

Effects of Artificial and Western Spruce Budworm (Lepidoptera: Tortricidae) Defoliation on Growth and Biomass Allocation of Douglas-Fir Seedlings

ZHONG CHEN,¹ THOMAS E. KOLB,^{1,2} AND KAREN M. CLANCY³

J. Econ. Entomol. 95(3): 587-594 (2002)

ABSTRACT Artificial defoliation has been used commonly to simulate defoliation by insect herbivores in experiments, in spite of the fact that obvious differences exist between clipping foliage and natural defoliation due to insect feeding. We used a greenhouse experiment to compare the effects of artificial and western spruce budworm (*Choristoneura occidentalis* Freeman) defoliation on the growth and biomass allocation of 3-yr old half-sib seedlings from mature Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco variety *glauca*] trees that showed phenotypic resistance versus susceptibility to budworm defoliation in the forest. Artificial clipping of buds mimicked the effects of budworm feeding on total seedling biomass when 50% of the terminal buds were damaged. However, artificial defoliation decreased seedling height, relative growth rate of height, and shoot: root ratio more than budworm defoliation, whereas budworm defoliation decreased stem diameter relative growth rate more than artificial defoliation. Half-sib seedling progeny from resistant maternal tree phenotypes had greater height, diameter, biomass, and shoot: root ratio than seedlings from susceptible phenotypes. We concluded that careful artificial defoliation could generally simulate effects of budworm defoliation on total biomass of Douglas-fir seedlings, but that the two defoliation types did not have equal effects on biomass allocation between shoot and root. Further, an inherently higher growth rate and a greater allocation of biomass to shoot versus root are associated with resistance of Douglas-fir trees to western spruce budworm defoliation.

KEY WORDS *Choristoneura occidentalis*, *Pseudotsuga menziesii*, biomass allocation, shoot:root ratio, herbivory

EFFECTS OF DEFOLIATION on the growth (Kulman 1965; Webb and Karchesy 1977; Ericsson et al. 1980; Piene and Little 1990; Osman and Sharrow 1993; Sanchez-Martinez and Wagner 1994; Krause and Raffa 1996; Lyttikainen 1999a, 1999b) and physiology (Britton 1988, Reich et al. 1993, Kolb et al. 1999, Vanderklein and Reich 1999) of conifer trees have been intensively studied. In these studies, plant response depended on defoliation intensity (Piene and Little 1990, Kolb et al. 1999), timing or season of damage (Osman and Sharrow 1993, Lyttikainen 1999b), defoliation history (Vanderklein and Reich 1999), plant genotype (Sanchez-Martinez and Wagner 1994), tree species (Krause and Raffa 1996, Vanderklein and Reich 1999), and the plant parts removed (Haukioja et al. 1990, Honkanen et al. 1994). Further, environmental factors such as fertilization (Honkanen et al. 1999), site fertility (Lim and Turner 1996), and elevated CO₂ (Kruger et al. 1998) can also influence tree response

to defoliation. These factors limit broad generalizations about effects of insect defoliation on conifers.

Some obvious differences exist between artificial defoliation used in numerous experiments and defoliation by insects. For example, artificial defoliation by clipping foliage or shoots rarely removes foliage at the same rate as defoliation due to insect feeding, and does not include possible effects of saliva, incomplete consumption (Baldwin 1990, Lyttikainen 1999a), or nutrient cycling from insect frass (e.g., Mattson and Addy 1975; Grace 1986; Hollinger 1986; Schowalter et al. 1986, 1991; Kolb et al. 1999). Despite these differences, artificial defoliation has been frequently used in experiments to mimic insect defoliation and determine effects of defoliation on growth and physiology of conifers (e.g., Reich et al. 1993, Osman and Sharrow 1993, Krause and Raffa 1996, Vanderklein and Reich 1999). Fewer studies have used insects to defoliate conifers in experiments (e.g., Kolb et al. 1999). The use of insect defoliation is more realistic, but adds logistical complexity to experiments and often results in high variation in the amount of defoliation amount within a treatment because of the difficulty of controlling insect feeding. Artificial and insect defoliation had similar effects on growth of lodgepole pine (*Pinus*

¹ School of Forestry, Northern Arizona University, Flagstaff, AZ 86011-5018.

² E-mail: tom.kolb@nau.edu.

³ USDA Forest Service Research and Development, Rocky Mountain Research Station, 2500 S. Pine Knoll Drive, Flagstaff, AZ 86001-6381.

contorta Dougl. ex Loud.) (Britton 1988), balsam fir [*Abies balsamea* (L.) Mill.] (Piene and Little 1990), and ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) (Sanchez-Martinez and Wagner 1994). However, we do not know whether artificial defoliation can be used to mimic effects of western spruce budworm (*Choristoneura occidentalis* Freeman) defoliation on growth and biomass allocation of interior Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco variety *glauca*].

The western spruce budworm is the most destructive defoliator of several important coniferous tree species including Douglas-fir (Brookes et al. 1987), one of the primary commercial timber tree species in western North America (Hermann and Lavender 1990, Harlow et al. 1996). Severe defoliation on Douglas-fir trees can decrease individual tree growth and stand productivity, and increase dieback and mortality (Alfaro et al. 1982, 1985; Brookes et al. 1987; Ferguson 1988; Campbell 1993). Budworm defoliation can vary among Douglas-fir trees in forest stands (Clancy et al. 1993) possibly because of genetic differences in resistance mechanisms among trees (Chen et al. 2001).

