**Title Page**

Pitch Pine Make A Stand On Fire-Absent Mt. Desert Island

Authors and affiliations:

Jeff Licht1 and Nicholas G. Smith2

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

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

Key words

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

**ABSTRACT**

Globally rare pitch pine (*Pinus rigida* Miller) is thought to depend on intermittent fire which encourages reproduction and niche preservation. At Mt. Desert island in Acadia National Park (ME, USA) a stand-replacing conflagration enveloped a portion of the island in 1947, however, there has been no recurrence. Indeed other populations on Mt. Desert island are unaffected by fire disturbance for over one hundred years. Loss of fire adaptations, like serotinous cones, climate change and outperforming evergreen competitors signal a shift in prospects depending on either resilience or buffering mechanisms. We quantified these through photosynthetic intrinsic water use efficiency, foliar nutrient status, allometry and soil moisture retention according to topographic gradients (9.5 to 404 m). Trees at upper elevations yielded significantly (*P*=0.004) greater water use efficiency (iWUEδ13C) electing adaptive stress resistance to growth. At one upper elevation, South Cadillac trail trees were the shortest (*P*=0.031), narrowest DBH (*P*=0.001) and narrowest canopy (*P*=0.035) in comparison with those at low-lying Gorham cliffs and Wonderland trail. At low lying elevations, especially Gorham Mountain cliffs, higher moisture retention (*P*=<0.0001) was significantly greater than other, more elevated sites. We determined fire on Mt. Desert is not necessary to promote resilience and long-term persistence in the absence of fire may be attributed to buffering in anticipation of other disturbance. Our findings provide key data to inform management efforts to reinforce pitch pine survival.

**INTRODUCTION**

On Mt. Desert Island in Maine in the Northeast USA, globally threatened pitch pine (*Pinus rigida* Miller) dwell at the edge of their domain. On the island, hereinafter MDI, species survival continues unabated despite fire suppression since the infamous 1947 conflagration. In many coastal Atlantic states further south, pitch pine is impacted by natural fire, or in its absence by anthropogenic fire (Carlo *et al* 2016); controlled burns (Foereid *et al* 2015) are a technique (Lee *et al* 2019) which reduces fuel and evergreen competition and opens canopies in pine barrens (Neill *et al* 2007). At MDI, though, pitch pine populations are just as persistent outside of the 1947 fire zone as inside it (Miller *et al* 2017), faring better than experts predicted in the past (Patterson Saunders and Horton 1983; Parshall *et al* 2003). Anomalous persistence at MDI in non-pyrogenic circumstances stimulates fact-finding by the authors to better understand resilience long after a fire event, or buffering in anticipation of another disturbance type.

We consider several premises. First, fire ecology scientists in Northeast USA (Jordan *et al* 2003) suggest wildfire is required every six to twenty-five years to perpetuate and rejuvenate pitch pine. At MDI, trees in undisturbed neighborhoods appear to engage similar seedling recruitment as trees in the post-1947 fire zone. This supposition leads us to propose a bifurcated model where trees either build a buffer capacity (*Bcapacity*) to reduce the shock of disturbance absence (Brand and Jax 2007) or build resilience capacity (*Rcapacity*) long after fire disturbance. As we shall explore further, each mode in its own way either promotes opportunistic individuals, or consolidation or expanded colonization.



**Figure 1**. Contorted but striking *Pinus rigida* specimen hiked out on an outcrop across from Gorham Mountain cliffs on the Park Loop Road at Mt. Desert Island.

Accepted wisdom (Ibáñez *et al* 2019) frames *Rcapacity* as recovery, in the absence of further fire disturbance. Nevertheless, in the case of former pyrogenic forests, it is not clear if recovery caused adaptive traits to disappear or if these are a result of intrinsic, as opposed to extrinsic, post-fire re-generation. During a sustained period of fire absence, physiological and morphological adaptations arise over many years (Little 1953). These include elimination of cone serotiny (Givnish 1981), thick bark and basal re-sprouting (Renninger *et al* 2013) in formerly fire-prone pitch pine ecosystems. A change in fire regimes (Jordan *et al* 2003) and suppression make it likely that any ongoing fire adaptive mechanisms (no longer required for stand sustenance) are wasted investments which could encourage under-competition with other evergreens (Buma *et al* 2013). At the same time, *Bcapacity* allows some forests, inexperienced in fire for more than one hundred years, to persist, through cushioning suited to climate adaptation.

Notwithstanding abiotic and biotic pressures (Harris *et al* 2012), the arc of pitch pine tends to be expressed as one side or the other of a dichotomy of growth or stress inoculation, colony retreat or expansion (Swanston *et al* 2018). *Bcapacity*, in our estimation, manifests especially where shade-intolerant pitch pine out-compete other evergreens: red spruce (*Picea rubens*), hemlock (*Tsuga canadensis*) and balsam fir (*Abies balsamea*) in bare, moisture-scarce soils. Where ledge features dominate, a contoured barren ecosystem (Howard and Stelacio 2011) replete with pitch pine takes advantage of gaps in multi-evergreen colonies (Lafon *et al* 2014). At Wonderland, for example, where ledge ecology exists, we suspect *Rcapacity* is traced in part to stored plant C availability (Butak 2014) central to carbon and nutrient economies (Wright *et al* 2004), a witness to greater tree longevity (Reich 2014) and testament to ecophysiological adaptation (Gururani Mohanta and Bae 2015) embodied as enhanced photosynthetic intrinsic water use efficiency (iWUEδ13C).

A fourth consideration is the effect of a particular ingredient enhancing *Rcapacity*, namely charcoal, in the form of soil pyrogenic carbon (PyC). PyC festoons Cadillac Mountain (Patterson Edwards and



**Figure 2**. Pitch pine populations on Mount Desert island examined in the context of fire presence (1947) or absence, as much as one hundred years or more on the west side of the island. Estimates of the extent of fire exposure shown in the right pane represent recent fire path extent (Miller et al 2014; Livingston, personal communication 2019).

