Red Spruce: Guidance for Seed Transfer Within the Eastern United States

Stephen R. Keller

Associate Professor, Department of Plant Biology, University of Vermont, Burlington, VT

Abstract

Red spruce (*Picea rubens* Sarg.) is a cool, temperate zone conifer that is widespread in the Northeastern United States and Canada and associated with fragmented, high-elevation mountainous areas of the Central and Southern Appalachians. The species prefers cool, moist climates with moderate summer temperatures and low exposure to drought stress. Red spruce is sensitive to cold stress, especially during midwinter thaws followed by abrupt return to subfreezing conditions. The species has low genetic diversity for an outcrossing, wind-pollinated conifer. Genetic data show an ongoing decline in effective population size exacerbated by more recent impacts of logging, fire, and acid rain. Red spruce naturally hybridizes with black spruce (*P. mariana* [Mill.] Britton, Sterns, & Poggenburg), which may provide a source of adaptive variation when reproductive barriers are overcome. Ongoing research suggests red spruce is vulnerable to climate change, especially where habitat fragmentation constrains natural opportunities for dispersal. Trait and genomic-based analyses of climate adaptation offer guidance for seed transfer and potential assisted migration within the species' range. Damage from insects and other pests is not widespread, but local outbreaks can cause damage to current-year growth and cone crops.

Introduction

Red spruce (*Picea rubens* Sarg.) is a shade-tolerant, coniferous tree that prefers cool, moist sites throughout mid to high elevations in the Appalachian Mountains and along coastal areas of Maine and the Canadian Maritime Provinces. Its geographic distribution shows a strong inverse latitude-elevation relationship, with red spruce occurring at its highest elevations in the Central and Southern Appalachians of West Virginia, Virginia, North Carolina, and Tennessee (most common above 3,300 ft [1,000 m]), more moderate elevations in the Adirondacks and Northern Appalachians of New York and New England (most common between 2,500 to 4,000 ft [750 to 1,200 m]), and near sea level in the northern Maritime forests (Cogbill and White 1991).

Red spruce is associated with a variety of forest types but is probably best known as a codominant member of high-elevation spruce/fir forests where it occurs with balsam fir (*Abies balsamea* [L.] Mill.) or Fraser fir (*A. fraseri* [Pursh] Poir.) in the northern or southern part of its range, respectively (figure 1). At lower mountain elevations, red spruce is a common component of mixed conifer-northern hardwood forests, where it commonly occurs with sugar maple (*Acer saccharum* Marshall), eastern hemlock (*Tsuga canadensis* [L.] Carrière), American beech (*Fagus grandifolia* Ehrh.), and yellow birch (*Betula alleghaniensis* Britt.) (Verrico et al. 2020). In high-latitude coastal areas of its range in Maine and Maritime Canada, red spruce is a dominant member of a cool, maritime-influenced conifer forest community. Elsewhere in the interior of its range, red spruce sometimes occurs in "frost pocket" wetland or bog sites in association with red maple (*Acer rubrum* L.), tamarack (*Larix laricina* [Du Roi] K. Koch), eastern hemlock, and with its closely related black spruce (*P. mariana* [Mill.] Britton, Sterns, & Poggenburg). In the Central and Southern Appalachian regions, red spruce is a foundational species that provides critical high-elevation, cool, shady habitat for a variety of regionally rare or endemic wildlife species (Byers et al. 2010) (figure 2).

Historically, red spruce was probably more widespread throughout both the northern and southern extents of its range and occupied additional areas with warmer climates than its

Figure 2. This red spruce forest in Spruce Knob, WV, shows structural diversity and recruitment from the understory. Cool, moist conditions at higher elevations (>4,000 ft [1,219 m]) in the Central Appalachians support the development of mature red spruce communities. Photo by Stephen R. Keller, 2013.

current distribution (Cogbill 2000, Van Gundy et al. 2012). Logging, fire, and atmospheric pollution (acid rain) have severely impacted red spruce and reduced its distribution and abundance, particular in lower elevation northern hardwood forests (Foster and D'Amato 2015, Koo et al. 2015, Siccama et al. 1982). In recent years, red spruce has been rebounding in growth and seedling recruitment at lower elevations, including recolonizing downslope in montane forests, suggesting a slow recovery from the legacies of land use and pollution (Foster and D'Amato 2015, Kosiba et al. 2018, Verrico et al. 2020, Wason et al. 2017).

