NOTE

Gypsy moth defoliation and N fertilization affect hybrid poplar regeneration following coppicing

Anurag A. Agrawal, Kevin R. Kosola, and Dylan Parry

Abstract: The interaction between insect outbreaks and forest health or tree plantation management has been considered rarely from an experimental approach. From 1996 to 1998, we experimentally created a gypsy moth outbreak that defoliated large plots of mature hybrid poplars, *Populus* ×*euramericana*, with half of the plots fertilized in a factorial design. The trees were harvested at rotation age in 1999, and we examined the mortality and regeneration of the coppiced (cut at the base) trees in the following growing season. Pre-treatment estimates of tree size strongly predicted the mortality and number of regenerating stems following harvest but not the height of those stems. Defoliation and fertilization each modestly increased tree mortality (10 and 6%, respectively), but the effects were not additive. Only defoliation had strong residual effects on the surviving trees: 25% fewer resprouting stems were produced by previously defoliated trees compared to undefoliated control trees.

Résumé : L'interaction entre les épidémies d'insectes et l'état de santé de la forêt ou l'aménagement des plantations d'arbres a rarement été examinée avec une approche expérimentale. De 1996 à 1998, nous avons créé expérimentalement une épidémie de spongieuse entraînant la défoliation de grandes parcelles de peupliers hybrides matures, *Populus* ×*euramericana*, où la moitié des parcelles avaient été fertilisées selon un plan factoriel. Les arbres ont été récoltés au terme d'une période de rotation en 1999 et nous avons examiné la mortalité et la régénération des tiges coupées durant la saison de croissance suivante. Les estimations pré-traitement faites à partir de la dimension des arbres prédisaient très bien la mortalité et le nombre de tiges produisant des rejets suite à la récolte mais pas la hauteur des rejets. La défoliation et la fertilisation ont toutes les deux augmenté légèrement la mortalité (respectivement 10 et 6 %) mais leurs effets n'étaient pas additifs. Seule la défoliation avait d'importants effets résiduels sur les tiges qui survivaient : parmi les arbres qui avaient été défoliés, 25 % moins de tiges produisaient des rejets comparativement aux arbres témoins non défoliés.

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Introduction

Insect outbreaks are thought to play a major role in deciduous forest productivity and dynamics (Mattson and Addy 1975; Karban 1980; Barbosa and Schultz 1988; Healy et al. 1997). In plantations, trees are grown on short rotations and, therefore, may have little chance to recoup losses in growth and yield caused by periodic episodes of defoliation. However, the effects of herbivore outbreaks in intensively managed forest and plantation settings are poorly understood. For management strategies relying on short rotations, especially those relying on tree regeneration from parental root stock following harvest, it is critical to examine the effects of previous defoliation on regeneration of trees following coppicing (vegetative propagation after harvest by cutting stems at the base). In coppicing systems, the growing environment experienced by the parent trees may directly affect the regenerating sprouts. The impacts of herbivores on sprout production in clonally reproducing species represent potential consequences for tree fitness. For example, factors slowing growth may allow overtopping by competitors, resulting in death, especially in fast-growing, early successional trees where competition for light is crucial (Kobe et al. 1995; Oliver and Larson 1996).

Poplars (*Populus* spp.) are one of the fastest growing temperate trees and have been used extensively in short-rotation plantations for fibre and in developing countries as a source of fuel. Plantations of hybrid poplar are typically managed under short rotations (4–10 years) and natural regeneration by adventitious sprouts growing from the stump (Ceulemans and Deraedt 1999). Ceulemans and Deraedt (1999) conclude that, although hybrid poplars are ideal for short-rotation forestry, further field research is required to maximize yield. Many trees in the genus *Populus* are preferred host plants for gypsy moth larvae (Liebhold et al. 1995), although there are

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large differences in performance on different species and clones within a species (e.g., Robison and Raffa 1997; Havill and Raffa 1999). In this study, we examined the effects of an experimentally created gypsy moth outbreak in a hybrid poplar plantation on tree mortality and regeneration after harvest. The broader study for which these large-scale plots were created (Scriber et al. 1999; Parry 2000; Kosola et al. 2001) included a fertilization treatment, factorially crossed with defoliation. We were thus able to examine interactive effects of fertilization and defoliation on poplar survival and productivity following harvest and regeneration. In particular, we hypothesized that defoliation by gypsy moth larvae would have negative effects on tree growth and mortality but that these effects would be ameliorated by fertilization.

