

RESTORATION OF RED SPRUCE FOREST: UNDERSTORY PLANT AND SOIL
RESPONSES TO CANOPY GAPS AT ROAN MOUNTAIN, NC

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TABLE OF CONTENTS

| | |
|---|----|
| List of Tables | iv |
| List of Figures | v |
| Abstract | vi |
| Chapter One: Introduction | 1 |
| Red Spruce and Fraser Fir as Key High-Elevation Species | 2 |
| Importance of Red Spruce and Fraser Fir to Biodiversity | 6 |
| Soil Respiration and Net Ecosystem Exchange as Measures of Ecosystem Function | 9 |
| Chapter Two: Methods | 16 |
| Gaps and Their Surroundings | 16 |
| Field Methods | 17 |
| Plant Observations | 17 |
| Response Measurement: Soil Respiration | 18 |
| Environmental Variables | 19 |
| Gap Characterization: Light and Canopy..... | 20 |
| Data Analysis | 20 |
| Chapter Three: Results | 22 |
| Physical Environment Responses | 22 |
| Vegetation Characteristics and Responses | 22 |
| Soil Respiration Responses | 23 |
| Chapter Four: Discussion | 26 |
| Chapter Five: Literature Cited | 35 |

LIST OF TABLES

Table 1. Canopy and light data response by gap type and location within gap40

Table 2. Seedling survival and growth means (standard deviation) for each gap size41

Table 3. Means (standard deviation) of percent cover on 30 m long, 1 m wide strip transects (two adjacent to a gap of each size, six total) of understory (less than 1 m in height) major plant taxa found at the study site42

Table 4. Means (standard deviation) of moss cover within soil collars by gap type, with total number of collars and their distribution in each gap type43

Table 5. Pearson’s correlation values for scarified and unscarified collar CO₂ efflux with soil temperature and soil moisture, run separately for each gap type44

Table 6. Repeated measures ANOVA output for strength of effect of gap size, week, and gap size-week interaction on soil CO₂ efflux readings, separated by scarified and unscarified collar types45

Table 7. Repeated measures ANOVA output for strength of effect of edge vs. center collar location, week, and location-week interaction on soil CO₂ efflux readings from 10 m gaps, separated by scarified and unscarified collar types46

LIST OF FIGURES

| | |
|---|----|
| Figure 1. Location of experimental spruce-fir stand at Roan Mountain, NC | 47 |
| Figure 2. Means and standard deviations for air temperatures over the 2021 growing season for each gap type | 48 |
| Figure 3. Means and standard deviations for soil temperature and soil moisture over the 2021 growing season for each gap type | 49 |
| Figure 4. Mean soil CO ₂ efflux values with standard deviation bars for unscarified (top) and scarified (bottom) center soil collars for each gap type | 50 |
| Figure 5. Mean soil CO ₂ efflux values with standard deviation bars for scarified and unscarified soil collars at edges of 10 m gaps | 51 |

ABSTRACT

RESTORATION OF RED SPRUCE FOREST: UNDERSTORY PLANT AND SOIL RESPONSES TO CANOPY GAPS AT ROAN MOUNTAIN, NC

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Red spruce-Fraser fir dominated forests are considered threatened in the southern Appalachian Mountains and are known to support a variety of rare and endemic species. Their range has diminished greatly due to human disturbance over the past century, and questions about their long-term persistence and ecosystem-level role as local carbon sinks have led to interest among land managers in assisting their health and regeneration. Spruce and fir seedling survival and growth may depend on soil conditions (e.g. disturbance, microbial activity) and environmental conditions (e.g. temperature, light) that affect resource availability. This study explored the effectiveness of 10 m-diameter and 3.5 m-diameter canopy gaps in boosting seedling growth and recruitment in one such forest at Roan Mountain with the goal of identifying a successful management strategy that mirrors historically natural processes. To investigate gap effects, I tracked seedling survival in gaps and uncut areas periodically from June to October 2021 and measured soil respiration weekly in the same areas. Soil respiration, or carbon exchange (CO_2 efflux) between the spruce-fir stand and surrounding environment, was used as an index for soil conditions and activity that may underlie seedling response. In addition to gap effects, soil disturbance (scarification) effects on soil respiration were investigated to account for possible

understory response to increased foraging by the federally endangered Carolina northern flying squirrel. To measure soil respiration, one soil ring was inserted in the center of each measurement area and a second was inserted beside it with duff removed in the top few centimeters of soil. Each 10 m gap was also given a second set of rings on the northern edge to test the effects of different angles and amounts of light. Spring, midsummer, and fall seedling census found that seedling survival was greater than 95% across the growing season in all gaps and uncut areas and that visible seedling growth was negligible (~0.5-1 mm). Weekly soil CO₂ efflux observations indicated that large gaps had lower efflux than both small gaps and uncut forest, but also that edges of large gaps had significantly higher efflux than centers of large gaps when soil was scarified. Strength of gap and within-gap-position effects also varied significantly with time when soil was scarified. Time was an important factor in soil CO₂ efflux with both disturbed and undisturbed soil. Results suggest that canopy gaps 10 m in diameter may have a negative effect on red spruce and Fraser fir seedling growth that diminishes toward the gap edge, and that smaller 3.5 m gaps may be a beneficial management tool for stimulating seedling activity in these ecosystems. Additionally, foraging-related soil scarification tended to impact soil respiration negatively, meaning that increased flying squirrel foraging could harm seedling regeneration. Connections between gap effects and soil scarification will therefore be important to monitor in the future depending on the extent to which restoration practices impact spruce-fir forest and Carolina northern flying squirrel populations.

CHAPTER 1: INTRODUCTION

Ecosystem-level physiological processes and their relation to ecosystem structure and species interactions have become an area of greater research interest as limits to our mechanistic understanding of those processes, and how they might be altered by climatic shifts, become more apparent (e.g. Ma et al. 2019). Species-level interactions are especially important when the communities in question contain rare or endemic species that are highly sensitive to environmental change. Understanding the changes different management practices may induce in the soil and among the primary producers in these cases is critical for preservation and restoration of threatened plant and animal species. The Appalachian red spruce-Fraser fir forest (*Picea rubens* and *Abies fraseri*, respectively), which is considered one of the most endangered ecosystems in the U.S. and has undergone changes in composition and health due to human disturbance over the past few centuries (White et al. 2012), is one such case where informed management is of high concern. A strong body of research has developed around describing the potential effects of spruce-fir forest management on both the principal tree species themselves (e.g. red spruce, Nowacki et al. 2010) and the varieties of plant and animal species that rely on them for foundational habitat and can alter them through activity such as soil foraging (e.g. Carolina northern flying squirrel (*Glaucomys sabrinus coloratus*), Thomas-Van Gundy and Sturtevant 2014).

This study investigated the effects of canopy gap creation on forest floor level response at Roan Mountain, a chain of peaks above 1500 m near the southern end of red spruce distribution in the Pisgah National Forest, Mitchell County, North Carolina. Roan Mountain and its associated bluffs cover about 19 km² (Bauer 2011). The region is characterized under the

Köppen climate system as a marine temperate climate averaging over 500 cm of precipitation annually with over 10% of total precipitation as snow (Tewksbury and Van Miegroet 2007, White et al. 2012). Historically dominated by spruce-fir forest like other high peaks in the area (>85% cover, White 1984, Bauer 2011), Roan Mountain was logged heavily in the 1930s along with many other relict spruce forest tracts. Logging was followed by wildfires and human disturbance that degraded the soil, destroying much of the regeneration potential from old-growth trees. The U.S. Forest Service acquired the land in the late 1930s and has since protected it from logging, allowing regeneration to begin (Bauer 2011). Stands are now of varying age and quality since many patches are growing on former clear-cut pasture, leading to interest from the Forest Service in improving individual tree quality through active management.

Red Spruce and Fraser Fir as Key High-Elevation Species

Red spruce is native to North America, thriving in cool, moist environments and requiring a shaded, but mostly bare, forest floor for greatest seed germination and seedling recruitment (Nowacki et al. 2010). Although the bulk of its distribution falls in its northern range, from the central Appalachians of West Virginia and Pennsylvania north into New England and Canada, high elevation regions in the southern Appalachians (above 1200 m) host substantial populations as well (Adams et al. 2010). Red spruce is found in cooler sub-climates within temperate environments and is characterized as a late-successional species (Dumais and Prévost 2007). Prior to the Industrial Revolution in the late 1800s, red spruce was a widespread high elevation species in the central Appalachians, but its range was reduced by more than 90% with the spread of clear-cutting for wood use and railroad construction (Rentch et al. 2016). In the southern Appalachians of North Carolina, red spruce and Fraser fir historically coexisted on high peaks, but spruce was sought by loggers there as well (Bauer 2011, White 1984). However,

difficult terrain on rocky outcroppings is thought to have protected much of the spruce-fir of the southern mountains (Pyle and Schafale 1988, White et al. 1985), although over 50% of red spruce was still lost from its southern range (White et al. 1985). This forest type rarely burns naturally (White 1984), so wildfires and subsequent soil degradation following logging disturbance resulted in spruce-fir stands being laid bare and colonized by more sun-tolerant hardwood species, restricting red spruce to smaller, cooler pockets in the understory where recruitment to higher canopy levels is reduced (Bauer 2011, Hayes et al. 2007, Dumais and Prévost 2014). Balsam woolly adelgid (*Adelges piceae*) infestation beginning in 1957 further harmed the habitat as Fraser fir canopy was lost, leaving standing dead fir with a spruce component and exposing even more bare ground to erosion (Jenkins 2003, Tewksbury and Van Miegroet 2007). These factors have converged over the last century to make red spruce forest one of the most threatened ecosystems in North America, and the red spruce-Fraser fir forest of the southern Appalachians one of the rarest in the world (Pyle and Schafale 1988, Hayes et al. 2007, White 1984).