In this study, we compared effects of artificial defoliation versus feeding by western spruce budworm larvae on growth and biomass allocation of young Douglas-fir seedlings in the greenhouse. Seedlings in our study were derived from mature trees that showed phenotypic resistance or susceptibility to budworm defoliation in the forest as determined by crown condition during a period of defoliation in late 1980s (Clancy et al. 1993, Clancy 2001). Our first objective in this study was to evaluate whether artificial defoliation could be used to mimic effects of budworm defoliation on the growth and biomass allocation of Douglas-fir seedlings; we hypothesized that artificial and budworm defoliation would have similar effects. Our second objective was to compare growth and biomass allocation responses to artificial and budworm defoliation among seedlings from phenotypically resistant and susceptible maternal trees. Based on the fact that phenotypically resistant trees grew faster than susceptible trees in the forest (Clancy et al. 1993), we expected that seedlings from these phenotypically resistant trees would have inherently higher growth rates than those from phenotypically susceptible trees, and that defoliation would not influence this difference.

Materials and Methods

Douglas-fir Half-sib Seedlings. Open-pollinated (or half-sib) seeds were collected between 1991 and 1994 from 12 pairs of mature Douglas-fir trees (ages ranged from 45 to 123 yr and averaged 79 yr) at two sites in Colorado (Deckers, and Buena Vista; 10 pairs) and one site in northern Arizona (Jacob Lake, two pairs). All three sites were located at elevations between 2,500 and 2,900 m and were dominated by Douglas-fir. A pair of trees was defined as two nearby trees (<30 m) within the same stand that were similar in

size (height and DBH) and microclimate (aspect and slope), but differed in the amount of crown damage during a budworm population outbreak in the late 1980s (Clancy et al. 1993). The resistant tree had a full and healthy crown (i.e., no significant sign of defoliation), whereas the crown of the susceptible tree was heavily damaged (loss of >67% of leaf area based on visual judgment) (Clancy et al. 1993). The open-pollinated seeds were sealed in labeled plastic bags and stored in a freezer at Rocky Mountain Research Station (RMRS) greenhouse, Flagstaff, AZ, until germination.

We germinated seeds in February 1998 in the greenhouse by sowing them in moist potting soil in container cells. The resulting seedlings were grown in container cells for one year and then transplanted to larger plastic pots (≈ 15 cm in diameter \times 20 cm in depth) filled with a mixture of peat and vermiculite for the following second and third years. The seedlings were grown in the RMRS greenhouse from spring 1998 to fall 2000 (i.e., three full growing seasons) with frequent watering (three times per week) and fertilization (once a week) during the growing season. Air relative humidity and temperature were varied seasonally to simulate field environmental conditions; this variation caused winter dormancy, spring budburst, and late-summer bud set to occur in a natural sequence each year. Maximum photosynthetic active radiation (PAR) in the greenhouse was $\approx 64\%$ of outdoor PAR.

Experiment Design. A completely random block, factorial design with five blocks was used for this study. Each block was located on a different bench in the RMRS greenhouse. Factors in the design were defoliation treatments (budworm defoliation, artificial defoliation, nondefoliation [i.e., control]) and maternal tree phenotypic traits (resistant versus susceptible). Each block contained 72 seedlings that were composed of three seedlings from each of the 24 families (i.e., 12 pairs of phenotypically resistant and susceptible trees). Three seedlings with similar size (i.e., in height and base stem diameter) from each family were randomly assigned to one of the three treatments within each block. In total, 360 seedlings were initially included in the study (5 blocks \times 3 treatments \times 2 traits \times 12 pairs).

Budworm and Artificial Defoliation. Both budworm and artificial defoliation treatments were designed to damage $\approx 50\%$ of the terminal buds on each seedling. The number of terminal buds was counted for those seedlings assigned to either budworm or artificial defoliation treatment. For the budworm defoliation treatment, we placed laboratory-reared third or fourth instar, nondiapausing budworm larvae on the seedlings (1 larva to five terminal buds) when $\approx 50\%$ of the buds on each seedling were in the fourth (columnar) developmental stage (Shepherd 1983). This approach maximized synchrony between the budworm larva feeding and bud burst. Following the protocol developed by Kolb et al. (1999), we visually monitored seedling damage and removed all larvae when $\approx 50\%$ of its terminal buds were consumed. Oc-

Table 1. ANOVA results for the effects of treatment and trait on the growth and biomass allocation of 3-yr-old Douglas-fir seedlings grown in greenhouse

