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HYBRID POPLAR PRODUCTIVITY AND SUITABILITY FOR THE FOREST TENT CATERPILLAR: A FRAMEWORK FOR EVALUATION

D.J. Robison and K.F. Raffa[1]

ABSTRACT.-- Fifteen hybrid poplar, Populus spp., clones were evaluated for growth, tolerance to defoliation, and suitability for the forest tent caterpillar, Malacosoma disstria. Poplar clones were ranked according to their suitability for M. disstria, as indicated by behavioral and developmental bioassays. Patterns of poplar growth characteristics and M. disstria preference and performance among the 15 clones were used to construct a productivity - suitability matrix. This matrix provides a framework for evaluating insect pest resistance in selected poplar clones and for considering clonal contributions to poplar-M. disstria interactions. The matrix concept and design incorporates both biologically and economically important criteria, and may facilitate similar evaluations for other important pests and crops.

INTRODUCTION

The potential value of woody biomass crops for multiple uses has fostered research and development with hybrid poplar. In northern North America, hybrids and selections within the genus Populus possess desirable characteristics and growth potential for short rotation intensive culture forest systems (Dickman and Stuart 1983). Knowledge of the silvics of the genus and appropriate silvicultural techniques has steadily advanced. However, the development of scientific theory and evaluation strategies to appropriately transfer these new technologies into biologically and economically acceptable practice has lagged. One area in which such evaluation strategies are needed is in the development and utilization of genetically based resistance to insects.

Insects on planted poplars have been cataloged, and several species including the cottonwood leaf beetle, Chrysomela scripta Fab., tarnished plant bug, Lygus lineolaris (Palisot de Beavois), and poplar-and-willow borer, Cryptorhynchus lapathi (L.), have become pestiferous (Moore and Wilson 1983). Dickman and Stuart (1983) report 24 insect species as major pests of Populus, and Moore and Wilson (1983) state that as many as 150 species are potentially injurious. While there is some tendency to consider insect damage as inevitable or to rely exclusively on traditional insecticidal control, there is also evidence of differential resistance among poplar clones (Abrahamson et al. 1990, Caldbeck et al. 1978, Harrell et al. 1981, Wilson and Moore 1985, 1986). This evidence, coupled with knowledge of plant defensive chemistry (Feeny 1976, Palo 1984), physiological balance between plant defenses and plant productivity (Bazzaz et al. 1987, Bryant et al. 1985, Loehle and Namkoong 1987), and research on resource utilization by poplar feeding insects (Bryant et al. 1987, Lindroth et al. 1988), suggests that natural resistance could potentially be enhanced to economically significant levels. Additionally, poplars have been targeted with some success for genetic improvement through the insertion of novel genes (Fillatti et al. 1986, Klopfenstein et al. 1989).

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The development and utilization of hybrid poplar clones resistant to insects depends upon many factors. Planting and silvicultural strategies need to consider the number and arrangement of clones, the size of clonal blocks (Burdon 1982, Heybroek 1984, Libby 1982), spacing, rotation age, number of coppice rotations expected, and site productivity and accessibility (Bowersox and Ward 1977, Dickman and Stuart 1983). Insect related considerations include behavioral and physiological characteristics, such as feeding guild, phenology, capacity for population growth, and susceptibility to insecticides. Tree improvement efforts demand knowledge of plant genetics, reproduction, tissue culture and genetic manipulation (McCown 1985, Zobel and Talbert 1984).

The integration of these factors will facilitate a comprehensive approach to insect pest management. Transferring information from laboratory, greenhouse and field experiments to production plantations poses many challenges to the successful utilization of plant-insect interaction theory and findings. The current study attempts to approach these challenges in a comprehensive manner and develop a preliminary framework for evaluating hybrid poplar-insect pest interactions, using the forest tent caterpillar, Malacosoma disstria Hbn.(Lepidoptera: Lasiocampidae), as a study insect.