Although associated with high-elevation or high-latitude areas in the Appalachian Mountains, red spruce is not a boreal species but rather a cool-temperate zone species (Dumais and Prévost 2007, White and Cogbill 1992). Red spruce appears to be limited by midsummer (July) temperatures (Cogbill and White 1991, Hamburg and Cogbill 1988), being sensitive to conditions of high temperatures during the growing season when adequate moisture is unavailable through precipitation, humidity, or cloud immersion (Day 2000, Hamburg and Cogbill 1988, Keller et al. in press, Lachmuth et al. 2023). Red spruce is also sensitive to cold temperatures during the fall and spring transition seasons (Yetter et al. 2021) and achieves only moderate cold tolerance in midwinter, incurring damage from temperatures below -40 °F (-40 °C) unlike true boreal spruce species in the northeast such as white spruce (*Picea glauca* Moench) and black spruce (DeHayes et al. 2001, Strimbeck et al. 2007). Winter injury to red spruce can also occur at less extreme temperatures when a midwinter warm period is followed by an abrupt return to cold. During these times, red spruce will temporarily deharden and resume

Figure 1. This montane red spruce forest in northern Vermont is typical of forest types between 2,500 and 3,500 ft (762 and 1,067 m) in elevation. Photo by Stephen R. Keller, 2019.

photosynthesis, resulting in susceptibility of current-year foliage to rapid transitions back to subfreezing temperatures (Schaberg 2000).

Red spruce seedling recruitment is best under partial shade. Photoinhibition damages seedlings exposed to full sunlight (Dumais and Prévost 2007, 2016). Due to its shade tolerance and slow growth habit, red spruce can persist in the understory for decades but requires canopy release to achieve its full growth potential (Rentch et al. 2016). Dominant canopy trees can persist for centuries as a late-successional species in the forest community. Red spruce can grow on a variety of substrates, from poorly drained bogs to exposed upland sites with shallow soils, but it commonly occurs on moist, slightly acidic soils with a well-developed humus layer (Spodosols).

During the last ice age, red spruce retreated to a southern refugium located in the unglaciated areas of the Carolinas and stretching westward toward the Mississippi River Valley, from which it recolonized northward after the glaciers retreated (Keller et al. in press, Lachmuth et al. 2023, Lindbladh et al. 2003, Watts 1979). After glaciation, red spruce may have retreated to a northern coastal refugium near the Canadian Maritimes during the mid-Holocene warm period, approximately 5,000 to 8,000 years ago, after which it is thought to have recolonized inland (Schauffler and Jacobson 2002).

Red spruce is most closely related to black spruce, from which it speciated during the Pleistocene glacial period, and with which it still overlaps geographically in areas from Pennsylvania northward (Jaramillo-Correa and Bousquet 2003). Red spruce and black spruce are known to hybridize naturally throughout their areas of sympatry (Capblancq et al. 2020, De Lafontaine et al. 2015, Jaramillo-Correa and Bousquet 2003, Perron and Bousquet 1997), and artificial hybrids are also possible through controlled crosses (Major et al. 2003, 2005). Despite overlapping ranges in the north, neither red spruce nor black spruce are closely related to white spruce, the latter of which shows closer phylogenetic relationships to western spruces (e.g., *Picea engelmanii* Parry ex Engelm. and *P. sitchensis* [Bong.] Carr.) (Feng et al. 2019, Lockwood et al. 2013).

Genetics

Red spruce is a diploid species (2n=24) with a very large genome (genome size of the closely related black spruce is ca. 18.3 Gbp [Lo et al. 2023]). Red spruce is also monoecious, producing separate male and female cones (figure 3) and has a wind-pollinated, outcrossing mating system. Based on the mating system and compared with other similar conifers (including black spruce), red spruce would be expected to have high genetic diversity and low population structure, but it does not meet these classic expectations (table 1). On the contrary, multiple genetic studies using a variety of marker types have shown red spruce to have quite low levels of genetic diversity compared with similar conifer tree species (Capblancq et al. 2020, Hawley and DeHayes 1994, Keller and Trott 2017, Perron et al. 2000). Low levels of diversity correspond to a bottlenecked effective population size (N_e) in red spruce that shows evidence of long-term decline over thousands of years, pre-dating more recent anthropogenic impacts (Capblancq et al. 2020, Jaramillo-Correa et al. 2015, Keller and Trott 2017).

Some of this initial reduction in N_e is attributable to the speciation event with black spruce, in which red spruce is

Figure 3. Reproductive structures in red spruce include male (left) and female (right) strobili. Photos by Brittany M. Verrico, 2017.

