# Oak at the Edge

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*You can access my codes here:* https://github.com/mykhanh0504/rxfire-oak

## Introduction

### *Quercus rubra* regeneration landscape at present

*Quercus rubra* L. (hereafter *Q. rubra*) is an economically and ecologically important tree species in the northeastern United States. It is a fast-growing species and thrives on a wide range of upland soils (Abrams 1992). Additionally, it is tolerant of heat, drought, and even ground fire (Abrams 2000). *Q. rubra* produces high-quality timber with high wood density, making it an important lumber commodity and prompting forest managers to be concerned with its sustainable regeneration (Dey and Schweitzer 2018). *Q. rubra* is managed for other ecological purposes as well. For example, it serves as a habitat and food source for many wildlife species, from birds like turkeys and jays to mammals like mice, squirrels, and deer, and even insects like weevils (Mcshea et al. 2007). *Q. rubra* drives their population dynamics with its high mast production occurring about every two years.

*Q. rubra* currently faces many regeneration challenges in the northeastern United States, and its recruitment will continue failing without timely and appropriate interventions. One such challenge is acorns becoming a major hard mast source for wildlife consumption since the demise of American chestnut and the spread of beech bark disease. This high seed predation deters successful advance regeneration outside of mast years (Mcshea et al. 2007). Moreover, if seeds are buried under a thick litter layer, the seed radicle may struggle to reach the mineral soil, and this can negatively affect epicotyl emergence (Arthur et al. 2012). Even when seedlings are established, they risk getting eaten, especially by deer (Mcshea et al. 2007). *Q. rubra* is also susceptible to some fungal pathogens including *Phytophthora* and *Armillaria*, which cause sudden oak death and Armillaria root rot respectively. Lastly, its shade intolerance retards its seedling recruitment when there is insufficient light in the understory (Nowacki and

Abrams 2008). Seedling growth might be slow due to competition from more shade-tolerant species such as *Acer rubrum* and *Fagus grandifolia*.

### Fire-oak hypothesis

Abrams (1992) hypothesized that prescribed fire might be crucial for oak regeneration. Fire has been integral to upland oak systems in the eastern United States for millennia. Pre-settlement fires occurred as a function of lightning strikes as well as native activities such as cooking, heating, seedbed preparation, hunting, ceramic manufacture, and communication. Burning continued with European settlement and pitched oak as the dominant species in periodically burned areas (Abrams 1992). Over time, *Q. rubra* became much more adapted to a periodic fire regime than other hardwoods and, as a result, can take advantage of the postfire environment. However, fire suppression became mainstream policy in the 1920s and promoted forest mesophication (Nowacki and Abrams 2008). As the eastern landscape becomes wetter and more shady, mesic microenvironmental conditions improve and favor the regeneration of shade-tolerant species. This positive feedback loop shrinks suitable habitats for shade-intolerant, fire-adapted species like *Q. rubra* over time. Therefore, it has been argued that it is necessary to bring back fire in a controlled manner to reverse the feedback loop and restore the upland oak ecosystems (Abrams 1992).

### Adaptive silviculture

The other important consideration for oak regeneration is that *Q. rubra* is projected to move further northward due to climate change (Peters et al. 2020). In New England, its distribution is projected to increase substantially by 2100 under both RCP 4.5 and 8.5 scenarios due to high adaptability. Nevertheless, adaptive silviculture can be implemented to ensure a seamless transition for the species north of its current range limit and contribute towards long-term resilience on the stand level (Nagel et al. 2017). Methods range from different ways of thinning and artificial planting to prescribed burns and combinations of them. Many previous studies have demonstrated that fire, alone or when combined with thinning, strengthens or re-establishes its dominance in different ecosystems by playing to its fire resistance and easing other regeneration limitations (e.g., Iverson et al. (2008), Granger et al. (2018), Bassett et al. (2020), Dee et al. (2022)). My study will build on this research and further explore its role in oak range expansion.

### Research questions and hypotheses

Six pairs of burn and control forest stands from four locations across the White Mountains ecoregion are picked for my study. They are part of a novel landscape-scale project implemented by the USFS over the past decade. There is a gradient of burn intensities and silvicultural treatments represented among these locations, along with variable burn intensity at smaller spatial scales within each stand. Assessment of how these factors have affected oak regeneration success will help to inform management considerations. The applied silvicultural prescriptions were all targeted towards oak regeneration, and my study investigates their results to answer the research questions below:

**Q1:** Does prescribed fire promote the recruitment of *Q. rubra* seedlings relative to other forest management practices, and if so, what mechanisms are at play?

**H1:** *Q. rubra* possesses fire-tolerant traits that give them an edge over more mesophytic species such as thick bark and deep roots (Abrams 1992). Mother oak trees hence have greater survival rates, giving them more time and better chances at reproducing while their competitors experience dieback (Dey and Schweitzer 2018). Prescribed fire burns can promote oak regeneration at any and all critical life stages including pollination, flowering, seed set, and germination (Arthur et al. 2012).

**Q2:** Does prescribed fire improve the growth of *Q. rubra* seedlings relative to other forest management practices, and if so, what key mechanisms are at play?

**H2:** Fire temporarily increases available nitrogen pools (Wan et al. 2001) and fluxes (Wang et al. 2014) and seedlings can take advantage of them to grow faster. Additionally, fire reduces pathogen loads that can negatively affect seedling growth (Filip and YangErve 1997). Once reaching an appropriate height and an appropriate density, *Q. rubra* seedlings can be more competitive against their mesophytic counterparts (Iverson et al. 2008).

