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Effects of repeated cottonwood leaf beetle defoliation on *Populus* growth and economic value over an 8-year harvest rotationDavid R. Coyle^{a,1,*}, Elwood R. Hart^{a,b}, Joel D. McMillin^{a,c}, Lita C. Rule^a, Richard B. Hall^a^a Iowa State University Department of Natural Resource Ecology and Management, Ames, IA 50011, USA^b Emeritus, Iowa State University Departments of Entomology and Forestry, Ames, IA, USA^c USDA Forest Service, Forest Health Protection, Flagstaff, AZ, USA

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ABSTRACT

The effects of 8 years of cottonwood leaf beetle, *Chrysomela scripta*, defoliation on growth and economic value of four *Populus* clones (91 × 04-03, D105, Eugenei, and NM2) was investigated in a split-plot randomized complete block design with unprotected and insecticide-protected plots. After 8 years clones 91 × 04-03 and D105 had significantly greater survival than Eugenei or NM2. This difference in survival was not attributed to chemical protection, and while not qualified, was most likely the result of disease and storm breakage. Protected trees had significantly greater height, diameter, and stem volume than unprotected trees, with clone 91 × 04-03 consistently growing the largest. Protected plots had greater basal area and stem biomass than unprotected plots, but branch biomass was greatest in unprotected plots. Differences in branch biomass were most likely due to loss of apical dominance, and subsequent increased branching, resulting from *C. scripta* defoliation. Aboveground biomass was unaffected by treatment because of the increased branch biomass of unprotected trees. Clone 91 × 04-03 responded the most positively to chemical protection, as stem volume of unprotected trees was over 30% less than in protected trees. A financial analysis of our data indicated that none of the clone × treatment combinations would be economically acceptable due to the high land costs in the midwestern US. However, the use of less expensive insecticides may make clone 91 × 04-03 an economically viable crop in this region.

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1. Introduction

Defoliating insects have varying impacts on tree growth, often depending on the timing, duration, and intensity of feeding (Kulman, 1971; Mattson and Addy, 1975). Plants have several ways of coping with defoliation, including nutrient reallocation, altering leaf size or canopy structure, or delaying senescence, and can exhibit positive or negative responses depending on the severity of defoliation (Trumble et al., 1993 and references therein). Plants often can withstand short periods of intense defoliation; however, repeated defoliation events may negatively impact plant growth,

defense, and reproduction (Crawley, 1983; Solomon, 1985; Trumble et al., 1993; Reichenbacher et al., 1996; Kosola et al., 2001). Deleterious effects of repeated defoliation have been shown in jack pine (*Pinus banksiana*) (Volney, 1998; Conway et al., 1999), balsam fir (*Abies balsamea*) (Piene, 1989), mountain birch (*Betula pubescens* ssp. *czerepanovii*) (Kaitaniemi et al., 1999), quaking aspen (*Populus tremuloides*) (Churchill et al., 1964), and several other hardwood species (Leininger and Solomon, 1995).

Populus selections are capable of significant yearly growth, and this trait makes them desirable for use in short-rotation woody crop systems that, in turn, feed into important industries such as wood products, fiber, and energy. Over 22,000 ha have been developed into *Populus* plantations in the US (Stanton et al., 2002). One of the most important challenges for successful *Populus* cultivation is repeated defoliation by insects, particularly the cottonwood leaf beetle, *Chrysomela scripta* (Coleoptera: Chrysomelidae) which is a major defoliator in young *Populus* (Salicales: Salicaceae) plantations (Morris et al., 1975; Burkot and Benjamin,

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1979; Harrell et al., 1981; Coyle et al., 2005). *Chrysomela scripta* feeding can result in seedling deformation, terminal damage, temporary loss of apical dominance (Burkot and Benjamin, 1979; Bingaman and Hart, 1992) increased susceptibility to pathogens (Klepzig et al., 1997), and mortality. These effects can elicit a range of responses in *Populus* growth depending on defoliation intensity (Bassman et al., 1982; Reichenbacher et al., 1996). For example, increasing defoliation levels resulted in decreased tree height, diameter, above- and below-ground biomass, as well as total biomass for all clones; however, over-compensatory growth occurred at the 25% defoliation level (Reichenbacher et al., 1996). Multiple defoliation events can have significant effects on tree growth and wood specific gravity over time (Bassman et al., 1982; Reichenbacher et al., 1996; Hall et al., 2001), and stresses on the trees early in the rotation may result in considerable losses in later growing seasons (Solomon and Oliveria, 1993; Reichenbacher et al., 1996; Kosola et al., 2001).

Potential long-term growth reductions resulting from *C. scripta* defoliation have been projected based on artificial defoliation studies (Bassman et al., 1982; Reichenbacher et al., 1996). While these studies suggest significant growth losses resulting from prolonged or intense *C. scripta* defoliation, it is not known if long term (>2 year) artificial defoliation has the same effect on *Populus* growth as natural defoliation. Furthermore, observations of *C. scripta* attacks in plantations indicate that attacks decline substantially after the first 3 or 4 years as the trees grow taller and the percentage of susceptible foliage decreases (Fang, 1997). Therefore, we designed a study to determine the impact of natural *C. scripta* defoliation on *Populus* biomass production over an 8-year rotation, typical of what might be used for a fiber or energy crop.

