Mortality and height growth losses of coniferous seedlings damaged by the black army cutworm[1]

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Growth and survival of seedlings were determined for 1 to 3 years following defoliation by black army cutworm, *Actebia fennica* (Tausch.). Ten data sets were collected on three sites and included four species of seedlings: interior Douglas-fir, *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco; lodgepole pine, *Pinus contorta* Dougl.; western larch, *Larix occidentalis* Nutt.; and Engelmann spruce, *Picea engelmannii* Parry. Mortality following defoliation cannot be assessed until after the flush in the next growing season because completely defoliated seedlings often regenerate new foliage and survive. More than 90% of the total mortality that did occur was detected at that time. Mortality of up to 39% occurred when seedlings were defoliated more than 60%; most of this occurred when planting was carried out concurrent with defoliation. Synergistic root stress effects caused by poor planting, dry sites, or drought significantly increased mortality. Height growth was significantly reduced when defoliation was greater than 60%; the greatest effects occurred when terminal bud destruction accompanied needle loss. Growth losses were greatest the year of defoliation; recovery of height growth of lodgepole pine was complete by the 2nd year on good growing sites. On poor sites, retardation of lodgepole pine height growth was still evident after 3 years.

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On a étudié pendant 1 à 3 années la croissance et la survie de semis défoliés par la légionnaire noir, *Actebia fennica* (Tausch.). Dix ensembles de données ont été recueillis dans trois sites sur quatre espèces de semis : Douglas taxifolié bleu, *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco; pin tordu, *Pinus contorta* Dougl.; mélèze occidental, *Larix occidentalis* Nutt.; et épinette d'Engelmann, *Picea engelmannii* Parry. On ne peut évaluer le taux de mortalité une fois que les arbres ont été défoliés qu'après l'apparition des pousses au cours de la saison de croissance suivante car, on peut souvent observer des semis complètement dégarnis sur lesquels se développe un nouveau feuillage et qui survivent. C'est à ce moment que s'est produit un taux de mortalité totale dépassant 90%. Une mortalité s'élevant jusqu'à 39% a été relevée chez les semis dont le taux de défoliation était supérieur a 60%; la majorité de ces cas ont été observés chez les semis dont la plantation et la défoliation ont eu lieu simultanément. Les facteurs d'agression synergiques sur les racines causés par une mauvaise plantation, le manque d'humidité dans les sites ou une sécheresse ont augmenté, de façon marquée, le taux de mortalité. La croissance en hauteur a été notablement réduite pour les semis défoliés à plus de 60%; les réductions les plus importantes ont été observées quand la destruction des bourgeons terminaux accompagnait la perte des aiguilles. Le ralentissement de la croissance a été maximale l'année de la défoliation proprement dite; les semis de pin tordu situés dans les sites où les conditions étaient favorables ont entièrement repris le retard de croissance en hauteur la 2ᵉ année. Dans les sites où les conditions étaient défavorables, les retards de croissance en hauteur des semis de pin tordu étaient encore évidents au bout de 3 ans.

Introduction

The black army cutworm, *Actebia fennica* (Tausch.) is widely distributed throughout the Northern Hemisphere (Clarke and Carew 1985; Humble *et al.* 1989; Pulliainen 1963). Prior to 1964, infestations in British Columbia were recorded only in agricultural situations (Allen and Wood 1973). Since that time, populations have caused severe damage in recently planted sites in many forest regions (Humble *et al.* 1989).

Extreme fluctuations of population levels are characteristic of the black army cutworm. One or 2 years after broadcast burning has been used for site preparation or following wildfires, many thousands of larvae suddenly appear and severely defoliate most vegetation, including coniferous seedlings. Larval distribution and subsequent damage is patchy throughout an infestation. The larvae feed initially on succulent herbaceous plants, and damage to seedlings occurs when the preferred vegetation is depleted. High populations on a given site generally last for 1 or occasionally 2 years and then disappear.

