Chapter 2
The Biology of Red Spruce

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2.1 Introduction

Red spruce (*Picea rubens*) is a medium sized, coniferous tree that grows in cool, moist climates, and acidic soils in eastern North America (Blum 1990; Fig. 2.1). It is a long-lived species with a slow growth rate due in part to its shade tolerance and subsistence in the understory for many years (Murphy 1917; Korstian 1937). Red spruce was first taxonomically described by the American botanist Charles Sprague Sargent in *Silva of North America—Vol. 12* (Sargent 1899). Modern taxonomy classifies red spruce as a gymnosperm in the family Pinaceae (International Plant Names Index 2022). Prior to the end of the nineteenth century, red spruce was common in many boreal and montane forests in eastern North America (Blum 1990; see Sect. 1.2.2 in Chap. 1). Extensive harvesting between the late 1800s and early 1900s dramatically reduced the area of red spruce occurrence (See Chap. 1). Today, red spruce communities are concentrated in three broad biogeographical regions—southern Appalachians, central Appalachians, and northern Appalachians (see Fig. 1.3 in Chap. 1).

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Fig. 2.1 Red spruce (*Picea rubens*) stand, Spruce Knob, Monongahela NF, West Virginia. Photo by USDA Forest Service

2.2 Life History

2.2.1 Reproductive Structure, Seed Production, and Seed Dispersal

Red spruce is monoecious with both male (i.e., pollen cone) and female (i.e., seed cone; Fig. 2.2) reproductive structures on the same tree, each forming on different branches. Pollen and seed cones differentiate the year preceding fertilization in mid to late summer. Pollen cones (length: 1.5–2.5 cm [0.6–1.0 in]) develop on axillary apices part of the distal shoots or terminal apices of proximal shoots. Initial pollen cone colors range from purple to red and turn yellow to brown upon maturity. Seed cones (length: 2.5–6 cm [1.0–2.4 in]) form at the tip of stems (terminal) and are initially erect with a greenish, slight purple tinge. Similar to other coniferous species, upon maturity the color of seed cones changes to a reddish to purplish brown and the cones gradually become hanging (pendulous) on the branches. Although pollen is released from late April to May, seed cones are only receptive to pollen a few days during this period.

Seed cones mature the following year in late August to October (Hart 1959; Safford 1974; Blum 1990; Farjon 2017), with seeds falling throughout late fall into



Fig. 2.2 Red spruce (*Picea rubens*) seed cone, Spruce Knob, Monongahela NF, West Virginia. Photo by Elizabeth Byers

winter. Periods for seed dispersal can be highly variable, ranging from October to March (Heinselman 1965; Safford 1974). The lightweight, winged seeds of red spruce are well suited for wind dispersal. Silvicultural studies of red spruce seed dispersal into forest openings show an effective seedling dispersal range of 61 m (200 ft; Frank and Bjorkbom 1973), with the greatest concentration of seeds 25–30 m (82–98 ft; Hughes and Bechtel 1997) from the forest edge, but potentially viable regeneration up to 100 m (328 ft) away from the seed tree Randall 1974).

Although red spruce trees may produce seeds starting at age 15 (Frank and Bjorkbom 1973), viable, large seed crop production does not begin until the ages of 30–50 years (Heinselman 1965; Safford 1974). The largest seed crops occur when individual trees enter the canopy into full, direct sunlight (Korstian 1937). Under these conditions red spruce produces the largest seed crops every 3–8 years, with smaller, less viable crops annually that may continue until mortality (Hart 1965; Blum 1990). In the southern region, two studies found contradictory results related to the percentage of filled seeds and seed mass with increasing elevation. Whereas Nicholas et al. (1992) observed a decrease with increasing elevation, a more recent study by Butnor et al. (2019) found an increase.

2.2.2 Seed Germination

Red spruce germination is epigeal (i.e., occurring above the ground; Safford 1974; Farjon 2017). Most seedling germination occurs the year following fertilization from May to July but may also occur in October immediately after release (Blum 1990). Germination success varies among substrates. Most mineral soil substrates that have high soil moisture holding capacities with moderate temperatures (20–30 °C [68–86 °F]) have the highest rates of successful germination (Frank and Safford 1970). Substrates with extensive bryophyte (non-vascular mosses, hornworts, and liverworts) layers also have successful germination rates due to their high water holding capacity and nutrient content (Dibble et al. 1999). Germination is lower in areas with thicker organic horizons and on decomposing coarse woody debris due to rapid desiccation, resulting from highly variable temperatures. Germination will not occur below 20 °C (68 °F), and significant injury resulting in high mortality occurs when temperatures exceed 33 °C (91 °F; Heinselman 1965; Safford 1974; Blum 1990). In Maine, Greenwood and McConville (2002) found germination rates of 33–83% when there was no water stress, with optimal daily temperatures of 20 °C (68 °F) and nightly temperatures of 10 °C (50 °F).

2.2.3 Seedling Establishment and Growth

Dry growing mediums and frost damage are major causes of mortality for red spruce seedlings growing in areas where organic horizons exceed 5 cm (2 in) or on decaying logs in the first year after germination (Blum 1990). Because seedlings slowly develop a shallow, fibrous root system, young roots may not penetrate deep enough to avoid zones of droughty or freezing conditions, leading to mortality. The upper areas of the soil are also prone to higher soil surface temperatures especially in open canopy areas with hotter and drier microclimates, with significant mortality occurring when soil surface temperatures exceed 46 °C (115 °F) for short intervals (Heinselman 1965; Safford 1974; Blum 1990). Seedling establishment is most successful under canopies reducing direct sunlight to moderate forest floor temperatures and retain moisture (Fig. 2.3).

Red spruce seedlings are typically established when they reach a height of 15 cm (6 in) due to a fibrous root system extending below organic and soil surface horizons that can generally survive drought or frost heaving conditions (Heinselman 1965; Frank and Bjorkbom 1973; Safford 1974). Once established, seedling growth may be reduced by interspecific competition with seedlings of competing conifers (e.g., Fraser fir [*Abies fraseri*]), deciduous trees, ericaceous shrubs, and herbaceous species whose diversity and abundance depends on elevation, and the amount and type of localized disturbance.