Two reports on our observations were made during the early development of these stands (Hall et al., 2001; Coyle et al., 2002). Over the first three growing seasons, trees protected from *C. scripta* defoliation by insecticides had grown over 2 m taller and up to 4 cm greater in diameter than unprotected trees, resulting in a 50–73% gain in stem volume for protected trees. These defoliation effects varied by *Populus* clone; a pure *P. deltoides* clone showed the greatest growth response in absence of defoliators. In addition, there was an increase in branching and forked terminals on defoliated trees (Coyle et al., 2002), 39–54% less basal area in unprotected stands, and up to a 4% loss in wood specific gravity (Hall et al., 2001). Our first objective was to determine the effects of defoliation that occurred during the early, highly susceptible plantation establishment years, over a complete harvest rotation, on growth and biomass of intensively managed *Populus*. We hypothesized that protected trees would exhibit increased growth and biomass when compared to unprotected controls, and that responses would vary among *Populus* clones.

The economic potential of *Populus* for fiber, energy, solid lumber, furniture and other uses is reflected in the increase of acreage planted to *Populus* by industry (Leavengood and Reed, 1997) as well as in farm-type or agroforestry approaches practiced by private small landowners in the US and other parts of the world (Clark et al., 1998; Jain and Singh, 2000; Robison-Avila, 2006; PAMUCEAF, 2007). Our second objective was to determine if management of early rotation defoliation would improve the profitability of intensively managed *Populus* plantations in the Midwest. The stand-level financial analyses presented in this paper pertain to a production system for biorenewable energy materials that could be established in agricultural regions such as the American Midwest. We expected differences in the financial performance of the protected versus the unprotected stands. The “average price” for biorenewables is a moving target because production and processing requirements for these materials are yet to be firmly established in the economy; thus alternative price levels are used to provide a range of possible financial trajectories

for the stands being examined. The environmental and other non-market contributions of such stands are not considered in the analyses, but they can be significant (Bateman and Lovett, 2000; Bowyer, 2001).

2. Materials and methods

The site, plant materials, and experimental design were described in greater detail in Coyle et al. (2000) and Coyle et al. (2002). A brief description follows.

2.1. Study area, plant material, and design

The research site was located at the Moore Farm near the Iowa State University Institute for Physical Research and Technology, located on the northwest edge of Ames, Iowa, USA. Glyphosate was applied to kill existing vegetation, and the study site was disked prior to planting study trees. Weeds were controlled mechanically as needed throughout the study.

Four *Populus* clones were planted: Eugenei, a *P. deltoides* Bartr. × *P. nigra* L. hybrid that is highly susceptible to *C. scripta*; NM2, a *P. nigra* × *P. maximowiczii* A. Henry hybrid with usually low susceptibility to *C. scripta*; and two pure *P. deltoides* clones, D105 (selected from a wild single tree seed collection by Dr. C. Mohn, University of Minnesota, USA) and 91 × 04-03 (Iowa State University breeding program clone exhibiting excellent growth potential). All *P. deltoides* clones are known to be susceptible to *C. scripta*.

A split-plot design was used with the four *Populus* clones planted in two treatments: protected (sprayed with insecticide to minimize *C. scripta* defoliation) and an unprotected control (*C. scripta* were allowed to naturally colonize and defoliate trees). The eight clone × 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 minimize any potential for interclonal competition and edge effects (Zavitkovski, 1981). Hardwood cuttings were grown in the greenhouse and outplanted as rooted cuttings during April 1998, at 2 m spacing within a row and 3 m between rows (Coyle et al. (2002) incorrectly reported tree spacing as 2.5 m × 3 m; the authors regret this error). A 9.5 m separation was maintained between the protected and unprotected sections of the block. All blocks consisted of a central four measurement trees surrounded by one border row of trees of the same clone. One additional row of buffer trees (I45/51, a *P. deltoides* × *P. nigra* hybrid) was planted along the outside edge of all the blocks.

2.2. Insecticide treatment

A combination of broad-spectrum and biorational insecticides were used to reduce *C. scripta* feeding (Coyle et al., 2002). Plots were treated twice in 1998 and once in 1999 with Novodor[®] (Abbott Laboratories, North Chicago, IL), a commercially available *Bacillus thuringiensis* subspecies *tenebrionis* formulation. Raven[®] (Ecogen Inc., Langehorne, PA), a commercially available *B. thuringiensis* subsp. *kurstaki* formulation, was applied twice in 1999, 2000, and 2001. Treatments coincided with peak larval hatch of each *C. scripta* generation. Both of these formulations have shown excellent control of *C. scripta* on this study site (Coyle et al., 2000). Sevin (Carbaryl [AI] 44.1%; Aventis CropScience, Research Triangle Park, NC), a broad-spectrum insecticide, was applied in May 2000 to control large numbers of post-winter emerging adults and again in August 2000 to control all *C. scripta* life stages. All chemical treatments were performed by licensed applicators following label directions. Plots were not treated from 2002 to 2005 because of low endemic *C. scripta* populations and the age of the trees being past the most susceptible stage for *C. scripta* attack.

Damage ratings (Fang and Hart, 2000) were over 4 and 3 times higher on unprotected trees in 1998 and 1999, respectively (Coyle et al., 2000). Treatments in 2000 and 2001 produced similar results (ERH and RBH, personal observation). Herbivory other than that of *C. scripta* was minimal. Additionally, we assumed there would be equal leaf disease levels (e.g., *Melampsora* leaf rust, *Marssonina* leaf blight, *Septoria* leaf spot) on both protected and unprotected plots and that chemical treatment had no impact on these pathogens. However, after three growing seasons increased *Septoria* levels coincided with increased *C. scripta* damage (Coyle et al., 2002), although this was not quantified.