******

**Figure 3**. Contour features are shown at four sites reveal dramatic differences between subalpine (St. Sauveur and South Cadillac) and coastal plain (Wonderland and Gorham cliffs) sites, each with *N*=15 trees (blue dots).

Maguire 1987), for example, and downslope pockets along the Park Loop Road. Below an otherwise infertile, glaciated bedrock (e.g., Ellsworth schist), charcoal remnants result in elevated soil C and mineral capacity. At higher elevations (incrementally between 190 and 404 m) where charcoal are found, sorption properties are similar to those revealed in an investigation of initial hydrophobic repulsion and later uptake in lignocellulosic charcoal (Licht and Smith 2018). In a later controlled study, investigators (Licht and Smith 2020) demonstrate the potency of residual charcoal whether as a result of forest fire or anthropogenic fire, to yield carbonates associated with negligible consumption of Ca, K and Mg(Kahl *et al* 2007). At lower locations we theorize PyC acts as a magnet for moisture retention to enable larger clusters and denser colonies of trees. The authors find subsurface PyC, undiminished by photorespiration and oxidation, spurs nutrient supply. Specifically, PyC in a glaciated ‘O’ soil layer (DeBano 1981) increase alkali cations (Kolden *et al* 2017) and solubilized minerals (Caldwell and Richards 1989) often resulting from thermal exfoliation (Shakesby and Doerr 2006).

A final premise concerns the influence of foliar C on *Rcapacity* or *Bcapacity* outcomes. To date there is no investigation of a combination of pitch pine biogeochemistry, elevation gradients and source-sink proximity for trees in the 1947 fire path. In previous studies of other species, scientists (Wang *et al* 2017) find greater carbon availability at higher elevation sites associated with stronger (less negative) iWUEδ13C outcomes and likely to be amplified by previous fire involvement (Chen Wang and Jia 2017). iWUEδ13C may be higher in some higher elevation populations at MDI. To answer this question, we aim to measure leaf level response between 160-404 m elevation, comprising historical fire effects on the one hand and long-term fire absence on the other. Fortuitously, at MDI, there exists a nearly ideal testbed to accumulate data to better clarify aspects of chemical geography (Star *et al* 2015) in precincts defined by fire history or its lack thereof. We anticipate our study will provide data to inform and inspire island management decisions (Stambaugh *et al* 2015).

**METHODS**

A US Department of the Interior (National Park Service) permit provided access to obtaining edaphic and needle data.

**Study Extraction Sites**

Fifteen trees at four sites at MDI in a factorially crossed fire history (Miller *et al* 2014) were investigated: (1) Wonderland trail between 9 and 25 m elevation (low elevation, outside the footprint of the 1947 fire), (2) Gorham cliffs between 24 and 36 m (low elevation, within the footprint), (3) St. Sauveur trail between 134 and 198 m (high elevation, outside the footprint) and (4) South Cadillac trail between 188 and 417 m elevation within the footprint. Distances between sampled trees and their five nearest, reproductively mature conspecific neighbors were measured in the four stands to calculate mean neighbor distance as a surrogate, but inverse, measure for stand density along with mean age (Mosseler Rajora and Major 2004).

**Laboratory MeasurementsCarbon and Nitrogen Stable Isotopes**C isotopic data of the needles (δ13C) of fully expanded leaf (needle cluster) of each species and accompanying soil samples was obtained. 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. C abundance or depletion according to δ13C was used to determine iWUE. As a product of carboxylation and diffusion (Lambers Chapin Pons 2006) iWUEδ13C represents δ13C unit/mL-1 percentage of photosynthesis, a sensitive long-term indicator of physiological change, i.e., growth versus stress inoculation. Foliar C and N were calculated using elemental analysis.**Foliar Elemental Analysis and Nutrient**Leaf tissue was obtained from excision of basal fascicle bundles at dbh; we acknowledge photosynthetic and nutrient measurements differ according to light environments impacted by the size (height and canopy) of tree subjects. 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 Perkins Elmer Elemental Analyzer ECS 4100 (Waltham, MA, USA) coupled with a Thermo Delta (Waltham, MA, USA) V+ IR-MS continuous flow isotope ratio mass spectrometer with a universal triple collector. Combustion gasses were separated on a gas chromatograph column, passed through a diluter and reference gas box, and introduced into the spectrometer. submitted for elemental analysis using Leco CN-2000 Carbon-Nitrogen Analyzer (Leco Corp., St. Joseph, MI) to determine C and N concentrations. The remainder of the same samples, 35 mL, 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 hotblock at 80 ◦C for 2 hours and diluted to 25 mL with 0.4 micron PTFE syringe filters. Analysis was focused on macro and micro inorganic extractable fractions (Ca, P, K, Mg, Al and Zn). **Soil Nutrient**Soils comprised uniformly similar shallow, homogeneous, low fertility characteristics (varying between .7-2.5 cm) and are usually overlain with rapidly drying needle duff (Day *et al* 2005) overlaying porous and acidic hornblende granite or Ellsworth schist. All sites were excavated similarly by hand trowel and soil probe (Accuproducts, Saline, MI, USA); aliquots were extracted from Oa-Ab horizon soil pockets of organic and mineral deposits within 50 cm of the tree base. 250 mL soil samples were sieved (#10) and measured in 2019. Drying was performed in an oven at 100°C for two d. Analysis was performed using a modified Mehlich method using inductively coupled plasma spectroscopy, pH measurement via proton activity of a 1:1 slurry and effective soil cation exchange capacity (CEC) via formic acid extraction. These methods are described previously (Lichtand Smith 2018). Bedrock C and N were calculated using elemental analysis.

**Gravimetric Moisture Retention**

70 mL samples were extracted from soils at fifteen tree locations at four sites, comprising <7.5 cm (Oa-Ab) horizon above bedrock to assess net moisture retention as a subset of soil moisture evaporation (*ψ*g), rather than depending on, say, matric potential (*ψ*m) to determine net evaporative loss or adsorption to surfaces. 50 g H2O were added to each aliquot. Soil moisture retention analysis was conducted according to the Fields method described previously (Lichtand Smith 2018). Retention effects of gravitational and evaporation forces was made on a wet basis where Wm=g H2O **●** g-1 moist soil; this method is described previously (Jingfang and Wenwei 2018).

