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Cottonwood leaf beetle (Coleoptera: Chrysomelidae) defoliation impact on *Populus* growth and above-ground volume in a short-rotation woody crop plantation

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Abstract

1 The impact of cottonwood leaf beetle *Chrysomela scripta* F. defoliation on four plantation-grown *Populus* clones was examined over three growing seasons. We used a split-plot design with two treatments: protected (by insecticides) and an unprotected control. Tree height and diameter at 1 m were measured annually and above-ground volume was calculated.

2 Protected trees of most clones had grown over 2 m taller after three growing seasons. Diameter differences ranged from over 1–4 cm larger on protected trees. Insecticide protection increased above-ground volume over 20 dm^3 in one clone, and at least 4 dm^3 in all others. *Chrysomela scripta* defoliation resulted in a 50–73% loss of above-ground volume. Defoliation also resulted in increased lateral branching and forked terminals on unprotected trees.

3 Defoliation impact varied among clone. The pure *Populus deltoides* clone 91 × 04-03 showed the greatest growth response to chemical protection, whereas clone NM2 (*P. nigra* × *P. maximowiczii*) responded the least.

4 Pest control is a key issue in short-rotation plantation management. Until adequate pest-resistant clones can be developed and natural enemy complexes better understood, chemical (biorational and organic) and cultural control may be used to reduce impacts of herbivorous pests.

Keywords Above-ground volume, chemical protection, *Chrysomela scripta*, defoliation impact, *Populus*, short-rotation forestry.

Introduction

Defoliating insects have varying impacts on tree growth, often depending on the timing, duration and intensity of defoliation (Kulman, 1971). However, plants have several ways of coping with defoliation, including nutrient reallocation, altering leaf size or canopy structure, or delaying senescence (Trumble *et al*., 1993). Plants can exhibit positive or negative responses depending on the extent of defoliation (Trumble *et al*., 1993 and references therein). Plants can often withstand short periods of intense defoliation; however, repeated defoliation may have negative impacts on plant growth, defence and reproduction (Crawley, 1983; Solomon, 1985; Trumble *et al*., 1993; Reichenbacker *et al*., 1996; Kosola *et al*., 2001).

Several studies have examined the effects of repeated defoliation on tree growth and physiology. Long-term defoliation by *Choristoneura pinus pinus* (Lepidoptera: Tortricidae) increased mortality (Volney, 1998) and decreased growth and volume accumulation in jack pine (*Pinus banksiana*) (Conway *et al*., 1999). Multi-year defoliation by *Choristoneura fumifera* (Lepidoptera: Tortricidae) caused growth rate reductions of up to 84% compared to pre-defoliation rates on balsam fir (*Abies balsamea*) (Piene, 1989). Kaitaniemi *et al.* (1999) simulated geometrid moth outbreak defoliation patterns on mountain birch (*Betula pubescens* ssp. *czerepanovii*) and detected no effect of low defoliation levels on tree growth. However, high levels of defoliation influenced tree growth and reproduction negatively. A 3-year *Malacosoma*

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disstria (Lepidoptera: Lasiocampidae) outbreak had negative effects on the growth of several hardwood species (Leininger & Solomon, 1995). *Populus tremuloides* suffered significantly reduced basal area, increased mortality and a higher susceptibility to secondary pathogens after several consecutive years of *M. disstria* defoliation (Churchill *et al*., 1964).

The cottonwood leaf beetle, *Chrysomela scripta* F., is a major defoliator in young *Populus* plantations (Salicales: Salicaceae) (Morris *et al*., 1975; Burkot & Benjamin, 1979; Harrell *et al*., 1981). *Chrysomela scripta* feeding can have a variety of effects, including seedling deformation, terminal damage and mortality (Burkot & Benjamin, 1979; Bingaman & Hart, 1992) and these add up to negative to positive impacts on *Populus* growth depending on defoliation intensity (Bassman *et al*., 1982; Reichenbacker *et al*., 1996). Furthermore, Fang & Hart (2000) demonstrated that *C. scripta* population levels were correlated with defoliation levels on *Populus*. For example, certain growth parameters of *Populus* clones were altered by simulated *C. scripta* defoliation after two growing seasons (Bassman *et al*., 1982; Reichenbacker *et al*., 1996). Increasing defoliation levels resulted in decreased tree height, diameter, above- and below-ground biomass, as well as total biomass for all clones; however, overcompensatory growth was found at 25% defoliation levels (Reichenbacker *et al*., 1996). Additional defoliation events in consecutive growing seasons further reduced tree growth (Bassman *et al*., 1982; Reichenbacker *et al*., 1996). Multiple defoliation events can have significant effects on tree growth over time, and stresses on the trees early in the rotation may result in considerable losses in later growing seasons (Solomon & Oliveria, 1993; Reichenbacker *et al*., 1996; Kosola *et al*., 2001).