2.3. Annual growth measurements

Height and stem diameter was measured during winter dormancy from 1998 through 2005. A metric pole was used to measure height in 1998–2001, and a clinometer was used to measure height in 2002 and 2003. Because of equipment error, height was not accurately measured in 2004. In 2005, height was measured on felled trees using a tape during the destructive harvest (see below). Diameter was measured at 1 m to avoid error associated with stump swell and because not all trees had reached diameter at breast height (1.4 m) by the end of the first growing season. Stem volume was estimated using the equation from Reichenbacher et al. (1996) that assumes the shape of young tree stems to be a cone:

$$\text{Volume (m}^3\text{)} = (\text{diameter}^2 \times \text{height}) \times \left(\frac{\pi}{12}\right) \quad (1)$$

2.4. Destructive harvest

Trees were harvested following the 2005 growing season. Trees were cut at a 20 cm stump height, and total tree height, as measured to ground level, was determined to the nearest 0.01 m. All branches were removed, and dead branches were discarded because they would have no role in most biomass end uses. Live branches for each tree were chipped, bagged and transported to the laboratory where they were dried to a constant weight and weighed to the nearest g. The stem was cut into sections (<50 kg), and the fresh weight of each segment (to the nearest 0.02 kg) was measured with a digital field scale (Intercomp, Minneapolis, MN). Before use, the field scale was tested against two laboratory scales with a series of 29 weights ranging from 1 to 50 kg (total field scale capacity). A small, systematic error in the field scale was detected and a regression equation was developed to correct field values to actual fresh weights:

$$\text{true fresh weight} = 0.999 * (\text{field scale weight}) + 0.0226(r^2 = 1) \quad (2)$$

This correction was applied individually to the field weight of each stem segment before the segment weights were summed to give the whole-tree stem fresh weight. After field weighing, discs were cut from the stem segments for dry weight determination. Three to six discs were taken from each stem depending on tree height, beginning with a basal disc taken just above the felling cut and one disc approximately every 4 m thereafter. For trees with co-dominant stems, one disk was taken from each stem at each sampling height. Discs were immediately sealed in plastic bags and placed in coolers. Discs were weighed to the nearest mg in the laboratory, oven-dried to a constant weight, and reweighed to the nearest mg. The dry weight/fresh weight ratio was then used to adjust the total stem fresh weight at harvest to an estimated dry weight at harvest. Average stem and living branch dry weights were used, along with the spacing between trees, and the survival rate, to calculate projected plantation yields on a MG/ha basis over the 8-year rotation. Differences in yield between protected and

unprotected stands were then subjected to an economic analysis of the costs and benefits of reducing *C. scripta* populations during the first 4 years with insecticide applications.

2.5. Statistical analyses

Individual tree height, diameter, calculated stem volume, and basal area were analyzed using a repeated-measures ANOVA (Proc Mixed, SAS Inc., Cary, NC) to test for overall treatment, clone, and year differences and their interactions. Survival (the proportion of surviving trees in each plot), stem, branch, and aboveground (stem + branch) biomass were analyzed at the conclusion of the rotation using an ANOVA (Proc Mixed, SAS Inc., Cary, NC) to examine the effects of clone, treatment, and the clone by treatment interaction. All means were compared using the Tukey–Kramer *t*-test. We used a significance level of $\alpha = 0.05$ for all statistical tests.

2.6. Financial analyses

The stand-level financial analyses used the perspective of private landowners or investors and employed the discounted cash flow method of evaluation. A real discount rate of 6% was used. Considering that the annual inflation rate was close to 3%, this gives the investor a 9% nominal rate of return. Several existing economic studies on *Populus* use 5%–6% real rates of interest (Bowersox and Ward, 1976; Strauss and Grado, 1997; Anderson and Luckert, 2007).

Two criteria used in the analyses are the net present value (NPV) and internal rate of return (IRR). The NPV is a straightforward discounted cash flow measure of project worth (Gittinger, 1982; Klemperer, 1996). Although use of NPV has a bias for large projects (Gregory, 1987), it is best for capital budgeting decisions because it indicates project size (Gunter and Haney, 1984), which could be a more important consideration for individual farmers or investors interested in biorenewable markets. Investments with positive NPVs are acceptable; the higher the NPV, the more attractive the investment. A NPV = 0 simply means that although the project is just “breaking even” the investor still earns the rate of return used in the evaluation which, in this case, is equivalent to the project’s IRR. The IRR is commonly applied by international institutions because of its simplicity (Gregory, 1987; Kohli, 1993). The higher the IRR is compared to an alternative rate of return, the better the investment’s financial performance. Quicksilver (Research Triangle Park, NC), a forestry financial investment program (Vasievich et al., 1984), was used to determine the financial criteria values.

Three pricing levels (\$66, \$55, and \$44) per dry MG were used to describe different possible earning trajectories for this 8-year rotation project to produce biorenewable energy material. This price range captured a series of farmgate prices for biorenewables that have been reported (Walsh et al., 2000; USDA/DOE, 2005; J.T. Tyndall, personal communication). A sensitivity analysis using the price farmers would need to be paid to enter the biorenewable market (\$66/MG) was performed so that prospective investors will see the financial consequences at five alternative interest rates.