**Field Measurements  
Allometry**Individual specimens served as a proxy for multiple trees nearby and were further characterized according to height, spread (canopy) and diameter. Height was estimated using nested, 2 m calibrated, lightweight aluminum rods (Garelick, St. Paul, MN, USA). Bole width was measured at 1.06 m dbh using a ProSkit electronic digital caliper (Amelia, VA, USA). Canopy spread was measured using the span between the same calibrated aluminum rods fixed with two landscape flags as a ground truth reference.   
**Remote sensing to locate colonies**  
A Kodak Trimble Juno 3B unit was used to obtain horizontal resolution of combined elevation, slope and aspect data plotted using between five and seven satellite telecommunication vehicles to maintain a maximum PDOP (Position Dilution of Precision). These data were differentially corrected and have estimated accuracies in the horizontal and vertical direction of 2 meters, while SA (selective availability) is set to zero. Data points are used to establish not only elevation but to compute fire event sink-source metrics. For analysis purposes we constructed two categories, assigning soil and tree aliquots to either a proximate fire-path or no fire-path exposure. Mapping was achieved through geospatial, remote sensing technology (Tierney *et al* 2012) used in the past to compare physiography and recalcitrant chemical biogeography, particularly in fire prone contexts (Szpakowski and Jensen 2019). Individual trees were randomly selected but a distance-between-subjects was observed, requiring 5m as a setback between specimens. Multiple satellite-configured GPS data (USGS 2m LIDAR 2010) determined coordinates for individual trees (Lubinski Hop and Gawler 2003; Kim 2010). ArcGIS (version 10) as well as slope, aspect and rose compass direction attributes. The aggregated data were reduced to mean values for each measurement category.

**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, five models were fit with the following dependent variables: iWUEδ13C, foliar and soil nutrient and soil moisture retention were log transformed to meet model assumptions of normality and heterogeneity of variances. All models were fit using the ‘lm’ function in R. Significance tests for each fixed factor was performed using the ‘anova’ function in R. Post-hoc Tukey’s tests were done to examine significant interactions between elevation and the presence of the 1947 fire using the ‘emmeans’ package (Lenth 2018) in R. All analyses were performed with R version 3.5.1 (R Core Team 2019). This section requires modification by Nick.

**RESULTS**

We found *Rcapacity* and *Bcapacity* were central to survival, despite fire absence from eighty to well over one hundred years, disparity in elevation gradients (12m to 404m), and connected by noteworthy pitch pine growth, iWUEδ13C, foliar chemistry and moisture retention outcomes. These findings build on previous results of field experiments conducted at a uniform elevation (89.2 m) where investigators (Licht and Smith 2020) examined response differences following seedling exposure to naturally occurring and anthropogenic fire PyC in a controlled setting. Here we examined leaf (needle) level dynamics at a landscape level absent experimental manipulation of fire.

**Foliar C, δ13C, N and δ15N**

Mean foliar C was 10% greater at trees at higher elevations such as St. Sauveur and South Cadillac trails but not significantly different from other sites (*P*=0.056). According to an earlier report, fire-involved as opposed to fire absent trees (Chen Wang and Jia 2017), especially those at upper locations, regulate photosynthesis to accent stress tolerance rather than growth. Our expectations of higher iWUEδ13C were confirmed at locations touched by fire in 1947 (*P*=0.004) shown in Table 1. Based on results obtained in another study (Kahl et al 2007), we conjectured differences in foliar N recalcitrancewould be minimal; in fact there was <5% difference in N availability among the four populations and δ15N was not a factor (*P*>.05). Likewise, foliar C/N ratios were not significantly different (*P*>.05).

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Table 1. Results from the mixed model analysis of variance for leaf C, leaf N, carbon to nitrogen ratios,** | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|  | **13C discrimination (δ13C) and 15N discrimination (δ15N)** | | | | | | | | | | | | | | | | |  | | |  | | |  | | | |  |
| Foliar analysis | | | Leaf C | |  | | Leaf N | |  | | Leaf C/N | |  | | δ13C | |  | | | δ15N | | |  | | | |  | |
|  | | |  | |  | |  | |  | |  | |  | |  | |  | | |  | | |  | | | |  | |
|  |  |  | |  | |  | |  | |  | |  | |  | |  | | |  | | |  | | |  |
|  | df | F | | P | | F | | P | | F | | P | | F | | P | | | F | | | P | | |  |
| Sites | 3 | 2.7439 | | **0.056** | | 0.8299 | | >.05 | | 0.676 | | >.05 | | 5.1792 | | **0.004** | | | 0.346 | | | >.05 | | |  |
| Residuals | 37 |  | |  | |  | |  | |  | |  | |  | |  | | |  | | |  | | |  |

**Foliar minerals**

Foliar mineral availability was significantly different at burned and unburned tree locations—those in the latter category featured significantly higher Ca (*P*<0.001), P (*P*=0.032), K (*P*<0.001) and Zn (*P*<0.008) noted in Table 2. Mg and Al contributions were not statistically different (*P*>0.05). At Gorham cliffs, based on our findings, we interpret elevation played an important role enhanced by pyrolytic recalcitrance. Despite determining substantially greater P availability at Gorham cliffs, that mineral along with N, were not significant factors attributed to growth in comparison with trees at another low elevation, Wonderland.

