Review

Responses of tree species to heat waves and extreme heat events

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ABSTRACT

The number and intensity of heat waves has increased, and this trend is likely to continue throughout the 21st century. Often, heat waves are accompanied by drought conditions. It is projected that the global land area experiencing heat waves will double by 2020, and quadruple by 2040. Extreme heat events can impact a wide variety of tree functions. At the leaf level, photosynthesis is reduced, photooxidative stress increases, leaves abscise and the growth rate of remaining leaves decreases. In some species, stomatal conductance increases at high temperatures, which may be a mechanism for leaf cooling. At the whole plant level, heat stress can decrease growth and shift biomass allocation. When drought stress accompanies heat waves, the negative effects of heat stress are exacerbated and can lead to tree mortality. However, some species exhibit remarkable tolerance to thermal stress. Responses include changes that minimize stress on photosynthesis and reductions in dark respiration. Although there have been few studies to date, there is evidence of within-species genetic variation in thermal tolerance, which could be important to exploit in production forestry systems. Understanding the mechanisms of differing tree responses to extreme temperature events may be critically important for understanding how tree species will be affected by climate change.

Key-words: drought, genotype, growth, heat stress, photosynthesis, respiration; stomatal conductance.

INTRODUCTION

Summertime extreme temperatures associated with prolonged heat waves, lasting for several weeks, now impact approximately 10% of land surfaces, up from only 1% in the 1960s (Hansen *et al*. 2012). An increase in the frequency and intensity of heat waves is expected to continue through the 21st century (Yao *et al*. 2013). Although there are several ways in which heat waves are delineated, broadly defined, they are periods of consecutive days where conditions are excessively hotter than normal (Perkins & Alexander 2013). Over the past several decades, worldwide, the number of record-breaking monthly temperature extremes has been

five times larger than it was from the late 19th through the mid-20th century (Coumou & Robinson 2013; Coumou *et al*. 2013). The five most extreme heat waves in Europe since 1871 have all occurred since 2000 (Barriopedro *et al*. 2011). The length of heat waves is also increasing. Della-Marta *et al*. (2007) reported that the length of summer heat waves in Western Europe has doubled and the frequency of hot days has tripled since 1880, indicating that climate is becoming more extreme. In fact, heat waves have contributed to a 0.5 °C increase in mean global temperature (Coumou & Robinson 2013; Coumou *et al*. 2013). This pattern is consistent with predictions that global warming will in part be driven by more frequent and intense high-temperature events (Coumou & Robinson 2013; Dulière *et al*. 2013).

Heat waves in combination with drought are common and intrinsically linked (Stéfanon *et al*. 2014). Together they produce positive feedbacks that intensify their effects. A decline in precipitation is usually associated with a decline in cloud cover and increased soil sensible heat flux and a reduction in air relative humidity, which can cause further increases in extreme temperatures. Higher temperature increases atmospheric vapour pressure deficit, which increases evapotranspiration resulting in more rapid soil drying and increased drought severity. Over the previous century, across the United States, the highest frequency of heat waves occurred in the drought years of the 1930s (Peterson *et al*. 2013). More recently, also associated with a major long-term drought at a regional level, the Western United States has had the highest frequency of heat waves in North America in the 2000s. Similarly, heat waves in Western and Central Europe are generally preceded by a lack of precipitation in Southern Europe (Vautard *et al*. 2007; Stéfanon *et al*. 2014).

Heat wave frequency is also increasing under wetter conditions. When temperature and precipitation were compared for the periods 1951–1977 and 1978–2004, it appeared that both hot/wet and hot/dry conditions were increasing substantially worldwide (Hao *et al*. 2013). Some parts of California in the Western United States have experienced an increase in midsummer humid heat waves, which have caused a disproportionate increase in night-time temperatures and less radiative cooling during the night (Guirguis *et al*. 2014). Since 1950, extremely hot days coupled with heavy precipitation events have become more common (Easterling *et al*. 2000; IPCC 2012).

Heat waves are already posing significant threats to plant survival and growth. The European heat wave in the summer of 2003 resulted in a 30% reduction in ecosystem gross primary production (Ciais *et al.* 2005). The 2010 Russian heat wave was the most extreme on record for that area and resulted in an estimated 50% reduction in gross primary production (Bastos *et al.* 2013). Drought and excessive heat across the Western United States in the last decade have caused widespread tree mortality (Allen *et al.* 2010). As these extreme events increase in frequency, it is imperative for us to understand how they will affect tree physiological processes and growth.

To date, the majority of research on the impact of heat waves has been restricted to either post-event analysis of the effects of heat waves on plant productivity or experiments on the short-term effects of high-temperature stress on plant physiology. This limitation in the scope of prior research is due in part to the random and unpredictable nature of heat waves, making observational studies difficult to plan and implement, and the difficulty in conducting experiments on extreme heat effects in the field. We are aware of only a few manipulative studies that investigated the effects of episodic heat waves on plant growth, and only three studies conducted on trees. One study on *Pinus taeda* and *Quercus rubra* seedlings exposed to repeated moderate (+6 °C) or extreme (+12 °C) heat waves in a greenhouse reported significant growth reductions caused by the +12 °C, but not the +6 °C heat wave (Bauweraerts *et al.* 2014). A second study on *Quercus alba* and *Quercus velutina* seedlings found that heat waves, applied by air heating and/or

soil heating, reduced photosynthesis and growth (Heckathorn, personal communication). Another study exposed naturally occurring arctic willow (*Salix arctica*), a small creeping shrub, to two consecutive 10 d heat waves of 8 °C and reported that, compared with a control treatment, the heat wave treatment initially increased growth, but subsequent growth was negatively impacted, possibly because of reduced capacity to tolerate cold weather (Marchand *et al.* 2005, 2006). Additionally, there have been a few studies in grasses (e.g. Wang *et al.* 2008), forbs (e.g. De Boeck *et al.* 2011) and crop systems (e.g. De Simon *et al.* 2013); however, because of differences in longevity among growth forms, it is difficult to extrapolate these findings to trees.

The effects of extreme high temperatures are seen in processes from the molecular level to the whole tree, and vary among species and within genotypes (Fig. 1). Drought and high light typically increase the damage caused by high temperatures. Of all the physiological processes in trees, the effect of heat on photosynthesis has received the most attention, and is evident in the list of cellular processes that have been reported to be affected by high temperatures on the right side of Fig. 1. Although less studied by comparison with photosynthesis, many other physiological processes in trees are affected by excessive heat, including respiration, transpiration, photorespiration and volatile organic compound (VOC) production, (centre, Fig. 1). At the scale of the whole tree, excessive heat can also cause a decrease in growth, leaf development and leaf area and when combined with drought, it can cause mortality (left side of Fig. 1). For some processes,
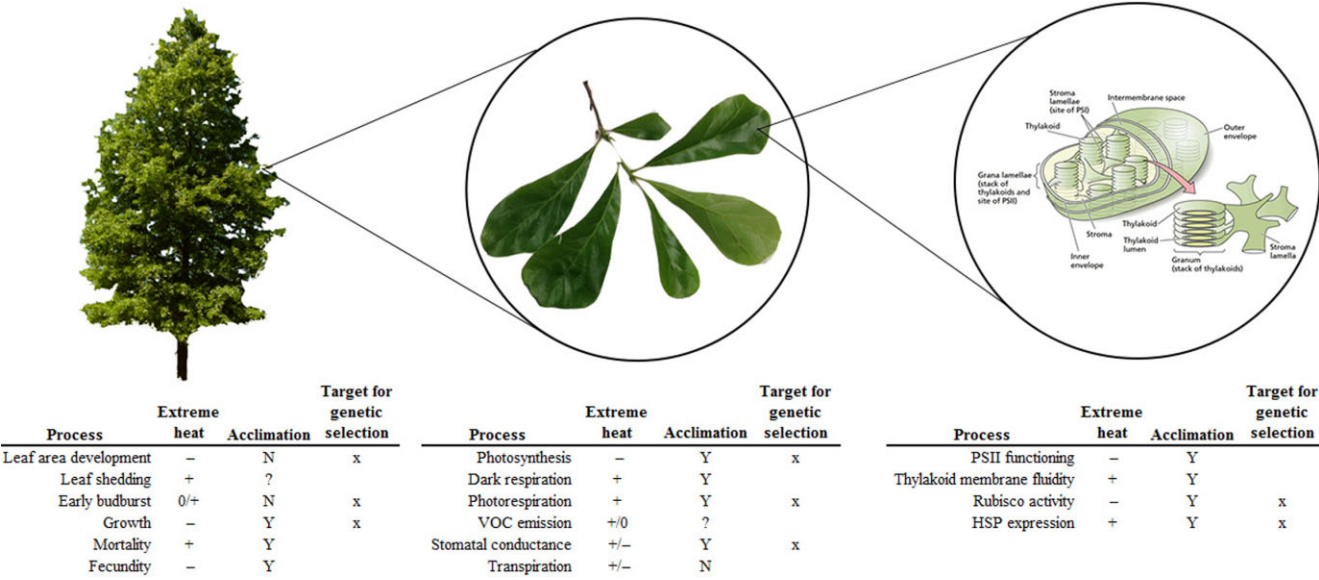

Process	Extreme heat	Acclimation	Target for genetic selection
Leaf area development	–	N	x
Leaf shedding	+	?	
Early budburst	0/+	N	x
Growth	–	Y	x
Mortality	+	Y	
Fecundity	–	Y	

Process	Extreme heat	Acclimation	Target for genetic selection
Photosynthesis	–	Y	x
Dark respiration	+	Y	
Photorespiration	+	Y	x
VOC emission	+/0	?	
Stomatal conductance	+/–	Y	x
Transpiration	+/–	N	

Process	Extreme heat	Acclimation	Target for genetic selection
PSII functioning	–	Y	
Thylakoid membrane fluidity	+	Y	
Rubisco activity	–	Y	x
HSP expression	+	Y	x

Figure 1. From right to left of the figure is a summary of known effects of high temperatures on trees at the cellular, leaf and whole plant scales. An increase, decrease or no change, in a process in response to high temperature is indicated by +, – and 0, respectively. More than one symbol associated with a process indicates between- or within-species variation. Y notes reported acclimation in response to exposure to high temperature; N indicates no acclimation has been reported; and ? indicates acclimation may exist, but evidence is limited. Known genotypic variation in the response of a process that may be useful for genetic selection for increased heat tolerance is indicated by (x). The processes listed are only a subset of those occurring at each scale, and indicate the current level of information available on the effects of extreme heat on trees. HSP, heat shock proteins; PSII, photosystem II; VOC, volatile organic compounds. Photographs of tree and leaves by R.O. Teskey. Diagram of chloroplast from Taiz and Zeiger (2010) and Becker (1986).

there is wide variation in the response of species or genotypes to extreme heat. Acclimation to heat is evident in many processes at each scale. Genetic variation in the response of processes to heat has received limited study in trees, but variation exists within species and could be exploited to improve heat stress tolerance in economically important species. All of these responses of trees to excessive heat, as well as the potential for genetic improvement in tolerance of heat stress, will be discussed in this review.