Response variable (units)	Treatment ^a		Trait ^b		Treatment × Trait	
	F _{2, 348}	P	F _{1, 348}	P	F _{2, 348}	P
Height, cm	8.77	0.000	13.21	0.000	0.73	0.484
Base diameter, mm	3.27	0.039	40.23	0.000	0.14	0.870
Height relative growth rate, %	5.52	0.004	5.80	0.017	0.41	0.669
Base diameter Relative growth rate, %	14.91	0.000	3.60	0.059	0.26	0.769
Branch dry mass, g ^c	3.80	0.023	24.31	0.000	0.53	0.591
Stem dry mass, g ^d	1.69	0.187	28.65	0.000	0.04	0.961
Root dry mass, g	3.56	0.029	14.14	0.000	0.70	0.496
Total dry biomass, g	3.05	0.049	27.08	0.000	0.11	0.899
Shoot: root ratio, g/g ^e	8.42	0.000	11.27	0.001	1.65	0.193

^a Artificial defoliation, budworm defoliation, and non-defoliation control.
^b Maternal parent tree was resistant versus susceptible to western spruce budworm defoliation.
^c Branch includes lateral branches and leaves/needles.
^d Stem includes main stem only.
^e Shoot includes branch, needle, and stem dry mass.

asionally, extra budworm larvae were added to seedlings to achieve the target level of defoliation. All budworm-defoliated seedlings were caged between 20 April and 20 May 2000 with gray nylon “No-see-um” netting (The Rain Shed, Corvallis, OR) that allowed ≈80% of full sunlight to penetrate to maintain larval staying on designed seedlings.

For the artificial defoliation treatment, we randomly clipped 50% of the terminal buds on seedlings

with scissors. The artificial defoliation started three days after the larvae were introduced. 1–2 buds were clipped daily to closely mimic the pace of budworm feeding; this process lasted up to 14 d. Seedlings in the artificial and control treatments were also caged as described above to keep growth conditions similar for all seedlings in the greenhouse. All cages were removed after the defoliation experiment ended on 20 May 2000. All seedlings were allowed to grow for

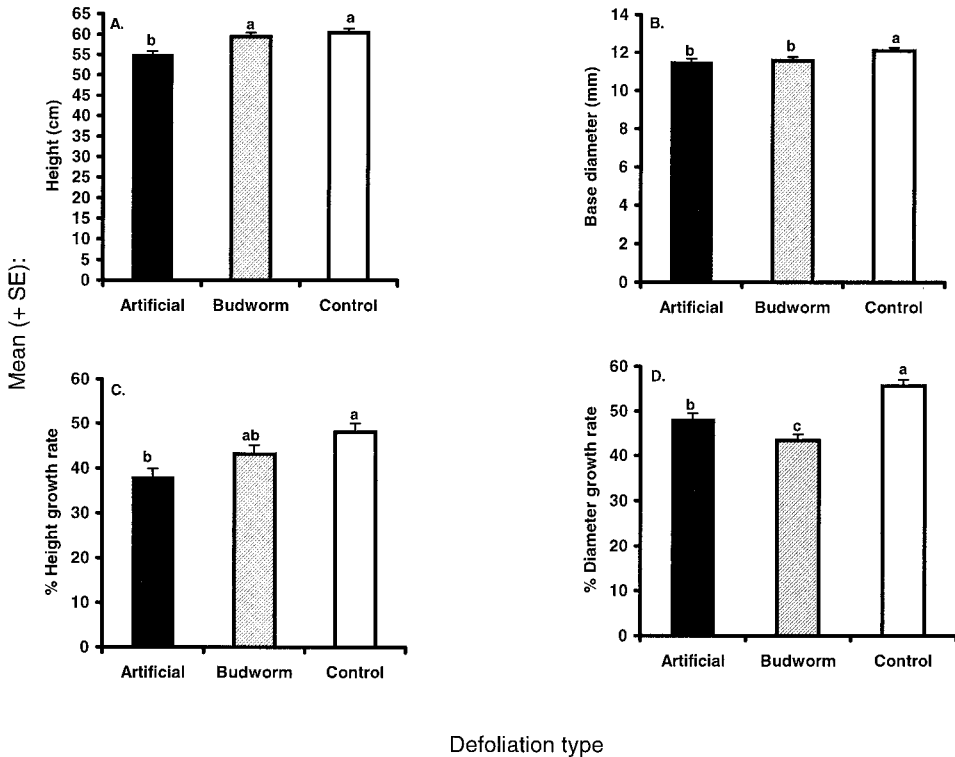


Fig. 1. Effect of defoliation type (artificial, budworm, and nondefoliated control) on average (LSMEAN ± 1 SE) height (A), stem base diameter (B), the relative growth rate (from April to August 2000 of height (C), and base diameter (D) of Douglas-fir seedlings. Bars sharing the same letter are not significantly different at $\alpha = 0.05$ (See Table 1 for ANOVA results) ($n = 120$ seedlings for the artificial and budworm defoliation treatments; $n = 118$ seedlings for the nondefoliated control).

