Commentary

A hot and dry future: warming effects on boreal tree drought tolerance

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By 2100, climate change is predicted to warm high-latitude summers by 3–8 °C (ACIA 2005, Christensen et al. 2007). High temperatures will become more common in the boreal region and, in the absence of significantly increased precipitation, drought frequency and intensity will increase. Much of the North American boreal consists of forests dominated by black spruce (*Picea mariana* (Mill.) B.S.P.), a major timber crop that dominates frequently flooded soils, but has shallow roots (<20 cm deep) and therefore experiences drought stress in the absence of frequent rain (Viereck and Johnston 1990). Black spruce growth is negatively impacted by heat, due in part to rapid soil drying from greater evapotranspiration (ACIA 2005, Angert et al. 2005). Increased temperatures and drought potentially threaten the dominance of black spruce in the boreal forest, and have been identified as major causes for the sharp increases in mortality rate of boreal tree species, including black spruce, that have occurred in North America since the 1960s (Peng et al. 2011).

Experiments investigating the response of black spruce to warming and drought provide insight into the mechanisms that underlie the reduced growth and increased mortality seen in this species in the field. Growth at elevated temperatures reduces the carbon balance of black spruce seedlings, which in turn limits growth, as well as reducing the root to shoot ratio, which may make trees more prone to drought stress (Way and Sage 2008a, 2008b, Way et al. 2011). Stomatal closure appears to be the main mechanism by which black spruce avoids lethal water stress (Blake and Li 2003), with conductance declining at relatively high leaf water potentials (−0.25 MPa) and complete closure observed below −1.5 MPa (Grossnickle and Blake 1986, Eastman and Camm 1995, Dang

et al. 1997). However, by reducing stomatal conductance to prevent water loss, seedlings substantially reduce their ability to assimilate carbon, which may further exacerbate heat-related growth declines.

In this issue of *Tree Physiology*, Balducci et al. (2013) look at how water stress affects xylem formation, gas exchange and survival in black spruce seedlings grown at elevated temperatures of +2 °C and +5 °C above the ambient. While a 32-day drought reduced stomatal conductance and photosynthesis, there was little evidence for an effect of temperature on these leaf-level parameters, which rapidly recovered fully after rewatering. But warming did alter the impact of drought on seedling survival: over 12% of the drought-stressed spruce died in the warmest treatment, compared with 2% in the ambient temperature environment. The drought also affected xylem formation over the season. When water was resupplied to the drought-stressed, ambient temperature-grown spruce had similar cambial activity to the ambient temperature, watered seedlings after 2 weeks of recovery. But growth at elevated temperatures delayed recovery of cambial activity for an extra 2 weeks, and reduced wood density. Overall, the effect of drought was much stronger than that of increased growth temperatures on the parameters examined, although the delayed recovery of growth and increased mortality from water stress at elevated temperatures implies that seedlings that develop in a warmer climate may be more vulnerable to drought.

While the cause of increased drought-related mortality in warm-grown spruce in Balducci et al. (2013) is unknown, it echoes recent trends seen in forest stands (Peng et al. 2011) and lends support to the concept that combined increases in heat and drought are responsible for rising mortality in boreal

species. However, there is some good news as well. The similarity in the development of and recovery from leaf-level stress across growth temperatures seen in Balducci et al. (2013) is encouraging, as it indicates that warming alone may not exacerbate water stress-induced damage to photosynthesis and leaf function. In fact, there are reasons to think that warming may even increase drought tolerance of photosynthesis. Exposure to high temperatures often increases the heat stability of photosystem II (PSII; Havaux 1993), through mechanisms such as chaperone protein expression (i.e., heat shock proteins; Vierling 1991), or changes in thylakoid membrane composition (Sharkey 2005). Water stress can induce similar protective mechanisms, such as an increased degree of saturation in thylakoid membrane lipids (Ferrari-Iliou et al. 1984, Prabha et al. 1985) and heat-shock protein expression (Ristic et al. 1998), so that drought increases the thermal stability of PSII (Havaux 1992, Ladjal et al. 2000). If the interaction between water stress and heat stress is reciprocal, and is due to similar physiological mechanisms, exposure to high temperatures should lead to greater drought tolerance (e.g., Yordanov et al. 1999).

Could warming help mitigate the effect of drought stress in black spruce needles? Figure 1 shows the effect of an elevated growth temperature treatment of 8 °C on the response of black spruce seedlings to drought (see figure legend for experimental details). In the drought treatment, leaf relative water content (RWC) declined linearly with shoot pre-dawn water potential (ψ_{PD}); there was no difference in the response of RWC to ψ_{PD} between growth temperatures (Figure 1A). But high temperature-grown trees maintained a higher maximum yield of PSII (measured as the dark-adapted ratio of variable to maximal chlorophyll fluorescence (F_v/F_m)) for a given ψ_{PD} in the drought treatment than trees from ambient temperatures (Figure 1B). Since F_v/F_m is relatively insensitive to drought and only declines when water stress becomes severe (Epron and Dryer 1992, Havaux 1992, Eastman and Camm 1995, Iijima et al. 2006, Ditmarova et al. 2010), this implies that the photosynthetic apparatus of leaves from elevated temperatures was more tolerant of low ψ_{PD} than trees grown at current temperatures. By the time declines in F_v/F_m were detected, about 50% of the needles on a seedling were brown, verifying that trees were extremely stressed. This concurs with Ditmarova et al. (2010), who also found that F_v/F_m did not decline in water-stressed spruce until just before the seedlings died.

