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On The Edge: Pitch Pine Persistence in the Absence of Fire Under the Influence of Elevation and Topographic Factors

Authors and affiliations:

Jeff Licht1, Risa McNellis2 and Nicholas G. Smith3

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

2, 3 Department of Biological Sciences, Texas Tech University, Lubbock, TX, USA 79409

Key words

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**ABSTRACT**

Globally rare pitch pine (*Pinus rigida*) is thought to depend on intermittent fire, which encourages reproduction and niche preservation. swith and without fire historyand,, at Mt. Desert Island in Acadia National Park (ME, USA). In 1947, a stand-replacing fire enveloped a portion of the island; since then there has been no recurrence of fire. Other populations on the island have been unaffected by fire disturbance for over 120 years. We measured tree height, diameter, stand density, foliar nutrients, and soil water retention at four sites across a gradient of fire history, elevation, and topography. Trees at higher elevation displayed greater water use efficiency, indicating a preference for stress resistance over growth. At lower elevation, soil water retention was higher and trees exhibited greater clustering (low distance between neighbors). However, fire accounted for a significant influence on foliar nitrogen. Our insights provide a means to a better understanding of how to promote pitch pine persistence in communities, at varying elevation and topography, where fire is absent, which dot the northeastern and mid-Atlantic U.S. coast.

**INTRODUCTION**

Over millennia, fire has been a constant disturbance in pitch pine (*Pinus rigida*) barrens, enabling persistence through reduced competition, added pyrogenic carbon (C) by way of post-fire charcoal, and long evolved adaptations. These adaptations include serotinous cones, which rely on the brief extreme heat of fire to release seeds (Givnish, 1981), thickened bark to withstand scorching, and epicormic sprouting following fire to provide additional photosynthetic stimulation. However, historic fire prevention and suppression has resulted in a significant loss of pitch pine barrens throughout the Northeast United States (Hanberry et al., 2012; Noss et al., 2006; Nowacki and Abrams, 2008), despite the occurrence of other forms of disturbance, such as land clearing and insect herbivory. Nevertheless, pitch pine communities do persist.

Interestingly, there has been a disappearance of fire-adaptive traits in pitch pines that no longer experience regular fire. For example, cone serotiny is low in jack pine populations in Maine that haven’t experienced fire in over 100 years (Conkey et al., 1995). Other traits, such as thick bark and epicormic re-sprouting (sprouting of needles from the trunk), have disappeared as well (xxx). One reason for the dissipation of adaptive traits are warmer temperatures and increasingly volatile changes in summer precipitation (xxx), in which fire-adaptive traits are not beneficial. Given the lack of a fire threat, pitch pine are also more directly competing with other evergreens (Nowacki and Abrams, 2008; Schwartz et al., 2016). A key question which arises is, in the absence of fire, what conditions favor the persistence of pitch pine communities?

Elevation and topography have been shown to be important factors in the dominance of pitch pine barrens due to their influence on the severity and extent of wildfires. Pitch pines favor dry, infertile soils with open forest canopies (Hanson, 2017; Nowacki and Abrams, 2008). Although pines vary in the aspect (or a position facing a particular direction) they occupy, areas with medium to high slopes often support pine communities due to good soil drainage (Hanson, 2017; Howard and Stelacio, 2011). Because of the strong positive relationship between elevation and precipitation, low elevation sites tend to have better established and more resilient pitch pine communities (Nowacki and Abrams, 2008), and persist even in the absence of fire. At higher elevations where moisture is higher, lack of fire removes the competitive advantage pitch pines have in outlasting nutrient- and moisture-demanding, late-successional species, which thrive in the high moisture and dense canopy conditions created when left undisturbed (Nowacki and Abrams, 2008; Schwartz et al., 2016). Elevational gradients have also been shown to have a strong impact on photosynthesis, with photosynthesis, stomatal conductance, and leaf N increasing with elevation (Bresson et al., 2009; Friend et al., 1989; Körner et al., 1986; Körner and Diemer, 1987). In addition, C13 isotope discrimination decreases with altitude and is associated with greater carboxylation efficiency at high altitudes (Chen et al., 2017; Körner et al., 1991; Zhu et al., 2010).