Populus species are capable of significant increases in yearly growth; this trait makes them desirable for use in short-rotation woody crop systems. Over 20 000 ha have been developed into *Populus* plantations in the U.S. (Stanton, 2001). At present, attributable damage and potential loss to *C. scripta* can only be projected based on artificial defoliation studies (Bassman *et al*., 1982; Reichenbacker *et al*., 1996) and impacts to terminal leaders (Fang & Hart, 2000). Although these studies suggest significant growth losses resulting from prolonged or intense *C. scripta* defoliation, it is not known if long-term (>2 year) artificial and natural defoliation have the same effect on *Populus* growth.

The objective of our study was to determine the impact of natural *C. scripta* defoliation on plantation *Populus* in the north central region of the United States through three growing seasons. This study was designed to test two hypotheses: (1) protected trees will exhibit increased growth and above-ground volume accumulation when compared to unprotected controls; and (2) growth and susceptibility to *C. scripta* defoliation will differ among *Populus* clones.

Methods

Plant material

Four *Populus* clones were used in this study. 'Eugenei' is a *P. deltoides* Bartr. × *P. nigra* L. hybrid that is highly susceptible to *C. scripta* attack. NM2 is a *P. nigra* × *P. maximowiczii* A. Henry hybrid with low susceptibility to *C. scripta* attack. Two pure *P. deltoides* clones were included to compare with the interspecies hybrid clones. Clone D105 was originally provided from a selection programme at the University of Minnesota. Clone 91 × 04-03 is one of the best clones to originate from the Iowa State University breeding programme in terms of growth potential. Both *P. deltoides* clones were known to be susceptible to *C. scripta* attack, as are all *P. deltoides* clones of which we are aware. Further criteria for clone selection included cutting availability, commercial value, adaptability to central Iowa, and low susceptibility to other damaging biotic agents (i.e. stem borers, *Septoria* stem canker, *Melampsora* leaf rust).

Study area and design

The research site was located at the Moore Farm near the Iowa State University Institute for Physical Research and Technology. This area is on an alluvial floodplain of Squaw Creek and is located on the north-west edge of Ames, IA, U.S.A. Roundup® herbicide (Monsanto Corp., St. Louis, MO) was applied to kill existing alfalfa groundcover in autumn 1997. The study site was cultivated in spring 1998 prior to tree planting. Hardwood cuttings were obtained from research plots adjacent to the study area. Cuttings were planted in Rootrainers® (Spencer LeMaire, Edmonton, Alberta, Canada) in February 1998 and were outplanted as rooted cuttings in the last week of April 1998.

A split-plot design was used with the four *Populus* clones planted in two treatments: protected (defoliation controlled with insecticide) and unprotected (*C. scripta* were allowed to naturally infest and defoliate trees). The eight treatment combinations were replicated in five blocks. Clones were assigned randomly to one of four positions within a block and were planted in 16 tree plots; only the four interior trees were measured to discount for interclonal competition. Rooted cuttings were planted at 2 m spacing within a row, 2.5 m between rows, and 9.5 m between protected and unprotected sections of the block. All blocks were surrounded by one row of buffer trees ('I45/51', a *P. deltoides* × *P. nigra* hybrid). Weeds were mowed as needed throughout the study.

