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You can access my codes here: <https://github.com/mykhánh0504/rxfire-oak>

Introduction

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 (Coble et al. 2017, Asbjornsen et al. 2021), 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 values 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 (Sork et al. 1993).

Q. rubra currently faces many regeneration challenges in the northeastern US, and its recruitment may continue failing without timely and appropriate interventions. Oak-dominated forests are at their peak capacity to produce acorns at present; however, if forest aging continued for the next 50 years without sufficient regeneration to maintain its age structure, a population bottleneck may ensue (Dey 2014). Acorns have become a major hard mast source for wildlife consumption since the demise of American chestnut and the spread of beech bark disease, but their production declines in older stands (McEwan and Muller 2006). Weevils can also make the acorns non-viable before they are fully mature. This high seed predation strongly limits successful advance regeneration outside of mast years (Mcshea et al. 2007). Moreover, seedling root penetration into underlying soils can be hindered by thick litter layers and can result in long and weak stems. (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 later in its life cycle including *Bretziella fagacearum* and *Armillaria mellea*, which cause oak wilt and Armillaria root rot respectively. While the former disease is spread from tree to tree through root grafts and travels longer distances by *Nitidulidae* and *Pseudopityophthorus spp.*, the latter grows parasitically on trees weakened by fire, drought, insects, or other diseases (Sander 1990). 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*.

Abrams (1992) hypothesized that ground fire might be crucial for oak regeneration. Fire has been integral to upland oak systems in the eastern US 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 pitch 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 against the backdrop of the “Big Burn” in 1910, the largest wildfire in the US history that spread across a million hectares in Idaho and western Montana (Nowacki and Abrams 2008). The newly established and extremely short-staffed US Forest Service was determined to codify suppression as the main tool to fire management. Its “10 AM” policy went into effect in 1935, requiring all forest fires to be suppressed before 10 AM the next day (Donovan and Brown 2007). Together with the 1911 Weeks Act that funded states with fire suppression plans, this policy kick-started almost a century of fire suppression legacy in the US. Fire absence has led to forest mesophication in the eastern landscape, a condition in which stands become wetter and more shady. It promotes mesic microenvironments

mental conditions, which in turn 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).

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, particularly in northern New York, Vermont, New Hampshire, and Maine, under both representative concentration pathways (RCP) 4.5 and 8.5 due to high adaptability. These scenarios are based entirely on greenhouse gas concentrations, assuming we follow the same industrial path as usual for RCP 4.5 (an increase of 4.5W/m² in radiative forcing between the years 1750-2100) or increase its intensity in RCP 8.5 (an increase of 8.5W/m² in the same period) (Joyce and Coulson 2020). This presents an opportunity for foresters, landowners, and scientists with an interest in *Q. rubra* regeneration to better understand regeneration concerns near its current Northern range limit so they can devise silvicultural strategies to introduce or increase its density as part of their species mix. Adaptive silviculture can be implemented to ensure this seamless transition 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 (Iverson et al. 2008, Granger et al. 2018, Bassett et al. 2020, Dee et al. 2022). This study will build on previous research and further explore prescribed fire's role in oak range expansion.

We studied six pairs of burn and control forest stands across the White Mountains ecoregion.

Three pairs were intentionally cut and burn to improve oak regeneration. Two other pairs lack an oak seed source but can provide insights into regeneration dynamics following prescribed burns. The last pair were unmanaged and experienced a wildfire instead, making it a fitting comparison. An additional pair was included for soil sampling, but not extensively studied beyond that. This study investigates whether prescribed fire promotes the recruitment of *Q. rubra* seedlings and improves their growth relative to other forest management practices. We hypothesized that *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 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 *Q. rubra* regeneration at any and all critical life stages including pollination, flowering, seed set, and germination (Arthur et al. 2012). Additionally, this study also strives to find clues to and shed light on the mechanisms at play. We hypothesized that 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 located in the approximately 320,000-ha White Mountains National Forest (WMNF) in New Hampshire (USA), three of which are part of a novel landscape-scale project guided by the forest's Land and Resource

Management Plan (1999-2005, (USDA Forest Service 2005)) and implemented by the USFS over the past two decades. They are paired by project and treatment date, with one stand harvested and the paired site harvested and burned (Table 1, Figure 1). One pair does not have any recent management history, but was sampled opportunistically following a wildfire that resulted in patchy mortality of canopy trees in a mature stand. The remaining two pairs at Bartlett Experimental Forest were burned rather opportunistically, as a way to study how a combination of clearcut and prescribed fire can impact overall vegetation regeneration.

Table 1: Six burn and control stand pairs for the study. Stands are paired by where they are located (SB, HOG, CF, or BEF, how they were harvested (shelterwood, seed tree, or clearcut), and that they were harvested concurrently.

