Effects of manual defoliation treatments and site type on balsam fir, black spruce and white spruce foliage production

by

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ABSTRACT

Defoliation level and site type are thought to influence tree response during spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreaks. We determined the effects of four manual defoliation treatments (0%-100% + bud removal of current foliage) for 3 years on balsam fir, black spruce, and white spruce trees, on four site quality classes (dry/poor, wet/poor, dry/rich, moist/rich), on foliage production. Number of shoots generally increased 12-59% with increasing cumulative defoliation. Shoot length generally decreased by 32% with increasing cumulative defoliation, especially on rich sites. Bud destruction resulted in 47% fewer shoots but 24% longer shoots during a 2-year recovery period. Trees on rich sites had 43% more shoots, 39% longer shoots, and 156% greater needle weight than on poor sites. The effects of site and defoliation varied between and within species, but site quality played an important role in production of shoots and needles and the tree's ability to withstand defoliation.

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Table of Contents

ABSTRACT ii
ACKNOWLEDGEMENTS iii
Table of Contents iv
List of Tables vi
List of Figures vii
1. INTRODUCTION 1
2. LITERATURE REVIEW 5
2.1 Effects of defoliation on tree photosynthetic rate 5
2.2 Effects of spruce budworm defoliation on foliage production 7
2.2.1 Number of shoots 8
2.2.2 Shoot length 9
2.2.3 Needle length 10
2.2.4 Needlefall 10
2.2.5 Foliage biomass 11
2.3 Effects of spruce budworm defoliation on tree growth 12
2.4 Effects of spruce budworm defoliation on tree mortality 13
2.5 Factors that influence tree response to defoliation 14
2.5.1 Species 14
2.5.2 Site 15
2.5.3 Defoliation severity 17
2.6 Manual defoliation studies on three host species and on other conifer species 17
3. METHODS 19
3.1 Study area and plot establishment 19
3.2 Defoliation treatments 20
3.3 Measurement of foliage variables 25
3.4 Data analysis 26
4. RESULTS 28
4.1 Defoliation period (1992-1994) 28
4.1.1 Number of shoots 28
4.1.2 Shoot length 32

4.1.3 Needle length 34
4.1.4 Needlefall 36
4.1.5 Needle weight 38
4.2 Recovery period (1995-1996) 40
4.2.1 Number of shoots 40
4.2.2 Shoot length 43
4.2.3 Needle length 45
4.2.4 Needlefall 48
4.2.5 Needle weight 49
4.3 Effects of bud destruction on foliage production 50
5. DISCUSSION 55
5.1 Effects of manual defoliation on foliage production 55
5.1.1 Number of shoots 55
5.1.2 Shoot length 56
5.1.3 Needle length 57
5.1.4 Needlefall 58
5.1.5 Needle weight 59
5.2 Effects of site quality on foliage production 61
5.3 Effects of species on foliage production 62
5.4 Application of results and future study 62
6. CONCLUSIONS 64
References 67
Curriculum Vitae

List of Tables

Table 1. Description of site conditions, species composition, and mean tree dimensions for trees in 12 plots in southern New Brunswick in 1992, prior to 3 years of manual defoliation treatments..... 24

Table 2. Mean height, DBH, and average growth increment by site type for the 240 sampled balsam fir, black spruce, and white spruce trees in the 12 sample plots in 1992 (before treatment began). 25

Table 3. ANOVA table showing the effects of species, site, cumulative defoliation (0%, 50%, 100% for number of shoots, shoot length, and needlefall; 0%, 50% for needle length and needle weight) on A) mean number of current-year shoots per tree, B) mean current-year shoot length per tree, C) mean current-year needle length per tree, D) mean needlefall of 1991 needles (1-year-old in the first year of defoliation treatments) per tree, and E) mean current-year needle weight per tree for the 240 sample trees during the defoliation period (1992-1994). 30

Table 4. ANOVA table showing the effects of species, site, defoliation treatment, and time since recovery on A) mean number of current-year shoots per tree, B) mean current-year shoot length per tree, C) mean current-year needle length per tree, D) mean needlefall of 1991 needles (1-year–old in the first year of defoliation treatments) per tree, and E) mean current-year needle weight per tree for the 144 sample trees during the recovery period (1995-1996). 41

Table 5. ANOVA of effects of species, site, and bud destruction (100% versus 100%+bud) on A) mean number of current-year shoots per tree, B) mean current-year shoot length per tree, C) mean current-year needle length per tree, D) mean needlefall of 1991 needles (1-year–old in the first year of defoliation treatments) per tree, and E) mean current-year needle weight per tree for the 72 sample trees during the recovery period (1995-1996)..... 52

List of Figures

Figure 1. Map of study area showing the location of 12 plots in southern New Brunswick. 22

Figure 2. Treated trees and manual defoliation treatments. 23

Figure 3. Mean number of current-year (1992-1994) shoots for five trees in each of the four site classes, tree species and levels of cumulative defoliation. Trees were manually defoliated by 50% or 100% each year from 1992-1994. Blue letters indicate significant differences ($p < 0.05$) among sites within a given species; red letters indicate significant differences among species within a given site; orange letters in brackets indicate significant differences among species, for all sites combined; green letters in brackets indicate significant differences among sites, for all species combined. 31

Figure 4. Mean shoot length (mm) of current-year shoots for five trees in each of the four site classes, three species, and levels of cumulative defoliation. Trees were manually defoliated by 50% or 100% each year from 1992-1994. Blue letters indicate significant differences ($p < 0.05$) among sites within a given species; red letters indicate significant differences among species within a given site; orange letters in brackets indicate significant differences among species, for all sites combined. 33

Figure 5. Mean needle length (mm) of current-year shoots per tree for five trees for each of the four site classes, three species, and levels of cumulative defoliation (control and 50%). Blue letters indicate significant differences ($p < 0.05$) among sites within a given species; orange letters in brackets indicate significant differences among species, for all site combined; green letters in brackets indicate significant differences among sites, for all species combined. 35

Figure 6. Mean needlefall of foliage produced in 1991 (%/tree) in 1994 (n=5) and 1996 (n=3) for each of the four site classes, three species, and four defoliation treatments. Needles produced in 1991 were 1-year-old in the first treatment year (1992), 3-years-old in the last treatment year (1994) and 5-years-old in 1996, the second recovery year. Green letters in brackets indicate significant differences ($p < 0.05$) of 3-year-old foliage among sites, for all species combined. Blue letters indicate significant differences ($p < 0.05$) of 5-year-old foliage among sites within a given species during the recovery period; red letters indicate significant differences ($p < 0.05$) of 5-year-old foliage among species within a given site during recovery period. 37

Figure 7. Mean current-year needle weight (g/tree) from 1992-1994 (treatment years D1-D3) and 1995-1996 (recovery years R1-R2) for three trees (harvested in 1996) in each of the four site classes, three species, and four defoliation treatments. Blue letters indicate significant differences ($p < 0.05$) among sites within a given species during the recovery period; red letters indicate significant differences ($p < 0.05$) among species within a given site during recovery period. 39

Figure 8. Mean number of current-year shoots produced per tree in two recovery years for three trees in each of the four site classes, three species, and four defoliation

treatments. Defoliation treatments ended in 1994, and the 144 sample trees were allowed to recover in 1995-1996. Blue letters indicate significant differences ($p < 0.05$) among sites within a given species; red letters indicate significant differences among species within a given site. 42

Figure 9. Mean length of current-year shoots (mm/tree) for three trees in each of the four site classes, three species, and four defoliation treatments. Defoliation treatments stopped in 1995, 144 trees were allowed to recover from 1995-1996. Brown letters indicate significant differences ($p < 0.05$) among treatments within a given species, site, and year. 44

Figure 10. Mean needle length of current-year shoots (mm/tree) for three trees in each of the four site classes, four defoliation treatments, and three species. Defoliation treatments stopped in 1995, 144 trees were allowed to recover from 1995-1996. Brown letters indicate significant differences ($p < 0.05$) among treatments within a given species, site, and year; blue letters indicate significant differences among sites within a given species in year 1; green letters indicate significant differences among sites within a given species in year 2; red letters indicate significant differences among species within a given site in year 1; and purple letters indicate significant differences among species within a given site in year 2. 47

1. INTRODUCTION

During outbreaks, spruce budworm (*Choristoneura fumiferana* (Clem.)) larvae repeatedly consume current-year foliage of balsam fir (*Abies balsamea* (L.) Mill.) and spruce (*Picea* spp.), leading to extensive host tree growth loss (Piene, 1980) and mortality (MacLean, 1980). Manual defoliation has been used to simulate defoliation by insect herbivores in experiments and is considered a good indication of a plant's response to a given type of damage (Piene, 2003). Foliage biomass per tree may be a better predictor of tree growth than defoliation level, which is used in most defoliation-based stand growth models. This is because in response to defoliation, trees may increase retention of older age-classes of foliage (Doran et al., 2017) and also increase production of new foliage, both of which affect tree growth. Understanding foliage production in response to defoliation is, therefore, an important component of models to predict tree growth response to defoliation.

Foliage is the tree's photosynthetic factory that permits tree growth, but defoliating insect attacks repeatedly remove foliage, strongly reducing photosynthetic capacity of host trees (Clark, 1961). Trees may increase photosynthetic rate in response to defoliation, i.e., photosynthetic compensation (Reich et al., 1993, Kolb et al., 1999, Vanderklein and Reich 1999). Such photosynthetic compensation, combined with internal reallocation of nutrients and carbohydrates to re-growing tissues (Schoonhoven et al., 1998), promotes tree recovery. Foliage biomass per branch of balsam fir is a function of number of shoots, mean shoot length, mean needle length, and percentage litterfall or defoliation per branch (Piene, 1983). Responses of these foliage variables

therefore determine overall tree foliage biomass, and thereby growth and recovery of trees that survive defoliation (Ostaff and MacLean, 1995).

Host tree species identify strongly influences the level of defoliation a tree experiences during spruce budworm attack (Régnière and Nealis, 2007; Hennigar et al., 2008). Susceptibility of host species to defoliation declines from balsam fir, white spruce (*Picea glauca* [Moench] Voss), red spruce (*Picea rubens* Sarg.), and black spruce (*Picea mariana* (Mill.) B.S.P.), with the three spruce species having about 72%, 41%, and 28%, respectively, as much defoliation as balsam fir (Hennigar et al., 2008). This may be because of differences in phenology, with black and red spruce opening buds about 10 days later than white spruce, which opens buds one or two days later than balsam fir (Blais, 1957). Lack of food leads to fewer spruce budworm larvae on black spruce. However, red spruce is more affected by budworm attack than black spruce, because young larvae can survive on old foliage of red spruce until the buds open (Greenbank, 1963). Thus, early larval populations do not decline and infestations are more persistent in red spruce stands than in black spruce stands. Generally, under similar levels of spruce budworm infestations, black spruce suffered less defoliation and lived longer than other host species (Greenbank, 1963).

In contrast to species, site moisture and fertility conditions have inconsistently influenced tree response to defoliation (Dupont et al., 1991; MacKinnon and MacLean, 2003). Balsam fir stands with higher soil moisture and fertility suffered 19% more defoliation than on wet/poor sites (MacKinnon and MacLean, 2003). Dupont et al. (1991) found that compared to xeric, mesic, and hydric fir stands, subhygric fir stands had the lowest vulnerability, with 27% mortality. Chen et al. (2017) failed to find strong

influences of site productivity and topographic characteristics on mortality and ingrowth. Sites with rich soil nutrients can provide more nutrients for trees to withstand defoliation. Piene (1980) found significant increases in percent P ($p < 0.01$), Mg ($p < 0.02$), and K ($p < 0.01$) in foliage from defoliated trees (75-100% defoliation) as compared to those from protected trees (with 0-25% defoliation). Similar results were found in other studies of concentrations of foliar nutrients in defoliated trees (e.g., Cook et al., 1978; Hoogesteger and Karlsson, 1992; Kolb et al., 1999). Defoliated trees may also have higher net photosynthetic rate caused by higher stomatal conductance on moisture rich sites, which provide greater water availability (Kruger and Reich, 1993; Reich et al., 1993).

In addition, other studies on the effect of defoliation severity and duration on foliage production of other conifer species have been published. 15-year-old young jack pine (*Pinus banksiana* Lamb.) in which all 1-year-old, 2-year-old, and 3-year-old foliage were manually removed produced distinctly yellowish foliage in the following year, with short needles densely distributed along shoots of reduced length (Neil, 1962). Lyytikäinen-Saarenmaa (1999) determined the responses of Scots pine (*Pinus sylvestris*) saplings to artificial clipping removal of current-year foliage and defoliation stress caused by sawfly larvae, and found that shoot lengths of artificially defoliated trees were significantly shorter than those of the controls, but in natural defoliation treatments, significant differences from the control were only found with 75% defoliation (33.4 versus 41.3 cm respectively). Kulman (1965) found that removal of all current-year needles of red pine (*Pinus resinosa* Ait.) trees reduced needle length by 19-32% after one year and increased length by 9-42% after two years.

In this study, a manual defoliation experiment was used to examine tree species

response to variable defoliation levels. More specifically, defoliation of 1.6-3.6 m tall balsam fir, black spruce and white spruce trees was conducted over a 3-year defoliation period (1992-1994) followed by a 2-year recovery period (1995-1996). Treatments included four levels of defoliation (0%, 50%, or 100% clipping of current-year needles, and a 100%+bud treatment clipping all current-year shoots per tree) on trees in four site quality classes (determined based on soil moisture and soil nutrient conditions: dry/poor, dry/rich, wet/poor, moist/rich). This resulted in twelve plots with 20 trees treated per plot (five trees in each defoliation class), for a total of 240 trees treated. The objective was to quantify the individual and interacting effects of manual defoliation severity, site type, and tree species on foliage production. Conifers maintain multiple age-classes (cohorts) of foliage, with one new cohort of needles produced each year, which we term current-year foliage. Foliage production was assessed in terms of mean number of current-year shoots, mean current-year shoot length, mean current-year needle length, mean needlefall of the 1991 age-class of needles (selected as the year prior to treatments), and mean current-year needle weight, over 5 years of defoliation treatments and recovery. In this study, we tested the following hypotheses and predictions: (1) during defoliation treatment years, cumulative defoliation will influence foliage production, with higher cumulative defoliation resulting in increased epicormic shoot production (Piene and Eveleigh, 1996), shorter shoot and needle length due to lack of carbohydrates and hormones (Piene and MacLean, 1999), increased old needle retention (Doran et al., 2017), and lower overall current-year needle production; (2) during recovery years, trees will prioritize recovery of foliage biomass (Ostaff and MacLean, 1995), by increased number of shoots, shoot and needle length, and old needle retention, resulting in

increased current-year needle weight. Trees in the 100%+bud removal and 100% defoliation treatment will have slower recovery owing to insufficient carbohydrates, hormones, and nutrients (Piene and MacLean, 1984); (3) trees on moist and rich sites will suffer less effects on number of shoots, mean shoot length, mean needle length, and needlefall during defoliation treatment years and have stronger ability to recover because these sites provide more water and nutrients for trees to resist defoliation and rapidly recover photosynthetic capacity (Brix, 1971; Lavigne et al., 2001; Piene, 2003).

2. LITERATURE REVIEW

The following sections provide a more in-depth review of previous studies of the effects of defoliation on tree photosynthetic rate, foliage production variables, tree growth and mortality, effect of species, site and defoliation severity, and manual defoliation studies.

2.1 Effects of defoliation on tree photosynthetic rate

Foliage plays an important role in a tree's function because it is the photosynthetic factory that permits tree growth. However, defoliating insect attacks repeatedly remove foliage, which strongly reduces photosynthetic capacity of host trees (Clark, 1961). Some studies have found that trees may increase photosynthetic rate in response to defoliation, i.e., photosynthetic compensation (Reich et al., 1993, Kolb et al., 1999, Vanderklein and Reich 1999), which, combined with internal reallocation of nutrients and carbohydrates to re-growing tissues (Schoonhoven et al., 1998), promotes tree recovery.

Reich et al. (1993) monitored subsequent growth, gas exchange and nutritional responses of red pine seedlings and trees that were subjected to manual defoliations of varying intensities in three experiments. In experiment 1, one of four treatments were applied to 2-year-old red pine seedlings: 50% of each needle was clipped by hand in spring (March); 50% of each current-year needle was clipped by hand in summer (July); both defoliations; or none. Results showed that both net photosynthesis and leaf conductance were 25-50% higher ($p < 0.01$) in defoliated than non-defoliated plants in May, six weeks after defoliation. In experiment 2, 4-year-old seedlings were randomly treated with either a 0, 25, 50, or 70% defoliation regime in August, and 1-year-old and 2-year-old needles were measured (current-year needles had not yet expanded). Photosynthetic rates in the 1-year-old and 2-year-old needles were highest in the 25% and 50% defoliated plants, respectively, and lowest in the controls (~ 6.5 versus 5.8 μmol m^{-2} s^{-1} and ~ 4.3 versus 3.8 μmol m^{-2} s^{-1}, respectively). In experiment 3, response of 11-year-old trees was monitored for 1 year following 0, 33, or 66% defoliation on each tree in July. Results showed that photosynthesis was highest in current-year and 1-year-old needles and then declined with increasing needle age. In all age classes, the 33% defoliated trees had higher photosynthetic rates than the 66% defoliated trees (mean of 10.28 versus 9.25 μmol m^{-2} s^{-1}). They concluded that 25-50% defoliation of plants stimulated net photosynthesis most.