Chemical treatment

A previous study applied two different biorational insecticides to this plantation to evaluate their efficacy for *C. scripta* control (Coyle *et al*., 2000). Protected plots were sprayed at a rate of 3.5 L/ha (1.5 quart/acre) on 31 July and 17 August 1998 and 20 May 1999 with Novodor® (Abbott Laboratories, North Chicago, IL, U.S.A.), a commercially available *Bacillus thuringiensis* subspecies *tenebrionis* formulation. Trees were sprayed with a 15.2-L (4 gallon) Solo® backpack sprayer at 40 psi. Raven® (Ecogen Inc., Langehorne, PA, U.S.A.), a commercially available *Bacillus thuringiensis* ssp. *kurstaki* formulation, was applied at a rate of 2.34 L/ha (1 quart/acre) with a 113.6-L (30 gallon) sprayer (Fimco, Sioux City, IA, U.S.A.) on

22 June and 29 July 1999. Raven also was applied on 17 June and 17 July 2000 at a rate of 7.02 L/ha (3 quarts/acre) using a 1056-L (400 gallon) orchard sprayer. The sprayer was set at a rate of 528 L/ha (200 gallon/acre) and pulled at a speed of 2.5–3 mph. Treatments coincided with each *C. scripta* generation's peak larval hatch. Both formulations have shown excellent control of *C. scripta* during the larval stage on this study site (Coyle *et al.*, 2000). *Bacillus thuringiensis* formulations generally show less efficacy to adult *C. scripta* (James *et al.*, 1999; Coyle *et al.*, 2000). In addition to the biorational insecticides, Sevin® XLR Plus (Carbaryl [AI] 44.1%; Aventis CropScience, Research Triangle Park, NC, U.S.A.), a broad-spectrum insecticide, was applied to the protected trees twice during the 2000 growing season. The aforementioned orchard sprayer was used to apply at a rate of 2.34 L/ha (1 quart/acre) on 2 May 2000 to control large numbers of postwinter emerging adults and again on 11 August 2000 to control all *C. scripta* life stages.

Our study estimated defoliation based on the damage rating scale of Fang & Hart (2000). Trees were rated from 0 (no defoliation on leaf plastochron index [LPI] 0–8) (Larson & Isebrands, 1971) to 4 (>75% defoliation on LPI 0–8 and feeding damage to the shoot) before and after chemical treatment. The LPI is a leaf numbering system whereby the newest fully expanded leaf on a terminal with a lamina length ≥3 cm is given the number 0; leaves are consecutively numbered toward the stem. Damage on LPI 0–8 was measured because these are the leaves most preferred for *C. scripta* feeding (Bingaman & Hart, 1992). Defoliation levels on protected and unprotected trees were nearly identical prior to the Novodor application, and increased significantly after chemical treatment on unprotected trees (Fig. 1; Coyle *et al.*, 2000). Raven was equally effective in minimizing *C. scripta* defoliation. Pre-application defoliation ratings were higher; however, ratings decreased in the protected trees after the Raven application (Fig. 2; Coyle *et al.*, 2000). These data show that both Novodor and Raven provided excellent protection from *C. scripta* defoliation.

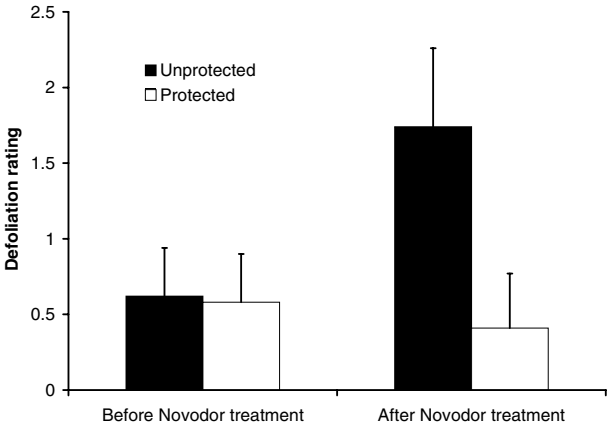

Figure 1 Combined defoliation ratings on four *Populus* clones in central Iowa, U.S.A., before and after Novodor application. Defoliation ratings were taken one week apart. Data from Coyle *et al.* (2000).

