

Agriculture and Forestry Climate change report card technical paper

6. Tree & stand growth & productivity

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Summary

This Technical Report:

1. Introduces observed and expected effects of rising temperature, elevated CO₂ and soil water availability on temperate forests;
2. Outlines current knowledge on impacts of climate change on tree phenology and reproduction;
3. Suggests forest management approaches and options suitable for adapting UK forests to climate change.

The key findings of the Technical Report are:

1. Temperature rise in the predicted band of 2-4°C in this century is likely to increase forest productivity in tree populations which are currently not at the southern boundary of species distribution, directly by increasing the rate of CO₂ assimilation and indirectly by lengthening the growing season **[high confidence]**.
2. Elevated CO₂ will stimulate forest net primary production, at least in the short term (1-2 decades). Any long-term stimulation is subject to limitation by other factors, notably water availability in the South and East and soil nutrient availability across the UK **[high confidence]**.
3. Unseasonal low or high soil water availability and high water table levels will negatively affect growth of species not adapted conditions of drought or flooding; this effect is very localised as it is moderated by soil type, topography and artificial drainage **[moderate confidence]**.
4. Increasing temperature has already resulted in documented shifts in phenology. Potential impacts on productivity can be both positive (longer growing season) and negative (suboptimal release from dormancy) **[high confidence]**.
5. Elevated CO₂ may delay autumnal senescence in broadleaved species, however, there is no indication whether this has an impact on productivity **[low confidence]**.
6. Rising temperature, elevated CO₂ and unseasonal fluctuation of soil water availability are expected to interfere with seed production, particularly with masting events which are important for natural regeneration of forests **[moderate confidence]**.
7. Higher winter temperature will affect natural regeneration by impacting on seed dormancy status of species and provenances that have a substantial chilling requirements to break seed dormancy **[high confidence]**.
8. Management plans for UK forests will have to adapt to increased uncertainty and to accommodate a greater variation in site conditions over the rotation, the length of which may become shorter **[high confidence]**.

Introduction

Environmental change has already had, and is expected to have a profound effect on UK forests, particularly because of the longevity of forest trees. Planting and management decisions taken today will have an impact on forest productivity and stability many decades hence. In all likelihood, trees planted today to fit a set of environmental constraints are likely to reach maturity under a different climate which may or may not negatively affect their performance. A wide range of interlinked ecosystem services is delivered by UK forests, alongside the traditional provisioning service of timber production. This technical paper, however, will focus on impacts on forest growth and timber productivity as other types of forest ecosystem services are dealt with elsewhere. Specifically, this report will consider the evidence for impacts of expected changes in average temperature, atmospheric CO₂ concentration, and changing patterns of precipitation and water table on UK forest function. Mirroring existing regional differences due to geography and topography, environmental change is expected to differentially affect various parts of the UK. Whilst intra-annual variation and the magnitude and frequency of extremes of some climatic variables do have significant influence of tree growth and survival, these factors are dealt with in Technical paper and will not be considered here.

This technical paper, therefore, will weigh up existing evidence for current and expected effects of environmental change on UK forests as a whole, and will illustrate the most relevant regional differences and contrasts. The paper considers effects of environmental change on tree growth, seasonality and phenology, forest rotation cycle, timber quality and species choice. The final section outlines current challenges in our understanding and suggests strategies for adaptation to change.

Tree growth and yield

Forest productivity is one of the most important processes that drive carbon, water and nutrient cycles globally. The magnitude and dynamics of the process, commonly referred to as tree or forest growth, strongly depend on carbon accumulation and allocation to different storage pools (Litton *et al.*, 2007) and their responses to key determinants, such as climate (Babst *et al.*, 2013), tree age (Pajtik *et al.*, 2011), and competition for nutrients and light (Sardans and Peñuelas, 2013). These mechanisms, together with forest management practices (Fahey *et al.*, 2009), form a complex set of constraints and drivers which influence carbon allocation to physiological processes that determine tree growth. Naturally, from a forest management point of view, it is the allocation to stemwood which is the most relevant, albeit this is still relatively poorly understood at large scales (Brüggemann *et al.*, 2011). Whilst some of the mechanisms and drivers affecting forest growth will functionally remain the same functionally, it is reasonable to expect that environmental change will have significant impact on carbon allocation in trees and therefore on tree and forest stand growth (Callaway *et al.*, 1994).

For the purpose of forest management, tree growth can be defined as the increase in aboveground dimensions of an individual tree through time (Weiskittel *et al.*, 2011). The tree dimensions most commonly measured in forest practice are height and diameter, mostly due to ease of observation but also because of their strong correlation with wood volume and biomass. Growth increment, or change in a dimension per unit of time, is commonly expressed in either absolute or relative terms. The use of relative growth is particularly useful when looking at the interaction between the environment and tree growth in young forest stands because of the rapid, initially non-linear accumulation of non-photosynthetic material such as stems, branches, and roots (Konôpka *et al.*, 2013). Patterns of growth vary according to tree species and growing conditions (Herault *et al.*, 2011), but in general height increases rapidly in young trees and then levels off at maturity, height increment approaches

zero in mature forest stands possibly as the result of hydraulic limitation (Ryan and Yoder, 1997; Sperry *et al.*, 2008).

Stem diameter, on the other hand, grows comparatively steadily over the lifespan of a tree (Hann *et al.*, 1991). Although annual increment tends to decline with age, increasing resource availability has been shown to boost diameter growth (Bebber *et al.*, 2004). It is very difficult to separate the effects of tree size and age on stem growth. Experimental grafting of shoots from donor trees indicates that the age of the donor does not affect shoot growth rates, but the size of the recipient does (Mencuccini *et al.*, 2005). These observations suggest that tree growth is influenced by tree size rather than age, suggesting that changing environmental conditions will differentially affect growth and productivity of trees of different size.