Kolb et al. (1999) grew 4-year-old, potted Douglas-fir seedlings in two soil types (desalt-derived, limestone-derived) with two levels of soil moisture (high, low) and manually applied three levels of western spruce budworm (*Choristoneura occidentalis* Freeman) defoliation (none, 30% and 60% defoliation) and two levels of frass and litter

produced by budworm feeding (with, without) over 2 years in a greenhouse environment. They found that heavily defoliated seedlings had significantly less biomass (mean of 22.3%) and higher net photosynthetic rate (23.85%) compared with non-defoliated seedlings ($p < 0.001$).

Vanderklein and Reich (1999) studied the effects of partial defoliation on photosynthesis and growth for field-grown seedlings of deciduous Japanese larch (*Larix leptolepis*) and evergreen red pine. The distal portion of each needle was removed by 0, 25, 50 or 75% in the first year (1990). Seedlings were defoliated either 0 or 50% in the second year (1991), regardless of previous defoliation treatments. Needles were collected to determine the leaf area and mass, which were used to calculate photosynthesis on a projected area or mass basis. Larch seedlings defoliated in 1991 had significantly higher (18%) photosynthetic rates on a mass basis than non-defoliated seedlings ($p = 0.054$). Red pine seedlings had significantly higher (15%) photosynthesis on an area basis ($p = 0.049$) in response to 50% defoliation in 1991, and also showed a linear increase (by as much as 50%) in photosynthesis on a mass and area basis with increasing 1990 defoliation intensity in 1991.

2.2 Effects of spruce budworm defoliation on foliage production

Defoliating insect attacks often bring about dramatic changes in vertical foliage distribution in the crown, especially those insects that not only decrease foliage weight but also destroy buds and shoots in the process (Piene and MacLean, 1999). Trees that survive the outbreak will recover depending on their ability to re-foliate, via changes in

foliage variables, such as lengths of shoots and needles, and the total number of shoots produced.

2.2.1 Number of shoots

Piene and MacLean (1999) established four treatments in young balsam fir stands: spaced and unspaced, defoliated and protected (annual insecticide spraying to prevent defoliation) and examined the foliage patterns every year throughout a spruce budworm outbreak cycle from 1976 to 1984 (including three years of 'recovery' from 1982-1984). They found that the number of shoots for protected spaced trees was significantly higher (1140 vs. 400 shoots/tree) than for the unspaced trees 8-13 years after spacing. However, no significant difference was found in shoot production between protected spaced and defoliated spaced trees, or between protected unspaced and defoliated unspaced trees in 1979, the fourth year of defoliation, as a result of the prolific production of epicormic shoots. Protected trees had the maximum number of shoots in the mid-crown, while the greatest number of shoots occurred in the lower crown of defoliated trees. In another study conducted by Ostaff and MacLean (1995), stands dominated by 60-80 year old balsam fir were divided into three groups according to different cumulative defoliation from 1974 to 1985 on Cape Breton Island. Trees in group 1 suffered the longest period of continuous cumulative defoliation (6-7 years from 1974-1980), while groups 2 and 3 sustained 4-5 years (1975-1977 and 1980-1981) and 3 years (1975-1977), respectively. In all groups, defoliation was nil or light from 1982 to 1985, allowing surviving trees to recover. In 1980, after three years of recovery, the number of shoots increased to 6.1 shoots/cm of branch length in group 3, more than trees in the other groups. Groups 1 and

2 reached their maximum shoot production in 1982, the second year of recovery following the cessation of defoliation (4.19 shoots and 6.69 shoots/cm of branch length), while group 3 decreased. Piene and MacLean (1984) also measured these foliage patterns for young, spaced balsam fir from 1979 to 1981 in 20 plots (involving moderately defoliated plots and severely defoliated plots) on the Cape Breton Highlands, Nova Scotia. They found that number of shoots was greater ($p < 0.001$) in moderately defoliated than in severely defoliated plots (means of 30 versus 8 shoots/10 cm branch length).

2.2.2 Shoot length

Shoot lengths of young balsam fir were generally reduced by defoliation, from 3.9 cm to 2.2 cm between protected spaced and defoliated spaced trees and from 4.0 cm to 2.2 cm between protected unspaced, defoliated unspaced trees (Piene and MacLean, 1999). Removal of needles (leaving buds) could cause reductions in carbohydrates and hormones, with the overall result being decreased shoot lengths (Piene and MacLean, 1999). Ostaff and MacLean (1995) found that shoot lengths increased after defoliation ended. In group 1 and 2 (6-7 and 4-5 years of defoliation), mean shoot length increased from 11-14 mm in 1980 to 21-27 mm in 1982, and group 3 (severe defoliation but only 3 years) had significantly greater mean shoot length than group 1 and 2 in 1980 (20.4 mm), 1981 (25.7 mm), 1984 (30.5 mm) after about 350% cumulative defoliation.

2.2.3 Needle length

In general, defoliation not only reduces shoot length, but it also shortens needle lengths (Piene and MacLean, 1999). In 1980, 1982 and 1984 (for unspaced trees), needles on defoliated trees (~ 9.1, 8.8, 9.2 mm/branch) were significantly shorter ($p = 0.001$) than on protected trees (~ 10.7, 10.7, 10.8 mm/branch). However, defoliation also resulted in significantly longer ($p = 0.001$) needles on defoliated spaced trees (~10.4 mm/branch) than on protected spaced trees (~10.0 mm/branch) in 1979, the fourth year of defoliation. The number of needle primordia, which is strongly influenced by the previous season's growing environment (Clements, 1970), was probably reduced in 1978, and then reduced the needle density in 1979, resulting in the abnormally long needles in that year (Piene and Percy, 1984).

2.2.4 Needlefall

Natural needlefall caused by defoliation is also an important factor in studying the effects of defoliation on foliage production. Conifers may adjust their foliage life spans to increase needle retention to compensate for losses of photosynthetic capacity to defoliation. Doran et al. (2017) reported that cumulative spruce budworm defoliation significantly increased needle longevity of balsam fir. They assessed defoliation and needle loss on 16 age classes of foliage on mid-crown branches sampled from 134 mature balsam fir trees and related it to needle age and cumulative defoliation (summed annual defoliation from 2012 to 2016). Results showed that for young foliage (< 9 years), increased cumulative defoliation caused lower needle survival, which resulted from backfeeding of spruce budworm on 5+-year-old foliage. While for older age classes (10-

16-year-old), 10-16% more foliage per age class was retained under severe defoliation than under light defoliation. Mean needle longevity of 50-year-old fir was almost double that for undefoliated 25-year-old fir (9.5 years vs 5.5 years).

2.2.5 Foliage biomass

Piene and MacLean (1999) showed that average foliage weight of defoliated trees throughout the spruce budworm outbreak cycle (from 1976-1984), except in 1976 at the start of the outbreak, was significantly lower ($p < 0.001$) than for the corresponding protected trees (mean of 1315 versus 410 g/tree). Foliage weight of defoliated trees decreased rapidly after 1976, and by 1981 they were almost completely defoliated. After 1981, foliage weight of trees that survived the budworm outbreak increased rapidly, due to prolific shoot production in 1979-1980.

Piene and MacLean (1984) presented two versions of foliage biomass of young spaced balsam fir, a potential biomass calculated based on needle and shoots dimensions and an actual biomass that included the effects of budworm defoliation in three successive years (1979-1981). Whether in protected plots or unprotected plots, both of these measures of biomass were significantly larger in the moderately defoliated plots than in the severely defoliated plots, with potential biomass averaging 31.2 and 14.6 g/10 cm branch length for protected, and 32.6 and 10.13 g/10 cm branch length for unprotected, and actual biomass averaging 20.13 and 4.73 g/10 cm branch length for protected and 19.0 and 2.33 g/10 cm branch length for unprotected, respectively.

Piene et al. (2003) examined foliage weight of young balsam fir throughout a 6-year (1976-1984) spruce budworm outbreak cycle. There were four treatments: spaced and

unspaced, defoliated and protected. In 1981, six years into the outbreak, foliage weight in defoliated plots reached its minimum levels, representing a reduction of 83.3 and 84.3% for spaced and unspaced stands, respectively, compared with the protected stand. For surviving trees, foliage weight recovery was very strong (three-fold to five-fold for spaced and unspaced plots, respectively) from 1981 to 1984, because of the release of suppressed buds damaged in 1977-1978. Still, spaced and unspaced stands had 37.5 and 68.5% lower foliage weight, respectively, at the end of the outbreak compared to protected stands.

2.3 Effects of spruce budworm defoliation on tree growth

Defoliation from spruce budworm feeding results in stem growth reductions of trees. It is well known that a spruce budworm outbreak causes reduced stem wood production, which is reflected in narrow annual tree growth rings. Piene (1980) determined growth reductions of spaced balsam fir that were first attacked by spruce budworm outbreak in 1976 (65-100% of current foliage consumed). Results showed that 80 to 100% defoliation of current-year foliage caused about 20% of the projected volume growth in the first year of spruce budworm feeding. However, responses of individual trees varied, with volume losses ranging from 11 to 42 % for trees that were 100 % defoliated. In the second year of defoliation, stem volume growth decreased by about 50%. MacLean et al. (1996) assessed the effect of spruce budworm cumulative defoliation from 1981 to 1987 on tree growth in a 35-year-old balsam fir stand. Trees were divided into five defoliation classes: 1-25%, 26-50%, 51-75%, 76-90%, and 91-100% via visual cumulative

defoliation rating. Specific volume increment was reduced by an average of 11, 55, 83, 70, and 83% for each class after six years of moderate to severe defoliation, respectively.

In terms of height growth, Mott et al. (1957) found that spruce budworm feeding was often most severe near the tops of trees. When a balsam fir dominant stand suffers years of defoliation resulting from spruce budworm, the attack will contribute to top killing in the third year (Miller, 1977). As a result, heights of living trees may be reduced by 0.5–4.0 m during outbreaks (Baskerville and MacLean, 1979). Alfaro et al. (2001) examined white spruce stand susceptibility to top-kill by spruce budworm in British Columbia, and found that 3-4 years of defoliation reached a maximum top-kill of 47.2%.

2.4 Effects of spruce budworm defoliation on tree mortality

If defoliation continues for several years, trees eventually die. Many studies on tree mortality during spruce budworm outbreaks in eastern North America were reviewed by MacLean (1980, 1985). Generally, tree mortality starts after 4-5 years of severe defoliation and mortality is generally complete by 10 years after the start of the infestation (MacLean 1980). Balsam fir stands start to die after three to five years of severe defoliation, whereas spruce stands have the ability of withstanding two more years of severe defoliation before mortality begins (Blais, 1985; Ostaff and MacLean, 1989). MacLean (1980) indicated that balsam fir was the most vulnerable species, with average mortality caused by budworm outbreaks in mature balsam fir, mature spruce, immature fir, and immature spruce stands averaging 85%, 42%, 36%, and 13%, respectively. Mortality in young balsam fir was 31-49% in spaced versus 11-32% mortality in unspaced plots, but in severely defoliation spaced young fir plots, mortality can reach up

to 94-100% (MacLean and Piene 1995). Average mortality was 10-22% higher in spaced than in unspaced fir plots. Alfaro et al. (2001) found that white spruce plots with 5-6 years of defoliation in British Columbia reached a maximum mortality of 30.4%.

2.5 Factors that influence tree response to defoliation

2.5.1 Species

Hennigar et al. (2008) quantified defoliation differences among all four host tree species over 9 years (1984 to 1992) in an extensive permanent sample plot network in New Brunswick. Results showed that on average, white spruce, red spruce, and black spruce had approximately 72%, 41%, and 28% as much defoliation as balsam fir, respectively. Several studies have indicated that spruce budworm can back-feed more readily on balsam fir than on spruce (Harper et al., 2003; Bouchard et al., 2005; MacLean, 2016). White spruce had longer shoot length and more rapid shoot growth than balsam fir, so that it can provide larvae 40% more food per unit of larvae population than balsam fir in young stands and 80% more food in mature stands (Greenbank, 1963).

High vulnerability (i.e., mortality or growth reduction) is generally associated with stands with a high proportion of balsam fir (Blais, 1983; MacLean, 1980). In addition, among the three host species of spruce, Baskerville and MacLean (1979) suggested that white or red spruce was more vulnerable to mortality than black spruce, which ranged from 0 to 24% in immature fir-spruce stands in New Brunswick. This may be partly because of differences in phenology, with black and red spruce opening buds some 10 days later than white spruce, which opens buds four days later than balsam fir (Blais, 1957; Greenbank, 1963). Thus young spruce budworm larvae may not achieve

adequate food from black spruce and as a result larvae may starve in the early instars or abandon the tree. However, red spruce is attacked more than black spruce, because young larvae can survive an old foliage of red spruce until the buds open. Thus, early larval populations do not decline and infestations are more persistent in red spruce than in black spruce stand (Greenbank, 1963). Generally, under similar level of spruce budworm infestations, black spruce suffered far less defoliation and live longer than other host species (Blais, 1957; Greenbank, 1963).

2.5.2 Site

Several studies have indicated that site quality may play a significant but inconsistent role in host tree defoliation and mortality (Dupont et al., 1991; MacKinnon and MacLean, 2003). Stands with more moisture and better nutrition suffered from more severe defoliation, given that fir on moist/rich sites sustained an average of 19% higher defoliation than on wet/poor sites (MacKinnon and MacLean, 2003). Sites with abundant moisture and nutrients support vigorous tree growth, providing increased available water contents and foliage nitrogen (Mattson and Haack, 1987; McKinnon et al., 1998) for budworms to survive, grow and breed (Schmitt et al., 1983; Mattson et al., 1991). Because of the higher rates of successful propagation, budworm populations may become vigorous, leading to more defoliation. However, Chen et al. (2017) reached an opposite conclusion that site potential productivity and topographic characteristics had little influence on spruce budworm-caused mortality and ingrowth. Despite exhibiting a large amount of variation, there were no significant relationships between mortality and

ingrowth and site characteristics, with all the site characteristics examined accounting for less than 1% of the variation in the response variables.

Dupont et al. (1991) studied a series of balsam fir stands with four different moisture regime classes (xeric, hydric, subhygric, and mesic fir stands) to determine vulnerability to mortality during a spruce budworm outbreak. The mortality results can be divided into three levels: xeric fir stands (85% mortality) and hydric fir stands (75% mortality) were the most vulnerable, mesic fir stands (45% mortality) showed a moderate level of mortality, while subhygric fir stands (27% mortality) had the lowest vulnerability. They explained their results by the hypothesis that with higher energy host trees reserve on good sites, trees are less vulnerable to spruce budworm damage (Hix et al., 1987; Waring, 1987). Overall, Dupont et al. (1991) concluded that trees with higher energy reserves are better able to produce new foliage following consecutive years of defoliation and sites with poor drainage not only have less water stress on trees, it may also act as a supplemental input of nutritional elements and oxygenated water, which led to a decreasing larval development rate, pupal weight, and a shrinking survival rate as well by increasing raw-fiber content of host trees foliage. In contrast, MacLean and MacKinnon (1997) found that moderate-well drained plots sustained more defoliation than imperfectly or poorly drained plots whether in the active budworm outbreak area (17% more current and 7% more cumulative defoliation), or in the more lightly defoliated area (7% more current and 5% more calculated cumulative defoliation).

2.5.3 Defoliation severity

Population of spruce budworms is the most direct representation of outbreak severity. The more spruce budworms that occur, the higher the defoliation will be. In addition, the characteristics of a high population level are comparatively high instar survival rates, especially late-instar survival (Régnière and Nealis, 2007).

In addition to the factors reviewed above, other factors such as hardwood content (Su et al., 1996; Needham et al., 1999), climate (Blais, 1958; Gray, 2008) and elevation (Bouchard and Auger, 2014; Magnussen et al., 2004) have also been suggested to influence host trees response to defoliation through the effects on spruce budworm population processes.

2.6 Manual defoliation studies on three host species and on other conifer species

Manual defoliation has been used to simulate defoliation by insect herbivores in experiments and is usually considered a good indication of a plant's response to a given type of damage. Piene and Little (1990) simulated defoliation resulting from spruce budworm by artificially removing foliage of 5-year-old balsam fir at the peak of the sixth instar period in the first 1, 2 or 3 years of a 3-year experiment. They applied seven treatments: manually remove 0, 33, 66, 90 or 100% of the current-year needles, clip all current-year needles by using scissors (clip treatment), or all current-year shoots severed using a razor blade at their base (100+ treatment). The foliage weight of clip treatment treated for 3 years was generally intermediate between that of the 90 and 100% treatment. And the 100+ treatment had a similar effect on foliage weight to the 100% treatment.