Costs and prices were adjusted for inflation using the Producer Price Index (US Bureau of Labor Statistics, 2007) for all commodities. Individuals (consumers) and businesses (producers) may use different inputs, so that inflation impacts should be accounted for using the appropriate measure when analyzing investment opportunities (Klemperer, 1996). Data on costs and prices were collected from Iowa State University publications and surveys on standardized rates (Edwards and Smith, 2002, 2006; Edwards, 2006), Iowa Department of Natural Resources (Iowa DNR, 2007), field practitioners (Kliver, 2005), and other published sources (Downing et al., 1996, 2004; Johnson and Wene, 2003;

Downing, 2005). Non-proprietary data used for the economic analyses are available from the authors upon request.

3. Results

3.1. Tree survival

Overall survival of protected trees ($66 \pm 0.04\%$) did not differ significantly from unprotected trees ($78 \pm 0.08\%$) ($F = 3.60$; d.f. = 1, 39; $P = 0.0760$). Survival of clones 91 × 04-03 and D105 was significantly greater than that of Eugenei or NM2 ($F = 12.04$; d.f. = 3, 39; $P = 0.0006$) (Table 1). The clone × treatment interaction significantly influenced survival ($F = 3.84$; d.f. = 3, 39; $P = 0.0303$), but not in a consistent pattern. Although chemical protection did not affect clones 91 × 04-03 and D105 survival compared with the unprotected plots, survival of the protected Eugenei and NM2 clones was less and significantly less, respectively, than unprotected trees (data not shown). Mortality of clones 91 × 04-03 and D105 occurred primarily during the third growing season, while the majority of Eugenei and NM2 mortality took place during the seventh and eighth growing seasons (Fig. 1). Mortality seemed to be related to increased severity of *Marssonina* leaf disease on Eugenei, greater susceptibility to *Septoria* canker development in both Eugenei and NM2 as stress from competition increased, and to top breakage in taller NM2 trees during wind and wet snowfall events. However, the specific reason for tree mortality was not recorded.

3.2. Individual tree growth

Protected trees were significantly taller (11.1%) than unprotected trees ($F = 130.02$; d.f. = 1, 28; $P < 0.0001$) after eight growing seasons. Height differed significantly among clones ($F = 8.42$; d.f. = 3, 28; $P = 0.0004$), and clone 91 × 04-03 was significantly taller than Eugenei (Table 1). Significant yearly increases in tree height also occurred ($F = 2048.99$; d.f. = 6, 436; $P < 0.0001$). While the clone × treatment interaction was not significant ($F = 1.82$; d.f. = 3, 28; $P = 0.1655$), the clone × time ($F = 8.27$; d.f. = 18, 436; $P < 0.0001$), treatment × time ($F = 38.89$; d.f. = 6, 436; $P < 0.001$), and clone × treatment × time interactions ($F = 1.81$; d.f. = 18, 436; $P = 0.0225$) all affected tree height significantly (Fig. 2). Clonal differences became readily apparent during the second and third growing seasons. Clone 91 × 04-03 responded the most positively to chemical protection after eight growing seasons, with protected trees growing approximately 15% taller than unprotected trees (Fig. 2). Conversely, protection from herbivores did not affect NM2 (protected trees were less than 1% taller than unprotected trees).

Stem diameter was over 13% larger in protected trees after eight growing seasons, a significant increase compared to unprotected trees ($F = 20.24$; d.f. = 1, 28; $P = 0.0001$). Stem diameter also differed significantly among clones after eight growing seasons ($F = 10.95$; d.f. = 3, 28; $P < 0.0001$), as clone 91 × 04-03 diameter was significantly greater than all others (Table 1). Diameter increased

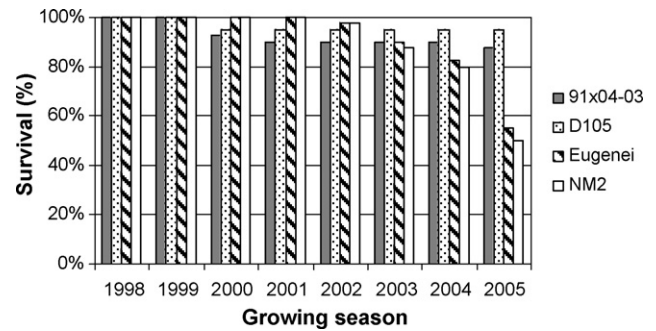


Fig. 1. Survival of four *Populus* clones over eight growing seasons in central Iowa, USA.

significantly each year ($F = 1064.40$; d.f. = 7, 503; $P < 0.0001$). The clone × time ($F = 6.01$; d.f. = 21, 503; $P < 0.0001$), treatment × time ($F = 13.22$; d.f. = 7, 503; $P < 0.0001$) and clone × treatment × time ($F = 2.41$; d.f. = 21, 503; $P = 0.0005$) interactions significantly affected stem diameter, but the clone × treatment ($F = 0.46$; d.f. = 3, 28; $P = 0.7094$) interaction did not. Differences in stem diameter between protected and unprotected trees declined after the fourth growing season; however, clone 91 × 04-03 again showed the most positive response to insecticide treatments, with protected trees approximately 27% greater in diameter than unprotected trees after eight growing seasons (data not shown, but see trends for stand basal area, Fig. 3).