Temperature

In temperate and especially in boreal climates, tree-ring chronologies indicate that mean temperature during the growing season is the main climatic factor affecting diameter growth (Nabeshima *et al.*; Miina, 2000). This is valid in both the short and long term; the start and duration of growth in a given growing season are related to mean annual temperature (Leikola and others, 1969), while inter annual variability in growth strongly reflects the temperature variation in summer temperature when tree growth usually peaks (Briffa *et al.*, 1990). In most trees, photosynthesis takes place at a fairly wide range of temperatures, and reversible changes and adaptation of photosynthetic processes are usually possible within a 10 °C to 35 °C band (Berry and Bjorkman, 1980). Looking at data from 19 gas exchange studies on trees and shrubs, Medlyn *et al.* (2002) showed that the optimum temperature for maximum rate of activity of the key primary CO₂ fixing enzyme, Rubisco, is around 29 °C in silver birch (*Betula pendula*), 43 °C in oak (*Quercus spp.*), 37 °C in silver fir (*Abies alba*) and 28 °C in Scots pine (*Pinus sylvestris*). These type of results suggest that trees in the UK currently grow in temperatures considerably below those at which maximum photosynthesis could occur. Measurements on temperate tree species in Australia have shown that net photosynthesis of at least 80% of maximum occurs over a 12–16 °C span of growth temperature, several times larger range than any temperature rise predicted for the UK over this century (Cunningham and Read, 2002). The ability of the temperate species to maintain maximum net photosynthesis over a greater range of growth temperatures is consistent with the large seasonal and diurnal variation in temperature in temperate climate zones. Looking at the global picture, tropical tree species may be near the high temperature threshold for photosynthesis that, if exceeded, will greatly reduce CO₂. This is not the case for temperate and boreal tree species growing in UK forests, where mean temperature is projected to rise by about 2-5°C by 2080s (Murphy *et al.*, 2009) from a current annual mean well below the critical threshold. These findings suggest that trees in colder environments may benefit from some degree of climate warming, but species in warmer environments will not (Figure 1). Increased rate of photosynthesis, however, may not directly translate to increased growth. Higher temperature is likely to stimulate autorespiration as well as photosynthesis, reducing the growth benefit resulting from rising temperature. Way and Oren (2010) in their review of tree growth responses to temperature predicted more variation in the response of high latitude and altitude tree species to a given temperature increase than for more warm-adapted species. Applied to UK conditions, it is therefore likely that stronger positive responses of trees and stands is to be expected in Scotland and at higher altitudes in England and Wales (where forest production is currently dominated by conifers), than at lower altitudes (predominantly broadleaves, but also containing large conifer stands). The scale of climate change predictions indicates that, in southern England, native broadleaf species may become unsuitable for timber production on drier soils. The planting of non-native species may therefore be considered to maintain woodland cover and ensure a viable hardwood timber industry (Broadmeadow *et al.*, 2009).

Atmospheric CO₂ concentration

Concurrent with, and indeed the main driver of, recent and predicted temperature increases, the rising atmospheric CO₂ concentration will have a significant effect on forest growth of forests. All tree species currently growing in the UK have the so-called C3 type of photosynthetic pathway (Sage *et al.*, 2011), which means that rising CO₂ concentration is likely to stimulate the rate of C fixation and increase C availability for allocation to tree biomass pools (Farquhar *et al.*, 1980). C3 photosynthesis does not become saturated at current (403 ppm at the time of writing) or near future CO₂ concentrations, therefore higher photosynthetic productivity of forest trees is to be expected. Early experiments looking at responses of tree species to doubling of atmospheric CO₂ concentration (mostly carried out on seedlings and young trees) indicated that the mean biomass accumulation due to doubled CO₂ is +38% for coniferous and +63% for broadleaved trees (Ceulemans and Mousseau, 1994). Later, Free Air CO₂ Enrichment (FACE) techniques were perfected and used to expose sections of developing or mature forests to elevated CO₂. Owing to growth limitation by other environmental factors and as the result of observing more mature trees, Norby *et al.* (2005) report that the response of forest net primary production (NPP) to elevated CO₂ is quite similar across a broad range of forest productivity, with a median stimulation of 23% for a doubling of CO₂ concentration. All FACE experiments have only exposed trees to elevated CO₂ for a fraction of their natural lifetime. Some of the slightly longer-term observations, such as in the FACE experiment on deciduous sweetgum (*Liquidambar styraciflua*), indicate that continuous exposure to elevated CO₂ leads to a decline in the NPP stimulation from 24% to 9% after 11 years (Norby *et al.*, 2010). Others show more mixed responses: exposing mature forest to a step-change in atmospheric CO₂ did not lead to any measurable stimulation of radial growth in broadleaf (Bader *et al.*, 2013) or conifer (Sigurdsson *et al.*, 2013) species. A FACE experiment investigating the response of a treeline ecosystem to elevated CO₂ over 9 years showed a differential response between species, larch trees showed increased ring width growth whereas pines did not (Dawes *et al.*, 2011).

One of the limitations of the initial FACE experiments was that they studied monoculture plantations, whereas most non-plantation forests are composed of tree species mixtures. The BangorFACE experiment assessed elevated CO₂ effects on monocultures and 2- or 3-species mixtures in a very young broadleaf stands of European beech (*Fagus sylvatica*), common alder (*Alnus glutinosa*) and silver birch (*Betula pendula*). Monocultures showed stemwood growth stimulation similar to other studies (Smith *et al.*, 2013b), whilst growth stimulation in mixtures resulted in larger root systems response rather than increasing stem growth (Smith *et al.*, 2013a). This finding highlights the fact that radial stem increment – although of key importance in commercial forestry – may not be the best indicator of forest response to elevated CO₂. In a wider ecological sense, measuring forest NPP might be more appropriate as it measures the amount of carbon (and thus energy) entering the forest ecosystem. NPP can be enhanced by elevated CO₂ after canopy closure, but current knowledge indicates that the stimulation may be downregulated by other environmental factors over time (Norby and Zak, 2011).