RESPONSE OF PHOTOSYNTHESIS, PHOTORESPIRATION AND RESPIRATION TO HIGH TEMPERATURES

In trees, the response of photosynthesis to high temperatures has received more study than responses of other physiological processes. This emphasis reflects the importance of photosynthesis as well as its sensitivity to heat (Berry & Bjorkman 1980; Salvucci & Crafts-Brandner 2004). The photosynthetic temperature optimum is often between 20 and 30 °C across boreal, temperate and tropical angiosperm and gymnosperm species (Teskey *et al*. 1995; Cunningham & Read 2003; Way & Sage 2008; Vargas & Cordero 2013). The temperature response curve of photosynthesis is often very broad and, in ambient CO_2 concentrations, high photosynthetic rates are often maintained at temperatures up to 35 °C (Sage *et al*. 2008). Positive net photosynthesis still occurs at temperatures above 40 °C, even in boreal species, for example *Picea mariana* (Way & Sage 2008), but species at warmer sites generally maintain positive net photosynthesis at even higher temperatures, for example +45 °C in the tropical species *Dipteryx oleifera* and *Zygia longifolia* (Vargas & Cordero 2013).

At high temperatures, the decline in net photosynthesis is attributed to numerous processes including increased photorespiration, increased mitochondrial respiration, inactivation of Rubisco attributed to reduced activity of Rubisco activase, decreased activity of photosystem II (PSII), and damage to the thylakoid membrane, which results in a reduction in ATP synthesis and increased thylakoid membrane permeability to H + ions (Crafts-Brandner & Salvucci 2004; Haldimann & Feller 2004; Hozain *et al*. 2010).

The increase in photorespiration with short-term increases in temperature has been attributed to changes in Rubisco specificity and differences in CO_2 and O_2 solubility (von Caemmerer & Quick 2000). Unfortunately, the enzymatic response of Rubisco to temperature has only been well characterized in a few species, including tobacco (*Nicotiana tabacum*) (Bernacchi *et al*. 2002), spinach (*Spinacia oleracea*) (Jordan & Ogren 1984) and *Arabidopsis* (Walker *et al*. 2013). The specificity was very similar among the species, suggesting that Rubisco specificity of trees may respond quite similarly to an increase in temperature. However, recent research also suggests that Rubisco specificity may change with thermal history (Cavanagh & Kubien 2014).

In addition to an increase in photorespiration, mitochondrial respiration, that is dark respiration, referred to here as respiration (*R*), has a much higher temperature optimum than photosynthesis (Fig. 2). A moderate increase
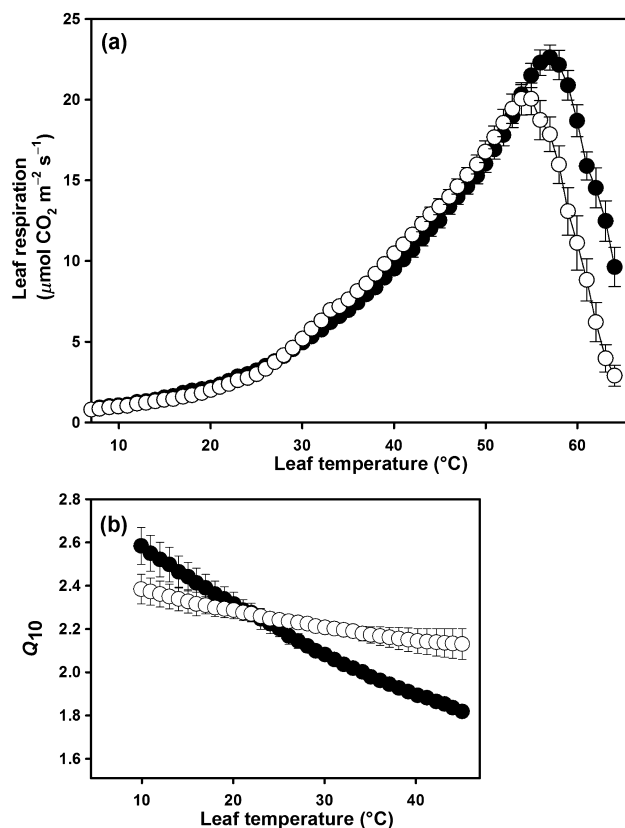

Figure 2. (a) Response of leaf respiration to temperature in *Eucalyptus pauciflora* trees growing at a field site in Australia measured in winter (filled circles) and summer (open circles). (b) Q_{10} modelled from measurements between 10 and 45 °C (redrawn from O'Sullivan *et al*. 2012).

in temperature can significantly reduce light-saturated net photosynthesis by increasing *R* (Crous *et al*. 2012). Respiration increases rapidly with temperature, often by 50 to 200% per 10 °C (equivalent to Q_{10} values of 1.5–3.0), which substantially reduces daily net carbon gain at high temperatures. The rate of increase is highly variable, depending on species, previous temperature exposure, time of year and many other factors. Maximum *R* often occurs at temperatures greater than 50 °C, for example 52 to 57 °C in *Eucalyptus pauciflora* at different times of the year (O'Sullivan *et al*. 2012), ~55 °C in *Populus tremula* (Hüve *et al*. 2012) and >45 °C in *Picea mariana* (Sage *et al*. 2008). At temperatures above the maximum, *R* decreases rapidly and severe cellular damage occurs at temperatures just above 60 °C (Kolb & Robberecht 1996).

High temperatures also cause a rapid consumption of carbohydrates for maintenance *R*. Hüve *et al*. (2012) found that *R* at 55 °C was eight times greater than at 20 °C in *Populus tremula*, and that after 30 min in the dark, the starch content of leaves decreased by 16% at 25 °C and 53% at 50 °C, compared with pretreatment starch content. They noted an especially rapid rise in *R* near the temperature optimum, which corresponded with the critical temperature

for PSII stability (T_c). A similar relationship between T_c and maximum R was observed in *E. pauciflora* (O'Sullivan *et al.* 2012).

Moderately high temperatures can lead to Rubisco activase limitation (e.g. in *Pic. mariana*, Sage *et al.* 2008), which is thought to be the primary constraint on A_{net} at those temperatures (Law & Crafts-Brandner 1999). In a review of C_3 plants, Galmes *et al.* (2013) showed that exposure to severe heat stress resulted in a reduction in initial Rubisco activity. The percentage of Rubisco in the active state decreased by about 30% in seedlings of both a boreal tree species, *Populus balsamifera*, and a temperate tree species, *Populus deltoides*, at 40 °C compared with 27 °C (Hozain *et al.* 2010). At higher temperatures, damage to the thylakoid membrane starts to occur. Heating up to 45 °C may reduce photosynthetic potential by affecting thylakoid membrane function. Work done in barley (*Hordeum vulgare*) demonstrated that heating can increase membrane fluidity and thylakoid proton conductance which can result in greater cyclic electron flow around photosystem I (PSI) (Bukhov *et al.* 1998, 2000). Additionally, moderate heating can stimulate dephosphorylation of numerous PSII core proteins, as observed in spinach (*Spinacia oleracea*) and *Arabidopsis* (Rokka *et al.* 2000; Vener *et al.* 2001).

Historically, PSII damage was considered a primary limitation to net photosynthesis with an increase in temperature (Santarius 1976; Santarius & Muller 1979; Berry & Bjorkman 1980; Enami *et al.* 1994); however, damage to PSII typically only occurs above 45 °C (Terzaghi *et al.* 1989; Thompson *et al.* 1989; Gombos *et al.* 1994; Cajanek *et al.* 1997). While physical damage by extreme temperature has been demonstrated, foliar damage by heat at lower temperatures is often associated with high light (Berry & Bjorkman 1980). For example, foliar damage to *Olea europaea* exposed to 38 °C was greater in high light than low light (Bongi & Long 1987).

In tree species, damage to PSII at temperatures below 40 °C is generally reversible. At temperatures above 40 °C (species- and exposure duration-specific), damage to PSII may be irreversible (Yordanov 1992). However, the critical temperature for PSII stability (T_c) is very sensitive to prior temperature exposure. An example of PSII sensitivity can be seen in the study of Ghouil *et al.* (2003) on *Quercus suber* seedlings from the Mediterranean region. In that study, plants were acclimated to six air temperatures from 10 to 40 °C in a growth chamber for 2 d, and photosynthetic characteristics were measured on the third day. The T_c ranged from 42 to 51 °C, with the lower T_c corresponding to an acclimation temperature of 10 °C, and the higher T_c to a temperature of 40 °C. The T_c of *Quercus macrocarpa* ranged from 43 °C to 48 °C and the T_c of *Quercus muehlenbergii* ranged from 46 °C to 50 °C measured in June and August, respectively, which corresponded with an increase in the maximum air temperature from 40 °C in June to 43 °C in August and an increase in the frequency of days when the maximum air temperature exceeded >40 °C from 1 in June to 15 in August (Hamerlynck & Knapp 1994). Critical temperatures of 48 °C and 52 °C were measured in *Quercus suber* and in *Quercus canariensis*, after acclimation for 5 days at 15 and
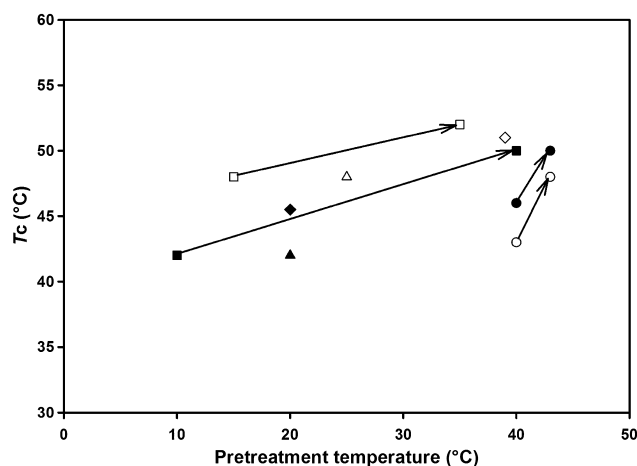

Figure 3. Critical temperature for PSII stability (T_c) for different tree species, compared with the pretreatment acclimation temperature. All T_c values were ≥42 °C. When species were subjected to different pretreatment temperatures in the same study, the values are connected by arrows. In each instance, a higher pretreatment temperature produced a higher T_c. Species were *Quercus muehlenbergii* (filled circle, Hamerlynck & Knapp 1994), *Quercus macrocarpa* (unfilled circle, Hamerlynck & Knapp 1994), *Quercus suber* (filled square; Ghouil *et al.* 2003), *Quercus canariensis* (unfilled square; Daas *et al.* 2008), *Picea glauca* (filled triangle, Bigras 2000), *Populus deltoides* (unfilled triangle, Hozain *et al.* 2010), *Ficus insipida* (unfilled diamond, Krause *et al.* 2013) and *Acer pseudoplantanus*, *Betula verrucosa*, *Fagus sylvatica*, *Fraxinus excelsior*, *Juglans rigia*, *Quercus robur* and *Quercus petraea* (all grown together and represented by a single data point, filled diamond, Dreyer *et al.* 2001).

35 °C, respectively (Daas *et al.* 2008). Plotting the pretreatment temperatures and T_c for these and other species revealed that T_c was high for all species and increased with acclimation temperature, suggesting that the capacity of PSII to resist thermal stress was not very different among species from boreal and temperate regions (Fig. 3). Factors in addition to temperature, such as dormancy or phenology, must also influence T_c, because T_c of field-grown *Eucalyptus pauciflora* was 46 °C in summer and 60 °C in winter (O'Sullivan *et al.* 2012). This result indicates the need for additional research on the underlying causes of seasonal variation in T_c as it is not clear why T_c was substantially higher in winter than in summer in that study.

