**Title Page**

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

Authors and affiliations:

Jeff Licht1, Nicholas G. Smith2 and Michael Day3

1School for the Environment, University of Massachusetts, Dorchester, MA, USA 02110

2Department of Biological Sciences, Texas Tech University, Lubbock, TX, USA 79409

3School of Biology and Ecology, University of Maine, Orono, Maine, USA, 04469

Key words

*Pinus rigida*, Pitch pine, Mount Desert Island, chemical geography, carbon, fire ecology

**ABSTRACT**

The health of fragile tree species is a concern in forests around the world. In the Northeastern United States, the absence of fire is thought to have a negative impact on the globally rare species, pitch pine (*Pinus rigida* Miller) because fire is essential for pitch pine reproduction and niche preservation. However, in some parts of the species range, stand-replacing conflagrations have occurred, including at the northeastern extreme of the species range limit in Acadia National Park (ME, USA) in 1947. Here, we examined pitch pine response to 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 to better understand the role that fire plays in sustaining this rare species. We found that 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. The individuals at this site were also shorter (*P*=0.031), had a narrower canopy (*P*=0.035), and a smaller dbh (*P*=0.001) than those closer to sea level. This result seems reasonable based on a conjecture 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 available foliar minerals Ca, P, K, Al and Zn, significantly more plentiful (on average *P*=<0.01). In summary, we found trees with a 100 year fire absence history exhibited self-preservation tendencies even amidst worsening biotic and abiotic pressures. Our analysis quantified tree and soil performance with specificity as to fire, geographic and topographic gradients to inform forest management decisions especially where prescribed fire is contemplated.

**INTRODUCTION**

The fragility of the globally rare pitch pine (*Pinus rigida* Miller) is nowhere more evident than in the Northeast United States, and particularly the northeastern extreme of the species range limit (Patterson Saunders and Horton 1983) in Acadia National Park (ME, USA). To obtain a better understanding of the impact of fire—either naturally occurring or anthropogenic-based—on forest health of pitch pines (Charpentier 2020) requires resolving the enigma of resilience of the species in the absence of fire. A dramatic conflagration disturbed the eastern half of Mt. Desert island in the Park in 1947 and since then wildfire has been suppressed (Pyne 2019). Investigators appreciate a unique opportunity to explore factors on the isolated pristine island—photosynthesis, foliar and soil nutrient, elevation and topography—with which to gauge globally rare pitch pine niche performance (Harris et al 2012).

Fire is a disturbance that can drastically alter the landscape of an ecosystem. Many species in fire-prone regions rely on fire to persist in their environment. For instance, fire may be necessary to create suitable niches for certain species or, more directly, to stimulate reproduction. Many species in these ecosystems expend energy on fire avoidance and tolerance. Additionally, fire is known to alter soil resource availability by increasing moisture and nutrient retention, conditions to which many species are adapted. Importantly, fire adaptations may be wasted investments if fires are suppressed, potentially causing fire-adapted species to be outcompeted and even lost from an ecosystem.

Current anthropogenic practices are now suppressing fire in many ecosystems, including the forests of the Northeastern United States. This suppression is potentially threatening the persistence of many species that are reliant on fire for survival and reproduction. In the Northeastern United States, the globally rare pitch pine (*Pinus rigida* Miller) is one potential loser in a fire suppressed environment. This is because XXXXXXXX.

A previous study (Jordan et al 2003) suggested that wildfire is required every ten years to perpetuate and rejuvenate pitch pine populations. Thus, a sustained fire absence may cause pitch pine decline (Copenheaver White and Patterson 2000) as it does for trees removed elsewhere from wildfire and other pertubations (Howard and Stelacio 2011). Besides the lack of pyrolysis other pressures exist. For instance, Day et al. (2005) asserted that pitch pine 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 (Fernandez *et al* 2015). Nonetheless, pitch pine still persists in some locations despite fire suppression, posing a conundrum to managers wanting to maintain the virility of this species. A significant delay in further pyrolysis does not necessarily signal an end to island wildfire (Pyne 2019), since fuel buildup continues unabated (Charpentier 2020).