On Mt. Desert Island in Acadia National Park (ME, USA), pitch pine dwell at the edge of their northeastern range (Fig. 1). In October 1947, an intense fire started just west of Bar Harbor, on the east side of the island (Miller et al., 2017), burning 17,188 acres in two weeks (Fig. 2A). Since then, fire suppression has been used at Mt. Desert Island to avoid the tragic consequences of such intense fires. According to our survey of seventeen populations on the island, trees are still recovering from the 1947 fire (xxx) and trees which were not burned persist despite expected dependence on fire intervals of 6-25 years (Jordan et al., 2003).

The fire, elevational, and topographic gradients at Mt. Desert Island provide a unique testbedto untangle connections and differences between disturbance and environmental factors and tree traits in pitch pines on the island (Fig. 2B). We hypothesized greater pitch pine growth and population expansion at low elevation sites as compared to high elevation sites, as a result of greater soil moisture retention and soil C that confer high growth functional traits such as more negative water use efficiencies. This expected increase in growth was hypothesized also to be the result of greater competition for resources at low versus high elevation. We also expected that upper ledge elevations would limit clustering (stand density), colonization, and expansion. We expected that the occurrence of the 1947 stand replacing fire would limit topographical differences because it would cause plants to adopt recovery persistence traits that confer low growth.

**METHODS**

**Study Sites**

We investigated fifteen pitch pine specimens at each of four sites at Mt. Desert Island (Tab. 1), factorially crossed in a fire history by elevation design: (1) Wonderland trail at an average 16.27 m elevation (low elevation, outside the footprint of the 1947 fire), (2) Gorham cliffs at an average30.74 m (low elevation, within the footprint), (3) St. Sauveur trail at an average 182 m (high elevation, outside the footprint) and (4) South Cadillac trailat an average 284.43 m (high elevation within the footprint). Elevation differences are more stark at higher elevations based on much longer transects. Soils at all four sites are porous, comprised of acidic hornblende granite or Ellsworth schist, and overlain with rapidly drying needle duff (xxx). In addition they are uniformly shallow, (varying between 0.7-2.5 cm), homogeneous, and low in fertility.

**Topography**

A Kodak Trimble Juno 3B was used to obtain horizontal resolution of data plotted using between five and seven satellite telecommunication vehicles to maintain a maximum Position Dilution of Precision. These data were differentially corrected and have estimated accuracies in the horizontal and vertical direction of 2 meters, while selective availability was set to zero. Multiple satellite-configured GPS data (USGS 2m LIDAR 2010) determined coordinates for individual trees (Lubinski *et al*. 2003) as well as slope and aspect attributes using ArcGIS (version 10). Mapping of this type of data has been used in the past to compare physiography and recalcitrant chemical biogeography, particularly in fire prone contexts (Szpakowski and Jensen 2019).

**Allometry**

We measured individual tree height, canopy spread and stem diameter of the bole at breast height (DBH). Tree height was estimated using a plastic clinometer (Kager, Lunenberg, MA USA) and 30 m tape. DBH was measured at 1.06 m using an expandable cloth measuring tape. Canopy spread across the first nodal branch expanse below the crown was measured using two calibrated, nested aluminum flags as a ground truth reference. This method was selected in order to sort out upper canopy spread x height differences where trees across all four stands with very similar height and DBH characteristics dominated.

**Clustering**Mean distances between sampled trees (*N* = 60) were calculated including up to five of their nearest, reproductively mature conspecific (within 5 m) neighbors (Churchill et al., 2013; Plotkin et al., 2002)—this method served as a surrogate, but inverse, measure for stand density (Mosseler et al., 2004).