FOLIAR DAMAGE FROM EXPOSURE TO HIGH TEMPERATURES

The temperature at which there is visible foliar damage from heat depends on species, duration of exposure and time of year. The damage threshold was as low as 44 °C in *Picea mariana*, a boreal species, when seedlings were exposed for 180 min (Colombo & Timmer 1992). This exposure produced visual symptoms of needle blanching on 40% of the plants, when assessed three weeks after the heat treatments. At a temperature just 2 °C higher (46 °C), 100% of the seedlings suffered damage when exposed for only 60 min. At
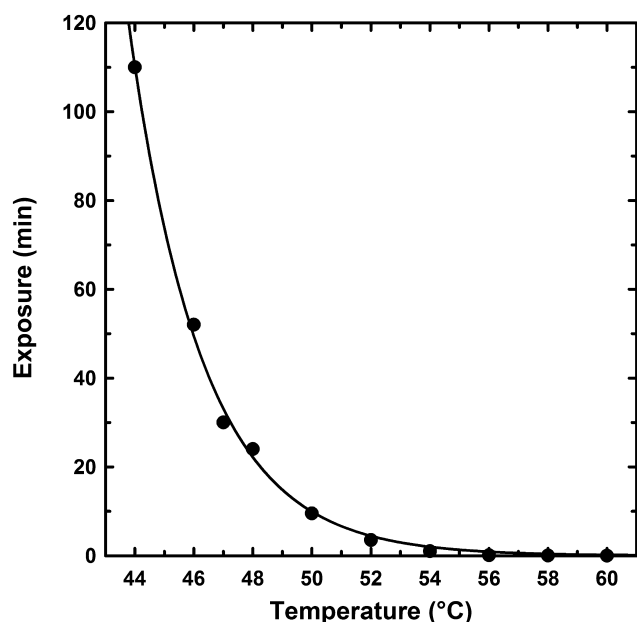
Figure 4. Relationship between temperature and duration of exposure resulting in damage to 50% of foliage in *Picea mariana* seedlings when assessed 3 weeks after treatment $[y = (5.095 \times 10^9)10^{(-0.4011\times)}, R^2 = 0.99]$ (redrawn from Colombo & Timmer 1992).

50 °C, 100% of the seedlings were damaged after an exposure of 10 min. There was a negative exponential relationship between the temperature and duration of heat exposure that resulted in foliar damage (Fig. 4). The length of exposure that would damage 50% of the foliage was almost an hour less at 44 °C compared with 46 °C. At higher temperatures the length of exposure required to induce damage decreased rapidly. In another boreal species, *Picea glauca*, a 30 min exposure to 48 °C produced 50% foliar damage (Bigras 2000). When compared with 100% foliar damage in *P. mariana* for the same exposure, it appears that *P. glauca* had different heat thresholds for direct damage.

In four temperate and four tropical evergreen tree species in Australia, the temperature causing 50% visible leaf damage (LT50) after an exposure for 30 min ranged from 47 to 54 °C, and was linearly correlated with the average maximum temperature of the hottest month at the origin location of the seeds or seedlings, which ranged from 19 to 31 °C (Cunningham & Read 2006). The LT50 values were substantially higher than the average maximum recorded temperature, but the 30 min exposure was relatively short, suggesting that LT50 might be lower if the exposure duration was longer. For *Pinus taeda* and *Q. rubra* from a warm temperate region where average maximum temperature is about 33 °C and the absolute maximum temperature has not exceeded 43 °C, seedlings of both species were able to tolerate daytime temperatures during the summer exceeding 50 °C, produced by supplemental heating, without any sign of visible damage (Ameye *et al.* 2012). Unfortunately, a clear pattern has not emerged about the relationship between species origin and the ability to tolerate high temperatures

without damage. A greater tolerance of high-temperature stress in species from warmer areas was supported by a study on temperate and tropical evergreen rain forest trees in Australia (Cunningham & Read 2006), but not by the study of Daas *et al.* (2008) who reported that thermal tolerance of PSII was not greater in *Quercus* species from the warmer Mediterranean region compared with those from the cooler European region.

The timing of the exposure is also critical. Excessive temperatures and heat waves are often considered summer phenomena, but during bud burst and leaf-out in the spring, considerably lower temperatures can cause substantial damage. Forests dominated by *Acer saccharum* trees growing in central Ontario Canada were exposed to 31.5 °C during leaf-out in May, an excessive temperature for a month in which the highest historical temperature was < 24 °C (Filewod & Thomas 2014). This high-temperature exposure caused mortality of emerging leaves ranging from 40% in the upper canopy to 21% in the lower canopy, resulting in an overall reduction of 65% in end-of-season cumulative leaf area index. Surviving preformed leaves and neo-formed leaves had a 36% reduction in photosynthetic capacity in early July compared with previous years. Photosynthetic capacity recovered by late July and early August, but the overall effect was a significant depression of seasonal carbon gain. Saplings had similar levels of leaf mortality and leaf scorch on surviving leaves, but produced very few new leaves (neo-formed leaves) after the heat event, indicating that there are ontogenetic differences in the capacity to recover from heat stress, perhaps related to stored carbohydrate availability. Precipitation was near normal throughout the growing season, and was not considered to have contributed to the damage. It is generally considered that an increase of 10–15 °C above ambient will produce heat shock or heat stress (Wahid *et al.* 2007), but in *A. saccharum* trees during budburst, an elevation of only 8 °C produced significant and long-lasting detrimental effects, indicating that timing of heat events is critical to their severity. Notably, there was little effect of the high temperatures on co-occurring species including *A. rubrum*, *Betula cordifolia*, *Fagus grandifolia* and *Prunus serotina*.

GROWTH

During the growing season, the impact of heat waves on growth can be significantly greater than the same amount of heat accumulated evenly over the same period (Bauweraerts *et al.* 2014). In that study, seedlings of *Pinus taeda* and *Quercus rubra* were exposed to one of three heat treatments from June to October: (1) a constant 3 °C elevation of the ambient temperature; (2) an alternating pattern of ambient temperature for 7 d, followed by a 7 d heat wave of ambient +6 °C; or (3) an alternating pattern of 21 d at ambient temperature followed by a 7 d heat wave of ambient +12 °C. The ambient +3 °C and the two heat wave treatments had the same monthly and growing season heat sum and mean air temperature. Repeated exposure to a 6 °C elevation of air temperature had no effect on leaf, stem, root or total biomass

at the end of the study in either species. However, compared with the treatment of constant +3 °C temperature elevation, the monthly +12 °C heat waves significantly reduced total growth as well as leaf, stem and root biomass in *Pinus taeda*, and total and root biomass in *Quercus rubra*. This study demonstrates that heat waves can have negative effects on growth that are more severe than the same amount of heat applied as a change in the average temperature. For perennial plants, the stress caused by an anomalously warm growing season can be long lasting, and cause a reduction in growth in subsequent years (Arnone *et al*. 2008).

Heat stress can also affect the timing of budburst and dormancy, and therefore the length of the growing season. When dormant excised terminal shoots collected from October through March from hybrid *Populus* trees received a 2 h exposure to temperatures ranging from 20 °C to 45 °C there was a significantly greater amount of budbreak induced by the short exposure to high temperatures, particularly in response to the 45 °C treatment (Wisniewski *et al*. 1997) (Fig. 5). Exposing dormant shoots of *Prunus persica* var. *nectariana* to a high temperature (50 °C for 1 h) transiently inhibited respiration, but hours later activated the pentose phosphate pathway, which may be the cause of early budburst induced by high temperatures (Tan *et al*. 2013). However, sustained exposure over a period of weeks to an unseasonably high temperature (21 °C) during dormancy was reported to significantly delay budburst in *Betula pendula*, *Betula pubescens* and *Alnus glutinosa* suggesting that, similar to direct damage from heat, the length of exposure to a temperature may substantially alter the response (Heide 2003). Findings in that study also emphasized the importance of the timing of the exposure to heat: for field-grown trees of the two *Betula* species, a mean September temperature of 14 °C, compared with the historical mean of 9 °C, delayed budburst in the following spring by approximately 20 days.

TOLERANCE AND AVOIDANCE OF THERMAL STRESS

Tolerance of heat stress can be conferred by prior exposure to moderately high temperatures. For instance, pretreatment of *Picea mariana* seedlings at 38 °C for 3 h per day for 6 days decreased and delayed direct damage to foliage subsequently exposed to 49 °C (Colombo & Timmer 1992) (Fig. 6). A 30 min exposure to 49 °C caused damage to 100% of the seedlings that did not receive the pretreatment, but damaged only 25% of pretreated seedlings. This increase in thermal tolerance was likely related to the synthesis of heat shock proteins (HSPs), which increased in the shoots receiving the heat pretreatment (Colombo & Timmer 1992; Colombo *et al*. 1992). A similar synthesis of several low molecular weight proteins was observed in young seedlings of *Pinus banksiana*, *Pinus taeda*, *Picea mariana* and *P. glauca* growing at 28 °C and exposed to 42 °C for 3 h (Gifford & Taleisnik 1994). These proteins were absent from the control plants that remained at 28 °C. There has been relatively little work on the molecular mechanisms of acquired thermal tolerance in
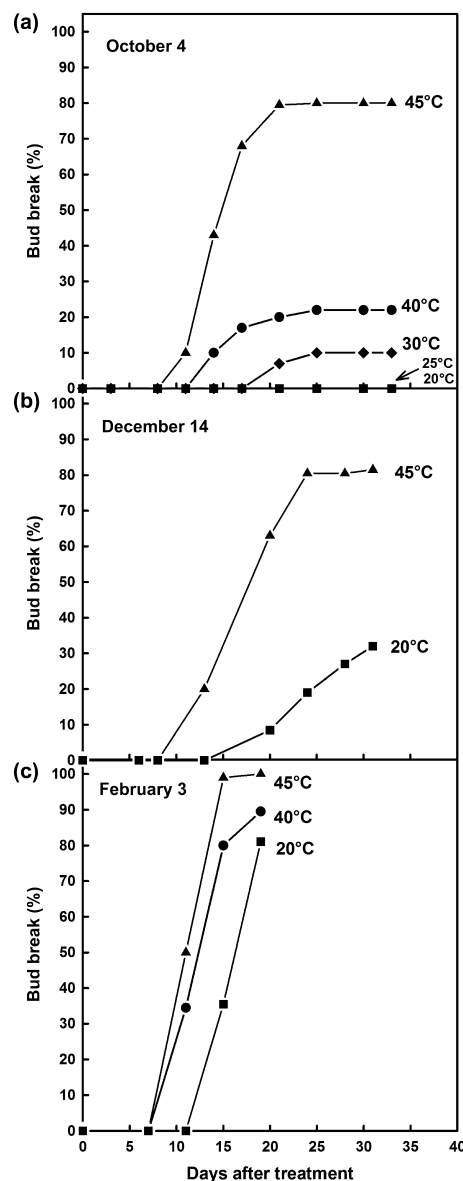

Figure 5. Cumulative percent budbreak in detached terminal shoots of *Populus nigra Charkowiensis* × *Populus nigra incrassata* exposed for 2 h to temperatures ranging from 30 to 45 °C in October (a), December (b) or February (c) during the dormant season. Shoots exposed to constant 20 °C served as controls (redrawn from Wisniewski *et al*. 1997).

tree species, but recently great progress has been made in agronomic species and *Arabidopsis* that indicates an important role for HSPs as well as abscisic acid, ethylene, hydrogen peroxide and salicylic acid in increasing tolerance to heat stress after either a short exposure to sub-lethal high temperatures or a gradual temperature increase to lethally high temperatures (Larkindale & Knight 2002; de Klerk & Pumisutapon 2008; Song *et al*. 2012).