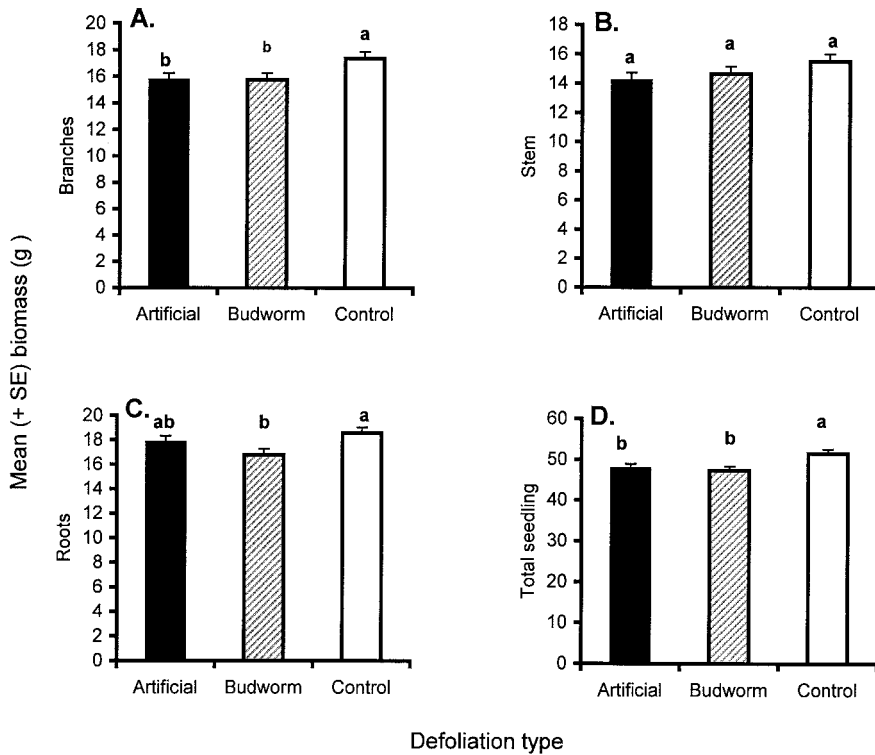


Fig. 2. The effect of defoliation type (artificial, budworm, and nondefoliated control) on average (LSMEAN \pm 1 SE) branches (A), stem (B), root (C), and total (D) biomass of Douglas-fir seedlings. Bars sharing the same letter are not significantly different at $\alpha = 0.05$ (See Table 1 for ANOVA results, and Fig. 1 for sample size). Branch includes lateral branches and leaves, stem includes the main stem only, and the total includes branch, leaves, and stem.

the whole summer until harvest in the end of August 2000.

Response Variables. The initial height and base stem diameter (\approx 1 cm above the soil surface in the pot) of seedlings were measured before the start of experiment in early April 2000. The growth of height and base diameter of all seedlings were measured once again at the end of August 2000 to determine their relative growth rate during the third growing season when the defoliation experiment was conducted. After that, all seedlings were harvested and partitioned into branches (including needles), stems, and roots. The roots were gently washed to remove the soil. All seedling components were oven dried at 75°C for 72 h and weighed. The shoot: root ratio for each seedling was calculated as the total above-ground dry mass (branches + stems) divided by the total below-ground dry mass (roots). Relative growth rate was calculated as [(growth measure in August - growth measure in April) / growth measure in April] \times 100%.

Data Analysis. We performed a fixed-effects analysis of variance (ANOVA) for each response variable with a general linear model: $y = \text{block} + \text{treatment} + \text{trait} + [\text{treatment} \times \text{trait}]$, where y represented each of the following response variables: seedling height, base stem diameter, relative growth rates of height and base diameter (from April to August 2000), biomass of each component, total biomass, and shoot: root ratio

($n = 358$, due to the death of two seedlings). Because two seedlings died during the experiment, the data were unbalanced. Thus, we used least square means (LSMEANS) to adjust the arithmetic means for missing data, and compared pair-wise differences among these LSMEANS at $\alpha = 0.05$. All data were approximately normally distributed as required for ANOVA; therefore, no data transformation was necessary. All calculations and statistical analyses were performed with SAS software (SAS Institute 1990).

Results

There were no detectable interactions between the defoliation treatment and tree trait for any seedling growth parameters ($P \geq 0.193$; Table 1). That is, Douglas-fir seedlings from mature trees that showed phenotypic resistance to budworm defoliation in the forest responded in a similar manner to the defoliation treatments, compared with seedlings from phenotypically susceptible mature trees. Therefore, we focused on the main effects of defoliation treatment and mature tree phenotypic traits.

Effects of Defoliation on Seedling Growth and Biomass. Defoliation treatment had significant effects on seedling height, base diameter, and the relative growth rates of height and base diameter from April to August 2000 ($P \leq 0.039$; Table 1). Compared with