**Foliar Isotope Analysis**

Maximizing seasonal data relative to active growth during the driest months of the summer was achieved by obtaining C isotopic data (δ13C) and N isotopic data (δ15N) of fully expanded leaves (needle cluster) of 15 individuals at each site. Sample fascicles were separated and dried for two days at 60 ◦C ground in a SPEX ball mill (Metuchen, NJ, USA), weighed to +/- 2 mg for leaf tissue and +/- 5 mg for soil using a Cole-Palmer (Vernon Hills, IL, USA) micro analytic balance and rolled in Costech (Valencia, CA, USA) 5 x 9 mm tin capsules. A Thermo Delta (Waltham, MA, USA) V+ IR-MS continuous flow isotope ratio mass spectrometer with a universal triple collector was used. Combustion gasses were separated on a gas chromatograph column, passed through a diluter and reference gas box, and introduced into the spectrometer. δ13C was used to indicate water use efficiency (iWUEδ13C) (Farquhar et al., 1989).

**Foliar Analysis**

Leaf tissue was obtained from excision of basal fascicle bundles at 1.06 m. 50 mL samples of needles were separated, cut and dried for two days at 60 ◦C. Then they were ground in a SPEX ball mill (Metuchen, NJ, USA), sieved to <10 mm, and <2 mL were fed to a Leco CN-2000 Carbon-Nitrogen Analyzer (Leco Corp., St. Joseph, MI) coupled with the spectrometer to determine C and N concentrations. 35 mL aliquots were submitted for standard plant tissue nutrient analysis using a TJA Model 975 AtomComp ICP-AES (Thermo Jarrell-Ash Corp., Franklin, MA). The method comprised submersion in a 5 mL trace-metal-grade HNO3 treatment, then refluxed on hot block at 80 ◦C for two hours and diluted to 25 mL with 0.4 micron PTFE syringe filters to access extractable macro and micro inorganics.

**Soil Analysis**

Soil C and N were calculated using elemental analysis in a similar fashion to method above for foliar samples. Soils were excavated by hand trowel and soil probe (Accuproducts, Saline, MI, USA); 70 mL samples were extracted at fifteen tree locations at four sites, from <7.5 cm (Oa-Ab) horizon above bedrock. In a laboratory, 50 g H2O were added to each aliquot to assess net water retention as a subset of soil moisture evaporation (*ψ*g) to determine net evaporative loss or adsorption to surfaces. Soil water retention analysis was conducted according to the Fields method (Lichtand Smith 2018). Retention effects of gravitational and evaporation forces was made on a wet basis where Wm=g H2O **●** (g moist soil)-1 (Qi et al., 2018).

**Statistical Analysis**

All data were analyzed using a similar linear model structure with elevation (high or low) and presence of the 1947 fire (yes or no) as categorical fixed factors. The interaction between elevation and presence of the 1947 fire was also included in each model. In total, 19 models were fit with the following dependent variables: tree height (m), canopy spread (m), DBH (cm), mean distance between neighbors (m), foliar carbon (C, %), foliar nitrogen (N, %), foliar C/N (unitless), foliar δ13C (‰), foliar δ15N (‰), foliar calcium (Ca2+ %), foliar phosphorus (P, %), foliar potassium (K+, %), foliar magnesium (Mg2+, %), foliar aluminum (Al+, ppm), foliar zinc (Zn, ppm), soil C (%), soil N (%), soil C/N (unitless), and soil water retention (%). Tree height, canopy spread, DBH, foliar P, foliar K+, foliar Zn and soil C/N were log transformed to meet model assumptions of normality and heterogeneity of variances. Soil water retention was arcsin square root transformed to meet model assumptions.

All linear models were fit using the ‘lm’ function in R (R Core Team 2019). Significance tests for each fixed factor was performed using the ‘anova’ function in R (R Core Team 2019). Post-hoc Tukey’s tests were done to examine significant interactions between elevation and the presence of the 1947 fire using the ‘emmeans’ package in R (Lenth 2018).

Because aspect data is circular in nature, we analyzed aspect using a Watson’s Two-Sample Test of Homogeneity as implemented in the R package ‘circular’ (Agostinelli and Lund 2017). Specifically, one-to-one comparisons were done between each site in all six possible combinations.