Piene (2003) carried out a study on the growth recovery from 1995 to 1997 of 60 12-year-old plantation white spruce following a 2-year period (1993-1994) of artificial defoliation and pruning, with four treatments: i) control undefoliated, ii) removal of 50% of the current-year foliage, iii) removal of all current-year shoots, iv) removal of all current-year shoots and all 1-year-old needles (in 1993) and all current-year shoots and all 3-year-old needles (in 1994). Following treatment, the location of buds and shoots were mapped in each of three whorls (whorls 1990, 1991, and 1992). The results demonstrated that all treatments increased shoot production. Shoot development (% buds that developed into shoots) for the 50% defoliation treatment exceeded the control treatment in 1994 (mean of 66% versus 98%) and 1995 (mean of 58% versus 90%), the first and second years of recovery. In terms of shoot length, the control treatment was greater than the 50% defoliation treatment from 1994 to 1996. Shoot length for the removal of all current-year shoots treatment completely recovered by 1996, the second year of recovery, but did not recover for the most severe removal of current-year and older foliage treatment. Number of shoots for the 50% treatment was greater than the control treatment in the first and second year of recovery, due to the great shoot development. Although the number of shoots increased in the most severe removal of current-year and older foliage treatment, the shoots had a yellow appearance. In addition, trees in the removal of all current-year shoots treatment triggered prolific shoot production thereafter (apical dominance was disrupted) and took one year to recover all foliage mass by almost doubling in 1995. However, trees in the most severe removal of current-year and older foliage treatment had slow recovery of foliage mass, possibly due

to root mortality which can be caused by light and severe defoliation (Redmond, 1959; Piene and Little, 1990).

In addition, several other studies of manual defoliation effects on conifer trees have been published. Neil (1962) manually removed all 1-year-old foliage or removed all 2-year-old and all 3-year-old foliage of 15-year-old young jack pine, both of which caused reduction in height growth by 0.21 m and 0.18 m, significantly different from that of trees in the control treatment. Lyytikäinen-Saarenmaa (1999) determined the responses of Scots pine saplings mean shoot length to artificial clipping using scissors and defoliation stress caused by sawfly larva. Results showed that in early-season treatments, the shoot lengths of artificially defoliated trees (27.7-32.9cm) were significant shorter than those of the controls (41.2-43.2 cm), but in natural defoliation treatments, significant differences from the control were only found with 75% defoliation (33.4 versus 41.3 cm). Kulman (1965) applied six defoliation treatments to 5-year-old red pine trees: (1) current-year, (2) one-year-old, (3) two-year-old, (4) current-year and one-year-old, (5) current-year and two-year-old, and (6) one-year-old and two-year-old. Results showed that removal of current-year needles reduced needle length by 19-32% after one year and increased length by 9-42% after two years.

3. METHODS

3.1 Study area and plot establishment

The study area was located in southern New Brunswick, where 12 square 30m x 30m plots were selected to represent balsam fir, white spruce, and black spruce, each on four

site quality classes (soil moisture and soil nutrient conditions: dry/poor, dry/rich, wet/poor, moist/rich) (Figure 1). Site quality was determined for each plot using the New Brunswick Forest Site Classification system (Zelazny et al., 1989) to determine site Treatment Unit, a large-scale landscape unit with a relatively narrow range of soil drainage and nutrient regimes based on vegetation type (VT) and soil type (ST). STs are defined based on assessment of plot soil profile characteristics and VTs are characterized by sampling dominant overstory and understory indicator plant species (Zelazny et al., 1989).

Detailed descriptions of each plot are presented in Table 1. Five of the plots (1, 4, 9, 11, 12) were located in plantations, three plots (2, 6, 10) were located in a "fill plantation" (i.e., partly planted), plots 3 and 7 were located in an area that was planted and then later thinned due to overabundance of competing balsam fir regeneration, plot 5 was located in a black spruce plantation that had a significant quantity of balsam fir regeneration, and plot 8 was located in a precommercially thinned spruce-fir stand that was mainly composed of balsam fir. Density of the plots ranged from 2000 stems/ha in plot 12 to 8989 stems/ha in plot 6. In three plots, there were scattered patches of dense clumps of black spruce (plot 2) or balsam fir (plots 5 and 6). Plot 11 had lots of maple (*Acer rubrum* and *Acer saccharum*) and birch (*Betula papyrifera*) suckering resulting from the thinning operation. The clumps and suckering resulted in a fairly high density for these plots. All 12 plots were composed mainly of spruce and fir with 16-19% small hardwood trees found in plots 1, 4, 7, 8, 9, and 11.

3.2 Defoliation treatments

Defoliation treatments began in the summer of 1992. In the fall of 1992, all trees in the 12 plots were mapped, identified by species, and measured for height, diameter at breast height (DBH), and stump diameter (Table 1). Additional measurements were taken only on treatment trees, including annual height increment from 1989 to 1992, mean height to base of live crown, and mean DBH (Table 2). Defoliation treatments were conducted for three years (1992-1994, termed years D1-D3). Using scissors, a specified amount of foliage was clipped off every current-year shoot on 240 sample trees (Figure 2), corresponding to four treatments: 1) 0% removal of current-year foliage (control); 2) 50% of foliage clipped from each current shoot; 3) 100% of foliage clipped from each current-year shoot; and 4) 100% of foliage and the bud clipped from each current-year shoot (i.e., current-year bud destruction). Treatments are termed 0%, 50%, 100%, and 100%+bud defoliation. The 100%+bud treatment was included to replicate extremely high spruce budworm populations, which can feed on the developing shoot early in the growing season and thus destroy the main axis and bud of the shoot as well as consuming all needles (Piene, 1989a). Random numbers were used to assign each treatment to five trees per plot (for a total of 20 treatment trees per plot). When treatments began, sample trees were 7-10 years old and averaged 2.3-4.1 m tall per plot (Table 2). Tree size (DBH) measured in 1992 did not differ among treatment trees within each plot. However, both height and DBH of sample trees in 1992 differed significantly among sites (trees on rich sites > on poor sites) and species (balsam fir > white and black spruce). When treatments ended, two of the five trees in each treatment per plot were harvested in 1994, and the remaining three trees per treatment, per plot (144 sample trees in total) were allowed to recover from 1995 to 1996 (termed years R1-R2) and then were harvested following

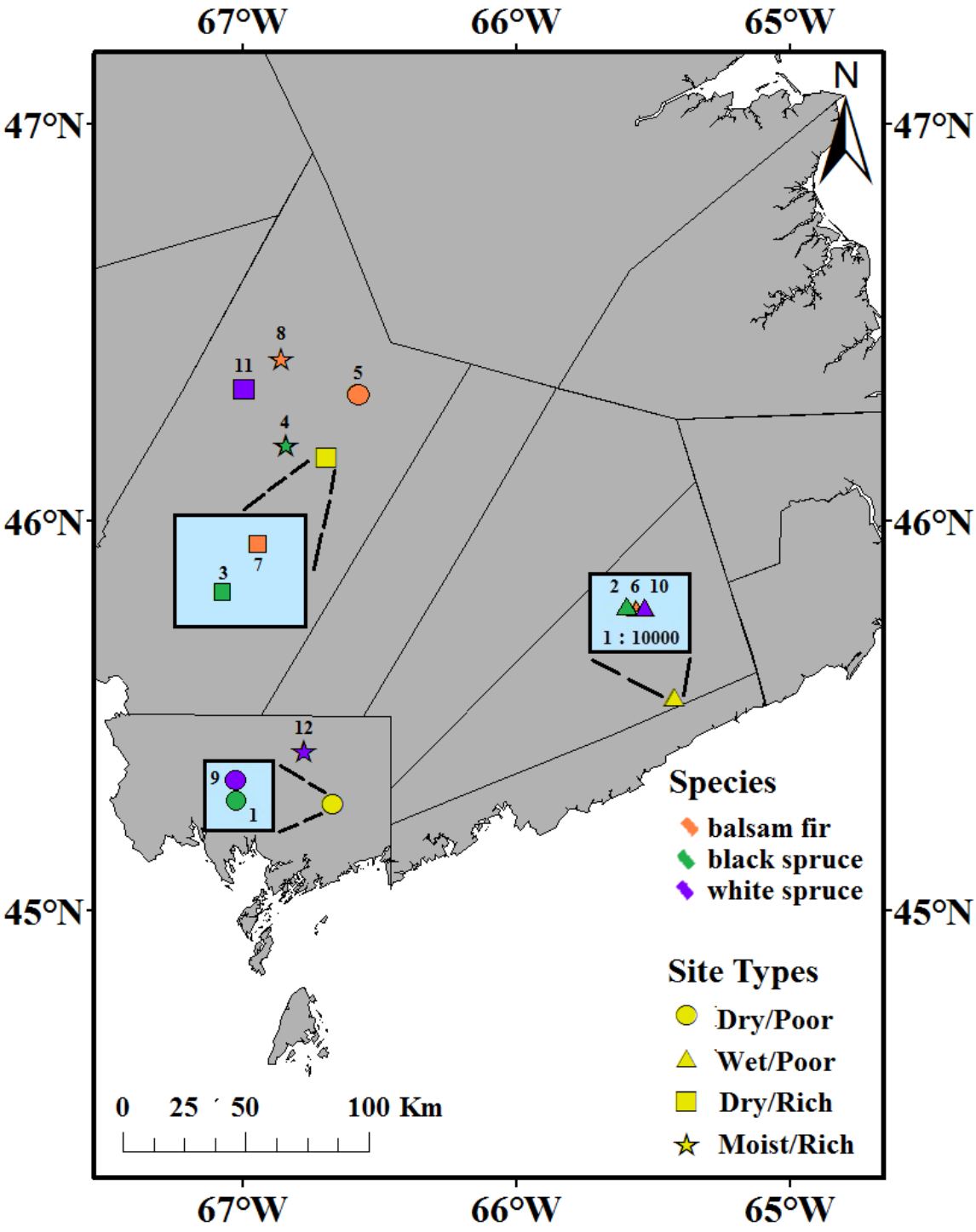


Figure 1. *Map of study area showing the location of 12 plots in southern New Brunswick.*

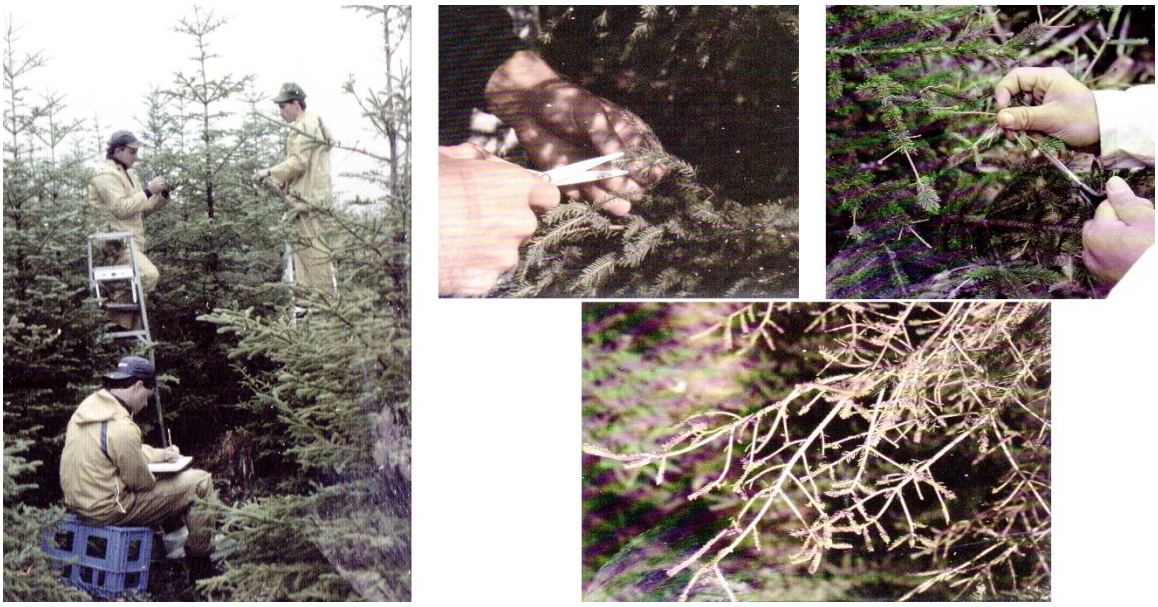


Figure 2. *Treated trees and manual defoliation treatments.*

completion of growth in the fall of 1996. We calculated cumulative defoliation each year by summing all defoliation treatments up to the current year (i.e. the cumulative defoliation of trees in the "50% treatment" was 50% in 1992, 100% in 1993, and 150% in 1994). Cumulative defoliation was used as a continuous variable for the analysis of tree response during the defoliation period. For the analysis of tree response during the recovery period, the defoliation treatment was used as a four-level categorical variable.

Table 1. *Description of site conditions, species composition, and mean tree dimensions for trees in 12 plots in southern New Brunswick in 1992, prior to 3 years of manual defoliation treatments.*

Plot	Sp.	Site description		Density (stems/ha)	Species composition (%)								Height (m)		DBH (cm)		Stump diam. (cm)		Crown width (m)	Age (yrs)
		Soil moisture	Soil nutrient		bF	wS	bS	rS	wB	rM	tA	sM	Mean	St dev	Mean	St dev	Mean	St dev		
1	bS	Dry	Poor	3833	1	0	71	0	26	0	0	0	2.19	0.04	2.48	0.09	4.16	0.12	1.7	8
2	bS	Wet	Poor	6744	18	16	64	1	1	0	0	0	1.89	0.02	1.61	0.04	3.52	0.06	1.2	8
3	bS	Dry	Rich	3100	42	1	47	0	0	1	8	0	3.56	0.08	4.85	0.13	6.34	0.17	1.6	8
4	bS	Moist	Rich	2989	5	1	71	0	0	15	1	0	2.56	0.06	3.12	0.12	5.13	0.16	1.8	8
5	bF	Dry	Poor	4633	59	1	34	3	0	0	4	0	1.59	0.02	1.67	0.06	3.53	0.06	1.0	7
6	bF	Wet	Poor	8989	46	18	12	25	0	0	0	0	2.13	0.02	1.97	0.04	3.45	0.05	1.3	7
7	bF	Dry	Rich	3292	45	9	25	1	0	6	13	0	3.08	0.08	5.04	0.15	6.63	0.18	1.6	10
8	bF	Moist	Rich	7860	49	1	0	6	17	15	5	0	2.12	0.04	2.59	0.12	3.64	0.11	1.7	10
9	wS	Dry	Poor	3956	0	59	0	15	21	1	0	0	2.38	0.04	2.82	0.06	5.52	0.14	1.7	8
10	wS	Wet	Poor	3756	32	39	4	24	2	0	0	0	2.04	0.03	2.05	0.06	3.68	0.07	1.6	7
11	wS	Dry	Rich	3023	17	39	0	0	3	24	5	10	2.24	0.04	2.10	0.09	4.09	0.12	1.6	7
12	wS	Moist	Rich	2000	0	96	0	4	0	0	0	0	3.02	0.06	4.27	0.13	7.93	0.17	1.6	7

Species abbreviations: bF balsam fir, bS black spruce, wS white spruce, rS red spruce, wB white birch, rM red maple, tA trembling aspen, sM sugar maple.

Table 2. *Mean height, DBH, and average growth increment by site type for the 240 sampled balsam fir, black spruce, and white spruce trees in the 12 sample plots in 1992 (before treatment began).*

Plot	Site description		Mean height (m)			Mean DBH (cm)			Average annual height increment [x] (m/year)		
	Soil moisture	Soil nutrient	bF	bS	wS	bF	bS	wS	bF	bS	wS
1, 6, 11	Dry	Poor	2.28	2.75	2.88	2.60	2.87	3.06	0.33	0.39	0.36
2, 7, 12	Wet	Poor	2.92	2.47	2.49	3.41	2.12	2.70	0.42	0.39	0.39
3, 8, 14	Dry	Rich	4.06	3.51	2.91	5.70	3.78	3.35	0.42	0.45	0.51
5, 9, 15	Moist	Rich	3.87	2.95	2.85	5.68	3.35	3.50	0.38	0.46	0.49

Species abbreviations: bF balsam fir, bS black spruce, wS white spruce.
[x]Annual height increment was calculated for the 1989-1992 period.

3.3 Measurement of foliage variables

Measurement of the number of shoots, shoot length, and needle length occurred once a year, in the Fall following completion of tree growth. Measurements of needlefall of older needles that were produced in 1991 (1-year-old in the first treatment year) and foliage weight per age class were collected at the time of harvest (1994 or 1996). One sample branch was randomly selected from every second whorl on each of the 240 sample trees for detailed shoot and needle measurements. Twenty shoots were selected from each foliage age class on each sample branch and measured for shoot length to the nearest mm. Lengths of five needles from the middle one-third (Piene, 1983) of each of the 20 randomly selected shoots from each age class (1989-1996) were measured to the nearest mm. Number of current-year shoots per branch was counted for every whorl and interwhorl branch each year. Cumulative needlefall was estimated visually for each age-class along the main branch axis and each second-order branch (i.e., branching off the main branch axis) (Piene, 2003), using seven classes: 0-10%, 11-20%, 21-40%, 41-60%, 61-80%, 81-99%, and 100%. We only analyzed the needlefall of the 1991 foliage age class in this report. Mean shoot length and mean needle length were calculated per

sample branch and tree, and total number of current-year shoots per whorl and per tree were calculated by summing the shoots on each whorl and interwhorl branch. Average percent needlefall of the 1991 foliage was calculated for each branch and for each treated tree.