Even after displacement and amidst decline, red spruce remains a foundation species at high elevations and northern latitudes because of its ecologically stabilizing effects on light profiles and forest floor chemistry (Dibble et al. 1999). Most remaining spruce-fir forest in the southeastern U.S was spared from disturbances severe enough to alter stand composition irreversibly (Van Miegroet et al. 2007, Pyle and Schafale 1988), making restoration a worthwhile goal. Furthermore, in the central Appalachians of West Virginia, red spruce is identified as the species that most strongly dominates forests with increasing elevation, as high geographic “knobs” (>1300 m) often are covered by pure spruce stands that then grade slowly into mixes of spruce/eastern hemlock/yellow birch and then into more hardwood cover and lower-elevation

understory species as elevation decreases (Mayfield and Hicks 2010). Both spruce-heavy zones and more mixed/hardwood forests can occur alongside and even encroach upon other rare and threatened ecotypes, including grassy or shrubby “balds” in the southern Appalachians including at Roan Mountain (Bauer 2011), adding another layer of complexity to conservation and management. In North Carolina, including in the largest patches of spruce-fir in Great Smoky Mountains National Park, red spruce tends to be the dominant mature tree species at the low end of the spruce-fir elevation range (1370-1650 m, Tewksbury and Van Miegroet 2007). Fraser fir becomes dominant at the highest elevations (above 1890 m) and the two species codominate at the middle elevations (Tewksbury and Van Miegroet 2007). Fraser fir often is the dominant seedling species in southern Appalachian forests characterized by mature red spruce, while red spruce seedlings dominate the forest floor beneath mature Fraser fir (Smith and Nicholas 1998). Additionally, *Betula* spp. tend to be less common in canopy gaps in the southern Appalachians (White et al. 1985). Forest floor seedling competition dynamics are thus different between the central and southern Appalachians.

Because red spruce is a principal component of high elevation forests at Roan Mountain and a late-successional species, the U.S. Forest Service and Appalachian Trail Conservancy aim to restore its habitat in such a way that multiple age classes can establish in the same stand, increasing resilience and genetic diversity. Advance regeneration, or the species variety and age classes of understory seedlings under 5 cm in stem diameter (Cavallin and Vasseur 2009, Dumais and Prévost 2014), is thus a primary concern at Roan Mountain. Occasional small-scale disturbance can create gaps in the canopy that increase light and wind exposure, allowing young red spruce and Fraser fir to establish in middle levels of the canopy. Gap-creating disturbances in the southern Appalachians are sometimes caused by lightning strikes, ice damage, or debris

avalanches depending on slope, but are most often caused by occasional wind events toppling mature trees (Busing 2004, White 1984, White et al. 1985). The frequency of disturbance events and the size of the gaps created is an important factor in overall stand composition and age class diversity (White et al. 1985, Dumais and Prévost 2014). Commercial clear-cutting of these forests, however, has caused many of them to grow back as densely packed, even-aged stands with stifled advance regeneration. “Partial forest cover” that leaves large enough periodic sun patches for growth of seedlings is described as the best for red spruce regeneration (Dumais and Prévost 2014, Dumais et al. 2019), and so there is interest in ways to achieve this state in natural settings. Further, small-scale plantings, which have been tested as a way to restore degraded red spruce stands, have shown that planting coupled with a canopy release can be beneficial both to red spruce and to companion tree species including balsam and Fraser fir (Dumais et al. 2020). Less information has been gathered on canopy release in purely natural seed banks, making that an aspect of interest to restoration planning.

Fraser fir is often found associated with red spruce in southern high elevation climates like those found in North Carolina, and historically was a codominant member of these forest canopies with a similar profile of optimal regeneration conditions (Nowacki et al. 2010). This species has also experienced disturbance-related mortality, especially over the past fifty years since the introduction of balsam woolly adelgid, which killed a significant number of mature trees (Busing 2004, Jenkins 2003). The adelgid has presented a significant threat to Fraser fir-associated forests because of its rapid spread and destructive feeding habit, which involves chewing in bark crevices of Fraser fir and injecting saliva that damages water-conducting cells and causes tree mortality (Jenkins 2003, Smith and Nicholas 1998, Bauer 2011). As a result, Fraser fir has experienced a loss of over two-thirds of adult trees across its range and faces

uncertain recovery conditions moving forward (Kaylor et al. 2016). Since Fraser fir can occupy a large canopy area, loss of mature trees can lead to openings that are highly vulnerable to increased ice and wind damage, which could contribute to the ongoing lackluster performance of red spruce (Busing 2004). With sufficient elevation, Fraser fir can begin to dominate stands with spruce interspersed, presenting another variation that the ecosystem can naturally return to under the right conditions and without extensive adelgid infestation (Jenkins 2003, Van Miegroet et al. 2007). Because of the close connection between the two tree species in the southern mountains, forest community studies, especially in zones of restoration concern, provide important information on their interaction with environmental variables.

Importance of Red Spruce and Fraser Fir to Biodiversity

Red spruce and Fraser fir have seen reduction in both number of individuals alive and overall genetic diversity (Kaylor et al. 2016, Capblancq et al. 2020), but they continue to anchor an ecosystem that features a unique and diverse plant community. More than 20 herbaceous forbs have been associated with the red spruce-Fraser fir (in the south) and red spruce-balsam fir (in the north) understory, including several varieties of *Vaccinium* and several lily, orchid, and violet species that increase the ecosystem's value as a genetic refuge (Dibble et al. 1999). Woody plants including Catawba rhododendrons (*Rhododendron catawbiense*) and scattered representatives of the neighboring northern hardwood forest type, including yellow birch (*Betula alleghaniensis*), American beech (*Fagus grandifolia*), and maples (*Acer* spp.) can occur in the understory and grow successfully in disturbed areas, adding to the overall plant biodiversity (Bauer 2011, Bird and McCleneghan 2005). Mycorrhizal diversity in the soil and moss diversity on the soil surface are known to further enhance biodiversity at Roan Mountain by providing

shelter and foraging opportunities for endangered species (Bird and McCleneghan 2005, Crespi et al. 2003).

Several vertebrate and invertebrate species, including three salamander species and one federally endangered arachnid as well as three endemic or migratory vertebrates, are closely associated with the spruce-fir ecosystem and make these areas critical refuges for biodiversity. Likely the best known of these species is the Carolina northern flying squirrel, a subspecies of genetically similar eastern montane flying squirrels, which is federally endangered and of high conservation interest (USFWS 2011a, NCWRC 2007). Key to its management is preservation and improvement of its disjunct habitat, which is restricted mainly to “sky islands” in the southern Appalachians that are dominated by spruce-fir, with minor components of eastern hemlock and hardwood species (Diggins et al. 2016). Flying squirrel nests have been observed in mature red spruce trees including those at the study site, leading to high interest among conservation groups and federal agencies in preserving mature spruce stands and bolstering recruitment since the squirrel uses red spruce for both shelter and foraging at all life stages. The species forages for symbiotic fungi that attach preferentially to fine roots of red spruce, and the soil scarifying that accompanies foraging creates minor disturbance in the top several centimeters of the surface (Diggins et al. 2016, USFWS 2011a). Since management that benefits red spruce at Roan Mountain is likely also to benefit northern flying squirrel populations, successful practices could result in more scarification, which could have implications for understory plant composition, red spruce seedling survival, and carbon storage in fine roots.

The distinct geography and geology of montane spruce-fir forests contribute to the ecosystem’s function as a refuge for floral and faunal genetic diversity. The mountaintops and outcrops that host these forests were formed by the recession of glaciers during the Pleistocene

that left behind grassy balds and boreal forests that are otherwise not found at such temperate latitudes (Crespi et al. 2003, Nowacki et al. 2010). The southern Appalachians have been identified as one of the greatest sources for montane diversification in North America (Hedin et al. 2015), and the sky island nature of the high elevation communities has resulted in disconnected habitat patches across the landscape mosaic that cause allopatry, meaning that populations of the same species may have distinct genetic markers depending on which mountaintop they occur. In the context of the current fragmentation of red spruce habitat that has resulted in low genetic diversity in many such stands with limited dispersal potential (Capblancq et al. 2020), restoration of stands and greater habitat connectivity become even more important.

The spruce-fir moss spider (*Microhexura montivaga*), an endemic arthropod, is another federally endangered species (USFWS 2011b) that shows distinct patterns by locality. Because its habitat consists exclusively of mossy boulders near red spruce stands, the spider is restricted to the same peaks as the forest type, including Grandfather Mountain, the Black Mountains, and Roan Mountain (Hedin et al. 2015, Jenkins 2003). Since the spider cannot disperse across unsuitable habitat between peaks, populations are isolated, and research has revealed genetic distinctions that have developed over time as the climate has changed, with especially strong divergence among the Roan Mountain population (Hedin et al. 2015). These observations provide evidence for the “refugia theory” of wildlife distribution (Haffer 1969), wherein plants and wildlife have competitive adaptations that allow them to “move” with an ecosystem as it moves over geologic time.

Another spruce-fir associated genus in our region, high elevation *Desmognathus* salamanders, followed the recession of the ecosystem as they sought high-quality, predator-free breeding habitat (Crespi et al. 2003). Each population of *D. wrighti*, in particular, is

physiologically adapted to high elevation and codistributed with red spruce, not inhabiting hardwood ravines between peaks. This results in a significant difference in genetic profiles by distance, which is not predicted by refugia theory but which reflects important geographic differences between the north side of the Asheville basin that includes Roan Mountain and the south side that includes the high peaks of the Smokies (Crespi et al. 2003). This genetic diversity and possible bottlenecks parallels that which occurs in red spruce and Fraser fir (Capblancq et al. 2020), underscoring the importance of maintaining and restoring the habitat wherever it occurs. Other threatened species of interest in the central Appalachians include the Cheat Mountain salamander (*Plethodon nettingi*), as well as vertebrate species including the southernmost populations of snowshoe hare (*Lepus americanus*) and several migratory birds such as northern goshawks (*Accipiter gentilis*) that are known to rely heavily on relict spruce-fir forests for shelter, breeding, and sustenance (Rentch et al. 2016). Given the importance of the Endangered Species Act and other federal programs to land management decisions, knowledge of red spruce habitat dynamics and their effects on species of concern is paramount, making studies related to ecosystem-level physiology in red spruce and Fraser fir appropriate for informing future action.

Soil Respiration and Net Ecosystem Exchange as Measures of Ecosystem Function

Net ecosystem exchange (NEE) accounts for elemental and nutrient fluxes into and out of a given area of habitat. A key component of NEE is soil CO₂ efflux or respiration, which includes carbon dioxide released from soil to the adjacent atmosphere. Soil respiration has broad implications for how much carbon an ecosystem adds to the atmosphere relative to that stored by growing plants (Chen et al. 2021, Ma et al. 2019, Kaur et al. 2010). Carbon stored in soils represents over 50% of terrestrial carbon and is equal to approximately double that stored in the

atmosphere (Chen et al. 2021, Kaur et al. 2010), and boreal and high elevation forests including southern Appalachian spruce-fir tend to have especially carbon-rich soils (e.g. Van Miegroet et al. 2007). Soil respiration is therefore an important carbon exchange pathway over large scales.