Stem volume was significantly greater (34%) in protected trees compared with unprotected trees after eight growing seasons ($F = 15.05$; d.f. = 1, 28; $P = 0.0006$), and there were significant differences in stem volume among clones as well ($F = 9.59$; d.f. = 3, 28; $P = 0.0002$) (Table 1). Stem volume of clone 91 × 04-03 was significantly greater than all other clones after eight growing seasons. Clones NM2 and D105 had greater volume than Eugenei, but were not different from each other. Stem volume significantly increased annually ($F = 337.84$; d.f. = 6, 436; $P < 0.0001$). The clone × time ($F = 10.53$; d.f. = 18, 436; $P < 0.0001$), treatment × time ($F = 11.69$; d.f. = 6, 436; $P < 0.0001$), and clone × treatment × time ($F = 3.12$; d.f. = 18, 436; $P = 0.0002$) interactions all affected stem volume significantly, while the clone × treatment interaction did not ($F = 1.07$; d.f. = 3, 28; $P = 0.3796$). Stem volume differences between protected and unprotected trees reached a plateau at the end of the fourth year. For clones Eugenei and NM2 there was a rapid decline in stem volume differences between treatments after the sixth growing season, when a disproportional number of the larger trees for these two clones died. Clone 91 × 04-03 again showed the most positive response to insecticide protection with protected trees approximately 36% greater in volume than unprotected trees after eight growing seasons. However, the volume losses for both 91 × 04-03 and D105 declined after the fourth growing season (Table 2).

Table 1
Growth differences (mean ± S.E.) among four *Populus* clones grown in central Iowa, USA after eight growing seasons

Measurement	Clone			
	91 × 04-03	D105	Eugenei	NM2
Survival (%)	87.5 ± 0.06a	95.0 ± 0.03a	55.0 ± 0.07b	50.0 ± 0.10b
Height (m)	17.1 ± 0.4a	16.4 ± 0.3ab	14.3 ± 0.4b	15.2 ± 0.6ab
Diameter (cm)	18.9 ± 1.0a	15.6 ± 0.6b	13.3 ± 0.6b	16.1 ± 1.1b
Stem volume (dm ³)	173.2 ± 20.1a	109.8 ± 8.1b	71.9 ± 8.8c	112.9 ± 18.1b
Basal area (m ² ha ⁻¹)	21.7 ± 1.9a	14.5 ± 1.3b	9.6 ± 0.7c	14.4 ± 1.2b
Stem biomass (kg ha ⁻¹)	70.1 ± 6.7a	60.4 ± 5.1b	26.0 ± 2.6c	36.9 ± 7.3b
Branch biomass (kg ha ⁻¹)	7.8 ± 0.8a	7.8 ± 0.9a	2.5 ± 0.5c	5.8 ± 1.3b
Aboveground biomass (kg ha ⁻¹)	77.9 ± 7.3a	68.2 ± 5.7ab	28.5 ± 3.0c	42.7 ± 8.4bc

Among clones within a measurement, means sharing a letter are not significantly different (Tukey's test, $\alpha = 0.05$).

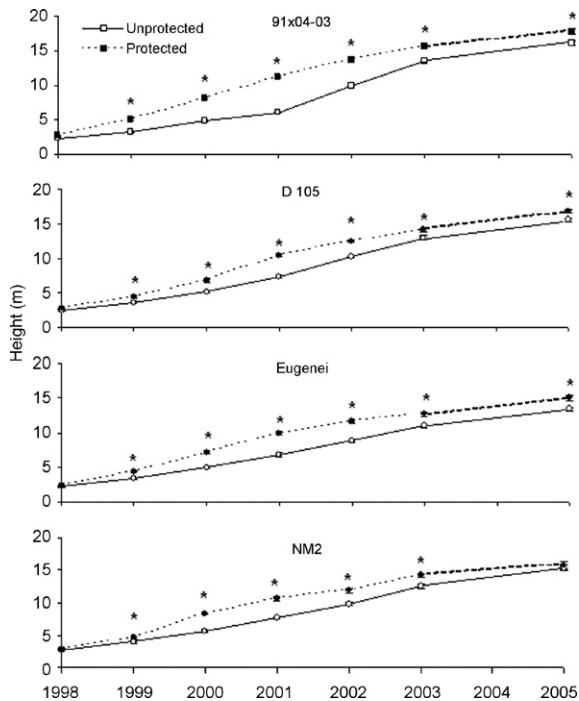


Fig. 2. Height (mean \pm S.E.) of four *Populus* clones after eight growing seasons in central Iowa, USA. Height data was not available for 2004. Within a clone, an asterisk (*) over a pair of points indicates a significant difference between unprotected and protected trees (Tukey's test, $\alpha = 0.05$).

3.3. Stand-level growth

Insecticide treatments increased basal area nearly 36% compared to unprotected plots, and this difference was significant ($F = 9.14$; d.f. = 1, 28; $P = 0.0053$). Basal area differed significantly over time ($F = 113.41$; d.f. = 7, 224; $P < 0.0001$) and among clones ($F = 10.90$; d.f. = 3, 28; $P < 0.0001$). Clone 91 \times 04-03 had significantly more basal area than all other clones, but there was no difference between NM2 and D105 (Table 1). Basal area was not affected by the clone \times treatment interaction ($F = 1.33$; d.f. = 3, 28; $P = 0.2859$). Plot basal area reflected the trends in diameter growth and mortality with the significant differences between protected and unprotected trees by the end of year 3 for all clones except NM2. The gap widened slightly for clones D105 and 91 \times 04-03 in the fourth year, and then stayed relatively constant through the eighth year. Size-related mortality of Eugenei and NM2 clones narrowed the gap in basal area in the eighth year, with the unprotected plots of NM2 actually having greater basal area at the time of harvest (Fig. 3). Clone 91 \times 04-03 had the greatest difference in plot basal area between protected and unprotected trees (26.0%), while protected plots with clone NM2 actually had a lower (63.2%) basal area than unprotected plots (Fig. 3). The clone \times time ($F = 5.46$; d.f. = 21, 224; $P < 0.0001$), treatment \times time ($F = 4.97$; d.f. = 7, 224; $P < 0.0001$), and clone \times treatment \times time interactions ($F = 2.14$; d.f. = 21, 224; $P = 0.0035$) all were significant.