**Table 2. Results of Analysis of Variance (ANOVA) for foliar mineral nutrient**

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | | |  |  |  |  |  |  |  |  |  |  |  |
|  |  | Ca |  | P |  | K |  | Mg |  | Al |  | Zn |  |
|  | df | F | P | F | P | F | P | F | P | F | P | F | P |
| Sites | 3 | 6.623 | **0.001** | 3.198 | **0.032** | 6.825 | **0.001** | 2.0252 | >.05 | 0.102 | >.05 | 4.456 | **0.008** |
| Residuals | 37 |  |  |  |  |  |  |  |  |  |  |  |  |

**Allometry**

Depending on location, trees differed significantly in Tukey’s tests according to height growth (*P*=0.031), canopy width (*P*=0.035) and dbh (*P*=0.001) especially where fire exposure and elevation co-occurred. Individual tree subjects along South Cadillac ridge trail were substantially shorter, narrower in canopy and smaller in dbh than their three counterparts (Table 3). We hypothesized trees at lower, burned elevations would exhibit more substantial growth than upper elevation trees. This hypothesis was confirmed as greater availability of foliar C coupled with greater environmental stress was more likely to be used for stress resistance rather than growth at higher elevations.

|  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Table 3. Results from analysis of variance (ANOVA) for plant height, canopy and dbh** | | | | | | | | | | |
|  |  | | | | |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |  |  |
|  |  | Height (cm) |  | Canopy (cm) | | DBH (cm) | |  |  |  |
|  |  |  |  |  |  |  |  |  |  |  |
|  | df | F | P | F | P | F | P |  |  |  |
| Sites | 3 | 3.3319 | **0.03** | 3.1881 | **0.035** | 6.8211 | **<0.001** |  |  |  |
| Residuals | 36 |  |  |  |  |  |  |  |  |  |

We anticipated symmetry between allometry, foliar C and iWUEδ13C and that result materialized.

**Soil organics**

Soil C concentration was approximately two times greater at Wonderland and St. Sauveur (*m*=24.5%) trails compared to those at South Cadillac trail and Gorham cliffs (*m*=13.2%) with Wonderland three times higher than South Cadillac trail (*P*=0.023) noted in Table 4. Except for a lower soil N at South Cadillac trail (.28%) compared to the others (.51%), there was no significant difference (*P*>.05) in soil N between groups. However, in the case of soil C/N, differences were statistically significant (*P*=.039), owing to a greater disparity in C contributions amongst tree groups.

**Table 4. Results from analysis of variance (ANOVA) for soil C and N nutrient**

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | |  | | |  | | |  | | |  | | |  | |
|  | | | | C | | |  | | | N | | |  | | C/N | | | |  | |  |
|  | df | | F | | | P | | | F | | | P | F | | | | P |  | |
| Sites | 3 | | 3.726 | | | **0.023** | | | 0.7197 | | | >.05 | 3.2896 | | | | **0.039** |  | |

|  |  |
| --- | --- |
| Residuals 37 |  |
|  |  |

**Soil minerals**

Elevation gradients discriminated presence or absence of soil minerals; we found St. Sauveur and Wonderland, unburned populations, collectively held greater Ca, P and Mg deposits but only K (*P*=0.019) and Al (*P*=0.027) were significantly, statistically higher (Table 5). Comparatively higher P at Wonderland was consistent with higher growth output compared to the other sites consistent.

|  |  |
| --- | --- |
| **Table 5. Results from analysis of variance (ANOVA) for soil nutrient** |  |
| |  |  |  |  |  |  |  |  |  |  |  |  |  |  | | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | |  |  | Ca |  | P |  | K |  | Mg |  | Al |  | Zn |  | |  | df | F | P | F | P | F | P | F | P | F | P | F | P | | Sites | 3 | 2.691 | >.05 | 1.753 | >.05 | 3.908 | **0.019** | 1.234 | >.05 | 3.564 | **0.027** | 1.536 | >.05 | | Residuals | 37 |  |  |  |  |  |  |  |  |  |  |  |  | |  |

**Soil moisture retention**

In the stressed environment on MDI, soil moisture retention, especially during peak PAR (photosynthetic active radiation) months, is crucial to survival in competition with other, larger evergreens. In a previous paper, investigators (Licht and Smith 2020) examined moisture retention in a controlled study of pitch pine exposed to natural and prescribed fire treatments with the result that charcoal PyC effects were found to add considerably to water retention outcomes. However, elevation was not a factor in that study. At MDI, we found few subsurface charcoal remnants (as compared to reports by Laird in 1993); nevertheless we

**Table 6. Results from analysis of variance (ANOVA) soil water retention**

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | | | | | | | | |
| Water retention | | df | F | P |  |  |  |  |
| Sites |  | 3 | 9.671 | **<0.0001** |  |  |  |  |
| Residuals |  | 36 |  |  |  |  |  |  |

stipulate higher soil C, as noted at Gorham cliffs, significantly increased moisture retention (*P*<0.0001), which was 45% greater than its nearest unburned cohort, St. Sauveur found in Table 6 (we may want to show percentage differences between the sites in a table or figure).

**Topographical x biogeochemical data**

Nick you had suggested analyzing the matrix components separately in order to tease out more ideas for explaining results (for example where trees on flat ledges are performing significantly differently than their sloped cliff counterparts). Compass regimentation, nutrient availability and photosynthetic output were aligned at south-facing Wonderland and to a lesser extent at southeast-facing Cadillac South trail and Gorham cliffs. A combination of factors favored Gorham cliffs pitch pine verticality (greatest vertical, *µ*=6.2 m)—contrasted with south-facing Wonderland trees achieving the widest canopy and southeast oriented South Cadillac trail trees deporting by far the smallest allometrics

**Table 7. Topographical x Biogeochemical data**

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Stand | x | y |  | Elevation | Slope | Aspect | Compass |
| CADST | -68.221 | 44.328 |  | 239.3 | 10.5 | 127.1 | SE |
| GM CLIFFS | -68.185 | 44.327 |  | 33 | 17 | 142 | SE |
| STSAUV | -68.326 | 44.310 |  | 172 | 15 | 252 | W |
| WONDER | -68.314 | 44.231 |  | 16 | 3 | 188 | S |

**DISCUSSION** **[perhaps an additional graphic would work in this section]**

Our study is the first to explain pitch pine *Rcapacity* and *Bcapacity* at formerly fire-present and long time fire-absent MDI sites. Previous research catalogued plant physiology and foliar nutrient of the species at Wonderland trail (Butak 2014); in this paper we examine four distinct populations at decidedly different elevations and distance from the 1947 fire experience. Our central findings are as follows: first, we found a line of demarcation between population foliar nutrient and elevation gradients where intrinsic water use efficiency was most pronounced in colonies of pitch pine where growth is compelled to give way to stress inoculation. Second, results were tied to colonies in terms of their sparseness or density, their consolidation in retreat, or, alternately, solitary or small groups of trees where a combination of fierce drying winds, low temperatures and infertility limit establishment and likely less sharing of eco resources. Third, we found evidence that not only identified the basis for an underlying dichotomy but distinct examples of pioneering opportunities in different ecosystems both remote and too formidable for their competitors.