Although low light levels slow seedling growth, red spruce is highly shade tolerant due to its foliar plasticity (Greenwood et al. 2008), increased resource allocation for



Fig. 2.3 Red spruce (*Picea rubens*) regeneration. Photo by USDA Forest Service

lateral versus height growth (Dumais and Prévost 2007), and its ability to photosynthesize with light levels found in sunflecks (Alexander et al. 1995). Given these factors, red spruce can survive extended periods in the understory and still respond to release treatments at 60–70 years (Nicholas et al. 1992), and even up to 150 years of age (Blum 1990). Since single-tree canopy disturbance is the most common disturbance type in red spruce and spruce-fir forests (see Chap. 5), this strategy is advantageous for a seedling to eventually reach the overstory.

Research across the entire red spruce range generally shows positive responses to silviculture prescriptions that mimic natural gap openings in the canopy that equate to changes in microenvironmental conditions. Specific silvicultural prescriptions relating to red spruce growth response are detailed in Chap. 8. Herein, we discuss seedling and sapling establishment in response to gap creation. Most silvicultural prescriptions aim to achieve an optimal light availability of 50% for red spruce seedlings (Seymour 1995; Moore et al. 2007; Dumais and Prévost 2014; Rentch et al. 2016). In the northern region in Québec, red spruce germination and establishment success depended on the type and size of gaps created in the canopy that influence the microenvironment (Dumais and Prévost 2007, 2008, 2014, 2016; Dumais et al.

2020). This research showed that although creating small (100m^2 [1076 ft^2]) gaps with a gradient of decaying wood and mosses initially appeared to be an optimum prescription, after 10 years seedling mortality appeared to increase compared to medium sized (100–300 m^2 [1076–3229 ft^2]) gaps, with larger (700 m^2 [7535 ft^2]) gaps having the lowest seedling survival.

In the central region, treatments with similar gap sizes were shown to increase red spruce seedling height and diameter growth by killing (but not removal) of more than 90% of the overstory competition with stem injection in gaps < 100 m^2 (1076 ft^2) and removal of 42% of overall basal area. Rollins et al. (2010) assessed seedling establishment across a plant community gradient and observed an increase in red spruce seedling establishment in the ecotone, a transitional zone of changing environmental conditions and species composition, between red spruce and deciduous communities. Red spruce seedling establishment also occurred in the red spruce-dominated study areas but was significantly reduced in the exclusively deciduous areas. Although creating small- to medium-sized gaps in the canopy is a viable silvicultural option to increase sapling red spruce growth and recruitment in the northern and central Appalachians, the size of gaps created in the southern Appalachians has not been well studied. Large gaps created by the death of hemlock (*Tsuga* spp.) and Fraser fir due to invasive insects (see Sect. 2.5.1) have caused overstory red spruce mortality due to wind throw (Busing 2004), indicating negative impacts of larger canopy gaps.

2.2.4 Forest Structure and Composition

Red spruce typically forms uneven-aged stands due to its persistance in the understory and is generally not released until gap formation in the canopy as domininant and co-dominant trees die (Blum 1990; Fraver and White 2005; Rentch et al. 2007; Rentch et al. 2016; see Fig. 2.1). Red spruce can also occur, although less frequently, as homogenous, single-aged stands due in part to historical clear-cut logging and subsequent fire activity (Korstian 1937; Allard and Leonard 1952) or large windthrow events (see Chap. 5). The high shade tolerance of red spruce allows seedlings and saplings to persist in the understory, potentially for decades (Blum 1990; D'Arrigo et al. 2012), which can make forest recovery slow after disturbances (Rollins et al. 2010).

Generally, red spruce growth rates are greater moving north to south due to a longer growing season in the more southern latitudes (Oosting and Billings 1951). The largest red spruce trees occur in old-growth forests, the majority of which occur in the Great Smoky Mountains in the southern Appalachians. For example, in the central and southern regions, stem diameters of larger trees may range from 54–61 cm (21–24 in; rarely exceeding 76 cm [30 in]), with maximum heights of 35 m (115 ft; Korstian 1937; Oostig and Billings 1951; Busing et al. 1988; Blum 1990; Soulé et al. 2012). However, the size and stature of red spruce in second growth stands following

timber harvesting tends to be reduced compared to old-growth counterparts (Korstian 1937; Schuler et al. 2002; Rentch et al. 2010).

Red spruce's productivity is impacted by a variety of factors. One important growth factor for red spruce throughout its entire range is age. Red spruce is a long-lived tree species with maximal ages reaching up to 400 years (Hart 1965), as evidenced by dendrochronological studies. As red spruce ages, biomass productivity, photosynthesis rates, and foliar efficiency can decline (Day et al. 2001). Older red spruce trees can comparatively exhibit more symptoms of decline than their younger understory counterparts affected by similar stressors (Adams and Stephenson 1989; Goelz et al. 1999). The age of suppressed red spruce is important as older trees are generally less responsive to release compared to their younger counterparts (Seymour and Kenefic 2002), although two studies that indicated a possible response up to 145 years (Safford and Young 1968; Frank and Bjorkbom 1973). In addition to age, crown architecture can be important when considering red spruce productivity and efficiency. Studies have shown that dominant canopy red spruce, with the largest crown sizes, generally have decreased growth efficiency (Seymour and Kenefic 2002; DeRose and Seymour 2009).

One method to assess site and stand productivity for tree species is site index (Brown 1962). Site index is commonly expressed as the height of an overstory tree at a reference base age, usually 50 years in eastern North America, and is based on the measurement of free-growing canopy trees (Geyer and Lynch 1987; Mathiasen et al. 2006). Site index curves can then be developed that estimate tree growth and hence potential stand productivity. Although traditional site index relationships have assessed red spruce productivity (Carmean et al. 1989), they are not reliable estimates because true age is used to predict height of red spruce. Red spruce is shade tolerarant and has extended periods of suppressed, slow growth (Rentch et al. 2007) that introduces inaccuracies into the development of site index curves.