The 1-year life cycle of the cutworm has been described by Wood and Neilson (1956) and by Humble *et al.* (1989). The dates of occurrence of each life stage vary from year to year depending on weather conditions, geographical location, aspect, and elevation. Emergence and flight of adult moths can occur from early July to mid-September. Oviposition takes place 2 to 5 weeks after emergence, and the overwintering stage is presumed to be young larvae. Nocturnal larval feeding begins as soon as the snow has melted in early spring, but daytime feeding occurs when night temperatures are too low to permit larval activity. The larvae pass through six instars in a 5- to 6-week period before pupating about mid-June; the pupal stage lasts for 3 or 4 weeks.

Larvae defoliate seedlings to various degrees, destroy terminal and lateral buds, and occasionally chew the bark. An assessment of the effects of this damage on the survival and

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TABLE 1. Sample size, initial seedling height, and percentage of seedlings exhibiting terminal bud damage by defoliation class, location, and time of planting

		Clearwater (1987), moist site	Invermere (1987), dry site			Golden (1988), medium site					
Defoliation class (%)	Parameters	Pine (con)	Pine (con)	D. fir (con)	Spruce (con)	Pine (con)	Pine (post)	D. fir (con)	D. fir (post)	Larch (con)	Larch (post)
0 (control)	Number of seedlings	45	86	45	172	22	106	103	63	10	169
	Initial height (cm)	11.0	13.5	16.7	21.3	19.4	24.6	24.2	25.1	30.0	38.9
1–30	Number of seedlings	68	52	85	170	40	115	108	32	18	160
	Initial height (cm)	11.1	14.0	16.5	22.0	20.4	22.9	24.6	24.4	28.9	40.4
	Terminal bud dead (%)	0	25	67	29	0	0	31	78	55	29
31–60	Number of seedlings	60	63	50	152	29	101	70	16	19	113
	Initial height (cm)	12.7	14.8	17.5	21.9	18.8	23.5	24.3	24.7	28.1	36.9
	Terminal bud dead (%)	0	30	84	75	0	0	26	100	53	31
61–99	Number of seedlings	50	112	42	157	46	80	49	61	15	107
	Initial height (cm)	11.8	15.2	17.2	22.0	17.8	24.3	25.1	25.2	27.2	37.6
	Terminal bud dead (%)	12	23	86	91	13	8	51	100	53	46
100	Number of seedlings	46	104	0	156	33	86	41	192	12	107
	Initial height (cm)	11.6	15.2	na*	22.4	18.6	23.4	23.9	26.0	26.0	36.5
	Terminal bud dead (%)	13	40	na*	95	33	49	78	100	50	95

NOTE: Pine, lodgepole pine; D. fir, interior Douglas-fir; spruce, Engelmann spruce; larch, western larch; con, defoliation occurred concurrent with planting; post, defoliation occurred 1 year after planting.
*No Douglas-fir seedlings could be found at Invermere with 100% defoliation.

TABLE 2. Percent seedling mortality by defoliation and terminal damage classes caused by black army cutworm

		Clearwater	Invermere			Golden					
						Pine		D. fir		Larch	
Defoliation (%)	Terminal bud	Pine (con)	Pine (con)	D. fir (con)	Spruce (con)	Con	Post	Con	Post	Con	Post
0 (control)	Alive	7.4	7.5	8.6	7.3	3.1	6.9	5.3	2.6	0.0	1.1
1–30	Alive	5.7	11.1	9.2	6.3	14.5	3.4	7.1	0.0	na	0.8
	Dead	na	5.9	5.9	1.8	na	na	5.3	0.0	na	0.0
31–60	Alive	4.9	1.6	0.0	0.0	9.5	1.9	1.8	na	na	0.0
	Dead	na	9.4	6.4	5.6	16.7	na	4.5	0.0	na	0.0
61–99	Alive	6.9	7.4	7.7	22.2	14.2	1.3	14.7	na	na	0.0
	Dead	0.0	15.5	5.6	6.5	22.2	0.0	26.3	0.0	na	6.9
100	Alive	9.7	8.8	na	9.1	44.2	10.2	37.5	na	na	12.5
	Dead	47.0	25.0	na	20.5	27.8	13.0	53.9	29.0	na	39.3
Combined (61–100)	Alive and dead	11.4	12.7	na	14.6	27.4	6.9	39.0	na	na	24.5