Essentially there is agreement amongst researchers and managers that it will be quite some time before fire reoccurs at MDI and then likely to be a minor nuisance compared to the earlier, catastrophic conflagration. Day *et al* (2005) concur, though there has been fuel buildup, emphasize higher summer and winter temperatures and moister autumns as the culprits for decline, rather than stand-replacing fire disturbance. Warming climate impacts the suitability of habitat and thus colonization tendencies of pitch pine to consolidate, regenerate or migrate (Day et al 2005; Lee *et al* 2019). Day Greenwood and White (2001) found an uptick in annual temperatures signaled increased leaf-air vapor pressure deficits, which negatively impact pitch pine stomata response and limit gas exchange. It is likely warming trends (Kunkel *et al* 2013) increase pitch pine difficulties in reproduction (Ledig Smouse and Hom 2015) and there is a suggestion of ‘mesophication’—negative feedback for shade intolerant trees (Nowacki and Abrams 2008) such as these. Recent climate change models anticipate negative impact on future vegetative status at MDI (Fernandez *et al* 2015) but the model does not specifically address the vicissitudes of pitch pine. However, Day *et al* 2005 suggest niche expansion is limited according to climate influence on loss of open space, a lack of enriched substrates and ‘safe sites’, though according to Niering (1987), constant climate change obviates the likelihood of an actual climax.

Some research (Butak 2014) points to photosynthesized C dedicated to growth rather than to stress resistance in flat, Wonderland trail ledges. Our findings confirm this result as well as opposite responses at South Cadillac trail and St. Sauveur trail. We theorized *Bcapacity* may be greater at the population level in Wonderland and Gorham cliffs where growth (rather than stress resistance) is most persistent; this theory reinforces the concept that charcoal availability is not pivotal to tree success. Specifically, investigators record St. Sauveur and Wonderland trail trees comprise denser and larger growing individuals; these are not attributable to charcoal effects. Findings by others appear to validate this impression based on reports of greater negative δ13C and higher soil moisture retention (Wang *et al* 2017; Chen, Wang and Jia 2017).One could argue that although charcoal remnants play a role in *Rcapacity* at burned-over communities at Cadillac Brook (well below the heights of South Cadillac trail) compared to nearby, lower, unburned Hadlock Brook, it does not appear to be a necessary benefactor to forest well-being. Scientists elsewhere ascribe importance to the agency of fire-induced sedimentary charcoal to produce soil C and N enrichment (Patel *et al* 2016) as measured in soil columns (Hart Horn and Grissino-Mayer 2008). This pattern was confirmed at burned sites near Cadillac mountain (Patterson Edwards and Maguire 1987; Laing 1993). We conjecture soil C persistence since the 1947 perturbance at burned-over areas such as South Cadillac trail reflects a failure of pyrogenic carbon removal (Doerr *et al* 2018), though elsewhere lower C availability is attributable to greater consumption by fungi (Luo *et al* 2017).

As to foliar N availability, scientists suggest acidified deposits may account for increased N deposition (Doerr *et al* 2018). This phenomenon is reported in fire-worn western pine forests (Pingree and DeLuca 2017). We noted lower foliar % N at Cadillac South trail than elsewhere and attribute post-fire loss to an ongoing lack of N sorption resulting from atmospheric N release (Patel *et al* 2019). Elsewhere, in pitch pine communities in New Jersey Pine Barrens, investigators report N is taken up by ectomycorrhizal pitch pine roots (Luo *et al* 2017) but there is some debate as to whether N in the form of NO3- is taken up by pitch pines at a meaningful level (Certini 2005). We lacked access to quantify those indicators at MDI, but suggest mineralization rates constitute a proxy for root N uptake, as others have asserted in δ15N measurement in pitch pine ecosystems (Inglett *et al* 2007).

We were unable to account for comparatively greater soil 15N at unburned sites (St. Sauveur, Wonderland) similar to those on Norumbega Mountain, portions of North Cadillac Mountain trail and lower South Cadillac trail. Limiting factor P provided clues as to niche capacity and chemical geography as discussed elsewhere (Verma and Jayakumar 2012); P availability at upper elevations at MDI contrasted with more modest availability at other, low-lying pinelands in New Jersey (Renninger *et al* 2013; Alkañiz *et al* 2018). Not surprisingly we were anxious to clarify why P sorption was so prominent in fire zone soils at South Cadillac trail, for example, in light of diminished growth there. One explanation for substantial P availability derives from an effect generated by charcoal remnants; however, lacking mycorrhizal studies we were unable to confirm the extent of P liberated from the charcoal working in tandem with ectomycorrhizal symbionts in 1947 fire precincts.

Our discussion of denser and taller trees at lower elevations is consistent with reports concerning non-glaciated populations in the New Jersey Pine Barrens (Mikita-Barbato *et al* 2015; Schafer and Bohrer 2016). Allowing for differences between disjunct communities, the authors found soil C and K alkali extractions were significantly higher for the Waterboro Barren cohort, with a decidedly greater disparity in available P, a limiting factor which tallied with % N (.39), is 50% higher than deposits at Cadillac South trail. Further, we note Mg and trace metal Zn (responsible for growth, enzyme and carbohydrate formation) micronutrient pulses at MDI thought to be associated with bedrock weathering occurred at a rate similar to earlier reports (Butak 2014). While foliar Zn was substantial at lower elevations availability grew fainter away from the coastline, up towards mountain summits, consistent with findings by others (Kolker *et al* 2013). However, in both Maine and New Jersey, *Rcapacity* may be illuminated by higher concentrations of foliar Ca, K, Mg, P, Al and Zn.