All analyses were performed with R version 3.5.1 (R Core Team 2019).

**RESULTS**

**Aspect**

Watson’s two sample t-tests indicated that the aspects of all sites differed with respect to one another except for the two sites that experienced the 1947 fire (Gorham cliffs and South Cadillac Trail), which had similar aspects (Fig. 3 and Tab. 2).

**Allometry and Clustering**

There was a significant interaction between fire and elevation on tree height (*P* < 0.01, Fig. 4A, Tab. 3) and DBH (P < 0.05; Fig. 4C and Tab. 3), with trees at higher elevation that experienced the 1947 fire being shorter than those at low elevation that did not experience the fire and having a smaller DBH than all other sites. Canopy spread tended to be reduced at high elevation (*P* < 0.01, Fig. 4B and Tab. 3), although Tukey’s tests revealed no difference between sites at α = 0.05. Distance between neighbors was greater at high elevation sites, particularly the one that experienced the 1947 fire (*P* < 0.01, Fig. 4D and Tab. 3).

**Foliar Isotopes**

Trees at higher elevations experienced less negative δ13C (*P* < 0.01, Fig. 5A and Tab. 4), reflecting greater water use efficiency, regardless of fire history. There were no significant differences between tree populations for δ15N (*P* > 0.05, Fig. 5B and Tab. 4)

**Foliar Nutrients**

On average, foliar C was greater at upper elevations, however the results were not statistically significant (*P* > 0.05, Fig. 5C and Tab. 4); nor was there a difference in C/N between sites (*P* > 0.05, Fig. 5E and Tab. 4). Our linear model suggested that fire accounted for a significant influence on foliar N (*P* < 0.05, Tab. 4), however post-hoc Tukey’s tests found no difference between sites at α = 0.05 (Fig. 5D).

Foliar Ca2+ was negatively impacted by increasing elevation (*P* < 0.001, Fig. 6A and Tab. 5). Our linear model suggested that foliar P was significantly higher at fire-involved sites (*P* < 0.01, Fig. 6B and Tab. 5), although this was not confirmed by post-hoc Tukey’s tests (Fig. 6B). Foliar K+ was reduced in the high elevation site that experienced fire as compared to the other sites (elevation x fire: *P* < 0.05, Fig. 6C and Tab. 5). Neither foliar Al+ nor Mg2+ differed by site (*P* > 0.05 in both cases; Fig. 6D, Fig. 6E, and Tab. 5). Foliar Zn concentrations were 9% lower in the high elevation sites than on the low elevation sites (*P* < 0.01, Fig. 6F and Tab. 5), due to a particularly strong reduction at the high elevation site that experienced fire.

**Soil Nutrients**

Soil C concentrations were greater at lower elevations (*P* < 0.05) and sites that did not experience the 1947 fire (*P* < 0.05, Fig. 7A and Tab. 6). Soil N did not vary between sites (*P* > 0.05, Fig. 7B and Tab. 6). Soil C/N was 15% lower at high elevation sites (*P* < 0.05, Fig. 7C and Tab. 6), but we found no significant disparity in C/N when either fire history or fire history x elevation interactions were examined (*P* > 0.05 in both cases).

**Soil Water Retention**

There was an interaction between elevation and fire history on soil water retention (SWR; *P* < 0.01, Fig. 7D and Tab. 6), with markedly higher values at Gorham cliffs, the low elevation site that experienced fire, as compared to other sites.

**DISCUSSION**

Elevation, as opposed to fire history, was the dominant driver of plant and ecosystem processes according to our measurements. We confirmed that trees at high elevation favored increased foliar water use efficiency (Chen et al., 2017; Körner et al., 1991; Zhu et al., 2010) over growth. Further, we found trees at higher elevation, particularly those in the former 1947 fire district, persevered despite noteworthy challenges including less density, greater distance between conspecific neighbors and evidence of less reproduction. At the highest elevations on South Cadillac trail, we expected to find the steepest slopes but they were far less inclined than those at Gorham cliffs. Topography was found to be instrumental in shaping population expansion especially in combination with elevation exclusive of disturbance effects. Of greater interest was the finding that, despite an absence of recent fire history at Wonderland (none since at least 1900 or so) contrasted with a much more recent fire event at Gorham cliffs, stand density, height, canopy spread, and DBH were higher at Wonderland.