## Methods

### Study sites

The selected pairs of burn and control forest stands for this study are paired by project and treatment date, with one stand harvested and the paired site harvested and burned (Table A, Figure 1). One pair does not have any notable management history, and its burn stand experienced wildfire instead. There is a gradient of burn intensities and silvicultural treatments represented among these projects, along with variable burn intensity at smaller spatial scales within each unit most probably due to topographical variables.

Table 1: Stand pairs in each study site

| Pair | Stand | Burn year | Harvest year | Harvest treatment |
|---|---|---|---|---|
| 1 | Stevens Brooks `SB_3/16B` | 2017 | 2010 | Shelterwood |
| 1 | `SB_5/15C` | - | 2011 | Shelterwood |
| 2 | Hogsback `HOG_20/2B` | 2017 | 2012 | Seedtree |
| 2 | `HOG_3/1C` | - | 2012 | Seedtree |
| 3 | Hogsback `HOG_28/2B` | 2018 | 2014 | Shelterwood |
| 3 | `HOG_12/2C` | - | 2013 | Shelterwood |
| 4 | Crawford Notch State Park `CF_B` | 2022 | - | - |
| 4 | `CF_C` | - | - | - |
| 5 | Bartlett Experimental Forest `BEF_44B` | 2021 | 2019 | Clearcut |
| 5 | `BEF_45C` | - | 2019 | Clearcut |
| 6 | Bartlett Experimental Forest `BEF_46B` | 2021 | 2019 | Clearcut |
| 6 | `BEF_46C` | - | 2019 | Clearcut |

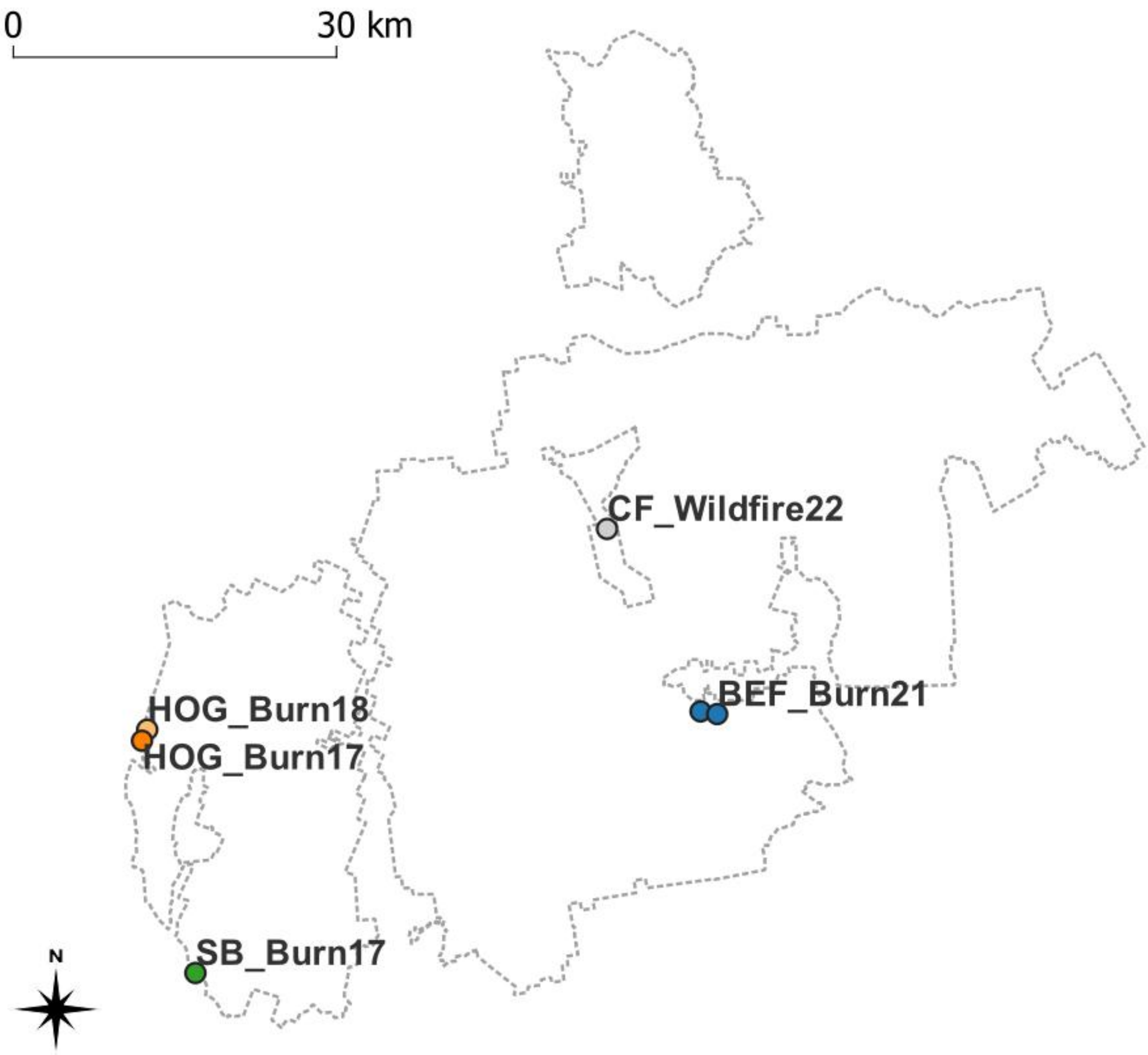


Figure 1: Map of the study sites

**Field data collection**

**Site characterization**

In summer 2023, a number of transects (anywhere between 50 and 225 m long) were laid 30 to 50 m apart in each study stand; they are either parallel or perpendicular from each other. They are marked by wooden stakes every 25 m. Along a transect is a series of 1 m² quadrats (hereafter referred to as “plots”) spaced 10 m apart from their centers. In total, there were 43 transects laid in 6 pairs of burn-control stands, amounting to 393 plots. Percent slope, aspect, microtopography, burn evidence, and oak litter presence were recorded for each plot. Percent slope was determined with a hypsometer and later validated with topography maps, and aspect with a compass. Microtopography was described qualitatively, using remarks like “slight slope,” “steep slope,” “mid slope,” “concave,” and “convex.” Burn evidence was confirmed with charcoal presence. Percent cover was estimated for bareground, woody debris, leaf litter, rock (which should all amount to 100%), as well as live vegetation at breast height and below. Woody species with diameter at breast height (DBH) smaller than 2 cm were identified and their stems counted.