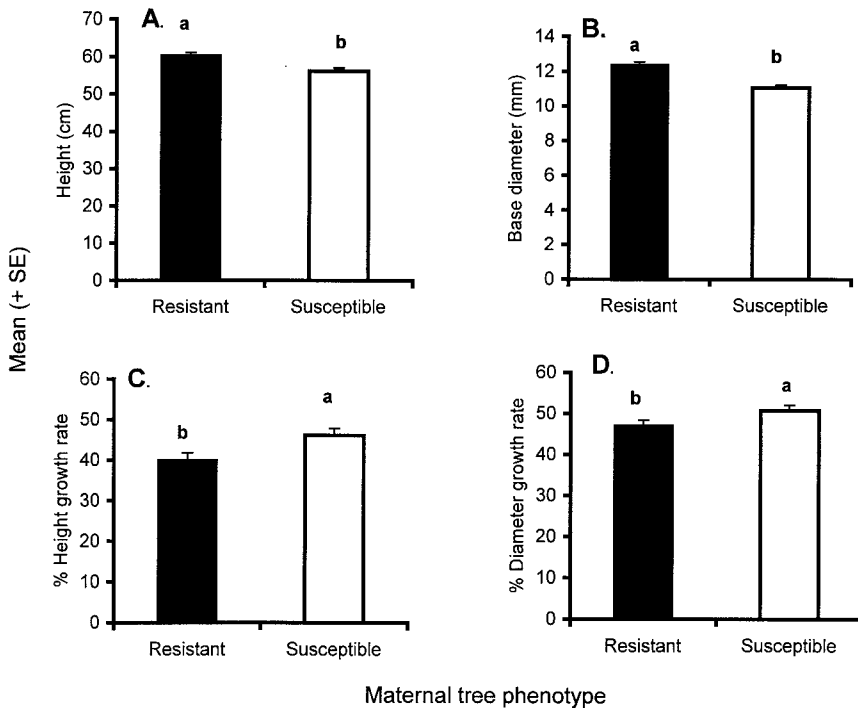


Fig. 3. Average (LSMEAN \pm 1 SE) height (A), stem base diameter (B), relative growth rate (from April to August 2000) of height (C), and base diameter (D) of Douglas-fir seedlings from maternal trees that were phenotypically resistant or susceptible to western spruce budworm defoliation in the forest. Bars sharing the same letter are not significantly different at $\alpha = 0.05$ (See Table 1 for ANOVA results) ($n = 178$ seedlings from resistant trees; $n = 180$ seedlings from susceptible trees).

nondefoliated seedlings, budworm defoliation did not significantly affect height (Fig. 1A) or the relative growth rate of height (Fig. 1C); however, it significantly decreased base stem diameter by $\approx 5\%$ (Fig. 1B), and the relative growth rate of base stem diameter by 29% (Fig. 1D). Artificial defoliation decreased seedling height by $\approx 10\%$ (Fig. 1A), base diameter by 5% (Fig. 1B), and their relative growth rates ($\approx 27\%$ in height, and 16% in base diameter) (Fig. 1C and 1D), compared with no defoliation. Artificial defoliation had a larger negative effect on relative growth rate of height than budworm defoliation (Fig. 1C), whereas budworm defoliation had a larger negative effect on the relative growth rate of base diameter (Fig. 1D).

Defoliation treatment also had a significant effect on branch and root biomass, and shoot: root ratio ($P \leq 0.029$), and had marginal effects on total biomass ($P = 0.049$) (Table 1). In contrast, defoliation treatment did not affect stem biomass ($P = 0.187$; Table 1). Both artificial and budworm defoliation decreased branch (Fig. 2A) and total biomass (Fig. 2D) similarly. Budworm defoliation reduced root biomass compared with the nondefoliation, whereas root biomass did not differ significantly between budworm and artificial defoliation (Fig. 2C).

Artificially defoliated seedlings had a significantly lower shoot: root ratio (1.68 ± 0.03) (LSMEAN \pm SE) than either budworm-defoliated (1.84 ± 0.03) or non-defoliated (1.79 ± 0.03) seedlings. Thus, artificial de-

foliation had a larger negative effect on above-ground biomass than below-ground biomass compared with budworm defoliation.

Effects of Phenotype on Seedling Growth and Biomass. In April 2000 (at the start of the experiment), average height and base diameter of half-sib seedlings from phenotypically resistant trees were 43.88 ± 0.69 cm (LSMEAN \pm SE) and 8.52 ± 0.13 mm, respectively, and both were significantly greater than those of seedlings from phenotypically susceptible trees (39.13 ± 0.69 cm in height, and 7.50 ± 0.13 mm in base diameter) (ANOVA, $P < 0.001$). Because the environment was the same for all seedlings in the greenhouse, differences in height and base diameter between the two groups of seedlings were attributed to their genotype. In other words, half-sib seedlings from resistant phenotypes had superior growth rate compared with those from susceptible phenotypes. In August 2000 (at the end of experiment), half-sib seedlings from resistant phenotypes continued to have significantly greater height (Fig. 3A) and base diameter (Fig. 3B) than those from susceptible phenotypes ($P < 0.001$; Table 1). However, relative growth rates of height and base diameter during the defoliation experiment (from April to August 2000) were greater for seedlings from susceptible phenotypes than those from resistant phenotypes ($P \leq 0.059$; Table 1) (Fig. 3C and D).