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

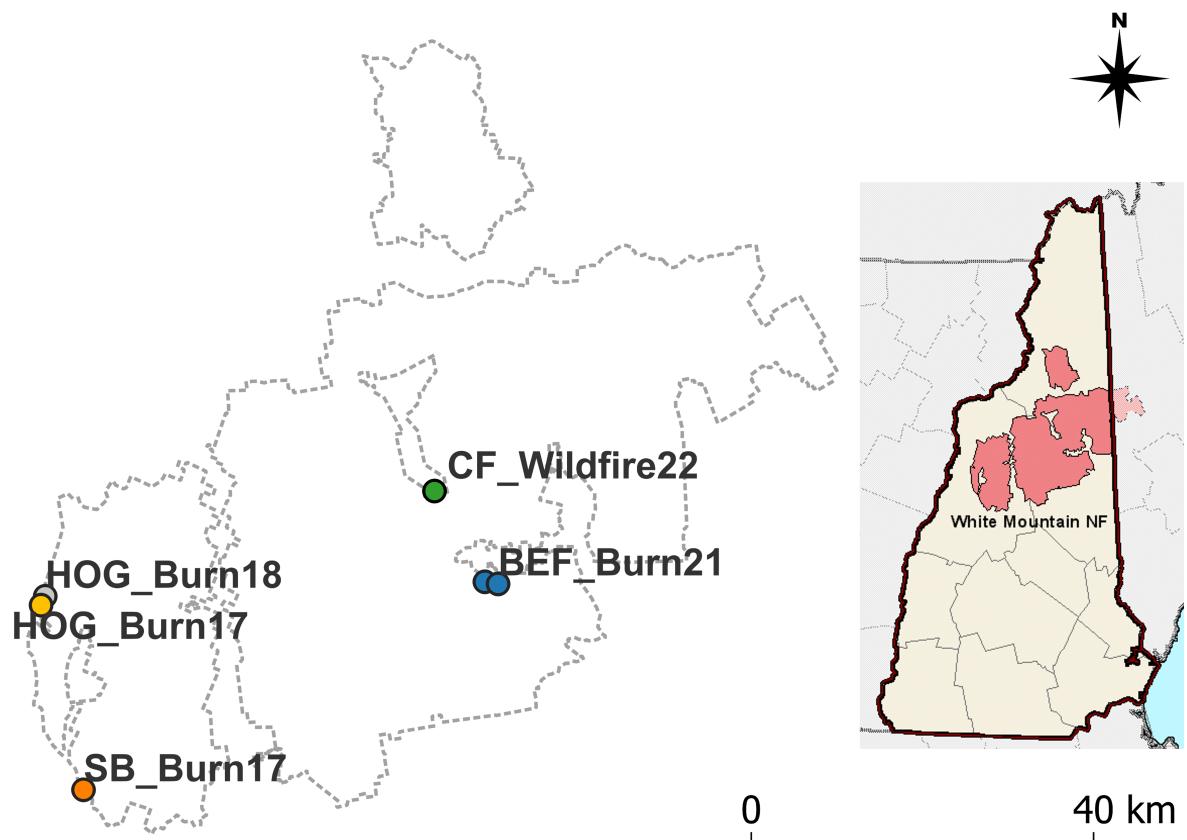


Figure 1: Map of where stand pairs are located. Burn years are displayed for burned stands, and a color is assigned to each pair: SB shelterwoods (1) in orange, HOG seed tree harvests (2) in yellow and shelterwoods (3) in grey, CF wildfire (4) in green, and BEF clearcuts (5, 6) in blue.

Stevens Brook (SB, Pair 1)

USDA FS 2005a, 1-16 to 1-22

The SB Project area is located in the Stevens Brook drainage in Rumney and Wentworth (Grafton County, NH) and spanning 400 ha of the WMNF (Figure 2). A 2009 pre-management field survey showed a forested landscape with well-defined forest roads. In the past half a century, management on this area was carried out to retain wildlife habitat and forest products e.g., timber, which was last harvested in the early 1990s (Fuller 2009). Following the field survey, the Alternative 2 plan was written up by a group of interdisciplinary resource specialists to address wildlife habitat management, vegetation, as well as transportation objectives laid out in the WMNF Forest Plan (USDA Forest Service 2005). With regards to vegetation, three goals are specified: (1) to diversify habitat type and age class, (2) to achieve a sustainable yield of commercial forest products like high-quality sawtimber, and (3) to promote residual tree health and vigor through harvesting, timber stand improvement, and prescribed burns (Fuller 2009). More specifically, the Plan expected to perpetuate more of the oak-pine habitat type and proposed a shelterwood harvest and prescribed fire in stand 5-15 to reinforce oak dominance. Evidently, stand 3-16 was cut and burned instead while stand 5-15 only received a cut.

Hogsback (HOG, Pairs 2-3)

HOG is part of the 2100-ha Oliverian Stewardship Project area, which comprises the Benton Range southern half in Benton and Warren (Grafton County, NH) (Figure 3). A pre-management survey showed a landscape dominated by hardwood, mostly mature with only a small area of young forest and no regeneration-age (0-9 years old) forest (Bayer 2010). Similar to the Stevens Brook project, this project aimed to produce a sustainable yield of commercial forest products

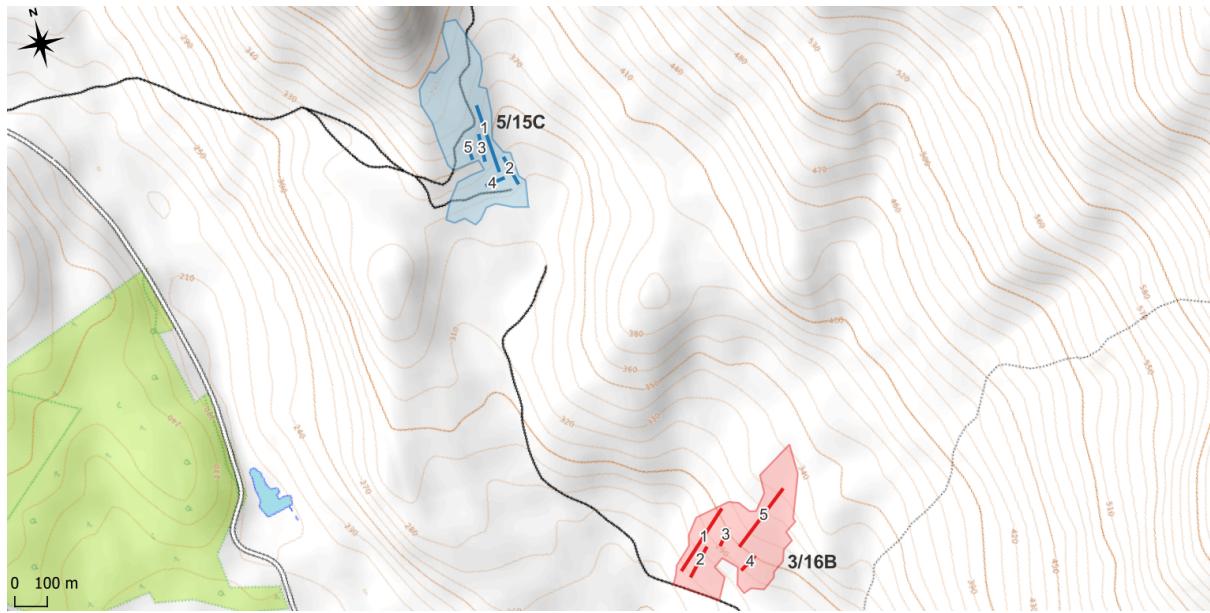


Figure 2: Map of Stevens Brook (SB, Pair 1) site. The burn stand is colored in red and the control stand in blue. Respective colored lines within the stands are transects establish for data collection.

and increase habitat diversity, especially for the regeneration age class, using timber harvesting. Unlike the SB area, however, the oak-pine forest type is less common. Prescribed burning was carried out on about 79 ha to maintain this forest type as well as reduce hazardous fuel loading. This management plan, officially called Alternative 3, was to ensure the provision of about 19300 m³ of forest products.