NOTE: Pine, lodgepole pine; D. fir, interior Douglas-fir; spruce, Engelmann spruce; larch, western larch; con, defoliation occurred concurrent with planting; post, defoliation occurred 1 year after planting; na, insufficient data were available ($n < 5$) within a damage class. Underlined means are significantly different from nondefoliated control means of the same column (t-test of percentages, $p \leq 0.05$).

growth of seedlings for up to 3 years following defoliation was the prime objective of this study. Interactions, including the time of planting in relation to time of defoliation, initial seedling height, planting quality, and drought following defoliation were also considered. The study was carried out within natural infestations in southeastern British Columbia from 1987 to 1989. The host species studied were interior Douglas-fir, *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco; lodgepole pine, *Pinus contorta* Dougl.; western larch, *Larix occidentalis* Nutt.; and Engelmann spruce, *Picea engelmannii* Parry. They are abbreviated in this paper as Douglas-fir, pine, larch, and spruce, respectively.

Materials and methods

Plots were established within current outbreaks, and as outbreaks usually last only 1 year, widely different locations had to be used each year, with a different combination of seedling species and growing conditions at each location. Plots were laid out near Clearwater and Invermere in 1987 and near Golden in 1988. Mortality and growth were determined each year up to and including growth for 1989. The location near Clearwater had abundant soil moisture and represented excellent growing conditions; it was located at 900 m on a 15% slope of south and west aspects and fell within the ICHmw3 Biogeoclimatic (BGC) subzone. The location near Invermere was on a poor growing site at 1400 m on a 30% slope of variable aspect; it fell within the ESSFdc1 BGC subzone. The location at Golden was

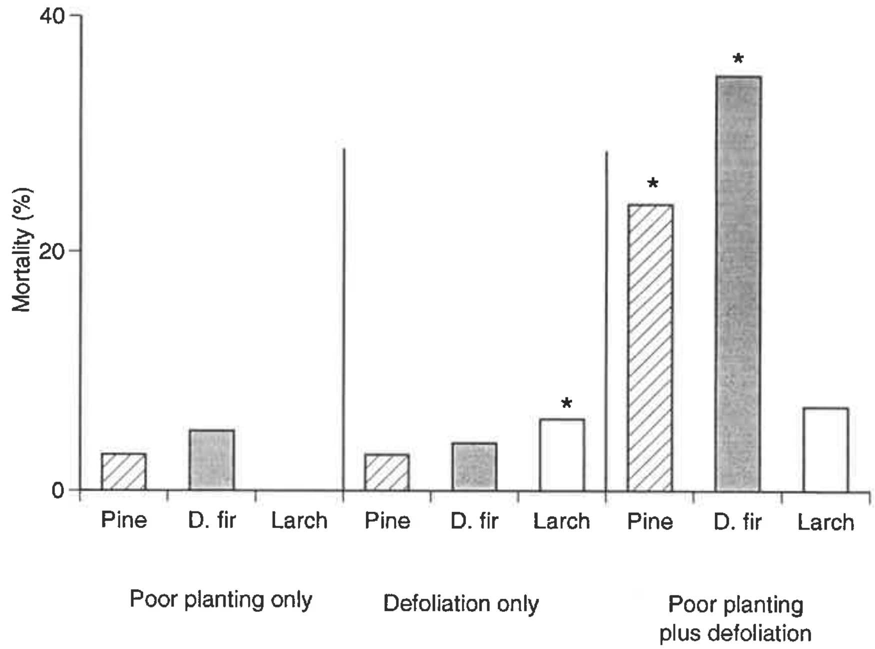

FIG. 1. Comparison of mortality by species between nondefoliated seedlings where mortality is due to poor planting only, well-planted seedlings defoliated 61% or more, and poorly planted seedlings that are also defoliated 61% or more, all at Golden, British Columbia. Pine, lodgepole pine; D. fir, interior Douglas-fir; larch, western larch. *, Mean is significantly different from the mean for planting only for that species (t-test of percentages, $p \leq 0.05$).