Precipitation and water table

Current climate change predictions indicate that the UK falls within a region with generally increasing precipitation, with projected increases of up to 10%, though some southern parts of the UK may experience decreases of up to 5% (Met Office, 2011). Seasonal distribution of precipitation is likely to be affected as well, with lower summer and higher winter precipitation totals predicted (Murphy *et al.*, 2009). At present, precipitation and resulting soil water availability appears sufficient to allow good rates of growth for most trees across the UK with the exception of East and South East regions which may experience summer water deficits, particularly on lighter or shallower soils. Evidence indicates that there are significant differences between tree species in their ability to maintain or recover from a dry spell in

term of timber productivity (Eilmann and Rigling, 2012) and survival (Peng *et al.*, 2011). Impacts of severe drought are not the focus of this paper (see Technical paper no 9, for impacts of extreme events), but persistent reduction of the amount of water available for uptake can have a negative impact on forest growth. A sequence of years with sub-optimal rainfall may result in a cumulative negative effect on growth, possibly leading to tree dieback (Allen *et al.*, 2010). As water availability is one of the main drivers of forest growth (Wagner *et al.*, 2012), and some indication of expected negative changes in forest productivity can be inferred from regions with climate similar to that predicted for the South East/ East of the UK, where selective growth reduction and tree dieback have been observed (Vayreda *et al.*, 2012). An interesting interaction between water use and elevated CO₂ occurs where elevated CO₂ reduces water vapour exchange between tree foliage and the surrounding atmosphere, leading to observations of increased water use efficiency (ratio of C accumulation to water loss) in forests. These, however, do not translate to increased tree growth (Andreu-Hailes *et al.*, 2011; Peñuelas *et al.*, 2011).

High water table and anoxic soil conditions may negatively affect tree growth in regions predicted to receive more precipitation in the future. Because the impact of excessive water supply is highly mediated by topography, this effect of climatic change will be very localised and likely to affect specific tree communities or stands (Lukac *et al.*, 2011). However, artificial drainage of organic or wetter soils is a common feature in much of plantation forestry in the UK, more intense precipitation may impact the performance of existing drainage systems. Restricted oxygen exchange between the root zone and the aerated environment due to high water content leads to hypoxia (Kreuzwieser *et al.*, 2003), which induces severe stress in tree root systems (Vartapetian and Jackson, 1997). Several tree species common in the UK have evolved mechanisms to deal with anoxic conditions in the soil, notably willows (*Salix spp.*), poplars (*Populus spp.*), common alder (*Alnus glutinosa*) and European ash (*Fraxinus excelsior*) (Drew, 1997). While high soil water content during the period of dormancy does not usually cause lasting damage, prolonged and frequent flooding during the growing season can severely limit growth of intolerant tree species (Figure 2). With specific reference to upland forest plantations growing in organic soils where water table management already is a key determinant of forest productivity (Skovsgaard, 2009), increased precipitation and prolonged flooding may confer an increasing risk of peatland encroachment, with adverse consequences for forest growth and regeneration (Crawford *et al.*, 2003).

In summary, rising temperature and atmospheric CO₂ concentration, together with stable or increasing precipitation in most of the UK but with changes seasonal patterns, are likely to have a combined positive effect on growth of trees and forests in the UK. Temperate tree species currently grow under a suboptimal temperature and CO₂ regime. Empirical evidence from tree ring studies carried out in permanent forest plots across Europe indicates that forest productivity has been steadily increasing over the last century (Pretzsch *et al.*, 2014). Present forest stands grow more rapidly, and accumulate a given standing volume earlier than comparable stands did a century ago (note possible contribution of N deposition (Magnani *et al.*, 2007); the growth trend is primarily based on a changed relationship between tree size and growth. Regional and local differences in other environmental factors such as soil drainage, nutrient availability and disturbance regimes are, however, likely to constrain positive growth response of forest trees.

Increasing temperatures since the 1950s have had a lower than expected effect in many Northern Hemisphere species (D'Arrigo *et al.*, 2008). This discrepancy is known as the 'divergence problem' in tree ring studies, with several possible explanations put forward; increased drought stress (Van Mantgem and Stephenson, 2007), shorter growing seasons caused by increased snowfall and therefore later snowmelt (Vaganov *et al.*, 1999), decreasing stratospheric ozone levels or changes in solar intensity (D'Arrigo *et al.*, 2008), or summer temperatures that are now exceeding the thermal optimum for growth of some species (e.g. white spruce (*Picea glauca*)) (D'Arrigo *et al.*, 2004). A new theory currently

being explored is that forest NPP does indeed react positively to elevated CO₂ and temperature, but the additional productivity is allocated to tree biomass pools other than stem (Li *et al.*, 2015). Because most existing observations of forest growth used only stem diameter measurements, such a shift in biomass allocation would be largely unreported.

Phenology, Growing season duration, Vernalisation & Dormancy

Annual developmental events such as bud-burst or flowering occur at specific times in different tree species. The timing of such development patterns is known as 'phenology' and is commonly affected by current and preceding environmental cues. For this reason, changes in climate have been observed to lead to changes in vegetation phenology (Chmielewski and Rötzer, 2001) and are often used as an indicator of environmental change (Kramer *et al.*, 2000). The large interannual variability in phenological events documented for European forests has often been explained by variation in cumulative temperature, global circulation patterns, or climate forcing factors such as solar cycles and the North Atlantic Oscillation (Badeck *et al.*, 2004). Climate change, which impacts mean temperature but also its annual fluctuation, is therefore also likely to have a direct and immediate impact on forest productivity and growth.

Temperature

Two key phenological events occur in UK forests each year – spring initiation (bud burst) and autumn cessation of growth. These two processes determine growth and biomass accumulation of trees by maximising the potential for photosynthesis during the most suitable period of the year, whilst minimising risk of damage to foliage and expanding tissues by low temperatures (Basler and Körner, 2012). In winter, trees in temperate and boreal climates undergo a period of dormancy, enabling them to withstand harsh climatic conditions. During this time, they require an accumulation of cold temperature days ('winter chill') to enhance the ability to trigger subsequent spring bud burst, summer flowering and seed production (Schwartz and Hanes, 2010). There is now unequivocal evidence that a measured decline in winter chill is apparent in the UK and in other parts of the globe (Baldocchi and Wong, 2008; Luedeling *et al.*, 2011). Little evidence of impacts exists for forest trees, but insufficient chilling is known to delay bud burst or decrease bud burst percentage (Samish, 1954). The actual range and duration of effective temperatures for chilling is poorly understood for forest trees, but cool and non-freezing temperatures between 2 and 4 °C and possibly up to 10 °C are thought to be most effective (Battey, 2000). Interspecific differences have been demonstrated, for example Norway spruce seems to require less chilling exposure than beech, oak or maple (Basler and Körner, 2012).