### Oak seedling measurements

If oak seedlings were present, they were tagged, aged, measured for height (cm) and diameter at root collar (DRC, mm), and checked for evidence of herbivory and pathogen damage. In summer 2024, they were resurveyed twice, once at the beginning and again at the end, to capture growth between the two growth seasons and within this season alone. More variables were added to this survey, including number of leaves and number of live and dead branches. Herbivory and pathogen damage were quantified percentage-wise as well as described qualitatively.

In the 5 m radius of each plot, trees were identified and measured for DBH, providing they were 2cm or larger. The number of oak seedlings was also counted. In summer 2024, oak seedling abundance was re-estimated twice, once at the beginning and again at the end of the season.

### LAI measurements

During the peak of the 2024 growth season, leaf area index (LAI) measurements were carried out at the center of each plot to quantify the amount of leaf material in its canopy. The LI-COR LAI-2200C Plant Canopy Analyzer was propped at knee height to simulate the light availability to seedlings and faced away from the sunlight direction. LAI data will be matched, calibrated, and analyzed using the LI-COR FV2200 software.

### Data visualization and analysis

Understory competition and overstory composition were visualized by bar graphs to illustrate the stand structures of each sites. Together with the annual 5-m radius oak seedling counts, these plot-level stem counts and estimated basal areas were scaled up to the stand level of per hectare. Box plot graphs of seedling counts and various abovementioned growth measurements as well as LAI measurements were also constructed. Suitable statistical analyses, mostly ANOVA with blocking, were carried out for each response variable to test if prescribed fire had an effect on them, and if so, whether it was significant. The entirety of data visualization and analysis took place in RStudio using multiple packages cited below.

## Results

Table 2: Species codes

| Species code | Scientific name | Common name |
|---|---|---|
| ABBA | *Abies balsamea* | Balsam fir |
| ACPE | *Acer pensylvanicum* | Striped maple |
| ACRU | *Acer rubrum* | Red maple |
| ACSA | *Acer saccharum* | Sugar maple |
| BEAL | *Betula alleghaniensis* | Yellow birch |
| BEPA | *Betula papyrifera* | Paper birch |
| BEPO | *Betula populifolia* | Gray birch |
| FAGR | *Fagus grandifolia* | American beech |
| FRAM | *Fraxinus americana* | White ash |
| OSVI | *Ostrya virginiana* | American hophornbeam |
| PIRU | *Picea rubens* | Red spruce |
| PIST | *Pinus strobus* | White pine |
| POGR | *Populus grandidentata* | Bigtooth aspen |
| POTR | *Populus tremuloides* | Quaking aspen |
| PRPE | *Prunus pensylvanica* | Pin cherry |
| PRSE | *Prunus serotina* | Black cherry |
| RUS | *Rubus spp.* | Brambles genus, including raspberries and blackberries |
| QURU | *Quercus rubra* | Northern red oak |
| TIAM | *Tilia americana* | American basswood |
| TSCA | *Tsuga canadensis* | Eastern hemlock |

### Stand characterization

### Understory competition

In burned stands, *Q. rubra* mainly competes with early successional seedlings e.g. *Rubus spp.* `RUS`, *A. rubrum* `ACRU`, *B. alleghaniensis* `BEAL` and stump sprouts e.g. *F. grandifolia* `FAGR`.