on a moderate to good growing site but subject to summer drought; it was located at 1050 m on a 25% slope of variable aspect in the ICHmk1 BGC subzone.

A number of plots were established at each location, each consisting of an inner circular portion of 4 m radius within which all seedlings were sampled and an outer portion consisting of the nearest 12 seedlings. The following data were recorded for each seedling: plot, species, time of planting and defoliation, defoliation class, terminal bud damage, and initial height.

An attempt was made to collect data on at least 60 seedlings within each cell of the data matrix (Table 1), but often these were not available. A cell was bounded by a combination of variables, which included 4 seedling species, 5 classes of visually estimated defoliation (0, 1-30, 31-60, 61-99, 100%), presence or absence of the terminal bud, and 2 periods of defoliation in relation to planting time. The last variable consisted of seedlings planted concurrent with the presence of feeding larvae and seedlings defoliated 1 year after planting. Each seedling was marked, and reassessments were made each year until the end of the study. Sufficient seedlings were often not available to fill every cell, and mortality resulted in the loss of samples in some cells during the study. In the case of larch, no outbreaks occurred within current planting operations; therefore, 74 seedlings were planted within a small outbreak in 1989 in order to obtain a small amount of data for this species. The average sample size was 78.3 seedlings per cell, and the total sample consisted of data on 3838 seedlings. In a preliminary analysis, no differences in mortality or growth could be detected between initial height classes. This variable was dropped in the final analysis.

One-, 2-, and 3-year reassessments consisted of noting mortality and measuring height growth of survivors at the end of each subsequent growing season. Mortality was attributed to defoliation, poor planting, or a combination of both. All dead seedlings were carefully excavated, and the roots were inspected for evidence of poor planting that could be implicated in seedling death (i.e., did seedlings have upturned roots, squashed plugs, or were they planted into rotten wood?). Height growth was measured in the autumn between the base of the newly formed bud and the basal scales of the previous terminal bud. When dieback extended below the current internode, a latent bud in an older internode usually developed in response to the damage and burst, giving rise to a replacement terminal (Fig. 1). In this case, a height loss occasionally occurred between the base of the new terminal bud and the basal scales of the previous terminal bud.

Mortality losses are binomial in form and therefore were tested statistically using a nonparametric one-tailed t-test for percentages (Fairchild 1959). The original height growth data were numerical in form, but no useful transformation was found that could handle a mixture of zero, negative, and positive data without causing a bias. In addition, there was considerable difference in growth rates between different years and plots, and often between different species combinations. Therefore, growth losses were expressed as percentages of growth of nondefoliated control trees measured each year at each site and plot; means were again compared using a t-test for percentages.

Results

Mortality

It was found that death could not be confirmed until one growing season after defoliation, as seedlings, even when completely defoliated, often set new buds and flushed later in the growing season or in the following year. One year after defoliation, 90% of the total mortality attributable to black army cutworm damage had occurred. Significant mortality was observed only in defoliation classes greater than 60% (Table 2). When defoliation was greater than 60%, 5 of the 7 combined data sets of defoliated seedlings had significantly greater mortality than the control (Table 2), and in 2 of the 7 combined sets of data, mortality was significantly greater when the terminal bud was killed compared with seedlings where the bud remained alive ($p \leq 0.05$, test of percentages). In the latter case, 2 additional data sets with small sample sizes had marginal levels of significance of $p = 0.07$ and 0.08.