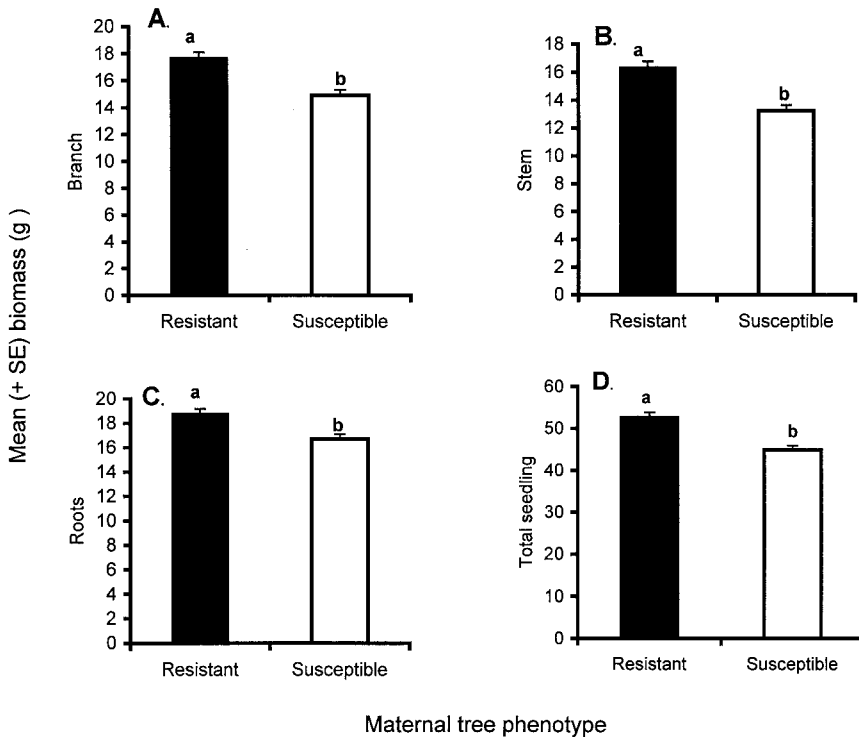


Fig. 4. Average (LSMEAN \pm 1 SE) biomass of branches (A), stem (B), root (C), and total (D) biomass of Douglas-fir from maternal trees that were resistant or susceptible to western spruce budworm defoliation in the forest. Bars sharing the same letter are not significantly different at $\alpha = 0.05$ (See Table 1 for ANOVA results, and Fig. 3 for sample sizes).

Total biomass and its components were greater for seedlings of resistant than susceptible phenotypes at the end of the study ($P = 0.000$; Table 1). For example, seedlings from resistant phenotypes had $\approx 19\%$ greater branch biomass (Fig. 4A), 23% greater stem biomass (Fig. 4B), 12% greater root biomass (Fig. 4C), and 18% greater total biomass (Fig. 4D) than seedlings from susceptible phenotypes. Furthermore, seedlings from resistant phenotypes had a greater shoot: root ratio (1.82 ± 0.02) than seedlings from susceptible phenotypes (1.71 ± 0.02) ($P = 0.001$; Table 1).

Discussion

We found that damage to 50% of terminal buds by either budworm feeding or gradual artificial clipping reduced total biomass of 3-yr-old Douglas-fir seedlings by $\approx 9\%$ (Fig. 2D). Kolb et al. (1999) reported that two consecutive years of budworm defoliation reduced total biomass of 5-yr old Douglas-fir seedlings by 11% when 30% of the terminal buds were damaged, and by 18% when 60% of the terminal buds were damaged. Overall, these findings and others (e.g., Osman and Sharrow 1993) suggest that Douglas-fir seedlings can tolerate occasional moderate to heavy defoliation without loss of substantial biomass. However, over-compensation in growth, where defoliated plants grow more than nondefoliated plants, did not occur in our study or in other studies with Douglas-fir seedlings

or saplings (Osman and Sharrow 1993, Kolb et al. 1999). The lack of over-compensation in growth in our study may have been due to the short duration of the experiment, or genetic or environmental factors that constrained mechanisms of compensatory growth. In contrast, over-compensation in growth has been reported for lightly defoliated Japanese larch [*Larix leptolepis* (Sieb. et Zucc) Gord] and red pine (*Pinus resinosa* Ait.) seedlings (Vanderklein and Reich 1999).

Although budworm and artificial defoliation had similar effects on total biomass of seedlings, the type of defoliation had different effects on some components of growth. For example, artificial defoliation had a greater negative effect on height relative growth rate (Fig. 1C), whereas budworm defoliation had a greater negative effect on diameter relative growth rate (Fig. 1D). One possible explanation for this difference is that artificial defoliation more severely suppressed leader growth than budworm defoliation because our artificial clipping removed buds completely and thus prevented shoot elongation, whereas some buds partially consumed by budworm larvae could elongate. Moreover, artificial defoliation significantly decreased shoot: root ratio compared with no defoliation, whereas budworm defoliation did not, suggesting a subtle effect of defoliation type on seedling biomass allocation. Perhaps budworm feeding reduced levels of hormones synthesized in young leaves that stimu-

late root growth (e.g., auxins, Kozłowski and Pallardy 1997) more than artificial clipping.

Overall, we concluded that gradual artificial removal of buds (e.g., over 14 d in our study) appropriately simulated effects of budworm feeding on most but not all characteristics of Douglas-fir seedling growth. Thus, we did not strongly reject our first hypothesis that artificial and budworm defoliation would have similar effects. This finding is consistent with other studies that have compared effects of artificial and insect defoliation on conifer seedlings and found little difference (Britton 1988, Sanchez-Martinez and Wagner 1994, Lyytikäinen 1999a). Our conclusion only applies to seedling growth for one summer after defoliation in the spring; long-term responses to defoliation were not addressed in our study, and could differ from short-term responses.