A short exposure to increased temperature also induces thermal tolerance of photosynthesis. Maximal PSII photochemical efficiency (F_v/F_m) decreased with increasing temperature from 42 to 50 °C in *Picea glauca* foliage, but plants
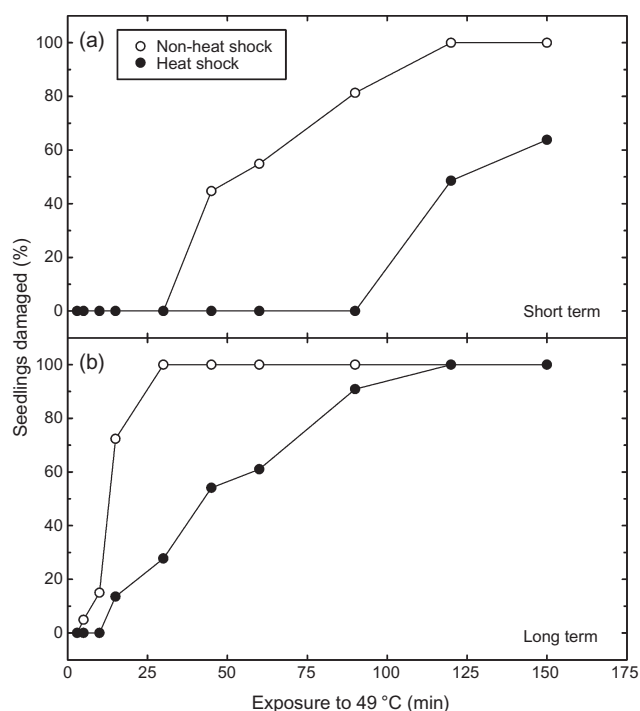
Figure 6. Percentage of seedlings exhibiting foliar damage after exposure to 49 °C for various time periods ranging from 3 to 150 min. Seedlings were evaluated immediately after heat exposure (short-term response, a) and after 3 weeks (long-term response, b). The greenhouse-grown *Picea mariana* seedlings were either preconditioned at 38 °C for 3 h per day for 6 consecutive days (heat shock treatment, filled circles) or not preconditioned (non-heat shock treatment, unfilled circles) (redrawn from Colombo & Timmer 1992).

preconditioned at 38 °C for 5 h had significantly higher F_v/F_m at temperatures up to 46 °C (Bigras 2000). Exposure to high temperatures increases thylakoid membrane fluidity, which may induce HSP expression. HSPs can desaturate membrane lipids, which results in a more thermally stable thylakoid membrane (Horvath *et al.* 2012). Above 46 °C, the preconditioning was ineffective, suggesting that higher temperatures were above the limit for thermal stability of PSII in this species (Bigras 2000). There are many reports of inhibition of Rubisco activase at temperatures above the thermal optimum of photosynthesis (Sage *et al.* 2008), including some for tree species (Haldimann & Feller 2004; Jin *et al.* 2010), but few studies have examined the effect of a rapid increase in temperature to >40 °C on activation states, and the results have been contradictory (Crafts-Brandner & Law 2000; Schrader *et al.* 2004). We are not aware of any study that examined the effect of thermal preconditioning on activation states or thylakoid membrane permeability above 40 °C.

Under most environmental conditions, a close correlation between photosynthesis and stomatal conductance is expected. Stomates close to reduce water loss, resulting in reduced photosynthesis. Alternatively, if biochemical limitations reduce photosynthesis, intercellular CO_2 increases, resulting in partial stomatal closure. However, in some plants, stomata remain open at high temperature even when photo-synthesis is significantly reduced and vapour pressure deficit (VPD) is very high (Schulze *et al.* 1973; Lu *et al.* 2000; Ameye *et al.* 2012). This response has been documented in only a few species and is not well understood, although it appears to be a strategy that uses transpirational cooling of the leaf to avoid or minimize heat stress. For example, during an imposed heat wave of 7 d, in which daily maximum air temperatures ranged from 47 to 53 °C, *Pinus taeda* and *Quercus rubra* seedlings had lower net photosynthesis on each day of the heat wave, but exhibited almost no change in stomatal conductance (g_s) (Ameye *et al.* 2012). In *Pinus taeda* seedlings, mean g_s was 0.12 mol H_2O m^{-2} s^{-1} at 37 °C and 0.09 mol H_2O m^{-2} s^{-1} at 50 °C. In *Quercus rubra* seedlings, mean g_s at 37 °C and 50 °C was 0.12 and 0.11 mol H_2O m^{-2} s^{-1}, respectively. In both species, the slope of the linear regression of g_s measured across that temperature range was not significantly different from zero. However, net photosynthesis declined by over 75% in both species over the same temperature range, and the regression slope was highly significant. VPDs during these measurements ranged from 4 to 8 kPa. Similarly, stomatal conductance of *Acer rubrum* changed very little, but net photosynthesis decreased to near zero, across a temperature range of 35 to 48 °C (Weston & Bauerle 2007). At lower temperatures, stomatal conductance typically decreases at a much lower range of VPD (Bongarten & Teskey 1986; Sandford & Jarvis 1986). At high temperatures, the lack of stomatal response to high VPD, or to decreasing net photosynthesis, indicates that trees were using transpiration as a mechanism to reduce the heat load on the leaves.

It is not known how many tree species have the capacity to utilize transpirational cooling to avoid extreme heat stress as it has been the subject of only a few studies. It may be more prevalent in trees that are adapted to growing in open, high light conditions. For example, in a study comparing two rainforest tree species, *Dipteryx oleifera*, a late successional species, had a significant reduction in both net photosynthesis and stomatal conductance at 37 °C compared with 27 °C, yet *Zygia longifolia*, an early successional species, had significantly reduced net photosynthesis, but no change in stomatal conductance at the higher, compared with the lower, temperature (Vargas & Cordero 2013).

Some of the most extreme temperatures that a tree can experience occur in the early seedling stage where the soil is exposed to full sun. Although mortality of young seedlings is often attributed to drought, within the boundary layer near the ground, the air can heat up to lethal temperatures on sunny days. In a study of young *Pinus ponderosa* seedlings in the field, the soil surface and the air at 5 mm above the ground reached temperatures in excess of 75 °C, but at 50 mm above the surface the temperature rarely exceeded 45 °C (Kolb & Robberecht 1996). The threshold stem temperature for seedling death was determined to be 63 °C for less than 1 min in that study. Seedlings with high stomatal conductance at the outset of the heat exposure survived, while those that had low stomatal conductance died. High transpiration resulting from high stomatal conductance reduced stem temperature by heat convection in rapidly moving water by as much as 30 °C during peak daylight hours

(leaf temperature was not measured). The mean maximum transpiration rate of the needles was 16.7 mmol H_2O m^{-2} s^{-1} at an air temperature of 60 °C, compared with 6.7 mmol H_2O m^{-2} s^{-1} at 35 °C. Using a model to predict stem temperature from air temperature and transpiration rate, Kolb & Robberecht (1996) determined that a transpiration rate of 16.7 mmol H_2O m^{-2} s^{-1} was adequate to prevent seedling mortality at a 1 min exposure to temperatures substantially >63 °C.

Elevated atmospheric [CO_2] can also mitigate the effect of heat stress. The temperature optimum for photosynthesis increases from about 20 °C at 180 μmol mol^{-1} [CO_2] to about 38 °C at 700 μmol mol^{-1} [CO_2] (Sage & Kubien 2007). Recovery in creosote bush (*Larrea tridentata*), a woody desert shrub, from a 9 d heat wave during which air temperatures reached 53 °C, was much faster in plants in elevated [CO_2] (700 μmol mol^{-1}) than those in ambient [CO_2] (360 μmol mol^{-1}) (Hamerlynck *et al.* 2000). During the heat wave, net photosynthesis was depressed in ambient [CO_2] but showed little change in elevated [CO_2] compared with before or after the event. In *Q. rubra* seedlings exposed to a 7 d heat wave of +12 °C, which also reached maximum temperatures > 50 °C, there was a significant reduction in net photosynthesis during the heat wave in an elevated [CO_2] treatment, but net photosynthesis remained higher than that of plants in an ambient [CO_2] treatment throughout the heat wave, as well as before and after (Bauweraerts *et al.* 2013). For *Pinus taeda* seedlings in that study, there was a decrease in biomass in response to the heat waves in both ambient and elevated [CO_2] treatments, but the relative reduction in growth in elevated [CO_2] was much less than that in ambient [CO_2]. The mitigating effect of elevated [CO_2] on carbon gain during short periods of heat stress is likely to extend to high-temperature periods throughout the growing season, if there is not substantial acclimation of photosynthesis to elevated [CO_2]. Elevated [CO_2] induces stomatal closure in many tree species, particularly broad-leaf deciduous species, which could preserve soil moisture and thereby increase water availability during warm periods, sustaining the beneficial effects of elevated [CO_2] on carbon gain (Long *et al.* 2004; Ainsworth & Rogers 2007). However, elevated [CO_2] also has the potential to exacerbate heat stress by reducing foliar cooling via transpiration (Urban 2003). In *Acer pennsylvanica*, heat stress had a significantly larger negative impact on short-term biomass accumulation (measured 35 d after a 1 d heat event) in elevated [CO_2] compared with ambient [CO_2], because of a reduction in g_s (Bassow *et al.* 1994).

Trees can produce numerous VOC, many in response to abiotic stresses (Joó *et al.* 2011; Šimpraga *et al.* 2011; Harrison *et al.* 2013). One of the most common VOC produced in response to short-term heat stress is isoprene, which is extensively synthesized in *Quercus* and *Populus* species (Rasmussen 1970) as well as in *Eucalyptus* (He *et al.* 2000) and *Picea* (Kempf *et al.* 1996). Additionally, monoterpenes, consisting of two isoprene molecules combined to form a cyclic compound, are synthesized by many other tree species (Harley *et al.* 2003) including *Pinus* (Kleist *et al.* 2012) and

Amazonian species (Kuhn *et al.* 2004). Typically, isoprene production increases with exposure to high temperature and high light. Isoprene emission may help stabilize photosynthetic complexes in the thylakoid membrane (Sharkey & Singsaas 1995). Additionally, isoprene may also confer high-temperature tolerance through an antioxidative role (Loreto & Velikova 2001).

Isoprene-emitting *Populus tremuloides* trees were able to cope with heat stress (36–39 °C) much better than *Betula papyrifera* trees, which do not emit isoprene. In fact, the *Populus tremuloides* clone that produced the most isoprene was able to tolerate the highest temperatures (Darbah *et al.* 2010). Additionally, isoprene production in sunlit leaves of *Quercus rubra* and *Q. alba* trees increased with temperatures of up to 42 °C (Sharkey *et al.* 1996). In *Q. alba*, g_s was lower and isoprene production was higher, compared with *Q. rubra*. The authors speculated that the higher g_s in *Q. rubra* resulted in greater evaporative cooling and a lower demand for isoprene production. Isoprene is not stored, but instead immediately emitted after production (Sharkey & Yeh 2001). However, monoterpenes and other VOCs can be stored in cells, where exposure to high temperatures induces lipid damage, causing the release of the VOC (Kleist *et al.* 2012).

HEAT AND DROUGHT

Although the direct effects of high temperature on trees can be severe, extreme high-temperature events under conditions of high soil moisture are relatively rare. The more common situation is to have simultaneous heat and drought events. A well-documented large-scale heat and drought event occurred in the summer of 2003 in Europe. July temperatures were up to 6 °C higher than long-term means and rainfall deficits were up to 300 mm, equivalent to 50% of annual precipitation in some locations. These conditions produced a 30% decrease in gross primary production over the European continent, making the region a net source of CO_2 (0.5 PgC per year) rather than a sink as it had been in previous years (Ciais *et al.* 2005). Some forests showed growth reductions of 50% (Bertini *et al.* 2011).

