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

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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); 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. We examined the enigma of pitch pine resilience 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 with varied geomorphology. We hypothesized trees at the highest elevations would yield greater photosynthetic intrinsic water use efficiency (iWUEisotope), a key metric of physiological performance; iWUEisotope was significantly (more negative) different between sites (*P*=0.004) and highest at upper elevations, St. Sauveur and South Cadillac trails. At South Cadillac trail, trees 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, whose growth is supported by more plentiful foliar C and minerals Ca, P, K, Al and Zn (on average *P*=<0.01). A combination of greater soil C, P, Ca, Mg (*P*=0.019), K and Al (*P*=0.027) at unburned locations, especially, Wonderland, added to greater soil moisture retention (*P*=<0.001). We found trees with a one-hundred-year fire absence history allocated more energy to growth than stress resistance amidst worsening biotic and abiotic pressures; a result noted at both low and upper elevations. The authors determined fire charcoal remnants were linked to growth, water use efficiency and soil moisture retention. Yet, enigmatic resilience of unburned tree stands depended on more aggressive growth-oriented photosynthesis, distributed nutrient and moisture than on charcoal remnants. New knowledge about soil and foliar mechanics provides forest managers with critical insights into pitch pine elasticity in the absence of fire.

**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; Parshall et al 2003). In fact, a previous study suggested that wildfire is required every six to twenty-five years to perpetuate and rejuvenate pitch pine (*Pinus rigida* Miller) populations (Jordan et al 2003). Still, at Mt. Desert island at Acadia National Park in Maine, members of the species not subjected to fire in the past one hundred years appear to be resilient to fire absence. Critically, this is not a case where pines are absorbing disturbance and reorganizing in response (such as survival of adult trees or seedling recruitment after loss of a stand) but rather coping with the shock of doing without fire and building resistance to that shock (Brand and Jax 2007). This paper is dedicated to resolving that enigma.

Pitch pine, like other species in fire-prone ecosystems, expend energy on fire avoidance and tolerance based on previous history of fire frequency. In the Northeastern USA, a combination of forest fire suppression and anthropogenic introduction of fire (Foereid et al 2015) have been used to manage pitch pines and their reproduction (Lee et al 2019)—at stands in Albany NY, Long Island NY, southern Connecticut and southeastern Massachusetts. Prescriptive fire intervention is used to reduce fuel, reduce evergreen competition and open canopies in pine-oak and pine barren forests (Neill et al 2007). On Mt. Desert island at Acadia National Park in Maine, however, prescriptive fire is rarely used (ANP WMP 2016) and, as a result, ongoing fire suppression creates a situation where both previous naturally burned and unburned communities offer themselves for comparison.

To investigate whether long term performance in burned preserves is similar to those in other populations untouched by fire we gather evidence. For example, fire adaptations such as cone serotiny (Givnish 1981), thick bark and basal re-sprouting (Renninger et al 2013) are disappearing due to a change in fire regimes (Jordan et al 2003) and those are seen in both burned and unburned forests. Given the perspective of suppression or non-occurrence, adaptations (Little 1953) appear to be wasted investments; not relinquishing these modifications may leave formerly needed fire-adaptations to be a cause for under competition with other plants in the community (Buma et al 2013). The uniqueness of the environment on Mt. Desert provides an ideal testbed to understand pitch pine resilience in the midst of fire absence and loss of these adaptations in fire-affected and unburned populations (Star et al 2015).

The sensitive nature of pitch pine resilience is undeniably undermined by the presence of abiotic and biotic pressures (Harris et al 2012) and requires a deeper explanation of community response than attributions of fire absence as the chief, overriding concern. 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). Anomalies like infertile, glaciated soil (e.g., Ellsworth schist) on Mt. Desert island and forest succession provide some explanation of limits on fragility. 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 vitality under the glare of intense sunlight coupled with limited nutrient and root moisture sorption. Further, where bare soil beckons (Lee et al 2019), infertility and moisture scarcity promote pioneering efforts enabling pitch pine to achieve ecosystem ‘facilitator’ status (Connell and Slatyer 1977). This is especially true in stressful locations less suited to evergreen competitors: red spruce (*Picea rubens*), hemlock (*Tsuga canadensis*) and balsam fir (*Abies balsamea*).

At burned sites, along Cadillac South Ridge trail or at the base of Cadillac cliffs, charcoal pyrogenic carbon (PyC) deposits act as a magnet for moisture retention despite what is, reportedly, initially hydrophobic repulsion by lignocellulosic charcoal (Licht and Smith 2020). Those authors found subsurface PyC from anthropogenic forest pyrolysis, undiminished by photorespiration and oxidation, spurred water retention and nutrient supply and increased photosynthetic intrinsic water use efficiency (iWUEisotope). As a result of natural or prescriptive fire, charcoal PyC yields carbonate additions (Licht et al 2017) resulting from negligible consumption of Ca, K and Mg(Kahl et al 2007). Additionally, an increase in alkali cations (Kolden *et al* 2017) in a glaciated ‘O’ soil layer (DeBano 1981) often result from thermal exfoliation (Shakesby and Doerr 2006) leading to an increase in solubilized minerals (Caldwell and Richards 1989) and perhaps greater gravimetric moisture retention. Natural and anthropogenic fire pyrolysis has been shown to impact the structure and function of pitch pine colonies (Carlo et al 2016) elsewhere; at Mt. Desert, improved moisture retention is a particularly well-shaped key which can unlock resistance to drought and wind disturbance.

Foliar nutrient enrichment promotes plant carbon and nutrient economies (Wright et al., 2004) and life history strategy (Reich 2014) and widens a primary focus on photosynthesis and water availability (Gururani Mohanta and Bae 2015). At Mt. Desert island there is a paucity of data shing a light on these factors and specifically on plant performance, measured for example by allometrics, or stand density,. Thus, an opportunity is present to acquire and interpret new data to improve an understanding of growth characteristics, especially as regards fire effects. Ecophysiological performance is an important discriminant and is studied at a flat, low elevation Wonderland trail (Butak 2014) using iWUEisotope. This measurement constitutes a cornerstone in the understanding of long-term seasonal growth. 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). What is not known is to what extent increased iWUE efficiency may be linked to fire effects and topographical factors such as elevation gradients, slope, and aspect on the island.

Here, we examine mechanisms underlying pitch pine resilience at sites at Mt. Desert (Figure 1). Specifically, given the perception that fire is a necessity, we hypothesize growth characteristics of individuals (height, stem diameter, canopy size) experiencing fire would be more robust as a result of greater soil C, higher (more negative) iWUEisotope, elevated accumulation of subsurface nutrient leading to higher leaf nutrition and moisture retention at a higher elevation. The use of multiple elevations and insights into biomorphology (Savinykh and Cheryomushkina 2015), elaborated with remote sensing technology, allow more flexibility to examine the generality of the responses.