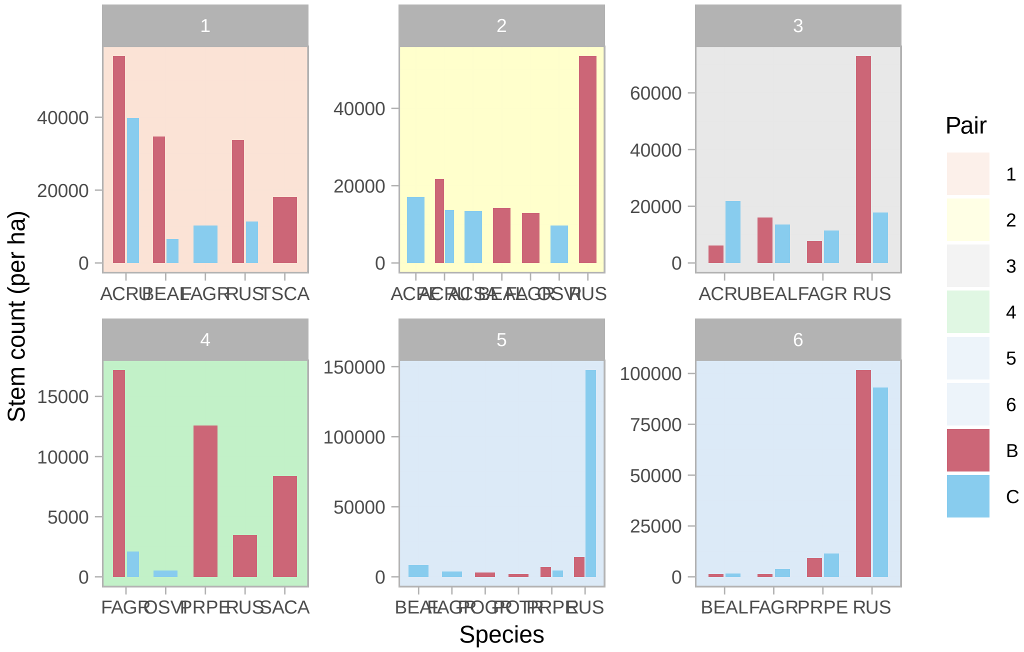


Figure 2: Stem density (per ha) of understory species in study stands

**Overstory composition**

Burn stands have lower overstory basal areas than control stands. Pairs 5 and 6 stand out especially due to their clearcut treatment i.e. absence of mature trees of 20 cm and above in DBH. Their compositions are also the least diverse, consisting of *Prunus* (`PRPE`,`PRSE`), *Populus* (`POGR`,`POTR`), and *Betula spp.* (`BEAL`,`BEPO`,`BEPA`). The remaining stands have a significant presence of mature *Q. rubra* as well as *Acer* and *Betula* spp. of mid-ranged DBH classes. Additionally, Pair 1's overstory composition includes a large basal area of high-DBH *Pinus strobus* `PIST`.

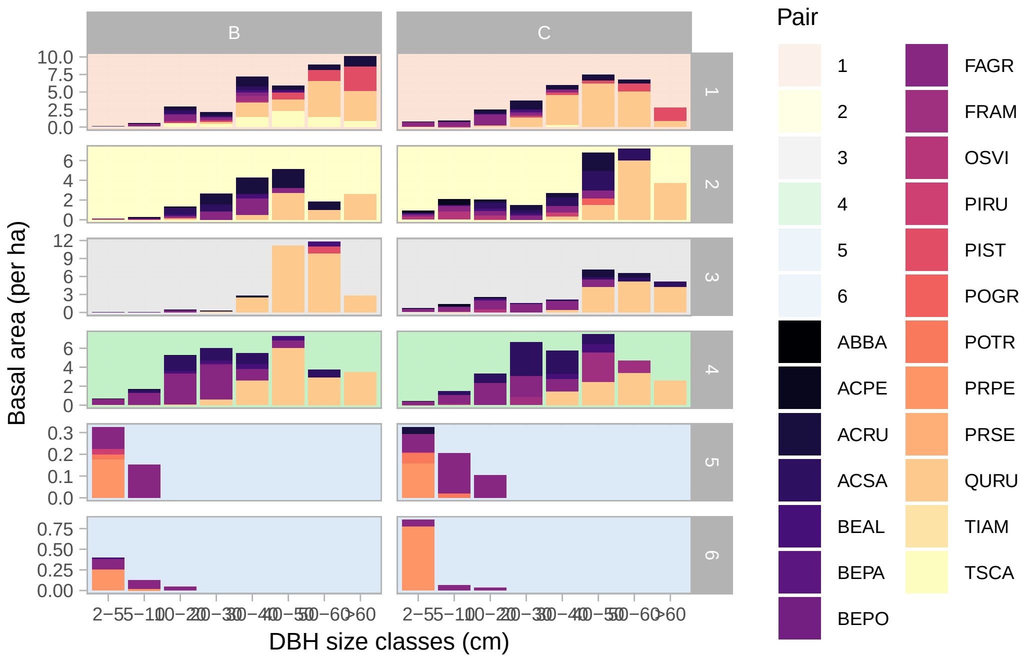


Figure 3: Basal area (per ha) of overstory species in study stands by DBH size classes

## Oak seedling density and measurements

### 2023 oak seedling density

Seedling density increased threefold in burned stands (2359+/-211 per ha) relative to control stands (778+/-121 per ha, $p<0.001$).

Table 3: Summarized statistics of 2023 oak seedling density per ha

| Disturbance | min | max | median | mean | sd | se |
|---|---|---|---|---|---|---|
| B | 0 | 17189 | 1146 | 2359.163 | 3045.723 | 211.183 |
| C | 0 | 12096 | 0 | 777.793 | 1637.060 | 120.686 |

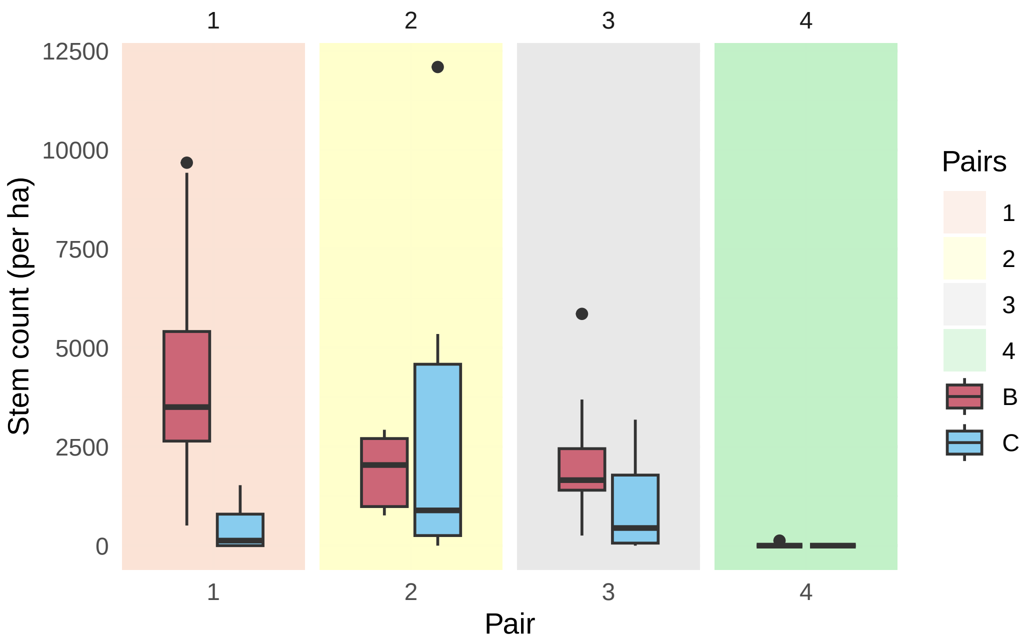


Figure 4: 2023 oak seedling density per ha of study stands

**2023 diameter at root collar (DRC, mm)**

DRC was greater for seedlings in burned stands (4.6+/-0.3 mm) versus control stands (3.3+/-0.3 mm, $p<0.01$).

