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Hydrologic position mediates sensitivity of tree growth to climate: Groundwater subsidies provide a thermal buffer effect in wetlands

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ABSTRACT

We evaluated the effects of hydrologic setting on the growth sensitivity of two conifer species to recent atmospheric climatic variability and change in a region experiencing a warming (annual Tmin: 0.07 °C/decade) and wetting trend (total annual PPT 9.8 mm/decade; 1911–2012). Tree-ring chronologies were constructed for the boreal disjunct balsam fir (*Abies balsamea*; n = 72; 1916–2012) and range-centered eastern white pine (*Pinus strobus*; n = 84; 1707–2012) at three forested, groundwater-fed wetlands (fens) and their neighboring uplands in New York State, USA. Soil temperature monitoring in 2010 confirmed that upland soils were significantly warmer than fen soils during the spring and summer months (11.5–13.9 °C; $p < 0.05$). Climate-growth relationships for *Abies balsamea* varied substantially based on hydrologic setting and season. Compared with a remnant upland population that showed an increasingly negative sensitivity to warm summer temperatures over time *A. balsamea* positioned in fens were less sensitive to recent warming. While atmospheric climate-growth relationships were more consistent across hydrologic settings for *Pinus strobus*, we still observed qualitatively different responses to atmospheric climate variables between fen and upland populations. Overall, the climate-growth relationships identified in this study suggest that relative to trees growing in mesic upland soils, growth sensitivity to warm ambient climate in summer is ameliorated by groundwater inputs. The climate modulating effects of groundwater on tree-growth observed in our study suggests that for temperate and boreal regions where fens are abundant further consideration of groundwater influences on climate-growth relationships is warranted.

1. Introduction

Global changes in temperature and precipitation have been linked to shifts in species distributions, altered patterns of forest productivity, and degradation of natural resources (e.g., Walther et al., 2002; Parmesan and Yohe, 2003; Iverson et al., 2008; Allen et al., 2010). Ecologists however, have long recognized the control topography – through its regulation of moisture and temperature balance – exerts over plant growth and forest species composition in complex terrain (e.g., Whittaker, 1956; Dobrowski, 2010). Variation in topographic setting (e.g., slope position, exposure, aspect) produces steep environmental gradients creating microclimates that diverge substantially from prevailing regional climate conditions (e.g., Hampe and Jump, 2011; Ashcroft and Gollan, 2013). Localized variation in climate (microclimate), particularly for soil moisture, plays a well-recognized role in shaping plant growth and community assembly in a changing climate (e.g., Daubenmire, 1974; Dobrowski, 2010; Anning et al., 2013). However, in certain hydrologic settings still relatively little is known about climate-growth relationships (e.g., Phipps, 1982; Edvardsson et al., 2015).

For instance, topographic relief and carbonate geology in glaciated regions often enable the flow of cool, mineral-rich groundwater to wetlands known as fens, which have historically buffered boreal populations from gradual changes in climate (Forsythe, 1974; Frederick, 1974; Nekola, 1999; Godwin et al., 2002; Hajek et al., 2009). While fens comprise a small percentage of the landscape in the temperate northeastern USA (Bedford and Godwin, 2003), forested wetlands influenced by groundwater are more common in boreal regions of North America and Eurasia where the diversity of hydrologic settings increases substantially (e.g., Vitt et al., 1995). Relative to other wetland types (e.g., marshes, bogs) where moisture availability is more closely linked to shorter-term fluctuations in precipitation and surface runoff,

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water levels in fens are more stable in the summer months (Godwin et al., 2002). The extent to which groundwater discharge alters climate-growth relationships for plants is poorly understood (Raney et al., 2014; Fernández-Pascual et al., 2015).

The northeastern USA has been experiencing a well-documented warming and wetting trend, with increasingly episodic precipitation events (e.g., Hayhoe et al., 2007; Bishop and Pederson, 2015). Global circulation models forecast continued warming and a shift to overall drier conditions with fewer, larger magnitude rainfall events in the Northeast, and less snowfall (IPCC, 2014). Such climate forecasts suggest that efforts are needed to improve our understanding of biotic responses to climate from understudied hydrologic settings such as forested fens. Dendroclimatology gives a long-term perspective on inter-annual woody plant growth responses to both site factors and changes in climate (e.g., Fritts, 1966, 1976; Tardif and Bergeron, 1997; Rodríguez-González et al., 2010), and this tool may help to clarify plant responses to climate change from unique hydrologic settings such as fens.

To quantify the effects of hydrologic setting on tree growth under changing climate, we studied microclimate variability and climatic controls of tree growth in the northeastern United States in two contrasting ecological settings: forested groundwater fed wetlands (fens) and nearby mesic uplands at a comparable elevation. We developed tree-ring chronologies from co-occurring tree species with primarily boreal (balsam fir – *Abies balsamea*) and temperate distributions (eastern white pine – *Pinus strobus*) to learn how climate-growth relationships might be influenced by differences in hydrologic setting (cooler, wetter fens and warmer, mesic uplands). We hypothesized that climate-growth relationships would vary by hydrologic setting and by species with respect to their range position (e.g., boreal disjunct populations of balsam fir vs. range-centered populations of white pine). We anticipated that tree growth in fens would be buffered from periods of higher summer air temperatures and those effects would be more pronounced for boreal species occurring near their climatic range limits (e.g., *Abies balsamea*) and less so for temperate species occurring near the center of their geographical range (e.g., *Pinus strobus*).