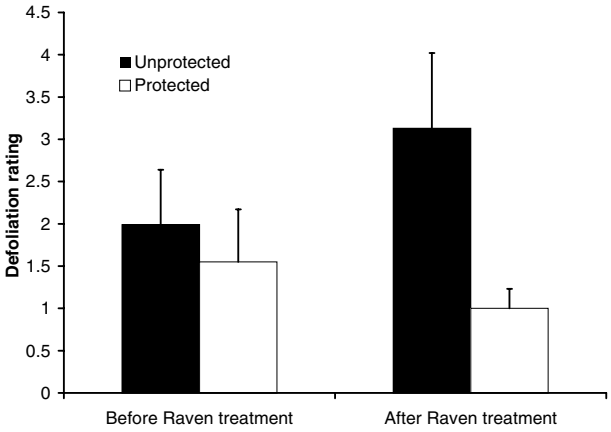

Figure 2 Combined defoliation ratings on four *Populus* clones in central Iowa, U.S.A., before and after Raven application. Defoliation ratings were taken one week apart. Data from Coyle *et al.* (2000).

Measurements and statistical analysis

Trees were measured each fall after leaf abscission for height (m) and stem diameter (cm) at 1 m. Volume (dm^3) was estimated using the equation (diameter^2 × height) × (π/12) from Reichenbacker *et al.* (1996). Data from the 1998–2000 growing seasons were analysed using a PROC MIXED repeated measures ANOVA (SAS Institute, 1999) to test for overall treatment, clone and year differences. The treatment × clone, treatment × year, clone × year and treatment × clone × year interactions also were tested. These interactions gave us a clearer picture of the actual effects that the chemical and clonal factors had on tree growth. Means were compared using the Tukey–Kramer *t*-test ($\alpha = 0.05$).

Foliar pathogens (e.g. *Melampsora* leaf rust, *Marssonina* leaf blight, *Septoria* leaf spot) and herbivory other than that of *C. scripta* were minimal on all clones and did not differ noticeably among split plot treatment within a clone. Small numbers of viceroy larvae, *Limentis archippus* (Cramer) (Lepidoptera: Nymphalidae), were observed on occasion, but damage by this insect was not measurable and was assumed to have no impact on our study.

Results

Defoliation impacts on tree height

Treatment, clone and year all affected tree height significantly after three growing seasons (Table 1). Protected trees grew much taller than unprotected trees ($F = 140.03$; d.f. = 1, 28; $P < 0.001$). Clones also differed significantly in height ($F = 5.23$; d.f. = 3, 28; $P = 0.005$). As expected, significant yearly increases in tree height occurred ($F = 2676.58$; d.f. = 2, 299; $P < 0.001$).

Several significant treatment interactions were observed, including a treatment × clone effect ($F = 3.40$; d.f. = 3, 28; $P = 0.032$). Clone 91 × 04-03 responded most positively to

Table 1 Growth parameters (mean ± SE) of four *Populus* clones exposed to two *C. scripta* defoliation treatments during the 1998–2000 growing seasons in central Iowa, U.S.A. Measurements were taken at the conclusion of each growing season

				Growing season		
Growth parameter	Clone	n^a	Treatment	1998	1999	2000
Height (m)	91 × 04-03	20	Unprotected	2.39 ± 0.13	3.30 ± 0.16	4.82 ± 0.20
		20	Protected	2.79 ± 0.09	4.95 ± 0.14	8.16 ± 0.16
	D105	20	Unprotected	2.53 ± 0.10	3.63 ± 0.08	5.17 ± 0.09
		20	Protected	2.80 ± 0.08	4.35 ± 0.11	6.82 ± 0.18
	Eugenei	20	Unprotected	2.25 ± 0.06	3.39 ± 0.09	4.98 ± 0.16
		20	Protected	2.46 ± 0.07	4.38 ± 0.11	7.17 ± 0.18
	NM2	20	Unprotected	2.72 ± 0.15	3.89 ± 0.19	5.66 ± 0.18
		20	Protected	2.80 ± 0.11	4.62 ± 0.12	8.22 ± 0.16
Diameter (cm)	91 × 04-03	20	Unprotected	1.87 ± 0.13	5.13 ± 0.35	7.18 ± 0.37
		20	Protected	2.24 ± 0.12	6.90 ± 0.25	11.23 ± 0.29
	D105	20	Unprotected	1.49 ± 0.07	3.75 ± 0.14	5.60 ± 0.18
		20	Protected	1.80 ± 0.08	4.91 ± 0.12	7.74 ± 0.20
	Eugenei	20	Unprotected	1.38 ± 0.07	3.54 ± 0.17	5.33 ± 0.29
		20	Protected	1.70 ± 0.10	4.74 ± 0.20	7.43 ± 0.26
	NM2	20	Unprotected	1.66 ± 0.11	4.74 ± 0.24	7.00 ± 0.32
		20	Protected	1.96 ± 0.08	5.90 ± 0.25	8.39 ± 0.34
Calculated volume (dm^3)	91 × 04-03	20	Unprotected	0.261 ± 0.038	2.663 ± 0.347	7.206 ± 0.862
		20	Protected	0.406 ± 0.047	6.520 ± 0.567	27.517 ± 1.649
	D105	20	Unprotected	0.162 ± 0.020	1.396 ± 0.117	4.363 ± 0.300
		20	Protected	0.252 ± 0.023	2.804 ± 0.172	10.936 ± 0.714
	Eugenei	20	Unprotected	0.125 ± 0.017	1.203 ± 0.136	4.112 ± 0.475
		20	Protected	0.210 ± 0.026	2.751 ± 0.268	10.871 ± 0.868
	NM2	20	Unprotected	0.234 ± 0.035	2.579 ± 0.330	7.843 ± 0.853
		20	Protected	0.298 ± 0.030	4.483 ± 0.423	15.912 ± 1.241