The gradual transition between dormancy and active growth involves numerous genetic, biochemical, physiological and anatomical alterations (Horvath *et al.*, 2010). The most important environmental drivers initiating growth following dormancy are temperature accumulation and photoperiod (daylength change). Photoperiodic responses in spring phenology are highly species dependent and still not well understood for most species. A possible explanation is that forest tree species commonly operate within a wide photoperiod envelope in which temperature has an overwhelming effect, particularly in cool years (Körner, 2006). In European forest tree species, photoperiod sensitivity is most pronounced in European beech (*Fagus sylvatica*) (Heide, 1993), but has also been observed in Norway spruce (*Picea abies*) (Partanen *et al.*, 1998), silver birch (*Betula pendula*) (Caffarra and Donnelly, 2011) and reported for a range of early and late successional species (Basler and Körner, 2012). Photoperiod is likely to interact at different stages of dormancy release; long photoperiods are likely to substitute for a lack of chilling (Heide, 1993) and decrease the thermal requirement for bud burst (Myking and Heide, 1995). A complete substitution of chilling by long photoperiods, however, does not appear likely to allow for dormancy release

without an impact on tree physiological response and reduced growth (Laube *et al.*, 2014). Chilling, photoperiod and temperature accumulation interact in a complex, species-specific manner which still remains to be clearly understood. Phenology of boreal and temperate trees is likely to be driven by differential climatic conditions and inter- and intraspecific genetic differences. The annual cycle of these trees is an integrated system, where one phase affects subsequent phases, resulting in delayed and cumulative impacts (Hänninen and Tanino, 2011).

Increasing temperatures are also expected to affect phenological processes in trees at the end of the growth season. In most temperate and boreal trees, dormancy is induced by a combination of low temperatures and decreasing daylength in autumn (Thomas and Vince-Prue, 1997). Some evidence points to the existence of independent pathways through which low temperature and photoperiod induce dormancy (Welling *et al.*, 2002), and in some species low temperatures alone seem to be sufficient to induce dormancy (Heide and Prestrud, 2005). Richardson *et al.* (2006) found that slightly less than 90% of the variation in autumn canopy senescence of sugar maple, American beech and yellow birch was accounted for by accumulated degree-days. An analysis of carbon uptake at 21 FLUXNET sites, where detailed measurements of CO₂ uptake and loss are studied continuously, has found that temporal anomalies affecting spring onset of productivity appear to have positive carry-over effects on productivity anomalies in the autumn of the same year, but also that later autumn senescence positively impacts on productivity in following spring (Richardson *et al.*, 2010). Keenan *et al.* (2014) observed a strong trend of earlier spring and later autumn when looking at 2 decades of forest phenological observations. Carbon uptake through photosynthesis increased considerably more than carbon release through respiration for both an earlier spring and later autumn (Figure 3). For the latitudinal range of the UK, it is worth noting that forests growing in the north of the country are less likely to benefit from delayed autumn senescence as their productivity is limited more by low light intensity than by low temperature later in the year (e.g. Suni *et al.* (2003)). By comparison, earlier spring onset of photosynthetic uptake might benefit productivity across the UK as, by the time this occurs, solar radiation is typically not limiting (Tanja *et al.*, 2003). Finally, the productivity of evergreen needle-leaf forests is less sensitive to phenology than the productivity of deciduous broadleaf forests (Richardson *et al.*, 2010), conifers typically initiate photosynthesis when air temperature reaches 5°C irrespective of dormancy status (Clement *et al.*, 2012).

Atmospheric CO₂ concentration

Natural autumnal senescence is also regulated by plant carbon–nitrogen and source–sink balance (Wingler *et al.*, 2004). The mechanism affecting cessation of photosynthesis can be traced to the optimisation of the nitrogen and carbon status of the plant (Keskitalo *et al.*, 2005). The strength of the plant's sink for photosynthate can positively influence photosynthetic responses to elevated CO₂ concentrations (Ainsworth *et al.*, 2004) and may also reduce the rate of senescence (Wingler *et al.*, 2004). Research into the autumnal senescence of forest trees indicates a large variability in response to elevated CO₂, with senescence advancing in some species (Norby *et al.*, 2003; Körner *et al.*, 2005), being delayed in other species (Rae *et al.*, 2006; Taylor *et al.*, 2008), or showing no effect (Asshoff *et al.*, 2006). In a study of poplar genotypes on two continents, Tallis *et al.* (2010) showed that elevated atmospheric CO₂ delayed autumnal senescence in a poplar (*Populus spp.*) forest canopy. At the canopy level, the declines in greenness (NDVI) and leaf area index (LAI) were both significantly delayed by elevated CO₂. To date, however, the findings on effects of elevated CO₂ independent of other factors are inconclusive and appear highly species specific (Asshoff *et al.*, 2006).

Precipitation and water table

While phenology and growth patterns of tropical forests show a very strong relationship with precipitation and resulting water availability (Borchert, 1994; Wagner *et al.*, 2012), however this link is far less evident in temperate and boreal forest because factors are more dominant. With regards to expected changes in climate and forest phenology in the UK, the following two aspects are worth exploring. First, spring onset of growth and subsequent forest productivity relies on synchrony with high soil water status. Flooding and water saturation of soil usually occur during the period of winter dormancy, without any negative impact on forest growth (Clark *et al.*, 2011). With continuing advancement of spring onset, there is a possibility of budburst co-occurring with a period of low soil oxygen status, with detrimental effects on the onset of tree growth. In mixed species forests, whether naturally regenerated or planted, periods of high soil water status have been observed to result in changes in tree species composition (Streng *et al.*, 1989). Second, soil water availability is one of the factors contributing to autumn senescence. While higher temperatures and elevated CO₂ may delay senescence, continuing low water availability in the south east of the UK may advance senescence and thus reduce the length of the growing season (Meier and Leuschner, 2008; Montserrat-Martí *et al.*, 2009). There is some evidence of an interaction between drought and elevated CO₂ affecting foliage senescence in deciduous temperate species (Tschaplinski *et al.*, 1995), although the exact mechanism or its impact are currently unknown.