2. Materials and methods

2.1. Study region

Our study is located at the main southern limit of fens in the northeastern USA in central New York State, where fens often support disjunct populations of boreal species (Forrester et al., 2005; Bedford and Godwin, 2003; Raney et al., 2014). This hydrologically diverse, glaciated region is characterized by cold snowy winters and warm wet summers (Riddle et al., 2014). Cover of boreal species declines rapidly as one transitions from fens to surrounding mesic upland soils, where forests are dominated by temperate northern hardwood species (Raney et al., 2014; Edinger et al., 2014). Between 1981 and 2010, annual air temperatures averaged 7.2 °C, with January minimums and July maximum averaging −11.4 °C and 25.7 °C, respectively. Total annual precipitation averaged 1088.3 mm and winter precipitation typically occurred as snow (Daly et al., 2008). Recent decades have experienced seasonally variable warming, increased total precipitation, and extended growing season length (Hayhoe et al., 2007; DeGaetano, 2009; Beier et al., 2012; Seager et al., 2012; Pederson et al., 2013). These factors make the northeastern US (and central New York) well suited for evaluating changes in tree-growth patterns under variable and changing climate while providing an opportunity to examine the effects of hydrological setting on tree-growth for co-occurring boreal and temperate species.

2.2. Study species

Balsam fir (*Abies balsamea* (L.) Mill.) approaches its southern range limits in New York State (NYS) where it occurs in cold, groundwater-fed fens disjunctly from its primarily boreal distribution (Little, 1971; Iverson et al., 2008; NYNHP, 2008). *Abies balsamea* is a relatively short-lived, medium sized (20–25 m tall), shade-tolerant, evergreen conifer species that occurs in habitats ranging from mountain ridges to wetlands in northern portions of North America (Wendel and Smith, 1990). *Abies balsamea* is very infrequent outside of fens in temperate portions of NYS (see Iverson et al., 2008), but the species is locally abundant with strong recruitment in groundwater-supported fens (Raney et al., 2014; Edinger et al., 2014).

A second evergreen conifer species included in our study was eastern white pine (*Pinus strobus* L.) – a temperate species occurring near the center of its overall geographic range in NYS. *Pinus strobus* is a moderately long-lived, large (40–50 m tall) species that occurs in both fens and uplands (Iverson et al., 2008; Edinger et al., 2014). *Pinus strobus* is intermediately shade-tolerant and although it can establish in relatively dry conditions, it responds well to moisture (Dovciak et al., 2003, 2005). *Pinus strobus* has greater heat tolerance than balsam fir with populations occurring naturally as far south as Alabama and as far north as Newfoundland (Little, 1971).

2.3. Study sites

Following a review of plant community occurrence records compiled from decades of field work in the region (NYNHP, 2008), we selected three accessible sites for sample collection where *Abies balsamea* and *Pinus strobus* co-occurred. We collected tree-ring (increment core) samples from closed canopy stands at Nelson Swamp, Beaver Creek, and Summit Lake Swamp in both mesic upland environments where soil moisture content reflected recent ambient conditions and in fens. For these and other fens in the region, local moisture balance is subsidized by groundwater discharge and to a lesser degree by surface water runoff. We focused our attention on hydrologic drivers of climate-growth relationships, by selecting drier upland sampling locations occurring within 600 m of fen populations, and by limiting elevation differences in between drier and wetter areas (Table 1; Fig. 1). In a companion study, Raney et al. (2014) over a four month monitoring period in 2009 found negligible differences in air temperature regimes between the fen and upland sample locations included in the current study.

While *A. balsamea* was abundant in fen environments and was sampled at all three of our study sites, this species was very infrequent on mesic soils lacking groundwater inputs in the study region. A relatively young upland population of *Abies balsamea* at the Beaver Creek site represented the lone population growing on mesic soils in the region and was sampled in its entirety (Fig. 1). *Pinus strobus* however, was abundant on both drier and fen soils and was sampled from both environments at all of our study sites. A timber harvest conducted at Nelson Swamp provided the opportunity to collect full cross-sections of old-growth *P. strobus* from an upland location, but resulted in fewer trees available for increment coring following 1995. Table 1 differentiates between the two sampling efforts for *Pinus strobus* at Nelson Swamp: Upland A denotes harvested crossections and Upland B denotes increment core samples collected in 2009 from trees that remained after the 1995 tree-harvest.

2.4. Sample collection and preparation

To maximize chronology length we preferentially selected older-appearing trees (i.e., taller trees with weathered, rough tex-