Low levels of mortality were attributed to defoliation alone in well-planted seedlings. Only in the case of larch was mortality due to defoliation higher than mortality due to poor

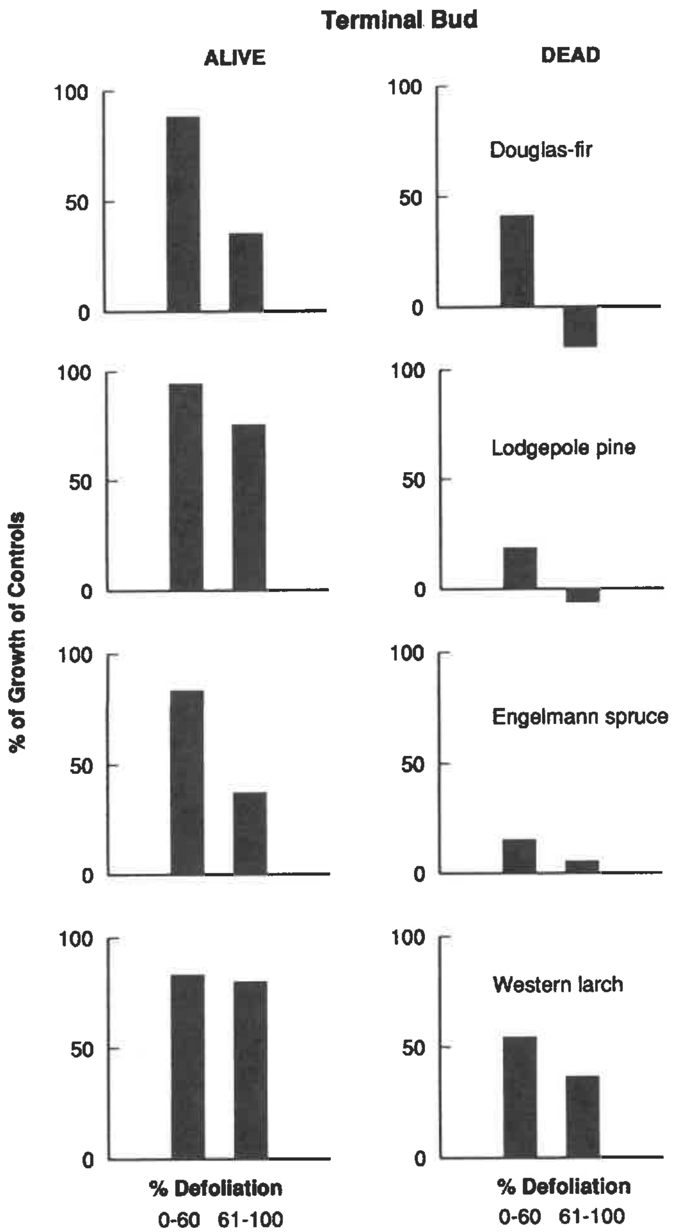

FIG. 2. Average seedling height growth as a percentage of nondefoliated controls for different species by defoliation and terminal bud survival classes.

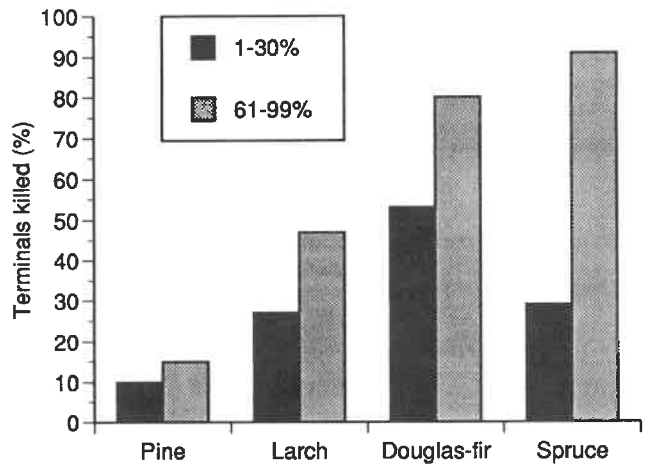

FIG. 3. Relationship between percentage of terminals killed and percent defoliation by species; averages are for combined data of both planting times. There was a significant difference between all percentages within each defoliation class except between western larch and spruce defoliated 1–30% (*t*-test of percentages $p < 0.01$). Pine, lodgepole pine; larch, western larch; Douglas-fir, interior Douglas-fir; spruce, Engelmann spruce.