Although protected plots had 22% more stem biomass than unprotected plots, insecticide treatments did not affect stem biomass significantly ($F = 1.51$; d.f. = 1, 16; $P = 0.2368$). Stem biomass differed significantly among clones ($F = 11.02$; d.f. = 3, 16; $P = 0.0001$), as clone 91 \times 04-03 had significantly more stem biomass than Eugenei and NM2 (Table 1). There was a significant clone \times treatment interaction ($F = 10.45$; d.f. = 3, 16; $P = 0.0005$). Clone 91 \times 04-03 had the greatest difference in plot biomass between protected and unprotected plots (45%, Table 3), while

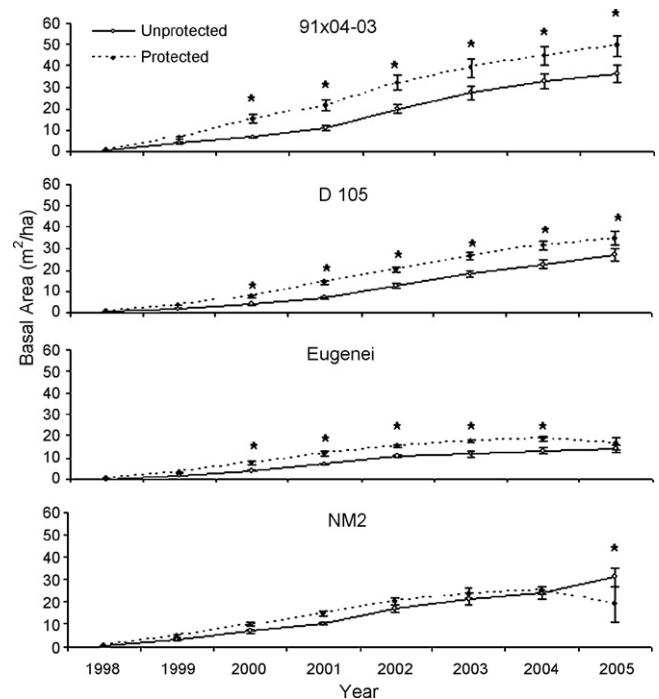


Fig. 3. Basal area (mean \pm S.E.) of four *Populus* clones after eight growing seasons in central Iowa, USA. Within a clone, an asterisk (*) over a pair of points indicates a significant difference between unprotected and protected trees (Tukey's test, $\alpha = 0.05$).

protected plots with clones Eugenei and NM2 had lower plot biomass than unprotected plots (Fig. 4), likely because of greater tree mortality in the protected plots.

Unprotected trees had over 8% more branch biomass than protected trees ($F = 5.24$; d.f. = 1, 16; $P = 0.0360$). Clones 91 \times 04-03 and D105 had greater amounts of branch biomass than Eugenei ($F = 5.12$; d.f. = 3, 16; $P = 0.0113$) (Table 1). There was a significant treatment \times clone interaction ($F = 7.07$; d.f. = 3, 16; $P = 0.0031$). Clone D105 had nearly the same branch biomass in either treatment, while clone 91 \times 04-03 had nearly 23% more branch biomass in the protected trees. In contrast, clones NM2 and Eugenei both had over 40% less branch biomass in the protected trees compared to unprotected trees (Fig. 4).

Overall, aboveground biomass was not affected by chemical protection ($F = 0.73$; d.f. = 1, 16; $P = 0.4057$) as protected plots had just over 6% more aboveground biomass. Aboveground biomass did, however, differ significantly among clones ($F = 11.86$; d.f. = 3, 16; $P = 0.0002$). Clone 91 \times 04-03 accumulated more aboveground biomass than clones NM2 and Eugenei (Table 1). There was a significant treatment \times clone interaction ($F = 10.69$; d.f. = 3, 16; $P = 0.0004$). Clones 91 \times 04-03 and D105 had over 34% more aboveground biomass in the protected plots, whereas clones Eugenei and NM2 had 17 and 51% less aboveground biomass, respectively, in the unprotected compared to the protected plots (Fig. 4).

3.4. Financial analyses

Because of the unexpected mortality in the NM2 and Eugenei plots that was not directly related to *C. scripta* defoliation, the financial analysis considered only clones 91 \times 04-03 and D105. At a 6% real rate of return, none of the stands proved to be financially acceptable (Table 3). The NPVs (adjusted to 2007 dollar values) were all negative, even at the highest stumpage price. Clone 91 \times 04-03 had a $-\$195/\text{ha}$ NPV (loss) and a 5.2% IRR, while D105

Table 2

Calculated 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.

	Year						
	1998	1999	2000	2001	2002	2003	2005
91 × 04-03	35.7	59.2	73.8	71.2	54.5	38.0	30.5
D105	35.8	50.2	59.6	60.7	42.2	28.9	20.6
Eugenei	40.3	56.3	62.4	59.6	41.7	27.3	23.2
NM2	21.4	42.5	50.9	48.1	32.6	32.1	16.0

Years 1998–2000 of this table first reported in Coyle et al. (2002). Data were not available in 2004.

had an NPV (loss) of $-\$947/\text{ha}$ and 1.6% IRR. The IRRs were positive only for the protected stands at the highest price level. These overall results were likely influenced by the land rental costs which accounted for almost half of the discounted total costs in the protected stands and about 58% in the unprotected stands. In fact, for the worst two cases ($\$44/\text{MG}$ price, unprotected stands for both clones), the discounted value of land rent alone was higher than the discounted value of the harvested biomass.