This insect is an oligophagous, univoltine, early season defoliator; features shared with a number of important Lepidopteran forest pests. In north central North America it is often associated with the aspens, Populus tremuloides Michx. and P. grandidentata Michx., and undergoes periodic outbreaks lasting four to six years every six to 16 years (Batzer and Morris 1971, Hodson 1941). Recently M. disstria was reported as a serious pest in a hybrid poplar research plantation[2], indicating that production plantations are at risk. Accordingly, the hybrid poplar-M. disstria association is both a useful model system and of economic importance.

Entomological and plant production factors must be considered in evaluating resistance (Painter 1941). Tree survival, growth rate, growth form, and tolerance to damage are important forest production considerations. Ecologically, the insect's behavioral and developmental responses to host plants, plant responses to insect pressures, and the influence of cultural conditions on pest biology, must be evaluated. In the M. disstria-poplar association, key areas of focus are adult ovipositional and larval feeding preference, larval performance, and capacity for population increase. Clonal tolerance to defoliation and inherent growth rate of the various clones are important plant variables. In the current study these parameters were evaluated individually, and then analyzed collectively to appraise how various factors might be manipulated to advance pest management through resistant clones.

EXPERIMENTAL APPROACH

Fifteen clones of hybrid poplar were selected to represent a broad taxonomic background and to maximize the probability of obtaining differential susceptibility to M. disstria (Table 1). Included among these selections were clones from the Leuce (aspens), Aigeiros (cottonwoods) and Tacamahaca (balsam poplars) sections of the genus Populus. Poplars were established from dormant hardwood cuttings in plastic pots in a glasshouse on the University of Wisconsin-Madison campus. Malacosoma disstria were obtained in 1988 as overwintering 1st instar larvae in eggs on aspens from outbreak populations on the Menominee Indian Reservation, Keshena, WI. All experimental insects were reared on foliage from glasshouse-grown poplar clones or on artificial diet (Grisdale 1985).

The following questions were addressed: 1) To what degree does M. disstria preference and performance vary among selected poplar clones? 2) What are the relative growth rates and foliar characteristics among the clones? 3) What are the relationships between poplar clones and their suitability for M. disstria? In conjunction with these questions, several ecological and silvicultural implications were addressed to help develop a framework for evaluation: 1) What are the relationships

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[2] E.A. Hanson, USDA For. Serv., No-Central For. Exp. Stn., Grand Rapids, MN; pers. comm. 1989.

Table 1.--Populus spp. clones evaluated.[1]

NC[2] No.	NE[2] No.	Other Name	Parentage[3]
5339	-	Crandon	alba x grandidentata
5260	-	Tristis #1	tristis x balsamifera
11505	388 & 88	-	maximowiczii x trichocarpa
5271	19	-	nigra Chark. x nigra Caud.
11004	-	Siouxland	deltoides x deltoides
5377	-	Wisc. #5	deltoides x nigra
11382	27	-	nigra Chark. x berolinensis
11396	49	-	maximowiczii x berolinensis
11445	280 & 157	-	nigra x laurifolia
5331	299	-	nigra Betulifolia x tricho.
11432	252	-	deltoides Angulata x tricho.
-	332	-	simonii x berolinensis
-	-	NM6	nigra x maximowiczii
-	-	DTAC2	deltoides Ang. x berolin.
5262	387	-	balsam. subcord-Cand. x berolin.

[1] Clonal material provided by: USDA North Central For. Exp. Stn., Rhinelander, WI; SUNY College of ESF, Syracuse, NY; and OMNR Fast Growing Forests Group, Brockville, ONT.

[2] NC and NE denote clonal designations by the USDA North Central For. Exp. Stn., and USDA No-Eastern For. Exp. Stn., respectively.

[3] All Populus spp. crosses.

between M. disstria host preference and larval performance? 2) How are patterns of poplar clonal growth, resistance and tolerance to defoliation, and M. disstria behavioral and developmental characteristics related? 3) How can information from these analyses be used to evaluate and develop more productive poplar clones?

METHODS

Foliar analysis was standardized for leaf position. Leaf number (position) was assigned by counting down from the most recent unfolded leaf (No. 1). Foliar nitrogen concentration and moisture content were determined from a composite sample of leaves 4, 5 and 6, by micro-Kjeldahl analysis and wet weight/dry weight analyses, respectively. Leaf toughness was measured as grams of force necessary to puncture the leaf surface with a penetrometer, for leaves 3-4 and 7-8.