Table 1. Summary of silvics, biology, and transfer considerations for red spruce

Red spruce *(Picea rubens)*	
Genetics	• Genetic diversity: low compared with other outcrossing conifers; long-term history of diversity decline • Genetic structure: three geographically distinct regions of genetic ancestry are the northern, midlatitude, and southern parts of the range; F_{ST} between regions = 0.02–0.03 • Gene flow: historically high within regions, though may be reduced due to habitat fragmentation and land use; gene flow between regions appears limited
Cone and seed traits	• Abundant cone crops every 3 to 8 years • Nonserotinous cones averaging 150,000 cleaned seeds/pound (330,000 seeds/kg) • Seeds disperse in late summer/early fall from cones produced that year • Seeds possess no physiological dormancy
Insect and disease	• Impacts on red spruce from insect pests and other diseases are generally low • Reductions in growth and vitality can arise during local outbreaks of spruce budworm, spruce coneworm, yellowheaded spruce sawfly, and eastern dwarf mistletoe • Eastern spruce gall adelgid is an introduced species that alters growth form of current-year shoots
Palatability to browse	• Low; not a preferred browse by deer or moose
Maximum transfer distances	• Intermediate tolerance to seed transfer (200–300 mi [322–483 km]) • Transfer to colder climates (more than 1.8 °F [2 °C] colder than the source) often results in cold damage and reduced growth • Transfer into warmer climates (5.4 to 9 °F [3 to 5 °C] warmer than source) may be tolerable but must be evaluated with consideration to temperature seasonality (warmer winters may benefit red spruce while warmer summers do not) and transpirational demand • Southern range-edge populations may be at risk for extirpation due to climate conditions near current thresholds, low genetic diversity, and habitat fragmentation
Range-expansion potential	• Regional stands in New England, northern New York, and eastern Canada are likely to expand northward but will still be constrained by long-range dispersal capacity • Opportunity for infilling in areas of former range where land-use change and other anthropogenic disturbances eliminated spruce during the last two centuries, especially at lower elevations • Regional populations in mid-Atlantic and Central and Southern Appalachians have limited range-expansion potential due to fragmentation and lack of continuous suitable climate habitats

thought to have diverged as a small, isolated subpopulation of black spruce during the Pleistocene glacial period and captured just a subset of its progenitor's genetic diversity (Jaramillo-Correa and Bousquet 2003, Perron et al. 2000). The trend toward declining N_e in red spruce has continued after its divergence with black spruce, with more recent bottlenecks dated to the mid to late Holocene (Capblancq et al. 2020, Jaramillo-Correa et al. 2015, Keller and Trott 2017). Low genetic diversity in red spruce has been associated with reduced seedling vigor under greenhouse conditions, particularly for seedlings originating from the southern part of its range (Capblancq et al. 2021).

At a landscape scale, red spruce shows genetic population structure between three geographically separated ancestry groups: the northern core of the range (New York, New England, and Canada), the southern fragmented range edge (Maryland south to North Carolina and Tennessee), and the margin or transition zone between the core and edge (bog sites in central and northern Pennsylvania) (figure 4). These three ancestry groups diverged ca. 8,000 years ago after glacial retreat and, while genetically distinct, there are only modest levels of divergence at nuclear loci, with F_{ST} (the proportion of genetic variance contained in a subpopulation relative to the total) of 0.02 to 0.03 (Bashalkhanov et al. 2013, Capblancq et al. 2020). Gene flow still occurs between regions but at a very low rate of 1 migrant exchanged every 4 to 20 generations, equating to an approximate maximum migration frequency between regions of 1 individual per 100 years (Capblancq et al. 2020).

