of Europe is the basidiomycete fungus *Gymnopus* (previously *Collybia*) *fusipes*. In the past it was considered a saprobe or weak parasite only able to colonise weakened trees (Phillips & Burdekin 1992), but from about 1980 onwards research has revealed this organism to be a primary pathogen (Delatour & Guillaumin 1984; Marçais & Delatour 1996) capable of causing serious root rot of mature oaks (suggested previously by Buller 1958). Disease develops very slowly and causes visible reduction in tree health only in advanced stages of infection (Marçais & Cael 2001). Both young healthy seedlings and vigorous mature trees are equally susceptible to infection.

The host range of *G. fusipes* is relatively restricted with pedunculate oak (*Q. robur*) and red oak (*Q. rubra*) the main hosts, i.e. the most susceptible and the most frequently reported cases, while sessile oak (*Q. petraea*) is less so (Buller 1958; Marçais *et al*. 1999, Piou *et al.* 2002, Camy *et al*. 2003a). Other species are documented as hosts and are listed in Piou *et al.* (2002) even though occurrences may be relatively rare. However, little information about *G. fusipes* in the UK is available and root rot caused by this fungus on oak is not well documented. No mention of this pathogen is made by either Peace (1962) or Morris and Perring (1974), who, prior to 1980, were considered the main British authorities on forest tree diseases and on all aspects of oaks respectively. Gibbs and Greig (1997) do mention *G. fusipes* in the context of its possible role in oak decline in Britain but there have not been any formal studies reported on its impact on oaks in the UK. Forest Research THDAS records of this pathogen mostly relate to oaks, with reports concentrated mainly in south-east England. The British Mycological Society, with records of this fungus dating back to 1865, produced a map showing that *G. fusipes* is widely distributed in north-east, central and south-east England, with smaller foci in East Anglia and the south-west (Fig B1). It has a limited known distribution in Scotland, Ireland and Wales.

Infection of oak by *G. fusipes* occurs in the collar region mainly from basidiospores (Marçais *et al*. 1998) and it does not spread from tree to tree via root contact (Marçais *et al*. 1998) in contrast to *Heterobasidion*. Colonisation is slow, with lesions developing on large roots and the root collar beneath the outer bark. Infected trees do not show any deterioration in crown health or sapwood increment until advanced stages of the disease hence the condition may not be realised for decades. *Gymnopus fusipes* destroys the deeply penetrating roots central to the root system working its way back to the horizontal supporting roots so windthrow can also be a problem (Marçais *et al*. 1999, Marçais *et al*. 2000). Soil moisture holding capacity is inversely correlated with disease severity; soils with low moisture holding capacity (e.g. sandy or sandy-loam over deep gravel soils) are associated with the most severe levels of disease (Camy *et al*. 2003a).

Figure B.1 Distribution records for *Gymnopus* (previously *Collybia*) *fusipes* throughout the UK, 1965-2005, produced by the British Mycological Society.



In the UK under a changing climate, the spread of disease and its impact will be highly dependent upon soil types, the species of oak in those areas and rainfall levels. In light, free draining soils with drier summers, disease is likely to become more severe and widespread. As there is no information available on how the pathogen responds directly to temperature, for example its influence on rates of colonisation or fruit body production, this makes quantitative assessment of the impact of CC difficult. However, in contrast to areas where drier summers are likely to prevail, in areas where soils are heavier and there is intermittent waterlogging *G. fusipes* is unlikely to be unable to survive since it is very sensitive to hypoxic conditions. In areas with intermittent waterlogging, Phytophthoras could play a more important part in oak decline, coupled with other weak pathogens such as *Armillaria gallica.*

Recently, oak decline in Britain has been characterised by different forms of the disorder given the names *acute oak decline* , where the damaging agents associated with the decline affect aerial tree parts, and *chronic oak decline* where poor root health is considered to underpin the condition (Denman & Webber 2009).