Materials and methods

From 1996 to 1999, the effects of an insect outbreak on trees were emulated by experimentally creating a sustained gypsy moth outbreak in replicated blocks of hybrid poplar trees (see Parry 2000; Kosola et al. 2001, for detailed information on the experimental design). The study was conducted in four 1-ha stands of a single clone of *Populus* ×*euramericana* cv. Eugeneii growing on the Long-Term Ecological Research site (42°24′N, 85°24′W, elevation 288 m) at Kellogg Biological Station in southwestern Michigan, U.S.A. (Marino and Gross 1988). This study area and design allow for long-term analyses and comparison with other systems because of the funding infrastructure. The trees were planted in 1987 (in a 1 × 2 m array) as rooted cuttings in a field that had been under agricultural cultivation for approximately 100 years. In each of the four stands, a 40 × 40 m block was located in the northeastern corner. Each block was partitioned using a split-plot design, with two herbivory treatments (i.e., defoliation and no defoliation), each split into a fertilized (100 kg $NH_4NO_3 \cdot ha^{-1} \cdot year^{-1}$) and unfertilized subplot. We applied prilled ammonium nitrate fertilizer with a 61 cm wide drop spreader, calibrated to apply 50 kg N/ha. The fertilizer was applied in two sets of perpendicular passes. Further site and planting details are outlined in Marino and Gross (1988), Parry (2000), and Kosola et al. (2001). Defoliation was achieved through the deployment of very large quantities (ca. 18 kg) of gypsy moth eggs in each year of the study (Parry 2000). The ensuing larvae created light defoliation in 1996 (≈20–40%), nearly complete defoliation in 1997 (≈75–100%), and moderate to severe defoliation in 1998 (≈40–90%). Gypsy moth populations collapsed by the end of 1998 and very little herbivory was evident in 1999. To minimize moth colonization of control trees, we used several manual and mechanical methods (Parry 2000). The combination of these methods was very effective in maintaining low gypsy moth densities (<<25% defoliation) in the control plots throughout the study (Parry 2000). At rotation age in the fall of 1999, all the trees were harvested. At this time, all trees in the plantation were mildly infected with a canker disease (*Septoria* sp.) (D. Dickmann, personal communication).

Diameter at breast height (DBH) was recorded from 40 trees in each subplot (i.e., each of the four factorial treatments) prior to the imposition of treatments in the fall of 1995. Additional DBH measurements were taken on a random subset of the surviving trees in 1999, prior to harvest. In June 2000, the first growing season after harvest and 2 years after defoliation and fertilization treatments had ceased, we determined the survival of individual trees, the number of new stems produced by each stump, and the maximum height of the resprouts in each plot. In addition, our analysis considered the effects of both pretreatment DBH of individual trees in 1995 and post-treatment DBH in 1999 on the regenerative ability of poplar trees after harvest. We employed logistic regression to test for effects of DBH on mortality and linear regression to test for effects of DBH on the number and height of resprouts.

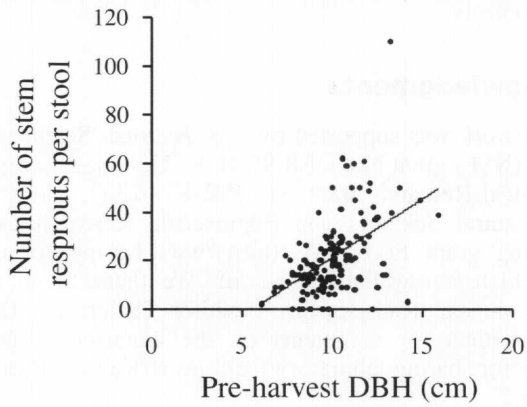
Using gypsy moth defoliation and fertilization as fixed effects and block as a random effect, we constructed mixed-model analyses to examine the consequences of our treatments on the regenerative ability of poplar trees. We had 16 subplots (total replicates), one for each block (four levels) × herbivory (two levels) × fertilization (two levels) treatment combination. Each of the 40 trees in each subplot was nested in the block × defoliation × fertilization interaction. Because block was an arbitrary factor included in the analyses to correct for variance associated with the different blocks, block × fertilization and block × defoliation × fertilization interactions were not included in the model ("model two" described by Newman et al. 1997). The block × defoliation interaction was included to account for the split-plot design. To examine the interactive effects of gypsy moth defoliation and fertilization on percent tree mortality, the mortality data was log transformed, because we were interested in the multiplicative null model for the interpretation of the interaction term (Sih et al. 1998). Log transformation allows such an interpretation and prevents the confounding problem of trees allowed to be affected (i.e., killed) twice by each factor (defoliation and fertilization) as in the additive model (Sih et al. 1998). The results obtained with log-transformed data were identical to those obtained with untransformed data. The percentage data were not further transformed; arcsine square root transformation did not improve the normality of the residuals. The number of stems produced by regenerating poplars was also log transformed to improve the normality of the residuals.