[a]In 2000 $n = 19$ for clone 91 ×04-03, Unprotected; 18 for clone 91 ×04-03, Protected; and 18 for clone D105, Unprotected.

chemical protection and were, on average, 41% taller than unprotected trees. Conversely, D105 responded the least to the chemical protection (protected trees were 24% taller than unprotected trees). Year × treatment ($F = 226.07$; d.f. = 2, 299; $P < 0.001$) and year × clone ($F = 6.94$; d.f. = 6, 299; $P < 0.001$) interactions also were significant. Protected trees were consistently taller than unprotected trees, and clonal differences became readily apparent during the second and third growing seasons (Table 1). NM2 was the tallest clone in all unprotected plots, and in all but one year in the protected plots.

Significant treatment × clone × year interactions were evident ($F = 5.35$; d.f. = 6, 299; $P < 0.001$). Differences in protected plots became apparent in the second and third growing seasons. After the second season, protected clone 91 × 04-03 trees were significantly taller than unprotected trees ($t = 6.87$; d.f. = 6, 299; $P < 0.001$). All unprotected trees were significantly shorter than protected trees of the same clone at the end of the third growing season. Clone 91 × 04-03 showed the most height loss in unprotected plots (Table 1). After three growing seasons, protected 91 × 04-03 trees were taller than protected D105 ($t = 5.22$; d.f. = 6, 299; $P < 0.001$) and Eugenei ($t = 3.79$; d.f. = 6, 299; $P < 0.035$) trees. NM2 protected trees also were significantly taller than D105 ($t = 5.88$; d.f. = 6, 299; $P < 0.001$) and Eugenei ($t = 4.42$; d.f. = 6, 299; $P < 0.004$) protected trees at the end of the third growing season (Table 1).

Defoliation impacts on tree diameter

Diameter was significantly greater in protected trees ($F = 64.30$; d.f. = 1, 28; $P < 0.001$). Significant clonal diameter differences also were apparent ($F = 21.47$; d.f. = 3, 28; $P < 0.001$). Diameter increased significantly each year ($F = 2265.50$; d.f. = 2, 299; $P < 0.001$).

In contrast to the height measurements, there was no significant treatment × clone effect ($F = 2.03$; d.f. = 3, 28; $P < 0.132$). However, the effects of treatment × year ($F = 75.38$; d.f. = 2, 299; $P < 0.001$) and clone × year ($F = 19.16$; d.f. = 6, 299; $P < 0.001$) were significant. Clone 91 × 04-03 had nearly 11 cm diameter after three growing seasons when protected, and again showed the most positive response to chemical protection. The percent diameter lost in clone NM2 declined in unprotected trees (compared with protected trees) after the third growing season.

A significant clone × treatment × year interaction occurred ($F = 5.58$; d.f. = 6, 299, $P < 0.001$). Diameter of the two largest clones, 91 × 04-03 and NM2, began to differentiate after the second growing season, and after the third season clone 91 × 04-03 protected trees had a significantly larger diameter than protected NM2 trees ($t = 7.03$; d.f. = 6, 299; $P < 0.001$). Both of these clones were significantly larger at 1 m than the other clone × treatment combinations.