B.5.2 Acute oak decline

Acute oak decline (AOD) is identified by dark patches of fluid exuding from cracks between the bark plates on trunks of established trees (>50 yrs-old); both *Q. robur* and *Q. petraea* can be affected. Underneath these bleeding areas of outer bark, there is extensive necrosis of the inner bark resulting in the formation of cavities. Two species of bacteria from the *Enterobacteriaceae*, *Brenneria goodwinii* and *Gibbsiella quercinecans* are consistently isolated from the necrotic tissue but not from healthy trees leading to the provisional conclusion that they play a significant role in causing the tissue necrosis that characterises AOD (Denman *et al.* 2010, Denman *et al.* 2014). In addition, the breeding galleries of the oak buprestid, *Agrilus biguttatus*, are almost always seen on the affected cambial-phloem interface of AOD symptomatic oaks, raising concerns that the beetle is contributing to the development of AOD, preventing recovery, or is even implicated in the spread of the bacteria associated with the bark necrosis (Denman *et al.* 2014).

Confirmed cases of AOD are within a distinct zone in England centred on the south east and the Midlands, but as far west as Wiltshire and Gloucestershire, and as far north as Manchester (Brown *et al.* 2015). This closely overlaps with the distribution of *A. biguttatus* and the distribution of this insect has expanded markedly in Britain since the mid-1980s (Brown *et al.* 2015). It has been hypothesised that a warming climate is a likely cause of the apparent increase in the *A. biguttatus* population (Broadmeadow & Ray 2005) which has apparently expanded from a relictual distribution, occurring in just a few ancient woodland sites such as the New Forest and Sherwood Forest to the distribution seen today (Brown *et al.* 2015). If *A. biguttatus* is expanding its range in response to climate change and does indeed contribute to the development of AOD, it signals a northerly expansion of AOD in the coming decades. In addition, as a complex decline syndrome, AOD is likely to be more damaging on drought stressed trees especially if placed under additional stress by the oak buprestid which is attracted to declining oaks for oviposition.

B.6 Canker diseases including latent pathogens and endophytes

Beech and oak are susceptible to species of *Biscogniauxia.* These are latent fungal pathogens with the potential to infect trees and remain asymptomatic for years until a factor such as drought stress triggers the development of disease. *Biscogniauxia* *nummularia* occurs on beech in southern Britain and causes cankers in the years following drought periods and particularly in areas with low rainfall and high temperatures (Hendry *et al*. 1998). *Biscogniauxia mediterranea* occurs in the Mediterranean region, and causes cankers on stems and branches of many broadleaved species but is particularly known as the cause of 'charcoal disease' of oaks. This disease is strongly associated with drought stress in trees (Vannini & Scarascia Mugnozza 1991, Desprez-Loustau *et al*. 2006, Capretti & Battisti 2007) and linked with the decline of various oak species, including pedunculate oak (*Q. robur*), in south-western Europe (Capretti & Battisti 2007). It is likely that both these diseases will expand their range northwards within the UK as a result of CC but measurable impact caused by *B. mediterranea* may take much longer (Desprez-Loustau *et al.* 2007).

A latent canker pathogen of potential future significance in the UK due to CC is *Botryosphaeria stevensii* (also known as *Diplodia mutila*). This fungus attacks a range of hosts, including ash, but is noted more for its ability to cause canker and dieback diseases of oak in the western Mediterranean region along with its close relative, *B. dothidea*. These fungi are associated with warmer temperatures (around 25 °C) and drought stress has been shown to increase the aggressiveness of *B. stevensii* on oak (*Q. robur*) (Ragazzi *et al*. 1999).

Sooty bark disease of sycamore is caused by the fungus *Cryptostroma corticale* which survives as latent infections in sapwood, but causes disease in response to water stress and high temperatures (Dickenson & Wheeler 1981). First reported on sycamore in London in the 1940's (Gibbs 1997), since then, disease outbreaks have occurred in the years immediately following hot, dry summers, particularly when the mean monthly temperature of more than one summer month equals or exceeds 23°C (Young 1978). The disease tends to occur predominantly in south east England (Gibbs, 1997) although it was reported as far north as Yorkshire in 1996 following the 1995 drought (FR THDAS database). This pathogen is expected to extend its northern range into Scotland under projected CC.