Increases in annual winter temperatures (Lesk *et al* 2017) coupled with an absence of fire (though not occult deposition) cause concern about a quite different disturbance—potential invasion within the next decade of a bark beetle, Southern pine beetle (*Dendroctonus frontalis* Zimmer). This pest (SPB) is already making its presence known in southern Massachusetts, Rhode Island and Connecticut to the south (Dodds *et al* 2018). Unless its progress is deterred by other insect predators (Coulson and Klepzig 2011) like double checkered clerid (*Thanasimus dubius*), it is possible pitch pines along with understory plants, butterflies and moth members of the Acadia ecosystem will suffer the same fate as others experience in more southerly locations (Lesk *et al* 2017). Trapping efforts at MDI, by the authors, in 2020, revealed no SPB presence. Other weather-related effects, including episodic drought, harsh winds and salt spray (Schmitt 2015; Fernandez *et al* 2015) and cold intolerance (Berang and Steiner 1985) are noted.

Day (personal communication) proposes still another factor which may modify *Rcapacity*, that is marine (occult) deposition on foliage and fall-through to bedrock derived from southeast and southerly mist and fog (Weathers *et al* 1986; Jagels *et al* 2002). It is reasonable to theorize nutrient aerosols trapped in foliage, or accumulating after fall-through onto weathered bedrock below, from summer to early fall deposition, affects maritime pitch pine ecosystems (Butak 2014). As with proximity to fire disturbance, we consider the likelihood there may be similarities in influence due to low elevations proximate to marine sources. Aside from the obvious presence of NaCl, we consider nitrate (NO3-) deposition from atmospheric sources—nitrate is measured by a spectrophotometer limit (acceptable at +/1 mg/L), in excessive quantities, above 10mg/L, at which point it is deemed toxic. Experiments are conducted in a pine barren to pinpoint contamination effects with titrated nitrate injections into ectomycorrhizae. However, experiments failed to boost aluminum toxicity (Shier and McQuattie 2008). At MDI, it would be helpful to determine the extent of NO3- presence as a function of microbial composition (Evans et al 2018) and quantify inhibition of pitch pine productivity.

Pitch pine is considered an important guardian of underlying heath communities at MDI; it is foundational as a necessary ecosystem component in a stressed environment, especially upper elevation cliffsides like South Cadillac trail. Rather than completely giving way to climate pressures, tree retreat into ever more sparse conditions reinforces their facilitator status (Connell and Slatyer 1977), as a species which explicitly maintains the livelihood of underlying flora through a sharing and distribution of ecoservices. Finally, our findings provide the means to enable forest management to discriminate between *Rcapacity* and *Bcapacity* impact on seedling recruitment (Patterson *et al* 2014). The National Park Service is tasked with promoting pitch pine as part of a long-term initiative—we provide data with which to inform decisions about which neighborhoods fall into a priority category to foster regeneration or encourage expansion or both. We furnish data to enable more accurate forecasts for how a particular intervention might be predicted to achieve a high-ranking objective.

**CONCLUSION**

We examined factors to enlighten scientific inquiry about the basis for pitch pine *Rcapacity* and *Bcapacity* according to variations in topographic gradients, selective preference for either growth to expand or stress tolerance to conserve, water use efficiency, soil moisture retention and selective retreat. We found pitch pine populations were buoyant, dedicating resources to accommodate contours and cliffs across elevation gradients and topography as they out-compete other evergreens. Our findings address a survival enigma taking place during a critical phase of the Anthropocene age, allowing the authors to provide insight to forest managers charged with preserving the future of these remarkable trees.

## Data Availability Statement

All data used in this article can be found at the following repository: <https://github.com/SmithEcophysLab/pitchpine/releases/tag/v1.0> (doi: [10.5281/zenodo.3600547](https://doi.org/10.5281/zenodo.3600547)).

## Author Contributions

JL and NS conceived the work, 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 in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved. JL carried out field collection, and conducted preparation for sample analysis at the EA-IRMS laboratory at Boston University under the direction of Robert Michener. At Texas Tech University, NS was responsible for performing C/N foliar evaluation, conducting statistical analyses and formulating figures and tables.

**ACKNOWLEDGEMENTS**

Professor Mike Day, University of Maine, lent critical expertise to selection of specific geographic sites used in the study. Cartographer Jill Phelps Kern created geospatial coordinate mapping. Remote sensing devices were supplied by Professor Tora Johnson, University of Maine. Field measurements were assisted by Mimi Licht and Laura Brumleve. Permitting, park data and accommodations were facilitated by Abraham Miller-Rushing, PhD, Emma Albee, Jesse Wheeler, William Gawley, PhD and Karen Anderson at Department of Interior, National Park Service, Mt. Desert Island, ME. Our thanks to several anonymous reviewers prior to submittal.

**ORCID**

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

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

**FUNDING INFORMATION**

This research was supported in part by funding at Texas Tech and a grant (P20AP00312) from the U.S. Department of Interior.

**REFERENCES**

Brand, F. and Jax, K. (2007). Focusing the meaning (s) of resilience: resilience as a descriptive concept and a boundary object. *Ecology and society*, *12*(1).

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

Butak, A. (2014). Vegetation Composition, Structure, and Ecophysiology of Maritime Ledge Ecosystems, University of Maine, Orono (<http://digitalcommons.library.umaine.edu/etd/2212>).

Caldwell, M. and J. Richards. 1989. Hydraulic lift: water efflux from upper roots improves effectiveness of water uptake by deep roots. *Oecologia,* 79, 1-5.

Carlo, N., Renninger, H., Clark, K., and Schäfer, K. (2016). Impacts of prescribed fire on Pinus rigida Mill. in upland forests of the Atlantic Coastal Plain. *Tree physiology*, *36*(8), 967-982.

Certini,G. (2005) Effects of fire on properties of forest soils: a review. *Oecologia* 143:1–10

Charpentier, J. (2020). Wildland Fire Disturbance - Recovery Dynamics in Upland Forests at Acadia National Park, Maine. Doctoral dissertation, Antioch University. <https://aura.antioch.edu/etds>

Chen Z,, Wang G. and Jia Y. (2017). Foliar d13C Showed No Altitudinal Trend in an Arid Region and Atmospheric Pressure Exerted a Negative Effect on Plant d13C, *Frontiers in Plant Science*, 8, 1-9.