Defoliation impacts on above-ground volume

Significant differences in above-ground volume were observed. Tree volume increased significantly in protected trees compared to unprotected controls ($F = 110.59$; d.f. = 1, 28; $P < 0.001$). Significant yearly increases also were apparent ($F = 942.85$; d.f. = 2, 299; $P < 0.001$). Volume differed significantly by clone ($F = 24.02$; d.f. = 3, 28; $P < 0.001$).

Significant differences in above-ground volume accumulation resulted from several interactions. The treatment × clone ($F = 10.23$; d.f. = 3, 28; $P < 0.001$) and clone × year ($F = 40.76$; d.f. = 6, 299; $P < 0.001$) interactions influenced tree volume significantly after three seasons. Also, the treatment × year ($F = 221.23$; d.f. = 2, 299; $P < 0.001$) interaction increased tree volume accumulation significantly.

Treatment × clone × year interactions were significant ($F = 22.22$; d.f. = 6, 299; $P < 0.001$). Chemical protection always resulted in increased volume (Table 1). 91 × 04-03 and NM2 were the two largest clones, with average above-ground volumes in the protected plots over 27 and 15 dm^3, respectively (Table 1). 91 × 04-03 had significantly more volume in protected plots than the next largest clone, NM2 ($t = 11.30$; d.f. = 6, 299; $P < 0.001$). NM2 had significantly more volume than the third largest clone, D105 ($t = 5.00$; d.f. = 6, 299; $P < 0.001$). Volume accumulation on Eugenei in protected plots was not significantly different than that of NM2 in untreated plots ($t = 3.04$; d.f. = 6, 299; $P < 0.277$). Above-ground volume lost from *C. scripta* defoliation ranged from 50 to over 73% after three growing seasons (Table 2). Clone NM2 was the least affected, whereas *C. scripta* defoliation caused the most volume loss on clone 91 × 04-03.

Discussion

This study demonstrated that, at least in the establishment phase, *C. scripta* can have a major negative impact on the productivity of short-rotation *Populus* plantations. High rates of biomass production will not be possible unless protective measures, such as the intensive spray programme used in this study, are applied. Indeed, the impact of *C. scripta* negated the potential growth superiority of our newly selected *P. deltoides* clone 91 × 04-03 when it was compared to the hybrid clone NM2 (Fig. 3). Considering the financial and environmental costs of such an intensive spray programme, it may be worthwhile to focus on developing resistant clones through conventional breeding and/or genetic transformation (Klopfenstein *et al*., 1997).

Table 2 Biomass volume lost (%) as a result of repeated *C. scripta* defoliation on four *Populus* clones grown under short-rotation intensive culture in central Iowa, U.S.A.

	Growing season		
Clone	1998	1999	2000
91 × 04-03	35.65	59.15	73.82
D105	35.80	50.20	59.63
Eugenei	40.32	56.29	62.39
NM2	21.41	42.48	50.94

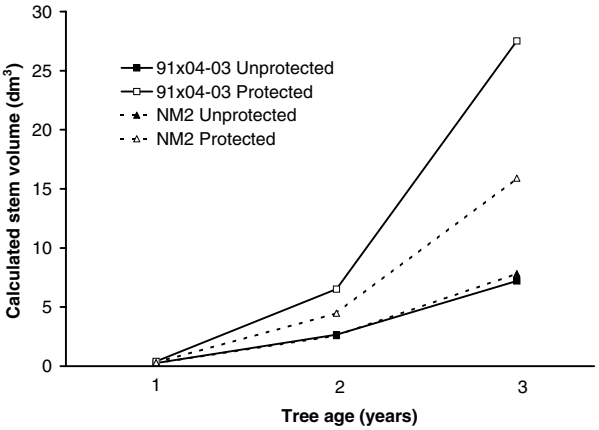

Figure 3 Mean calculated stem volume of clones 91 × 04–03 and NM2 over three growing seasons in central Iowa, U.S.A.