Heterotrophic soil respiration, half of total soil respiration, includes respiration by soil microbes and soil-dwelling heterotrophs while autotrophic respiration, the other half, includes respiration output from plant roots and their associated mycorrhizae and symbionts (Ma et al. 2019, Pacific et al. 2008). Total soil respiration combines an estimate of ecosystem processes, including nutrient cycling and decomposition, as well as plant fine root growth, providing a view of the ecosystem's baseline life processes (Chen et al. 2021). As soil CO₂ efflux represents the largest transfer of carbon from terrestrial environments, a better understanding of how it responds to changing climatic conditions is a valuable research goal (Kim et al. 2010).

Commonly, soil respiration is measured using a portable flux chamber such as an LI-8100 (LicOR Biosciences, Lincoln, NE) paired with PVC soil collars (e.g. Chen et al. 2021, Shi et al. 2012). In this way, a major component of ecosystem respiration can be tracked week to week during short growing seasons.

Environmental factors, such as temperature and water availability, affect activity of every organism in the soil and thus also affect the carbon entering and exiting the system. Like other biological processes, soil respiration has a moisture optimum beyond which carbon emitted decreases, and in the field some systems can show a negative correlation between soil moisture and respiration depending on how wet or dry the season has been (Moyano et al. 2013, Chi et al. 2021). Physical properties of the soil and geologic history also have long-term effects on water and nutrient transfer through the substrate, which impacts microbe communities and all associated inputs and outputs (Bukombe et al. 2021). Soil temperature is often the primary driver

of variation in soil respiration and can have effects that overpower those caused by structural or chemical factors such as addition of fertilizer (Grave et al. 2015). Because of their strong effects, soil temperature and moisture are generally considered alongside soil respiration data.

Biomechanics of soil CO₂ efflux are not fully understood, and field studies have shown that the amount of carbon respired and variability in efflux measurements can vary spatially within an ecosystem due to temperature and moisture variation (Kim et al. 2010, Ma et al. 2019, Dore et al. 2014). Re-wetting of soil after drought is known to have significant positive effects on soil respiration because of both heterotrophic and autotrophic activity (Kim et al. 2010), and soil temperature and moisture have both been shown to increase soil respiration as long as fine roots are not physically damaged (Kaur et al. 2010). Accordingly, soil CO₂ efflux tends to be higher in moist riparian areas and can vary spatially as exposure and water holding capacity change (Pacific et al. 2008). Air and soil CO₂ concentration can also cause efflux to vary, and it has been hypothesized that these environmental variables combined with temperature and moisture levels predict soil respiration more strongly than plant communities do (Kim et al. 2010, Kaur et al. 2010). Disturbance of either the soil surface or the surrounding vegetation can have additional effects on soil respiration, as burning can reduce it and forest stand thinning can have variable effects by location (Sullivan et al. 2010). Agriculture-linked disturbance has been shown in some instances to increase soil respiration slightly (Grave et al. 2015), while trampling or soil compaction from forest harvesting may cause decreases in soil respiration during warm months and increases during cold months (Goutal et al. 2012). Thus, type of disturbance (e.g. foraging, trampling, fire, vegetation loss) coupled with seasonal factors and general spatial variability in CO₂ efflux even at small scales of space and time (Dore et al. 2014) make soil respiration responses unique to each microenvironment. Surface soil scarification from squirrel

foraging is the most likely form of disturbance to affect Roan Mountain forests, making the connection between scarification and soil CO₂ efflux important to monitor when applying management practices that could benefit Carolina northern flying squirrels.

Climate change has spurred a growing interest in how high altitude and polar ecosystems will respond to changes in temperature and moisture, and soil respiration has been used as a proxy for that response. Coniferous boreal forests comprise nearly a third of the total forested area on earth (Chi et al. 2021), and the relatively slow growth of coniferous trees leads to high amounts of wood and other “maintenance” biomass that stores carbon long-term, making these forests important sinks for carbon. These systems experience climate warming effects disproportionately, with more average temperature increase during the non-growing season than the growing season and strong drought effects, making their ecosystem exchange responses over long time periods important (Chi et al. 2021). Soil respiration in coniferous forests tends to be significantly lower than in their deciduous, evergreen broadleaf, and mixed counterparts (Ma et al. 2019), meaning that CO₂ exits the system from roots and microbes at a comparatively lower rate. As a result, these systems act as long-term carbon sinks, an effect that can be enhanced when there is a significant component of woody herbaceous plant species on the forest floor (Rhyti et al. 2021). Research in central Canadian boreal forest has also found that tree species mixture can have a strong effect on soil respiration, with heterotrophic respiration normally increasing as a forest stand trends away from a monoculture (Chen et al. 2021). Soil physical properties and regional geologic history can also affect nutrient availability to the plant community and the quality of available carbon stock (Bukombe et al. 2021), making soil-level response and land use history important to consider in alpine and boreal areas, which hold a significant amount of global soil carbon (Rhyti et al. 2021). Since red spruce-Fraser fir forests

occur in these regions southward to the southern Appalachians, these findings provide reason to expect that they can act as local carbon sinks and may show significant soil responses to both short-term changes (e.g. canopy gaps) and long-term environmental pressure (e.g. higher mean annual temperatures).

Southern Appalachian spruce-fir forests, and the variety of species that rely on them for habitat, have been driven into progressively smaller and less-connected patches of space, and that trend is expected to continue and possibly intensify in the coming decades. Evidence from earth's boreal forests, which are the best parallel to the sky islands of the red spruce, indicates that heat and drought stress will be a driver of further range shifts in dominant species such as Canadian black spruce (*Picea mariana*), with yet-unknown effects on net primary productivity (Girardin et al. 2016). Although an increase in mean annual temperature combined with higher ambient CO₂ concentrations is expected to increase primary productivity in most plant species, spruce and fir included, the linked effects of those factors on soil water availability and autotrophic respiration could be negative, thereby limiting the amount of productivity possible in those species adapted to colder environments (Girardin et al. 2016). Carbon isotope analyses have confirmed the connection between higher temperatures and lower productivity in black spruce as expressed in smaller tree ring width in drought-impacted years (e.g. Walker et al. 2015). Slope aspect can be another important variable, as north-facing stands of black spruce showed signs of moisture stress following winters with high snowfall, which depressed spring soil temperatures and prevented much early wood production during an already short growing season (Walker et al. 2015). Since this species is closely related to red spruce, similar patterns could be expected at high elevations in our region, meaning that restoration of the ecosystem across a wider range and measurement of ecophysiological variables across different patches of

spruce-fir forest are increasingly important going forward. However, some southern Appalachian spruce-fir soil carbon analyses have found patterns that deviate from those predicted, including higher soil respiration in fall months in Great Smoky Mountains National Park despite lower soil temperatures (e.g. Tewksbury and Van Miegroet 2007, Van Miegroet et al. 2007). More data from southern spruce-fir is therefore needed to inform predictions.

Expanding understanding of spruce-fir habitat dynamics and soil CO₂ efflux therein is especially important as climate change effects become more apparent. Conservation studies on a variety of different species have concluded that shifts to more northern latitudes are in progress, and analogously, so are shifts to higher elevations, as montane species follow cooler conditions upslope and experience commensurate changes in their interaction networks (Roth et al. 2014, Speed et al. 2012). Models predict that red spruce will also follow this trend, likely being pushed to higher elevations and correspondingly into smaller geographic pockets (e.g. Rentch et al. 2010). Since stands of old growth forest are especially linked to greater genetic diversity of tree species and greater overall ecosystem adaptability to changing conditions, proper restoration practices to maintain mature spruce and allow seedlings to reach the canopy may become increasingly important (Mosseler et al. 2002).

Spruce-fir forests, due to the trees' physiology, have historically required small-scale natural disturbances to open room in the understory and canopy, and management practices that more closely mirror this history are likely to be more successful at maintaining the ecosystem's genetic diversity (Rentch et al. 2016, White et al. 1985). These ecosystems also include carbon-rich forest soils derived from their geologic history and lack of fire (Van Miegroet et al. 2007), making their combination of soil carbon and carbon contained in growing trees and debris an important variable for projecting climate change resilience. Past studies have found that soil

respiration in southeastern spruce-fir is much lower than in other temperate coniferous forests (Tewksbury and Van Miegroet 2007) and that combined effects of wind disturbance, balsam woolly adelgid damage to Fraser fir, and mean annual temperature increase create heterogeneity in the ecosystem's spatial and temporal carbon exchange patterns (Van Miegroet et al. 2007).

Overall, this project augments the body of knowledge on spruce-fir restoration ecology by investigating soil respiration in canopy gaps under both undisturbed and foraging-scarified soil conditions. Though spruce stand health and history have been tracked in parts of the Great Smoky Mountains where stands are contiguous in small patches (e.g. Busing 2004), regeneration potential for a spruce-fir forest that flanks another threatened ecosystem in the form of the grassy balds at Roan Mountain in northwestern North Carolina has not been tested. Canopy-gap restoration dynamics of spruce seedlings have been examined in the central Appalachians due to the presence of Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*, Rentch et al. 2010), but neither canopy gap silvicultural treatment nor effects of Carolina northern flying squirrel foraging on soil respiration have been described for the southern Appalachians outside of the Great Smoky Mountains.

Specific research questions were:

1. Do different canopy gap sizes affect understory seedling survival within a single growing season?
2. Do large and small gaps, and position within large gaps, have different quantitative effects on soil respiration compared to uncut patches of forest?
3. Does scarification of leaf litter and duff (comparable to flying squirrel foraging activity) have a measurable effect on soil respiration compared to undisturbed patches within the same gaps?

CHAPTER 2: METHODS

Gaps and Their Surroundings

Ten plots for canopy gaps were marked in the fall of 2020 in suitable stands of spruce-fir forest with understory recruitment near Carver's Gap, about 100-200 m below Roan Mountain's peak. Mature trees whose removal would enhance the stand's overall health were identified by the U.S. Forest Service and cut with a chainsaw in January 2021 to create immediate canopy gap space around the center of each plot. Stumps were left in place while trunks and branches were cut and piled in the least obtrusive spot possible, usually downslope of the plots but in some cases in the edge of a gap. The two stands for the project were located on the east-facing slope of Roan Mountain at approximately 1700 m elevation on the North Carolina side of the state line, with six gaps/two untreated in the higher stand and four gaps/two untreated in the lower stand (Figure 1).