We destructively sampled two trees per treatment per species in 1994, and the remaining three trees per treatment were destructively sampled following completion of tree growth in 1996. For each tree, foliage was weighed fresh for all branches per whorl, and sample branches were clipped and combined by foliage age, separated into needles and twigs for each age class, dried at 65°C for 48 h, cooled in a desiccator and weighed to the nearest 0.01 g. Needle weight per tree by year was calculated.

3.4 Data analysis

Linear mixed-effects models (shown below, [1] and [2]) were used to test for the effects of site, cumulative defoliation (or defoliation treatment), and tree species on the number of shoots, shoot length, needle length, and needle weight per tree. The Maximum Likelihood fitting method was used to fit models. Number of shoots, shoot length, needle length, and needle weight were continuous response variables, while cumulative defoliation was treated as a continuous explanatory variable, and site, species, defoliation treatment, and bud destruction (i.e., comparison of 100%+bud treatment with 100%) were treated as categorical explanatory variables. Since we had repeated measurements over multiple years per tree, trees had random effects. During the defoliation period (1992-1994), 100% and 100%+bud treatments removed all current-year needles, thus we only analyzed the effects of 0% and 50% treatments on needle length and needle weight.

The 100%+bud treatment also removed all current-year shoots, thus it was also excluded in the analysis of defoliation effects on number of shoots and shoot length. During the recovery period (1995-1996), all four treatments were included in the analysis. Linear model [3] was used to compare the effects of the 100% and 100%+bud treatments in each recovery year. Since needlefall data were only collected at the time of harvest (1994 or 1996), there were no repeated measures on each tree, so a standard linear model [4] was used for the analysis of needlefall of older (1991 age class) foliage in the defoliation and recovery periods. Our full models were:

[1] defoliation period (1992-1994):

Number of shoots | Shoot length | Needle length | Needle weight

= Site x Species x Cumulative defoliation + (1|Tree)

[2] recovery period (1995-1996):

Number of shoots | Shoot length | Needle length | Needle weight

= Site x Species x Treatment x Time since recovery + (1|Tree)

[3] analysis comparing 100% and 100%+bud treatments in each recovery year:

Number of shoots | Shoot length | Needle length | Needlefall | Needle weight

= Site x Species x Bud destruction

[4] analysis of needlefall of 1991 foliage in defoliation or recovery period:

Needlefall = Site x Species x Cumulative defoliation (or Treatment),

where Site x Species x Cumulative defoliation (or Treatment) tested whether the effect of one of these variables depends (is conditional) on the level of one of the other variables. If the interaction terms (2-way and 3-way interactions) were not significant, then we removed them from the model and re-ran the reduced model. The number of shoots and

needle weight response variables were transformed (natural logarithm) after examining model residuals to correct for obvious deviations from normality. Then, visual inspection of the model residuals did not reveal any obvious deviations from homoscedasticity or normality via residual plots and Q-Q plots. Our null hypothesis was that no differences in number of shoots, shoot length, needle length, needlefall, or needle weight would be detected (at a significance level of ($\alpha = 0.05$) between different site types, species, and cumulative defoliation (or defoliation treatment). Post hoc Tukey's HSD tests were used to test for significant differences in number of shoots, shoot length, needle length, needlefall, and needle weight between site types, species, and cumulative defoliation (or defoliation treatment).

All data analyses were conducted using R 3.3.1 (R Development Core Team, 2016). The "lme4" package (Bates et al., 2019) was used to conduct the linear mixed-effects modeling analyses. The "MuMIn" package (Bartoń, 2019) was used for calculation of marginal (based on the fixed effects) and conditional R^2 values (incorporating random effects) of models. The "lsmeans" package (Lenth, 2018) was used for post hoc Tukey's HSD tests, and the "ggplot2" package (Wickham et al., 2019) was used to produce all graphs.

4. RESULTS

4.1 Defoliation period (1992-1994)

4.1.1 Number of shoots

Significant interactions for Site x Species ($F = 3.77$, $p = 0.001$), Site x Cumulative

defoliation ($F = 12.48$, $p < 0.001$), and Species x Cumulative defoliation ($F = 17.12$, $p < 0.001$) (Table 3A) indicate that the mean number of shoots per tree differed among site types and among species, but both depended upon cumulative defoliation. Marginal R^2 and conditional R^2 indicate that 49% and 82% of variance was explained by the fixed variables (site, species and cumulative defoliation) and by both the fixed and random variables (tree), respectively (Figure 3).

Post hoc HSD tests showed that there were positive trends of the number of shoots versus cumulative defoliation for 10 out of 12 species-site combinations (purple regression lines in Figure 3; all except 3D and 3J). Black spruce on the dry/rich site responded most strongly to cumulative defoliation (Figure 3G), with about 2.4 times more current-year shoots per tree with 300% defoliation than with no defoliation. Cumulative defoliation values of 100, 200, and 300% in the 100% treatment are equivalent to complete removal of one, two, and three age classes of needles, respectively. For example, two years of 50% defoliation treatment equates to 100% cumulative defoliation, the same as one year of 100% defoliation. Specific significant differences in number of shoots among sites (blue letters in Figure 3) included: balsam fir, rich sites > dry/poor site (means of 2210 versus 1300 current-year shoots/tree); black spruce, moist/rich site > wet/poor site (means of 4730 versus 2700 shoots/tree); and white spruce, dry/rich site > poor sites (3670 versus 2130 shoots/tree). Comparing tree species on all sites (red letters in Figure 3), black spruce had significantly (39-189%) more shoots than balsam fir on all sites and produced 89% and 85% more shoots than white spruce on the dry/poor and moist/rich sites, respectively. White spruce had significantly (41-53%) more shoots than balsam fir on dry site

Table 3. *ANOVA table showing the effects of species, site, cumulative defoliation (0%, 50%, 100% for number of shoots, shoot length, and needlefall; 0%, 50% for needle length and needle weight) on A) mean number of current-year shoots per tree, B) mean current-year shoot length per tree, C) mean current-year needle length per tree, D) mean needlefall of 1991 needles (1-year-old in the first year of defoliation treatments) per tree, and E) mean current-year needle weight per tree for the 240 sample trees during the defoliation period (1992-1994).*

Source of variation	**df**	**A) Mean number of current-year shoots/tree**		**B) Mean current-year shoot length /tree (mm)**		**C) Mean current-year needle length/tree (mm)**		**D) Mean needlefall of 1991 needles/tree (%)**		**E) Mean current-year needle weight/tree (g)**	
		F	***p***	***F***	***p***	***F***	***p***	***F***	***p***	***F***	***p***
Site	3	3.65	**0.013**	32.32	**< 0.001**	15.63	**< 0.001**	3.45	**0.024**	15.82	**< 0.001**
Species	2	51.64	**< 0.001**	16.07	**< 0.001**	93.29	**< 0.001**	2.31	0.110	0.55	0.579
Cumulative defoliation	1	143.21	**< 0.001**	60.17	**< 0.001**	0.83	0.364	3.03	0.088	14.23	**< 0.001**
Site x Species	6	3.77	**0.001**	8.76	**< 0.001**	2.82	**0.012**	0.78	0.587	1.94	0.079
Site x Cumulative defoliation	3	12.48	**< 0.001**	2.28	0.078	5.63	**< 0.001**	0.78	0.511	0.46	0.708
Species x Cumulative defoliation	2	17.12	**< 0.001**	20.43	**< 0.001**	6.73	**0.001**	0.18	0.982	0.13	0.876
Site x Species x Cumulative defoliation	6	1.79	0.100	1.87	0.084	1.44	0.200	0.20	0.975	1.04	0.400

p values ≤ 0.05 are indicated in bold font.
Site: four site types – dry/poor, wet/poor, dry/rich, and moist/rich.
Species: three host tree species - balsam fir, black spruce, and white spruce.

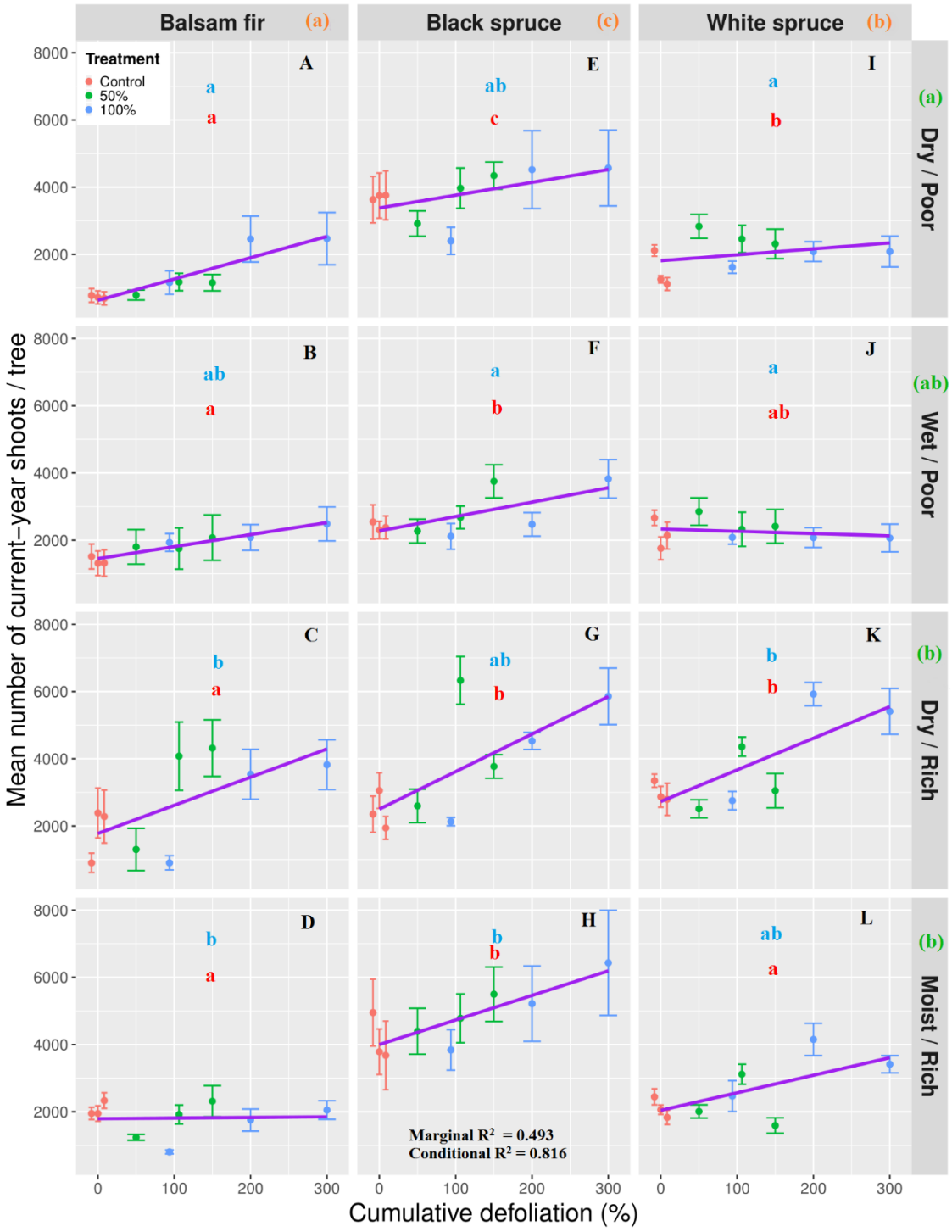


Figure 3. *Mean number of current-year (1992-1994) shoots for five trees in each of the four site classes, tree species and levels of cumulative defoliation. Trees were manually defoliated by 50% or 100% each year from 1992-1994. Blue letters indicate significant differences ($p < 0.05$) among sites within a given species; red letters indicate significant differences among species within a given site; orange letters in brackets indicate significant differences among species, for all sites combined; green letters in brackets indicate significant differences among sites, for all species combined.*

Overall, trees responded to increasing cumulative defoliation by increasing the number of shoots produced. Trees on rich sites produced 36% more shoots than on poor sites, especially on the dry/rich site (green letters in brackets in Figure 3). Balsam fir had the fewest shoots (mean of 1900 shoots/tree), only about one-half that on black spruce, which had 64% more shoots than white spruce except on the dry/rich site (orange letters in brackets in Figure 3).

4.1.2 Shoot length

Significant interactions for Site x Species ($F = 8.76$, $p < 0.001$; Table 3B) and Species x Cumulative defoliation ($F = 20.43$, $p < 0.001$; Table 3B) indicate that site and cumulative defoliation had significant effects on mean current-year shoot length per tree but that these effects depended on species. Marginal R^2 and conditional R^2 indicate that 48% and 77% of variance was explained by the fixed variables (site, species and cumulative defoliation) and by both the fixed and random variables (tree), respectively (Figure 4).

Post hoc HSD tests showed that mean shoot length declined with increasing cumulative defoliation for 9 out of 12 species-site combinations (purple trend lines in Figure 4), while shoot length increased only for balsam fir on two sites (Figure 4A and 4D). Mean shoot length of black spruce declined more strongly with increasing cumulative defoliation on dry sites (mean of 30% declines from 0 to 300% defoliation; purple trend lines in Figure 4E and 4G), while shoot length of white spruce decreased most in response to cumulative defoliation on rich sites (mean of 34% reduction from 0 to 300% defoliation; purple trend lines in Figure 4K and 4L) and on the wet/poor site

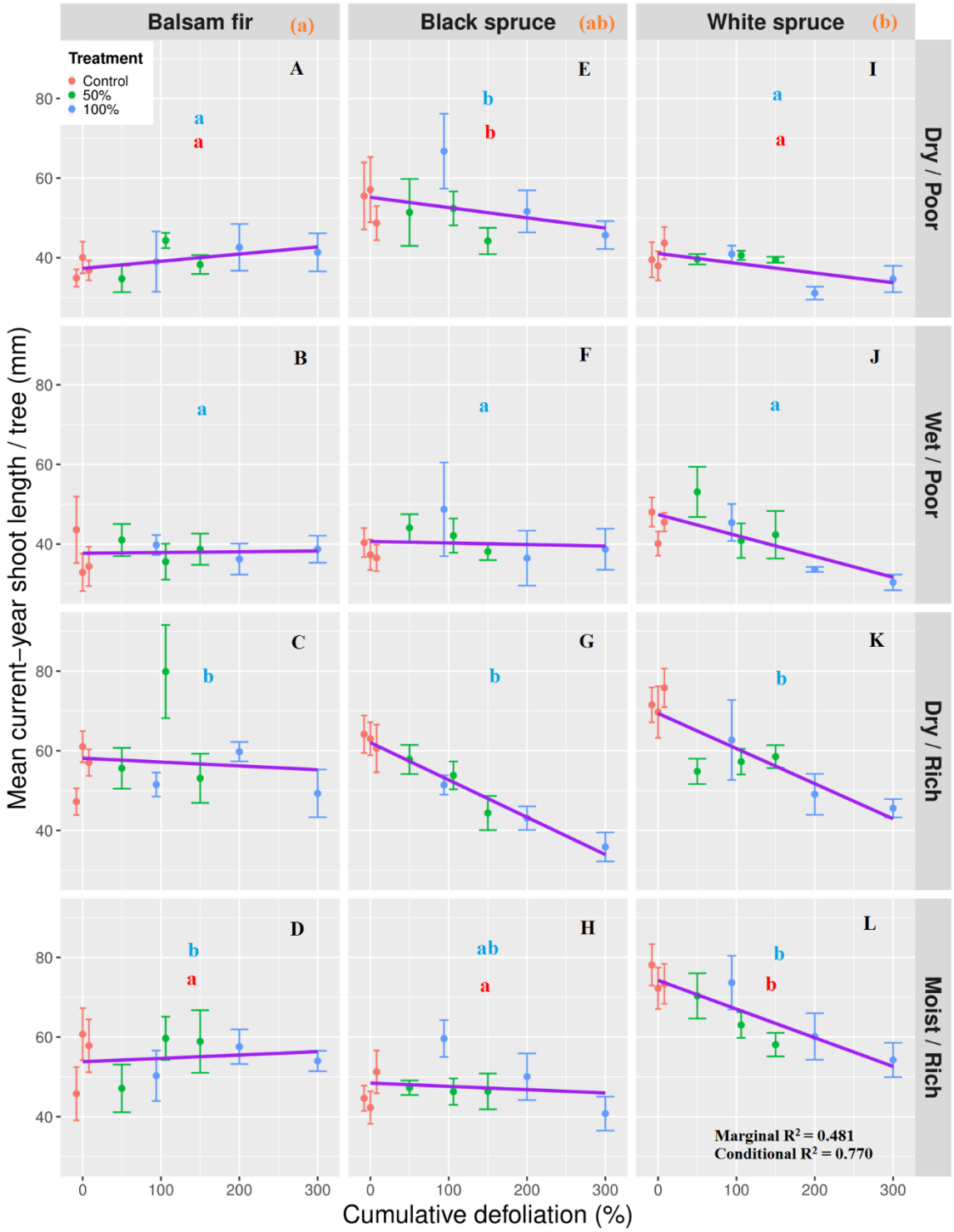


Figure 4. *Mean shoot length (mm) of current-year shoots for five trees in each of the four site classes, three species, and levels of cumulative defoliation. Trees were manually defoliated by 50% or 100% each year from 1992-1994. Blue letters indicate significant differences ($p < 0.05$) among sites within a given species; red letters indicate significant differences among species within a given site; orange letters in brackets indicate significant differences among species, for all sites combined.*

(32% declines from 0 to 300% defoliation; purple trend line in Figure 4J). For balsam fir and white spruce, trees had significantly longer shoots on rich than on poor sites (balsam fir: means of 56 versus 39 mm/tree; white spruce: 64 versus 40 mm/tree), while for black spruce, trees on dry sites had longer shoots than the wet/poor site (means of 53 versus 40 mm/tree, blue letters in Figure 4).