At a more local scale within regions, population differentiation in the nuclear genome among populations is typically quite low ($F_{ST} < 0.01$) consistent with its wind-pollinated mating system (Keller and Trott 2017, Verrico 2021). Cytoplasmic genomes (mitochondria and chloroplast) show limited haplotype variability in red spruce
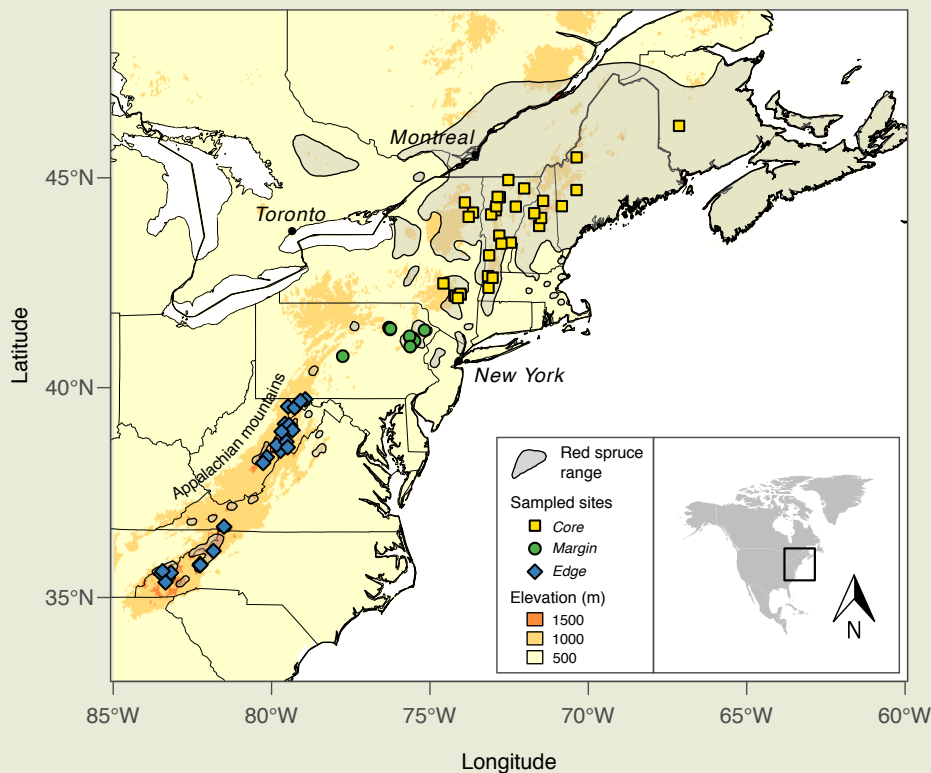
Figure 4. Range-wide structure of genetic ancestry in red spruce. Symbols denote the 65 populations (N=340 individuals total) sampled for exome-capture genomic sequencing by Capblancq et al. (2020). Colors denote genetic ancestry clusters based on principal component analysis of single-nucleotide polymorphisms (SNPs), which separated samples genetically into three regional clusters: a southern range edge (blue), a midlatitude margin (green), and a northern range core (yellow).

range (Capblancq et al. 2020, de Lafontaine et al. 2015, Perron and Bousquet 1997). Areas of advanced introgression between red spruce and black spruce can also be found in wetlands and bogs of Pennyslvania. Natural hybrid genotypes with a mix of red spruce and black spruce genetic ancestry show positive heterosis for growth in common garden experiments (Prakash et al. 2022). In contrast, controlled crosses between red spruce and black spruce suggest reduced seed viability and slightly negative heterosis for growth among surviving first-generation hybrids (Major et al. 2003, 2005). The reduced seed set along with the ecological (habitat) separation is probably sufficient to keep the two species distinct, even in the face of occasional hybridization.

Molecular studies shed further light by showing that the barriers to hybridization vary considerably across the genome with some gene loci forming strong isolating barriers, while other loci are highly permeable to introgression (de Lafontaine et al. 2015). Further, genomic studies show that backcrossing of hybrids with red spruce occurs more frequently than backcrossing to black spruce, suggesting introgression is directional and occurs more easily toward red spruce (de Lafontaine and Bousquet 2017). Ongoing studies of natural advanced generation backcrosses suggests that introgression introduces adaptive variation into red spruce (which is otherwise low in genetic diversity), which may facilitate its adaptation along climatic gradients (Prakash and Keller, unpublished data). Synthesizing across these studies indicates that hybridization between red spruce and black spruce (1) is relatively common in the north, (2) is likely selected against in the first generation as a result of reduced seed viability, (3) backcrosses preferentially with red spruce in cases where hybrids survive to maturity, and (4) may increase adaptive potential in red spruce populations due to introgression of genetic diversity from advanced generation backcrossing.

relative to black spruce, and a trend for greater population structure in mitochondrial DNA (dispersed through seed) than chloroplast DNA (dispersed through pollen), consistent with higher levels of gene flow through pollen (Gérardi et al. 2010, Jaramillo-Correa and Bousquet 2003).