A 2 m-wide unmarked trail separated the two areas, creating two clusters of treatments in the overall study area. Gaps were spaced approximately one mature spruce tree height (~17 m) apart to minimize interference, but due to space constraints the distance between some small and large gaps was reduced to approximately 10 m. Large gaps, which had the most potential for spatial interference, were spaced at least 17 m apart from each other in all cases. Since no equipment was used to remove timber, the soil surface in the gaps was left undisturbed after tree removal and open except where timber piles covered 10-15% of the ground in three plots. Legacy trees, worth maintaining for their age or biological shelter value, were marked for protection and gaps were otherwise randomly placed throughout the stands to provide a representative sample of the understory for measurement of the response across all replicates.

The gaps were roughly round in shape and two different size classes: five “small” 3.5 m diameter plots, and five “large” 10 m diameter plots. This size difference approximated a single tree gap versus a two-to-four tree gap, which mirrors what wind-, ice-, or lightning-related mortality would most likely cause in a natural setting (Rentch et al. 2010). Gaps much larger than this have been shown to lead to overexposure of the seedlings to light, wind, and heat at ground level, which can harm seedlings rather than “release” them into the next level of the understory (Rentch et al. 2010). Uncut control plots were established in nearby areas of the spruce-fir stands that had no canopy opening, allowing comparison between gap and no-gap settings in addition to the comparison between gap sizes. These were intended to allow for growth monitoring and soil respiration baseline data collection in a closed-canopy environment similar to a spruce stand with no gaps. They were placed in such a way that interference from both artificial and natural gaps would be minimized and nearby vegetation would be representative of what occurs throughout the understory. Two controls each were placed in the upper and lower stands, with at least 15 m between them to provide representative average measurements. These were analyzed as “gaps” with no canopy opening.

Field Methods

Plant Observations

Three different methods for tracking plant growth responses on the forest floor were applied at the beginning of the 2021 growing season in early June, repeated in the middle in early August, and repeated again at the end in mid-October. The first method involved measurement of vertical height of random immature trees (less than 7 cm in stem diameter) in the understory of each gap and near each control. The second method involved placement of a 1x1 meter quadrat in each gap and near each control that contained a mixture of seedlings (less than 4 cm in height,

negligible stem diameter) and observing the number alive and dead at each time point. Seedlings were counted in each of the two gap sizes plus uncut controls and pooled across individual gaps such that 50 seedlings could be observed for each treatment, the most that could be measured without going beyond gap boundaries. The third involved running six 30 m strip transects (three in the upper stand, three in the lower) in October 2020 before gap creation in areas of the stands adjacent to expected gap sites. A 100 m tape measure was used to measure these, and then used to measure off 1x1 m quadrats at every meter of the 30 m transect, alternating sides. Vegetation within each quadrat was then identified as either red spruce, Fraser fir, moss, or deciduous species and a visual estimate of percent canopy cover of non-mature individuals was taken. This measurement was done again in October 2021 to test for noticeable differences.

Response Measurement: Soil Respiration

To measure soil respiration, PVC collars were inserted into all 10 gaps and all 4 controls at the minimum necessary soil depth required to be stable, creating a soil microenvironment within each collar that included a representative sample of soil microbes and fine red spruce and Fraser fir roots that was alive and actively metabolizing. Live seedlings within collars were clipped. Collars were 20 cm in diameter and 11.5 cm in height, and were inserted 3-6 cm into the soil surface. An LI-8400 portable flux chamber (LI-COR Biosciences, Lincoln, NE) was used to measure CO₂ efflux from each ring at weekly intervals on average throughout the growing season, from approximately June 1 to October 15, 2021. Each 10 m gap received a collar near the marked center of the plot and another on the northern edge so that responses to different amounts of ambient light could be tracked, while all 3.5 m plots received collars only in the center, with the exception of one that had three trees removed and was thus large enough for edge collars as well. Each uncut control received two soil collars in the plot center with no edge.

Soil scarification was included in the study as an independent subset of soil collars to account for effects of possible future increase in Carolina northern flying squirrel foraging. An additional PVC collar was added next to the initial collar in every gap and control such that there were two collars side-by-side with approximately a collar width between them: one had undisturbed soil within it while the other had random surface scratching and duff removal, with the disturbance not exceeding 4 cm in depth to avoid excessive soil mixing. Each 10 m gap thus had four PVC collars (one scarified and one undisturbed in the center, another identical pairing at the northern edge) while each 3.5 m gap and control had two (one such pairing in the center). One 3.5 m gap had its scarified soil ring lost during the season and, as such, only had an unscarified ring.

Environmental Variables

Because of the close association between soil respiration and environmental variables including soil temperature, soil moisture, and air temperature, those three variables were tracked throughout the growing season for differences between gap sizes that may have corresponded to patterns in CO₂ efflux or plant growth. A TDR 350 soil probe (Spectrum Technologies, Aurora, IL) was used to measure soil temperature and moisture each time soil respiration was measured. Additionally, iButton Thermochron and Hygrochron autonomous temperature loggers (iButtonLink LLC, Whitewater, WI) were placed 3-5 cm above the soil surface in metal holders in each gap. Ambient temperatures were measured continuously at 30-minute intervals starting in mid-May 2021 and continuing throughout the growing season June-October, with readings downloaded in the field every 3-5 weeks. The iButton loggers were placed between the center and edge rings of every 10 m gap to give a representative sample of the air temperature in the gap overall. Collected data was then averaged by month.

Gap Characterization: Light and Canopy

Canopy cover and light measurements were taken in tandem at a single time point late in the growing season to quantify gap effects on the understory light regime. An LI-1400 light meter (LI-COR Biosciences, Lincoln, NE) with the quantum sensor attachment was used at midday on a clear day in late October 2021 to quantify the amount of photosynthetically active radiation (400-700 nm wavelength) reaching the forest floor in each gap and control on the average “clear” day with no cloud immersion. In taking the light readings, a transect was walked starting at the center of each plot between the two soil rings and proceeding to the plot edge in each cardinal direction, with the reading recorded at 1 m intervals and the average of the four median readings calculated.

Canopy cover was measured at the end of the growing season using four handheld spherical densiometers, with measurements taken by four different observers using the standard method of one reading at chest height in each of the four cardinal directions. Measurements were taken with the observer standing above each set of soil rings so that canopy cover could be compared directly with soil respiration, meaning that any gap with both center and edge rings also had center and edge canopy cover. Since the canopy remained unchanged throughout the growing season and no snags or branches presented the threat of imminent gap size changes in either stand, one measurement was suitable.

Data Analysis

Soil respiration was analyzed using repeated measures analysis of variance (RANOVA) via linear mixed effects modeling to account for repeated sampling of each soil collar weekly over the observation period. RANOVA was used to test for significant effects of time, gap size,

and soil collar positioning within gap where applicable, as well as interactions of treatment variables with time, using base R and the Rstatix package in R version 4.1.2 (R Core Team 2016). This analysis was done separately for scarified and unscarified collar sets, and separately for gap centers (which included all three gap sizes) and gap edges (which included only large gaps). Means and standard deviations were calculated for soil CO₂ efflux values for each gap type by week. Means were calculated for soil temperature and soil moisture by gap type by week, as well as for air temperature by month. Pearson's correlation coefficients were calculated for the relationship between soil respiration (scarified and unscarified separately), soil temperature, and soil moisture using the Tidyverse package in R (R Core Team 2016). Light meter and canopy cover data were collected and used to provide context for conditions in different gap sizes. One-way analysis of variance (ANOVA) was used to test for significant differences in environmental metrics between treatment means at a significance level of 0.05. ANOVA was performed on soil temperature, soil moisture, air temperature, light meter, and canopy cover data and was blocked through time for soil temperature, soil moisture, and air temperature to account for seasonality.

CHAPTER 3: RESULTS

Physical Environment Responses

Air temperatures tended to be between 0.1 °C and 1 °C higher in 10 m gaps than in 3.5 m gaps or uncut areas, with the difference more pronounced during the warmer months of June, July, and August, corresponding to the first 13 weeks of the growing season (Figure 2). Ten-meter gaps had significantly higher average air temperatures than 3.5 m gaps and uncut plots in June, and significantly higher air temperatures than 3.5 m gaps in July ($F = 24.88$, $df = 2$, $p = 0.001$ for June; $F = 8.152$, $df = 2$, $p = 0.036$ for July). Differences between gap size treatments were minimal thereafter. Uncut areas and 3.5 m gaps tended to have comparable air temperatures throughout the season. Light availability at ground level was approximately 150% higher in 10 m gaps than in 3.5 m gaps or uncut plots, which corresponded with 8-10% more overstory canopy openness both at plot center and extending up to 5 m away (Table 1). Tree removal created edge effects in both gap sizes that led to high standard deviations in light values. Photosynthetically active radiation (PAR) differed among treatments near gap centers but not at gap edges ($F = 30.39$, $df = 2$, $p = 1.81e-09$ for centers; $F = 2.033$, $df = 2$, $p = 0.142$ for edges). There was also a significant difference in canopy cover between the treatments ($F = 10.60$, $df = 2$, $p = 5.41e-04$). Overall, 10 m gaps admitted significantly more light and had significantly lower canopy cover than 3.5 m gaps and uncut controls, which were similar in light and canopy.

Vegetation Characteristics and Responses

Survival of small red spruce and Fraser fir seedlings was 96% or greater throughout the growing season in all gap types, with total average height growth of seedlings only near 1 mm across the season for all gap types as well (Table 2). The study area was characterized by 10-

30% more cover of Fraser fir than red spruce in the understory, but a generally high cover of both, as no transect survey found cover of either species lower than 25% (Table 3). Three deciduous species (*Vaccinium*, *Rhododendron*, and *Betula* spp.) were observed in the study area, with none having more than four individuals in or near a gap. Moss was generally abundant at the study site, with percent cover often surpassing that of conifer seedlings. Because of this, soil collars often contained soil that was partially covered with moss, with a randomly selected collar likely to have 25% or more of its soil covered (Table 4). All soil collars had relatively similar moss cover across treatments (ranging between 25% and 50% averaged over eight or more soil collars) such that soil respiration data were not disproportionately impacted by moss presence in any one soil collar set.

Soil Respiration Responses

Soil temperature and soil moisture showed opposite trends over the growing season: soil moisture tended to increase when soil temperature decreased (Figure 3). Although soil temperature showed the same pattern as air temperature during the warmest part of the growing season between weeks 6-13, it peaked several weeks later, corresponding with the lowest weekly soil moisture values of the season. Soil temperature did not differ significantly among the three gap sizes ($F = 0.975$, $df = 2$, $p = 0.599$); 10 m gaps were only 0.5-1 °C warmer than 3.5 m gaps early in the season and warmer by less later. Soil moisture was 5-10% higher in 10 m gaps at most sampling times, with 3.5 m gaps being 5% higher, or less, in moisture than controls (Figure 3). Soil moisture differed among treatments throughout the growing season ($F = 6.608$, $df = 2$, $p = 0.024$), with 10 m gaps having higher soil moisture than 3.5 m gaps or uncut areas.