In general, increasing cumulative defoliation resulted in shorter shoot lengths of black spruce and white spruce (means of 54 versus 41 mm/tree for 0 versus 300% defoliation). However, the decline was not noticeable for balsam fir (means of 47 versus 46 mm/tree for 0 versus 300% defoliation). Trees on rich sites had about 15 mm (35%) longer shoots than on poor sites (Figure 4). White spruce had the longest shoots (mean of 57 mm/tree; orange letters in brackets in Figure 4), except on the dry/poor site where mean shoot length of black spruce was 36% longer than white spruce (red letters in Figure 4).

4.1.3 Needle length

Results showed that there were significant interactions for Site x Species ($F = 2.82$, $p = 0.012$), Site x Cumulative defoliation ($F = 5.63$, $p < 0.001$), and Species x Cumulative defoliation ($F = 6.73$, $p = 0.001$) (Table 3C). Marginal R^2 and conditional R^2 indicate that 70% and 92% of variance was explained by the fixed variables (site, species and cumulative defoliation) and by both the fixed and random variables (tree), respectively (Figure 5).

Post hoc HSD tests showed that for balsam fir, trees on rich sites had longer needles than on poor sites (means of 14.1 versus 11.8 mm/tree), while for white spruce, only trees

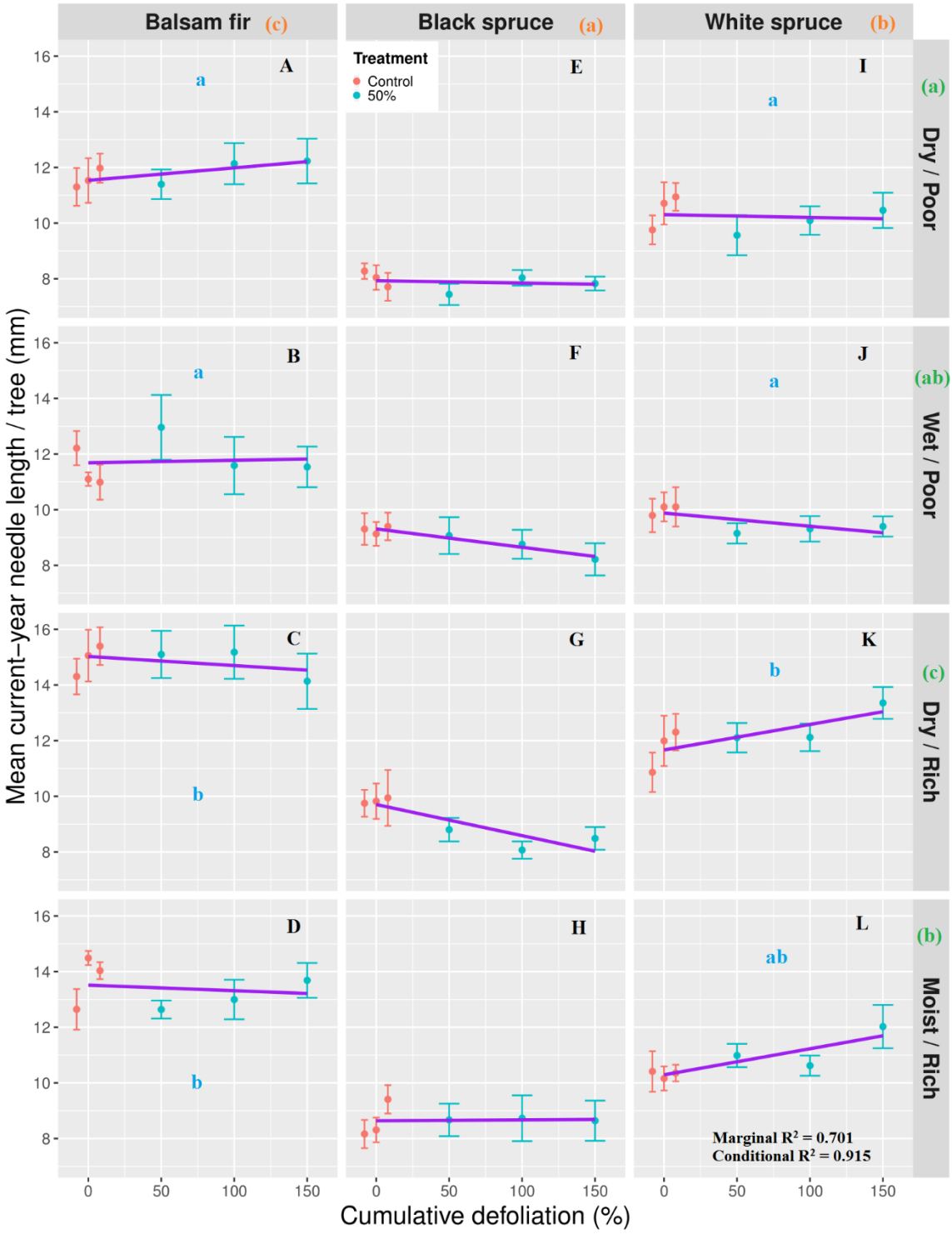


Figure 5. *Mean needle length (mm) of current-year shoots per tree for five trees for each of the four site classes, three species, and levels of cumulative defoliation (control and 50%). Blue letters indicate significant differences ($p < 0.05$) among sites within a given species; orange letters in brackets indicate significant differences among species, for all site combined; green letters in brackets indicate significant differences among sites, for all species combined.*

on the dry/rich site had longer needles than on poor sites (12.1 versus 10.0 mm/tree, blue letters in Figure 5). There were no significant differences of mean needle length among sites for black spruce.

In summary, cumulative defoliation had no significant effect on mean length of current-year needles. Among the three tree species, balsam fir had 22% longer mean current-year needle length than white spruce, which had 23% longer mean needles than black spruce (means of 13.1 versus 10.7 versus 8.7 mm/tree; orange letters in brackets in Figure 5). Trees on rich sites had 15% longer needles than poor sites, especially for balsam fir and white spruce (green letters in brackets in Figure 5).

4.1.4 Needlefall

Mean needlefall of 1991 foliage was only significantly affected by site ($F = 3.45$, $p = 0.024$; Table 3D) during the defoliation treatment years (i.e., by 1994, when the 1991 needles were 3 years old). Trees on the moist/rich site lost the least 3-year-old needles (about 16%, green letters in brackets in Figure 6), while mean needlefall of 1991 foliage on the dry/poor site was about 29%. No significant differences were found among cumulative defoliation treatments or among species.

A similar analysis was completed on the mean needlefall of the 1989 and 1990 foliage. Mean needlefall of 1989 and 1990 foliage were significantly affected by site (1989: $F = 11.66$, $p < 0.001$; 1990: $F = 10.41$, $p < 0.001$) and species (1989: $F = 5.58$, $p = 0.007$; 1990: $F = 4.71$, $p = 0.014$). Trees on rich sites had an average of 21% lower needlefall of 1989 and 1990 foliage than on poor sites. White spruce had 14% higher needlefall of 1989 and 1990 foliage than the other two species. No significant differences

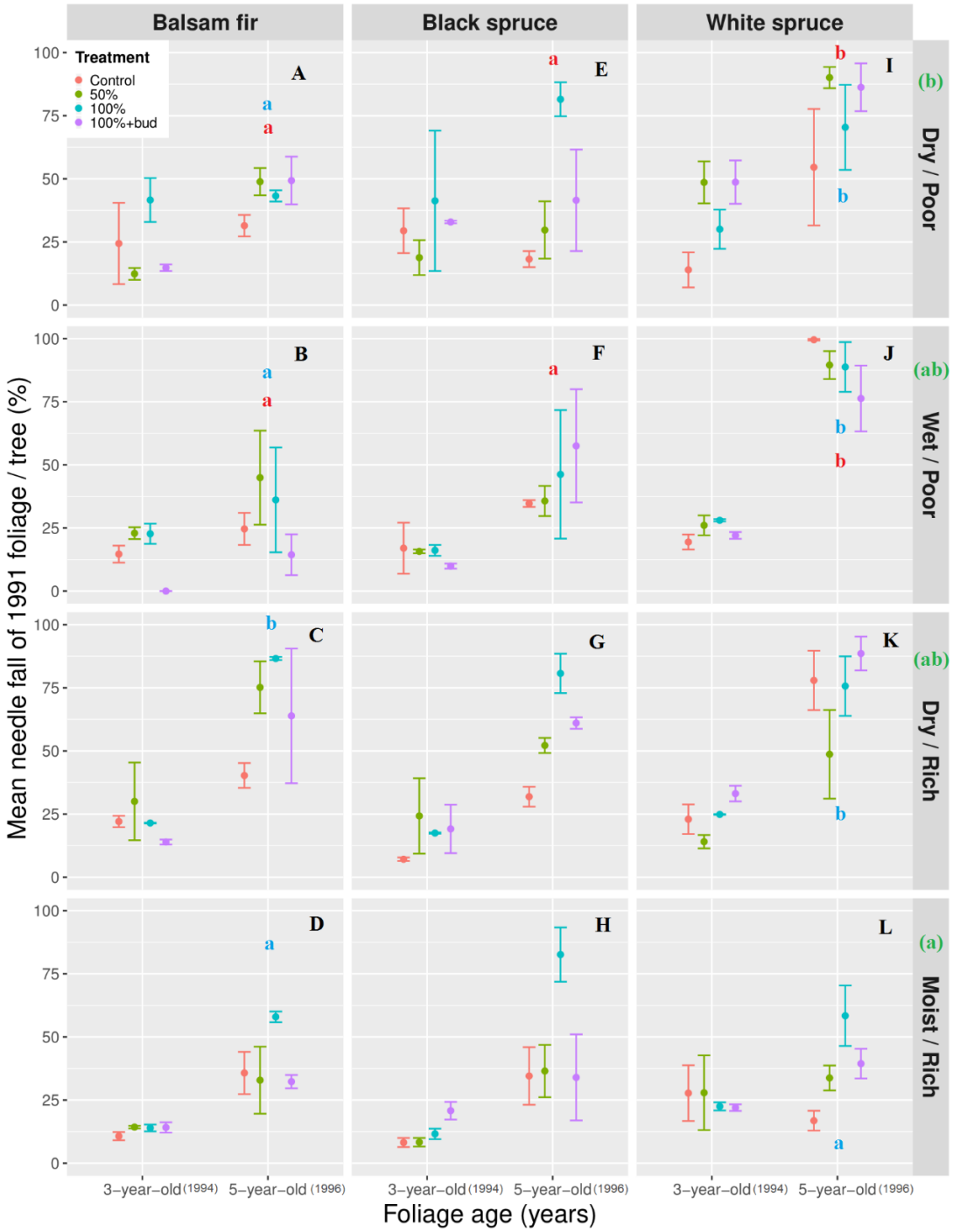


Figure 6. *Mean needlefall of foliage produced in 1991 (%/tree) in 1994 (n=5) and 1996 (n=3) for each of the four site classes, three species, and four defoliation treatments. Needles produced in 1991 were 1-year-old in the first treatment year (1992), 3-years-old in the last treatment year (1994) and 5-years-old in 1996, the second recovery year. Green letters in brackets indicate significant differences ($p < 0.05$) of 3-year-old foliage among sites, for all species combined. Blue letters indicate significant differences ($p < 0.05$) of 5-year-old foliage among sites within a given species during the recovery period; red letters indicate significant differences ($p < 0.05$) of 5-year-old foliage among species within a given site during recovery period.*

were found among cumulative defoliation treatments.

4.1.5 Needle weight

For the defoliation period (1992-1994), we only analyzed the effects of the control versus 50% defoliation on the current-year needle weight per tree (Table 3E) as all needles were removed by the 100% and 100%+bud treatments. Results showed that there were no significant interactions, but mean current-year needle weight per tree was significantly affected by site ($F = 15.82$, $p < 0.001$) and by cumulative defoliation ($F = 14.23$, $p < 0.001$; Table 3E). Marginal R^2 and conditional R^2 indicate that 32% and 79% of variance was explained by the fixed variables (site, species and cumulative defoliation) and by both the fixed and random variables (tree).

It was obvious that defoliation treatment would decrease needle weight in all 12 species-site combinations (Figure 7, years D1-D3), because the treatment removed 50% of needles on every current-year shoot on the trees. Trees on rich sites had significantly greater current-year needle weight than on poor sites (means of 620 versus 270 g/tree). Trees in the 50% treatment had 32-57% greater current-year needle weight per tree than trees in the control in the third year of defoliation among sites.

Overall, increasing cumulative defoliation from 0% to 150% resulted in 49-57% reductions of mean needle weight of current-year needles. Trees on rich sites had 142-144% greater mean current-year needle weight per tree, but responded to cumulative defoliation more strongly than on poor sites (49-57% versus 32-48% reductions; Figure 7).

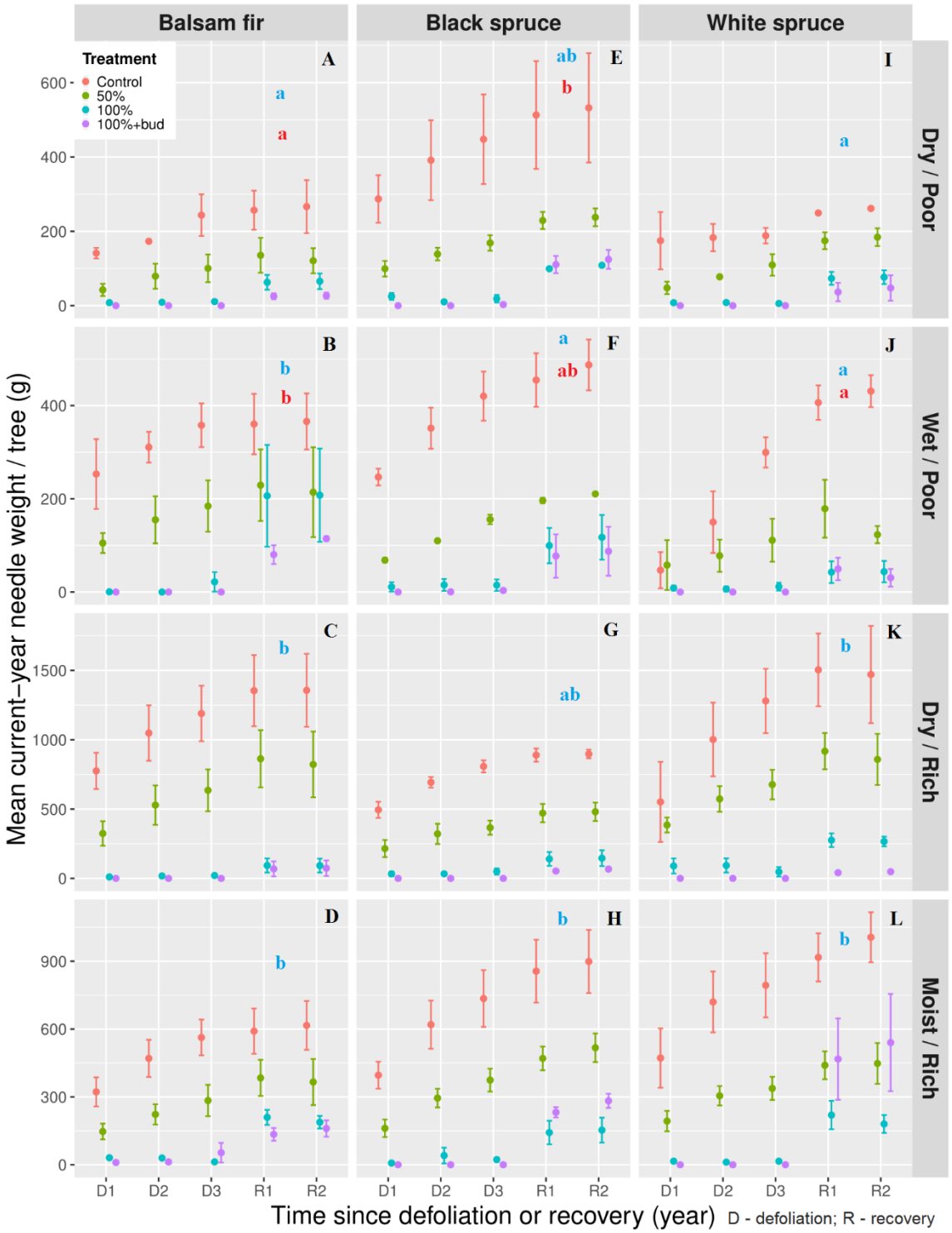


Figure 7. *Mean current-year needle weight (g/tree) from 1992-1994 (treatment years D1-D3) and 1995-1996 (recovery years R1-R2) for three trees (harvested in 1996) in each of the four site classes, three species, and four defoliation treatments. Blue letters indicate significant differences ($p < 0.05$) among sites within a given species during the recovery period; red letters indicate significant differences ($p < 0.05$) among species within a given site during recovery period.*

4.2 Recovery period (1995-1996)

4.2.1 Number of shoots

During the recovery years 1995-1996, mean shoot production was significantly affected by a 4-way interaction for Site x Species x Treatment x Time since recovery (F = 5.39, $p < 0.001$; Table 4A). This indicated that during the recovery period, mean number of current-year shoots per tree differed among sites, species, and treatments, and this depended on the time since recovery (i.e., first and second years of recovery).

