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Research paper

Warming and elevated CO_2 alter tamarack C fluxes, growth and mortality: evidence for heat stress-related C starvation in the absence of water stress

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Climate warming is increasing the frequency of climate-induced tree mortality events. While drought combined with heat is considered the primary cause of this mortality, little is known about whether moderately high temperatures alone can induce mortality, or whether rising CO_2 would prevent mortality at high growth temperatures. We grew tamarack (*Larix laricina*) under ambient (400 p.p.m.) and elevated (750 p.p.m.) CO_2 concentrations combined with ambient, ambient +4 °C and ambient +8 °C growth temperatures to investigate whether high growth temperatures lead to carbon (C) limitations and mortality. Growth at +8 °C led to 40% mortality in the ambient CO_2 (8TAC) treatment, but no mortality in the elevated CO_2 treatment. Thermal acclimation of respiration led to similar leaf C balances across the warming treatments, despite a lack of photosynthetic acclimation. Photosynthesis was stimulated under elevated CO_2, increasing seedling growth, but not leaf C concentrations. However, growth and foliar C concentrations were lowest in the +8 °C treatments, even with elevated CO_2. Dying 8TAC seedlings had lower needle C concentrations and lower ratios of photosynthesis to respiration than healthy 8TAC seedlings, indicating that C limitations were likely the cause of seedling mortality under high growth temperatures.

Keywords**:** acclimation, carbohydrates, climate change, J_{max}, non-structural carbohydrates, survival, V_{cmax}.

Introduction

With atmospheric CO_2 concentrations increasing at ~2.0 p.p.m. per year, global temperatures are projected to increase 2.0–4.5 °C by the year 2100 (Cramer et al. 2014). Warming is most extreme in high northern latitudes, which could experience temperature increases of more than 8 °C by the end of the century (Serreze et al. 2000, Oppenheimer et al. 2014). These increased temperatures and atmospheric CO_2 concentrations have already intensified climatic stress on vegetation, leading to greater tree mortality globally. Since 1970, there have been over 88 documented large-scale tree mortality events, and tree mortality has been identified as a major contributor to future vegetation shifts (Allen et al. 2010, 2015). Many forest mortality events have been linked to global change-related droughts, where high temperatures and drought occur simultaneously. Tree die-offs have therefore been largely attributed to water stress causing either hydraulic failure (i.e., catastrophic xylem cavitation) or carbon (C) starvation (where low stomatal conductance suppresses photosynthetic C gains, but respiratory C losses remain high) (Allen et al. 2010, Mcdowell and Sevanto 2010, Anderegg et al. 2012, Sevanto et al. 2014, Adams et al. 2017, Hartmann et al. 2018).

Tree die-offs are already proving to be detrimental to the boreal biome. In high latitude regions in North America, boreal tree species had mortality rate increases of up to 4.7% per year between 1963 and 2008 (Peng et al. 2011), likely due to climate change. But while warming was positively correlated with mortality rates for all plots in Peng et al. (2011), water