CO₂ efflux trends varied with environmental conditions: low efflux values corresponded to low soil temperature and high soil moisture, while high efflux values corresponded to high soil temperature and lower soil moisture (Figures 3 and 4). Over the growing season, soil CO₂ efflux showed little correlation with soil moisture (range -0.20 - +0.26; Table 5) in all gap and soil scarification treatments. Soil temperature was more strongly correlated with efflux in most cases, especially in scarified rings in uncut and 3.5 m gaps, where Pearson's correlation coefficients were 0.53 and 0.65, respectively (Table 5). The exception to this trend was 10 m gaps, where Pearson's coefficients for soil moisture were larger than those for soil temperature in both scarification treatments (0.27 vs. 0.13 scarified, 0.26 vs. 0.16 unscarified; Table 5). Both variables were positively correlated with soil CO₂ efflux in all but one case: soil moisture had a correlation coefficient of -0.2 for scarified collars in 3.5 m gaps.

Gap size effects were not significant for unscarified collars ($p > 0.05$), but effects of time and the time-size interaction were significant (Table 6). Unscarified collars in all three gap types, with center and edge efflux values averaged for 10 m gaps, showed values within 0.5 $\mu\text{mol}/(\text{m}^2\cdot\text{s})$ of one another during most weeks, with peaks for all three in week 16 of observation at efflux values of 4.89 (± 0.15) $\mu\text{mol}/(\text{m}^2\cdot\text{s})$ for uncut areas, 4.24 (± 0.77) $\mu\text{mol}/(\text{m}^2\cdot\text{s})$ for 3.5 m gaps, and 4.30 (± 1.39) $\mu\text{mol}/(\text{m}^2\cdot\text{s})$ for 10 m gaps (Figure 4). Most values for unscarified collars fell between 3.5 and 4.5 $\mu\text{mol}/(\text{m}^2\cdot\text{s})$.

In contrast to unscarified collars, scarified collars often produced similar efflux values for 3.5 m gaps and controls (all readings within 0.5 $\mu\text{mol}/(\text{m}^2\cdot\text{s})$ of each other after week 2) and lower values for 10 m gaps, with 10 m gap readings lower by as much as 1.13 $\mu\text{mol}/(\text{m}^2\cdot\text{s})$ in week 9 and only approaching readings from uncut areas in week 12 (Figure 4). The majority of readings from scarified collars fell between 2.5 and 3.5 $\mu\text{mol}/(\text{m}^2\cdot\text{s})$, with peak values in week

13 for uncut areas ($4.06 (\pm 0.47) \mu\text{mol}/(\text{m}^2 \cdot \text{s})$), week 16 for 3.5 m gaps ($3.94 (\pm 0.61) \mu\text{mol}/(\text{m}^2 \cdot \text{s})$), and week 12 for 10 m gaps ($3.19 (\pm 0.95) \mu\text{mol}/(\text{m}^2 \cdot \text{s})$) (Figure 4). However, as in the unscarified collar set, there was no significant effect of gap size alone for scarified collars ($p > 0.05$, Table 6). Instead, there was a significant effect of time and a significant interaction between time and gap size with respect to efflux readings (Table 6).

Soil CO_2 efflux readings from edges of 10 m gaps followed a similar seasonal pattern to readings from gap centers but often were higher, especially when comparing scarified edge rings to scarified center rings in 10 m gaps (Figures 4 and 5). The majority of readings for scarified edge rings fell between 3.0 and 3.5 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$ with a maximum of 4.02 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$ in week 10 and minimum of 2.53 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$ in week 15 (Figure 5). This contrasts with readings for 10 m gap scarified center rings, half of which fell between 2.5 and 3.0 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$ with only two readings higher than 3.0 during the observation period (Figure 4). Most unscarified edge values fell between 3.25 and 4.0 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$ with a maximum of 4.57 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$ in week 16 and minimum of 2.70 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$ in week 3 (Figure 5). These tended to be greater than readings for unscarified center rings, which fell between 3.0 and 3.75 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$ with a maximum of 4.44 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$ in week 13 and minimum of 2.77 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$ in week 3 (Figure 4). RANOVA testing of edge vs. center collar location within 10 m gaps indicated, as in the gap size analysis, that time had a significant effect on soil CO_2 efflux for both scarified and unscarified collar readings ($p = 5.71\text{e-}07$ and $p = 1.44\text{e-}17$, respectively, Table 7). In this analysis, however, the interaction of the location variable with time was significant for scarified collars ($p = 3.80\text{e-}04$) but not significant for unscarified collars ($p > 0.05$, Table 7). This suggests that the location effect varied in strength depending on time for scarified collars, but not for unscarified collars.

CHAPTER 4: DISCUSSION

Sudden large openings in the canopy, such as those generated by the multi-tree removal in the present study, have been linked to light- and heat-related stress that can stunt regeneration and growth of red spruce and other shade-adapted species (Dumais and Prévost 2008, Rentch et al. 2016). However, red spruce and Fraser fir at Roan Mountain often experience cloud immersion, which affects photosynthesis, water relations, and other physiological factors, buffering such changes to an extent and enabling the ecosystem to persist long-term (Berry et al. 2014). Seedlings tend to have unique physiology adapted to maximize nutrient uptake and photosynthesis during cloud immersion, which also makes them more sensitive to environmental change (Berry and Smith 2013). The survival of over 95% of all observed seedlings throughout the growing season suggests that neither the 10 m gaps nor the 3.5 m gaps allowed enough light or heat to create excessively stressful conditions.

Additionally, although 10 m gaps allowed more light and had slightly higher average soil and air temperatures than smaller gaps and uncut areas, they also tended to have higher average soil moisture. Across all 10 m gaps, 3.5 m gaps, and uncut areas, soil moisture tended to be inversely related to soil temperature, meaning that the higher soil moisture in 10 m gaps relative to smaller gaps could stem from reduced water uptake by nearby roots or reduced transpiration. This finding also suggests that conditions were never warm enough to dry out the soil or desiccate the vegetation, which aligns with the high seedling survival observations. It is thought that increased exposure to direct sun can lead to reduced cold tolerance in red spruce seedlings that causes winter desiccation and needle damage (Hadley and Amundson 1992), suggesting that mortality could follow as winters pass at the study site and making periodic seedling inventory a good idea in the experimental gaps. However, continuation of normal cool, cloudy conditions at

the study site may help maintain higher photosynthetic rates and leaf conductance values as well as more favorable vapor pressure deficits in seedlings (Berry and Smith 2013), all of which can minimize environmental stress effects caused by the gaps.

Average air temperatures in gaps, including 10 m gaps that often produced lower soil respiration values, were within the range of maximum photosynthetic rate for mature red spruce, which is known to fall between 15-20 °C (Walter et al. 2017). Further, air temperatures were in this range for three months in 10 m gaps, but only for two months in 3.5 m gaps and uncut areas. If 10 m gaps continue to reach optimal temperature a month sooner than the surrounding forest, red spruce and Fraser fir could benefit over multiple seasons. The lack of competition from forbs and deciduous species at the study site may also assist survival of red spruce and Fraser fir seedlings, and is unsurprising as red spruce tends to grow best on shallow, acidic, low fertility soils that inhibit such competition (Walter et al. 2017, Li et al. 2020). The overall low red spruce and Fraser fir seedling mortality combined with the temperatures observed for summer and fall 2021 indicate no short-term negative effect from gaps.

Seedling survival did not appear to be impacted by any gap size or lack thereof, as nearly all seedlings counted survived the entire growing season without showing browning or other signs of stress. The high similarity in seedling survival among treatments and locations suggests that the few seedlings that died may have died by chance or been affected by inadvertent mechanical disturbance (either from collar insertion or timber piling). Red spruce and Fraser fir grow slowly (< 5 cm/yr) and take a few years to acclimate to partial canopy openings (Dumais and Prévost 2008, Dumais and Prévost 2014), making the lack of response in terms of height growth unsurprising for an initial growing season. Rentch et al. (2016) report that neighboring tree removal can produce a relatively quick vertical and DBH growth response in plantation-

grown red spruce, although this may require multiple growing seasons to play out in a natural setting. Understory mortality, especially of Fraser fir seedlings and suppressed individuals 2 m or shorter in height, was raised as a possible outcome for both gap sizes by collaborators prior to treatment, but the high observed survival and lack of apparent damage to the larger fir specimens suggests treatment may generally have more positive effects.

Research from plantation red spruce used in gap experiments in degraded red spruce-balsam fir habitat in the northern Appalachians has suggested that gaps 100-300 m² in area, or 10-20 m in diameter, show the greatest potential for red spruce regeneration (Dumais et al. 2020). When combined with a partial stand cut, or “group selection harvest,” these gaps alter the light microenvironment strongly without allowing hardwood competitors to overtake the area (Dumais and Prévost 2007, Dumais et al. 2020), suggesting that the gaps used in the present study could similarly control competition (if competitors are abundant in the seed bank) since they are smaller. It is possible that cumulative gap effects over seasons could increase seedling mortality in the future (Dumais et al. 2020), but since seedlings at the study site are native to the seed bank, and not transplanted, this is less likely to occur. In terms of height growth, the same canopy gaps that benefit red spruce are also known to benefit fir species, which may even benefit more than spruce from increased light levels (Dumais and Prévost 2014). Thus, it will be important to monitor not only survival but also comparative vertical growth of the two conifer species at the Roan Mountain study site since most gaps in the study sites contained both red spruce and Fraser fir.

For soil respiration, undisturbed soil and smaller canopy gaps, or even no gap, tended to correspond with higher soil respiration values even though no data suggested conditions, such as excessively dry or wet soil, that would depress soil respiration in large gaps. This trend was most

clearly seen with unscarified collars vs. scarified collars for edge vs. center in 10 m gaps, where unscarified efflux was greater than scarified for 78% of observations. Gaps were created by cutting and removing trees, but stumps were left in the ground such that the surrounding soil architecture could remain as unchanged as possible and disturbance could be introduced solely through surface scratching within select soil collars. The method of tree removal prevented tip-up mounds from forming and drastically changing the topsoil in gaps. Though the soil disturbance used in this study was meant to mimic Carolina northern flying squirrel foraging, it also provides information about general physical disturbance that could come from other sources, such as foot traffic or harvesting. Scarification involved moving and mixing the litter layer with surface topsoil and duff, which can alter the soil climate by allowing more light infiltration (Zummo and Friedland 2011). This can lead to overall increases in carbon lost to respiration (Zummo and Friedland 2011), which was not seen in this study. Non-fire-related soil disturbance effects on efflux are not commonly evaluated in the literature, making the dynamic seen in this study interesting.