Black spruce on the moist/rich site had substantially more current-year shoots, especially trees in 100% treatment (nearly 12500 shoots/tree) than all other species-site-treatment values (Figure 8H). In other species-site combinations, most trees had fewer than 5000 shoots/tree, except for balsam fir in the 50% treatment on the dry/rich site in the first recovery year, which had 5740 shoots/tree (Figure 8C). In the first recovery year, trees defoliated of 50% and 100% of needles for 3 years produced 6% and 27% more current-year shoots than control trees, respectively, while 100%+bud treatment had 47% fewer current-year shoots than control trees. In the second recovery year, 50%, 100%, and 100%+bud treatment trees had 12%, 79% and 12% more current-year shoots than the control (Figure 8).

Post hoc HSD tests showed black spruce had significantly (168%) more current-year shoots per tree in the recovery years than balsam fir and white spruce, except on the dry/rich site (red letters in Figure 8). Trees on rich sites produced 49% more shoots per tree in the recovery years than on poor sites in most species-site combinations (blue letters in Figure 8C, 8H, 8K, and 8L).

Overall, trees undergoing the 100% defoliation treatment for 3 years produced 30-

Table 4. *ANOVA table showing the effects of species, site, defoliation treatment, and time since recovery on A) mean number of current-year shoots per tree, B) mean current-year shoot length per tree, C) mean current-year needle length per tree, D) mean needlefall of 1991 needles (1-year–old in the first year of defoliation treatments) per tree, and E) mean current-year needle weight per tree for the 144 sample trees during the recovery period (1995-1996).*

Source of variation	df	A) Mean number of current-year shoots/tree		B) Mean current-year shoot length /tree (mm)		C) Mean current-year needle length/tree (mm)		D) Mean needlefall of 1991 needles/tree (%)		E) Mean current-year needle weight/tree (g)	
		F	***p***	***F***	***p***	***F***	***p***	***F***	***p***	***F***	***p***
Site	3	14.10	**< 0.001**	89.12	**< 0.001**	14.54	**< 0.001**	8.19	**< 0.001**	31.56	**< 0.001**
Species	2	69.64	**< 0.001**	11.93	**< 0.001**	257.03	**< 0.001**	18.63	**< 0.001**	3.29	**0.040**
Treatment	3	25.37	**< 0.001**	23.43	**< 0.001**	2.71	**0.047**	11.53	**< 0.001**	110.80	**< 0.001**
Time since recovery	1	18.96	**< 0.001**	243.76	**< 0.001**	55.17	**< 0.001**	/	**/**	6.79	**0.010**
Site x Species	6	8.80	**0.001**	6.49	**< 0.001**	5.02	**< 0.001**	7.75	**< 0.001**	5.80	**< 0.001**
Site x Treatment	9	4.06	**< 0.001**	3.35	**< 0.001**	1.26	0.263	1.25	0.276	5.99	**< 0.001**
Species x Treatment	6	2.30	**0.038**	7.21	**< 0.001**	7.78	**< 0.001**	3.04	**< 0.001**	0.87	0.517
Site x Time since recovery	3	35.10	**< 0.001**	19.06	**< 0.001**	42.86	**< 0.001**	/	/	0.33	0.804
Species x Time since recovery	2	18.20	**< 0.001**	41.13	**< 0.001**	5.62	**0.004**	/	/	4.05	**0.019**
Treatment x Time since recovery	3	91.43	**< 0.001**	18.06	**< 0.001**	71.59	**< 0.001**	/	/	7.48	**< 0.001**
Site x Species x Treatment	18	2.71	**< 0.001**	2.40	**0.002**	1.28	0.209	1.12	0.350	1.67	0.052
Site x Species x Time since recovery	6	17.02	**< 0.001**	13.83	**< 0.001**	18.71	**< 0.001**	/	/	1.93	0.079
Site x Treatment x Time since recovery	9	6.95	**< 0.001**	1.67	0.102	6.70	**< 0.001**	/	/	1.23	0.279
Species x Treatment x Time since recovery	6	8.98	**< 0.001**	2.97	**0.009**	0.69	0.661	/	/	1.62	0.148
Site x Species x Treatment x Time since recovery	18	5.39	**< 0.001**	2.61	**< 0.001**	2.30	**0.004**	/	/	1.36	0.161

p values ≤ 0.05 are indicated in bold font.

Site: four site types – dry/poor, wet/poor, dry/rich, and moist/rich.

Species: three host tree species - balsam fir, black spruce, and white spruce.

Treatment: four defoliation treatments – 0%, 50%, 100% removal of current-year needles, and 100%+ bud (removal of all current-year shoots).

Time since recovery: one year since treatment (1995), and two years since treatment (1996).

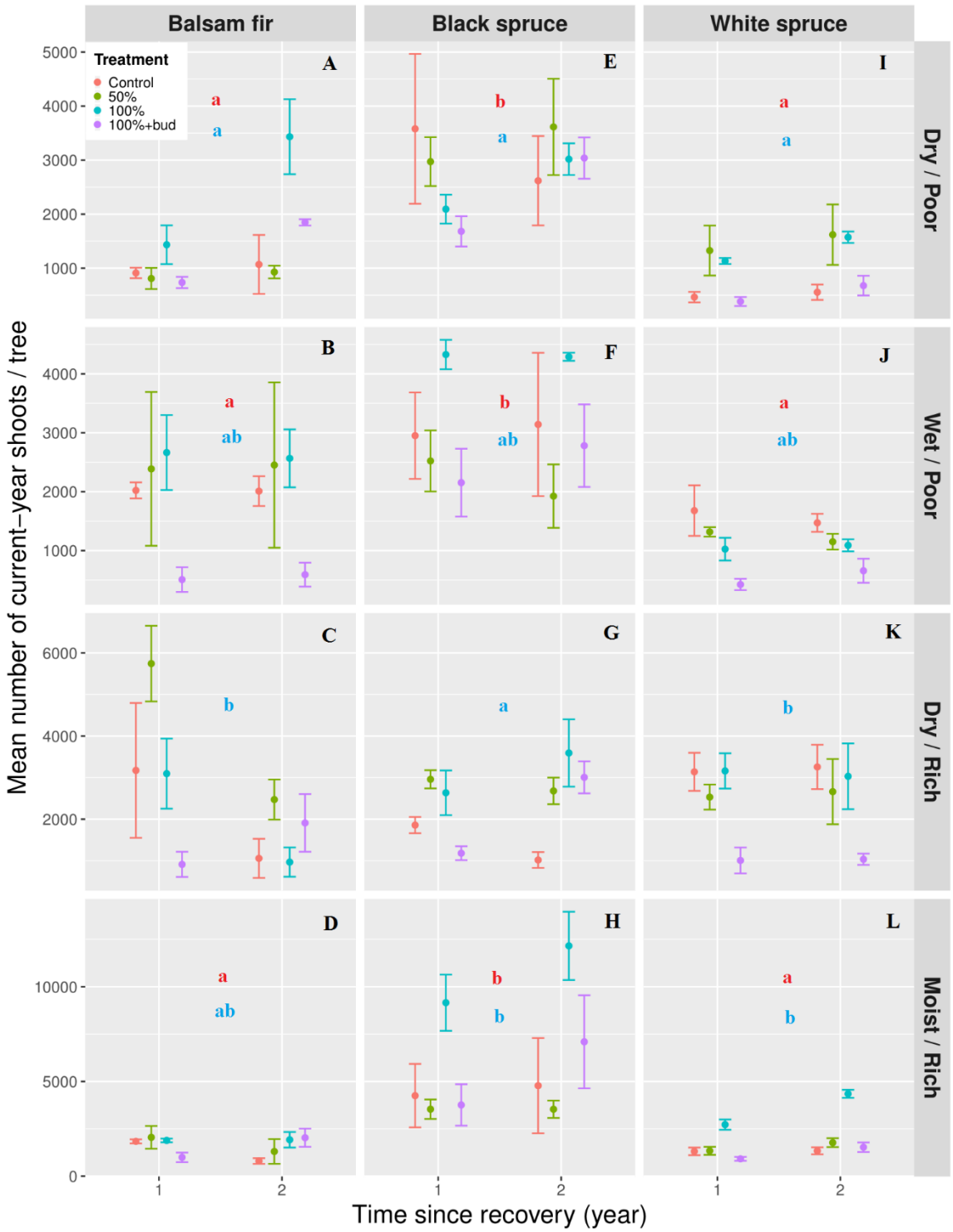


Figure 8. *Mean number of current-year shoots produced per tree in two recovery years for three trees in each of the four site classes, three species, and four defoliation treatments. Defoliation treatments ended in 1994, and the 144 sample trees were allowed to recover in 1995-1996. Blue letters indicate significant differences ($p < 0.05$) among sites within a given species; red letters indicate significant differences among species within a given site.*

167% more shoots than control trees in the 2-year recovery period for 8 out of 12 species-site combinations, especially for black spruce on wet sites (Figure 8F and 8H). The 50% defoliation treatment also stimulated trees to produce 6-189% more shoots than control trees for 7 out of 12 species-site combinations, especially for balsam fir on the dry/rich site (means of 4110 versus 2120 shoots/tree; Figure 8C) and for white spruce on the dry/poor site (means of 1470 versus 510 shoots/tree; Figure 8I). The 100%+bud removal treatment led to an average of 20% fewer shoots than the control treatment during the recovery period. Trees on rich sites produced 49% more shoots per tree in the recovery years than on poor sites.

4.2.2 Shoot length

A significant 4-way interaction for Site x Species x Treatment x Time since recovery occurred again for mean current-year shoot length per tree during recovery period (F = 2.61, $p < 0.001$; Table 4B), which indicated that mean current-year shoot length per tree differed significantly among sites, species, and treatments, and these depended on the time since recovery.

Compared to the control, the 50% defoliation treatment resulted in 7-31% reductions of mean shoot length per tree during the 2-year recovery period for 10 out of 12 species-site combinations (Figure 9, except 9A and 9B). The 100% defoliation treatment decreased mean shoot length per tree by 15-45% during the 2-year recovery period for 6 out of 12 species-site combinations (Figure 9C, 9D, 9G, 9J, 9K, and 9L), especially on rich sites. However, for balsam fir on poor sites, the 100% defoliation treatment increased mean shoot length by 19-20% over the control trees during the recovery period (Figure

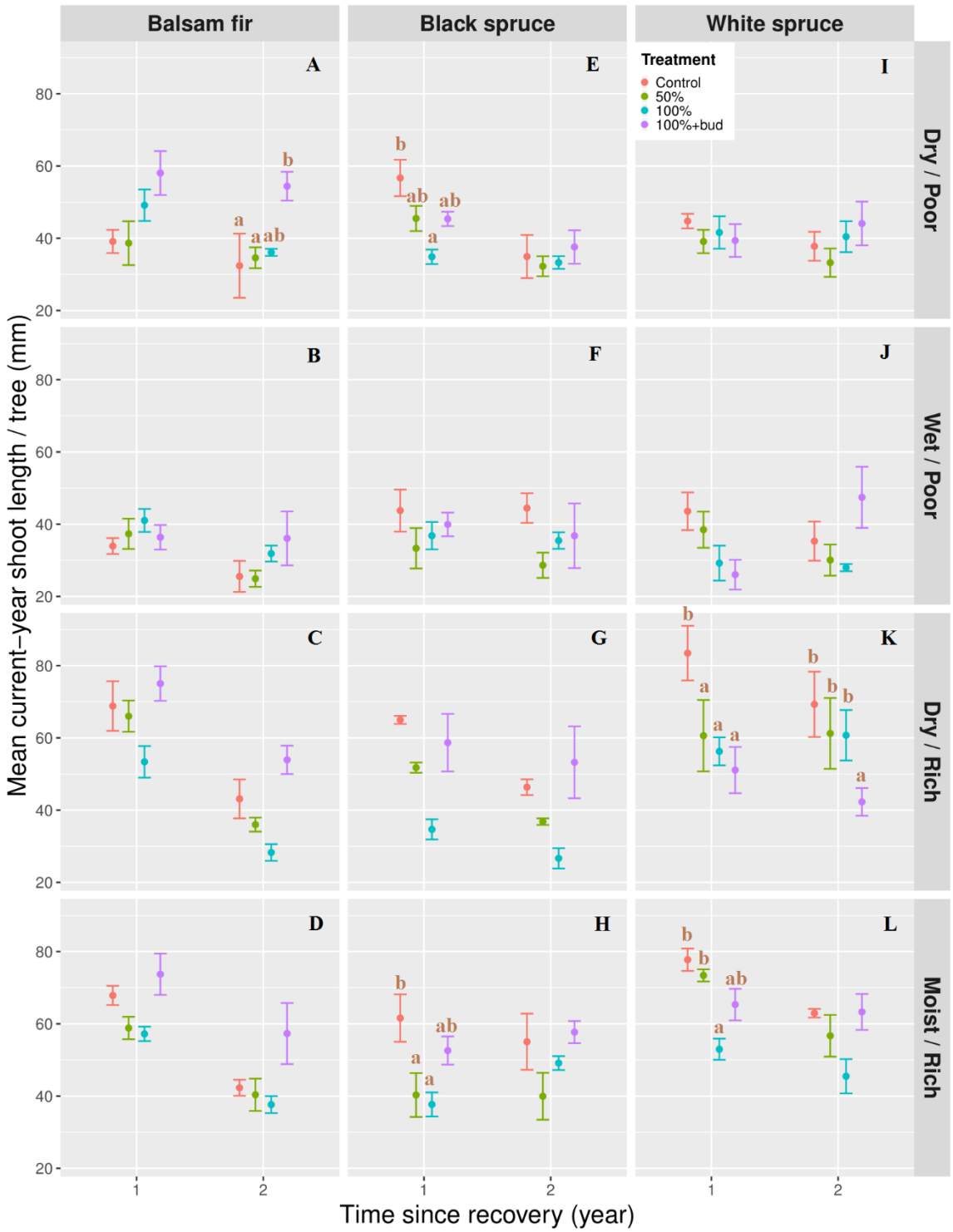


Figure 9. *Mean length of current-year shoots (mm/tree) for three trees in each of the four site classes, three species, and four defoliation treatments. Defoliation treatments stopped in 1995, 144 trees were allowed to recover from 1995-1996. Brown letters indicate significant differences ($p < 0.05$) among treatments within a given species, site, and year.*

9A and 9B).

Post hoc HSD tests showed that in the first year of recovery, mean shoot length of black spruce in the control had significantly (62%) longer shoots than in the 100% treatment on the dry/poor, and (53-63%) longer shoots than in the 50% and 100% treatments on the moist/rich site (brown letters in Figure 9E and 9H); for white spruce, control trees had significantly (47-48%) longer shoots than 100% treatment trees on rich sites (brown letters in Figure 9K and 9L). In the second year of recovery, balsam fir in the 100%+bud treatment had an average of 57% longer shoots than other treatments (brown letters in Figure 9A); for white spruce, trees in the 100%+bud treatment had an average of 34% shorter shoots than other treatments on the dry/rich site (brown letters in Figure 9K).

In summary, for black spruce and white spruce, mean shoot length decreased with increasing defoliation treatment, especially on rich sites, while mean shoot length of balsam fir trees increased with defoliation treatment on poor sites. Balsam fir in the 100%+bud treatment had 20-56% longer shoots than in the control, except in the first recovery year on the wet/poor site, while for black spruce and white spruce, bud destruction led to an average of 13% shorter shoots in most species-site combinations. Trees on rich sites produced 29-57% longer shoots than on poor sites (Figure 9).

4.2.3 Needle length

Mean needle length also had a significant 4-way interaction for Site x Species x Treatment x Time since recovery during the recovery period ($F = 2.30$, $p = 0.004$; Table 4C). Thus, site, species and treatment had significant effects on mean needle length per

tree, but all effects depended on time since recovery.