Although limited, there have been improvements to estimate red spruce site productivity using site index relationships in northern and central regions (Nicholas and Zedaker 1992; Seymour and Fajvan 2001; Yetter et al. 2021a). In the northern region, Seymour and Fajvan (2001) quantified free-to-grow conditions and alternate periods of tree suppression to adjust site index curves. Most recently, Yetter et al. (2021a) developed suppression-corrected age-height pair and DBH-height pair site index models in the central Appalachians (Fig. 2.4). Red spruce was sensitive to several climatic (e.g., number of frost-free days, extreme temperature over a 30-year period) and geographic (e.g., elevation) variables which can affect growth (Yetter et al. 2021a, 2021c). Appropriate site index curves for red spruce in the southern region still need to be developed.

2.2.5 Stand Dynamics

Forest dynamics in red spruce stands are typically controlled by wind (Busing and Pauley 1994; Busing 2004), ice (Nicholas and Zedaker 1989), and individual tree

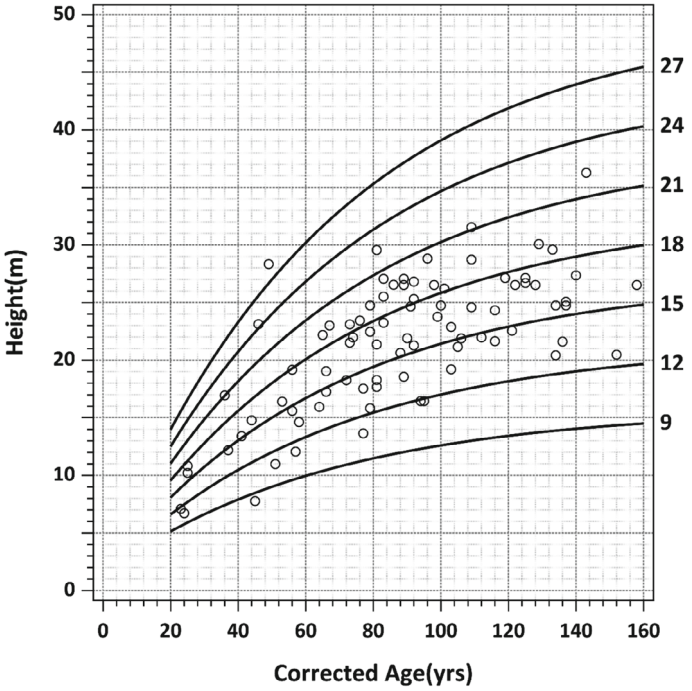


Fig. 2.4 Red spruce (*Picea rubens*) site index curves developed from a model of height- and suppression-corrected age. Individual lines are base age 50 site index curves. Open circles represent sample trees ($n = 83$). Adapted from Yetter et al. (2021a)

mortality (Cogbill and White 1991), although larger historical disturbance events caused by forest insects, large blowdown events, and landslides have been documented (Hopkins 1891, 1899; Murphy 1917; Korstian 1937; Cook and Johnson 1989; see Chap. 5). Gap dynamics of second-growth red spruce stands in the central region of West Virginia indicate that gaps are most frequently created by the death of American beech (*Fagus grandifolia*) due to beech bark disease (Rentch et al. 2010). Unfortunately, these typical gaps formed in the central Appalachians of West Virginia generally close before red spruce can reach the canopy, and restoration efforts require active management (i.e., thinning and release) to promote subsequent canopy openings to allow advanced red spruce regeneration to ascend to the overstory in hardwood dominant stands (Rentch et al. 2010; see Chap. 8). Gap phased dynamics in mixed stands of spruce-fir in the Great Smoky Mountains of North Carolina and Tennessee indicated a trend of replacement of canopy species, with Fraser fir prominent at higher elevations (White et al. 1985; Busing 1996).

In mixed-species stands of red spruce with a fir component, balsam woolly adelgid (*Adelges piceae*), a non-native insect, can lead to mortality of fir trees (Creed et al. 2004). In particular, Fraser fir is susceptible to balsam woolly adelgid and infestations can negatively impact fir regeneration while not impairing red spruce regeneration

(Stehn et al. 2013). Infestation with balsam woolly adelgid can in turn lead to an increased amount of coarse woody debris (Creed et al. 2004; Rose and Nicholas 2008). Past insect infestation of Fraser fir in Great Smoky Mountains National Park led to improved growth rates of red spruce in the stand, but mortality of red spruce increased due to increased wind exposure (Busing and Pauley 1994; Busing 2004).

Predation from herbivores has minimal impact on red spruce regeneration because the species has low palatability to many browsers, such as white-tailed deer (*Odocoileus virginianus*). Browse resistance provides a competitive advantage for red spruce regeneration over competing hardwood species, such as red maple and yellow birch (Griscom et al. 2011). In contrast, competition from other plant species limits spruce regeneration. For example, *Rhododendron* stems can grow into dense thickets and can negatively affect regeneration of red spruce (Adams and Stephenson 1989). In canopy gaps created by beech bark disease, American beech sprouts can grow fast and may end up filling canopy gaps with infected beech saplings, which takes up available space and resources for red spruce regeneration (Van Miegroet et al. 2007; Rentch et al. 2016).

2.3 Abiotic and Biotic Stressors

The interaction of abiotic and biotic stressors affects the reproduction, growth, and distribution of red spruce in the central and southern Appalachians (Harmon et al. 1984). Examples of abiotic stressors include extreme weather events such as ice storms (Nicholas and Zedaker 1989) and windstorms (Busing 2004), fire (Moore et al. 2002), and pollutant deposition, whereas biotic stressors include pests and pathogens. Stressors are also influenced by historical activities, including exploitative timber harvesting (Adams 1999) and climate change. For example, at the turn of the twentieth century extensive extractive harvest logging and subsequent fires caused significant soil erosion and nutrient loss from the ecosystem that reduced soil fertility and limited red spruce reproduction, growth, recovery, and potential restoration. More than a century after pre-industrial logging occurred, mountain slopes devoid of trees are still seen in Great Smoky Mountains National Park (Harmon et al. 1984).