Beech is known to become infected by a fungal disease, *Nectria coccinea*, which is more prevalent on beech in the south of Britain, indicating a preference for warmer temperatures. *Nectria coccinea* invades the bark of beech colonised by the bark-feeding insect, *Cryptococcus fagi*, killing bark and cambium which can lead to the death of branches and entire trees. The combination of fungus and insect causes 'beech bark disease'. It has been suggested that drought may render beech susceptible to direct infection by *N. coccinea* (Lonsdale, 1980), although studies have not been conducted to confirm this.

Unexpected impacts of drought stress on Sitka spruce (*Picea sitchensis*) in eastern Scotland were observed following a severe drought year in 2003, when rainfall was exceptionally low from June until November, with soil moisture deficits of 200 mm or above for four consecutive months. Mortality occurred with groups of trees and surviving trees had varying types of damage (Green *et al.* 2009). An unidentified species of canker-causing fungus *Phomopsis* was isolated consistently from lesions and underlying stained wood of the drought-affected trees. The likely explanation is that this is another example of a latent fungal pathogen with the potential to infect trees and remain asymptomatic for years until drought stress triggers disease development. This disorder is likely to become more frequent on Sitka spruce if more episodes of severe drought occur.

B.7 Insect-vectored diseases

Insects are important vectors of many plant diseases. Higher temperatures are likely to result in faster development rates and therefore rapid increases in populations of insect vectors that disseminate pathogens, but also allow them to extend to tree populations at higher elevations and further north (see section A in this review).

Some of the most commonly vectored tree pathogens are the bluestain fungi (generally species of *Ophiostoma*, *Leptographium* and *Ceratocystis*), which depend on bark beetles for dissemination and entry into suitable host species. For example, drought stressed or wind blown Scots pine is generally considered to be more susceptible to attack by the bark beetle, *Tomicus piniperda* (Gibbs & Inman 1991, Gregory & Redfern 1998). *Tomicus piniperda* also transmits bluestain fungi such as *Leptographium* spp. which invade the phloem and sapwood of infected trees, causing staining which reduces timber quality, and may even cause tree mortality. Drought stress may also increase the susceptibility of Scots pine sapwood to direct infection by *Leptographium* (Croisé *et al*. 2001).

Larch trees subject to drought stress appear to show increased susceptibility to attack by the bark beetle, *Ips cembrae*, which is a vector for the fungus *Ceratocystis laricicola* (Redfern *et al*. 1987). This fungus invades the sapwood of damaged trees, causing blue staining and associated losses in timber quality, and may also cause dieback and death of entire trees (Redfern *et al*. 1987). It is expected that damage due to these insect-vectored diseases will increase in frequency across Britain under climate change, as the activity of the beetles and the growth of the fungi are favoured by higher temperatures.

Not only conifers but also broadleaved trees suffer from bark beetle transmitted pathogens. Dutch elm disease is caused by the fungus, *Ophiostoma novo-ulmi*, which is spread by the beetles *Scolytus scolytus* and *S. multistriatus*. They introduce the pathogen into the tree during feeding by adult beetles, and it then invades the xylem of infected trees and disrupts water transport, causing foliar wilting and tree death. Although Dutch elm disease is established and widespread throughout much of the UK, it is still extending north. Since the beetle prefers warmer temperatures (approximately 21° C and above) for flight (Fairhurst & King 1983), it is likely that recent warmer summers in the north of Scotland have resulted in increased flight episodes and thus disease expansion. With CC, it is possible that Dutch elm disease will extend to cause damage to wych elm populations (*Ulmus glabra*) throughout the north of Scotland.