During drought periods, cloudiness is reduced, which increases solar radiation and heating of land surfaces and reduces air relative humidity. The resulting increases in VPD cause increased transpiration, further drying the soil and creating a positive feedback loop that accelerates and magnifies the effects of the drought. The combination of heat and drought has contributed to tree mortality worldwide (Allen *et al.* 2010). In many instances, after the trees have been stressed by several years of drought and high temperatures, insects and diseases are the primary agents of death (Breshears *et al.* 2005; Kurz *et al.* 2008; Allen *et al.* 2010). Warming in the Western United States has accelerated soil drying, and has been implicated in increased tree mortality throughout the region (van Mantgem *et al.* 2009).

The simultaneous occurrence of heat and drought events can impose considerable strains on tree function. The European drought of 2003 provided several examples of the

negative effects of concurrent heat and drought on physiological processes in trees. In *Quercus pubescens* growing in the Swiss Alps, leaf temperatures were generally higher than air temperatures, and often exceeded 40 °C on many days in June, July and August (Haldimann *et al*. 2008). As expected, net photosynthesis was reduced throughout the day. Intercellular CO_2 concentrations were high, indicating that the suppression of photosynthesis was due to biochemical limitations rather than stomatal closure. Leaves increased their concentration of carotenoids, which added protection against photooxidative damage, likely at the expense of growth. There was a reduction in chlorophyll concentration, a down-regulation of PSII, and an increase in dissipation of electrons through alternative pathways. The heat and drought event also caused stomatal closure, as well as early senescence of leaves of *Q. pubescens* (Zweifel *et al*. 2006). It is uncertain whether the leaves senesced because of excessive heat damage, or as a response to maintain the tree hydraulic system by reducing transpiration (Zweifel *et al*. 2007). In a study of 18 tree species during the 2003 heat and drought event, García-Plazaola *et al*. (2008) reported that most species had decreased chlorophyll, ascorbate, and chlorophyll fluorescence (*Fv/Fm*) and increased tocopherol and xanthophyll cycle pigments, which would increase protection against excessive light energy in the chloroplast.

In most circumstances, trees are able to cope well with high ambient temperatures (>40 °C) for short durations as long as they have a sufficient water source. This water is used to cool the leaves evaporatively by transpiration, but also to cool stem tissues convectively through heat transfer (Kolb & Robberecht 1996). Thus, at high temperatures, drought impedes the capacity to cool tissues to temperatures below the damage threshold. Drought and extreme temperatures are often interconnected, and may induce similar cellular damage and secondary stresses, such as osmotic and oxidative stress, which often activate similar cell signalling pathways and cellular responses, such as the production of stress proteins, up-regulation of antioxidants, and accumulation of compatible solutes (Wang *et al*. 2003). The effect of this striking interconnection between soil drought and extreme temperatures is not, however, limited to responses of living cells, but also exists at the whole-tree transport level, including xylem transport, phloem transport and their interaction, because extreme temperatures translate into atmospheric drought, which in turn causes increased transpiration. Thus, while exposed to both dry soil and a dry atmosphere caused by extreme temperatures, trees must maintain hydration to avoid a whole-system transport failure, which would ultimately lead to tree death (Anderegg *et al*. 2012). In a heat wave experiment on *Q. rubra* seedlings, Bauweraerts *et al*. (2013) observed that transpiration of seedlings in a low soil water treatment significantly decreased as a week-long +12 °C heat wave progressed, and that transpiration was significantly lower after the heat wave than prior to the heat wave. This behaviour was absent in well-watered seedlings. Therefore, selection for drought resistance may also be important for selection for heat and extreme temperature resistance.

GENETIC IMPROVEMENT FOR EXTREME TEMPERATURES

One of the great challenges for forestry is to select genotypes that are suitable for growth in the new climatic conditions that will be present in the 21st century. These future conditions include an increase in extreme heat events with increased frequency and duration of summer heat waves, increased fluctuations in temperature and an increase in monthly maximum temperatures throughout the year. There has been relatively little study of the response of trees to these conditions. Research into genetic engineering of some crop and model species to improve production of HSPs is a promising area of investigation (Grover *et al*. 2013) that could be adapted to tree species. Short-term exposure to high temperatures has resulted in expression of HSPs and increases in reactive oxygen species, redox response enzymes and certain regulatory proteins (Suzuki *et al*. 2012). These responses appear to contribute to the maintenance of physiological functioning during heat stress. Other compounds such as abscisic acid, salicylic acid, hydrogen peroxide, ethylene and beta-amionbutyric acid may mediate responses to heat stress, although what pathways or mechanisms these signals induce or regulate is not well understood (Ham *et al*. 2013).

We know from the few studies on trees that exist that there is variation in the response of genotypes to excessive heat. An *Acer rubrum* genotype from a warm temperate area (Florida) had higher net photosynthesis than one from a cool temperate area (Minnesota) at temperatures up to 48 °C (Weston & Bauerle 2007). Bigras (2000) examined the response of 12 open-pollinated families of *Picea glauca* to 30 min of heat from 42 to 50 °C, and found that families with superior height performance were the most sensitive to heat stress, compared with those families with intermediate or inferior rates of height growth. This finding is similar to the results from many screening tests for drought tolerance in trees in that there is often a trade-off between stress tolerance and productivity. Generally, faster-growing tree genotypes originate in fertile and moist areas and allocate less carbon belowground, and are less water-use efficient, than genotypes that develop in less resource-rich areas. In a trial of 33 *Populus deltoides* × *Populus trichocarpa* genotypes, the most productive genotypes in well-watered conditions were the least tolerant of moderate water deficits (Monclus *et al*. 2009). In a comparison of the traits of *Eucalyptus globulus* clones from several breeding programmes, faster-growing genotypes were the least water-use efficient (Pita *et al*. 2005). As drought and heat stress often co-occur it may be most fruitful to simultaneously screen genotypes for both drought and heat tolerance and avoidance characteristics. Looking for these types of responses among genotypes, especially in genotypes from the warmest portion of a species range where the growing season is extended, may be critical to selecting families and clones for superior performance under the heat and drought conditions that are expected to increase globally in the future.

There are many provenance trials in place for economically important tree species worldwide that are being

re-examined to evaluate potential growth of different geno-types in response to climate change. It is evident that even improved half- and full-sibling families have high levels of genetic and phenotypic variation (Aspinwall *et al.* 2013). Determining the selection traits that will improve productiv-ity of managed stands in the future is an important unre-solved question in tree breeding. Responses to temperature, drought, nutrients and CO_2 may all be important in the novel climate of the future. Provenances from warmer areas usually have faster growth than those from cooler areas (e.g. Savva *et al.* 2007; Leites *et al.* 2012), so genotypic variation in response to temperature can be exploited to increase growth in managed tree species in the future warmer climate.

Whether traditional breeding practices are appropriate for producing the most suitable genotypes for the rapidly chang-ing climate predicted in the 21st century is also an important issue. While it is possible to breed for desirable traits, this process is slow and does not guarantee results (Harfouche *et al.* 2011). Wahid *et al.* (2007) reviewed the difficulties in breeding crop plants for thermotolerance using traditional protocols, which generally involve growing breeding materials in a hot environment to identify superior-performing plants or lines. In brief, the difficulties include: identifying genetic resources, understanding the complexity of heat tolerance mechanisms, evaluating which stages of the life cycle are most susceptible to heat stress, distinguishing between heat tolerance and inherent growth potential and determining selection criteria. Most of the same difficulties apply to the breeding of trees, with the addition of a much longer life cycle, which severely limits the speed at which trials can be conducted. Despite these complications, for a few crop species some acceptable heat-tolerant cultivars have been developed and released, and traditional breeding trials continue [e.g. Farnham & Bjoerkman 2011; Cairns *et al.* 2013; Hossain *et al.* 2013; Sadras *et al.* 2013; Alemayehu *et al.* 2014 in broccoli (*Brassica oleracea*), maize (*Zea mays*), wheat (*Triticum aestivum*), field pea (*Pisum sativum*) and barley (*Hordeum vulgare*), respectively].

Genetic engineering of trees has great potential to provide rapid improvement in heat and drought tolerance of trees by utilizing introduced genes gained from research on other plant types, which is much farther along than it is in trees (Harfouche *et al.* 2011). Recent progress in molecular and biotechnological techniques has improved the prospects for development of thermotolerance in plants. Some molecular mechanisms of the heat–stress response have been eluci-dated (Qu *et al.* 2013) and quantitative trait loci (QTL) for some stress-adaptive traits have been identified. For example, (Xue *et al.* 2012) exposed rice (*Oryza sativa* L.) plants to heat stress and found significantly increased lipid peroxidation and antioxidative enzyme activity after 24 h at high tempera-tures compared with control plants. They subsequently iden-tified 11 differentially expressed genes between the two groups that were associated with the heat stress response. In another study, Wei *et al.* (2013) identified a major locus on rice chromosome 9, which controls heat tolerance up to 48 °C in a local rice cultivar. Ali *et al.* (2013) crossed a heat-tolerant variety of primitive wheat (*Triticum turgidum*) with 10 heat-

susceptible genotypes to develop 19 families. These families were phenotyped for heat tolerance and genotyped to iden-tify associated QTL, which mapped up to three chromo-somes. Results of these and similar studies in many crop species exemplify the first steps in using advanced methods to engineer heat stress tolerance in plants. A review by Harfouche *et al.* (2011) highlighted some of the advance-ments made in genetic modification of trees, including species of the genera *Populus*, *Eucalyptus*, *Pinus*, *Picea*, *Castanea* and *Ulmus*. While modification has primarily been done to improve growth rates and disease or fungal resistance, some work has been done to increase drought tolerance in *Pinus* (Tang *et al.* 2007), and salt (Wang *et al.* 2010) and cold toler-ance in *Populus* (Guo *et al.* 2009). Similar work to induce heat stress tolerance in commercially planted tree species is also possible if genetic regulation of heat stress responses can be elucidated.

However, little has been done to determine the genetic mechanisms of thermotolerance in trees. Salazar *et al.* (2013) analysed xylem transcription profiles of three *Eucalyptus* species intensively used in breeding programmes and found that the expression of genes encoding small HSPs was great-est in *Eucalyptus urophylla*, the species best adapted to a tropical climate and considered most robust, and lowest in *E. globulus*, which is adapted to subtropical/temperate cli-mates. *E. urophylla* has been used in breeding programmes for its resistance to drought and diseases (Turnbull 2000), and these results suggest that it might also provide useful germplasm for heat resistance. In another study on *Populus simonii*, a heat-resistant species with wide distribution in China, Wang *et al.* (2012) identified 35 microsatellite markers from heat stress transcription factors that could be useful in marker-assisted breeding of stress-resistant germplasm. A similar negative relationship between drought resistance and wood quality/productivity has been observed among prov-enances in other tree species (Wells 1983; Danjon 1994; Eilmann *et al.* 2013).

Molecular and biotechnological methods, along with clonal tissue culture propagation, show great promise for tree breeding because they can overcome some of the limitations imposed by the long life cycle of trees. With these techniques, germplasm can be identified, modified and reproduced without waiting multiple years or decades for the completion of the tree reproductive cycle. However, it is not certain whether transgenic trees will gain regulatory and societal approval.