In summary, on-going environmental change does and will have significant effects on forest growth and productivity. Some of the positive effects are related to improved growth conditions as a result of temperature and atmospheric CO₂ concentration being closer to physiological optimum. Lengthening of the growing season as a result of increasing temperature also increases the period suitable for photosynthesis. At the same time, the costs of mistimed phenology caused by changing abiotic drivers could be significant: advanced bud-burst can lead to death or extensive tissue damage due to frost in frost-prone areas notably in Scotland but also elsewhere, but delayed bud-burst could lead to loss of productivity in drought prone regions in the South/East. Indirect effect of changes in tree phenology include the mistiming of key events across trophic levels in forest ecosystems (Bauer *et al.*, 2010; Walther, 2010), i.e. changes in the relationship between the producer and consumer groups. Such disruption could have a long-term impact on forest productivity via disturbance of energy and nutrient cycles (Cleland *et al.*, 2007; Luo, 2007), temporal disruption of species interactions (Tylianakis *et al.*, 2008; Bauer *et al.*, 2010) and possibly lead to loss of forest ecosystem services (Lindner *et al.*, 2010; Walther, 2010).

Natural regeneration: seed production, masting events, seed quality and germination

Effects of climate change on seed production in unmanaged forests is likely to be one of the key long-term mechanisms which will drive their development in the future. Seed quantity and quality control the regeneration processes and the ability of tree species to spread to new locations (Ibanez *et al.*, 2008). Most tree species exhibit distinctive inter-annual patterns of seed production characterised by spatial synchronicity (e.g. Burrows and Allen (Burrows and Allen, 1991)), periodicity (e.g. Allen *et al.* (2012), Greene *et al.* (2004)) and high variability (e.g. Greene *et al.* (2004), Herrera *et al.* (1998)). Several hypotheses have been put forward to explain the development of synchronous and highly variable seed production, such as predator satiation (Crawley and Long, 1995), increased pollination efficiency (Koenig *et al.*, 1994) and resource dynamics (Danielson and Frommer, 2013; Koenig and Knops, 2014). The ability to produce seed in sufficient quantity and with the capacity to germinate at the right time may increasingly become a challenge to many forest tree species as seed production is controlled by the interaction of several factors affected by environmental change.

Temperature

Seed production, in particular masting events characterised by a very large crop of seed produced in some years, have been shown to correlate closely with temperatures during current and preceding years. Low temperature and increased moisture availability during the resource build-up period lasting approximately two years prior to seedfall, has been linked to increased seed production across populations of various tree species (e.g. Piovesan *et al.* (2001)). This effect of cooler conditions contrasts with impacts of higher temperatures during floral primordia development about 1 year prior to seedfall (e.g. Övergaard *et al.* (2007), Schauber *et al.* (2002)) and warmer post-flowering episodes negatively affecting successful seed development (e.g. Richardson *et al.* (2005)). Combinations and specific timing of precipitation and temperature patterns explain most of the interannual variation in tree seed production (Allen *et al.*, 2014). Smaill *et al.* (2011) have shown that masting events can be predicted from temperature patterns with high reliability in New Zealand mountain beech forests, but these effects can be modified by soil resource availability (Tanentzap *et al.*, 2012). Some observed effects appear divergent: seed viability of white spruce (*Picea glauca*) in the interior of Alaska is strongly and positively related to summer temperatures over the period of primordia development, but total seed production is negatively related to temperature over the same period (Roland *et al.*, 2014). Temperature appears to be the dominant factor directly (flowering phenology) and indirectly (resource availability for seed filling) influencing frequency of masting events (Allen *et al.*, 2014). Since UK climate change predictions indicate a trend towards higher temperatures during both vegetative and dormant periods, together with altered annual precipitation patterns, it is reasonable to expect that the existing pattern of masting events will be disturbed. It is however not possible to indicate the size or the direction of this disturbance.

Temperature is a key environmental factor which also regulates dormancy and germination of seeds (Bewley, 1997). An increasingly warmer climate may impact on the natural regeneration of tree species that have a chilling requirement (Broadmeadow *et al.*, 2005). Tree species vary in the temperature range required for breaking dormancy; from narrow (Washitani and Kabaya, 1988) to wide (Vleeshouwers and Bouwmeester, 2001). Changes in both the severity and duration of low winter temperatures may therefore have species-specific effects, with a higher proportion of seed may remain dormant in some species compared to others (Walck *et al.*, 2011). Relatively small changes to weather may have a profound effect on tree species regeneration. For example, under laboratory conditions, a simulated mid-winter warm period of as little as 24 h under laboratory conditions reduced spring germination and induced secondary dormancy in non-germinated herbaceous seeds (Ter Borg, 2005).

Atmospheric CO₂ concentration

Many of the tree species exposed to high CO₂ in FACE or OTC (Open Top Chamber) studies have been found to produce more seeds than at ambient CO₂. If this effect proves to be long-lasting, natural regeneration of future forests may be less limited by seed supply. Seed production is thought to represent very high energy and nutrient investment. Increased seed numbers produced at high CO₂ are, however, often correlated with reduced seed quality in a range of species (Jablonski *et al.*, 2002). Growth under elevated CO₂ led to an 85% greater number of fruits in sour orange (*Citrus aurantium*) trees over 17 years without affecting individual fruit mass (Kimball *et al.*, 2007). Similarly, Stiling *et al.* (2004) found increased acorn production, but no change in acorn mass or viability for oak species (*Quercus spp.*) in a scrub-oak community, while Way *et al.* (2010) found greater seed production in loblolly pine (*Pinus taeda*) grown in elevated CO₂. The latter study reported no decrease in seed quality, while a marked shift towards greater participation of individual trees in stand reproduction was observed. After 3 years of high CO₂ fumigation, loblolly pine trees were twice as likely to be reproductively mature and produced three times as many cones and seeds as trees in current ambient CO₂ concentration (LaDeau and Clark, 2001).