Soil respiration is often considered to have two main “compartments”: plant fine root respiration and respiration from rhizosphere microbes; these are autotrophs and heterotrophs respectively (e.g. Kelting et al. 1998, Ma et al. 2019). This metric is known to be linked closely with soil temperature and moisture (e.g. Ma et al. 2019, Moyano et al. 2013), and specifically tends to be positively associated with soil temperature and by extension with higher light levels (Kaur et al. 2010). In this context, the present study’s lower observed efflux values in centers of large gaps relative to edges is interesting, as soil temperatures, moisture levels, and light levels all tended to be higher in 10 m gaps and thus could have been expected to induce greater respiration in either heterotrophs or autotrophs. Since the two respiration components were not

segregated in this study, an increase in either autotrophic or heterotrophic respiration would have affected overall values, indicating that neither was increased enough by the conditions to raise the average. The greater soil moisture in 10 m gaps suggests that temperatures in 10 m gaps were never high enough to dry out the soil, which could be a positive sign for red spruce and Fraser fir regeneration as both species require moist soil to establish (Nowacki et al 2010, Rentch et al. 2016). Soil respiration data from forests codominated by these species is scarce in the literature, making these findings valuable.

Soil respiration oscillated across the growing season in keeping with the gradual increases and decreases in temperature over weeks that is common at Roan Mountain. Overnight low temperatures consistently dropped below 9 °C and as low as 2 °C, with daytime highs not exceeding 13 °C, until approximately June 4, explaining in part the low initial efflux values since soil respiration tends to be reduced at low temperatures (Ma et al. 2019, Moyano et al. 2013). The study site was regularly under at least 1 cm of snow cover until at least the end of April, meaning that efflux had likely come up from even lower values over the month prior to data collection. Once daytime high temperatures stabilized between 21 °C and 24 °C in mid-July, soil respiration increased by between 10% and 50% depending on plot, which would coincide with increased net primary productivity and fine root respiration in understory seedlings (Ma et al. 2019). The significance of the time effect in both RANOVAs corresponds with environmental data that suggests a growing season peak with high air temperatures from late July to late August.

Soil CO₂ efflux can be used as an index for growth and fine root nutrient uptake by seedlings and saplings in forested systems and provides information about forest carbon sequestration (Kelting et al. 1998). Low average values indicate that carbon is staying in the

system and that root/microbe activity and plant growth may be low, while higher average values suggest the opposite. At the study site, carbon is likely stored at a relatively high rate among mature trees as in other evergreen forests (Rhyti et al. 2021), with mountaintop soil properties and seedlings that are currently germinating contributing to carbon lost to the atmosphere. Following from this, it appears that the often-higher efflux values found in controls compared to large gaps may indicate that red spruce and Fraser fir are performing fairly well without intervention at Roan Mountain. Other mapping and growth evaluations from the central and southern Appalachians have supported this idea, even suggesting that red spruce is naturally regenerating at a satisfactory level in montane areas (Nowacki et al. 2010, Rentch et al. 2016). Short growing seasons at Roan, which tend to be between 100-150 days/yr as in other parts of the southern Appalachians (Tewksbury and Van Miegroet 2007), may also play a role in the observed efflux pattern as decomposition of roots after tree removal may not increase enough to affect total soil respiration until a future season. Continued monitoring would be needed to evaluate the pattern more fully.

The end of clear-cutting and subsequent slash fires 80-100 years ago in areas with a red spruce and Fraser/balsam fir presence in the seed bank is also thought to have allowed nutrient cycling to restore the soil such that red spruce can germinate more successfully, especially where hardwood species, which have high root and stem turnover rates, have, or had previously, colonized (Mayfield and Hicks 2010). The scarcity of many hardwood species, especially *Betula* spp., in southern Appalachian high elevation seed banks (White et al. 1985, White 1984, Busing 2004) and lack of mature hardwoods near the study site means that spruce-fir may be even more likely to benefit from restoration practices since competition is low. This contrasts with spruce-fir in other areas such as West Virginia (e.g. Mayfield and Hicks 2010, Rentch et al. 2016) or the

northeastern U.S. and Canada (e.g. Nowacki et al. 2010, Dumais and Prévost 2014). One aim of silvicultural practices is to increase red spruce sapling growth rates, release them into higher canopy strata, and diversify stand age class (Mayfield and Hicks 2010). Results from this study support the idea that inducing single-tree or small multi-tree gap disturbances, such as the 3.5 m gaps used in this study, may help reach those goals. Squirrel-related soil scarification affected soil respiration in gap size treatments as well, as scarified rings in large gaps generally had the lowest efflux of all. The comparatively high soil respiration values for scarified rings seen in the smaller gaps in this study indicate increased metabolic activity in seedling roots in those treatments, which could translate to the regeneration we hope to see even with greater flying squirrel foraging. However, some research has suggested that alpine spruce forest, such as that found in the Austrian Alps, may show no net soil respiration response to canopy gaps regardless of whether advance regeneration is occurring (Mayer et al. 2017), so monitoring over multiple seasons would be necessary to evaluate gap effects on soil respiration specifically, especially as it responds to the combination of gap size and soil scarification.

The present study controlled for living plant contributions to efflux within collars to the extent possible, but the structure of the forest floor and litter layer at Roan Mountain prevented total exclusion. Both vascular and non-vascular plants are known to emit CO₂ at high enough rates to cause efflux readings to skew higher, and for this reason studies that use collars commonly clip live vegetation (e.g. Ma et al. 2019, Rhyti et al. 2021). Where present, small conifer seedlings and shoots of herbaceous plants including *Vaccinium* spp. were clipped, but several moss species were ubiquitous at the study site as is typical for boreal forests (e.g. Rhyti et al. 2021). Approximately half of all soil collars, evenly distributed between scarified/unscarified treatments and all gap sizes, had some level of moss present within them that could not be

avoided since moss had a 50% or greater ground cover in most gaps. Moss grows well in the dark, wet conditions typical of the site and often supports red spruce and Fraser fir seedlings because of its ability to trap water, making it hard to exclude from the design. This may have inflated efflux readings overall but not affected treatment values relative to one another because of the wide distribution of moss cover. Moss may have helped reduce spatial variation between gaps by trapping water, holding topsoil in place, and creating continuous ground level vegetation cover in many areas. Moss will continue to impact soil and vegetation dynamics at Roan Mountain, though differences between its impact on soil respiration and that of random spatial heterogeneity may be difficult to determine.

Climate effects, including increases in mean annual temperature and diminished cloud cover, could impact the red spruce-Fraser fir forest at Roan Mountain in future seasons and have extensive effects on the plant and soil communities. Increased soil acidification from acid rain could cause further issues in red spruce stands where acid deposition is already known to be a problem (Koo et al. 2014, Mayfield and Hicks 2010, Ribbons 2014). Red spruce specifically could face physiological issues, such as longer winter dormancy caused by higher winter temperature effects on abscisic acid breakdown (Koo et al. 2014). Its relatively low genetic diversity (Capblancq et al. 2020) and need for cool conditions at high altitude (Koo et al. 2014, Ribbons 2014) could therefore jeopardize its abundance at Roan Mountain, possibly lowering soil respiration at the study site if red spruce is injured by climate or if hardwoods begin to colonize.

Overall, data from this study suggest that large, multi-tree canopy gaps may not be the most efficient method for red spruce restoration at Roan Mountain. Smaller gaps often had similar or greater soil CO₂ efflux, which may indicate greater root and microbe activity because

of the combination of slightly more light with enough protection to prevent desiccation. However, edges of large gaps had higher soil respiration, meaning that the more variable light conditions created by the edge effect could have more positive effects on spruce-fir advance regeneration than the more uniform high light conditions at the center of the gap. Multiple field seasons will be needed to evaluate red spruce and Fraser fir seedling growth dynamics as well as competitive dynamics between the conifers and hardwood competitors following recruitment. Further monitoring of soil CO₂ efflux and seedling growth in controls will also be necessary as the two conifer species may be regenerating to an extent without active management. As they relate to forest management at Roan Mountain, results of this study indicate that 10 m gaps show diminished soil respiration, and that scarification like that caused by Carolina northern flying squirrel foraging also tends to decrease soil respiration. These outcomes suggest that spruce and fir recruitment may be lower in large gaps than in small gaps but higher at the edge than in the center, and that a greater flying squirrel presence that could follow successful restoration may negatively affect recruitment in subsequent seasons. Thus, pairing a survey of flying squirrel nesting at Roan Mountain with continued regeneration monitoring in both gaps and uncut controls would provide valuable information for managing spruce-fir stands at the site in the long term.

CHAPTER 5: LITERATURE CITED

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Table 1. Canopy and light data response by gap type and location within gap, including medians and standard deviation of photosynthetically active radiation (PAR) with boxplots depicting spread of values, as well as means and standard deviation of percent overstory canopy cover. Center refers to the area from the marked center of the gap extending 2 m in any direction, while edge refers to the area from 2 m to the true gap edge in any direction.