Mixed-model analyses of variance were conducted in SAS PROC MIXED (SAS Institute Inc. 1999). SAS PROC MIXED is a superior procedure to traditional general linear model analyses of mixed-model ANOVAs, because it employs restricted maximum likelihood methods to fit the statistical structure to the data (SAS Institute Inc. 1999). Degrees of freedom for F tests of fixed effects were estimated using the Satterthwaite approximation (SAS Institute Inc. 1999). As suggested by the SAS Institute Inc. (1999), the likelihood-ratio χ^2 test was employed for tests of the random effects. The likelihood-ratio χ^2 tests the hypothesis that the variation due to the random effect is greater than 0 and is a one-sided single degree of freedom test.

Results

The diameter of poplar trees in 1995 (pretreatment DBH) was a strong predictor of survival and regeneration after harvest in 1999 (DBH (cm) in 1995, alive = 10.353 ± 0.092

Fig. 1. Correlation between diameter at breast height (DBH) in November 1999 (just before harvest) and number of new stem sprouts per stool (n = 134) in June 2000 for hybrid poplar trees at Kellogg Biological Station's Agroecology Long-Term Ecological Research site.



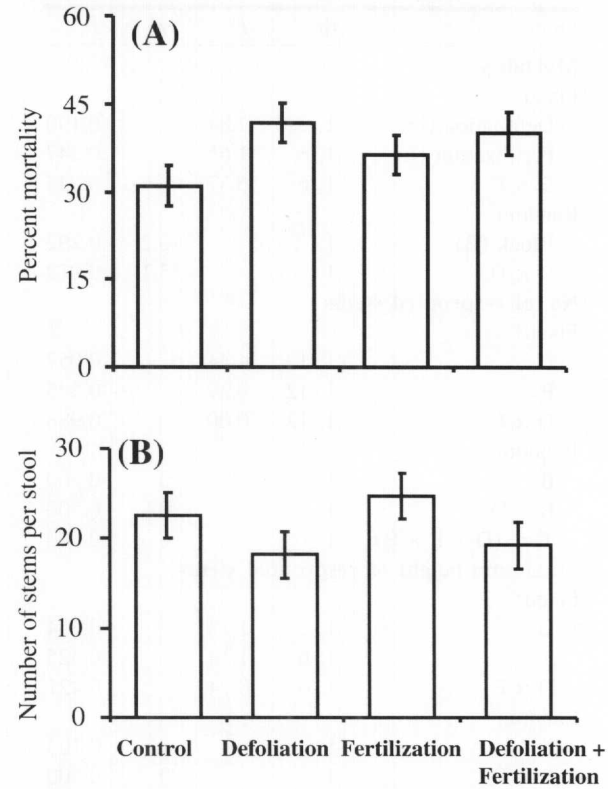
(mean ± SE), dead = 8.142 ± 0.168; logistic regression, n = 527, χ^2 = 182.263, df = 1, P < 0.001). In addition, we measured diameters of a subset of live trees in 1999 (post-treatment DBH) before harvest; these DBH values did not predict mortality (i.e., lack of regeneration) after harvest (logistic regression, n = 134, χ^2 = 2.153, df = 1, P < 0.142). In this case, we had little statistical power because among measured trees; only seven trees died between the pre- and post-harvest measurement. The pre-harvest DBH of trees was a significant predictor of the number of regenerating stems produced post-harvest (linear regression, R^2 = 0.252, $F_{[1,132]}$ = 44.409, P < 0.001; Fig. 1) but was a poor predictor of maximum height of the resprouts (linear regression, R^2 = 0.001, $F_{[1,125]}$ = 0.132, P = 0.717). The range of resprout height was from 14 to 114 cm (65.1 ± 1.9 (mean ± SE)).

Three successive years of defoliation by gypsy moths increased mortality following harvest by 10%. Prior fertilization increased mortality by 6% compared with controls. However, these effects were not additive, and overall mortality of trees in plots that had experienced both gypsy moth defoliation and fertilization was only 9% higher than controls (Fig. 2*a*, Table 1). Defoliation by gypsy moths decreased the number of stems produced by the surviving trees by 25% compared with controls, while fertilization had no effect (Fig. 2*b*, Table 1). The number of new stems produced by the poplars was not correlated with the maximum height of those stems (n = 284, Pearson correlation: Bartlett χ^2 = 2.018, df = 1, P = 0.155). There was no detectable effect of the gypsy moth defoliation treatment or fertilization on the maximum height of new poplar stems (control, 62.965 ± 5.699 cm (least-squares mean ± SE); gypsy moth, 54.971 ± 5.806 cm; fertilizer, 63.767 ± 5.723 cm; gypsy moth and fertilizer, 62.476 ± 5.778 cm; Table 1).