2.3.1 Abiotic Stressors

Prior to 2000, most research on the abiotic stressors of red spruce forests in the central and southern Appalachians focused on understanding the effects of pollutant exposure and deposition on high elevation red spruce ecosystems (Eagar and Adams 1992; Rentch et al. 2010). Although these regional red spruce forests are confined to remote, high peaks, they are exposed to concentrated, high levels of pollutants originating from the midwestern and southern U.S. that are carried eastward on prevailing atmospheric patterns. Sources of this pollution include point sources (coal

power plants emissions) and diffuse sources (automobile exhaust). Air masses are forced over the mountains, resulting in higher rainfall and cloud immersion at high elevations that concentrate pollutants such as ground level ozone, carbon monoxide, sulfur dioxide, and nitrogen dioxide. The levels of pollutant emissions from industrial sources increased from the 1950s through the 1990s but then declined due to the Clean Air Act, which focused on reducing pollution from point sources. Although passed in 1970, the Clean Air Act was strengthened by amendments in 1990 that helped reduce pollution levels (Mohnen 1992; Moore et al. 2002; Banks 2013; Lawrence and Baily 2021). As the successful impact of the Clean Air Act became increasingly apparent, research shifted to investigating questions relating to ecosystem recovery.

Research on the effects of pollutant deposition and exposure in Appalachian red spruce forests increased in the 1980s following initial observations that spruce populations were declining in the northern Appalachians and Europe (Eagar and Adams 1992). During this period the term *acid rain* was used to describe the acidic precipitation that formed when sulfur and nitrogen oxide pollutants combined with atmospheric water to become sulfuric and nitric acids. However, pollutant exposure includes both dry and wet forms. Clouds, mist, and fog may be more important pathways for pollutants as wet deposition in certain regions than rain. In addition, these high elevation forests may be even more vulnerable since the soils found in these environments are naturally acidic and low in buffering capacity due to low cation availability (Moore et al. 2002).

2.3.2 Biotic Stressors

When immature, red spruce is generally resistant to most native insects and diseases, and it is not until maturity that tree health may be affected (Blum 1990). Most research specific to insects and diseases is based on red spruce systems in the northern Appalachians and Canada, with limited studies specific to the central and southern regions. In the central Appalachians, research has focused on determining whether various spruce gall adelgids (e.g., eastern spruce gall adelgid [*Adelges abietis*] and *Cytospora* cankers [*Leucostoma kunzei*]) influence red spruce health (see Sect. 6.6.2 in Chap. 6). Two studies suggested that although spruce gall adelgids and *Cytospora* cankers were observed in several areas of West Virginia, they did not generally appear causing a decline in the overall health of individual red spruce trees (Audley and Skelly 1994; Audley et al. 1998). Spruce gall adelgid species, like aphids, form galls at the apex or base of new shoots depending on the species. Although unsightly and causing branch tips to weaken, infestations generally do not cause significant damage to individual trees and are mostly confined to single, scattered trees in a stand. Similarly, *Cytospora* cankers can damage branches and cause deformities, but they rarely translate to tree mortality. Similar results were also found for red spruce in the southern region. Bruck (1989) conducted a survey of diseases and insects on red spruce and Fraser fir in the Black Mountains of North Carolina and found the

influence on individual tree health by the fungi and insects observed on red spruce was minor.

In contrast to minimally damaging biotic agents specific to red spruce in the central and southern Appalachians, other plant species associated with red spruce forests in these regions have been dramatically affected. Two specific examples of tree species include the eastern hemlock and Fraser fir. In the central Appalachians, hemlock woolly adelgid (*Adelges tsugae*) has caused significant mortality to eastern hemlock, occurring mixed stands with red spruce. In the southern Appalachians, Fraser fir occurs with red spruce at higher elevations and significant mortality has been caused by the balsam woolly adelgid (*Adelges piceae*, see Sect. 6.6.2.2 in Chap. 6) since its introduction and spread in the 1960s (Eagar and White 1984). Although it has been suggested that the deposition of atmospheric pollutants may have increased the vulnerability of the mature Fraser fir to balsam woolly adelgid infestation (McLaughlin et al. 1995), evidence has not been found to support this hypothesis (Lee et al. 1997). Although atmospheric deposition is a regional abiotic stressor, the timing and pattern of Fraser fir mortality in this region directly followed the geographic pattern of balsam woolly adelgid spread rather than a pattern associated with levels of pollutant deposition (White 1984).

The long-term persistence of Fraser fir in these ecosystems is uncertain. Fraser fir is a shade tolerant species that produces abundant regeneration (Peck 1990). Because the stems do not become vulnerable to balsam woolly adelgid attack until they are large enough to develop bark crevices, the initial waves of Fraser fir mortality left behind a high density of younger trees that enable recovery for Fraser fir populations (Smith and Nicholas 1998; Bowers and Bruck 2010; Lusk et al. 2010; McManamay et al. 2011; White et al. 2012; Kaylor et al. 2017). The health of young Fraser fir is further evidence that the balsam woolly adelgid was the principal agent of Fraser fir mortality rather than pollutant exposure. What is uncertain is whether the patches of existing healthy Fraser fir will survive long enough to provide seeds for future generations and open the possibility of long-term persistence of Fraser fir (Dale et al. 1991; Smith and Nichols 2000). Fraser fir develops bark fissures prior to cone production (Eagar and White 1984), suggesting Fraser fir may continue to decline despite the current recovery. It is possible that Fraser fir and balsam woolly adelgid continue to coexist in a dynamic patch system. In this system, balsam woolly adelgid would become locally scarce in young Fraser fir stands that had not developed bark crevices, possibly allowing Fraser fir reproduction through delayed recolonization of balsam woolly adelgids. The current patchiness of Fraser fir populations due to the previous balsam woolly adelgid infestation, combined with the geographically isolated Fraser fir forest populations, may also impact long-term viability of this tree species. Another possibility for long-term persistence of Fraser fir forests is the possibility that clones of Fraser fir are putatively resistant to balsam woolly adelgid produced sesquiterpenes after an adelgid feeding period of 20 weeks (Thomas et al. 2022). While it is not known whether these compounds are responsible for resistance to adelgids, Thomas et al. (2022) argued that they may be useful indicators of genetically resistant genotypes.