Trees growing in elevated CO₂ reached reproductive maturity sooner and at smaller size. Later in the same experiment, a larger proportion of trees produced seed in elevated CO₂ compared to ambient (Ladeau and Clark, 2006), accompanied by a doubling of pollen production (Way *et al.*, 2010). Due to the short-term nature of elevated CO₂ studies compared to the long-term pattern in seed production, no firm conclusions as to the effects on masting events can be drawn. To date, observations indicate high interannual variability. For example, seed mass of paper birch (*Betula papyrifera*) was significantly increased in only one out of three years in elevated CO₂ – grown trees, while germination rates of seed produced in elevated CO₂ were significantly higher in two of three years (Darbah *et al.*, 2008). Any differences in the response to elevated CO₂ between forest tree species will have important consequences for future forest community composition. Tree species that exhibit pronounced growth responses to high CO₂ could further enhance their competitive ability by also producing more seeds through continued reproductive allocation (Way and Oren, 2010).

Precipitation and water table

Sufficient water availability preceding and during seed production has frequently been found as a factor significantly affecting seed quantity and quality. Because water availability during winter and early spring is not predicted to decrease, it is summer which may influence seed production in UK tree species is summer drought, particularly in the drought-prone parts of the country. In a long-term data set on reproductive and vegetative growth of holm oak (*Quercus ilex*) in Mediterranean woodland, the annual seed crop was always affected by environmental factors related to the precipitation pattern (Pérez-Ramos *et al.*, 2010). Seed production was strongly dependent upon water availability at initial (spring) and advanced (summer) stages of the acorn maturation cycle, whereas the final step of seed development was negatively affected by the frequency of torrential-rain events. The latter observation might be of relevance to the success of oak reproduction in the UK where climate change predictions indicate an increased frequency of extreme weather events. Similarly, Espelta *et al.* (2008) found that inter-annual differences in summer water stress modified the likelihood of abortion during acorn ripening and enforced within- and, particularly, between-species synchrony and population variability in acorn production in holm oak (*Quercus ilex*) and downy oak (*Quercus humilis*). In Sweden, on the other hand, Drobyshev *et al.* (2010) found that drought stress itself was not correlated to the occurrence of mast years in European beech (*Fagus sylvatica*). In an environment with similar water availability to that of the north of the UK, the role of water availability in controlling beech masting behaviour appeared limited due to a sufficient amount of growing season precipitation. Water availability, however, may be an important factor in controlling masting behaviour in other parts of the distribution range of beech, with drought having been identified as the main factor affecting beech masting patterns in Europe and eastern North America (Piovesan and Adams, 2001). Significant interaction between precipitation and temperature controls seed production and masting behaviour in many species. For example, cone yield of Mediterranean stone pine (*Pinus pinea*) has been shown to strongly respond to signals from these two environmental factors (Mutke *et al.*, 2005).

In summary, reproductive success of forest trees depends on strong synchrony between weather patterns, seed production and germination. Environmental change is likely to influence all of these processes via changes in timing of key events, alterations of resource availability and by changing the combinations of ecological conditions necessary for successful establishment of a cohort of seedlings. Key factors influencing seed yield and its quality are temperature fluctuations during several years preceding a masting event, together with water availability during seed growth and temperature profile during the winter following seed dispersal. The few observations that are available indicate, that differences between tree species in their sensitivity to environmental factors exist, leading to the

suggestion that environmental change will alter forest regeneration dynamics and therefore species composition of naturally regenerated forests in the future.

Although this section deals with natural regeneration, and therefore excludes plantation forestry, there are some similarities in the way the two pathways of forest renewal will be affected by climate change. Plantation sector relies on seed stock of provenance suitable for prevailing environmental conditions. Effects of climate change on seed production and viability are of minor importance to this process, but increased occurrence of spring droughts or winter waterlogging will negatively impact the success of forest plantation establishment. Plantation forestry will have to widen its range of tree species provenances to suit predicted climatic conditions, but also adapt forest planting methods to minimise the risk of tree crop failure.

Implications for forest management: rotation length, timber quality and species choice

Environmental change affects some of the key factors which drive fundamental biological processes in plants and will therefore impact development of forest ecosystems. Ongoing change is likely to affect the distribution, structure, composition, and function of forest ecosystems. This profound change will need to be managed to ensure forests will continue to provide services essential to society (Millar *et al.*, 2007). As outlined in preceding sections, rising temperature, increasing concentration of atmospheric CO₂ and altered precipitation regime will all alter forest growth, phenology and reproduction. This section details the implications of expected changes for the management of UK forests.

Temperature

According to the latest UK climate projections (UKCP09), average temperatures in southern England are predicted to increase by 4.2 °C in summer and 3.5 °C in winter by 2080, implying that trees planted today would be subjected to temperature conditions prevailing in regions two to three degrees of latitude further south (Figure 4) (Hubert and others, 2007). In the absence of other limiting factors, faster ontogenetic development of individual trees as a result of increasing temperature is likely to reduce the time necessary to reach target size, theoretically allowing for higher yield class and shorter rotations or increased standing biomass. In the UK, any increase in productivity resulting from higher temperatures is likely to be modified by drought in some regions, especially in the south, south-east and central England (Broadmeadow *et al.*, 2005), but also see Technical paper 9. It is expected that predicted climates will not be suitable for growing certain trees for timber in some combinations of soil and climatic conditions. This implies that a change of management goals due to longevity existing stands (delivering other ecosystem services, Technical paper 10.) or a change of species/provenance may be necessary in the future. Current policy of planting local or provenances verified for past conditions aims to maximise productivity by growing trees adapted to local climate, which will however not be in existence within several decades. It has been argued that local adaptation by forest trees is dynamic (Brown, 1997) and that traits involved in local adaptation of temperate and boreal trees appear to be the product of small effects of many genes (Aitken *et al.*, 2008). Managed genetic diversity may be harnessed to establish long-term viability of forest tree populations, but recruitment of new genotypes into existing populations suffers from forest fragmentation prevalent in the UK (Cavers and Cottrell, 2015). On the continent, natural gene flow with pre-adapted alleles from warmer climates may promote adaptation and migration at the leading edge, but even widespread species with large populations will likely suffer an adaptational lag for a few generations.