Several studies have evaluated the effects of natural insect defoliation on plantation *Populus*. Solomon & Oliveria (1993) examined the effects of a poplar tentmaker, *Clostera inclusa* (Lepidoptera: Notodontidae), outbreak on older (6–12 year old) *Populus* plantations. Defoliation intensities up to 90% were observed, resulting in higher mortality and significant diameter and height reductions. *Chrysomela scripta* defoliation also can increase susceptibility to secondary pests and pathogens (Bassman *et al*., 1982; Dickmann & Stuart, 1983). We found no mortality in our study directly attributable to *C. scripta* defoliation; however, five trees (3%) died during our study. All died during the 2000 growing season; mortality was attributable to *Septoria musiva* Peck stem canker. These deaths were possibly an indirect effect of repeated *C. scripta* defoliation and subsequently weakened tree defences. Up to 92.5% terminal mortality and a 4- to 8-week premature leaf drop on one-year-old *Populus* in Mississippi was caused by *Chaitophorus populicola* (Homoptera: Aphididae) defoliation (Solomon, 1986). *Lymantria dispar* L. (Lepidoptera: Lymantriidae) defoliation significantly reduced *Populus* growth, canopy light transmission, carbon allocation and nitrate uptake over a 3-year period (Kosola *et al*., 2001).

Previous studies have examined the effect of mechanical defoliation on *Populus* growth parameters (Bassman *et al*., 1982; Reichenbacker *et al*., 1996). Uniform artificial defoliation did not affect tree growth at low (0–40%) levels, but height and diameter reductions in excess of 20% occurred at high (75–80%) levels (Bassman *et al*., 1982). Reichenbacker *et al*. (1996) recorded increased tree growth at low defoliation levels (0–25% of LPI 0–8) and a 34% reduction in above-ground volume at high defoliation levels (75%). Although simulated defoliation studies often are indicators of what might happen in natural systems, the precise physical and chemical plant–insect interactions of natural herbivory are absent.

We studied the impact of natural *C. scripta* defoliation on four plantation-grown *Populus* clones for three field

seasons. All insecticide applications in 1998 and those for generations 1 and 2 in 1999 controlled *C. scripta* defoliation effectively. However, phenological asynchrony in the third generation of 1999 made precise identification of peak larval hatch impossible. Also, on 23 July 1999 all trees in both treatments were severely defoliated on LPI 0–8 as a result of adult movement into the protected trees from both the unprotected trees and other areas of the Moore Farm. The application of Raven on 29 July 1999 controlled the first part of the third *C. scripta* generation, but in hindsight another application one week later would have been needed to control the second half of the third and beginning of the fourth *C. scripta* generation effectively. Trees recovered slightly, leafing out at the tips of the terminals. Residual protection continued for approximately 2 weeks, as damage ratings taken 6 and 13 August 1999 showed lower defoliation in protected plots. However, damage ratings taken 20 August showed no differences between protected and unprotected trees. All *C. scripta* life stages could be found in both treatments beginning in early August, and by 31 August 1999 no clear *C. scripta* generation was evident. Most lateral branches and several terminal leaders had set bud by this time. Terminal growth was apparent only on clone NM2. Greater control was accomplished in 2000, primarily as a result of the Sevin applications. However, large numbers of adult beetles emigrated from surrounding plantations, resulting in some defoliation and terminal damage on the protected trees during *C. scripta* generations 3 and 4.

Our results suggest that damage by natural *C. scripta* defoliation can be greater than that predicted from similar artificial defoliation studies (Bassman *et al.*, 1982; Reichenbacker *et al.*, 1996), despite the fact that protected trees suffered from defoliation during the second growing season. Height growth in the first 2 years was slightly greater than that obtained by Reichenbacker *et al.* (1996), yet less than that reported in Bassman *et al.* (1982). However, trees in the study by Bassman *et al.* (1982) were irrigated. Diameter growth in our study was slightly less than that observed in Reichenbacker *et al.* (1996); however, their study measured diameter at 0.2 m, whereas we measured at 1 m. Our observed diameters were greater than those in Bassman *et al.* (1982). However, diameter comparisons between studies are difficult to make because of the many factors that influence diameter, including stand density, clonal differences and abiotic factors such as site and climate conditions.