Table 4: Summarized statistics of 2023 oak seedling measurements

| Disturbance | variable | min | max | median | mean | sd | se |
|---|---|---|---|---|---|---|---|
| B | Height_cm | 5.00 | 182.00 | 13.750 | 24.314 | 25.944 | 2.349 |
| B | DRC_mm | 1.05 | 17.54 | 3.650 | 4.614 | 3.161 | 0.286 |
| B | nlive_branches | 1.00 | 18.00 | 2.000 | 3.022 | 3.119 | 0.331 |
| B | ndead_branches | 0.00 | 35.00 | 2.000 | 3.079 | 4.969 | 0.527 |
| C | Height_cm | 4.30 | 184.00 | 14.000 | 19.780 | 25.619 | 3.178 |
| C | DRC_mm | 1.12 | 17.37 | 2.875 | 3.348 | 2.297 | 0.287 |
| C | nlive_branches | 1.00 | 4.00 | 1.000 | 1.327 | 0.585 | 0.081 |
| C | ndead_branches | 0.00 | 7.00 | 1.000 | 1.385 | 1.402 | 0.194 |

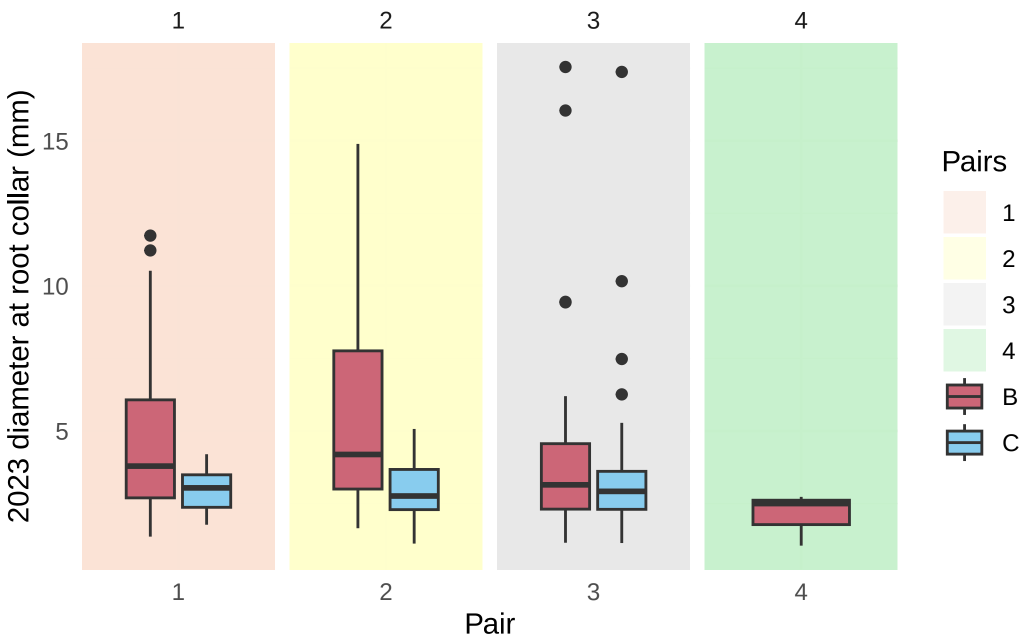


Figure 5: 2023 seedling DRCs by study stands

**2024 extension growth (cm)**

Extension growth was greater for seedlings in burned stands (6.43+/-0.5 cm) versus control stand (2.6+/-0.4 cm, p<0.001).

Table 5: Summarized statistics of 2024 oak seedling measurements

| Disturbance | variable | min | max | median | mean | sd | se |
|---|---|---|---|---|---|---|---|
| B | Height_cm | 1.55 | 263.00 | 18.00 | 31.105 | 35.808 | 2.465 |
| B | Extension_growth_cm | 0.00 | 38.00 | 3.50 | 6.432 | 7.306 | 0.503 |
| B | DRC_mm | 0.86 | 27.58 | 3.92 | 5.170 | 3.939 | 0.271 |
| B | nleaves | 2.00 | 100.00 | 8.00 | 15.864 | 20.540 | 1.414 |
| B | nlive_branches | 1.00 | 38.00 | 2.00 | 3.578 | 4.398 | 0.303 |
| B | ndead_branches | 0.00 | 37.00 | 2.00 | 3.858 | 5.983 | 0.412 |
| C | Height_cm | 6.00 | 225.00 | 15.00 | 21.414 | 29.999 | 2.773 |
| C | Extension_growth_cm | 0.00 | 40.30 | 1.60 | 2.622 | 4.190 | 0.387 |
| C | DRC_mm | 1.44 | 22.55 | 2.85 | 3.530 | 2.937 | 0.272 |
| C | nleaves | 2.00 | 100.00 | 4.00 | 6.940 | 12.943 | 1.197 |
| C | nlive_branches | 0.00 | 31.00 | 1.00 | 1.880 | 2.986 | 0.276 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| C | ndead_branches | 0.00 | 25.00 | 2.00 | 2.410 | 3.265 | 0.302 |