Although the balsam woolly adelgid does not attack red spruce itself, a sudden loss of the Fraser fir canopy in an old-growth forest in the Great Smoky Mountains caused compensatory mortality in red spruce by increasing spruce mortality to wind damage and windthrow (Busing and Pauley 1994). Another study showed that Fraser fir mortality from balsam woolly adelgid caused increased overstory red spruce mortality from 2 to 4% per year, with 70% of the dead canopy stems resulted from wind (Busing 2004). The increase in wind damage was especially marked on exposed topographic positions, such as ridgelines. As is shown in this example, the interaction between biotic and abiotic stressors can be difficult to separate.

Unlike the balsam woolly adelgid, the hemlock woolly adelgid feeds on the needles of all age classes of eastern hemlock, including younger stems, and there is no *window of escape* for this tree species as described for Fraser fir. Research has not focused on the indirect effects of the sudden loss of eastern hemlock co-dominant stems on red spruce forests in the central Appalachians, and it is uncertain what effect the loss of eastern hemlock will have on the lower elevation range of red spruce where these species co-occur. Attempts to identify and establish biocontrol agents for the hemlock woolly adelgid are now underway (Mayfield et al. 2020).

2.3.2.1 Acid Rain and Pollutant Deposition

Pollutant deposition increases with increasing elevation in mountainous regions, and studies have used this gradient to contrast red spruce response to various levels of exposure (Berry et al. 2014). The increase in pollutant deposition with elevation is due to increases in precipitation and cloud immersion. Cloud immersion contributes one-third to one-half of all water sources at upper elevation sites (Aneja et al. 1992; Reinhardt and Smith 2008b). In addition, cloud-intercepted water is more acidic (pH 2.5–4.5) than rainwater (pH 3.5–5.5; Aneja et al. 1992). Deposition of nitrogen oxides can be higher in cloud-intercepted water than in rainwater or dry deposition (Isil et al. 2022). Spruce-fir forests in the southern Appalachians are immersed in clouds 25–40% of the time and on 65% of all days annually (Aneja et al. 1992; Reinhardt and Smith 2008a, Berry et al. 2014; see Sect. 1.4.2 in Chap. 1). An important research need is to understand how these cloud immersion periods will change in duration, timing, and elevation as local climates change and what effect these changes will have on spruce-fir forests. Regardless of whether upwind pollutant emissions increase or decrease, the delivery of sulfuric and nitric acids will vary with precipitation and cloud exposure and may shift under contemporary rapid climate change.

As noted previously, pollutant emissions increased from the 1950s through the 1990s but then decreased with improved amendments to the Clean Air Act in 1990. Even areas with similar elevations and time periods may experience differences in pollutant exposure and deposition due to site specific microenvironmental differences. For example, no significant effect of acid deposition on spruce-fir forests in the central and southern Appalachians for elevations ranging from 980–1750 m (3215–5740 ft; Bryant et al. 1997). However, the Spruce-Fir Research Cooperative did find significant acidification effects in forests with elevations of 1800 m (5900

ft; Adams and Eagar 1992). Although the results of Bryant et al. (1997) did not show a significant effect of acidification, the systems sampled may have already begun recovery at the time of sampling due to the 1990 Clean Air Act amendments compared to the Spruce-Fir Research Cooperative data collected 5–10 years prior (Banks 2013). Pollutant exposure and deposition in high elevation forests has raised several lines of questions: (1) whether the deposition caused a short-term decline of red spruce; (2) whether the deposition caused a long-term acidification of soils; and (3) whether a reduction of soil nutrients due to the initial acidification would affect red spruce growth and aquatic ecosystems receiving runoff from the acidified terrestrial ecosystems. Although questions remain about the short- and long-term effects of acidic deposition, climate change may now be playing an outsized role in the resiliency of these spruce-fir forests and interacting with current pollution levels to impact mortality (Koo et al. 2014).

2.3.2.2 Pollutant Impacts on Red Spruce Growth and Mortality

Many studies have evaluated the impacts of pollutant deposition on red spruce growth and mortality in the Appalachians. In the northern region, evidence clearly showed pollutants slowing growth and increasing mortality starting in the 1960s (Adams and Eagar 1992). However, it is more difficult to ascertain obvious growth patterns for spruce-fir forests in the central and southern Appalachians. Some studies found growth declines in red spruce in the central and southern regions (Adams et al. 1985; McLaughlin et al. 1990, 1998; Adams and Eagar 1992; McLaughlin and Percy 1999; Elias et al. 2009; White et al. 2014). One study by Webster et al. (2004) found growth declined from the 1940s to the 1970s but that these declines reversed after the 1970s. Other studies found no growth rate declines in red spruce for these regions (Busing and Wu 1990; Cook and Zedaker 1992; Johnson et al. 1992; Goelz et al. 1999; Soulé 2022). Due to these mixed results, it is difficult to make definitive statements about the direct influence of pollutant deposition on red spruce mortality in the central and southern Appalachians (Reams et al. 1993; McLaughlin et al. 1994). Since 2000, most research has indicated no decline in red spruce growth rates (Bowers and Bruck 2010; Lusk et al. 2010), with some studies showing increases (Hornbeck and Kochenderfer 1998; Soulé 2022).