Sensitivity analyses (Table 4) using five alternative rates of return (0, 2, 4, 5 and 6%) at $\$66/\text{MG}$ price level show NPVs were positive at the four lowest rates for clone 91 × 04-03, and at only 0% for clone D105, all in protected stands. From these results, the best investment option was to use clone 91 × 04-03, accept the 5% real rate of return from the investment, and expect an NPV of $\$41/\text{ha}$. These results concur with the findings of significant growth advantages of clone 91 × 04-03 protected stands, as shown in Figs. 2 and 3.

Unprotected stands require higher biomass prices to break-even compared to protected stands. At 6% real rate of discount and adjusted to 2007 dollar values, breakeven prices ranged from $\$76-\$86/\text{MG}$ for protected stands and from $\$94-\$101/\text{MG}$ for unprotected stands. For clones 91 × 04-03 and D105, the price of protection with insecticides was worth an average reduction of $\$16/\text{MG}$ in the break-even prices; i.e., investors will need break-even prices $\$16/\text{MG}$ higher than when insecticides are used. This reduction represents 20% of the breakeven prices for the protected stand. Between clones, 91 × 04-03 had better (lower) break-even prices, by as much as about $\$10$ and $\$7$ per MG lower for protected and unprotected stands, respectively.

4. Discussion

Defoliation can be quite detrimental to a *Populus* plantation during the first several years of growth. Artificial defoliation levels of 75% over 2 years resulted in a 31% height decrease and 26% diameter decrease in Mississippi (Tucker et al., 2004). After 2 years, an artificial defoliation level of 75% caused volume reductions of 33% in Iowa (Reichenbacher et al., 1996) and 69% in Wisconsin (Bassman et al., 1982). To our knowledge, this paper reports the only study that has examined the impact of natural *C. scripta* damage in field conditions over a full harvest rotation. We found

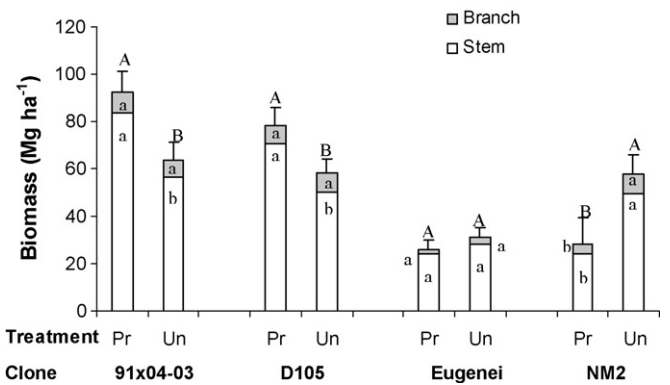


Fig. 4. Biomass (mean ± S.E.) of four *Populus* clones after eight growing seasons in central Iowa, USA. Within tissues for each clone, means sharing a small letter are not significantly different (Tukey's test, $\alpha = 0.05$). Within clones, means of total aboveground biomass for trees of each treatment sharing a capital letter are not significantly different. Standard errors and capital letters are for total aboveground biomass.

losses in stem volume of 50–74% for four *Populus* clones over the first 3 years (Coyle et al., 2002), but those losses decreased to a range of 16–31% by the final harvest reported here. In a similar system, high (>70%) *Phratora vulgatissima* feeding on 4 and 5-year-old *Salix viminalis* reduced stem volume 32 and 39% in successive years (Björkman et al., 2000). Leaf beetle damage is believed to be insignificant on older trees because of the reduced proportion of susceptible foliage (Coyle et al., 2005). Our data support this notion because the impact on growth was greatest after the third growing season, declining yearly thereafter.

The best IRR for commercial stands, based on this study, was 5.2% for protected clone 91 × 04-03 (Table 3), which accumulated biomass at an annual rate of 11.5 MG/ha over 8 years. Without protection from *C. scripta*, the IRR for even the most productive clone in this study is negative. These results clearly indicate the financial challenges and policy implications if the productive agricultural soils of the midwestern US (with the associated high land rental rates) are to be used for producing renewable bioenergy materials such as *Populus*. The costs of production and economic returns from growing switchgrass (*Panicum virgatum*) as an energy crop in this region are similar to or slightly less favorable than for *Populus* (Solow et al., 2005). With the increasing prices of fossil fuels, cost of producing ethanol from corn, and rising environmental concerns, *Populus* selections are one energy alternative that should warrant a much closer look. Continuing efforts at reducing costs and increasing yields are needed, as these analyses pertain only to *Populus* grown for biorenewable energy materials; the potential stream of costs and benefits may vary for *Populus* grown for different production objectives.

