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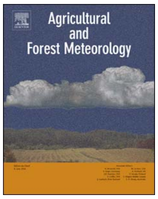

Growth and cold hardening of European aspen seedlings in response to an altered temperature and soil moisture regime

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ABSTRACT

During the autumn, plants undergo a physiological process of cold hardening to limit damage caused by the low temperatures of winter. Under a warming climate, plants may be less cold hardened and hence more susceptible to the effects of a sudden temperature drop. During the growth season of 2010–2011, growth and cold hardening of European aspen (*Populus tremula* L.) seedlings from native wild populations were examined under ambient and projected climate scenarios in greenhouses at the Haapastensyrjä research station in Southern Finland. Using locally obtained seedlings, we manipulated temperature and soil moisture during the normal growth period and then subjected them to an artificial freezing treatment during September–November 2010. At the end of the experiment, we determined seedling height, survival and the extent of stem damage, and analysed their variation with mixed effect models.

Among the treatments tested, temperature was the main factor affecting survival, cold hardening, and frost damage to seedlings. The higher temperature (4 °C increase) of the 2100 future climate regime was associated with a 35% decrease in seedling survival (from 66 to 31%) during the growing period. Increased irrigation had a positive, but considerably weaker effect on seedling survival (improved survival by ca. 8%). Height of seedlings after the first growth season was enhanced by increased soil moisture and temperature, but these effects were negated the following spring by increased frost damage caused by warmer growth conditions. Although cold hardiness increased as the season progressed, increase of temperature by 1 and 4 °C severely diminished it, and survival after the freezing dropped from 55% (control) to 48% and 14%, while stem damage increased from 58% (control) to 90% and 96%, respectively. These results suggest that regeneration of north European aspen might become burdened in a warmer climate. Although survival was clearly affected, several seedlings grown under the future climate regimes survived freezing and overwintered with negligible damage, suggesting an adaptive capacity of the local population. The intraspecific competition that occurred as a side effect of the experimental setup also affected cold hardening, suggesting that stand structure might be managed to improve the resilience of aspen to frost damage.

1. Introduction

Climate is one of the main factors that determines the distribution of tree species and forest productivity (Hickler et al., 2012; Lindner et al., 2010). Climatic changes will affect forest ecosystems with ecological and economic consequences (Hanewinkel et al., 2012). While the shifts in species composition appear inevitable, the effect of a changing climate on forest productivity may vary on a regional basis and according to the resident flora (Lindner et al., 2010). In Central Europe, warming will likely decrease forest productivity due to the increased incidence of drought and pests (Bolte et al., 2009; Maracci et al., 2005). At high northern latitudes, warmer temperatures and elevated atmospheric CO_2 could increase the productivity of boreal forests (Battipaglia et al., 2013; Bergh et al., 2003; Kellomäki et al., 1997), but this effect could likely be limited by increased evapotranspiration (Trajkovic et al., 2005; Wilmking et al., 2004) and the potential damage caused by water deficit and severe frosts (Rixen et al., 2012; Schreiber et al., 2013; Weng and Parker, 2008). Compared to conifers, broadleaves in Northern Europe are expected to benefit from climate change and increase in economic importance (Drobyshev et al., 2012; Kellomäki and Kolström, 1992; Reich and Oleksyn, 2008).

Although climatic and edaphic factors determine productivity of the forest ecosystems (Pastor and Post, 1985), the early development, establishment, and growth rate of seedlings is a critical period with

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profound effects on the composition and performance of the stand (Urban et al., 1993; Stott and Loehle, 1998). Given that height increment is influenced by climate (Jansons et al., 2014), conditions experienced during the first few years after planting may affect inter-species competition and hence structure of the stand (plantation). Thus, stand composition might be influenced by frost damage to shoots (Schreiber et al., 2013; Hänninen, 2006; Pearce, 2001), especially as a consequence of rapid shifts in temperature (Rixen et al., 2012). To minimize such damage, trees have evolved physiological mechanisms, through which they become cold hardened (Beck et al., 2004; Welling et al., 2002), when cell water content is reduced (Welling et al., 2002) and the concentration of antifreeze compounds is increased (Cox and Stushnoff, 2001). The timing and efficiency of cold hardening varies among species and regions, and this accounts for the differences observed in susceptibility to frost and cold (Schreiber et al., 2013; Weng and Parker, 2008). In autumn, cold hardening is induced by a shortening photoperiod and cessation of growth that proceeds gradually, while the occurrence of frosts accelerate the process (Beck et al., 2004; Welling et al., 2002). Warmer periods in autumn and winter may delay or otherwise disrupt cold hardening (Anisko et al., 1994; Saxe et al., 2001; Welling et al., 2002), and such events subject trees to frost damage wrought by rapid temperature shifts (Rixen et al., 2012; Schreiber et al., 2013), which are becoming more frequent (IPCC, 2013; Marino et al., 2011). Cold hardening can also be influenced by water deficit affecting tree vigour (Siminovitch and Cloutier, 1983) and development of defence reaction (Welling et al., 2002) via alterations of nutrient reserves and formation of antifreeze compounds (Cox and Stushnoff, 2001; Ögren et al., 1997) or changes in physiological processes (Rixen et al., 2012).

European aspen (*Populus tremula* L.) is a fast-growing species with a short rotation that performs well in commercial plantations (Tullus et al., 2012). In Northern Europe, aspen is a softwood grown for bioenergy (Tullus et al., 2012) and the production of high-quality paper (Ranua, 2002). Under future climate scenarios, aspen is expected to increase productivity and become a more attractive species to Fennoscandian foresters (Drobyshev et al., 2012; Jansons et al., 2014; Lasch et al., 2010). As such, information on its development under a warmer and wetter or drier climate would form the basis of sustainable forest management practices.