Red spruce exhibits patterns of local adaptation to climate at both local and regional scales. At the trait level, common garden estimates of genetic variation in budbreak and budset shows clinal patterns of trait variation along climatic gradients of elevation and latitude (Butnor et al. 2019, Prakash et al. 2022, Verrico 2021). Evidence also indicates that plasticity in budbreak timing shows locally adapted genetic variation in response to gradients in climate seasonality (Prakash et al. 2022). At the molecular level, clinal adaptation in stress response genes is evident along seasonal gradients of temperature and precipitation, as well as historic air pollution (Bashalkhanov et al. 2013, Capblancq et al. 2023).

As noted previously, red spruce and black spruce are capable of hybridization. Naturally occurring hybrid genotypes occur in the northern part of the red spruce

Seed-Transfer Considerations
While not grown commercially, red spruce is the focus of active restoration and reforestation efforts for conservation of biodiversity, especially in the southern

portions of the range where logging and fire have severely reduced its former range (Adams and Stephenson 1989). Consideration of seed sourcing and transfer guidance for red spruce comes from a variety of sources, including climate models, provenance trials, progeny tests, and genomic analyses. Climate-based species distribution models generally predict a severe contraction of red spruce's range by the end of this century (Beane and Rentch 2015, Koo et al. 2014, Lachmuth et al. 2023) with overall decreases in importance values over much of its existing range (Peters et al. 2020). These forecasts raise awareness that seed sourcing for reforestation and restoration should take into consideration both current and future climates (Walter et al. 2017).

Several provenance trials exist for red spruce (Morgenstern et al. 1981, Wilkinson 1990) that offer insight into the response of red spruce growth to climate transfer distance (TD = test site climate – seed source climate). A recent study of trials in Maritime Canada showed that growth (height and diameter at breast height [DBH]) measured on adult trees responded most to TD based on temperature variables and less so to precipitation (Li et al. 2020). In these trials, growth response of warm-climate provenances was negatively affected by seed transfer into colder test sites (negative TD); conversely, cold provenances benefited slightly from transfer into warmer test sites, up to 5.4 °F (3.0 °C) warmer than the source climate. These responses were strongest for climate variables associated with growing season length (frost-free period and growing degree days), pointing to risk of cold damage and thus slower growth upon transfer to colder climates. It is important to note that all the test sites and most of the source provenances in Li et al. (2020) were northerly (eastern Canada), so the data do not necessarily capture the response of midlatitude and southern provenances to warming above their baseline.

A recent test evaluated red spruce progeny from 340 mothers sampled from 65 provenances across the range and grown in raised beds at 3 test sites stratified by latitude (Vermont, Maryland, and North Carolina) (Prakash et al. 2022). The three test sites were generally warmer than the climate at the seed sources (Prakash et al. 2022), producing a range of TD values (based on mean annual temperature) from 7.2° F (4 °C) colder to 22 °F (12 °C) warmer than the source climate. Seedlings showed a decrease in first-year height increment growth with increasingly warmer TDs (figure 5). In their second year, growth declined under both the coolest and warmest TDs, but was resilient to, or even slightly benefited from, moderate warming (5.4 to 9 °F [3 to 5 °C]). A related analysis that considered the influence of a broader set of 11 climate variables, including different aspects of seasonal temperature as well as precipitation and humidity-related variables, found a consistent reduction in seedling height growth with increasing transfer distance away from the source climate (Capblancq et al. 2023, Lachmuth et al. 2023).
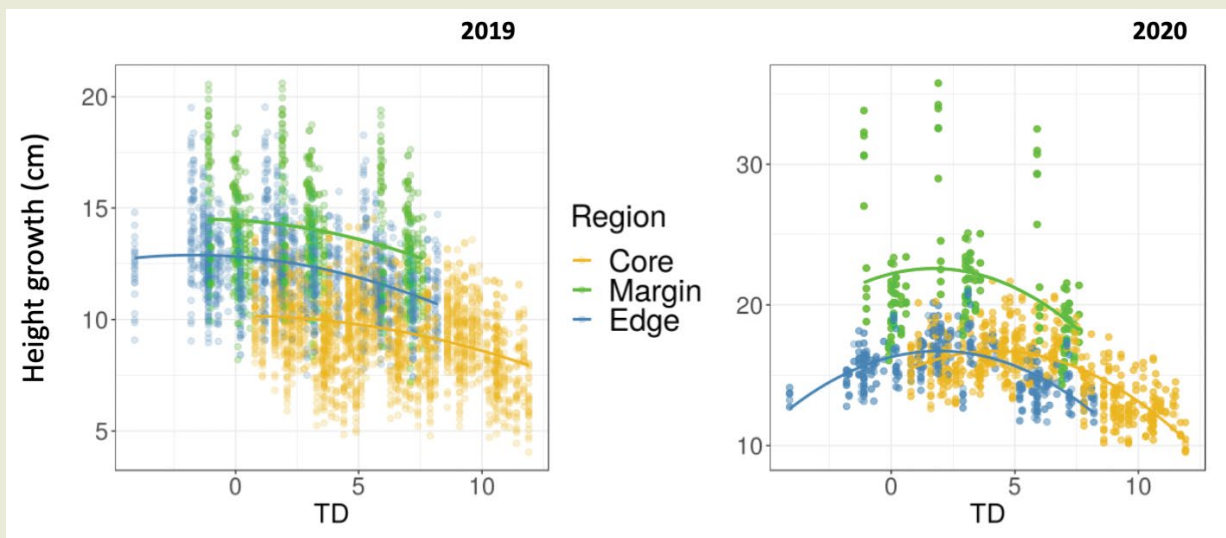