Perhaps the most important growth indicator is above-ground stem volume (Eaton, 2000). *Chrysomela scripta* defoliation decreases *Populus* leaf area, thus decreasing the tree's ability to capture solar radiation and add volume. With the exception of energy plantations where the entire tree is utilized, stem volume is the only merchantable tissue (Kenney *et al.*, 1993). Our results agreed with those of Bassman *et al.* (1982) and Reichenbacker *et al.* (1996) in that defoliation can and does reduce tree growth and above-ground volume accumulation.

Previous studies have examined the effect of chemical protection on *Populus* growth parameters (Abrahamson *et al.*, 1977; Solomon, 1985). Chemical treatment consistently resulted in 80–90% less *C. scripta* defoliation in 2- and 3-year-old cottonwood plantations. Furthermore, trees receiving chemical protection during the second and third growing seasons averaged 1.25 m taller than controls at the end of three growing seasons. Our study showed much greater growth differences between protected and control trees; height differences attributable to defoliation suppression in our study ranged from 1.65 (clone D105) to 3.34 m (clone $91 \times 04\text{-}03$) after three growing seasons. Diameter measurements in protected plots also were much larger in our study; increases up to 4.05 cm were obtained when *C. scripta* defoliation was minimized. These differences between studies were probably caused by the insecticide treatment in the first year of tree growth.

Height, diameter and volume in our protected plots were comparable to, and sometimes larger than, that in other studies (Ceulemans *et al.*, 1992; DeBell *et al.*, 1997; Scarascia-Mugnozza *et al.*, 1997). We obtained above-ground volume measurements from 2.8 to 6.5 dm^3 in pure species after two growing seasons; these values were greater than those in a study by Ceulemans *et al.* (1996). Both pure species and hybrids used by Ceulemans *et al.* (1992) and Scarascia-Mugnozza *et al.* (1997) accumulated more above-ground volume than ours after three growing seasons. Hybrids used in their studies differed from the ones used in our study; however, a longer growing season and irrigation were probably the more important factors influencing growth.

In other studies, hybrid clones tended to outperform pure species (Ceulemans *et al.*, 1992; DeBell *et al.*, 1997; Scarascia-Mugnozza *et al.*, 1997). We did not explicitly test this hypothesis, and attained varying results in our study. The hybrid clone NM2 grew taller than the pure *P. deltoides* clones D105 and $91 \times 04\text{-}03$ in protected plots. However, both diameter and volume were greater in protected plots of $91 \times 04\text{-}03$, our largest clone. Also, the hybrid Eugenei had the smallest diameter and volume of the clones used. Clone $91 \times 04\text{-}03$ in protected plots accumulated greater volume amounts after 3 years (Table 1). However, clone $91 \times 04\text{-}03$ lost over 73% above-ground volume as a result of *C. scripta* defoliation after three growing seasons (Table 2). Furthermore, the percent volume lost (Table 2) due to *C. scripta* defoliation indicates that clone NM2 and $91 \times 04\text{-}03$ would show the least and most economic benefit, respectively, from chemical protection.

The benefits of biorational pesticide use include high specificity, rapid degradation and practically no harm to non-target organisms (Tabashnik, 1994; Bauer, 1995). However, *C. scripta* can develop resistance to *Bacillus thuringiensis* formulations in the laboratory (Bauer *et al.*, 1994). An integrated pest management approach incorporating various management tactics should be used to manage and control insect resistance to biorational pesticides (Tabashnik, 1994; Bauer, 1995; Coyle *et al.*, 2002). Repeated use of the same chemical control method will inevitably lead to insect resistance.

Because the proportion of leaves preferred by *C. scripta* decreases with tree age, it is generally thought that *C. scripta* is a major pest of young plantation *Populus* only.

However, we do not know when *C. scripta* defoliation ceases to influence tree growth significantly. Our study showed that *C. scripta* defoliation reduced tree growth significantly after three growing seasons. Efforts will be made to continue this study to determine if the trends seen here continue or change over time. Results generated from this study will provide critical information on management options to determine the impact of *C. scripta* population levels, defoliation and subsequent impact on plantation *Populus* growth.

This study demonstrated the effects of long-term defoliation on plantation *Populus* growth and volume accumulation. The effects of *C. scripta* defoliation can be severe and cause significant growth and economic losses. Plantation managers need to be aware of and adequately control *C. scripta* if *Populus* is to be a viable option for energy, pulp and solid wood production in short-rotation woody crop plantations.

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