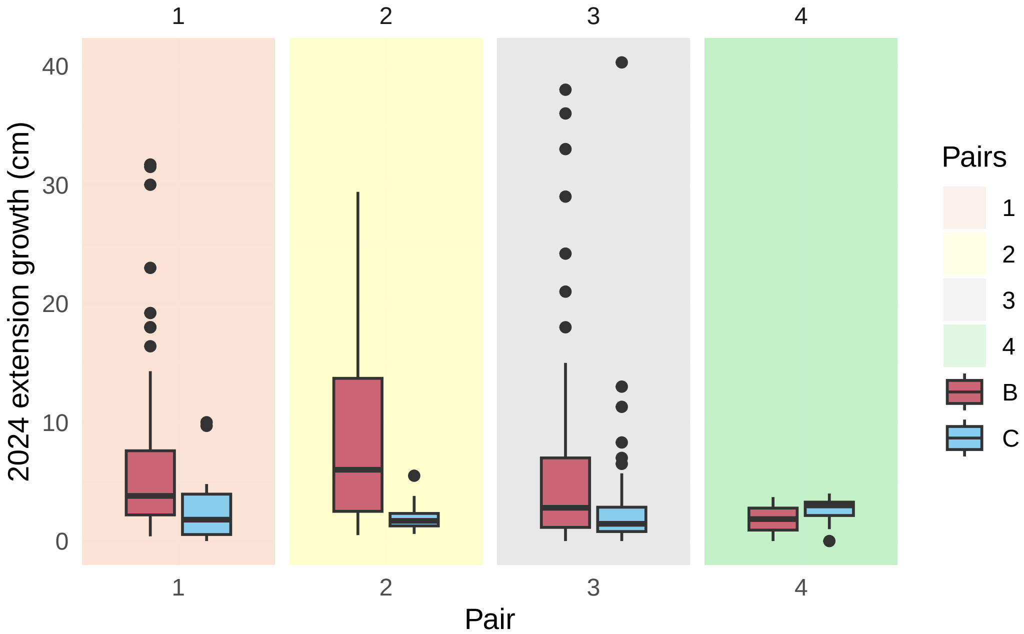


Figure 6: 2024 seedling extension growths by study stands

**2024 number of live branches**

There were more live branches per seedling in the burned stands than the control stands, respectively 4+/-0 and 2+/-0 (p<0.001).