Natural and anthropogenic fire pyrolysis have been shown to impact the structure and function of pitch pine (Carlo et al 2016). For instance, a previous study found that the charcoal pyrogenic carbon was important for subsurface water retention and nutrient supply, which impacted the water use efficiency of the pines (Licht and Smith 2020). Nonetheless, the study did not address the impact of alterations to competition that resulted from fire absence (Lee et al 2019), leaving it still unclear as to what factors regarding fire are most important for the persistence of pitch pine.

The fragility of pitch pine is nowhere more evident than in the northeastern extreme of the species range limit (Patterson Saunders and Horton 1983) in Acadia National Park (ME, USA). Interestingly, a dramatic conflagration disturbed the eastern half of Mt. Desert island in the park in 1947 and since then wildfire has been suppressed (Pyne 2019), providing an ideal testbed for understanding pitch pine-fire dynamics.

Soil dynamics on Mt. Desert island are well prescribed within the pitch pine enclaves; glaciated edaphics are the rule (e.g., Ellsworth schist) as opposed to sandy or gravelly loam (Entisols and Ultisols) in most other pitch pine refugia in the Northeast US. Well-drained and infertile soils at Mt. Desert provide competitive advantages to pitch pine in competition with red spruce (*Picea rubens*), hemlock (*Tsuga canadensis*) and balsam fir (*Abies balsamea*). Spread proceeds more quickly where bare soil beckons (Lee et al 2019), allowing pitch pines to migrate to stressful locations less suited to other, bigger competitors. Once situated by themselves, they may be better enabled to balance the scales of growth and stress resistance.

When used in concert with data on plant growth, foliar traits can provide 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) that can be backed up using growth data. There are few data on plant traits at Mt. Desert island with the exception of a single study at Wonderland trail (Butak 2014). In that study, photosynthetic intrinsic water use efficiency (iWUE) was conducted to frame long-term seasonal growth, but was not examined in the context of fire. 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.

Juvenile pitch pine nurse evergreen competitors. As time passes, this counterintuitive irony untangles as intense sunlight coupled with soils infertile from root sorption thrusts pitch pine into a more enviable position. In both burned and unburned locales, growth or retreat to achieve escape from others is dependent on how much advantage is enjoyed in sorption of available organic and mineral deposits. Immediately after wildfire or prescribed fire events carbonate availability is noted (Licht and Smith 2020) as there is negligible pyrolytic consumption of Ca, K and Mg(Aber et al 1998; Kahl et al 2007).

The absence of fire may increase alkali cations (Kolden *et al* 2017), specifically in an ‘O’ soil layer (DeBano 1981) and perhaps, as has been suggested earlier (Butak 2014), there is a connection between an absence of fire and greater availability of solubilized minerals (Caldwell and Richards 1989) at Wonderland. Alternately, what is worth noting at burned sites is the impression that pyrogenic carbon deposits act as a magnet for moisture retention despite what are, reportedly, initially hydrophobic repulsion by lignocellulosic-based charcoals (Licht and Smith 2020). Soil moisture retention, boosted by carbonates is critical to pitch pine well-being (Licht and Smith 2020); the contrast between retention and soil history (burned or unburned), including thermal exfoliation effects (Shakesby and Doerr 2006), provides potential to further distinguish those intra-system effects.

Here, we used the 1947 fire on Mt. Desert island to examine the mechanisms underlying the impact of fire on the growth and survival of pitch pine. To do this, we measured growth metrics along with foliar traits and soil characteristics at four sites in a factorial fire by elevation design. The fours sites included a high and low elevation site that experienced the 1947 fire and a high and low elevation site that did not experience the fire. Specifically, we hypothesized that the growth of the individuals experiencing the fire would be greater and that this would be correlated to greater iWUE and leaf nutrition, as well as greater soil nutrition. The use of multiple elevations allowed us to examine the generality of the response.