The aim of this study was to evaluate the growth, survival, and development of cold hardiness in first-year aspen seedlings subjected to current and future (i.e., elevated temperature and altered soil moisture) climate regimes. We hypothesized that elevated temperature increases seedling growth, but reduces cold hardiness and, consequently, increases the risk of frost damage. We also assumed that increased soil moisture would improve growth and plantlet vigour, hence cold hardiness.

2. Material and methods

2.1. Experimental design

The experiment was conducted at the Haapastensyrjä research station of the Natural Resources Institute Finland in southwest Finland (60°37′N, 24°25′E). Climate at the study site was mild; during 1980–2009, the mean annual temperature was +4.6 °C and the mean annual precipitation was 590 mm (data from Haapastensyrjä meteorological station). During the study period, the mean monthly temperature ranged from +21.6 °C in July 2010 to −12.1 °C in February 2011 (Fig. 1A). Although during most of the period, temperature conditions were similar to the long-term estimates, November and December 2010, and February 2011 were colder (by ca. 2, 6 and 5.5 °C, respectively), and July 2010 was ca. 5 °C warmer compared to the 30-year mean. An increased range of daily temperature was observed in May 2010, August 2010, and February 2011. The frost-free period in 2010 lasted from May 5 to October 1. Mean temperature during that period was +13.2 °C and the temperature sum above +5 °C was 1487 °C.

Growth and freezing experiments were conducted in 2010 and the results were determined in spring 2011 (Fig. 2). Seed material was obtained from the controlled full-sib crossing of four mature female and three male aspens (plus-trees) growing in local wild stands distributed 60°37–38′N and 24°25–27′E. Crossing was done on covered cut branches in March 12 2010 (Stanton and Villar, 1996). Initially, about 10,000 seeds per full-sib family were sown in vefi-boxes on April 12 and grown for five weeks in a heated greenhouse maintained 4 °C above ambient, and with abundant moisture to ensure germination and early development. The most vital seedlings were then transplanted into Lännen B15 boxes with 48 (8 × 6) containers with 644 cm^3 volume (9 cm spacing between planting places), filled with pre-fertilized peat "NPK 16-4-17". Groups of four seedlings (four in a row) belonging to each of 12 full-sib families were randomly planted within 13 boxes, replicated five times. Boxes were randomly placed on movable growing tables in the greenhouse. In total, 65 boxes (13 boxes in five replications for each treatment combination) were planted with 3120 seedlings (48 seedlings per box). During the experimental period, boxes and tables were circulated weekly to minimize edge effects. No additional fertilizer was supplied during the experiment.

To examine the effects of future climate scenarios on the early growth of aspen, seedlings were subjected to a control and four different combinations of temperature and soil moisture. Each combination of treatments and control were applied in a separate isolated compartment of the greenhouse (one per combination). The temperature regime was altered according to the A1 B scenario for near (2030) and distant (2100) future climate projections for Finland (Jylhä et al., 2009). For the 2030 and 2100 scenarios, temperature was maintained in the real time regime (i.e. 24/7) at ca. 1 and 4 °C above ambient, respectively, throughout the entire period of the experiment (reaching temperature sums of 1759 and 2381 °C, respectively; Fig. 1B) by an automatic conditioning system. Yet it prevented temperature from falling below ca. −7 °C. To assess the effect of changes in the amount of precipitation, each temperature treatment was combined with two soil moisture regimes of 1.6 mm m^{-2} day^{-1} (dry) and 3.1 mm m^{-2} day^{-1} (wet) of irrigation, which are above and below the long-term mean precipitation of the vegetation period in the study region (ca. 2.4 mm m^{-2} day^{-1}). In all cases, irrigation was supplied automatically (by sprinklers) on Mondays, Wednesdays, and Fridays between 10:00 and 11:00 when ambient temperature was > 0 °C. The control conditions were: unaltered ambient temperature and irrigation of 2.4 mm m^{-2} day^{-1} (the long-term mean). The estimated reference evapotranspiration (Trajkovic, 2005) during the growing period was ca. 1.5, 1.7, and 1.8 mm m^{-2} day^{-1} when temperature was not altered, and increased by 1 and 4 °C, respectively. The photoperiod was not altered, i.e. all seedlings were grown under the local natural light climate. Inventory of the experiment was conducted on September 6 2010.

Development of cold hardiness was evaluated during a 13-week period from September 7 (DOY = 249) to November 30 (DOY = 333) 2010. Every Tuesday within that period, a set of five boxes (one box from each of four treatment combination and the control) was transferred to the freezing chamber. Prior to the treatment, seedling height (height of the uppermost terminal bud) from the soil level was measured to the nearest mm. The freezing treatment consisted of a gradual decrease of temperature by 3 °C/h until reaching −10 °C, where seedlings were maintained for two hours during the night before the temperature was allowed to gradually (by 1 °C/h) return to ambient. Seedlings were put on a thermo-isolated surface and peat-filled boxes were placed around the experimental material to limit edge effects and to protect the root system, hence the soil was not frozen. Following treatment, boxes were returned to their original locations in the greenhouse. All seedlings received the treatment by December 1 2010, after that, all material was transferred to a covered plastic greenhouse where it received natural (unaltered) photoperiod for the rest of the dormant period. The temperature was altered partially, as