CONCLUSIONS

It is clear that there is much to be learned about how high temperatures and heat waves affect trees. The level of stress caused by high temperatures is determined by many things, including exposure temperature, duration of exposure, ability to tolerate or rapidly acclimate, time of year and soil water availability. Trees are well adapted to survive transient extreme heat events, although these events reduce carbon gain and growth. Heat stress and drought stress are often linked, and each tends to amplify the stress caused by the

other. Mortality from drought is far more likely than mortality from heat stress, but the severity of drought stress, and the speed of its onset, is greatly increased under high temperatures. Similarly, drought can exacerbate the effect of heat stress. For example, a common response to drought stress is to close stomata to reduce water loss, but heat stress can be much more severe when transpirational cooling is reduced. At this time, we do not know how many tree species employ this mechanism to cool their leaves, although some clearly do. Compared with other physiological processes, including growth, we know more about the effect of heat on photosynthesis, but even that knowledge is limited. We have yet to determine differences in thermal tolerance across temperature gradients within and across biomes or in the amount of genetic variation in high-temperature tolerance within species. These issues present opportunities for research that will expand our knowledge of how trees acclimate and adapt to their environment. There are also ample prospects for the use of both traditional and modern genetic techniques to improve resistance to high-temperature stress of economically important trees, particularly because this has not been the focus of breeding programmes to date. Decisions about trait and gene selection are complicated by a lack of understanding of how trees respond physiologically to the combination of heat waves and drought. For example, selection for drought avoidance traits such as deep root systems that could supply more water would be advantageous for heat tolerance, but would likely reduce stem biomass production. However, it is imperative that more attention is focused on these problems, given the long life of trees, the extended period between planting and harvest of most economically important species, and our rapidly changing climate.

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REFERENCES

Ainsworth E.A. & Rogers A. (2007) The response of photosynthesis and stomatal conductance to rising [CO2]: mechanisms and environmental interactions. *Plant, Cell & Environment* **30**, 258–270.

Alemayehu F.R., Frenck G., van der Linden L., Mikkelsen T.N. & Jorgensen R.B. (2014) Can barley (*Hordeum vulgare* L. s.l.) adapt to fast climate changes? A controlled selection experiment. *Genetic Resources and Crop Evolution* **61**, 151–161.

Ali M.B., Ibrahim A.M.H., Malla S., Rudd J. & Hays D.B. (2013) Family-based QTL mapping of heat stress tolerance in primitive tetraploid wheat (*Triticum turgidum* L). *Euphytica* **192**, 189–203.

Allen C.D., Macalady A.K., Chenchouni H., Bachelet D., McDowell N., Vennetier M., . . . Cobb N. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* **259**, 660–684.

Ameye M., Wertin T.M., Bauwereaerts I., McGuire M.A., Teskey R.O. & Steppe K. (2012) The effect of induced heat waves on *Pinus taeda* and *Quercus rubra* seedlings in ambient and elevated CO₂ atmospheres. *The New Phytologist* **196**, 448–461.

Anderegg W.R.L., Berry J.A. & Field C.B. (2012) Linking definitions, mechanisms, and modeling of drought-induced tree death. *Trends in Plant Science* **17**, 693–700.

Arnone J.A. 3rd, Verburg P.S., Johnson D.W., Larsen J.D., Jasoni R.L., Lucchesi A.J., . . . Schimel D.S. (2008) Prolonged suppression of ecosystem carbon dioxide uptake after an anomalously warm year. *Nature* **455**, 383–386.

Aspinwall M.J., King J.S. & McKeand S.E. (2013) Productivity differences among loblolly pine genotypes are independent of individual-tree biomass partitioning and growth efficiency. *Trees* **27**, 533–545.

Barriopedro D., Fischer E.M., Luterbacher J., Trigo R.M. & Garcia-Herrera R. (2011) The hot summer of 2010: redrawing the temperature record map of Europe. *Science* **332**, 220–224.

Bassow S.L., McConnaughay K.D.M. & Bazzaz F.A. (1994) The response of temperate tree seedlings grown in elevated CO₂ to extreme temperature events. *Ecological Applications* **4**, 593–603.

Bastos A., Gouveia C.M., Trigo R.M. & Running S.W. (2013) Comparing the impacts of 2003 and 2010 heatwaves in NPP over Europe. *Biogeosciences Discussions* **10**, 15879–15911.

Bauweraerts I., Wertin T.M., Ameye M., McGuire M.A., Teskey R.O. & Steppe K. (2013) The effect of heat waves, elevated [CO₂] and low soil water availability on northern red oak (*Quercus rubra* L.) seedlings. *Global Change Biology* **19**, 517–528.

Bauweraerts I., Ameye M., Wertin T.M., McGuire M.A., Teskey R.O. & Steppe K. (2014) Water availability is the decisive factor for the growth of two tree species in the occurrence of consecutive heat waves. *Agricultural and Forest Meteorology* **189–190**, 19–29.

Becker W.M. (1986) *The World of the Cell*. pp. 254–255. The Benjamin/Cummings Publishing Company, Menlo Park.

Bernacchi C.J., Portis A.R., Nakano H., von Caemmerer S. & Long S.P. (2002) Temperature response of mesophyll conductance: implications for the determination of Rubisco enzyme kinetics and for limitations to photosynthesis *in vivo*. *Plant Physiology* **130**, 1992–1998.

Berry J. & Bjorkman O. (1980) Photosynthetic response and adaptation to temperature in higher plants. *Annual Review of Plant Physiology and Plant Molecular Biology* **31**, 491–543.

Bertini G., Amoriello T., Fabbio G. & Piovosi M. (2011) Forest growth and climate change: evidences from the ICP-Forests intensive monitoring in Italy. *iForest – Biogeosciences and Forestry* **4**, 262–267.

Bigras F.J. (2000) Selection of white spruce families in the context of climate change: heat tolerance. *Tree Physiology* **20**, 1227–1234.

Bongarten B.C. & Teskey R.O. (1986) Water relations of loblolly pine seedlings from diverse geographic origins. *Tree Physiology* **1**, 265–276.

Bongi G. & Long S.P. (1987) Light-dependent damage to photosynthesis in olive leaves during dhilling and high-temperature stress. *Plant, Cell & Environment* **10**, 241–249.

Breshears D.D., Cobb N.S., Rich P.M., Price K.P., Allen C.D., Balice R.G., . . . Meyer C.W. (2005) Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences of the United States of America* **102**, 15144–15148.

Bukhov N.G., Boucher N. & Carpentier R. (1998) Loss of the precise control of photosynthesis and increased yield of non-radiative dissipation of excitation energy after mild heat treatment of barley leaves. *Physiologia Plantarum* **104**, 563–570.

Bukhov N.G., Samson G. & Carpentier R. (2000) Nonphotosynthetic reduction of the intersystem electron transport chain of chloroplasts following heat stress. Steady-state rate. *Photochemistry and Photobiology* **72**, 351–357.

von Caemmerer S. & Quick W.P. (2000) Rubisco: physiology *in vivo*. In *Photosynthesis: Physiology and Metabolism* (eds R.C. Leegood, T.D. Sharkey & S. von Caemmerer), pp. 85–113. Springer, Dordrecht.

Cairns J.E., Crossa J., Zaidi P.H., Grudloyma P., Sanchez C., Luis Araus J., . . . Atlin G.N. (2013) Identification of drought, heat, and combined drought and heat tolerant donors in maize. *Crop Science* **53**, 1335–1346.

Cajanek M., Stroch M., Lachetova I., Kalina J. & Spunda V. (1997) Characterization of the photosystem II inactivation of heat-stressed barley leaves as monitored by the various parameters of chlorophyll *a* fluorescence and delayed fluorescence. *Journal of Photochemistry and Photobiology* **47**, 39–45.

Cavanagh A.P. & Kubien D.S. (2014) Can phenotypic plasticity in Rubisco performance contribute to photosynthetic acclimation? *Photosynthesis Research* **119**, 203–214.

Ciais P., Reichstein M., Viovy N., Granier A., Ogee J., Allard V.,. . . Valentini R. (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* **437**, 529–533.

Colombo S.J. & Timmer V.R. (1992) Limits of tolerance to high temperatures causing direct and indirect damage to black spruce. *Tree Physiology* **11**, 95–104.

Colombo S.J., Colclough M.L., Timmer V.R. & Blumwald E. (1992) Clonal variation in heat tolerance and heat-shock protein expression in black spruce. *Silvae Genetica* **41**, 234–239.

Coumou D. & Robinson A. (2013) Historic and future increase in the global land area affected by monthly heat extremes. *Environmental Research Letters* **8**, 034018.

Coumou D., Robinson A. & Rahmstorf S. (2013) Global increase in record-breaking monthly-mean temperatures. *Climatic Change* **118**, 771–782.

Crafts-Brandner S.J. & Law R.D. (2000) Effect of heat stress on the inhibition and recovery of the ribulose-1,5-bisphosphate carboxylase/oxygenase activation state. *Planta* **212**, 67–74.

Crafts-Brandner S.J. & Salvucci M.E. (2004) Analyzing the impact of high temperature and CO2 on net photosynthesis: biochemical mechanisms, models and genomics. *Field Crops Research* **90**, 75–85.

Crous K.Y., Zaragoza-Castells J., Ellsworth D.S., Duursma R.A., Löw M., Tissue D.T. & Atkin O.K. (2012) Light inhibition of leaf respiration in field-grown *Eucalyptus saligna* in whole-tree chambers under elevated atmospheric CO_2 and summer drought. *Plant, Cell & Environment* **35**, 966–981.

Cunningham S.C. & Read J. (2003) Do temperate rainforest trees have a greater ability to acclimate to changing temperatures than tropical rainforest trees? *The New Phytologist* **157**, 55–64.

Cunningham S.C. & Read J. (2006) Foliar temperature tolerance of temperate and tropical evergreen rain forest trees of Australia. *Tree Physiology* **26**, 1435–1443.

Daas C., Montpied P., Hanchi B. & Dreyer E. (2008) Responses of photosynthesis to high temperatures in oak saplings assessed by chlorophyll-a fluorescence: inter-specific diversity and temperature-induced plasticity. *Annals of Forest Science* **65**, 304–306.

Danjon F. (1994) Stand features and height growth in a 36-year-old maritime pine (*Pinus pinaster* Ait.) provenance test. *Silvae Genetica* **43**, 52–62.

Darbah J.N.T., Sharkey T.D., Calfapietra C. & Karnosky D.F. (2010) Differential response of aspen and birch trees to heat stress under elevated carbon dioxide. *Environmental Pollution* **158**, 1008–1014.

De Boeck H.J., Dreesen F.E., Janssens I.A. & Nijs I. (2011) Whole-system responses of experimental plant communities to climate extremes imposed in different seasons. *The New Phytologist* **189**, 806–817.

De Simon G., Alberti G., Delle Vedove G., Peressotti A., Zaldei A. & Miglietta F. (2013) Short-term cropland responses to temperature extreme events during late winter. *Biogeosciences* **10**, 5545–5553.

Della-Marta P.M., Haylock M.R., Luterbacher J. & Wanner H. (2007) Doubled length of western European summer heat waves since 1880. *Journal of Geophysical Research-Atmospheres* **112**, D15103.

Dreyer E., Le Roux X., Montpied P., Daudet F.A. & Masson F. 2001. Temperature response of leaf photosynthetic capacity in seedlings from seven temperate tree species. *Tree Physiology* **21**, 223–232.

Dulière V., Zhang Y. & Salathé E.P. (2013) Changes in twentieth-century extreme temperature and precipitation over the Western United States based on observations and regional climate model simulations*. *Journal of Climate* **26**, 8556–8575.

Easterling D.R., Meehl G.A., Parmesan C., Changnon S.A., Karl T.R. & Mearns L.O. (2000) Climate extremes: observations, modeling, and impacts. *Science* **289**, 2068–2074.

Eilmann B., de Vries S.M.G., den Ouden J., Mohren G.M.J., Sauren P. & Sass-Klaassen U. (2013) Origin matters! Difference in drought tolerance and productivity of coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.)) provenances. *Forest Ecology and Management* **302**, 133–143.