Half-sib seedlings from resistant maternal trees had greater growth and biomass over 3 yr than seedlings from susceptible trees, suggesting a greater genetic capacity for rapid growth for resistant phenotypes (Figs. 3 A and B and 4). However, in the third year of the study (when we conducted the defoliation experiment), seedlings of resistant trees had a smaller relative growth rate in height and diameter than seedlings of susceptible trees (Fig. 3 C and D). This difference in relative growth rate was likely caused by greater size of the resistant seedlings compared with the susceptible seedlings at the beginning of the third growing season, as relative growth rate is well known to decline as plant biomass increases (Evans 1972, Hunt 1978). Our results on genetic variation in seedling growth rate are consistent with radial growth rates of resistant and susceptible mature trees in the forest: mature trees that showed resistance to budworm defoliation had greater radial growth rate than trees that were highly susceptible to budworm defoliation (Clancy et al. 1993). These findings suggest genetic control of growth rate in Douglas-fir trees, and a possible linkage between growth rate and resistance to budworm defoliation.

High growth rate may promote Douglas-fir resistance to budworm defoliation by reducing the amount of damage per tree because the large number of buds present on fast growing trees exceeds budworm-feeding capacity. Also, high growth rate and rapid crown development may promote rapid crown recovery after budworm defoliation. Seedlings of resistant phenotypes had a higher shoot: root ratio than seedlings of susceptible phenotypes, suggesting greater biomass allocation to crown development for resistant phenotypes. However, we found no difference in growth response to either artificial or budworm defoliation between progeny from resistant and susceptible phenotypes during this one-year defoliation experiment (see treatment \times trait interactions in Table 1). Thus, we failed to reject our second hypothesis that defoliation type would not influence inherent differences in growth rate among progeny. Such difference in growth response to defoliation among progeny might occur in subsequent years after defoliation, but this could not be addressed in our short-term study.

In conclusion, artificial defoliation that simulates the intensity and timing of budworm larva feeding can be used to study the tolerance of Douglas-fir seedlings to western spruce budworm defoliation. However, artificial and budworm defoliation may differ in their effects on seedling biomass allocation between shoot and root. Half-sib seedlings from resistant mature tree phenotypes had a greater capacity for fast growth than seedlings from susceptible phenotypes, suggesting that an inherently high growth rate is associated with resistance of Douglas-fir trees to western spruce budworm defoliation.

References Cited

- Alfaro, R. I., G. A. Van Sickle, A. J. Thomson, and Z. Wegwitz. 1982. Tree mortality and radial growth loss caused by the western spruce budworm in a Douglas-fir stand in British Columbia. *Can. J. For. Res.* 12: 780-787.
- Alfaro, R. I., A. J. Thomson, and G. A. Van Sickle. 1985. Quantification of Douglas-fir growth losses caused by western spruce budworm defoliation using stem analysis. *Can. J. For. Res.* 15: 5-9.
- Baldwin, I. T. 1990. Herbivory simulations in ecological research. *Trends Ecol. Evol.* 3: 91-93.
- Britton, R. J. 1988. Physiological effects of natural and artificial defoliation on the growth of young crops of lodgepole pine. *Forestry* 61: 165-175.
- Brookes, M. H., J. J. Colbert, R. G. Mitchell, and R. W. Stark (eds.). 1987. Western spruce budworm. USDA For. Ser. Tech. Bull. 1694.
- Campbell, R. W. 1993. Population dynamics of the major North American needle-eating budworms. USDA For. Ser. Res. Pap. PNW-RP-463.
- Chen, Z., T. E. Kolb, and K. M. Clancy. 2001. Mechanisms of Douglas-fir resistance to western spruce budworm defoliation: bud burst phenology, photosynthetic compensation and growth rate. *Tree Physiol.* 21: 1159-1169.
- Clancy, K. M. 2001. Biochemical characteristics of Douglas-fir trees resistant to damage from the western spruce budworm: patterns from three populations, pp. 115-124. *In* R. Alfaro et al. (eds.), Protection of world's forest from insect pests: advances in research. International Union of Forestry Research Organizations, Vienna, Austria.
- Clancy, K. M., J. K. Itami, and D. P. Huebner. 1993. Douglas-fir nutrients and terpenes: potential resistance factors to western spruce budworm defoliation. *For. Sci.* 39: 78-94.
- Ericsson, A., S. Larsson, and O. Tenow. 1980. Effects of early and late season defoliation on growth and carbohydrate dynamics in Scots pine. *J. Appl. Ecol.* 17: 747-769.
- Evans, G. C. 1972. The quantitative analysis of plant growth. Blackwell, Oxford, UK.
- Ferguson, D. E. 1988. Growth of regeneration defoliated by spruce budworm in Idaho. USDA For. Ser. Res. Pap. INT-463.
- Grace, J. R. 1986. The influence of gypsy moth on the composition and nutrient content of litter fall in Pennsylvania oak forest. *For. Sci.* 32: 855-870.
- Harlow, W. M., E. S. Harrar, J. W. Hardin, and F. M. White. 1996. Textbook of Dendrology. McGraw-Hill, New York.
- Haukioja, E., K. Ruohomaki, J. Senn, J. Suomela, and M. Walls. 1990. Consequence of herbivory in the Mountain birch (*Betula pubescens* spp. *tortuosa*): importance of the functional organization of the tree. *Oecologia* 82: 238-247.