B.8 New Threats

Undoubtedly already established pathogens will expand their northerly ranges with CC. However, there is little precise data on the distribution of many tree pathogens, so it will be difficult to distinguish between expansion into new areas or newly detectable levels of activity brought about through the direct or indirect impact of climate change. With fast generation times, pathogens also have the ability to adapt much faster than their host trees, thereby increasing the likelihood of severe impacts. Some pathogens such as *Phytophthora* have also shown they have the propensity for hybridisation, increasing their potential for radical change and ability to infect new hosts.

Pathogen introductions via global trade pathways raise a further problem. The plant trade is considered a major pathway for the accidental introduction of plant pathogens and the growing amount of plant trade between southern European countries and Britain within the EU trading block must inevitably provide increased opportunities for pests and pathogens from this region to arrive in Britain. A changing climate may then make the establishment of some these non-native pathogens more likely.

Several quarantine pathogens that have either recently arrived in Europe or steadily extended their northern range but are still absent from Britain are likely to pose a major threat. The most prominent examples are chestnut blight (*Cryophonectria parasitica*) and pitch canker (*Gibberella circinata* also known as *Fusarium circinatum*). Following its introduction into North America at the end of the nineteenth century, chestnut blight spread over five decades throughout all the main chestnut (*Castanea dentata*) areas and virtually destroyed all mature chestnut trees. In 1938, the pathogen was discovered in Italy and once again spread steadily, establishing in most parts of southern Europe where chestnuts are cultivated by the late 1960s. It is now present throughout much of France and still expanding northwards, with new records of the chestnut blight disease occurring yearly, especially in the north west (Brittany). Both *Castanea* and *Quercus* species are susceptible to this canker causing pathogen. CLIMEX modelling suggests that *C. parasitica* occurrence is favoured by increased precipitation and a warmer, drier summer climate (Desprez-Loustau *et al.* 2007) so CC is likely to increase the suitability of many parts of northern France and southern Britain for it. In 2011 an incursion of chestnut blight was discovered in England on recently planted chestnut trees imported from France (Hunter *et al.* 2013). Diseased trees were then found at a further nine recently planted locations (most from the same supplying nursery), but eradication efforts appear to have been successful and the disease is no longer considered to be present in the UK. However, a changing climate is likely to favour establishment and spread if more accidental introductions of chestnut blight occur in future.

Pitch canker is a more recent arrival in Europe, with formal reports of the disease in Spain in 2005, although informal records suggest the first findings were made in 1998 (Landeras *et al.* 2005) and more recently in Italy (Carlucci *et al.* 2007). Prior to this it was known mainly for the damage it caused in North America. Many *Pinus* species have been recorded as hosts as well as Douglas fir (*Pseudotsuga menziesii*). Shoots, branches, exposed roots and trunks can all be infected. The tops of trees and ultimately entire trees can be killed by this fungus, which is spread via moist winds and insect vectors (EPPO 2005). Moisture is required for infection, and a combination of precipitation and warm temperatures favour the pathogen, (Watt *et al*. 2011) and it is especially severe in California in close proximity to the coast (Gordon *et al*., 2001). Parts of East Anglia could be ideal for this pathogen especially with projected climate change.

The arrival of another new invasive pathogen from Europe, the ash dieback fungus *Hymenoscyphus fraxineus* (formerly *Chalara fraxinea*), probably dates back to the late 1990s but was unidentified at that time (Gross *et al.* 2014). It contrasts with chestnut blight and pitch canker because it is still largely absent from southern Europe, but since its discovery in Poland it has spread west across much of the natural distribution of *Fraxinus excelsior* (common ash) including the UK where it was first detected in 2012. Ash dieback disease causes high levels of tree mortality, but so far there has been little if any analysis of how the future of this epidemic could be shaped by climate change. The fruiting bodies produced mainly during July and August in the form of delicate apothecia that occur on dead, fallen leaf material, are easily desiccated and may be affected by dry summer conditions. However, the rapid spread and large-scale occurrence of the pathogen also suggest that it readily tolerates a wide range of environmental conditions.