Barring severe climate change predicted by high-emission scenarios, forest ecosystems will adapt to climate change in time. However, it is the role of forest management to minimise

any reduction in timber yield during the transition from one forest type to another (Kellomäki *et al.*, 2008). Suboptimal conditions for some species may occur in certain regions, especially at the trailing edge of current geographical distribution, which will require artificial shortening of the rotation and replacement by more suitable species. It is currently difficult to quantify the transitional cost in productivity, however a study of species range changes in North America has shown that three fifths of the tree species currently show the pattern expected for a population undergoing range contraction, rather than expansion, at both northern and southern boundaries (Zhu *et al.*, 2012). About a fifth of tree species show a pattern consistent with a northward shift (20.7%) and only 4.3% are consistent with expansion at both range limits. One forest management approach currently under discussion is assisted migration; *i.e.* planting provenances from a region with climatic conditions similar to that of future climates (Gray *et al.*, 2011; Koralewski *et al.*, 2015). Most trees in commercial forestry in the UK are planted, assisted migration of provenances or species would therefore entail selection of genotypes not currently considered suitable for a particular location. Given the uncertainty in climate change predictions, a policy supporting planting of a range of provenances or of mixed-species forests may be one of the ways to ascertain continuity of forest cover in the future.

Atmospheric CO₂ concentration

Increasing concentration of atmospheric CO₂ will positively affect growth of UK forests, although probably not all species to the same degree and not in perpetuity as the stimulation will likely be constrained by other limiting factors. Nevertheless, in a positive interaction with rising temperature, an increase in productivity due to elevated CO₂ is predicted. Evidence shows that exposing forests to air with future concentration of CO₂ may lead to faster development (Norby *et al.*, 2005), earlier reproductive maturity (Ladeau and Clark, 2006), alteration of competition (Smith *et al.*, 2013a) and changes in understory dynamics (Souza *et al.*, 2010). However, most of the available data describing effects of elevated CO₂ on forests originate from experiments which cover only a fraction of normal forest rotation and therefore any inference as to the effects of elevated CO₂ on rotation length and its management are uncertain.

A few reports offer evidence on effects of elevated CO₂ on wood properties, indicating variable responses. In conifers, wood density increased (Kilpeläinen *et al.*, 2003) or was unaffected (Ceulemans *et al.*, 2002) or was found to be clone specific (Kostiainen *et al.*, 2014). Cell wall thickness of tracheids increased in Monterey pine (*Pinus radiata*) (Atwell *et al.*, 2003), but decreased in Siberian larch (*Larix sibirica*) (Yazaki *et al.*, 2001). The few studies on responses of wood chemical composition to elevated CO₂ report no significant effects in longleaf pine (*Pinus palustris*) Mill. (Runion *et al.*, 1999), Scots pine (*Pinus sylvestris*) (Kilpeläinen *et al.*, 2003) or Monterey pine (Atwell *et al.*, 2003). Blaschke *et al.* (2002) observed a decrease in lignin concentration in beech (*Fagus sylvatica*), as did Anttonen *et al.* (2001) in trembling aspen (*Populus tremula*). Increase in soluble sugars and starch were found to increase in aspen clones, but not systematically (Kaakinen *et al.*, 2004). Hence, currently it is not possible to draw any inference about effects of elevated CO₂ on timber quality and any resulting adaptations of forest management that might be required.

Conclusion

This report aims to illustrate effects of predicted climate change on forest growth, phenology and reproduction. Available evidence is imperfect as many of the key drivers of change interact and are correlated. The long life cycle of most tree species makes it difficult to observe impacts of changing environmental factors over an entire length of forest rotation. Existing experimental and observational data must be supplemented by process-based modelling studies which make use of climate predictions to explore forest growth potential in

the future. A forest ecosystem comprises many material and energy cycles, it is reasonable to expect that it will take decades to centuries before it adapts to a new set of environmental conditions. Moreover, any trees planted today are expected to persist and grow both in current and in future climates. As outlined in this paper, climate change will affect forest growth directly by affecting tree physiology, but also indirectly by altering the function of the whole forest ecosystem. Interaction with other organisms, including many pests and diseases, will determine the impact of climate change on UK forests.

Given these constraints and the uncertainty inherent to future climate predictions, a greater focus on tree diversity may be necessary. Planting forests which contain a range of provenances, a range of species or even a range of forest stand types may be required to guarantee continuity of the provision of ecosystem services, including timber production. Naturally, moving away from monocultures and single provenance stands implies greater complexity of forest management methods and probably a yield penalty because not all trees will be able to exploit a wide set of environmental conditions to the maximum.

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Figure 1. Range of growth responses to warming. Adapted from Way and Oren (2010).

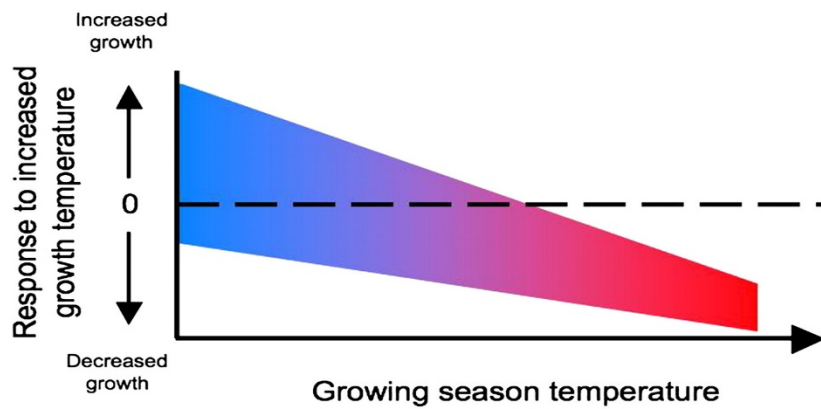


Figure 2. Sensitivity of broadleaf tree species to anoxic conditions within the rooting zone. Adapted from Lukac (2011).