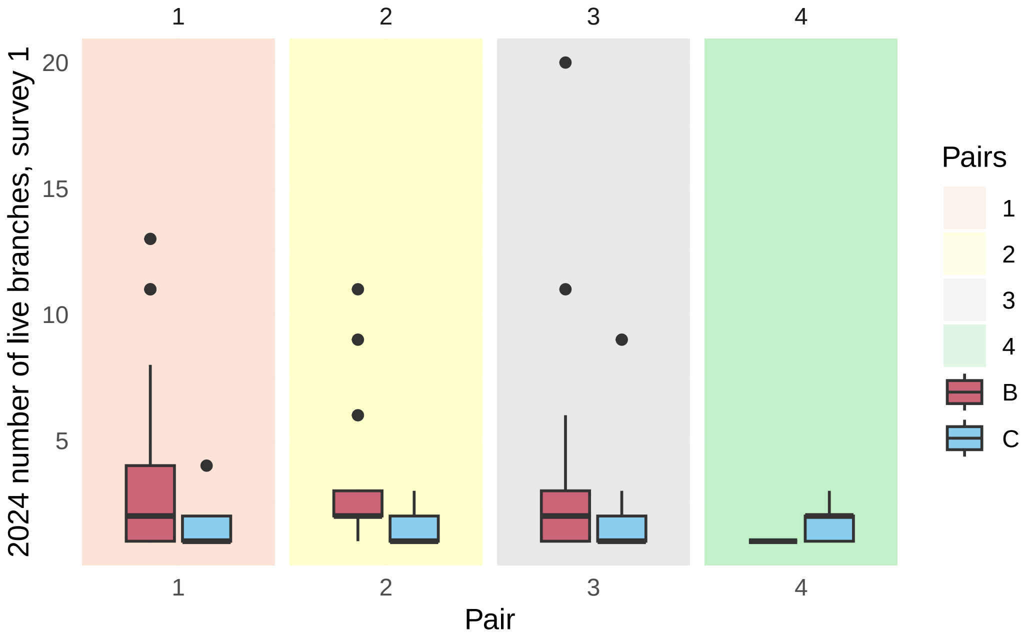


Figure 7: 2024 number of live branches per seedling by study stands and surveys

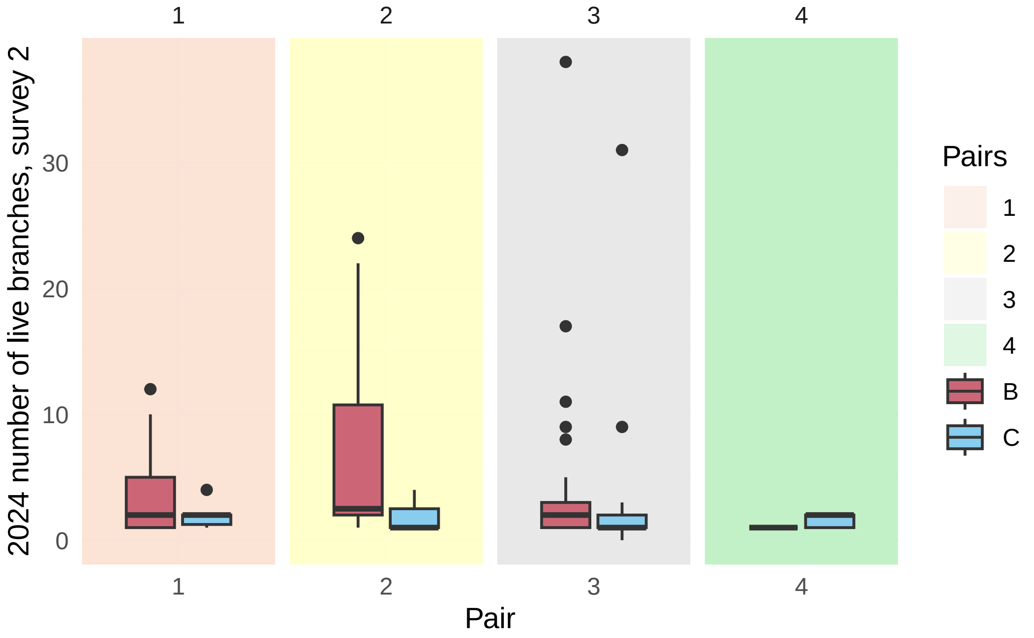


Figure 8: 2024 number of live branches per seedling by study stands and surveys

**2024 number of leaves**

Seedlings in burned stands sprouted more leaves (16+/-1) than in control stands (7+/-1, p<0.001).

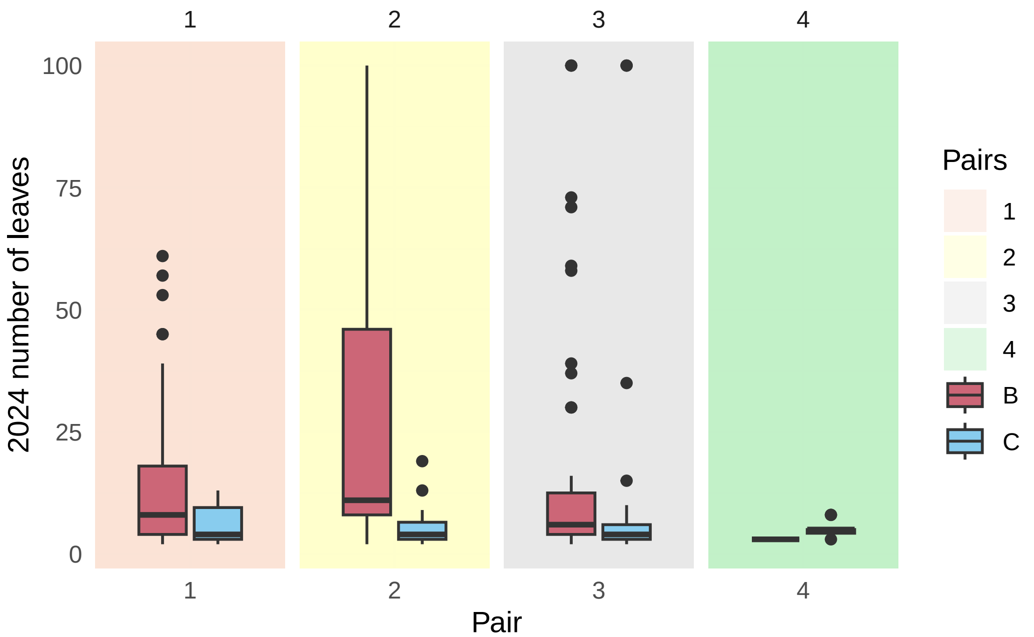


Figure 9: 2024 number of leaves per seedling by study stands

### Leaf Area Index (LAI)

Burned stands have lower LAI values (averaging 3.2+/-0.2) than control stands (5.4+/-0.2, p<0.001).

Table 6: Summarized statistics of LAI values

| Disturbance | min | max | median | mean | sd | se |
|---|---|---|---|---|---|---|
| B | 0 | 9.233 | 2.928 | 3.159 | 2.136 | 0.150 |
| C | 0 | 9.825 | 5.915 | 5.400 | 2.347 | 0.176 |