Even at high elevation ledge communities, we found little compelling empirical evidence that fire is necessary in pitch pine population perpetuation at Mt. Desert Island. This assertion is partly confirmed by the disappearance of serotiny and epicormic sprouting (xxx), found formerly at higher sites on Cadillac mountain three decades ago (xxx). Fire return intervals have lengthened at Mt. Desert Island to the point where they tend to be too intermittent to perpetuate previous fire resistance traits. A shift back to fire, accompanied by a re-introduction of serotinous characteristics, is not impossible in the future; however, current climate projections suggest the reoccurrence of fire is unlikely (Fernandez *et al.* 2015). Despite the absence of fire, fire remnants, such as anthropogenic fire charcoal (PyC) endure long after the 1947 event (Miller et al., 2017). PyC is associated with greater foliar water use efficiency, negligible consumption of Ca2+, K+, and Mg2+,and enhanced soil moisture holding capacity (Licht and Smith, 2020). On Mt. Desert Island, we found higher foliar water use efficiency(via δ13C) at high elevations at both burned and unburned sites, consistent with reported outcomes for non-glaciated populations in flat, sand plain New Jersey Pine Barrens (Schafer and Bohrer, 2016) and elsewhere (Chen et al., 2017; Körner et al., 1991; Zhu et al., 2010). There is evidence from previous investigations that post-fire PyC remnants endure in the soil layer (DeBano 1981) and that this increases alkali cations (Kolden *et al.* 2017), solubilize minerals (Caldwell and Richards 1989) and thermal exfoliation (Shakesby and Doerr 2006). From the standpoint of reproduction, the absence of fire, at locations such as Wonderland trail (Butak 2014), does not appear to be slowing down expansion in that flat-sloped region nor in ledge locations (e.g., St. Sauveur) that we and others (Howard 2010) have studied. One could argue that charcoal remnants very probably play a role in recovery capacity at burned-over Cadillac Brook (below the heights of South Cadillac trail), but it is not known to what extent these benefit the larger ecosystem. Developing further insights into the ecological stoichiometry of pitch pine at Mt. Desert Island marks a step in achieving a firmer understanding of the relationship between biogeochemistry, fire history and topography.

Our foliar nutrient results derived from burned and unburned sites are similar to those reported by others in New Jersey (Renninger et al., 2013) and indicate that historical fire reduced soil C. There was also a strong reduction in soil C with elevation. However, foliar C was similar across sites, inconsistent with findings by others in New Jersey (Renninger et al., 2013, Alkañiz *et al.* 2018), complicating the soil-plant connection. The interaction between elevation and foliar nutrient is still not resolved; foliar Zn availability was higher at lower elevations at Mt. Desert Island. This result was consistent with findings by others in another New Jersey investigation (Kolker *et al.* 2013). Our findings led us to speculate that persistence capacity may be tied to higher concentrations of foliar Ca2+ and K+.

Climate is already considered a more significant arbiter of population decline than the absence of stand-replacing fire disturbance (xxx). Recent climate change models anticipate a negative impact on future vegetative status at Mt. Desert Island due to changes in precipitation patterns, disturbance regimes, soil moisture, pest and disease outbreaks, and nonnative invasive species (Fernandez et al., 2020; Swanston et al., 2018), but these do not specifically address the adaptability of pitch pine nor the extent to which plasticity is shaping tendency towards persistence. What has been clear for almost three decades is the effect of global climate change on physiological traits. Day et al. (2001) found that an uptick in annual temperatures signaled increased leaf-air vapor pressure deficits that negatively impacted pitch pine stomatal conductance and limited gas exchange. In a related report, scientists found warming trends increased pitch pine reproductive difficulties (Ledig et al., 2015). This included weather-related effects such as episodic drought, harsh winds, and salt spray (Schmitt 2015; Fernandez *et al.* 2015) as well as conditions that increased cold intolerance (Berang and Steiner 1985). Increases in annual winter temperatures coupled with an absence of fire cause concern about a quite different disturbance—potential invasion within the next decade of an herbivore, Southern pine beetle (*Dendroctonus frontalis* or ‘SPB’; Lesk et al., 2017).