Larval preference among the 15 clones was evaluated in petri dish bioassays. Each dish contained an excised leaf disk from each clone. Six 2nd instar or four 4th instar larvae were allowed to feed for 24 or 18 hours, respectively. At the end of the feeding period, the area of each leaf disk consumed was estimated by a dot grid method and preference expressed as the percent of leaf disk consumed. Total feeding per dish was used as a covariate in the analysis.

Preliminary investigations into adult M. disstria oviposition preference among the clones were conducted in $1m^3$ cages containing a single plant of each clone. Thirty or 60 female pupae and an equal number of male pupae were introduced into each cage. Moths were allowed to eclose, mate and oviposit, and preference was evaluated by counting the number of egg bands on each clone. Statistical analyses were not conducted.

M. disstria performance was evaluated under controlled conditions (laboratory) and in an open-air glasshouse. In the laboratory 10 first instar larvae were introduced into plastic rearing boxes containing excised whole leaves from specific clones. Larvae were allowed to develop, and performance was measured as development time to pupation, and female pupal fresh weight and width. In the glasshouse, a single egg band containing 60 to 80 eggs was hung within cages containing three plants of the same clone. All eggs hatched within 24 hours of each other. After 14 days of feeding, approximately 20 larvae were removed from each cage and weighed.

Clonal tolerance to loss of photosynthetic area was measured by artificially defoliating plants over a 30 day period. This approximates the natural rate of insect feeding (Hodson 1941). Height growth of control and defoliated plants were measured 10 days after the final treatment, and tolerance computed as the percent growth of defoliated trees, to control trees. Initial height was used as a covariate in the analysis.

Statistical analyses among clones were conducted by the General Linear Models (ANOVA) procedure, and among measured variables Pearson product-moment correlations were calculated (SAS 1982).

RESULTS

Height growth varied significantly among clones after three and a half months, and ranged from 60 to 140 cm (alpha=.05). Foliar nitrogen (2.4 to 4.2 %), moisture (75 to 82 %) and leaf toughness also varied significantly among clones (alpha=.05). Foliar toughness was significantly different among clones for both leaf positions tested.

Feeding preference by 2nd instar larvae varied significantly among clones, ranging from 0.6 to 43.9 percent consumption of leaf disks (alpha=.05). Fourth instar preference also varied significantly among clones, ranging from 11.1 to 50.7 percent leaf disk consumption (alpha=.05). These two behavioral measures, however, were not significantly correlated with each other.

Preliminary investigations on adult M. disstria oviposition have indicated that clonal preferences may exist. However, in these glasshouse bioassays many females failed to oviposit and so more conducive experimental conditions need to be devised. Further studies are underway to develop more sensitive adult bioassay techniques and to test for preferential differences among clones.

In laboratory performance bioassays, M. disstria development varied significantly among clones (alpha=.05). Development time ranged from 31 to 52 days, female pupal width ranged from 5.8 to 8.3 mm, and female pupal fresh weight ranged from 165 to 477 mg, among clones. In glasshouse performance bioassays, larval fresh weights varied greatly among clones (0.88 to 59.83 mg) (alpha=.05), with three clones, DTAC2, NM6 and NC5339 being rejected by the larvae.

Significant differences among clones in tolerance to artificial defoliation were found (65 to 98 % tolerance) (alpha=.05).

DISCUSSION AND FRAMEWORK DEVELOPMENT

Plant hosts which foster larger and more rapidly developing insects, particularly if selectively preferred, are likely to contribute to increasing insect populations and damage. Plant defense (resource availability) theory suggests that the impact of insect pressures depends in part on a physiological balance among plant defenses, reproductive effort and productivity (Bazzaz et al. 1987, Bryant et al. 1985, Loehle and Namkoong 1987). These factors are environmentally mediated, with defenses being both constitutive and induced, and productivity being a combination of inherent growth rate (a species or varietal characteristic), tolerance to loss of photosynthetic area, carbon and nutrient allocation amongst plant parts, and site productivity. These factors coupled with plant age, previous history and cultural conditions contribute to overall plant resistance to pests. Thus the coupling of heritable pest resistance with production forestry objectives requires consideration of the type and intensity of the resistance mechanism, and its relationship with plant productivity. Additionally, the integration of improved genetic pest resistance with production values requires that ecological considerations such as pest biotype evolution, secondary pests, effects on natural enemies and resistance stability, be addressed (Painter 1941, Raffa 1989).