Crawford Notch State Park (CF, Pair 4)

This 2400-ha state park was acquired in 1913 by the State of New Hampshire, as a result of a bill passed in 1912 to protect the northern region of Hart's Location from excessive timber harvest (NH State Parks 2010). Our study stand (CF) is specifically situated at the south end of the notch, through which a railroad has run since 1875. In May 2022, the Bemis Fire burned 106 acres uphill from the train tracks for 14 days (Angers 2022). Other than that, the stand has been unmanaged since its acquisition, with disturbance patches primarily formed by windthrow (Foster and Reiners 1983). The study vegetation zone is a northern hardwood-spruce phase forest

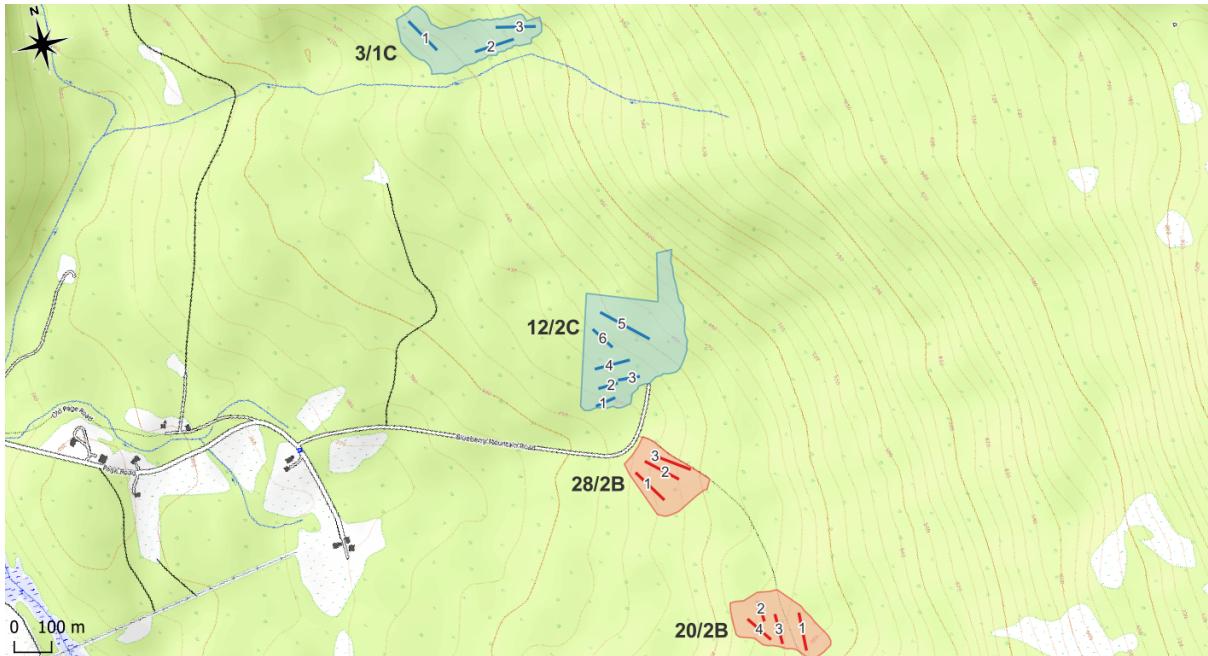


Figure 3: Map of Hogsback (HOG, Pairs 2-3) site, with 20/2B and 3/1C being the seed tree harvests and 28/2B and 12/2C being shelterwoods. Burn stands are colored in red and control stands in blue. Respective colored lines within the stands are transects establish for data collection.

at the lowermost portion of the slope up to an elevation of 700 m, dominated by *A. grandifolia*, *A. saccharum*, and *B. alleghensis*.

Bartlett Experimental Forest (BEF, Pairs 5-6)

1050 hectares were set aside by the US Forest Service in 1931 to conduct research on the ecology and management of northern forest ecosystems, including forest dynamics and structure as well as wildlife relationship with forest management (Figure 5) (Gamal-Eldin 1998). The forest was chosen for its typical New England conditions in terms of soils, elevation gradients, climate, and tree species composition. It was selectively logged through the late 19th into the early 20th century for high-value timber, fuel, and building roads. At present, different silvicultural systems are implemented in different compartments to be studied over a long period of time (Leak and Yamasaki 2011). With regards to the even-aged silvicultural treatment, three compartments were clear-cut in 2018, and half of each also received prescribed fires in 2021.



Figure 4: Map of Crawford Notch (CF, Pair 4) site. The burn stand is colored in red and the control stand in blue. Respective colored lines within the stands are transects establish for data collection.

Whole tree harvesting as such promoted multi-species composition, especially allowing the successional paper birch and aspen to regenerate. The ultimate goal is to make Bartlett a mixed stand with multiple age classes, a diverse tree species composition, and appropriate levels of stocking.

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,

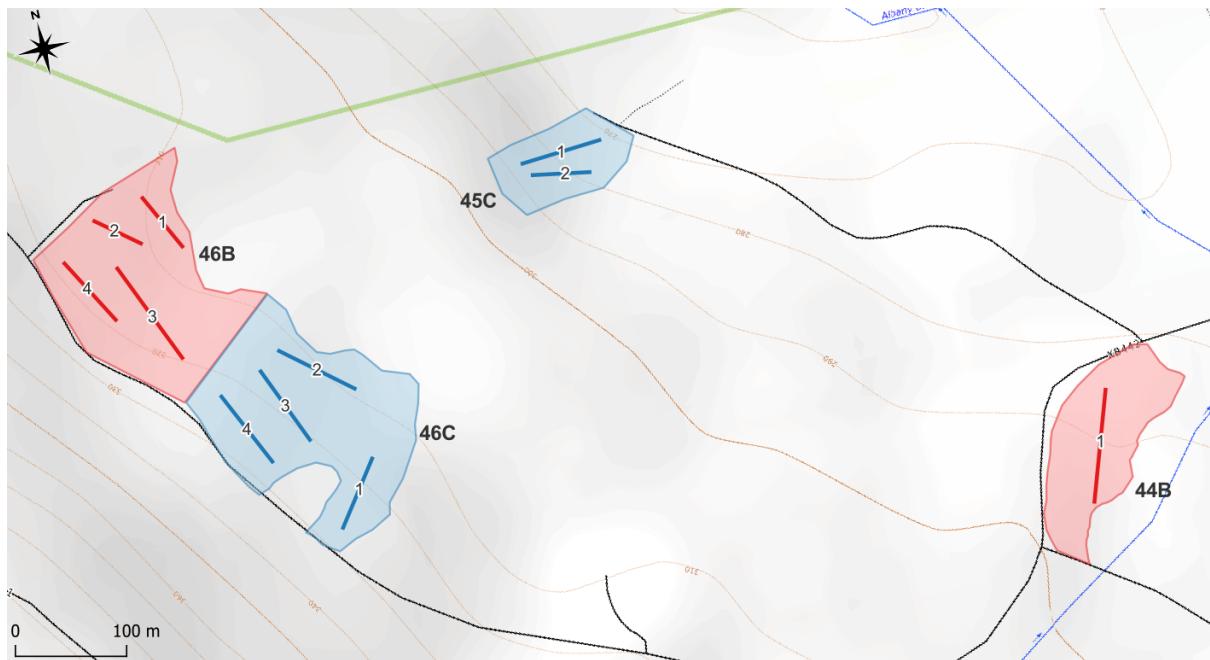


Figure 5: Map of Bartlett (BEF, Pairs 5-6) site. The burn stand is colored in red and the control stand in blue. Respective colored lines within the stands are transects establish for data collection.