Enami I., Kitamura M., Tomo T., Isokawa Y., Ohta H. & Katoh S. (1994) Is the primary cause of thermal inactivation of oxygen evolution in spinach PS II membranes release of the extrinsic 33 kDa protein of of Mn? *Biochimica et Biophysica Acta* **1186**, 52–58.

Farnham M.W. & Bjoerkman T. (2011) Evaluation of experimental broccoli hybrids developed for summer production in the Eastern United States.

Hortscience: A Publication of the American Society for Horticultural Science **46**, 858–863.

Filewod B. & Thomas S.C. (2014) Impacts of a spring heat wave on canopy processes in a northern hardwood forest. *Global Change Biology* **20**, 360–371.

Galmes J., Aranjuelo I., Medrano H. & Flexas J. (2013) Variation in Rubisco content and activity under variable climatic factors. *Photosynthesis Research* **117**, 73–90.

García-Plazaola J.I., Esteban R., Hormaetxe K., Fernández-Marín B. & Becerril J.M. (2008) Photoprotective responses of Mediterranean and Atlantic trees to the extreme heat-wave of summer 2003 in Southwestern Europe. *Trees* **22**, 385–392.

Ghouil H., Montpied P., Epron D., Ksontini M., Hanchi B. & Dryer E. (2003) Thermal optima of photosynthetic functions and thermostability of photochemistry in cork oak seedlings. *Tree Physiology* **23**, 1031–1039.

Gifford D.J. & Taleisnik E. (1994) Heat-shock response of *Pinus* and *Picea* seedlings. *Tree Physiology* **14**, 103–110.

Gombos Z., Wada H., Hideg E. & Murata N. (1994) The unsaturation of membrane-lipids stabilizes photosynthesis against heat-stress. *Plant Physiology* **104**, 563–567.

Grover A., Mittal D., Negi M. & Lavania D. (2013) Generating high temperature tolerant transgenic plants: achievements and challenges. *Plant Science* **205–206**, 38–47.

Guirguis K., Gershunov A., Tardy A. & Basu R. (2014) The impact of recent heat waves on human health in California. *Journal of Applied Meteorology and Climatology* **53**, 3–19.

Guo X.H., Jiang J., Lin S.J., Wang B.C., Wang Y.C., Liu G.F. & Yang C.P. (2009) A ThCAP gene from *Tamarix hispida* confers cold tolerance in transgenic *Populus (P. davidiana × P. bolleana)*. *Biotechnology Letters* **31**, 1079–1087.

Haldimann P. & Feller U. (2004) Inhibition of photosynthesis by high temperature in oak (*Quercus pubescens* L.) leaves grown under natural conditions closely correlates with a reversible heat-dependent reduction of the activation state of ribulose-1,5-bisphosphate carboxylase/oxygenase. *Plant, Cell & Environment* **27**, 1169–1183.

Haldimann P., Galle A. & Feller U. (2008) Impact of an exceptionally hot dry summer on photosynthetic traits in oak (*Quercus pubescens*) leaves. *Tree Physiology* **28**, 785–795.

Ham D.-J., Moon J.-C., Hwang S.-G. & Jang C.-J. (2013) *Molecular Biology Reports* **40**, 6709–6720.

Hamerlynck E.P. & Knapp A.K. (1994) Leaf-level responses to light and temperature in two co-occurring *Quercus* (Fagaceae) species: implications for tree distribution patterns. *Forest Ecology & Management* **68**, 149–159.

Hamerlynck E.P., Huxman T.E., Loik M.E. & Smith S.D. (2000) Effects of extreme high temperature, drought and elevated CO_2 on photosynthesis of the Mojave Desert evergreen shrub, *Larrea tridentata*. *Plant Ecology* **148**, 183–193.

Hansen J., Sato M. & Ruedy R. (2012) Perception of climate change. *Proceedings of the National Academy of Sciences of the United States of America* **109**, E2415–E2423.

Hao Z., AghaKouchak A. & Phillips T.J. (2013) Changes in concurrent monthly precipitation and temperature extremes. *Environmental Research Letters* **8**, 034014.

Harfouche A., Meilan R. & Altman A. (2011) Tree genetic engineering and applications to sustainable forestry and biomass production. *Trends in Biotechnology* **29**, 9–17.

Harley P., Otter L., Guenther A. and Greenberg J. (2003) Micrometeorological and leaf-level measurements of isoprene emissions from a southern African savanna. *J. Geophysical Res.*, **108**D13, 8468, doi:10.1029/2002JD002592.

Harrison S.P., Morfopoulos C., Dani K.G.S., Prentice I.C., Arneth A., Atwell B.J., . . . Wright I.J. (2013) Volatile isoprenoid emissions from plastid to planet. *The New Phytologist* **197**, 49–57.

He C.R., Murray F. & Lyons T. (2000) Monoterpene and isoprene emissions from 15 *Eucalyptus* species in Australia. *Atmospheric Environment* **34**, 645–655.

Heide O.M. (2003) High autumn temperature delays spring bud burst in boreal trees, counterbalancing the effect of climatic warming. *Tree Physiology* **23**, 931–936.

Horvath I., Glatz A., Nakamoto H., Mishkind M.L., Munnik T., Saidi Y., . . . Vigh L. (2012) Heat shock response in photosynthetic organisms: membrane and lipid connections. *Progress in Lipid Research* **51**, 208–220.

Hossain A., Sarker M.A.Z., Saifuzzaman M., da Silva J.A.T., Lozovskaya M.V. & Akhter M.M. (2013) Evaluation of growth, yield, relative performance and heat susceptibility of eight wheat (*Triticum aestivum* L.) genotypes

grown under heat stress. *International Journal of Plant Production* **7**, 615–636.

Hozain M.I., Salvucci M.E., Fokar M. & Holaday A.S. (2010) The differential response of photosynthesis to high temperature for a boreal and temperate *Populus* species relates to differences in Rubisco activation and Rubisco activase properties. *Tree Physiology* **30**, 32–44.

Hüve K., Bichele I., Ivanova H., Keerberg O., Pärnik T., Rasulov B., . . . Niinemets Ü. (2012) Temperature responses of dark respiration in relation to leaf sugar concentration. *Physiologia Plantarum* **144**, 320–334.

IPCC (2012) *Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation*. A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change (eds Field C.B., Barros V., Stocker T.F., Qin D., Dokken D.J., Ebi K.L., Mastrandrea M.D., Mach K.J., Plattner G.-K., Allen S.K., Tignor M., Midgley P.M.), 582 pp. Cambridge University Press, Cambridge UK and New York NY USA.

Jin S.H., Li X.Q., Zheng B.S. & Wang J.G. (2010) Response of the photosynthesis and antioxidant systems to high-temperature stress in *Euonymus japonicus* seedlings. *Forest Science* **56**, 172–180.

Joó É., Dewulf J., Amelynck C., Schoon N., Pokorska O., Šimpraga M., . . . Van Langenhove H. (2011) Constitutive versus heat and biotic stress induced BVOC emissions in *Pseudotsuga menziesii*. *Atmospheric Environment* **45**, 3655–3662.

Jordan D.B. & Ogren W.L. (1984) The CO_2/O_2 specificity of ribulose 1,5-bisphosphate carboxylase oxygenase: dependence on ribulosebisphosphate concentration, pH and temperature. *Planta* **161**, 308–313.

Kempf K., Allwine E., Westberg H., Claiborn C. & Lamb B. (1996) Hydrocarbon emissions from spruce species using environmental chamber and branch enclosure methods. *Atmospheric Environment* **30**, 1381–1389.

Kleist E., Mentel T.F., Andres S., Bohne A., Folkers A., Kiendler-Scharr A., . . . Wildt J. (2012) Irreversible impacts of heat on the emissions of monoterpenes, sesquiterpenes, phenolic BVOC and green leaf volatiles from several tree species. *Biogeosciences* **9**, 5111–5123.

de Klerk G.-J. & Pumisutapon P. (2008) Protection of in-vitro grown *Arabidopsis* seedlings against abiotic stresses. *Plant Cell, Tissue and Organ Culture* **95**, 149–154.

Kolb P.F. & Robberecht R. (1996) High temperature and drought stress effects on survival of *Pinus ponderosa* seedlings. *Tree Physiology* **16**, 665–672.

Krause G.H., Cheesman A.W., Winter K., Krause B. & Virgo A. 2013. Thermal tolerance, net CO_2 exchange and growth of a tropical tree species, *Ficus insipida*, cultivated at elevated daytime and nighttime temperatures. *Journal of Plant Physiology* **170**, 822–827.

Kuhn U., Rottenberger S., Biesenthal T., Wolf A., Schebeske G., Ciccioli P., . . . Kesselmeier J. (2004) Seasonal differences in isoprene and light-dependent monoterpene emission by Amazonian tree species. *Global Change Biology* **10**, 663–682.

Kurz W.A., Dymond C.C., Stinson G., Rampley G.J., Neilson E.T., Carroll A.L., . . . Safranyik L. (2008) Mountain pine beetle and forest carbon feedback to climate change. *Nature* **452**, 987–990.

Larkindale J. & Knight M.R. (2002) Protection against heat stress-induced oxidative damage in *Arabidopsis* involves calcium, abscisic acid, ethylene, and salicylic acid. *Plant Physiology* **128**, 682–695.

Law R.D. & Crafts-Brandner S.J. (1999) Inhibition and acclimation of photosynthesis to heat stress is closely correlated with activation of ribulose-1,5-bisphosphate carboxylase/oxygenase. *Plant Physiology* **120**, 173–181.

Leites L.P., Robinson A.P., Rehfeldt G.E., Marshall J.D. & Crookston N.L. (2012) Height-growth response to climatic changes differs among populations of Douglas-fir: a novel analysis of historic data. *Ecological Applications* **22**, 154–165.

Long S.P., Ainsworth E.A., Rogers A. & Ort D.R. (2004) Rising atmospheric carbon dioxide: plants FACE the future. *Annual Review of Plant Biology* **55**, 591–628.

Loreto F. & Velikova V. (2001) Isoprene produced by leaves protects the photosynthetic apparatus against ozone damage, quenches ozone products, and reduces lipid peroxidation of cellular membranes. *Plant Physiology* **127**, 1781–1787.

Lu Z., Quinones M.A. & Zeiger E. (2000) Temperature dependence of guard cell respiration and stomatal conductance co-segregate in an F2 population of Pima cotton. *Australian Journal of Plant Physiology* **27**, 457–462.

van Mantgem P.J., Stephenson N.L., Byrne J.C., Daniels L.D., Franklin J.F., Fule P.Z., . . . Veblen T.T. (2009) Widespread increase of tree mortality rates in the Western United States. *Science* **323**, 521–524.

Marchand F.L., Mertens S., Kockelbergh F., Beyens L. & Nijs I. (2005) Performance of High Arctic tundra plants improved during but deteriorated after exposure to a simulated extreme temperature event. *Global Change Biology* **11**, 2078–2089.

Marchand F.L., Kockelbergh F., van de Vijver B., Beyens L. & Nijs I. (2006) Are heat and cold resistance of arctic species affected by successive extreme temperature events? *The New Phytologist* **170**, 291–300.

Monclus R., Villar M., Barbaroux C., Bastien C., Fichot R., Delmotte F.M., . . . Brignolas F. (2009) Productivity, water-use efficiency and tolerance to moderate water deficit correlate in 33 poplar genotypes from a *Populus deltoides × Populus trichocarpa* F1 progeny. *Tree Physiology* **29**, 1329–1339.