- Hermann, R. K., and D. P. Lavender. 1990. *Pseudotsuga menziesii* (Mirb.) Franco, Douglas-fir. In *Silvics of Northern America*. USDA For. Ser. Agric. Handb. 654: 527.
- Hollinger, D. Y. 1986. Herbivory and the cycling of nitrogen and phosphorus in isolated California oak trees. *Oecologia* 70: 291-297.
- Honkanen, T., E. Haukioja, and J. Suomela. 1994. Effects of simulated defoliation and debudding in needle and shoot growth in Scots pine (*Pinus sylvestris*): implications of plant source/sink relationships for plant-herbivore studies. *Funct. Ecol.* 8: 631-639.
- Honkanen, T., E. Haukioja, and V. Kitunen. 1999. Responses of *Pinus sylvestris* branches to simulated herbivory are modified by tree sink/source dynamics and by external resources. *Funct. Ecol.* 13: 126-140.
- Hunt, R. 1978. *Plant growth analysis*. Edward Arnold, London.
- Kolb, T. E., K. A. Dodds, and K. M. Clancy. 1999. Effect of western spruce budworm defoliation on the physiology and growth of potted Douglas-fir seedlings. *For. Sci.* 45: 280-290.
- Kozłowski, T. T., and S. G. Pallardy. 1997. *Physiology of woody plants*. Academic, New York.
- Krause, S. C., and K. F. Raffa. 1996. Differential growth and recovery rates following defoliation in related deciduous and evergreen trees. *Trees Struct. Funct.* 10: 308-316.
- Kruger, E. L., J. C. Volin, and R. L. Lindroth. 1998. Influences of atmospheric CO₂ enrichment on the responses of sugar maple and trembling aspen to defoliation. *New Phytol.* 140: 85-94.
- Kulman, H. M. 1965. Effects of artificial defoliation of pine on subsequent short needle growth. *For. Sci.* 11: 90-98.
- Lim, W.H.L., and I. M. Turner. 1996. Resource availability and growth responses to defoliation in seedlings of three early successional, tropical woody species. *Ecol. Res.* 11: 321-324.
- Lyytikäinen, S. P. 1999a. Growth responses of Scots pine (*Pinaceae*) to artificial and sawfly (Hymenoptera: Diprionidae) defoliation. *Can. Entomol.* 131: 455-463.
- Lyytikäinen, S. P. 1999b. The responses of Scots pine, *Pinus sylvestris*, to natural and artificial defoliation stress. *Ecol. Appl.* 9: 469-474.
- Mattson, W. J., and N. D. Addy. 1975. Phytophagous insects as regulators of forest primary production. *Science* 190: 515-522.
- Osman, K. A., and S. H. Sharrow. 1993. Growth responses of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) to defoliation. *For. Ecol. Manage.* 60: 105-117.
- Piene, H., and C.H.A. Little. 1990. Spruce budworm defoliation and growth loss in young balsam fir: artificial defoliation of potted trees. *Can. J. For. Res.* 20: 902-909.
- Reich, P. B., M. B. Walters, S. C. Krause, D. W. Vanderklein, K. F. Raffa, and T. Tabone. 1993. Growth, nutrition and gas exchange of *Pinus resinosa* following artificial defoliation. *Trees Struct. Funct.* 7: 67-77.
- Sanchez-Martinez, G., and M. R. Wagner. 1994. Sawfly (Hymenoptera: Diprionidae) and artificial defoliation affects above- and below-ground growth of ponderosa pine seedlings. *J. Econ. Entomol.* 87: 1038-1045.
- SAS Institute. 1990. *SAS/STAT user's guide*. SAS Institute. Cary, NC 27513.
- Schowalter, T. D., W. W. Hargrove, and D. A. Crossley. 1986. Herbivory in forest ecosystems. *Annu. Rev. Entomol.* 31: 177-196.
- Schowalter, T. D., T. E. Sabin, S. G. Stafford, and J. M. Sexton. 1991. Phytophage effects on primary production, nutrient turnover, and litter decomposition of young Douglas-fir in western Oregon. *For. Ecol. Manage.* 42: 229-243.
- Shepherd, R. F. 1983. A technique to study phenological interactions between Douglas-fir buds and emerging second-instar western spruce budworm, pp. 17-20. In M. Montgomery (eds.), *Forest defoliator-host interactions: a comparison between gypsy moth and spruce budworms*. USDA For. Ser. Gen. Tech. Rep. NE-85.
- Vanderklein, D. W., and P. B. Reich. 1999. The effect of defoliation intensity and history on photosynthesis, growth and carbon reserves of two conifers with contrasting leaf lifespan and growth habits. *New Phytol.* 144: 121-132.
- Webb, W. L., and J. J. Karchesy. 1977. Starch content of Douglas-fir defoliated by the tussock moth. *Can. J. For. Res.* 7: 186-188.

Received for publication 6 July 2001; accepted 31 January 2002.