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The Enigma Of Pitch Pine Survival In Fire Absent Populations At Acadia National Park

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**ABSTRACT**

The health of fragile tree species is a concern in forests around the world. In the Northeastern United States, the absence of natural fire is thought to have a negative impact on the globally rare species pitch pine (*Pinus rigida* Miller). This is because fire is considered essential for pitch pine reproduction and niche preservation. In the northeastern extreme of pitch pine’s range, a stand-replacing conflagration enveloped a portion of Acadia National Park (ME, USA) in 1947 but there has been no recurrence since then. Within populations on the eastern side of Mt. Desert island in the Park we examined the enigma of pitch pine proclivities amidst the demise of natural fire using data from forty locations in and outside of the 1947 fire footprint along an altitudinal (12 to 404 m) gradient. We found photosynthetic intrinsic water use efficiency, a key metric of physiological performance, was significantly (more negative) higher (*P*=0.004) at an unburned upper elevation, St. Sauveur trail than trees at other locations. At previously burned South Cadillac trail, individuals along this path were shorter (*P*=0.031), had a narrower canopy (*P*=0.035), and a smaller dbh (*P*=0.001) than trees at other, sea level, sites. These results are likely due to the fact that pitch pine at lower elevation have less need to compensate for moisture loss, wind and cooler temperature effects and instead push photosynthetic growth supported by significantly more plentiful foliar minerals Ca, P, K, Al and Zn (on average *P*=<0.01). Unburned sites with higher mineral availability and overall lower elevation were significantly better at soil moisture retention (*P*=<0.001). In summary, we found trees with a one-hundred-year fire absence history allocated more energy to growth than stress resistance amidst forecasts for worsening biotic and abiotic pressures. Our analysis has the capacity to explain at least some of the reasons for the survival enigma as well as provide data to inform forest management decisions about soil and foliar mechanics which differ between burned and unburned populations.

**INTRODUCTION**

Fire is a disturbance that can drastically alter the landscape of a forest ecosystem. Indeed, so can its absence. In the Northeastern USA, and in the state of Maine in particular (Miller et al 2017), many species rely on natural fire to stimulate reproduction and preserve population niches (Patterson Saunders and Horton 1983). In fact, a previous study suggested that wildfire is required every six to twenty-five years to perpetuate and rejuvenate pitch pine populations (Jordan et al 2003). Several species in fire-prone ecosystems, like pitch pine (*Pinus rigida* Miller), expend energy on fire avoidance and tolerance based on previous history of fire frequency. Yet, recently, in the Northeastern USA, anthropogenic activities have suppressed fire frequency. As a result, fire adaptations such as cone serotiny (Givnish 1981), thick bark and basal re-sprouting (Renninger et al 2013) are disappearing in pitch pine colonies due to a change in fire regimes (Jordan et al 2003). From that perspective, adaptations (Little 1953) may be wasted investments, potentially causing fire-adapted pitch pine to be outcompeted by other plants in the community (Buma et al 2013).

For some time, fire suppression, due to concerns for nearby human populations, has been offset by selective, prescriptive fire intervention to reduce fuel, reduce evergreen competition and open canopies (Neill et al 2007). On Mt. Desert island at Acadia National Park in Maine, prescriptive fire is rarely used and, as a result, ongoing fire suppression creates a situation where both naturally burned and unburned communities both exist in a harsh, quite varied, topography. Where fire ecology and topographic variants intersect, it is unknown whether long term benefits found in burned preserves outlast those in populations untouched by fire. The uniqueness of the environment on Mt. Desert provides an ideal testbed to understand pitch pine-fire dynamics and address important conservation questions (Star et al 2015).

Pitch pine fragility is more complex than reducing an explanation of community response to a lack of fire. Day et al (2005) assert pitch pines are poised to decline at a more rapid pace due as much to higher summer and winter temperatures and moister autumns, as stand-replacing disturbances like fire. These concerns are shared by other Maine scientists (Copenheaver White and Patterson 2000) and are confirmed elsewhere where the species is removed from wildfire and other perturbations (Howard and Stelacio 2011). The fragile nature of pitch pine endurance is underscored by experience in a severe environment of abiotic and biotic pressures (Harris et al 2012). Yet tenuousness is partly offset by anomalies like glaciated edaphics on Mt. Desert island (e.g., Ellsworth schist). Upon entering their juvenile phase, pitch pine shade and nurture evergreen competitors for up to a decade relying on their greater adaptability to infertile soils to gain a competitive edge in a barren ecosystem. As time passes, seeming delicacy morphs into a complex and unexpected capacity of near vitality under the glare of intense sunlight coupled with limited nutrient and moisture root sorption. Further, where bare soil beckons (Lee et al 2019), pioneering efforts enable their ecosystem ‘facilitator’ status (Connell and Slatyer 1977), accelerating establishment in stressful locations less suited to evergreen competitors: red spruce (*Picea rubens*), hemlock (*Tsuga canadensis*) and balsam fir (*Abies balsamea*).

At burned sites, such as along Cadillac South Ridge trail, pyrogenic carbon deposits (Laing 1993), embroidered by thermal exfoliation (Shakesby and Doerr 2006), act as a magnet for moisture retention despite what is, reportedly, initially hydrophobic repulsion by lignocellulosic charcoal (Licht and Smith 2020). In fact those authors found charcoal pyrogenic carbon (PyC) from anthropogenic forest pyrolysis spurred subsurface water retention and nutrient supply, increasing photosynthetic intrinsic water use efficiency (iWUEisotope). Indeed, as a result of natural or prescriptive fire, charcoal PyC yields carbonate additions (Licht and Smith 2020) resulting from negligible consumption of Ca, K and Mg(Aber et al 1998; Kahl et al 2007). Additionally, an increase in alkali cations (Kolden *et al* 2017) in a glaciated ‘O’ soil layer (DeBano 1981) is reported to increase availability of solubilized minerals (Caldwell and Richards 1989) and moisture retention. This phenomenon has been suggested as an artifact of soils at Wonderland trail (Butak 2014). Natural and anthropogenic fire pyrolysis has been shown to impact the structure and function of pitch pine colonies (Carlo et al 2016); at Mt. Desert, improved moisture retention is a key to unlock the means to defeat punishing drought, winds and runoff.

Used in concert with data on plant growth and soil characteristics, knowledge of foliar traits provides substantial information about plant carbon and nutrient economies (Wright et al., 2004) and life history strategy (Reich 2014). For instance, foliar traits can reveal mechanisms underlying tradeoffs between growth and abiotic stress resistance (Gururani Mohanta and Bae 2015) underscored by growth data. There are little data on plant traits, especially allometrics, at Mt. Desert island with which to better understand and interpret influence of fire absence on ecophysiology. However, at Wonderland trail at least (Butak 2014), iWUEisotope was studied as a framework for understanding long-term seasonal growth; however, there was no burned population elsewhere used for comparison. Previous findings suggest iWUEisotope increases with elevation (Wang et al 2017) and is greater in fire-involved as opposed to fire absent trees (Chen Wang and Jia 2017). We seek to clarify how increased efficiency may be linked to elevation gradients or, perhaps, to other, explanatory variables such as slope and aspect.

Here, we examined the mechanisms underlying the impact of fire at four sites serving as a proxy for at least nine niches at Mt. Desert (Figure 1). Specifically, we hypothesized that growth characteristics of the individuals not experiencing fire would be greater as a result of greater (more negative) iWUEisotope and leaf nutrition, as well as enhanced soil nutrition. The use of multiple elevations allowed us to examine the generality of the response.