O'Sullivan O.S., Weerasinghe K.W., Evans J.R., Egerton J.J., Tjoelker M.G. & Atkin O.K. (2012) High-resolution temperature responses of leaf respiration in snow gum (*Eucalyptus pauciflora*) reveal high-temperature limits to respiratory function. *Plant, Cell & Environment* **36**, 1268–1284.

Perkins S.E. & Alexander L.V. (2013) On the measurement of heat waves. *Journal of Climate* **26**, 4500–4517.

Peterson T.C., Heim R.R., Hirsch R., Kaiser D.P., Brooks H., Diffenbaugh N.S., . . . Wuebbles D. (2013) Monitoring and understanding changes in heat waves, cold waves, floods, and droughts in the United States: state of knowledge. *Bulletin of the American Meteorological Society* **94**, 821–834.

Pita P., Cañas I., Soria F., Ruiz F. & Toval G. (2005) Use of physiological traits in tree breeding for improved yield in drought-prone environments. The case of *Eucalyptus globulus*. *Investigación Agraria. Sistemas y Recursos Forestales* **14**, 383–393.

Qu A.-L., Ding Y.-F., Jiang Q. & Zhu C. (2013) Molecular mechanisms of the plant heat stress response. *Biochemical and Biophysical Research Communications* **432**, 203–207.

Rasmussen R.A. (1970) Isoprene: identified as a forest-type emission to atmosphere. *Environmental Science & Technology* **4**, 667–671.

Rokka A., Aro E.M., Herrmann R.G., Andersson B. & Vener A.V. (2000) Dephosphorylation of photosystem II reaction center proteins in plant photosynthetic membranes as an immediate response to abrupt elevation of temperature. *Plant Physiology* **123**, 1525–1535.

Sadras V.O., Lake L., Leonforte A., McMurray L.S. & Paull J.G. (2013) Screening field pea for adaptation to water and heat stress: associations between yield, crop growth rate and seed abortion. *Field Crops Research* **150**, 63–73.

Sage R.F. & Kubien D.S. (2007) The temperature response of C3 and C4 photosynthesis. *Plant, Cell & Environment* **30**, 1086–1106.

Sage R.F., Way D.A. & Kubien D.S. (2008) Rubisco, Rubisco activase, and global climate change. *Journal of Experimental Botany* **59**, 1581–1595.

Salazar M.M., Nascimento L.C., Oliveira Camargo E.L., Goncalves D.C., Neto J.L., Marques W.L., . . . Guimaraes Pereira G.A. (2013) Xylem transcription profiles indicate potential metabolic responses for economically relevant characteristics of Eucalyptus species. *BMC Genomics* **14**, 201.

Salvucci M.E. & Crafts-Brandner S.J. (2004) Relationship between the heat tolerance of photosynthesis and the thermal stability of rubisco activase in plants from contrasting thermal environments. *Plant Physiology* **134**, 1460–1470.

Sandford A.P. & Jarvis P.G. (1986) Stomatal responses to humidity in selected conifers. *Tree Physiology* **2**, 89–103.

Santarius K.A. (1976) Sites of heat sensitivity in chloroplasts and differential inactivation of cyclic and noncyclic photophosphorylation by heating. *Journal of Thermal Biology* **1**, 101–107.

Santarius K.A. & Muller M. (1979) Investigations on heat-resistance of spinach leaves. *Planta* **146**, 529–538.

Savva Y., Denneler B., Koubaa A., Tremblay F., Bergeron Y. & Tjoelker M.G. (2007) Seed transfer and climate change effects on radial growth of jack pine populations in a common garden in Petawawa, Ontario, Canada. *Forest Ecology and Management* **242**, 636–647.

Schrader S.M., Wise R.R., Wacholtz W.F., Ort D.R. & Sharkey T.D. (2004) Thylakoid membrane responses to moderately high leaf temperature in Pima cotton. *Plant, Cell & Environment* **27**, 725–735.

Schulze E.-D., Lange O.L., Kappen L., Bushbom U. & Evenari M. (1973) Stomatal responses to changing temperature at increasing water stress. *Planta (Berl.)* **110**, 29–42.

Sharkey T.D. & Singsaas E.L. (1995) Why plants emit isoprene. *Nature* **374**, 769.

Sharkey T.D. & Yeh S.S. (2001) Isoprene emission from plants. *Annual Review of Plant Physiology and Plant Molecular Biology* **52**, 407–436.

Sharkey T.D., Singsaas E.L., Vanderveer P.J. & Geron C. (1996) Field measurements of isoprene emission from trees in response to temperature and light. *Tree Physiology* **16**, 649–654.

Song L., Jiang Y., Zhao H. & Hou M. (2012) Acquired thermotolerance in plants. *Plant Cell, Tissue and Organ Culture (PCTOC)* **111,** 265–276.

Stéfanon M., Drobinski P., D'Andrea F., Lebeaupin-Brossier C. & Bastin S. (2014) Soil moisture-temperature feedbacks at meso-scale during summer heat waves over Western Europe. *Climate Dynamics* **42,** 1309–1324.

Suzuki N., Koussevitzky S., Mittler R. & Miller G. (2012) ROS and redox signalling in the response of plants to abiotic stress. *Plant, Cell & Environment* **35,** 259–270.

Šimpraga M., Verbeeck H., Demarcke M., Joó É., Pokorska O., Amelynck C., . . . Steppe K. (2011) Clear link between drought stress, photosynthesis and biogenic volatile organic compounds in *Fagus sylvatica* L. *Atmospheric Environment* **45,** 5254–5259.

Taiz L. & Zeiger E. (2010) *Plant Physiology*. p. 173. Sinauer Associates, Sunderland.

Tan Y., Li L., Leng C., Li D., Chen X. & Gao D. (2013) Respiratory response of dormant nectarine vegetative buds to high temperature stress. *Journal of Integrative Agriculture* **12,** 80–86.

Tang W., Newton R.J., Li C. & Charles T.M. (2007) Enhanced stress tolerance in transgenic pine expressing the pepper CaPF1 gene is associated with the polyamine biosynthesis. *Plant Cell Reports* **26,** 115–124.

Terzaghi W.B., Fork D.C., Berry J.A. & Field C.B. (1989) Low and high-temperature limits to PSII: a survey using trans-parinaric acid, delayed light-emission, and f0 chlorophyll fluorescence. *Plant Physiology* **91,** 1494–1500.

Teskey R.O., Sheriff D.W., Hollinger D.Y. & Thomas R.B. (1995) External and internal factors regulating photosynthesis. In *Resource Physiology of Conifers* (eds W.K. Smith & T.M. Hinckley), pp. 105–140. Academic Press, London.

Thompson L.K., Blaylock R., Sturtevant J.M. & Brudvig G.W. (1989) Molecular basis of the heat denaturation of photosystem II. *Biochemistry* **28,** 6686–6695.

Turnbull J.W. (2000) Economic and social importance of *Eucalypts*. In *Diseases and Pathogens of Eucalypts* (eds P.J. Keane, G.A. Kile, F.D. Podger & B.N. Brown), pp. 1–9. CSIRO Publishing, Collingwood, VIC, Australia.

Urban O. (2003) Physiological impacts of elevated CO_2 concentration ranging from molecular to whole plant responses. *Photosynthetica* **41,** 9–20.

Vargas G.G. & Cordero S.R.A. (2013) Photosynthetic responses to temperature of two tropical rainforest tree species from Costa Rica. *Trees* **27,** 1261–1270.

Vautard R., Yiou P., D'Andrea F., de Noblet N., Viovy N., Cassou C., . . . Fan Y. (2007) Summertime European heat and drought waves induced by winter-time Mediterranean rainfall deficit. *Geophysical Research Letters* **34,** L07711.

Vener A.V., Harms A., Sussman M.R. & Vierstra R.D. (2001) Mass spectrometric resolution of reversible protein phosphorylation in photosynthetic membranes of *Arabidopsis thaliana*. *The Journal of Biological Chemistry* **276,** 6959–6966.

Wahid A., Gelani S., Ashraf M. & Foolad M.R. (2007) Heat tolerance in plants: an overview. *Environmental and Experimental Botany* **61,** 199–223.

Walker B., Ariza L.S., Kaines S., Badger M.R. & Cousins A.B. (2013) Temperature response of *in vivo* Rubisco kinetics and mesophyll conductance in *Arabidopsis thaliana*: comparisons to *Nicotiana tabacum*. *Plant, Cell & Environment* **36,** 2108–2119.

Wang D., Heckathorn S.A., Mainali K. & Hamilton E.W. (2008) Effects of N on plant response to heat-wave: a field study with prairie vegetation. *Journal of Integrative Plant Biology* **50,** 1416–1425.

Wang L., Wang B.-L., Wei Z.-Z., Du Q.-Z., Zhang D.-Q. & Li B.-L. (2012) Development of 35 microsatellite markers from heat stress transcription factors in *Populus simonii* (Salicaceae). *American Journal of Botany* **99,** E357–E361.

Wang W., Vinocur B. & Altman A. (2003) Plant responses to drought, salinity and extreme temperatures: towards genetic engineering for stress tolerance. *Planta* **218,** 1–14.

Wang Y.C., Qu G.Z., Li H.Y., Wu Y.J., Wang C., Liu G.F. & Yang C.P. (2010) Enhanced salt tolerance of transgenic poplar plants expressing a manganese superoxide dismutase from *Tamarix androssowii*. *Molecular Biology Reports* **37,** 1119–1124.

Way D.A. & Sage R.F. (2008) Thermal acclimation of photosynthesis in black spruce [*Picea mariana* (Mill.) BSP]. *Plant, Cell & Environment* **31,** 1250–1262.

Wei H., Liu J., Wang Y., Huang N., Zhang X., Wang L., . . . Zhong X. (2013) A dominant major locus in chromosome 9 of rice (*Oryza sativa* L.) confers tolerance to 48 degrees C high temperature at seedling stage. *The Journal of Heredity* **104,** 287–294.

Wells O.O. (1983) Southwide pine seed source study: loblolly pine (*Pinus taeda*) at 25 years. *Southern Journal of Applied Forestry* **7,** 63–71.

Weston D.J. & Bauerle W.L. (2007) Inhibition and acclimation of C₃ photosynthesis to moderate heat: a perspective from thermally contrasting genotypes of *Acer rubrum* (red maple). *Tree Physiology* **27,** 1083–1092.

Wisniewski M., Sauter J.J., Fuchigami L. & Stepien V. (1997) Effects of near-lethal heat stress on bud break, heat-shock proteins and ubiquitin in dormant poplar (*Populus nigra Charkowiensis × P. nigra incrassata*). *Tree Physiology* **17,** 453–460.

Xue D.-W., Jiang H., Hu J., Zhang X.-Q., Guo L.-B., Zeng D.-L., . . . Qian Q. (2012) Characterization of physiological response and identification of associated genes under heat stress in rice seedlings. *Plant Physiology and Biochemistry* **61,** 46–53.

Yao Y., Luo Y., Huang J. & Zhao Z. (2013) Comparison of monthly temperature extremes simulated by CMIP3 and CMIP5 models. *Journal of Climate* **26,** 7692–7707.

Yordanov I. (1992) Response of photosynthetic apparatus to temperature stress and molecular mechanisms of its adaptations. *Photosynthetica* **26,** 517–531.

Zweifel R., Zimmermann L., Zeugin F. & Newbery D.M. (2006) Intra-annual radial growth and water relations of trees: implications towards a growth mechanism. *Journal of Experimental Botany* **57,** 1445–1459.

Zweifel R., Steppe K. & Sterck F.J. (2007) Stomatal regulation by microclimate and tree water relations: interpreting ecophysiological field data with a hydraulic plant model. *Journal of Experimental Botany* **58,** 2113–2131.