During the development of a forest, growth rates of trees change due in part to the competition for resources (e.g., light, nutrients) that may be further influenced by pollutants. At the start of a stem exclusion phase, the growth rate of red spruce declines due to increased stem crowding and hence increased competition for limited resources. During this phase, when there is a constant crown size and leaf area, even if biomass production is constant, tree-rings become narrower as tree circumference increases. In addition, red spruce is a late successional shade-tolerant species and therefore undergoes episodes of prolonged suppressed growth before it reaches the canopy. For example, growth declines in 25% of red spruce trees in the northern Appalachians after 1967, especially at higher elevations, but the growth decline was not greater than historical levels (LeBlanc et al. 1992). Yet, understanding specific

influences of growth, and growth metrics in general, can be difficult to interpret (Reams et al. 1993; McLaughlin et al. 1994).

Understanding the influence of pollutants on red spruce growth rates is difficult to ascertain and most studies did not find an increase in mortality in these regions directly related to pollution (Bruck and Robarge 1988; Busing et al. 1988; McLaughlin et al. 1990, 1998; Cook and Zedaker 1992; Johnson et al. 1992; Busing and Pauley 1994; Smith and Nicholas 1999). Although Busing and Pauley (1994) observed an increase in red spruce mortality (2–4% per year) in an old-growth spruce-fir forest in the Great Smoky Mountains, the authors attributed this increase to the sudden loss of the co-dominant Fraser fir canopy trees and hence increased wind exposure to the remaining red spruce trees. Most studies after the 2000s have found no increase in red spruce mortality and potentially an increase in red spruce recruitment in certain systems (Nowacki et al. 2010; Mathias and Thomas 2018).

2.3.2.3 Acidification Effects on Red Spruce

Although it does not appear that pollutant deposition has created an ongoing decline in red spruce populations in the central and southern Appalachians, research has shown there is a more chronic, longer-term issue—ecosystem acidification. In areas of the Appalachians impacted by acid deposition, exposure to sulfuric and nitric acids in rainwater and cloud-intercepted water leaches cations from red spruce needles (Joslin et al. 1988; Robarge et al. 1989; McLaughlin et al. 1990, 1991; Thornton et al. 1990, 1992, 1994; Sayre and Fahey 1999; Crim et al. 2019). Foliar concentrations of calcium (Ca) and magnesium (Mg) in red spruce had decreased by more than 50% compared to the 1960s, while in Fraser fir concentrations had decreased from 25 to 50% (Shepard et al. 1995). A study showed significant levels of Ca and Mg leached from red spruce foliage when an acidic water solution (pH 3.1) was applied, especially in the spring when the outer cuticle on young needles may not have completely formed (Sayre and Fahey 1999). Evidence of foliar leaching, which can cause leaf mortality, is also supported by observed differences between water captured as throughfall compared to that in open areas, with throughfall containing twice the concentration of Ca, Mg, and other plant nutrients (Joslin et al. 1988; Johnson et al. 1991; Joslin and Wolfe 1992).

Soils with high concentrations of aluminum (Al) competitively inhibit calcium uptake, an important nutrient for structure in plants. Aluminum displaces certain cations from the surface of soil particles at low pH, causing reduced calcium plant uptake and increased likelihood of leaching. Ratios between certain nutrient cations, especially Ca and Al, have been proposed as indexes of acidification for both plant tissue and soil solutions (Shortle and Smith 1988). The risk of decline in red spruce increased as the Ca:Al ratio decreased, where the risk was 50% at a Ca:Al ratio of 1.0, 75% risk at 0.5, and near 100% risk at 0.2 (Cronan and Grigal 1995). In the southern Appalachians, Ca:Al ratios were among the lowest on record, suggesting the possibility of that aluminum toxicity could reduce root growth in the future (Robarge et al. 1989).

2.3.2.4 Acidification Effects on the Physiology of Red Spruce

Several physiological effects occur in red spruce due to acidification. One physiological effect is due to low Ca levels in cellular membranes of foliage. These low Ca levels are due to foliar and soil leaching, detailed above. Lower Ca levels in the membranes of cells decrease the cold hardiness of red spruce foliage, potentially translating to foliar damage during cold winter temperatures (Thornton et al. 1994; DeHayes et al. 1999; Schaberg et al. 2000). This connection between Ca deficiency in foliage and cold hardiness as a cause of spruce mortality in the northern Appalachians may help explain why central and southern red spruce populations did not show the same increased mortality as northern areas due to less severe winters (Johnson 1992; Johnson et al. 1992; McLaughlin et al. 1993). However, exposure to acid cloud water and ozone can still cause the loss of cold tolerance even in the southern Appalachians (Thornton et al. 1992, 1994). Another physiological effect from acidification is increased respiration and decreased photosynthesis (McLaughlin et al. 1990, 1991, 1993; Pier et al. 1992; McLaughlin and Percy 1999) that was correlated with foliar Ca and Ca:Al ratios. Red spruce trees with lower foliar Ca and Ca:Al ratios had less photosynthesis, higher respiration, hence indicating stressed conditions. Other physiological effects include cellular membrane disruption that causes foliar injury, including needle speckling (DeHayes et al. 1999) and stomatal cell functioning that can lead to a lessened response to water stress (Borer et al. 2005). Since acidification decreases Ca:Al ratios, those levels can become toxic to fine root growth, reducing the uptake of nutrients critical to growth (Shortle and Smith 1988; Robarge et al. 1989; Cronan and Grigal 1995). Because red spruce systems are generally Ca deficient and because Ca is critical to the physiology of red spruce, research has examined the effects of amending sites with Ca and other base cations to ameliorate ecosystem acidification. Adding Ca to red spruce sites in the southern Appalachians can improve foliar Ca at high elevation red spruce sites, but not sites at lower elevation (Van Miegroet et al. 1993; Joslin and Wolfe 1994).

2.3.2.5 Recent Reductions in Pollutant Deposition and Improvements in Forest Health

Studies have reported Ca, Mg, and Ca:Al ratios improved from the 1990s to the 2000s, suggesting the 1990 Clean Air Act amendments reduced atmospheric deposition of pollutants in the southern region of red spruce (Blintz and Butcher 2007; Rosenberg and Butcher 2010; Wilson and Butcher 2012). Recently, Schwartz et al. (2022) reported significant declines in acid deposition in the Great Smoky Mountains. Similar trends were observed in the northern Appalachians, with a 40–50% reduction in acidic deposition, improved soil pH, and a reduction in soil Al at certain locations (Lawrence et al. 2011, 2015; Lawrence and Bailey 2021). Although acidic deposition had decreased significantly, soil recovery is probably at an early stage and additional research is required to understand linkages between terrestrial and aquatic systems as this relates to forest health (Lawrence and Bailey 2021). Improved forest health

in red spruce forests was also observed in Canada following air quality regulations (Kosiba et al. 2018).