In many instances the origins and/or arrival of apparently new pathogens are not detected until they are established and sometimes widespread. Climate change is likely to exacerbate this potential. One such example is a new disease causing bleeding canker of horse chestnut that has arisen in Europe and is caused by the bacterial pathogen, *Pseudomonas syringae* pathovar *aesculi* (Webber *et al*. 2007). Surveys have revealed the disease is now established in many parts of England, Wales and southern and western Scotland (Forestry Commission 2008). Evidence indicates that the epidemic in Europe has most likely resulted from the recent introduction of a single genotype of the bacterium, highlighting the risks posed by the accidental introduction of exotic pathogens to new geographical locations (Green *et al.* 2010). Details are also gradually emerging about disease epidemiology (Steele *et al.* 2010, Mullett & Webber 2013; Laue *et al*. 2014). Possibly the series of milder, wetter winters over the past few years has already aided the spread of *P. syringae* pv *aesculi* across the UK, but premature defoliation by strong winds in spring and summer could also expose unprotected leaf traces allow direct entry of the bacterium into the shoots (Billing 2011).

In general, tree diseases caused by *Pseudomonas* species are most prevalent in regions with cool, wet climates where they are thought to be spread mainly in wind-blown rain (eg Hattingh *et al.* 1989, Kennelly *et al.* 2007). In line with this, the *P. syringae* pv *aesculi* epidemic on horse chestnut appears to be geographically limited to north-western Europe where cool, wet climatic conditions prevail, and the pathogen may well be disseminated in wind or rain since lesions on branches are almost certainly initiated by aerial inoculum (Steele *et al*. 2010). Based on the predicted warmer, drier summers of the future, other bacterial diseases caused by different pathovars of *Pseudomonas syringae* might be expected to decrease because of the requirement for moisture and high humidity. This may, however, be counteracted by enhanced survival in soil during milder winters, and increased opportunities for dispersal and infection offered by severe rain and wind storms and the damage associated with these events (Boland *et al*. 2004).

Apart from these pathogen threats in Europe, many other pathogens from around the world may have increased opportunities to establish in Britain as the climate becomes more compatible, and trees come under higher levels of physiological stress and are therefore more likely to succumb to opportunist pathogens.

B.10 Gaps in evidence

A number of key evidence gaps exist in relation to CC and tree pathogens and we suggest how these might be addressed in the future.

- Systematic review is required of the full range of pathogens that are potentially key agents of forest disturbance over the next 50 years; these are likely to differ between conifers and broadleaf hosts. Phytophthoras, which can be root attacking or aerial, pose particular problems because they are environmentally persistent, highly mobile pathogens that attack a range of host tissues and often have wide host-ranges. They are also commonly found in nurseries and therefore most likely to be spread via the plant trade and have proved in many instances to be highly adaptable and invasive when exposed to new environments and hosts.

- Information on the abundance and impact of most pathogens is scant, even those considered economically and environmentally important. Monitoring and sampling of key pests/pathogens as part of systematic, integrated surveys are needed to provide critical information on the responses of key pest/pathogens to both short-term climatic fluctuations as well as longer-term climate trends.

- Routine deployment of molecular tools for accurate, rapid detection of pathogens could enable early confirmation of the presence (or absence) of important target pathogens during surveys. They can also be used to study aspects of tree host-pathogen interactions, for example in evaluating resistance in host genotypes to pathogen infection.

- There is insufficient ecological and epidemiological understanding of the direct environmental effects of temperature and moisture on key pathogens, particularly in relation to pathogens which attack roots or persist in soil. For example, there is virtually no available information on the performance of these agents in relation to soil temperatures, water potential and availability.

- There are few cases where pathogen behaviour and disease damage under different climatic scenarios can be predicted with confidence to assess possible regional changes in distribution and abundance. Poor historical climatic and pathogen distribution data also make comparisons and validation difficult.

- There is a lack of observational and experimental studies on the epidemiology of pathogens at the margins of their range, which might improve the characterisation of pathogen populations, to distinguish between population cycles and expansions.

- Experimental evidence on the effects of tree physiology on forest pathogens, particularly in relation to resistance mechanisms and how these are affected by external factors such as water availability and drought.