Post hoc HSD tests showed that in the first recovery year, balsam fir trees in the 100%+bud treatment had significantly (35-42%) longer current-year needles than control and 50% treatment trees on the dry/poor site, and significantly (32-34%) longer needles than control, 50%, and 100% treatment trees on the most/rich site (brown letters in Figure 10). In the first recovery year, balsam fir had significantly (54% and 79%) longer current-year needles than black spruce and white spruce on the moist/rich site; in other three sites, balsam fir had significantly (17-29%) longer needles than white spruce, which had significantly (18-61%) longer needles than black spruce (red letters in Figure 10). In the second recovery year, white spruce trees in the 50% and 100% treatment had significantly (44-62%) longer needles than 100%+bud treatment trees (brown letters in Figure 10). On the wet/poor and dry/rich site, balsam fir had significantly (54% and 37%) longer needles than black spruce and white spruce; on the dry/poor and moist/rich sites, balsam fir had significantly (25-33%) longer needles than white spruce, which had significantly (36-39%) longer current-year needles than black spruce (purple letters in Figure 10). In the first recovery year, balsam fir trees on the moist/rich site had 12-20% longer needles than on poor sites; while white spruce trees on the dry/poor site had 18% longer current-year needles than on the moist/rich site (blue letters in Figure 10). In the second recovery year, balsam fir trees on the dry/rich site had 22% longer needles than on the dry/poor site, trees on which had 16% longer needles than on the wet/poor site; black spruce trees on the dry/rich site had 22-36% longer needles than on poor sites; white spruce trees on rich sites had 20-27% longer needles than on the wet/poor site (green letters in Figure 10).

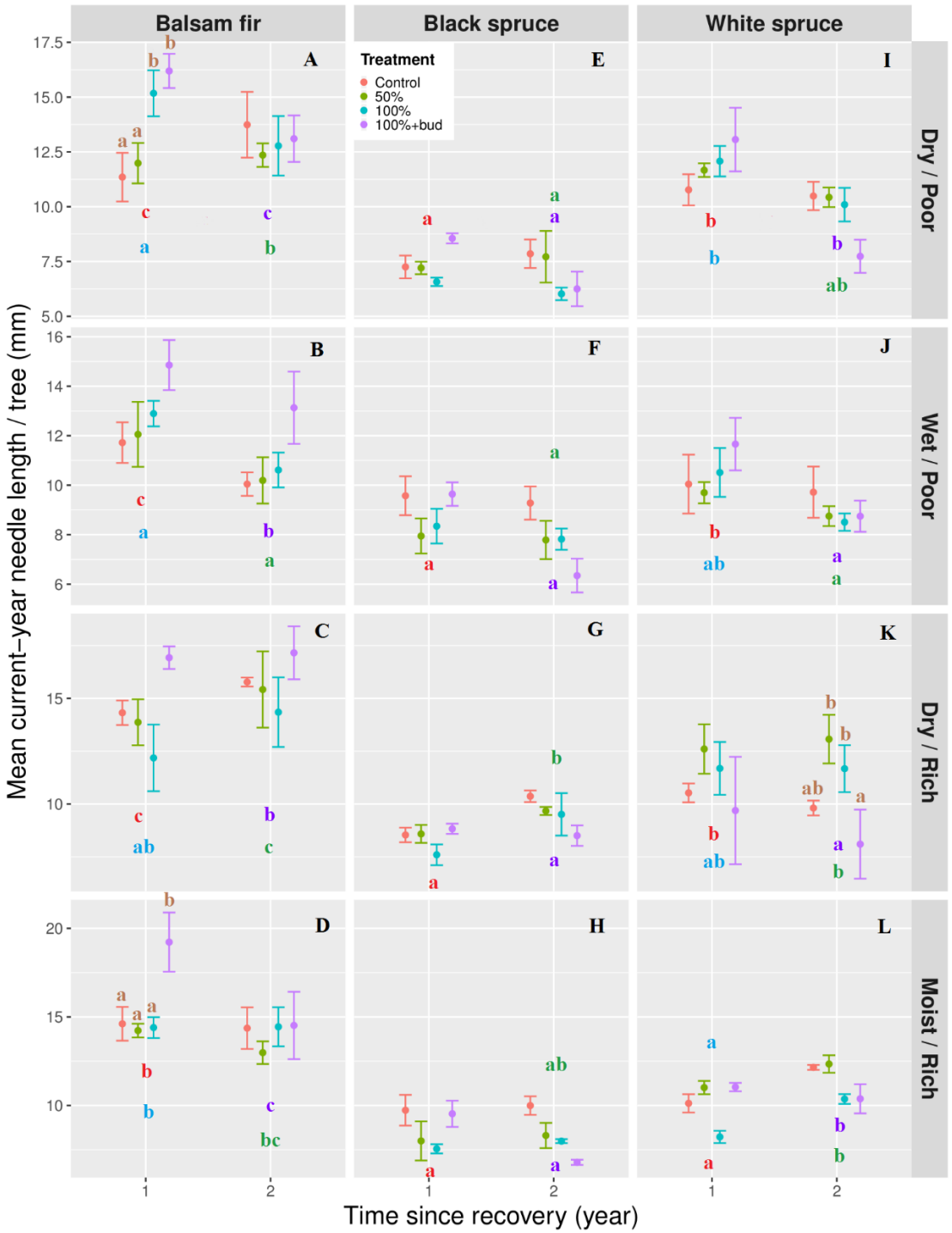


Figure 10. *Mean needle length of current-year shoots (mm/tree) for three trees in each of the four site classes, four defoliation treatments, and three species. Defoliation treatments stopped in 1995, 144 trees were allowed to recover from 1995-1996. Brown letters indicate significant differences ($p < 0.05$) among treatments within a given species, site, and year; blue letters indicate significant differences among sites within a given species in year 1; green letters indicate significant differences among sites within a given species in year 2; red letters indicate significant differences among species within a given site in year 1; and purple letters indicate significant differences among species within a given site in year 2.*

In summary, balsam fir had 48% longer mean current-year needle length per tree than black spruce and white spruce. Trees on rich sites produced 17% longer mean current-year needle length of balsam fir than on poor sites. Treatment had no significant effects on needle length during the 2-year recovery period for most species-site combinations.

4.2.4 Needlefall

Significant interactions Site x Species ($F = 7.75$, $p < 0.001$) and Species x Treatment ($F = 3.04$, $p < 0.001$; Table 4D) indicated that mean needlefall of 1991 foliage differed among sites and treatments, and both depended on species.

Post hoc HSD tests showed that for balsam fir, 1991 foliage had significantly (22-35%) more needlefall on the dry/rich site than on other sites (blue letters in Figure 6), especially 100% treatment trees. However, comparing sites for white spruce, mean needlefall of 1991 foliage, by 1996, on the moist/rich site was significantly (36-52%) lower than on other sites (blue letters in Figure 6). On poor sites, mean needlefall of 5-year-old foliage of white spruce was about twice of that of balsam fir and black spruce (red letters in Figure 6). For white spruce, no significant differences in mean needlefall of 5-year-old foliage were found among control, 50% and 100% treatments; while for balsam fir, trees in the 100% treatment had 22% higher mean needlefall of 5-year-old foliage than in the control (Figure 6); for black spruce, mean needlefall of 5-year-old foliage was 45% higher than that of trees in the control and 50% treatments (Figure 6).

Overall, 5-year-old foliage of the 100% treatment trees had 14-27% greater mean needlefall than trees in the other treatments. White spruce had 37-45% greater mean

needlefall of 5-year-old foliage than balsam fir and black spruce on poor sites. Balsam fir growing on the dry/rich site had the greatest mean needlefall of 1991 foliage (about 66% / tree). Mean needlefall of 1991 foliage of white spruce was lowest on the moist/rich site (about 37% / tree).

Results of similar analyses of needlefall of 1989 and 1990 foliage showed that defoliation treatment affected needlefall of 6- and 7-year-old foliage (1989: $F = 4.24$, $p = 0.007$; 1990: $F = 4.16$, $p = 0.008$). However, needlefall of 6- and 7-year-old foliage was close to 100% in most species-site combinations, which reflected senescence and dropping off of older needles.

4.2.5 Needle weight

Significant interactions for Site x Species ($F = 5.80$, $p < 0.001$), Site x Treatment ($F = 5.99$, $p < 0.001$), Species x Time since recovery ($F = 4.05$, $p = 0.019$), and Treatment x Time since recovery ($F = 7.48$, $p < 0.001$) indicated that mean current-year needle weight per tree differed among species and treatments, and both depended on site type and time since recovery (Table 4E).

During the 2-year recovery period (R1 and R2 in Figure 7), trees on rich sites had an average of 172% greater needle weight than trees on poor sites (means of 490 versus 180 g/tree; Figure 7), especially for the control and 50% treatment trees on the dry/rich site for balsam fir (mean of 1100 g/tree; Figure 7C) and white spruce (mean of 1190 g/tree; Figure 7K). It was clear that defoliation treatment had an increasing negative effect on mean current-year needle weight per tree (means of 730 versus 140 g/tree from 0 to 100% treatment). In the first recovery year, trees in the 50%, 100%, and 100%+bud

treatment had 30-57%, 43-93%, and 49-97% reductions of current-year needle weight compared to control trees across species and sites. In the second recovery year, trees in the 50%, 100%, and 100%+bud treatment had 30-71%, 43-82%, and 46-97% reductions of current-year needle weight compared to control trees (Figure 7).

Post hoc HSD tests showed that on the dry/poor site, black spruce had the greatest mean current-year needle weight, and on the wet/poor site, balsam fir had 31% greater needle weight than white spruce (means of 210 versus 160 g/tree; red letters in Figure 7). For balsam fir, trees on the dry/poor site had 49-82% reductions of mean needle weight than on other sites (blue letters in Figure 7A); for black spruce, mean needle weight on the moist/rich site was 100% greater than on the wet/poor site; for white spruce, trees had 300% greater needle weight on rich sites than on poor sites (blue letters in Figure 7).

In general, mean current-year needle weight per tree in the recovery years still decreased in response to increasing defoliation treatment. The 50% treatment resulted in 30-57% and 30-71% reductions of current-year needle weight per tree in the first and second recovery years. Trees in the 100% and 100%+bud treatments had greater reductions in the first recovery year (43-93% and 49-97%), and still recovered slowly in the second year (43-82% and 46-97%). Trees on rich sites produced 172% greater needle weight than on poor sites in the recovery years. Black spruce had 47-59% greater mean current-year needle weight per tree on poor sites than the other two species (Figure 7), while white spruce had 25-38% greater needle weight per tree than the other two species on rich sites (Figure 7).

4.3 Effects of bud destruction on foliage production

Because the 100%+bud treatment also destroyed all current-year buds, analysis comparing the 100% and 100%+bud treatments in each recovery year was conducted to determine the effects of bud destruction on foliage production. Number of current-year shoots per tree in the recover years for the 100% and 100%+bud treatments showed that there were significant interactions for Site x Species ($F = 6.26$, $p < 0.001$ in 1995; $F = 2.98$, $p = 0.034$ in 1996) and Species x Bud destruction ($F = 3.23$, $p = 0.043$ in 1995; $F = 4.15$, $p = 0.018$ in 1996); and in the second recovery year, the Site x Bud destruction interaction was also significant ($F = 2.98$, $p = 0.034$; Table 5A). This indicated that site and the bud destruction treatment (i.e., 100%+bud removal) had significant effects on mean number of current-year shoots per tree 1 and 2 years following the treatment, and both depended on species. In the second recovery year, mean number of shoots also differed among sites, which depended on bud destruction treatment. Post hoc HSD tests showed that in the first recovery year, trees in the 100% defoliation treatment produced significantly (24-424%) more shoots per tree than trees in the 100%+bud removal treatment across sites and species (Figure 8). In the second recovery year, only white spruce 100% treatment trees had significantly (66-193%) more shoots per tree than 100%+bud trees (Figure 8).

Comparison of results of mean current-year shoot length per tree for 100% and 100%+bud treatment trees showed that in the first year of recovery, Site x Species ($F = 4.05$, $p < 0.001$) and Species x Bud destruction interactions ($F = 6.62$, $p = 0.002$) were significant (Table 5B); in the second year of recovery, the Site x Species x Bud destruction interaction was significant ($F = 4.27$, $p < 0.001$; Table 5B), which was caused by species (the Site x Bud destruction interaction was not significant). Thus, mean shoot

Table 5. *ANOVA of effects of species, site, and bud destruction (100% versus 100%+bud) on A) mean number of current-year shoots per tree, B) mean current-year shoot length per tree, C) mean current-year needle length per tree, D) mean needlefall of 1991 needles (1-year–old in the first year of defoliation treatments) per tree, and E) mean current-year needle weight per tree for the 72 sample trees during the recovery period (1995-1996).*

Source of variation	df	A) Mean number of current-year shoots/tree				B) Mean current-year shoot length /tree (mm)				C) Mean current-year needle length/tree (mm)				D) Mean needlefall of 1991 needles/ tree (%)		E) Mean current-year needle weight/tree (g)			
		1995		1996		1995		1996		1995		1996		1996		1995		1996	
		F	***p***	***F***	***p***	***F***	***p***	***F***	***p***	***F***	***p***	***F***	***p***	***F***	***p***	***F***	***p***	***F***	***p***
Site	3	15.14	**< 0.001**	3.58	**0.016**	44.44	**< 0.001**	25.17	**< 0.001**	1.57	0.200	23.54	**< 0.001**	3.76	**0.017**	11.07	**< 0.001**	11.34	**< 0.001**
Species	2	41.20	**< 0.001**	29.66	**< 0.001**	6.48	**0.002**	12.18	**< 0.001**	164.36	**< 0.001**	140.70	**< 0.001**	8.47	**< 0.001**	1.19	0.308	1.77	0.175
Bud	1	81.35	**< 0.001**	2.98	0.087	0.81	0.369	24.52	**< 0.001**	31.69	**< 0.001**	5.38	**0.022**	7.50	**0.009**	58.79	**< 0.001**	49.99	**< 0.001**
Site x Species	6	6.26	**< 0.001**	4.01	**0.001**	4.05	**< 0.001**	3.80	**0.002**	4.81	**< 0.001**	3.55	**0.003**	2.67	**0.026**	1.78	0.109	2.18	0.050
Site x Bud	3	2.98	**0.034**	2.55	0.059	0.93	0.426	0.79	0.500	1.44	0.235	0.96	0.416	0.63	0.598	4.80	**0.003**	4.67	**0.004**
Species x Bud	2	3.23	**0.043**	4.15	**0.018**	6.62	**0.002**	4.87	**0.009**	8.74	**< 0.001**	12.15	**< 0.001**	2.15	0.129	0.82	0.442	0.87	0.423
Site x Species x Bud	6	0.93	0.478	1.53	0.173	0.70	0.653	4.27	**< 0.001**	1.05	0.398	1.22	0.300	0.73	0.627	0.44	0.851	0.71	0.641
Residuals	118																		

p values ≤ 0.05 are indicated in bold font.

Site: four site types – dry/poor, wet/poor, dry/rich, and moist/rich.

Species: three host tree species - balsam fir, black spruce, and white spruce.

Bud: bud destruction – 100% (no), and 100%+bud (yes).

length of 100% and 100%+bud treatment trees differed among sites and with the bud destruction treatment, and both depended on species. Post hoc HSD tests showed that in the first year of recovery, balsam fir trees in the 100%+bud treatment had significantly (2-42%) longer mean current-year shoot length than in the 100% treatment except on the wet/poor site, while white spruce trees in the 100%+bud treatment had significantly (7-10%) shorter mean shoot length than in the 100% treatment except on the moist/rich site (Figure 9). In the second year of recovery, for balsam fir and black spruce, trees in the 100%+bud treatment had significantly (5-99%) longer shoots per tree than in the 100% treatment (Figure 9).

Comparison of results of mean current-year needle length per tree for 100% and 100%+bud treatment trees showed that in both recovery years, Site x Species (1995: $F = 4.81$, $p < 0.001$; 1996: $F = 3.55$, $p = 0.003$) and Species x Bud destruction interactions (1995: $F = 8.74$, $p = 0.002$; 1996: $F = 12.15$, $p < 0.001$) were significant (Table 5C). This indicated that mean needle length of 100% and 100%+bud treatment trees differed among sites and bud destruction treatments, and both depended on species. Post hoc HSD tests showed that in the first recovery year, balsam fir and black spruce in the 100%+bud treatment had 7-30% longer mean needle length per tree than in the 100% treatment (Figure 10). In the second recovery year, black spruce and white spruce trees in the 100%+bud treatment had significantly (1-12%) shorter mean needle length than in the 100% treatment in most species-site combinations, but balsam fir in the 100%+bud treatment had significantly (1-23%) longer mean needle length than in the 100% treatment (Figure 10).

Comparison of results of mean needlefall of 1991 foliage for 100% and 100%+bud

treatment trees showed that the Site x Species interaction was significant ($F = 2.67$, $p = 0.026$), indicating mean needlefall of 5-year-old foliage differed among sites, and depended upon species. The bud destruction term was also significant ($F = 7.50$, $p = 0.009$; Table 5D). Post hoc HSD tests showed that 100% treatment trees had 13-32% higher mean needlefall of 5-year-old foliage than 100%+bud treatment trees for 8 out of 12 species-site combinations (Figure 6B, 6C, 6D, 6E, 6G, 6H, 6J, and 6L).