2.3.2.6 Ozone Exposure Effects on Red Spruce

One pollutant receiving more attention in recent years is ground-level ozone. This pollutant can form in remote areas when sunlight provides the energy for a chemical reaction between nitrogen oxides (NO_x), released during fossil fuel combustion, and volatile organic compounds, a broad term that includes several classes of airborne compounds that derive from both human and natural sources. Examples of volatile organic compound sources include the burning of fossil fuels, forest fires, and repellants or toxins that reduce insect attack released by tree species (Montero-Montoya et al. 2018).

Ground-level ozone can also be transported from urbanized areas by atmospheric patterns, like other pollutants previously discussed. Ground-level ozone is considered a pollutant because it can cause significant damage to the foliage of plants. Like acid deposition in the central and southern regions of red spruce, ground-level ozone has been found to increase with elevation, especially during the summer months (Aneja et al. 1992; Neufield et al. 2019).

Although ground-level ozone has been shown to cause significant foliar damage in certain plant species, most research to date generally shows minimal direct effects on red spruce foliage, physiology, and growth (Laurence et al. 1989; Kohut et al. 1990; Thorton et al. 1990, 1992, 1994; Pier et al. 1992; Rebbeck et al. 1993). The earliest studies looked at ground-level ozone effects on seedling height, branching, mass of stem, needle and roots, biomass production, and rate of photosynthesis. No direct or interactive effects were observed when ozone was combined with acidic wet deposition. Even studies using elevated levels of ozone (0.5–2.0 times ambient levels) combined with simulated acid precipitation have found no significant effects of either pollutant, alone or in combination (Laurence et al. 1989; Kohut et al. 1990).

A few studies showed differences in red spruce response to ozone, mainly when combined with water from clouds. One such study showed elevated ozone effected red spruce physiology (Rebbeck et al. 1993). Differences were not observed with ambient ozone levels, but there was a 29–40% reduction in photosynthesis in young red spruce when ozone was elevated to 75 and 150 ppb above ambient. Stomatal conductance was also higher in juvenile stems, indicating that ozone uptake may be as much as twice as high as on older stems and that seedlings will have different responses than canopy branches of established trees. Another study in the central and southern Appalachians found a significant effect of combining ozone with cloud water. Thornton et al. (1992) found lower foliar Ca and Mg concentrations and higher respiration rates for both seedlings and mature trees of red spruce compared to ozone only treatments. They also observed increased height growth for seedlings with the ozone and cloud water treatment, possibly due to a fertilization effect from nitrogen and sulfur in the cloud water. It is clear from the mixed results of these studies

that additional research is needed to understand the effects that ozone, including its interactions with atmospheric precipitation, have on red spruce ecosystems.

2.4 Climate Change

The spruce-fir forests of southeastern North America occur at the highest elevations in Appalachian Mountains and depend on the cool, wet conditions that occur at these elevations. As the climate changes, environmental conditions supporting these montane ecosystems is also likely to change, possibly creating upslope migration of these forests. Among the trees of eastern North America, red spruce has been classified one of the most vulnerable tree species to climate change (Rogers et al. 2016). Similar to other long-lived trees, red spruce is vulnerable to changing climatic conditions because of its long generation time, inability to migrate northward at the southern parts of its range, and low genetic diversity (Potter et al. 2010; see Chap. 7). Analyzing changes in mean temperatures and the seasonal progression of temperatures are also important metrics to understand the effects of climate change in these ecosystems (Day 2000). Red spruce seedlings, saplings, and the radial growth of mature trees are sensitive to hot and dry summers (Yetter et al. 2021c) and some future environmental changes might be favorable to red spruce productivity. Higher atmospheric CO_2 levels (if water and nitrogen are not limiting), longer growing seasons, and the moderation of winter temperatures, may also increase red spruce productivity (Yetter et al. 2021c). However, it is also possible that an earlier release from winter dormancy may increase vulnerability to late frosts (Koo et al. 2014; Soulé 2022), possibly offsetting productivity gains.

Cloud immersion and precipitation can have mixed effects on red spruce populations (Yetter et al. 2021c). Although these environmental variables are responsible for most of the pollutant deposition in these forests, red spruce is sensitive to summer heat and drought and depends on high elevation habitats with high humidity and water supply. Cloudy days have been found to have both positive (Johnson and Smith 2006; Reinhardt and Smith 2008a; Berry and Smith 2012, 2013) and negative (Yetter et al. 2021c; Soulé 2022) effects on red spruce photosynthesis. Red spruce growth rates in the central Appalachians decreased with hot summer temperatures, but increased with fall temperatures, indicating that warming climates would have a net negative effect on red spruce growth (Yetter et al. 2021b). In the northern Appalachians, a tree ring analysis between 1925 and 2012 found that higher temperatures outside the traditional growing season were related to increased growth (Kosiba et al. 2018). In Massachusetts, red spruce populations were sensitive to both temperature and precipitation, with a negative growth response to the regional warming that had occurred over the last 100 years (Ribbons 2014). Although the effect of climate change on precipitation and cloud immersion is critical to spruce-fir forests (Berry et al. 2014), it is hard to predict (Berry and Smith 2013). Some have asserted that the average cloud ceiling sets the lower boundary of spruce-fir forests, and this cloud ceiling is moving up in elevation in some areas of the Appalachians, as in the north, or stable or decreasing

in other areas, such as in the south (Richardson et al. 2003). Cloud immersion may also affect microclimatic conditions during regional warm periods, wherein low elevations experience higher heat effects, but high elevation sites experienced mitigated temperatures due to low cloud cover (Fridley 2009). Therefore, high-elevation spruce-fir forests may have buffering effects during extreme regional heat events due to cloud immersion, providing suitable microclimates for long-term persistence despite regional warming. See Sect. 7.2.2 in Chap. 7 for additional information on how climatic variation and extreme weather events influence the physiology of red spruce.