microtopography, burn evidence, and *Q. rubra* 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 at the plot scale was confirmed with charcoal presence. Surface cover was estimated in categories including bare soil, woody debris, leaf litter, and rock. Live vegetation cover below breast height was also estimated visually. Woody species with diameter at breast height (DBH) smaller than 2 cm were identified and their stems counted.

Composite soil samples of the top 10 cm representing each study site were collected along study transects in fall 2023 to characterize soil parameters of relevance to seedlings.

***Q. rubra* seedling measurements**

If *Q. rubra* 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 in June and again in August, to quantify growth between the two growth seasons and within this season alone. At this time, we also counted the number of leaves and number of live and dead branches. Herbivory and pathogen damage were quantified percentage-wise as well as described qualitatively.

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

***Q. rubra* leaf and root sample collection**

In 2024, an 8-mm-diameter hole punch was used to collect foliar tissues from tagged *Q. rubra* seedlings in study plots along established transects. For every tagged seedling, 3-10 punch samples were collected depending on the total number of leaves present to achieve representative C and N concentrations for analysis. As for roots, samples were destructively obtained from *Q. rubra* seedlings in study stands but outside of established transects. Soils surrounding each seedling were gently excavated to reveal a lateral root, which was then followed and collected in its entirety to the extent possible, ensuring that all tertiary roots were preserved. Samples were brought back to the lab to be analyzed for ectomycorrhizal and arbuscular mycorrhizal colonization rates.

LAI measurements

During the peak of the 2024 growth months, leaf area index (LAI) measurements were made at the center of each plot to quantify the light. The LI-COR LAI-2200C Plant Canopy Analyzer was positioned at ~50 cm height to assess the light availability to seedlings. LAI data was then matched, calibrated, and analyzed using the LI-COR FV2200 software.

Lab processing of collected samples

Soil

Soil samples were air-dried, homogenized, and sieved to 2 mm. They were then sent to the University of New Hampshire Cooperative Extension in December 2023 to be tested for soil pH and concentrations of calcium (Ca), magnesium (Mg), potassium (K), phosphorus (P), lead (Pb), and organic matter (OM). In February 2025, more samples were sent to the Pennsylvania State University College of Agricultural Sciences' Agricultural Analytical Services Laboratory to be tested for nitrate nitrogen (NO_3^-) and ammonium nitrogen (NH_4^+).

Isotope weighing of leaf punches

Leaf punches were oven-dried at 60°C overnight and stored in air-tight conditions. They were then subsampled using a razor blade and packed in 8*5-mm tin capsules to achieve samples weighing 3 ± 1 g. A total of 66 samples and [] duplicates were put in the 96-well cell plate and sent to the Washington State University Stable Isotope Core Laboratory to analyze for %C, %N, C:N ratio, as well as C and N isotope ratios.

Data visualization and analysis

Plot-level stem and seedling counts and basal areas were expressed 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 analysis of variance (ANOVA) with blocking, were carried out in RStudio version 2024.12.1.563 for each response variable to test for hypothesized differences between prescribed fire and control pairs. Data visualization and analysis packages included `forcats`, `ggplot2`, `tidyverse`, `dplyr`, `gt`, `car`, `rstatix`, and `kableExtra`.

Results

Table 2: List of four-letter codes for common woody species (and brambles genus) at the study sites.

Species code	Scientific name	Common name
ABBA	<i>Abies balsamea</i>	Balsam fir
ACPE	<i>Acer pensylvanicum</i>	Striped maple
ACRU	<i>Acer rubrum</i>	Red maple
ACSA	<i>Acer saccharum</i>	Sugar maple
BEAL	<i>Betula alleghaniensis</i>	Yellow birch
BEPA	<i>Betula papyrifera</i>	Paper birch
BEPO	<i>Betula populifolia</i>	Gray birch
FAGR	<i>Fagus grandifolia</i>	American beech
FRAM	<i>Fraxinus americana</i>	White ash
OSVI	<i>Ostrya virginiana</i>	American hophornbeam

Species code	Scientific name	Common name
PIRU	<i>Picea rubens</i>	Red spruce
PIST	<i>Pinus strobus</i>	White pine
POGR	<i>Populus grandidentata</i>	Bigtooth aspen
POTR	<i>Populus tremuloides</i>	Quaking aspen
PRPE	<i>Prunus pensylvanica</i>	Pin cherry
PRSE	<i>Prunus serotina</i>	Black cherry
RUS	<i>Rubus spp.</i>	Brambles genus, including raspberries and blackberries
QURU	<i>Quercus rubra</i>	Northern red oak
TIAM	<i>Tilia americana</i>	American basswood
TSCA	<i>Tsuga canadensis</i>	Eastern hemlock

Stand characterization

In the understory of the burned stands, *Q. rubra* mainly competes with early successional seedlings e.g. *Rubus spp.*, *A. rubrum*, *B. alleghaniensis* and stump sprouts e.g. *F. grandifolia* (Figure 6). *Rubus* is prevalent in all but Pair 4, ranging from 14000 individuals per hectare in Pair 5 to 101786 in Pair 6. *A. rubrum* was abundant only among Pairs 1, 2, and 3 and is more abundant in burned stands than in control stands e.g., with a seedling density of 56818 per hectare in the former versus 39783 in the latter in Pair 1. *B. alleghaniensis* follows a similar pattern while *F. grandifolia* is most common in Pair 4, especially the burned stand with 17209 seedlings per hectare compared to 2105 in the control stand.