In some regions, the use of the interspecies hybrids of *P. deltoides* × *P. nigra*, *P. deltoides* × *P. trichocarpa*, *P. deltoides* × *P. maximowiczii* (*suaveolens*), or *P. nigra* × *P. maximowiczii* has lowered planting costs by allowing use of unrooted cuttings for planting stock and has raised yields from hybrid vigor (Stettler

Table 3

Chrysomela scripta impact on biomass production and economics over an 8-year rotation for two *P. deltoides* clones

Clone treatment	Average dry wt. (kg)		Branch/stem ratio	Survival	Stand yield (MG/ha)	\$66/MG stumpage & 6% real rate of return	
	Branch	Stem				Net present value (\$/ha)	Internal rate of return
91 × 04-03 protected	5.8	55.8	9.3	90%	92.3	−195	5.2
91 × 04-03 unprotected	5.0	39.9	10.9	85%	63.6	−11,255	−1.0
D105 protected	4.6	42.4	10.9	100%	78.3	−947	1.6
D105 unprotected	5.1	33.4	15.2	90%	57.7	−1571	−3.2

Table 4

Net present values per hectare (adjusted to 2007 dollar values) at five alternative real rates of return at \$66/MG for four categories of stands

Real rate of return (%)	Clone 91 × 04-03		Clone D105	
	Protected	Unprotected	Protected	Unprotected
0	1664	-242	466	-746
2	914	-657	-108	-1087
4	303	-989	-572	-1357
5	41	-1130	-769	-1470
6	-195	-1255	-947	-1571

et al., 1996; Stanturf et al., 2001). The severity of *Septoria* canker disease in the midwestern US has precluded the use of many interspecies hybrid clones (Ostry and McNabb, 1986). We included two interspecies hybrid clones (NM2 and Eugenei) in this study that were being recommended for use in the region. However, disease severity increased over time and, along with some storm breakage of NM2 stems in years 7 and 8, these clones were failing by the end of the experiment. Similar problems with the Eugenei and NM2 (also NM6) clones were observed in all other Iowa plantings during this same time frame. We no longer recommend planting these clones in this region.

Using a broad spectrum insecticide (Sevin) for all treatments, instead of biorational insecticides such as Novodor and Raven, would have lowered costs and improved the financial picture, although all results would still be financially unacceptable at 6% real rate of discount. These changes translate to as high as 25% improvement in the NPVs, and 38% improvement in the IRRs. The improvements are better for clone 91 × 04-03 than for D105. However, Sevin can have detrimental impacts on some natural enemies (Smith and Krischik, 2000), including *Coleomegilla maculata* (Coleoptera: Coccinellidae), a ladybird beetle known to inhabit intensively managed hardwood plantations and prey on *C. scripta* (Head et al., 1977; Jarrard, 1997; DRC, personal observation). One promising avenue for decreasing pest management costs as well as harm to beneficial insects during the first part of the rotation is the use of the systemic insecticide imidacloprid (Tenczar and Krischik, 2006). By infusing the insecticide into hardwood cuttings via a pre-plant soaking in imidacloprid solution, *C. scripta* damage through the first (and to an extent, second) year in the field is greatly reduced (Tenczar and Krischik, 2006). The need for more expensive field sprays during the first year would be eliminated along with the associated financial carrying costs. Although imidacloprid is not completely benign to natural enemies, it is a better option than Sevin (Tenczar and Krischik, 2006).

Another modification in insecticide use might pay dual dividends of reducing treatment costs and increasing yields. Our results confirm that there is compensatory growth in trees damaged by leaf beetle feeding, as was suggested by Reichenbacher et al. (1996). As shown by the height growth of unprotected trees (especially clones 91 × 04-03 and D105) after 2001, the last year of heavy *C. scripta* damage, there is a recovery period where the unprotected trees are growing faster in height than their protected counterparts. We believe one part of this compensatory growth is the temporary loss of apical control when *C. scripta* damage stem terminals. This releases lateral buds lower on the current-year-growth increment to develop as branches. Potentially, damaged trees end up having more leaf area for a period of time until these branches are shaded out by continued canopy development. This study was not designed to quantify canopy-level changes, but we did observe more branch production in unprotected 3 and 4-year-old trees that was still visible at the time of harvest (Fig. 5). Although our harvest results at age eight showed that protected trees had more total live branch weight, the



Fig. 5. Branching characteristics of unprotected (left) and protected (right) 8-year-old trees of clone 91 × 04-03. The lower dead branches had been removed from the protected trees at the time of the photograph while the unprotected trees had not been cleaned of their lower dead branches. Unprotected trees of clone 91 × 04-03 consistently had more branching along the stem for the first four growth increments than did protected trees of that clone.

ratio of branch to stem weights was higher for unprotected trees in all four clones (Table 3; Eugenei: 9.8 vs. 7.3, NM2: 15.4 vs. 14.7). It would be worthwhile to test for a positive stand-yield effect of allowing some *C. scripta* damage at strategic points in tree development, while controlling *C. scripta* damage at other periods. For example, foregoing or delaying *C. scripta* treatment for the second generation in the third growing season could be used to increase canopy size for the rest of that season on into the fourth and possibly fifth growing seasons. However, a considerable amount of research would be required on this strategy before we would recommend it to growers.

We have focused on selections of intraspecies *P. deltooides* hybrids for the north central region. Unfortunately, no useful level of resistance to *C. scripta* has yet been found in *P. deltooides* clones; the two clones used in this study (D105 and 91 × 04-03) are representative of the lack of *C. scripta* resistance we have seen in all other clones. Newer selections are giving higher biomass yields, but only when *C. scripta* damage is low (Riemenschneider et al., 2001). The use of *P. deltooides* clones transformed to express coleopteran strains of the *Bt* toxin could be a solution, but many technical and regulatory obstacles remain for that option (Strauss et al., 2004). Improved tree cultivars for the Midwest through traditional breeding or genetic modification has potential, but for now, improved growth with reduced-cost *C. scripta* management, especially chemical protection during the first few years of plantation establishment, is our recommended strategy.

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