Conclusions and forward look

For aggressive pathogens such as Dutch elm disease or ash dieback, climate change effects on tree physiology are likely to be minor compared to the importance of tree genetics and pathogen dispersal. For others, climate change is likely to play a major role in defining levels of damage. With foliar pathogens such as *Dothistroma septosporum* and some aerial Phytophthoras, the impact is likely to be direct and rapid especially when environmental optima for sporulation, dispersal and infection are reached. Likewise, for insect pests threshold temperatures are critical for emergence and flight. Moreover, once disease levels reach critical thresholds they may not return to earlier levels even after particular climatic extremes that caused the outbreak have finished. Other tree pathogens such as root rot and decay fungi are long-lived and operate over long periods, even millennia. These include pathogens such as *Heterobasidion*, *Armillaria* and *Gymnopus*, and their visible effects may take decades to appear. In these instances the indirect influence of climate change on tree physiology may be much more crucial. Based on the relatively limited information available for most pathogens on their temperature and moisture requirements it is possible to define their climatic envelope, and even assign risk levels to key agents (see Table B1). However, trying to predict how a changing climate will influence the interactions between pathogens and tree physiology is difficult and complex.

Commercial forestry in Britain is currently dependent on a relatively limited panel of species. The dominant conifer species, Sitka spruce, accounts for around one half (51%) of the conifer area in Great Britain, followed by pine (~28% %) and larch (~10%). For deciduous genera, oak and birch dominate, comprising around 17% and 18% respectively of the broadleaved cover, with ash, sycamore and beech also considered important species at 12%, 8% and 7% respectively of the broadleaf area

(Forestry Commission, 2014). Based on current evidence forestry trees such as pine, larch, oak, beech and sycamore, which together make up more than a third of forest cover in Britain, are at risk from known pathogens that are either predicted to or might have an increased impact due to climate change. However, the major forestry species Sitka spruce is presently largely unscathed by any of the recently introduced pathogens. Instead it appears most at risk to threats driven by indirect effects of climate change such as drought stress, making it most vulnerable to root rot and latent pathogens, particularly the latter when planted on drought prone sites or insect pests such as *Elatobium abietinum* which is predicted to become an increasing threat to spruce plantantations in the future due to milder winters. Increased rotation length as part of continuous cover forestry might also increase the risk from root rot pathogens but is probably more likely to increase the risk of windthrow.

Adaptation efforts to counter climate change impacts has partly focussed on tree species or provenance choice to off-set the negative impacts on survival and growth. Some of these strategies might also be deployed to counter certain pests and pathogens. There is already some evidence to suggest there are differences in susceptibility of different provenance of various pine species to Dothistroma needle blight (Fraser *et al.* 2015) and their potential under future climate change scenarios should be considered. Other approaches also include creating a more diverse and structurally-varied vegetation or use of wider spacing (Read *et al.* 2009). The latter might also reduce disease levels of foliar pathogens such as Dothistroma by increasing air movement in stands and making environmental conditions less conducive for infection and sporulation. Diverse species mixtures could also have the additional beneficial effect of reducing the potential for pest and pathogen spread, for example by minimising roots grafts, making the conditions for successful aerial dispersal and infection more demanding.

However, the appearance of new threats has already undermined several species identified for consideration when developing climate change adaptation measures. Plans to use Corsican pine (*P. nigra* spp. *laricio*) have been largely adandoned with the upsurge in Dothistroma needle blight; *Fraxinus angustifolia* has proved highly susceptible to ash dieback (*Hymenoscyphus fraxineus*) which threatens ash populations across Europe, and is also likely to be susceptible to Emerald Ash Borer should it arrive in Europe (Straw *et al.* 2013). Other examples include loss of *Nothofagus obliqua* which is now routinely infected and killed by *Phytophthora pseudosyringae*; whilst sweet chestnut continues to be at risk from chestnut blight which is now widespread in neighbouring European countries. Therefore, greater awareness of pest and pathogen threats alongside improved biosecurity around the selection of planting stock and wider measures are critical to the success of adaption measures for the future.