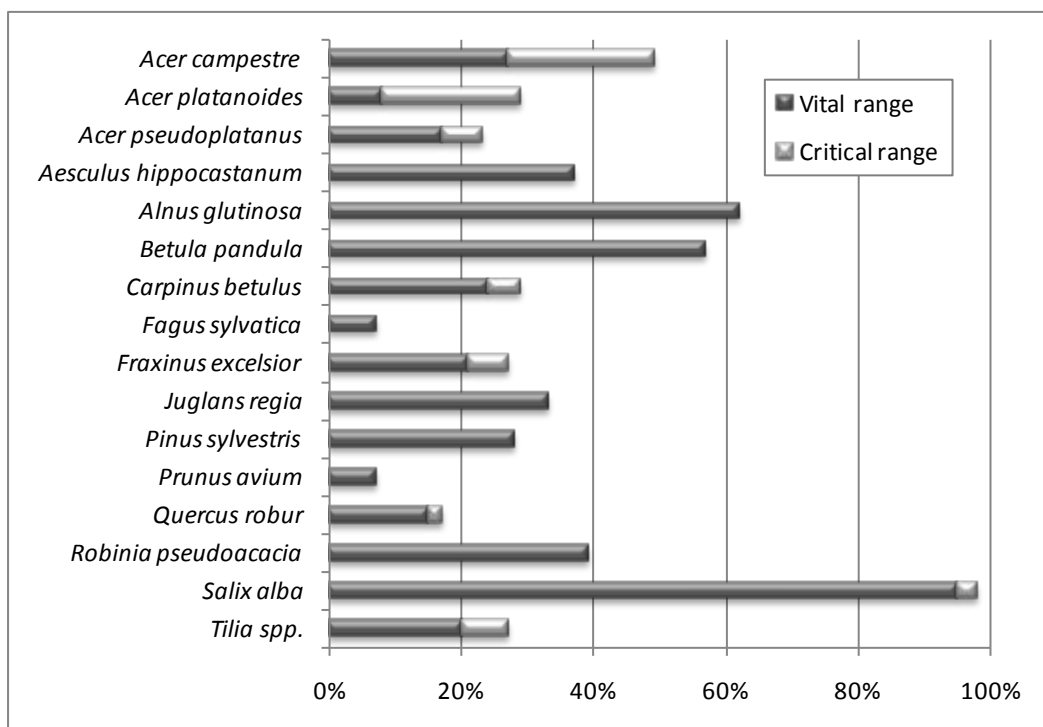


Figure 3 Phenological adaptations to warmer climate. Adapted from Keenan *et al.* (2014).

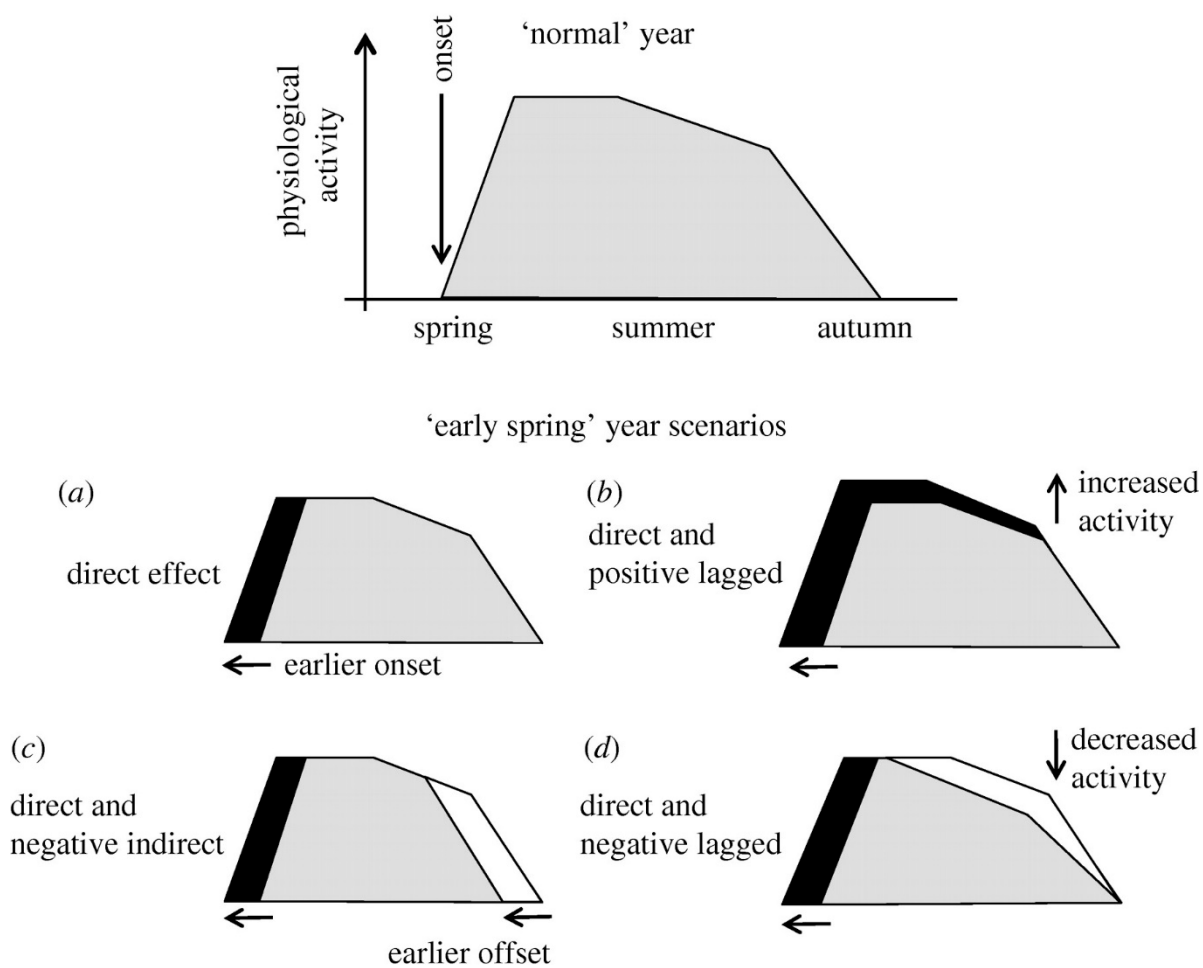


Figure 4. Predicted changes in the geographical distribution of oak. Adapted from Hubert *et al.* (2007).