The current study revealed that correlations among the insect preference and performance variables were rare. Only a single significant (non-trivial) relationship, between 2nd instar larval preference and laboratory reared female pupal performance (weight, width) (r=.60, alpha=.1), was observed. Thus various measures of plant suitability for a particular insect are not necessarily related, signaling the need for caution in the use of single factor evaluations of clonal resistance to insects.

Correlations among the plant and insect characteristics measured indicated that foliar nitrogen and toughness were not significantly related to any measure of insect preference or performance (alpha=.1). Foliar moisture content was moderately correlated with 2nd instar preference (r=.5, alpha=.1). Other foliar characteristics, such as phenolic glycosides and other allelochemicals may be important (Bingaman and Hart 1989, Bryant et al. 1987, Lindroth et al. 1986).

Clonal growth rates were not significantly correlated with any measure of insect preference or performance (alpha=.1). The absence of any apparent direct tradeoff between growth and resistance contradicts some aspects of the resource availability hypothesis (Bryant et al. 1985).

Because individual parameters of insect preference or performance were of little value in denoting levels of clonal resistance, and because there were no simple relationships between plant and insect characteristics, a suite of traits must be considered. Such an analysis can be unwieldy, and so a systematic way of examining several factors together is needed. A matrix analysis provides an efficient tool for such an evaluation.

Figure 1 illustrates a proposed Productivity - Suitability Matrix for evaluating plant-insect interactions. Clones can be evaluated for productivity and suitability for insects, and potential directions of tree improvement considered. For example, in Figure 1 clones NC5271 and NM6 are both productive and tolerant of defoliation. However, NM6 is resistant to M. disstria while NC5271 is susceptible. This suggests that pest resistance improvement be a priority for NC5271, but not necessarily for NM6. Thus the matrix facilitates an examination of clonal characteristics, and the relative advantages and disadvantages of improving plants already resistant to insects, versus those which are susceptible. This same approach may also help guide decisions as to whether improvement should strive for additive, synergistic or novel mechanisms of resistance, and what physiological or growth costs are acceptable.

From the 15 clones studied, clones with both high and low suitability for M. disstria corresponding to various portions of the height growth - tolerance to defoliation matrix were identified. Clones listed in Figure 1 have been positioned in a relative fashion, but could be placed quantitatively, and a response surface generated by developing a 3rd axis to represent plant suitability for the insect. Alternative and/or additional plant and insect characteristics could be incorporated into the matrix. The framework permits an evaluation of each clone's relative characteristics in regard to productivity and resistance

	- - - - - - - -TOLERANCE TO DEFOLIATION- - - - - - -		
	High Tolerance		Low Tolerance
High Growth	NC5271 (S,S) NM6 (R,R)	?	NC11004 (S,S)
	NC11432 (R,i)	DTAC2 (i,R)	NC11396 (i,i)
HEIGHT GROWTH		NC11445 (R,i) NC11382 (S,i) NC5331 (i,R)	NC5377 (S,S)
Low Growth	NC5262 (R,i) NC11505 (i,R)	?	?

Location of clones refers to height growth and defoliation tolerance characteristics. Letters in parentheses following clonal designations refer to M. disstria preference and performance results, respectively; R=resistant, S=susceptible, i=intermediate. A question mark indicates where no clone was found with this combination of traits.

Figure 1.--Productivity-suitability matrix for the hybrid poplar-M. disstria association.

to M. disstria. A generalized pest guild matrix, or a suite of matrices could be used to consider the interactions between several pests and a particular crop. The identification of primary pests, silvicultural objectives and ecological implications, coupled with use of a productivity - suitability matrix, provides a rational approach for integrating genetic pest resistance with production objectives.

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