planting (Fig. 1). However, when defoliated seedlings were subjected to other stress factors that affected root growth, there were synergistic effects on mortality. Douglas-fir and pine at Golden suffered much higher mortality than would be expected through the additive effects of defoliation and poor planting acting separately (Fig. 1). A drought (approximately 60% of normal precipitation in May) occurred in 1988 following planting at Golden. Average mortality for pine in this case was 27.4% for seedlings defoliated 60–100% (Table 2), whereas average mortality in the previous year at Invermere and Clearwater, when precipitation was near normal, was significantly less at 12.7 and 11.4%, respectively ($p < 0.02$, test of percentages).

A comparison of time of defoliation as related to time of planting can be made with pine and Douglas-fir at Golden (Table 2). When there was 61–99 or 100% defoliation and the terminal bud was killed, greater mortality occurred when defoliation was concurrent with planting than when defoliation occurred 1 year later ($p < 0.05$, *t*-test of percentages).

Height growth loss

The impact of defoliation and terminal damage upon subsequent height growth is given in Table 3 as a percentage of the undefoliated control seedlings of the same species growing on the same site. The average percent growth was significantly different within the four damage classes ($p < 0.001$, test of percentages). Nonterminally damaged seedlings with less than 60% defoliation did not have significantly less height growth than nondefoliated control seedlings, but those with more than 60% defoliation did have significantly less growth than controls.

Height growth of seedlings defoliated 1 year after planting was reduced about the same or more than that of seedlings defoliated concurrent with planting (Table 3). This was evident in the growth rates of pine, Douglas-fir, and larch growing on the same site during the same years.

Similar trends in losses between damage classes occurred with all species (Fig. 2). Larch suffered the least and Douglas-fir the most, with an average 18% dieback occurring below the current internode in the most severely attacked class.

There were large differences between tree species within the same defoliation class in the percentage of seedlings that lost terminal buds (Fig. 3); Douglas-fir and spruce were the most susceptible. Even at low levels of defoliation, over half of the terminals on Douglas-fir seedlings were killed, while pine suffered little terminal damage even at high levels of defoliation. These differences could be related to many factors, such as the relative palatability of 1-year-old needles of different species or the time of larval feeding as related to the time of bud development. Further studies should be carried out to determine this point.

Height growth relative to control trees for areas where 3 years of data were available is given in Fig. 4. Loss of height growth was most noticeable in the year of attack, particularly when the terminal bud was also destroyed. In