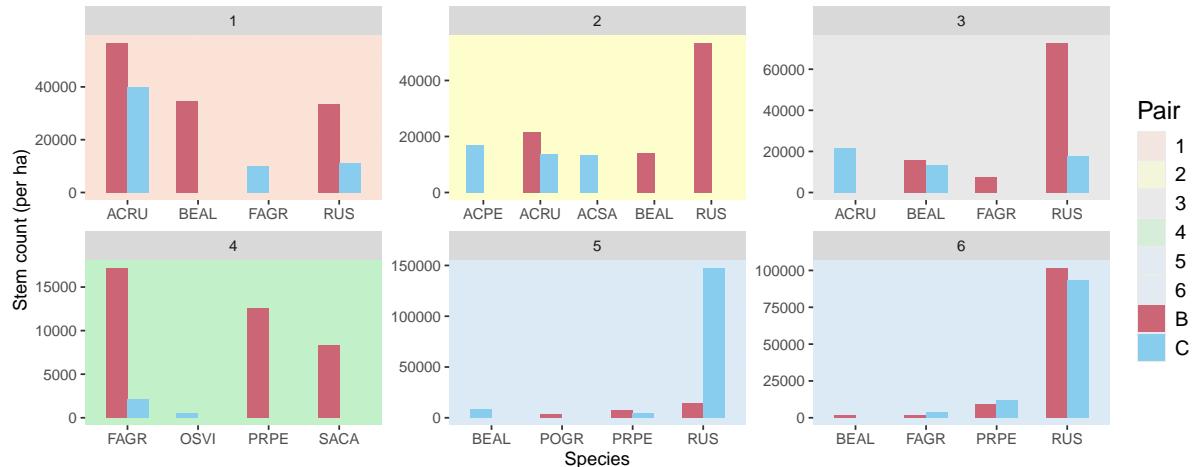


Figure 6: Stem density per hectare of the most abundant understory species in 2023 by stand pairs.

Study stands' basal areas are a reflection of their harvesting methods more than whether or not they were burned (Figure 7). Having been clearcut more recently and hence absent of trees of 20 cm and above in DBH, Pairs 5 and 6 have substantially lower basal areas, all under 1 m² per hectare, compared to others with 18.3 (burned stand in Pair 2) to 37.9 m² (burned stand in Pair 1). Their compositions are also the least diverse, consisting of *Prunus*, *Populus*, and *Betula spp.*. 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*.

Figure 8 shows basal areas of mature trees of 30 cm and above in DBH by whether they were dead standing or alive at the time of survey. *Q. rubra*'s basal areas were about 10 m²/ha across all stands, far exceeding those of other dominant genera. More standing dead trees were recorded in the burned stands, with *F. grandifolia* suffering the highest mortality rate.

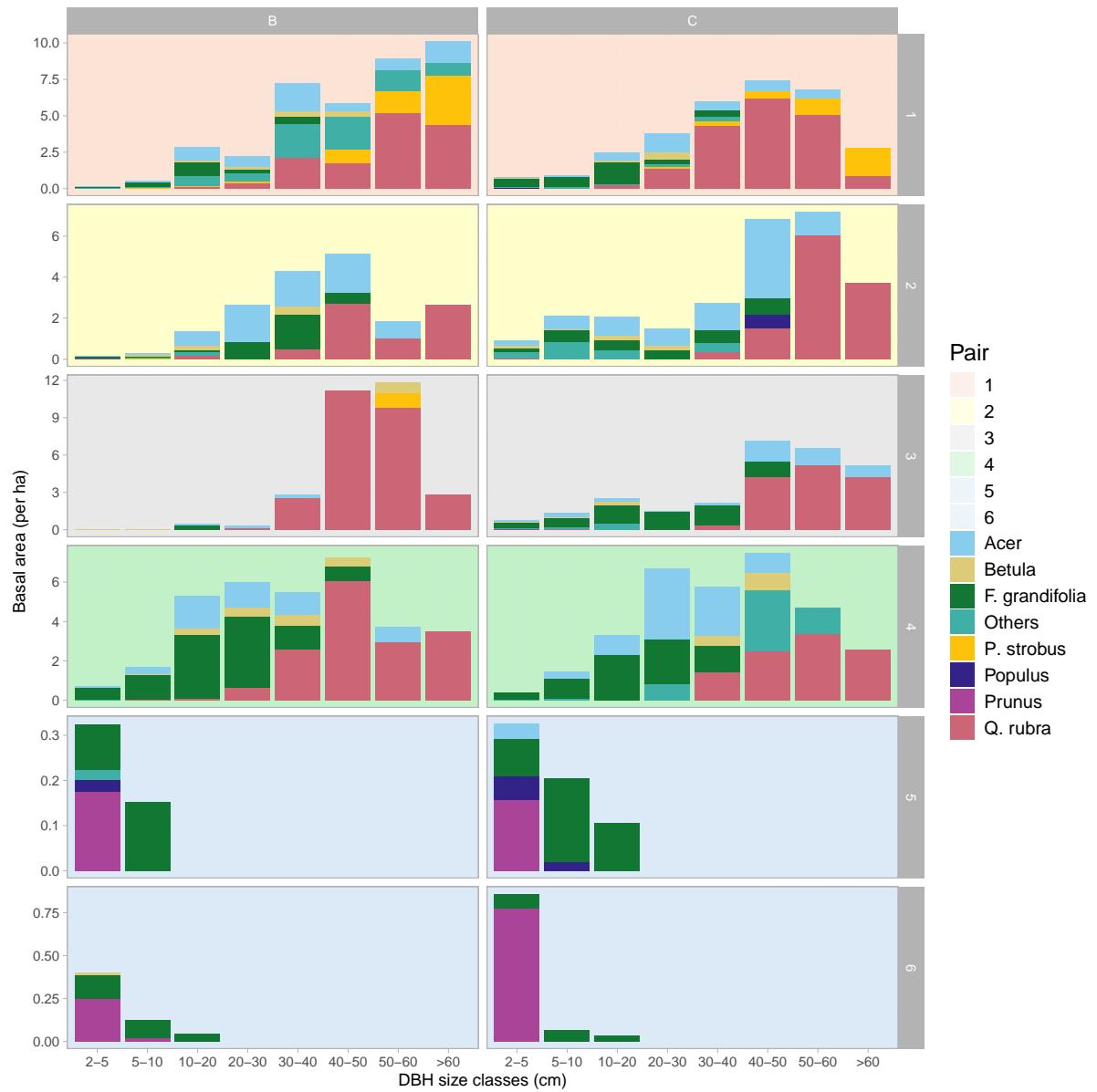


Figure 7: Basal area per hectare of overstory species in 2023 (y-axis) by burn treatments (columns), study stands (rows), and DBH size classes (x-axis).