Figure 5. Red spruce seedling height growth after 1 year (2019) and 2 years (2020) postplanting into outdoor raised bed common gardens varied by climate transfer distance (TD = test site − source) based on mean annual temperature (°C) and regional genetic ancestry groups (core, margin, and edge) assigned based on genomic data (see also figure 4). Height growth data were reanalyzed from Prakash et al. (2022).

The entire set of findings on red spruce transfer indicate that red spruce has a negative growth response to seed transfer toward sites that are both warmer and drier (e.g., higher evaporative demand) than its source climate, and that simple proxies of temperature or geographic distance alone are likely insufficient to properly evaluate the transfer impact. If based solely on mean annual temperature, it appears that red spruce can tolerate, or even benefit from, moderate warming (figure 5) likely reflecting its sensitivity to frost damage (Li et al. 2020). Best practice would thus be seed transfers into areas where current and future climate will most closely match the historic source climate, considering the combined effects of both growing season temperature and precipitation/humidity, while also being mindful to avoid risk of frost damage under colder transfers. This practice meshes well with dendrochronology studies in red spruce, which show an overall growth benefit from warmer winters (i.e., less cold damage) alongside negative growth impacts of warmer and drier conditions during the growing season (Kosiba et al. 2018, 2013; Yetter et al. 2021). Ongoing work is aimed at integrating knowledge of local adaptation from quantitative genetics (St. Clair et al. 2022) and population genomics (Lachmuth et al. 2023a, 2023b) into multivariate climate transfer models to help predict optimal seed sources and recipient sites for planting under current and future climate. These genetically informed approaches are under continued development and are available as online tools to provide an additional resource for making seed-transfer decisions (https://fitzlab.shinyapps.io/spruceApp/ and https://seedlotselectiontool.org/sst/).

Insects and Diseases

Red spruce is the target of a few pests but none that have achieved high levels of impact across broad landscapes. Perhaps the most damaging insect pest is the spruce budworm (*Choristoneura fumiferana* Clemens), a native insect that damages buds and current-year shoots of red spruce, especially when growing sympatrically with balsam fir. An important seed pest in some areas is the spruce coneworm (*Dioryctria reniculelloides* Mutuura & Munroe), whose larvae tunnel into developing seed cones and consume the seeds; this can sometimes have considerable local impact on the seed crop (figure 6). In some areas, yellowheaded spruce sawfly (*Pikonema alaskensis* Rohwer) larvae will feed on new needle growth and cause high impacts locally. The eastern spruce gall adelgid (*Adelges abietis* L.) is an introduced pest from Europe that primarily attacks Norway spruce but is occasional on red spruce, with its nymphs feeding at the base of current-year twigs and creating pineapple-shaped galls. The parasitic plant eastern dwarf mistletoe (*Arceuthobium pusillum* Peck) primarily

Figure 6. These red spruce cones in northern Vermont show damage incurred by spruce cone worm (*Dioryctria reniculelloides*). Note the small entrance holes visible on the cones and the brown discoloration indicating seed predation. Photo by Stephen R. Keller, 2017.

infects black spruce but can also be common on white spruce and red spruce (in its northern range), producing the characteristic "witches' broom" growth form, reducing growth, increasing susceptibility to other stressors, and in some cases causing mortality (Baker et al. 2006).

Address Correspondence to:
Stephen Keller, Department of Plant Biology, 111 Jeffords Hall, University of Vermont, Burlington, VT 05405; email: srkeller@uvm.edu; phone: 802–656–5121.

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