**Title Page**

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 stations 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 higher (*P*=0.004) at a previously burned upper elevation, South Cadillac trail. Individuals strung along this path were also shorter (*P*=0.031), had a narrower canopy (*P*=0.035), and a smaller dbh (*P*=0.001) than those at several sea level aggregations. 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). 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). 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. In fact, a previous study suggested that wildfire is required every ten years to perpetuate and rejuvenate pitch pine populations (Jordan et al 2003). Yet, recently, in the Northeastern USA, anthropogenic activities have suppressed fire frequency. As a result, fire adaptations such as cone serotiny (Givnish 1981) are disappearing in pitch pine colonies due to a change in fire regimes (cite?). 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 common, harsh island environment. Nonetheless, it is unknown whether long term benefits found in burned preserves outshine 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.

Pitch pine fragility is more complex than the 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 have been 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). Ironically, glaciated edaphics on Mt. Desert island (e.g., Ellsworth schist) enable a more competitive edge for pitch pines in mixed barren ecosystem; upon entering their juvenile phase, pitch pine shades and nurtures evergreen competitors for up to a decade. As time passes, the picture of fragility morphs into a more complex and unexpected image of near vitality under the glare of intense sunlight coupled with limited nutrient and moisture root sorption. These factors provide a backdrop for competition with red spruce (*Picea rubens*), hemlock (*Tsuga canadensis*) and balsam fir (*Abies balsamea*). Further, where bare soil beckons (Lee et al 2019), pioneering efforts enable accelerated establishment in stressful locations less suited to these other, broader competitors.

At burned sites, such as those 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, Licht and Smith (2020) found that charcoal pyrogenic carbon from anthropogenic forest pyrolysis spurred subsurface water retention and nutrient supply, increasing photosynthetic intrinsic water use efficiency (iWUE). Indeed, as a result of natural or prescriptive fire, charcoal yields carbonate addition (Licht and Smith 2020) resulting from negligible consumption of Ca, K and Mg(Aber et al 1998; Kahl et al 2007). An increase in alkali cations (Kolden *et al* 2017) in a glaciated ‘O’ soil layer (DeBano 1981) has been 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) through the influence of sufficient moisture to enable trees to defeat punishing drought, winds and runoff.

Used in concert with data on plant growth, 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), iWUE was studied as a framework for long-term seasonal growth; howver, there was no burned population for comparison. Previous findings suggest that iWUE increases with elevation (Wang et al., 2017) and is greater in fire-involved as opposed to fire absent trees (Chen Wang and Jia 2017). Nonetheless, it is unclear how this increased efficiency may influence growth nor to what extent elevation gradients may play a role.

Here, we examined the mechanisms underlying the impact of fire at four sites serving as a proxy for more than eighteen niches at Mt. Desert. Specifically, we hypothesized that growth characteristics of the individuals experiencing fire would be greater and that this would be the result of greater iWUE and leaf nutrition, as well as enhanced soil nutrition. The use of multiple elevations allowed us to examine the generality of the response.

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Added references  
Miller, D., Castañeda, I., Bradley, R., & MacDonald, D. (2017). Local and regional wildfire activity in central Maine (USA) during the past 900 years. *Journal of Paleolimnology*, *58*(4), 455-466.

Buma, B., Brown, C. D., Donato, D. C., Fontaine, J. B., & Johnstone, J. F. (2013). The impacts of changing disturbance regimes on serotinous plant populations and communities. *BioScience*, *63*(11), 866-876.

Wright IJ, Reich PB, Westoby M et al. (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821.

Reich PB (2014) The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto. *Journal of Ecology*, **102**, 275–301.

Wang H, Prentice IC, Davis TW, Keenan TF, Wright IJ, Peng C (2017) Photosynthetic responses to altitude: an explanation based on optimality principles. *New Phytologist*, **213**, 976–982.