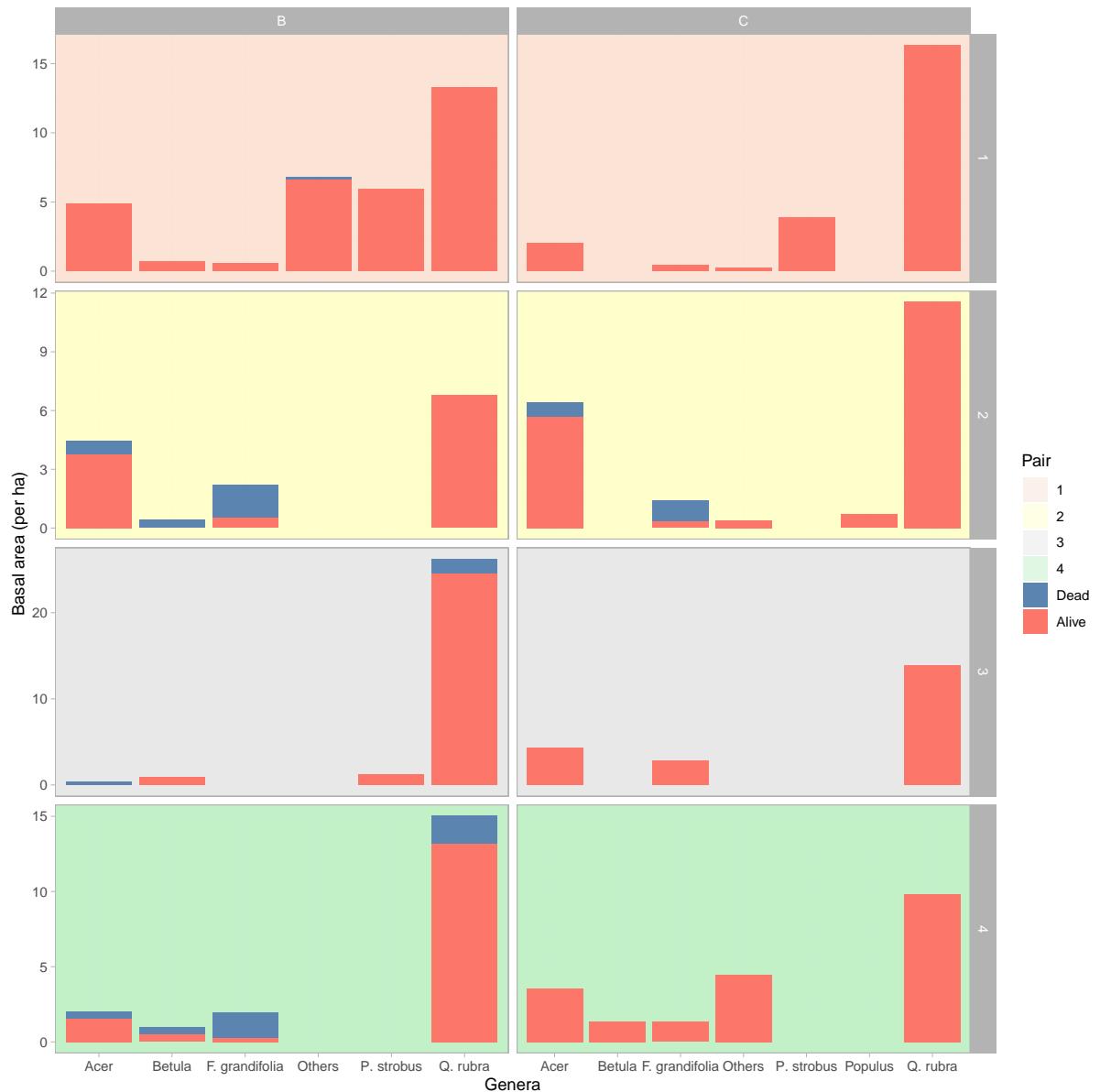


Figure 8: Basal area per hectare of dead/alive overstory trees with DBH ≥ 30 cm in 2023 (y-axis) by burn treatments (columns), study stands (rows), and genus (x-axis).

Q. rubra seedling density and measurements

2023 seedling density

Seedling density increased threefold in burned stands (2887 \pm 240 per ha) relative to control stands (1030 \pm 154 per ha, $p<0.001$) (Table 3).

Table 3: Summarized statistics of *Q. rubra* seedling density per hectare in 2023.

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

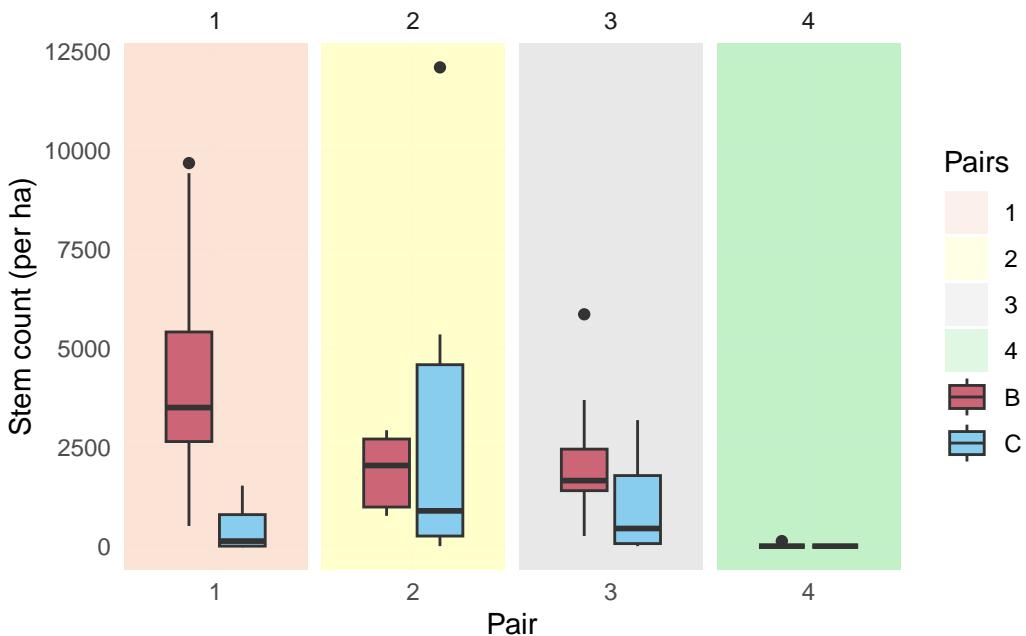


Figure 9: *Q. rubra* seedling density per hectare in 2023 (y-axis) by stand pairs (x-axis), error bars = ± 1 SE.