Discussion

The long-term consequences of repeated defoliation on subsequent tree growth and mortality varies among forest communities. For example, Wickmann (1980) observed an increase in growth of surviving white fir trees after severe defoliation by Douglas-fir tussock moth. Gypsy moth out-

Fig. 2. Effects of 3 years of experimental gypsy moth defoliation and fertilization on the (least square) mean ± SE (A) mortality and (B) number of resprouted stems per stool of hybrid poplars at Kellogg Biological Station's Agroecology Long-Term Ecological Research site.



break defoliations have been implicated in the decline of oaks in many eastern North American deciduous forests (Niemela and Mattson 1996; Healy et al. 1997). In our study, successive years of defoliation in *Populus* plantations clearly had long-term detrimental effects on stand growth and productivity. We found that mortality increased by 10% in defoliated plots compared with controls. A previous study that employed artificial defoliation found that only heavy defoliation caused a growth reduction in hybrid poplars (Bassman et al. 1982). Although *Populus* clones may vary in their tolerance to herbivory, we expect that repeated defoliation will generally decrease productivity.

As expected, we also found that defoliation led to a 25% decrease in coppice growth (stem production; Fig 2B). However, contrary to our expectations, fertilization during defoliation did not lead to a significantly increased capacity for stem production in coppiced trees (Fig. 2B), despite previous observations of increased growth by fertilized plots during defoliation (Kosola et al. 2001). Fertilization effects on tree vigor apparently dissipated more quickly than defoliation effects; neither defoliation nor fertilization treatments were applied in 1999. Tree diameter growth was similar in all treatments during this recovery year (Kosola et al. 2001). Possibly, fertilization increased aboveground tree growth without affecting (or at the cost of) regeneration ability.

In our plantation sites, mortality in control plots was relatively high (30%). It is possible that this mortality, and the irregular spacing of trees that resulted, may have increased

Table 1. Mixed-model analysis for effects of gypsy moth defoliation and fertilization on mortality, number of resprouted stems, and maximum height of resprouted stems of hybrid poplars using SAS PROC MIXED.

Source	df	F	χ^2	P
Mortality				
Fixed*				
Defoliation (D)	1, 3	2.84		0.190
Fertilization (F)	1, 6	1.65		0.247
D × F	1, 6	6.37		0.045
Random†				
Block (B)	1		0.2	0.292
B × D	1		5.1	0.012
No. of resprouted stems				
Fixed*				
D	1, 12	4.44		0.057
F	1, 12	0.39		0.545
D × F	1, 12	0.00		0.988
Random†				
B	1		0	0.500
B × D	1		0	0.500
Trees(D × F × B)	1		0	0.500
Maximum height of resprouted stems				
Fixed*				
D	1, 3	1.18		0.354
F	1, 6	1.14		0.325
D × F	1, 6	0.74		0.421
Random†				
B	1		1.6	0.103
B × D	1		0	0.500
Trees(D × F × B)	1		3.8	0.026

*df calculated using the Satterthwaite approximation.
†Likelihood-ratio χ^2 test for random effects.

variability in our results. Typically, poplar plantations are harvested a couple of years earlier than our 12-year harvest (Ceulemans and Deraedt 1999). We interpret the relatively high mortality as self-thinning leading to mortality of the smaller trees (Kosola et al. 2001). We found that the combination of gypsy moth defoliation and fertilization slightly increased mortality relative to controls but in a non-additive fashion. Why did defoliation increase tree mortality in unfertilized plots only (Fig. 2A) and fertilization increase tree mortality in undefoliated plots but not in defoliated plots? One possibility is that fertilization generally reduces the root/shoot ratio of plants. If fertilized plants had decreased root biomass compared with controls, then reduced root storage may have contributed to lower regeneration (i.e., higher mortality) after harvest. In other words, we speculate that self-thinning was accelerated by fertilization.

The management of plantations is complicated by several factors including stand age, herbivore outbreaks, and soil fertility. Because short-term poplar management relies on regeneration from parental root stock following harvest, impacts of herbivore outbreaks are potentially great. In addition, several unmeasured influences and their interactions could relate to optimal management. Potential interactions between herbivory, fertility, and disease could strongly influence tree mortality and regeneration. Irrespective of such interactions, ultimately our results point to relatively strong effects of defoliation on post-harvest regeneration, with surviving trees producing 25% fewer resprouting stems than controls.

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