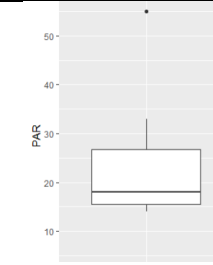

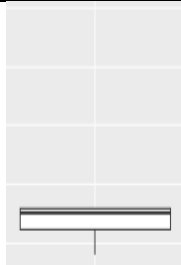
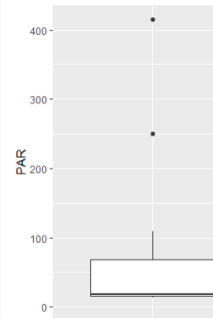
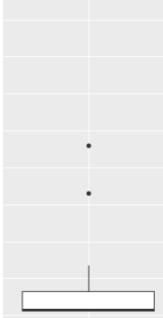

| Response | 10 m Gap | 3.5 m Gap | Uncut |
|---|--|---|--|
| <i>Center</i> | | | |
| |  |  |  |
| PAR ($\mu\text{mol}/(\text{m}^2 \cdot \text{s})$) | 18.0 (± 9.9) | 7.0 (± 4.0) | 7.5 (± 1.7) |
| Canopy Cover (%) | 88.3 (± 4.8) | 96.4 (± 1.7) | 98.6 (± 1.4) |
| <i>Edge</i> | | | |
| |  |  |  |
| PAR ($\mu\text{mol}/(\text{m}^2 \cdot \text{s})$) | 18.0 (± 98.5) | 7.8 (± 65.5) | 6.6 (± 18.1) |
| Canopy Cover (%) | 90.1 (± 3.4) | 95.6 (± 1.5) | 98.8 (± 1.1) |

Table 2. Seedling survival and growth means (standard deviation) for each gap size. Survival rate describes the proportion of seedlings alive in a 1x1 m quadrat during the sampling month (n=50 for all treatments). Height growth describes the average growth of the surviving seedlings in mm since the last growth survey.

| Response | 10 m Gap | 3.5 m Gap | Uncut |
|--------------------|---------------------|---------------------|---------------------|
| <i>May</i> | | | |
| Survival rate | 0.98 | 1.00 | 0.96 |
| Height growth (mm) | - | - | - |
| <i>July</i> | | | |
| Survival rate | 0.96 | 1.00 | 0.96 |
| Height growth (mm) | 0.30 (± 0.20) | 0.50 (± 0.40) | 0.25 (± 0.10) |
| <i>October</i> | | | |
| Survival rate | 0.96 | 0.98 | 0.96 |
| Height growth (mm) | 0.40 (± 0.20) | 0.50 (± 0.20) | 0.50 (± 0.30) |

Table 3. Means (standard deviation) of percent cover on 30 m long, 1 m wide strip transects (two adjacent to a gap of each size, six total) of understory (less than 1 m in height) major plant taxa found at the study site.

| Taxon | 10 m Gap (% Cover) | 3.5 m Gap (% Cover) | Uncut (% Cover) |
|--------------------------|---------------------------|----------------------------|------------------------|
| <i>Picea rubens</i> | 29 (± 4) | 36.5 (± 3.5) | 30 (± 10) |
| <i>Abies fraseri</i> | 60 (± 5) | 45 (± 5) | 50 (± 10) |
| <i>Vaccinium</i> spp. | 0.5 (± 0.5) | 1 (± 0.5) | 1 (± 0.5) |
| <i>Rhododendron</i> spp. | 1 (± 0.5) | 3 (± 1) | 0 (± 0) |
| <i>Betula</i> spp. | 1 (± 0.5) | 0 (± 0) | 0 (± 0) |
| Moss (unidentified) | 55 (± 5) | 75 (± 1) | 35 (± 5) |

Table 4. Means (standard deviation) of moss cover within soil collars by gap type, with total number of collars and their distribution in each gap type.

| Gap Type | Number of Collars | Center Collars | Edge Collars | Moss Cover (%) |
|-----------------|--------------------------|-----------------------|---------------------|-----------------------|
| 10 m diameter | 20 | 10 | 10 | 25 (± 18) |
| 3.5 m diameter | 11 | 9 | 2 | 50 (± 36) |
| Uncut | 8 | 8 | 0 | 33 (± 15) |

Table 5. Pearson’s correlation values for scarified and unscarified collar CO₂ efflux with soil temperature and soil moisture, run separately for each gap type. Only collars located in gap centers were used in this analysis.

| Environmental Metric | 10 m Gap Flux | 3.5 m Gap Flux | Uncut Flux |
|-----------------------------|----------------------|-----------------------|-------------------|
| <i>Scarified</i> | | | |
| Soil Temperature (°C) | 0.134 | 0.653 | 0.531 |
| Soil Moisture (%) | 0.265 | -0.200 | 0.048 |
| <i>Unscarified</i> | | | |
| Soil Temperature (°C) | 0.161 | 0.328 | 0.337 |
| Soil Moisture (%) | 0.255 | 0.085 | 0.144 |

Table 6. Repeated measures ANOVA output for strength of effect of gap size, week, and gap size-week interaction on soil CO₂ efflux readings, separated by scarified and unscarified collar types. Edge and center ring readings for 10 m gaps were averaged for the analysis. * denotes a statistically significant effect of the variable effect on efflux as expressed by the p value, with a significance threshold of $p = 0.05$.

| Effect | Degrees of Freedom | F | p |
|--------------------|---------------------------|----------|-----------|
| <i>Scarified</i> | | | |
| Size | 2 | 2.624 | 0.276 |
| Week | 17 | 16.18 | 2.67e-07* |
| Size:Week | 34 | 2.301 | 9.00e-03* |
| <i>Unscarified</i> | | | |
| Size | 2 | 0.421 | 0.704 |
| Week | 17 | 29.36 | 2.51e-09* |
| Size:Week | 34 | 3.085 | 7.36e-04* |

Table 7. Repeated measures ANOVA output for strength of effect of edge vs. center collar location, week, and location-week interaction on soil CO₂ efflux readings from 10 m gaps, separated by scarified and unscarified collar types. * denotes a statistically significant effect of the variable effect on efflux as expressed by the p value, with a significance threshold of p = 0.05.

| Effect | Degrees of Freedom | F | p |
|--------------------|---------------------------|----------|-----------|
| <i>Scarified</i> | | | |
| Location | 1 | 5.436 | 0.080 |
| Week | 17 | 5.111 | 5.71e-07* |
| Location:Week | 17 | 3.164 | 3.80e-04* |
| <i>Unscarified</i> | | | |
| Location | 1 | 0.179 | 0.689 |
| Week | 17 | 13.57 | 1.44e-17* |
| Location:Week | 17 | 1.385 | 0.165 |



Figure 1. Location of experimental spruce-fir stand at Roan Mountain, NC. Stand area is outlined red with experimental gaps and controls dotted within as of the time cuts were made in January 2021. Two uncut control areas were unmapped in the leftmost cluster as they were established after treatment.

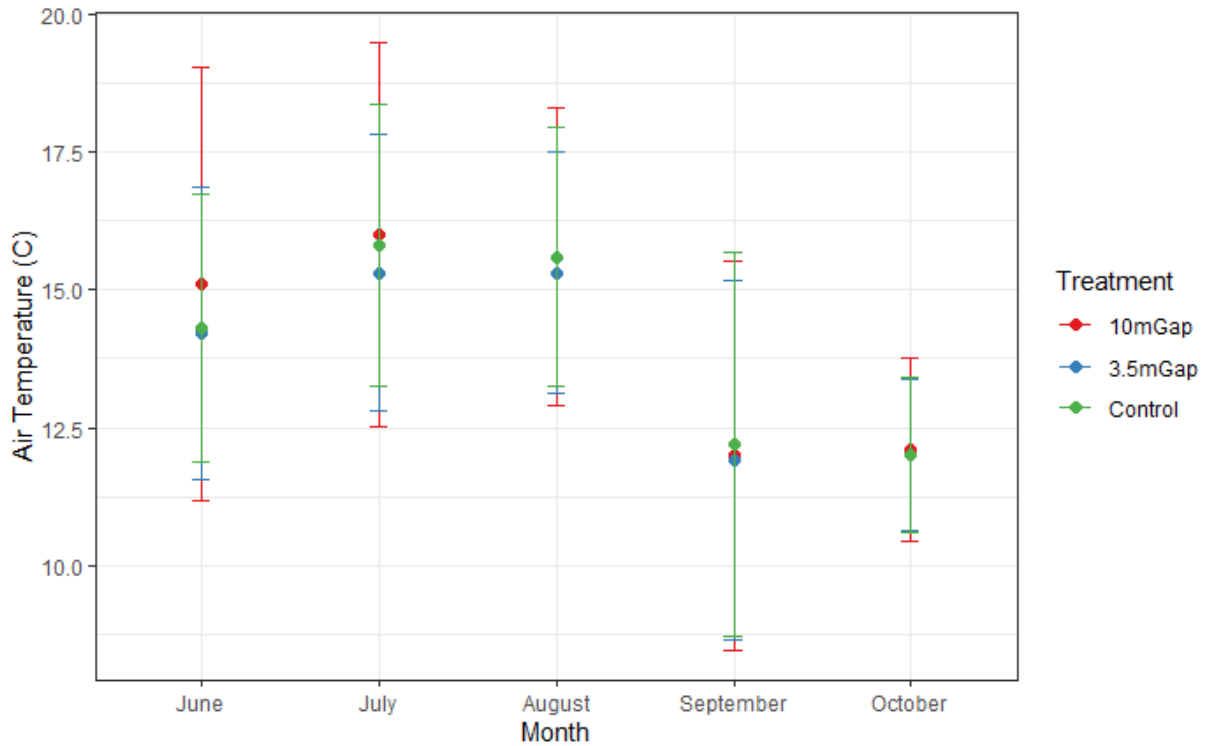


Figure 2. Means and standard deviations for air temperatures over the 2021 growing season for each gap type. Each month name denotes a specific set of weeks of the growing season starting with week 1 and ending with week 18. June: weeks 1-5. July: weeks 6-9. August: weeks 10-13. September: weeks 14-16. October: weeks 17-18.