Connell, J. and Slatyer, R. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist*, *111*(982), 1119-1144.

Coulson, R. and Klepzig, K. (2011). Southern Pine Beetle II. Gen. Tech. Rep. SRS-140. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 153-160.

Day, M., Schedlbauer, J., Livingston, Greenwood, M., White, M. and Brissette, J. (2005). Influence of seedbed, light environment, and elevated night temperature on growth and carbon allocation in pitch pine (*Pinus rigida*) and jack pine (*Pinus banksiana*) seedlings. *For Ecol & Manag*, *205*(1), 59-71.

Doerr, S., Santin, C., Merino, A., Belcher, C., and Baxter, G. (2018). Fire as a removal mechanism of pyrogenic carbon from the environment: effects of fire and pyrogenic carbon characteristics. *Frontiers in Earth Science*, *6*, 127.

Dunne, J., Saleska, S., Fischer, M. and Harte, J. (2004). Integrating experimental and gradient methods in ecological climate change research. *Ecology*, *85*(4), 904-916.

Evans, S., Dueker, M., Logan, J. and Weathers, K. (2019). The biology of fog: results from coastal Maine and Namib Desert reveal common drivers of fog microbial composition. *Science of the Total Environment*, *647*, 1547-1556.

Fernandez, I., Schmitt, C., Birkel, S., Stancioff, E., Pershing, A., Kelley, J., Runge, J., Jacobson, G. *et al* (2015). Maine’s climate future: 2015 update. University of Maine, Orono, ME. 24 pp.

Foereid, B., Lehmann, J., Wurster, C., and Bird, M. (2015). Presence of black carbon in soil due to forest fire in the New Jersey pine barrens. *J. Earth Sci. Eng.* 5, 91–97. doi: 10.17265/2159

Greenwood, M., Livingston, W., Day, M., White, A. and J. Brissette. (2002). Contrasting modes of survival by jack and pitch pine at a common range limit. *Canadian Journal of Forest Research*, 32, 1662-1674.

Gururani, M., Mohanta, T. and Bae, H. (2015). Current understanding of the interplay between phytohormones and photosynthesis under environmental stress. *International journal of molecular sciences*, *16*(8), 19055-19085.

Harris, T., Rajakaruna, N., Nelson, S. and P. Vaux. (2012). Stressors and threats to the flora of Acadia National Park, Maine: Current knowledge, information gaps, and future directions. *Journal of the Torrey Botanical Society*, 139 (3), 323-344.

Hart, J., Horn, S. and Grissino-Mayer, H. (2008). Fire history from soil charcoal in a mixed hardwood forest on the Cumberland Plateau, Tennessee, USA1. *The Journal of the Torrey Botanical Society*, *135*(3), 401-410.

Howard, L. and Stelacio, M. (2011). Fire and the development of high-elevation pitch pine communities in northeastern West Virginia. *Bulletin of the New Jersey Academy of Science*, *56*(2), 19-23.

Ibáñez, I., Acharya, K., Juno, E., Karounos, C., Lee, B. R., McCollum, C., ... & Tourville, J. (2019). Forest resilience under global environmental change: Do we have the information we need? A systematic review. *PloS one*, *14*(9), e0222207.

Inglett, P., Reddy, K., Newman, S., and Lorenzen, B. (2007). Increased soil stable nitrogen isotopic ratio following phosphorus enrichment: historical patterns and tests of two hypotheses in a phosphorus-limited wetland. *Oecologia*, *153*(1), 99-109.

Jagels, R., M. Jiang, S. Marden, and J. Carlisle. 2002. Red spruce canopy response to acid fog exposure. Atmos. Res 64:169–178

Jingfang, Q., and Wenwei, L. (2018). A survey about characteristics of soil water retention curve. In *IOP Conference Series: Earth and Environmental Science* (Vol. 153, No. 6, p. 062076). IOP Publishing.

Jordan, M., Patterson III, W. and Windisch, A. (2003). Conceptual ecological models for the Long Island pitch pine barrens: implications for managing rare plant communities. *Forest Ecology and Management*, *185*(1-2), 151-168.

Kahl, J., Nelson, S., Fernandez, I., Haines, T., Norton, S., Wiersma, G. ... and Rustad, L. (2007). Watershed nitrogen and mercury geochemical fluxes integrate landscape factors in long-term research watersheds at Acadia National Park, Maine, USA. *Environmental monitoring and assessment*, *126*(1-3), 9-25

Kunkel, K., L. Stevens, S. Stevens, L. Sun, E. Janssen, D. Wuebbles, and Dobson, J. (2013). Regional climate trends and scenarios for the US national climate assessment: Part 1. Climate of the Northeast United States. NOAA technical report NESDIS 142-1. Washington, DC. 87 pp.

Lafon, C., H. Grissino-Mayer, S. Aldrich, G. DeWeese, W. Flatley, L. La-Forest, and Hoss, J. (2014). Three centuries of Appalachian fire history from tree rings. Pp. 99–103 *in* T.A. Waldrop, ed., Wildland Fire in the Appalachians: Discussions among Managers and Scientists. General Technical Report SRS-199. USDA Forest Service, Southern Research Station, Asheville, NC

Lambers, H., Chapin, F. and Pons, T. (2006). Photosynthesis, respiration and long distance transport. In *Plant Physiology Ecology*: 11-99, Springer, New York.

Ledig, F., Smouse, P. and Hom, J. (2015). Postglacial migration and adaptation for dispersal in pitch pine (Pinaceae). *American journal of botany*, *102*(12), 2074-2091.

Lee, C., Robinson, G., Robinson, I., and Lee, H. (2019). Regeneration of pitch pine (Pinus rigida) stands inhibited by fire suppression in Albany Pine Bush Preserve, New York. *Journal of forestry research*, *30*(1), 233-242.