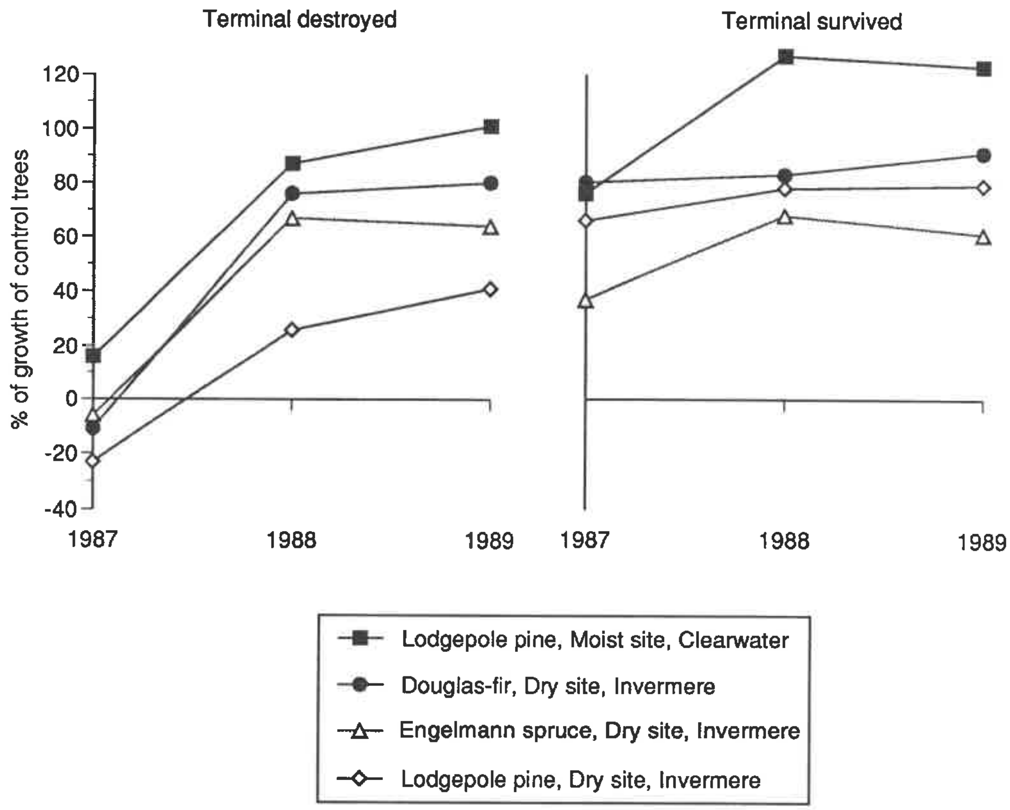

FIG. 4. Recovery of height growth of trees defoliated 61–100% in 1987 concurrent with planting and measured for 2 subsequent years, expressed as a percentage of growth on nondefoliated control trees.

TABLE 3. Height growth for the year of attack expressed as a percentage of nondefoliated controls for each species and location by defoliation and terminal bud survival class

		Clearwater	Invermere			Golden					
						Pine		D. fir		Larch	
Defoliation (%)	Terminal bud	Pine (con)	Pine (con)	D. fir (con)	Spruce (con)	Con	Post	Con	Post	Con	Post
0–60	Alive	96	82	95	83	107	75	86	81	83	73
	Dead	na	18	10	15	na	na	69	77	54	25
61–100	Alive	76	66	na	37	96	53	35	na	80	51
	Dead	15	−23	na	5	45	7	−18	−52	36	19

NOTE: Pine, lodgepole pine; D. fir, interior Douglas-fir; spruce, Engelmann spruce; larch, western larch; con, defoliation occurred concurrent with planting; post, defoliation occurred 1 year after planting; na, insufficient data were available ($n < 5$) within a damage class. Underlined means are significantly different from nondefoliated control means (t-test of percentages, $p \leq 0.05$).

some cases there also was significant dieback and a loss of height. On the moist site at Clearwater, competition from herbaceous plants was evident and inadvertent sheep grazing reduced the competition around the defoliated trees but not the controls. This resulted in more growth on the recovering trees than on the control trees.

On the moist site at Invermere, growth of pine had essentially recovered by the 2nd year, while on the dry site height growth was severely affected and slow to recover, particularly when the terminal bud was destroyed. Growth of defoliated trees on the dry site recovered to between 40 and 80% of that of the control trees in the 2nd year, with little change in the 3rd year. The percent growth for trees for the 2 years of data available at Golden followed similar patterns to those at Invermere. Thus, on dry and medium sites it appears that damaged trees exhibited below-normal growth rates for at least 3 years. Further monitoring should be carried out to determine the duration of these effects.

Discussion

Mortality or height growth was affected only when defoliation was greater than 60% or the terminal bud was lost. Lewis (1980) found similar effects with *Pinus elliottii* Engelm. in that reductions in height growth only occurred when defoliation was 75% or more. When both severe defoliation and bud loss occurred together, mortality increased and growth essentially ceased for the year of attack.