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, Figure 10).

Table 4: Summarized statistics of *Q. rubra* seedling measurements in 2023.

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

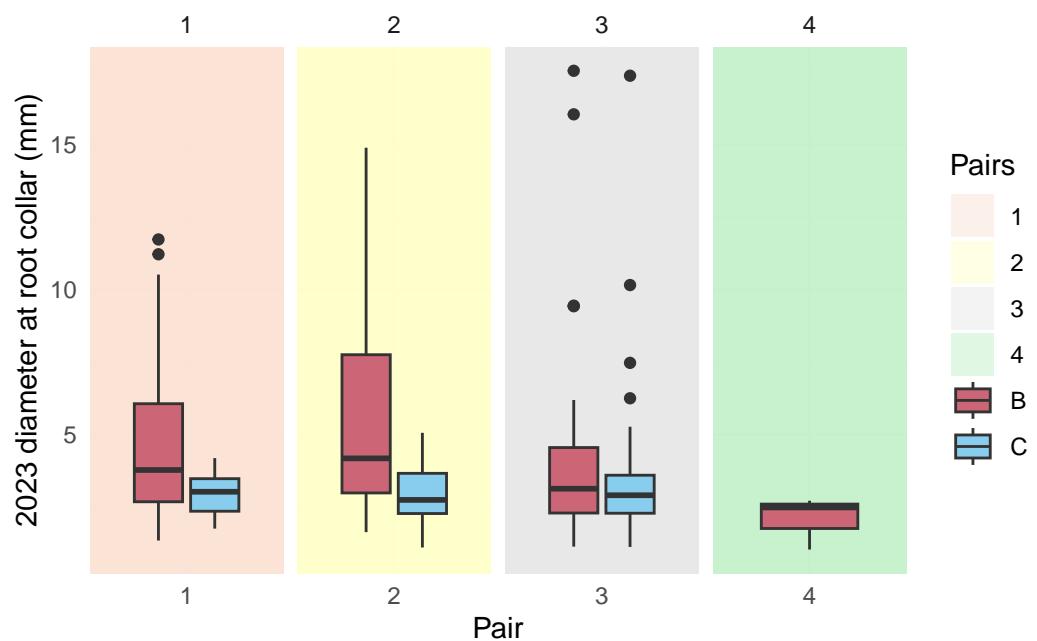


Figure 10: *Q. rubra* seedling diameters at root collar in 2023 (y-axis) by stand pairs (x-axis), error bars = ± 1 SE.

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, Figure 11).

Table 5: Summarized statistics of *Q. rubra* seedling measurements in 2024.

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

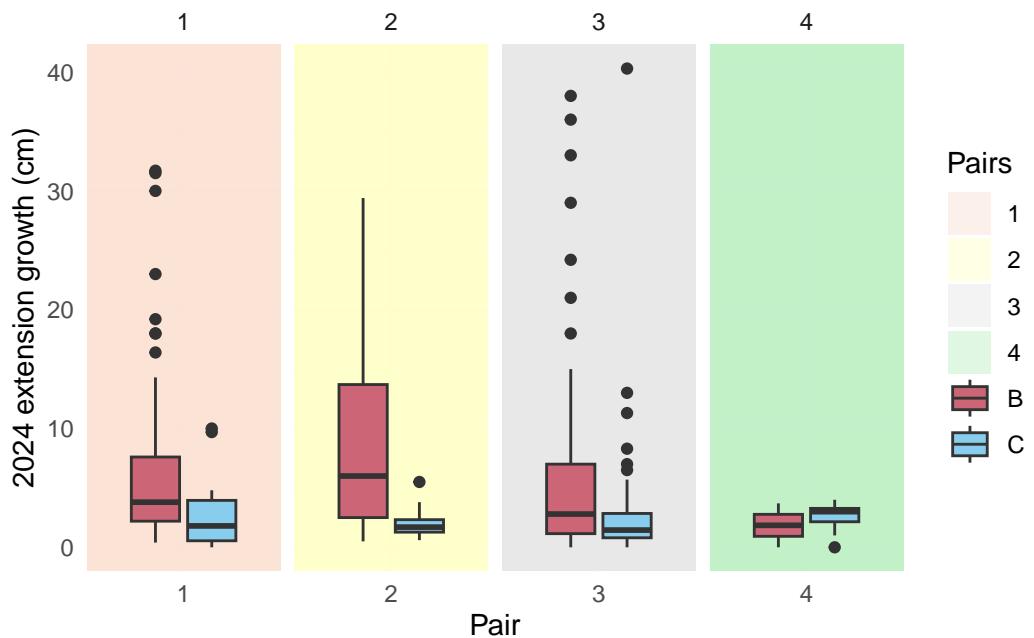


Figure 11: *Q. rubra* seedling extension growths in 2024 (y-axis) by stand pairs (x-axis), error bars = ± 1 SE.

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 ($p<0.001$) (Table 5, Figure 12).

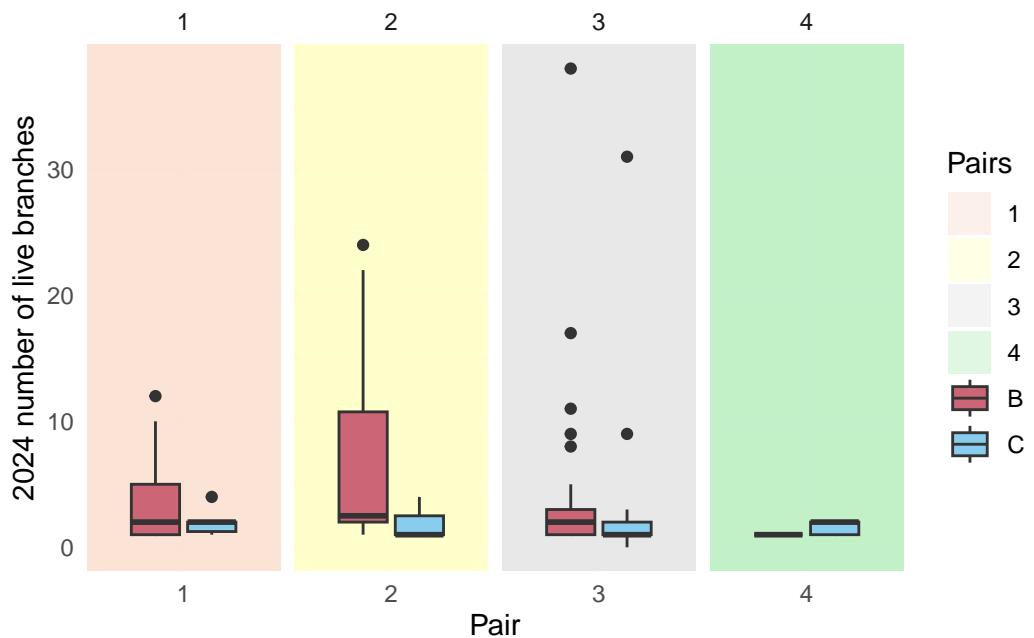


Figure 12: Number of live branches per *Q.rubra* seedling in 2024 (y-axis) by stand pairs (x-axis), error bars = ± 1 SE.