Although deer browsing and rodent damage historically impeded tree survival in pine barrens (Ledig et al., 2013), SPB has already paid a deadly visit to Long Island NY (Dodds et al., 2018). Unless SPB’s progress is deterred by other insect predators like double checkered clerid (*Thanasimus dubius*; Coulson and Klepzig, 2011), it is possible that pitch pines along with understory plants, butterflies and moth members of the Acadia ecosystem will suffer the same fate experienced in more southerly locations (Lesk et al., 2017). According to several authors (Day et al., 2005; Lee et al., 2019) warming climate impacts habitat suitability and pitch pine tendencies to consolidate, regenerate or migrate may be in jeopardy, through a combination of diminished open space capacity, loss of enriched substrates and elimination of suitable habitats (Day et al., 2005).

Pitch pine is considered an important indicator of underlying heath communities at Mt. Desert Island; it is foundational as a necessary ecosystem component in a stressed environment (xxx). Despite increasing climate pressures, tree retreat into ever more sparse conditions reinforces their facilitator status (Connell and Slatyer, 1977) for this species explicitly maintains the livelihood of underlying flora through a sharing and distribution of ecoservices. Our findings may be used by other scientists (Fuller and Quine, 2016) to better understand how pitch pine in other ecosystems, outside of the Northeast U.S., take advantage of elevation and topographic parameters to gain advantage over competitors. The present data yields a firmer purchase on current regeneration and expansion concepts—essential to an appreciation of influences on persistence in the absence of forest or prescribed fire.

**CONCLUSION**

We found elevation and topography signaled adaptivity effects (growth, expansion into greater stand density) which account for greater growth and stand density on more hospitable terrain, with little impact from fire history. This is undoubtedly due to the fact that fire return intervals are so infrequent as to reduce recovery features found elsewhere (e.g., where cone serotiny and epicormic sprouting still prevail). Flat and ledge pitch pine populations exhibited greater buoyancy than trees in more strenuous cliff situations. We also identified a selective preference for either growth at low elevations or stress tolerance at high elevations using multiple plant and ecosystem metrics. Our findings unravel part of the enigma about persistence in a post-fire milieu during a critical phase of the Anthropocene age. At lower elevations, which represent the vast majority of pitch pine populations in the Northeast US, we predict newly pioneered locations reflect a continuation of persistence signaled by significant differences in density, slope and aspect. At a time when continued climate change may tip the scale away from survival, our findings encourage the use of our data by forest managers to better understand the imposition of fire absence on flat and ledge communities.

## Data Availability Statement

Data used in this article can be found at the following repository: <https://github.com/SmithEcophysLab/mtDesertIsland_Pinusrigida> (DOI:10.5281/zenodo.4663255). Additional soil inorganic data is available at this site.

## Author Contributions

JL and NGS conceived the work. JL, RM, and NGS contributed substantially to the interpretation of the data and to drafting the manuscript, gave final approval of the version submitted, and agreed to be accountable for all aspects of the work. Questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved. JL carried out sample collection and field measurements, conducted soil water retention tests and prepared samples for EA-IRMS analysis. NS performed C/N foliar analysis. NGS and RM conducted statistical analyses and formulated figures and tables.

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**ORCID**

Jeff Licht: <https://orcid.org/0000-0002-2248-2050>

Risa McNellis: https://orcid.org/0000-0002-3538-9269

Nicholas Smith: <https://orcid.org/0000-0001-7048-4387>

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