With climate warming, it is probable that intense drought will increase in the boreal forest, if for no other reason than accelerated evapotranspiration, and temperatures equivalent to the warming used by Balducci et al. (2013) will become common (ACIA 2005, Christensen et al. 2007). These higher temperatures may enhance leaf-level drought tolerance in black spruce, reducing the ψ_{PD} where severe photosynthetic stress occurs (Figure 1B), and they do not appear to aggravate drought-induced damage of leaf function (Balducci et al. 2013). This
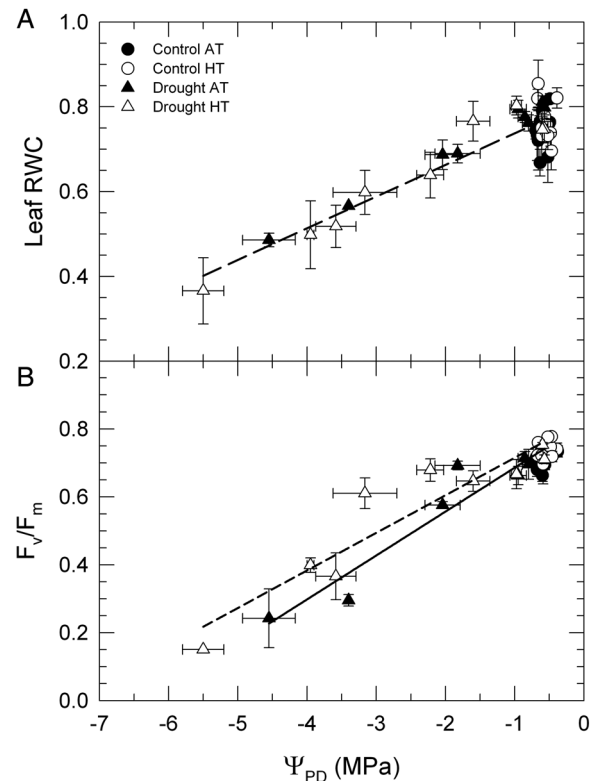

Figure 1. Effects of elevated growth temperatures on leaf physiological parameters under drought stress. A total of 350 1-year old black spruce seedlings were grown for 3 months in 3.8-l pots filled with peat moss in each of two climate-controlled greenhouses with vapour pressure deficits of 1.4–1.7 kPa. The ambient-temperature (AT) room was set to 22/16 °C day/night temperatures to mimic conditions from the seed provenance site; the high-temperature (HT) room was set to 30/22 °C. Water was then withheld from half of the seedlings in each room (drought treatment) for 40 days; the other half continued to receive ample water. Drought tolerance of photosynthesis was measured on six seedlings per treatment per day using the F_v/F_m on dark-adapted needles (PAM-101, Walz, Effeltrich, Germany). Immediately afterward, whole shoot ψ_{PD} was measured with a pressure chamber (PMS Instruments, Corvallis, OR, USA) and the leaf RWC was assessed. Figures show the relationship between ψ_{PD} and (A) RWC, and (B) F_v/F_m, in well-watered (circles) and drought-treated (triangles) spruce grown at AT (filled symbols and solid lines) or HT (open symbols and dashed lines). Means ± SE, $n = 2$–6. In (A), no difference between treatments ($P = 0.18$), long-dashed line fit to all data: $r^2 = 0.84$; (B) significant difference between growth temperatures ($P < 0.0001$), solid line fit to AT: $r^2 = 0.93$; short-dashed line fit to HT: $r^2 = 0.87$.

could be significant, because drought in the boreal is often short-term in duration, developing rapidly in the gap between summer rains (Larsen 1980). More studies on how drought stress and temperature interact are needed to improve our ability to predict how elevated growth temperatures and drought will affect ecologically and economically important species such as black spruce. Also, multi-factor experiments that examine the combined effects of rising temperatures and CO_2 concentrations on drought stress in trees, such as recent work by Duan et al. (2013) and Lewis et al. (2013), are key for making realistic predictions of tree responses to future climate scenarios. Given

the recent increase in tree mortality due to climate-related drought stress (Adams et al. 2010, Allen et al. 2010), particularly in unmanaged boreal forest stands (Peng et al. 2011), determining how key tree species will cope with drought in the future is a critically important research question.

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