2024 number of leaves

Seedlings in burned stands sprouted more leaves ($16+/-1$) than in control stands ($7+/-1$, $p<0.001$) (Table 5, Figure 13).

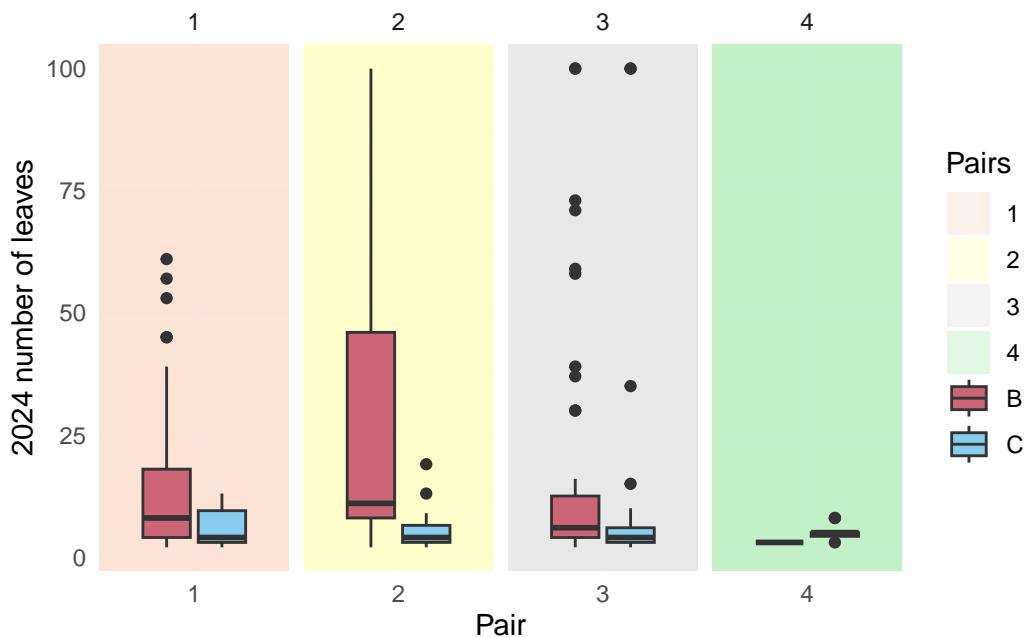


Figure 13: Number of leaves per *Q. rubra* seedling in 2024 (y-axis) by stand pairs (y-axis), error bars = ± 1 SE.

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, Figure 14).

Table 6: Summarized statistics of leaf area index (LAI) values in 2024.

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

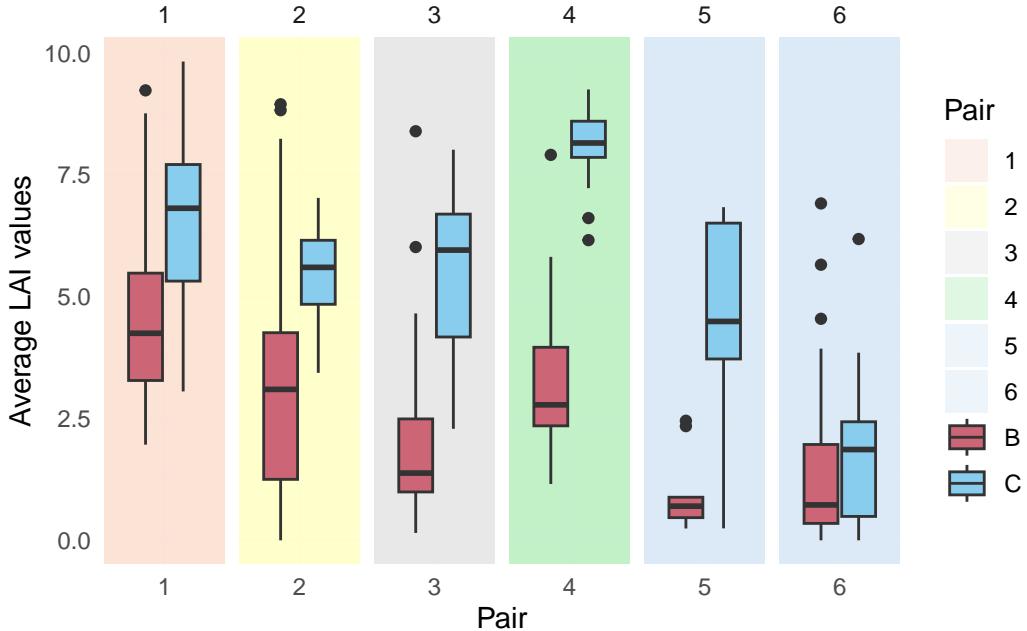


Figure 14: Leaf area index (LAI) values in 2024 (y-axis) by stand pairs (x-axis), error bars = ±1 SE.

Leaf nutrient content

Discussion

Q. rubra seedling recruitment by prescribed fire

Q. rubra seedling density in burned stands is nearly triple that in control stands, supporting the hypothesis that prescribed fire promotes seedling recruitment (Figure 9). We did not find any significant effect the different cutting treatments may have had on such recruitment; though the cuttings took place at different years, making it not a true comparison. When these cutting treatments took place, management left behind mostly *Q. rubra* trees in the highest DBH size classes, 30 cm and above (Figure 7). The mother trees survived the burns better than their mesophytic competitors (Figure 8) and possibly took advantage of their regrowth time to reproduce

(Dey and Schweitzer 2018). Their survival rates are higher due to thicker bark 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 nitrogen cycling, which in turns releases more of it into the soil (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). For example, *Conotrachelus spp.* and *Curculio spp.* and could be killed by fire while exiting from fallen acorns or while in the forest floor layers attempting to reach the soil. Fire consumption of the forest floor removes their hiding areas and presents them to greater predation by small mammals. 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. [MORE CONNECTIONS TO OTHER MEASUREMENTS HERE] 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.

Conclusion

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