Lesk, C., Coffel, E., D'Amato, A., Dodds, K., and Horton, R. (2017). Threats to North American forests from southern pine beetle with warming winters. *Nat. Clim. Change* 7, 713–717. doi: 10.1038/nclimate3375

Licht, J. and Smith, N. (2018). The influence of lignocellulose and hemicellulose biochar on photosynthesis and water use efficiency in seedlings from a Northeastern US pine-oak ecosystem. *Journal of Sustainable Forestry*, *37*(1), 25-37.

Licht, J. and Smith, N. (2020). Pyrogenic Carbon Increases Pitch Pine Seedling Growth, Soil Moisture Retention, and Photosynthetic Intrinsic Water Use Efficiency in the Field. *Frontiers in Forests and Global Change*, *3*, 31.

Lubinski, S., Hop, K., & Gawler, S. (2003). US Geological Survey-National Park Service Vegetation Mapping Program, Acadia National Park, Maine. *Project Report*.

Luo, J., Walsh, E., Miller, S., Blystone, D., Dighton, J., and Zhang, N. (2017). Root endophytic fungal communities associated with pitch pine, switchgrass, and rosette grass in the pine barrens ecosystem. Fung. Biol. 121, 478–487. doi: 10.1016/j.funbio.2017.01.005

McDowell, N., Allen, C., Anderson-Teixeira, K., Aukema, B., Bond-Lamberty, B., Chini, L., ... & Hurtt, G. 2020. Pervasive shifts in forest dynamics in a changing world. *Science*, *368* (6494).

Miller, K., Mitchell, B., Curtin, P. and Wheeler, J. 2014. Forest Health Monitoring, Northeast Temperate Report, 2006-2013 NPS/NETN. <https://www.amazon.com/stream>

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

Mosseler, A., Rajora, O. and Major, J. (2004). Reproductive and genetic characteristics of rare, disjunct pitch pine populations at the northern limits of its range in Canada. *Conservation Genetics*, *5*(5), 571-583.

Niering, W. (1987). Vegetation dynamics in relation to plant community management. *Conservation Biology*, 1 (4), 287-295.

Nowacki, G., and Abrams, M. (2008). The demise of fire and “mesophication” of forests in the eastern United States. *Bioscience* 58, 123–138.

Parker, J., Fernandez, I., Rustad, L., and Norton, S. (2001). Effects of nitrogen enrichment, wildfire, and harvesting on forest-soil carbon and nitrogen. *Soil Science Society of America Journal*, *65*(4), 1248-1255.

Parshall, T., Foster, D., Faison, E., MacDonald, D., and Hansen, B. (2003). Long-term history of vegetation and fire in pitch pine–oak forests on Cape Cod, Massachusetts. *Ecology* 84, 736–748. doi: 10.1890/0012-9658(2003)084

Patel, K., Jakubowski, M., Fernandez, I., Nelson, S., and Gawley, W. (2019). Soil Nitrogen and Mercury Dynamics Seven Decades After a Fire Disturbance: a Case Study at Acadia National Park. *Water, Air, & Soil Pollution*, *230* (2), 29.

Patterson, T., Maxwell, R., Harley, G., Oliver, J., Speer, J., Collins, S., ... & Russell, C. (2016). Climate–Growth Relationships of Pinus rigida (Mill.) at the Species’ Northern Range Limit, Acadia National Park, ME. *Northeastern naturalist*, *23*(4), 490-500.

Patterson, III, W., Saunders, K. and Horton, L. (1983). Fire regimes of the coastal Maine forests of Acadia National Park. U.S. Department of the Interior, National Park Service, North Atlantic Region, Office of Scientific Studies, Boston, Mass. Publ. OSS 83-3.

Patterson, III, W., Edwards, K. and Maguire, D. (1987). Microscopic charcoal as a fossil indicator of fire. *Quaternary Science Reviews*, *6*(1), 3-23.

Pingree, M. and DeLuca, T. (2017). Function of wildfire-deposited pyrogenic carbon in terrestrial ecosystems. *Frontiers in Environmental Science*, *5*, 53.

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

Renninger, H., Clark, K., Skowronski, N. and Schäfer, K. (2013). Effects of a prescribed fire on water use and photosynthetic capacity of pitch pines. *Trees*, *27*(4), 1115-1127.

Shakesby, R. and Doerr, S. (2006). Wildfire as a hydrological and geomorphological agent. *Earth-Science Reviews*, *74*(3-4), 269-307.

Schier, G. and McQuattie, C. (1996). Response of ectomycorrhizal and nonmycorrhizal pitch pine (Pinus rigida) seedlings to nutrient supply and aluminum: growth and mineral nutrition. *Canadian journal of forest research*, *26*(12), 2145-2152.

Stambaugh, M., J. Varner, R. Noss, D. Dey, N. Christensen, R. Baldwin, R. Guyette, B. Hanberry *et al*. 2015. Clarifying the role of fire in the deciduous forests of eastern North America: Reply to Matlack. *Conservation Biology* 29:942–946

Star, J., Fisichelli, N., Bryan, A., Babson, A., Cole-Will, R. and Miller-Rushing, A. (2015). Acadia National Park climate change scenario planning workshop summary, National Park Service.

Swanston, C., Brandt, L., Janowiak, M., Handler, S., Butler-Leopold, P., Iverson, L., et al. (2018). Vulnerability of forests of the Midwest and Northeast United States to climate change. *Clim. Change* 146, 103–116. doi: 10.1007/s10584-017-2065-2

Szpakowski, D. and Jensen, J. (2019). A review of the applications of remote sensing in fire ecology. *Remote Sensing*, *11*(22), 2638.

Verma, S., & Jayakumar, S. (2012). Impact of forest fire on physical, chemical and biological properties of soil: A review. *Proceedings of the International Academy of Ecology and Environmental Sciences*, *2* (3), 168.

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

Weathers, K., Likens, G., Bormann, F., Eaton, J., Bowden, W., Andersen, J., ... & Huth, P. (1986). A regional acidic cloud/fog water event in the eastern United States. *Nature*, *319* (6055), 657-658.

Wright, I., Reich, P., Westoby, M., Ackerly, D., Baruch, Z., Bongers, F., ... & Flexas, J. (2004). The worldwide leaf economics spectrum. *Nature*, *428*(6985), 821-827.