Längstrom and Hellqvist (1989), Carlson (1977), and Britton (1988) showed that severe defoliation of the coniferous species Norway spruce, *Picea abies* (L.) Karst.; Scots pine, *Pinus sylvestris* L.; white spruce, *Picea glauca* (Moench) Voss; and lodgepole pine reduced seedling root growth. Kelly and Mecklenburg (1978) found similar effects when working with the deciduous species *Betula pendula* Roth; decreases in root elongation were proportional to the degree of defoliation. Lavender and Hermann (1970) found that substances necessary for root growth of Douglas-fir came from the foliage and not the buds, and that artificially defoliated seedlings produced little or no roots. The essential substances were probably photosynthate, i.e., sugars and starch (Etter and Carlson 1973; Parker 1974). Parker (1979) found that the starch and sucrose contents of red oak (*Quercus rubra* L.) roots decreased as defoliation increased. In defoliated *Populus* ×*euramericana* cv. Negrito de Granada plants, $^{14}CO_2$ photosynthate was shifted to expanding shoots and lateral branches from the roots (Bassman and Dickmann 1985). This alteration in translocation patterns occurred within 24 h of defoliation.

In the present study, when other stress factors that affected root growth were present in addition to black army cutworm defoliation, there was an additive effect and mortality rates increased significantly in both pine and Douglas-fir. Usually poor planting and drought were the complicating factors. This result is supported by the work of Parker and Patton (1975), who found that drought and defoliation acting together on black oak, *Quercus velutina* Lam., seedlings resulted in lower starch contents than either factor acting alone. When seedlings are planted, root hairs grow into the surrounding soil to establish contact with a source of water and nutrients. If root growth is blocked or reduced by defoliation, then the seedlings may not survive. If another factor comes into play that also affects root growth, such as drought or poor planting, there appears to be a synergistic effect that places the seedlings in double jeopardy.

If defoliation occurred 1 year after seedlings were planted, there was significantly less mortality than when defoliation occurred concurrent with planting. By then root systems would have become established and the risk of mortality reduced. Lavender and Hermann (1970) found that root growth of seedlings in autumn was negligible and root establishment into the soil would not occur until the following spring. Therefore, planting in the autumn to avoid concurrent planting with a threatening population the following spring would be of little value.

At all levels of defoliation, Douglas-fir suffered a large amount of bud destruction. Spruce suffered similarly when defoliation was high but not at low levels of defoliation. In contrast, pine suffered very little bud destruction. This may explain why Douglas-fir seems to suffer higher mortality within each damage class than pine at Golden, where there is comparable data. However, susceptibility of different species cannot be ascertained properly until a replicated study can be undertaken of outbreaks within plantations of mixed species where defoliation, terminal bud destruction, height growth, and mortality can be determined on seedlings exposed to the same population density on the same site.

When terminal buds were destroyed, all species suffered severe growth losses the 1st year, but after new buds were formed and flushed the next spring, seedlings grew at rates related to their defoliation levels. This trend is consistent with data presented by Längstrom and Hellqvist (1989) and Hoffman and Steiner (1965).

There was a dramatic difference in recovery rates of pine growing on different sites. On the moist, fast-growing site near Clearwater, initial growth loss was less and recovery rapid as compared with the dry site near Invermere. At Clearwater, growth rates were close to normal by the 2nd year even for trees with terminal bud destruction. Opportunities should be sought to make similar site comparisons for other species.

The nature of the site should be considered, at least for pine, in pest management programs for black army cutworm. On a moist site not susceptible to drought, if a high level of planting quality is maintained, mortality should not exceed normal planting losses and most damaged seedlings should recover height growth rates within a year. However, as indicated in this study, mortality can be significant on poor growing sites, particularly those subject to drought. Poor planting will aggravate the problem. Height growth is slow to recover on poor sites, and 3 years after the attack, damaged seedlings were still falling behind adjacent nonattacked seedlings.

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