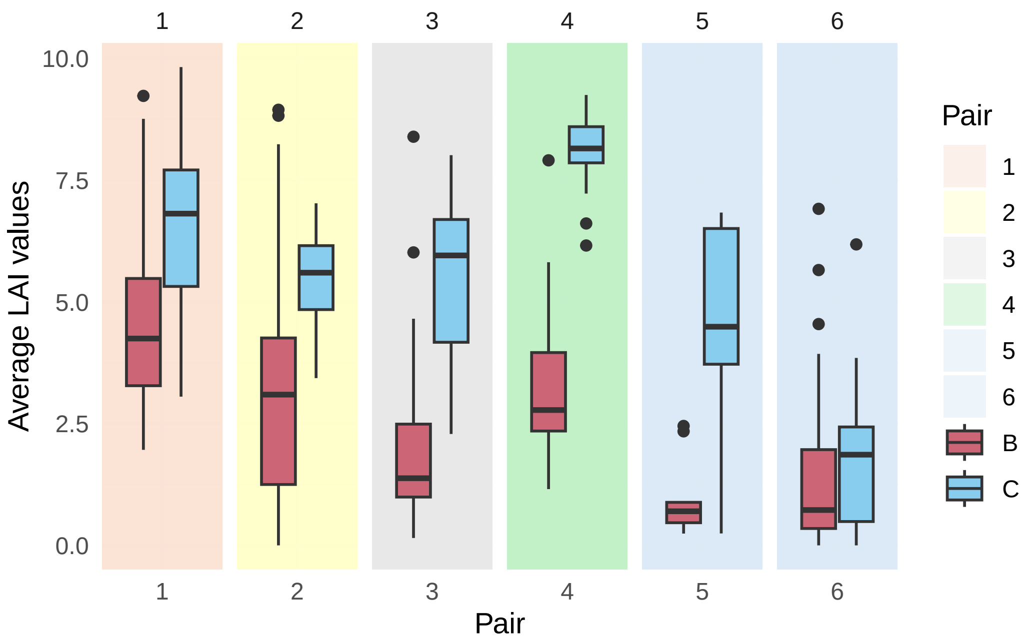


Figure 10: LAI values by study stands

## Discussion

### *Q. rubra* seedling recruitment by prescribed fire

*Q. rubra* seedling density in burned stands is triple that in control stands, supporting the hypothesis that prescribed fire promotes seedling recruitment (Figure 4). The different cutting treatments did not have significant effects on such recruitment. When these cutting treatments took place, management intentionally left behind mostly *Q. rubra* trees in the highest DBH size classes (Figure 3). The mother trees survived the burns better than their mesophytic competitors and possibly took advantage of their regrowth time to reproduce (Dey and Schweitzer

2018). Their survival rates are higher due to thicker barks and rapid compartmentalization, among other factors. There is evidence that acorn production is positively correlated to tree vigor i.e full-crowned dominant trees of larger DBHs produce more acorns (Bogdziewicz et al. 2020). Even though acorn production is also dependent on tree genetics (Smith et al. 2022), meaning that “good” producers are more likely to yield larger crops, thinning and burning to release the healthiest-looking individuals raises the chance of achieving better yields.

Additionally, fire can alter soil resource supply by accelerating nutrient cycling and hence releasing more of them (Chapin and Vitousek 2012). A sudden increase in nitrogen availability in the nitrogen-limited temperate forest (Bae et al. 2015) may help promote flowering and acorn production (Callahan et al. 2008). In terms of acorn germination success, fire is assumed to decrease acorn herbivory, which can lead to nonviable seeds or low-vigor seedlings, by interfering with insects’ life cycle portions spent in the soil (Riccardi et al. 2004). Another benefit fire provides is lessening the litter thickness, which in turns aids root penetration and avoids long and weak stems growing through thick litter (Hutchinson et al. 2024).

It is also worth evaluating fire effects on competitors at the germination and seedling establishment stage. Fire can reduce seed bank abundance (Schuler et al. 2010), but it is more likely that the seed bank remains abundant after one-time burns like in our study. In the understory, early successional seedlings are plentiful, mostly comprising *Rubus spp.*, *A. rubrum*, and *Betula spp.* (Figure 2). The latter two produce high volumes of wind-dispersed seeds that germinate well in the postfire exposed mineral soil. *A. rubrum*, together with *F. grandifolia*, also have strong sprouting responses to disturbances. Prescribed burns can only be considered an effective management tool for *Q. rubra* regeneration if their effects are net positive.

### ***Q. rubra*** **seedling growth promoted by prescribed fires**

Diameter at root collar and extension growth are significantly greater for *Q. rubra* seedlings in burned stands versus control stands (Figures 5-6). Seedlings in burned stands also have more leaves and live branches (Figures 7-9). They might have grown bigger diameter-wise by taking advantage of the temporary increases in available nitrogen pools (Wan et al. 2001) and fluxes (Wang et al. 2014) immediately after fires to store carbon into the stems. On the other hand, the significantly larger annual extension growths and leaf and branch sproutings in the past two summers imply that the positive fire effects still linger 3-7 years post-treatment. Forest recovery generally takes decades after a major disturbance. Cuevas-González et al. (2009) found that effect duration is dependent on the dominant forest type. Yang et al. (2017) echoed the same sentiments, highlighting that stands in higher latitudes experience it for longer. Other variables include vegetation density, richness, and abundance: dense areas tend to recover slower while plant species richness and abundance increase with more time elapsed since fire (Smith-Ramírez et al. 2022).

While mesophytic competitors experience dieback and invest their resources in regrowing, *Q. rubra* seedlings make use of nutrients, space, and light that are more available than ever (Figure 10) to grow taller vertically and horizontally as well as produce leaves to expedite photosynthesis. These photophilic seedlings put on twice the number of live branches (Figures 7-8) and leaves (Figure 9) in the burned stands compared to the control stands. While the mechanisms at play remain unclear, a 2023 mesocosm experiment growing acorns in soils collected from study pairs 4 also showed that seedlings in burned soils have greater DRCs than those in control soils (Cleavitt et al. *in prep*). The study design isolated the effects of burned soils by having acorns sourced from the same mother tree and soils from the same locations to minimize genetic and micro-topographical differences respectively. Arbuscular mycorrhizal fungi (AMF), a symbiotic network that exchanges nutrients with plant roots, was hypothesized to colonize burned soils more extensively but the differences among soil treatments were insignificant. The next step in this investigation of mycorrhizal fungal colonization is analyzing seedling roots harvested from the study sites, in which ectomycorrhizal (EcMF) structures are expected as well.

**Limitations**

One major limitation of this study is that specific burn dates are unknown. Knowing only the burn years makes determining when vegetation started its post-disturbance recovery a difficult job, especially when early successional species only take a few months to regenerate and take up space. On top of that, no pre-treatment vegetation surveys were done to have meaningful within-site comparisons. Our between-site comparisons can be impacted by confounded variables like differences in micro-topography, soil properties, and existing seed banks. Lastly, *Q. rubra* is known to allocate more resources belowground in the first few years than aboveground (Kolb et al. 1990). While destructive harvesting of tagged seedlings lies outside of this project, their belowground structures would have provided a more comprehensive understanding of what role fire plays in this resource allocation.

## Citations

### R packages


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