2.5 Genetics

Understanding genetic diversity is an important variable to consider when assessing long-term species viability in a region. Populations may develop regional adaptations to local abiotic and biotic stressors. Although these adaptations may be well-suited for conditions in one region, they may not translate favorably to another. Yet these regional adaptations are important for maintaining a high level of genetic diversity that allow populations to possibly endure anomalous events, such as rapid environmental changes. They may also assist species in dealing with longer term climatic changes as are occurring in our modern world. Populations that become increasingly isolated have reduced gene flow (i.e., bottleneck effect), which increases genetic inbreeding and equates to decreased genetic diversity. Isolated populations experiencing this cycle of reduced genetic diversity are at a higher risk of not developing positive adaptations in rapidly changing conditions, potentially contributing to their disappearance from the landscape.

A mostly continuous *genetic core* of red spruce ranges from the Canadian Maritimes west into east-central Canada, south through New England into the Adirondack and Catskill Mountains of New York, with small disjunct populations occurring further west in Algonquin Park, Ontario (Major et al. 2015). Although there are small populations in Pennsylvania, the two largest disjunct populations occur in the central (West Virginia) and southern (Virginia, North Carolina, and Tennessee) Appalachian Mountains (see Fig. 1.3 in Chap. 1). The gene flow for these disjunct populations in the central and southern regions was initially constrained by the last glaciation at the end of the Pleistocene, but exacerbated by the destructive logging at the end of the nineteenth century, creating isolated fragmented populations as *sky islands* of spruce-fir in the southernmost part of its range (see Chap. 1). In addition to these genetically isolated regions, research has shown genetic variation decreasing significantly from the *geneticcore* to trailing edge populations (Hawley and DeHayes 1994; Prakash et al. 2021), with higher instances of inbreeding in the central and southern Appalachians (Capblancq et al. 2021), thus highlighting the isolation and lack of gene flow between disjunct populations. Due to these combined genetic attributes, it is uncertain whether the central and southern regions contain sufficient genetic variation to survive the increased warming expected with climate change

(Capblancq et al. 2020; Prakash et al. 2021). See Chaps. 7 and 9 for more information on climate change impacts and adaptation solutions employing ecological genomics.

Some of the earliest red spruce genetics research, although limited, was done in Canada (Fowler et al. 1988; Blum 1990). In the early 1990s, research began looking at how genetic diversity might help explain red spruce declines across the eastern U.S. The earliest studies suggested that because genetic diversity of red spruce was relatively uniform across the entire range, this species was poorly suited to adjust to sudden environmental changes, which could contribute to its decline in certain areas (DeHayes and Hawley 1992). The authors noted that populations with increased genetic variability had higher vigor compared to populations with less genetic variability, suggesting these populations may be more resilient and capable of maintaining viable populations in the future. Although old-growth forests are thought to have high genetic diversity due to their stand age and dynamics, evidence suggests they may suffer similar genetic diversity limitations if they have small population sizes (Mosseler et al. 2003). Despite potential limitations of genetic diversity in smaller populations, it is still important to characterize phenotypic variations of populations, regardless of their size, due to the potential for selecting seed sources for restoration efforts. For example, phenotypic variation was observed on climate-associated traits, with seeds collected along an elevational gradient on Kuwohi Mountain (a.k.a., Clingmans Dome) in Tennessee (Butnor et al. 2019) suggesting that seed sources might be able to be transferred from lower to higher elevation populations to achieve successful restoration of red spruce in the southeastern U.S. Interestingly, the same relationship was not observed on material collected along an elevational gradient on Mt. Mitchell in North Carolina (Butnor et al. 2019). It is possible that an unknown seed source was used to artificially regenerate the red spruce populations in the area that was replanted on Mt. Mitchell after extensive resource exploitation in the early to mid-twentieth century (Davis 1930; Frothingham 1931; Minckler 1940).

Understanding the unique regional phenotypic and genotypic variation that may improve the chances of future survival in the context of changing abiotic and biotic stressors may be key in successfully maintaining and expanding existing red spruce populations (Beane 2010; Thomas et al. 2014; Koo et al. 2015; Andrews 2016). The acceptance and use of climate change adaptation tools like assisted species migration has increased in recent years as an option to maintain or restore ecosystems (Vitt et al. 2010; Thomas et al. 2014). This concept tries to match the viability of specific phenotypic and/or genotypic variation to future modeled climatic scenarios. For plants, this usually requires determining the genetic variation of species in a specific area, assessing adaptations in relation to biotic and abiotic stressors, and moving genetic sources to areas predicted to experience similar conditions under future climate models. For red spruce, this area of research is in its initial stages (Butnor et al. 2019; Capblancq et al. 2020).

2.6 Conclusion

Red spruce has been an integral part of eastern forest landscapes due to its natural resiliency as a shade tolerant, slow-growing, medium-sized conifer with the ability to thrive under harsh environmental conditions. Although historical human influences, such as exploitive logging and fires, dramatically reduced the area occupied by red spruce in the eastern forests, the species is gradually expanding due to natural processes and significant restoration efforts led by groups such as CASRI and SASRI. These groups are using silvicultural prescriptions to increase gap dynamics to improve red spruce growth in existing forests, and planting seedlings in areas with the genetics to match future climatic model predictions that will hopefully improve resiliency in specific areas. However, there are still potential obstacles for the future of red spruce. The interaction of pollution and climate change on species survival, especially in the southern region, is uncertain. Climate change may also influence cloud and fog development, which is critical to red spruce in the southern Appalachians. Future pests and pathogens are unknown, as are invasive species. Despite these potential headwinds, much progress continues to be made in expanding the range of red spruce throughout the entire Appalachian Mountains.

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