Table B1

Analysis of the risk posed by major pathogens present in Britain in relation to climate change (1-5 + low to high risk)

Pathogen	**Disease symptoms**	**Affected genera/species**	**Likelihood of increased activity**	**Potential impact**	**Level of risk**
Foliar pathogens					
Marssonina spp.	Leaf spots, shoot blights, branch and stem cankers on young trees	Poplar, birch and willow	Low–moderate	Moderate[3]	2
Erysiphe spp.	Mildew causing leaf and shoot blight	Oak	Moderate–high	Moderate	3
Venturia spp.	Death of leaves and shoots	Poplar and willow	Low	Moderate	2
Melampsora spp.	Death of leaves, premature leaf fall	Poplar and willow	High	Moderate–high[4]	4
Dothistroma septosporum	Needle death, premature defoliation and tree mortality	Pines, especially Corsican, lodgepole and now Scots pine	High	High	5
Diplodea pinea	Shoot blight, top dieback, and cankers on stem and branches	Pines, particularly black pine	Moderate–high[1]	Moderate[1]	4
Phytophthora spp., e.g. *P. ramorum, P. pseudosyringae*	Leaf and shoot blights, stem cankers and mortality	Larch, beech, sweet chestnut, Southern beeches	Moderate[2]	High	4
Root rots					
Heterobasidion annosum	Decay and mortality (particularly of young trees)	All conifers	Moderate–high	High	4
Armillaria spp.	Decay, tree decline and mortality	Wide range of conifers and broadleaves	Moderate–high	Moderate[5]	4
Gymnopus fusipes	Decay, tree decline and mortality	Predominantly oak	Moderate	Low–moderate[6]	3
Phytophthora spp., e.g. *P. cinnamomi, P. alni, P. cambivora*	Root death, bleeding canker and mortality	Wide range of broadleaves	High	High[7]	5
Stem cankers					
Bacterial diseases	Bleeding stem canker, shoot tip die back, gummosis	Broadleaf species, e.g. alder, ash, cherry, horse chestnut and oak	High	Moderate–high	5
Stress related or latent pathogens					
Biscogniauxia spp	Strip cankers and dieback	Beech and oak	Moderate–high	High[8]	3
Botryosphaeria stevensii	Cankers and dieback	Ash and oak	Moderate	Low[1]	2
Cryptostroma corticale	Bark death and dieback	Sycamore	High	Low-moderate	2
Nectria coccinea	Bark death	Beech	Moderate	Moderate[9]	3
Hymenoscyphus fraxineus	Cankers, dieback, mortality	Ash	Low	High	3
Phomopsis spp	Bark cracking and stem lesions	Spruce and larch	Moderate	Low	2
Other established diseases					
Ophiostoma novo-ulmi	Vascular wilt (Dutch elm disease), mortality	Elm	Moderate	High	2
Ophiostoma and *Ceratocystis*	Bluestain of wood and bark death	Pines and other conifers	High	Moderate-high[10]	4

1 Impact could be especially high in nurseries, but also recognised as an endophyte which can be very damaging to stressed trees.
2 Some of the aerial Phytophthoras infect best at moderate temperatures (18–22°C) with high humidity, but can persist over hot summers via resting spores.
3 Moderate but localised impact, dependent on species involved.
4 Likely to have a high impact on clonal polar/willow biomass crops but this will be localised.
5 Main impact may still be on ornamental rather than commercial plantation/woodland species, although increased incidence of Armillaria attack on commercial forestry species is being recorded in the Forest Research Tree Health Diagnostic and Advisory Service database.
6 Low to moderate impact reflects the long time-scales before damage becomes apparent.
7 High impact anticipated because of root death interacting with drought.
8 Common species affected although the impact may be high but localised.
9 Losses likely to be increased by stems snapping in severe wind and rain storms.
10 High temperatures likely to favour not only the fungi but also the insect vectors

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