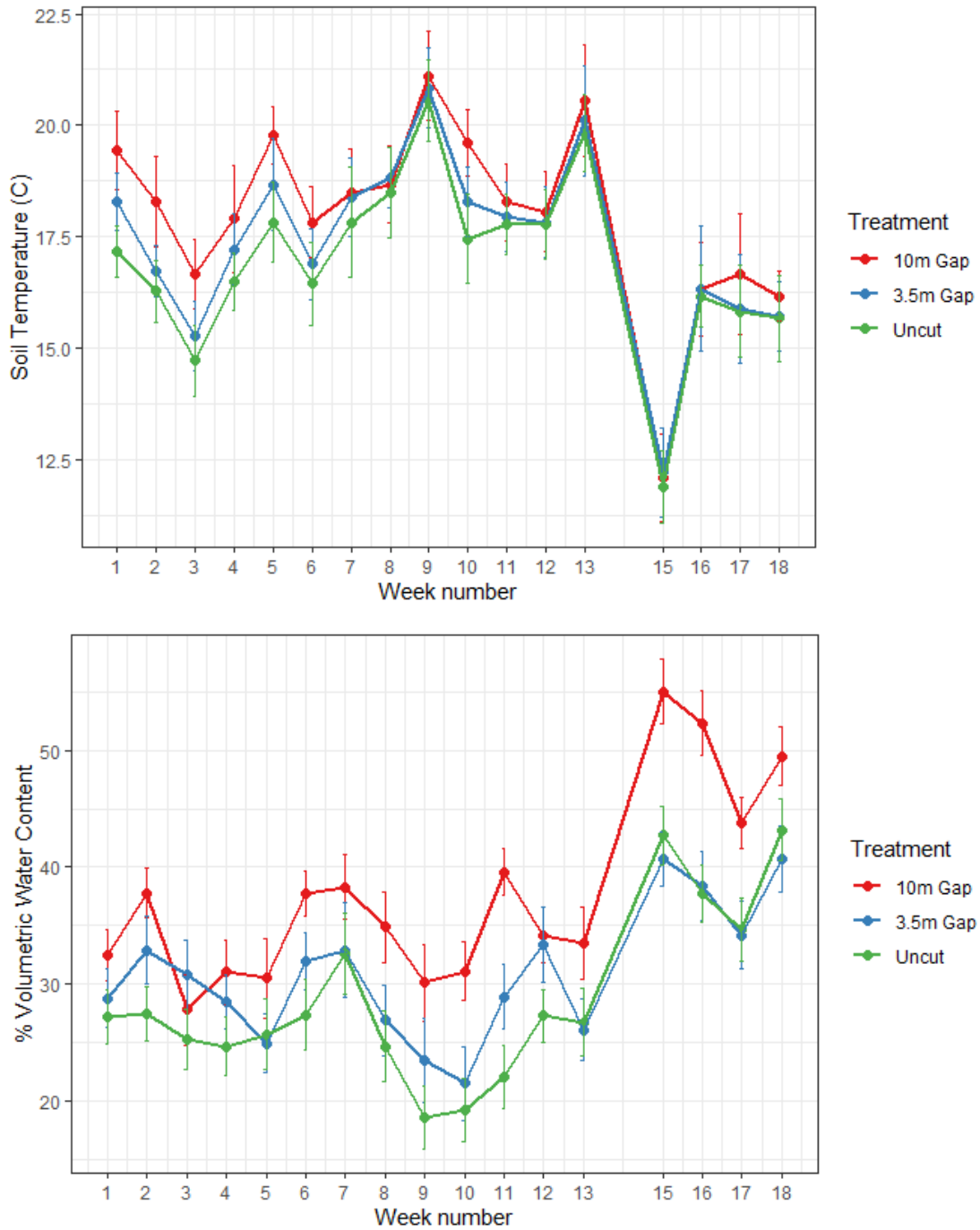


Figure 3. Means and standard deviations for soil temperature and soil moisture over the 2021 growing season for each gap type. Week 1 denotes the start of sampling on 6/4/21 and week 18 denotes the end on 10/14/21, with readings interspersed by 7 days on average. Data missing for week 14 due to equipment availability.

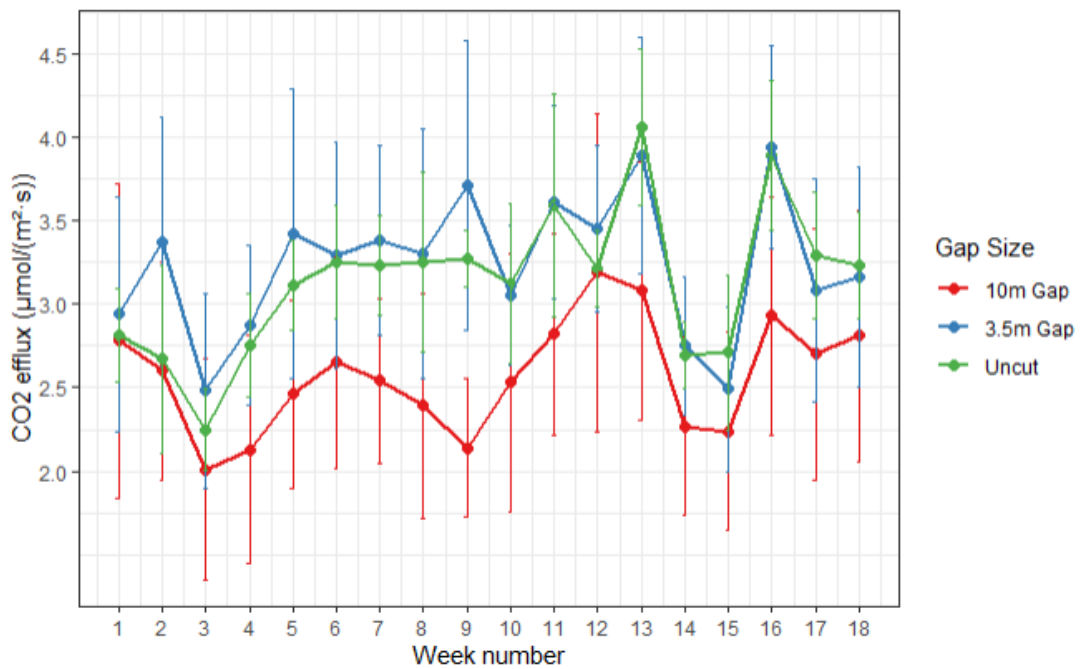
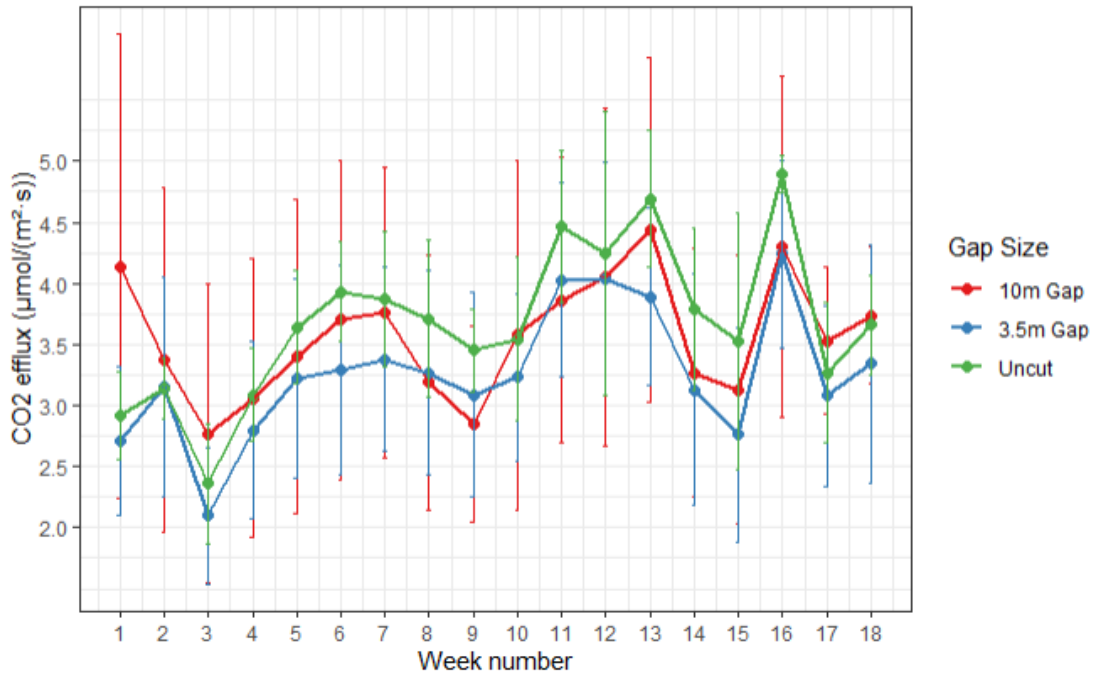


Figure 4. Mean soil CO₂ efflux values with standard deviation bars for unscarified (top) and scarified (bottom) center soil collars for each gap type. Week 1 denotes the beginning of readings on 6/4/21 and week 18 denotes the final readings on 10/14/21, with readings interspersed every 7 days on average.

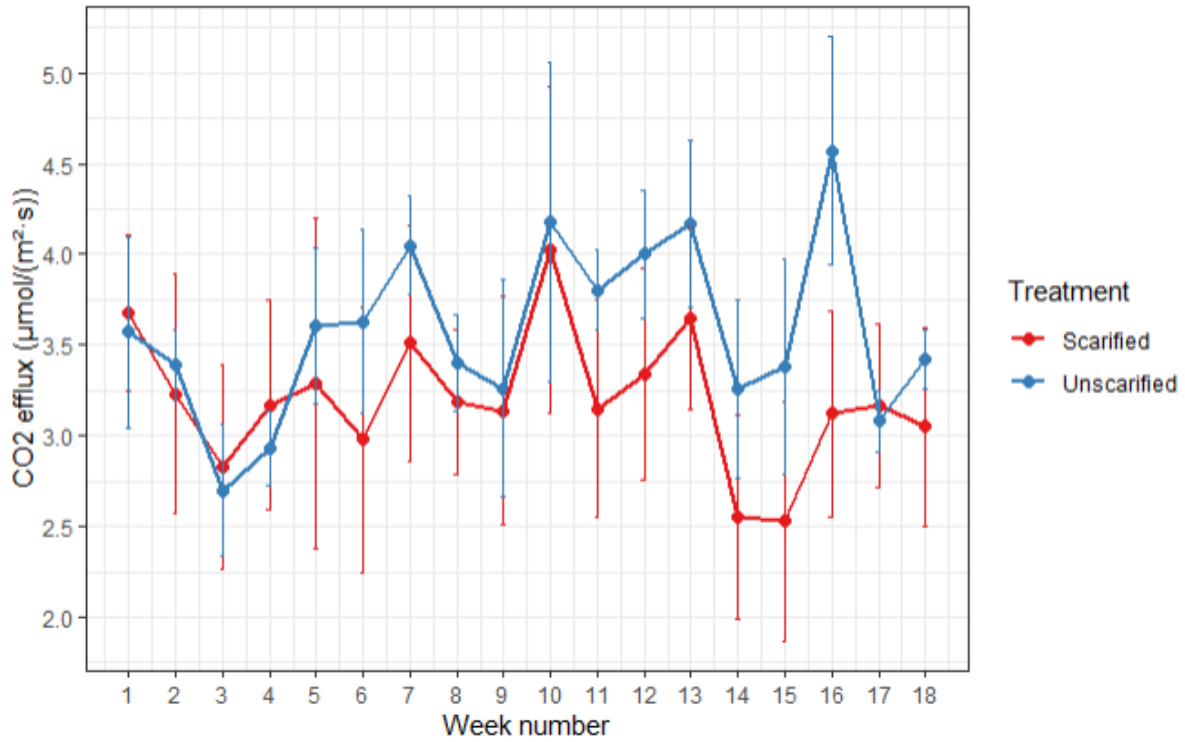


Figure 5. Mean soil CO₂ efflux values with standard deviation bars for scarified and unscarified soil collars at edges of 10 m gaps. Week 1 denotes the beginning of readings on 6/4/21 and week 18 denotes final readings on 10/14/21, with readings interspersed every 7 days on average.