Comparison of results of mean current-year needle weight per tree for 100% and 100%+bud treatment trees showed the interactions for Site x Bud destruction for both recovery years were significant (1995: $F = 4.80$, $p = 0.003$, 1996: $F = 4.67$, $p = 0.004$; Table 5E). Species had no significant effects on needle weight during the recovery years (1995: $F = 1.19$, $p = 0.308$, 1996: $F = 1.77$, $p = 0.175$; Table 5E). Thus, mean current-year needle weight per tree differed among sites, which depended on bud destruction. Post hoc HSD tests showed that during the recovery period, trees in the 100% treatment had significantly (31-186%) greater mean needle weight of current-year needles per tree than in the 100%+bud treatment except on the moist/rich site. However, bud destruction increased mean current-year needle weight per tree by 74-152%, compared to the 100% treatment on the moist/rich site for black spruce and white spruce (Figure 7H and 7L).

In summary, in the first recovery year, trees in the 100% treatment had 24-424% more current-year shoots, and 13-32% greater current-year needle weight per tree (except on the moist/rich site) than in the 100%+bud treatment. Bud destruction led to 2-42% longer shoots of balsam fir than in the 100% treatment except on the wet/poor site but 7-10% shorter shoots of white spruce except on the moist/rich site compared. Balsam fir and black spruce in the 100%+bud treatment had 7-30% longer needles than in the 100%

treatment. In the second recovery year, white spruce in the 100% treatment had 66-193% more shoots than in the 100%+bud treatment. Bud destruction increased shoot length of balsam fir and black spruce by 5-99%, needle length of balsam fir by 1-23%, and needle weight of black spruce and white spruce on the moist/rich site by 74-152%, while it decreased needle length of black spruce and white spruce in most species-site combinations by 1-12%. Mean needlefall of 5-year-old foliage in the 100% treatment was 13-32% higher than in the 100%+bud treatment.

5. DISCUSSION

5.1 Effects of manual defoliation on foliage production

5.1.1 Number of shoots

Our results showed that during the defoliation period, trees responded to increasing cumulative defoliation by increasing the number of current-year shoots produced; for all species and sites combined, trees that sustained 100%, 200%, and 300% cumulative defoliation had averages of 12%, 45%, and 59% more shoots than trees in the control, respectively. During the 2-year recovery period, trees undergoing the 50% and 100% treatments produced 6-189% (for 7 out of 12 species-site combinations) and 30-167% (8 out of 12 species-site combinations) more shoots than control trees. However, combining all species and sites, the 100%+bud removal treatment led to an average of 47% and 20% fewer shoots than on the 100% treatment trees and control trees, respectively. Several previous studies suggested that balsam fir responded to defoliation and destruction of terminal buds by producing epicormic shoots from latent buds, thus increased shoots after defoliation (Piene and Percy, 1984; Piene, 1989b; Piene and Eveleigh, 1996). Piene

(2003) also found that white spruce in the 50% defoliation treatment had 32% more shoots than in the control in the first and second recovery years, which was similar to our results.

However, artificial defoliation of young Scots pine (*Pinus sylvestris* L.) that did not include bud destruction resulted in no significant difference in bud production between treated and control trees for three years after treatment (Ericsson et al., 1980). Piene and MacLean (1984) found that number of shoots was significantly greater ($p < 0.001$) in moderately defoliated than in severely defoliated plots. They explained that trees in severely defoliated plots did not have sufficient carbohydrates, hormones, and nutrients. Most trees in the severely defoliated plots ultimately died, indicating that with high spruce budworm populations and defoliation, the stand could not recover to any operable level and can be considered completely destroyed.

5.1.2 Shoot length

During the defoliation period, increasing cumulative defoliation (from 0 to 300%) resulted in 2-42% shorter current-year shoot length for black spruce and white spruce in all 8 species-site combinations. During the recovery period, 50% and 100% treatment resulted in 8-31% and 1-45% reductions of mean shoot length compared to control treatment (for 10 out of 12 species-site combinations). For black spruce and white spruce, trees in the 100%+bud treatment had 5-39% shorter shoots for 6 out of 8 species-site combinations, while balsam fir in the 100%+bud treatment trees had 15-57% longer shoots in all species-site combinations than the control. Trees in the 100%+bud treatment had 2-58% longer shoots than in the 100% treatment for 10 out of 12 species-site

combinations. Results from Piene and MacLean (1999) showed that shoot lengths were generally reduced 44-45% by defoliation, from 3.9 cm to 2.2 cm between protected spaced and defoliated spaced trees and from 4.0 cm to 2.2 cm between protected unspaced, defoliated unspaced trees. Removal of needles caused reductions in carbohydrates and hormones, resulting in decreased shoot lengths (Piene and MacLean, 1999).

This was also observed for other species: (1) for artificially defoliated red pine, when either the old needles were removed (Kozlowski and Winget, 1964) or current foliage was removed singly or in combination with 1- or 2-year-old foliage (Kulman, 1965), shoot length declined by 50% or 38-63%; (2) for jack pine, the most severe reduction in shoot length occurred when removing the current foliage (O'Neil, 1962); (3) for Scots pine (Ericsson et al., 1980), reductions in shoot lengths were found in the second and third year of defoliation when current in combination with 1-year-old foliage was removed (early or late in the growing season: 43% or 54%).

5.1.3 Needle length

During the defoliation period, cumulative defoliation had no significant effect on mean length of current-year needles. During the recovery period, no significant differences were found among the 0, 50%, and 100% treatment trees. However, bud destruction increased mean current-year needle length of balsam fir and black spruce , compared to trees in the 100% treatment, by 7-30% in the first recovery year and decreased mean needle length of black spruce and white spruce by 1-23% in the second recovery year, for 6 out of 8 species-site combinations. Piene and MacLean (1999) found

that 3 years of severe defoliation resulted in unusually long needles in the fourth year of defoliation. They explained that the number of needle primordia, which could be strongly influenced by the previous season's growing environment (Clements, 1970), was probably reduced in the third year of defoliation, and then reduced the needle density in the following year, resulting in the abnormally long needles in that year (Piene and Percy, 1984). However, Kulman (1965) found that after removing current foliage in mid-summer, red pine had 19-32% shorter average needle lengths after one year and 9-42% longer average needle lengths after two years. This might relate to destruction of tree's photosynthetic capacity which provides nutrients to development of needles (Clark, 1961).

5.1.4 Needlefall

During the defoliation period, cumulative defoliation had no significant effects on mean needlefall of 3-year-old foliage. During the recovery period, balsam fir and black spruce in the 100% treatment had significantly (22% and 45%) higher mean needlefall of 5-year-old foliage than in the control. In contrast, some previous results have suggested that conifers may adjust their foliage life spans to increase needle retention to compensate for losses of photosynthetic capacity to defoliation. Doran et al. (2017) reported that cumulative spruce budworm defoliation significantly increased needle longevity of balsam fir. For young foliage (< 9 years), increased cumulative defoliation caused lower needle survival, which resulted from backfeeding of spruce budworm on 5+-year-old foliage. However, for older age classes (10-16-year-old), 10-16% more foliage per age class was retained under severe defoliation than under light defoliation. Mean needle

longevity of 50-year-old fir was almost double that for undefoliated 25-year-old fir (9.5 years vs 5.5 years). The 5-year-old foliage in our study were young foliage in Doran et al. (2017) study, thus, our results supported their conclusion that cumulative defoliation caused lower needle survival, i.e. higher needlefall. Further analysis needs to be done on older foliage which produced before 1991 to determine whether trees suffered cumulative defoliation would increase old needle retention to compensate for decreased photosynthetic capacity.

5.1.5 Needle weight

Increasing cumulative defoliation from 0 to 150% reduced mean current-year needle weight by 49-57%. During the recovery period, mean current-year needle weight per tree had a decreasing pattern as a response to increasing defoliation percentage. The 50% defoliation treatment resulted in 30-57% and 30-71% reductions of needle weight per tree in the first and second recovery years, while the 100% and 100%+bud treatments caused greater reductions in the first recovery year (43-93% and 49-97%), and slow recovery in the second year (43-82% and 46-97%). Bud removal reduced mean current-year needle weight per tree by 7-83% for 9 out of 12 species-site combinations, compared to 100% treatment; while it increased needle weight of black spruce and white spruce on the moist/rich site by 74-152%.

Defoliation that removes needles can leave the buds deprived of the source of carbohydrates and other nutrients that are necessary for bud-forming processes, resulting in fewer and smaller buds formed, leading to a decreased needle weight in the following year (Piene and MacLean, 1999). In addition, remaining older foliage has lower

photosynthetic capacity than the current-year foliage which was repeatedly removed (Clark, 1961; Reich et al., 1993). These factors may explain why reductions of mean current-year needle weight of trees in the recovery years in the 100% and 100%+bud treatments was greater than in the 50% treatment.

Foliage weight is a function of number of shoots, mean shoot length, mean needle length, and natural needlefall. Although trees in the 50% and 100% defoliation treatments produced 6-167% more shoots than in the control in most species-site combinations, they also had 8-31% and 1-45% shorter shoots than in the control. In addition, mean needlefall of 5-year-old foliage in the 100% treatment was an average of 22% and 45% higher than in the control for balsam fir and black spruce, respectively. Thus, mean shoot length and natural needlefall are more important variables to determine foliage weight in our study.

It is interesting that black spruce and white spruce in the bud destruction treatment increased mean current-year needle weight on the moist/rich site during the 2-year recovery period. The destruction of the terminal bud has been shown previously to result in epicormic shoot production, which is one of the main factors contributing to the rapid growth recovery (Piene and Percy, 1984; Piene, 1989b; Ostaff and MacLean, 1995). However, during the recovery period, the number of shoots in the 100%+bud treatment decreased by 47% compared to that in the 100% treatment. One possibility to explain this phenomenon is that moist/rich site could compensate as the source of carbohydrates and other nutrients that were deprived by needles and buds removal, thus supported trees to recover rapidly (Piene, 2003).

Similar results have been observed for young balsam fir trees in other studies, either following artificial early-season defoliation of current foliage for 3 years (defoliation

versus control treatment: means of 80 versus 180 g/tree) (Piene and Little, 1990) or during a spruce budworm outbreak (mean decreases of 84% of that on trees in protected plots) (Piene et al., 2003).

5.2 Effects of site quality on foliage production

In this study, nutrition (soil richness) had a stronger influence than soil moisture on foliage growth. During the defoliation period, trees on rich sites had 36% more current-year shoots, 35% longer current-year shoots, 15% longer current-year needles, and 139% greater current-year needle weight than on poor sites (590-660 g/tree on rich sites versus 260-270 g/tree on poor sites, with the wet/poor site the lowest) combining all treatments and species. Mean needlefall of 3-year-old foliage on the moist/rich site was 22% lower than on the dry/poor site. During the recovery period, trees on rich sites had 49% more current-year shoots, 43% longer current-year shoots, 13% longer current-year needles, and 172% greater current-year needle weight than on poor sites (430-550 g/tree on rich sites versus 160-190 g/tree on poor sites, with the dry/poor site the lowest) combining all treatments and species. Mean needle fall of 5-year-old foliage on the moist/rich site was 43% lower than on the dry/rich site.

Trees absorb nutrients and moisture from the soil to develop buds and withstand defoliation, while trees on poor sites might be deprived of essential nutrients or have insufficient or excess moisture, resulting in a decrease in production of needle primordia formed in the bud (Piene, 2003), and then fewer shoots, shorter shoots, and less foliage weight. Nitrogen, which is transformed through photosynthesis by foliage, is very important for foliage growth. Higher foliar nitrogen levels have previously been

associated with increased photosynthetic rates (Brix, 1971; Lavigne et al., 2001), which might explain our results. In addition, balsam fir trees on the rich site plots were 3 years older than on poor sites, they had larger crowns and greater height (Table 1); mean height and DBH of sample trees on rich sites were significantly (28% and 52%) greater than on poor sites (Table 2). Results of effects of DBH alone showed that shoot length, needle length and needle weight were significantly affected by DBH, with greater DBH resulted in longer shoots and needles, and greater needle weight.

5.3 Effects of species on foliage production

During both defoliation and recovery periods, black spruce had the most current-year shoots; white spruce had the longest shoots; and balsam fir had the longest needles. Mean needlefall of 5-year-old white spruce foliage was 21% higher than balsam fir and black spruce. During the recovery period, black spruce had 53% greater mean current-year needle weight than the other two species on poor sites; while on rich sites, white spruce had 36% greater needle weight than the other two species.

Greenbank (1963) also found that white spruce had longer shoot length and more rapid shoot growth than balsam fir (similar to our results that white spruce had the longest mean current-year shoots). In addition, balsam fir had the lowest mean current-year needle weight during the recovery period, which may contribute to other studies finding that balsam fir is the most susceptible among host species (Blais, 1983; MacLean, 1980).

5.4 Application of results and future study

Mean number of current-year shoots, shoot length, and needle weight were most strongly affected by cumulative defoliation. With increasing cumulative defoliation, the effects on number of shoots and shoot length of black spruce and white spruce were stronger on rich sites than on poor sites (i.e. trees increased more shoots by 1700-3500 versus 500-1200/tree, and decreased shoot length by 4-28 versus 1-16 mm/tree from 0-300% cumulative defoliation). Mean current-year needle weight of all three species responded more strongly to cumulative defoliation on rich sites than on poor sites (i.e. current-year needle weight per tree decreased more severely on rich sites, by 240-580g versus 90-260g/tree from 0-150% cumulative defoliation). Erdle and MacLean (1999) concluded that stem growth reduction of balsam fir, white spruce, and red-black spruce were similar for a given amount of cumulative defoliation. Our results suggested that the increase of number of shoots and the shoot length reduction of black spruce and white spruce on the dry/rich site were similar for a given amount of cumulative defoliation. The foliage weight reduction of balsam fir and white spruce were similar on the dry/rich site for a given amount of cumulative defoliation. These results and a parallel study assessing stem volume growth via stem analysis of the sample trees will permit calibration of a foliage-based stand growth model (Baskerville and Kleinschmidt, 1981). Based on our results, effects of defoliation on number of shoots, shoot length, and needle weight are most important and necessary and should be functionally included in a foliage-based stand growth model. Nonetheless, some other influence factors were not included in this study, such as climate, hardwood content etc., which merit further research.

However, there are some limitations of this study. We applied 0, 50%, 100%, and 100%+bud treatments on trees in this study, but they had no significant effects on mean

current-year needle length and mean needlefall of 1991 foliage. Maybe we could reclassify the defoliation treatment levels and get more cumulative defoliation levels to explore the effect of defoliation severity on foliage growth. We also collected older foliage data before 1992, which can be used to more rigorously analyze the effects of defoliation and site on needlefall of more foliage age classes. In addition, given the pseudo replication of site, DBH of sample trees in 1992 can be introduced as a fixed factor in the existing linear models. DBH of sample trees in 1992 was significantly larger on rich sites, which probably resulted in more shoots and possibly longer shoots and needles. If DBH is significant and some site or species interactions become non-significant, this suggests that the testing of site and species differences could be confounded by DBH differences between sites and species. Future study can focus on these topics.

6. CONCLUSIONS

Several key results were evident from this study:

(1) During the defoliation period, higher cumulative defoliation resulted in 290-1370 more current-year shoots per tree by epicormic shoot production, 2-29 mm shorter current-year shoots for black and white spruce due to lack of carbohydrates and hormones, and 90-440 g/tree lower overall current-year needle production.

(2) During the recovery period, defoliated trees prioritized recovery of foliage biomass by producing 400-6150 more current-year shoots per tree, while mean current-year shoot length decreased by 5-25 mm, resulting in 80-1450g/ tree lower current-year needle

weight than control trees. Trees in the 100%+bud removal and 100% defoliation treatment had slower recovery of current-year needle weight (only recovered 3-11% in a year) owing to insufficient carbohydrates, hormones, and nutrients, except for black spruce and white spruce in the 100%+bud treatment on the moist/rich sites.

(3) Trees foliage production on rich sites was two to three fold that on poor sites, but they also responded more strongly to the cumulative defoliation by decreasing 190-320 g/tree greater needle weight during the defoliation period. They had stronger ability to recover (two to four fold more foliage production on rich sites than on poor sites) mainly because of sufficient nutrients for trees to resist defoliation and rapidly recover photosynthetic capacity.

(4) Three species host trees recovered foliage biomass by different ways as response to defoliation. Black spruce generally prioritized producing more shoots, while white spruce and balsam fir enhanced shoot length and needle length, respectively.

These results supported some of our hypotheses and predictions that 1) during the defoliation period, cumulative defoliation resulted in more shoots, shorter shoot length, and lower overall current-year needle production; 2) during the recovery period, trees prioritize recovery of foliage biomass by increased number of shoots, and bud destruction resulted in slower recovery of trees; 3) trees on rich sites had stronger ability to resist defoliation and recover foliage production than on poor sites. However, we rejected some hypotheses and predictions that 1) cumulative defoliation did not substantially affect needle length and needlefall in this study; 2) during the recovery period, trees did not increase shoot length and needle weight to prioritize recovery of foliage biomass, defoliation treatments still resulted in shorter shoots and lower overall current-year

needle production; 3) it seemed nutrients played a more important role than moisture in the development of shoots and needles and the tree's ability to withstand defoliation, because in most species-site combinations, trees on the dry/rich site had the best foliage growth.

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