

CHAPTER 7

Insects pests of *Populus*: coping with the inevitable

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Introduction

Trees in the genus *Populus* (the aspens, cottonwoods, poplars, and their hybrids) are highly regarded for their phenomenal potential for producing wood. This reputation derives from their high physiological capacity for exploiting light- and nutrient-rich environments. They are classic examples of "growth-dominated" plant species, i.e., ones that consistently allocate a high proportion of their gathered resources to several key growth-enhancing processes, such as continuous foliage canopy enlargement, during a prolonged growing season.

Tradeoffs: high growth, low resistance to pests

As desirable as fast growth traits are, they may often come at an expense, i.e., a tradeoff with other desirable traits. For example, some high-growth-adapted plants may exhibit poor stress resilience, and high susceptibility to pathogens, insects, and vertebrate herbivores (Chapin et al. 1993; Herms and Mattson 1997). For example, in North America, the number of insects and mites commonly found on the 12 species of *Populus*, at least 300 species, ranks among the highest on any native tree genus (Drooz 1985; Ives and Wong 1988; Peterson and Peterson 1992). In Europe, the recorded total number is almost twice as large, about 525 species of insects and mites (Delplanque et al. 1998). The pathogens are just as numerous, there being more than 250 species of decay fungi on just *Populus*

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tremuloides (Newcombe 1996). Some very excellent, color handbooks are now available to permit rapid identification of the most common and most important pests (for North America, see Ostry et al. 1989 and Ives and Wong 1988; for Europe, see Delplanque et al. 1998).

What this means is that *Populus* trees are prone to have large numbers of insect and pathogen species that attack them. Moreover, this typically translates into many kinds of injuries that can often be quite substantial and detrimental. For example, a midsummer survey of foliage damage in a 3-year-old trembling aspen sucker stand, regenerated after a logging clearcut in western Upper Michigan, revealed that of nearly 8000 sample leaves examined from several hundred plants, only a paltry 5% completely escaped insect injury.

Practically every single leaf in the young stand was injured to some degree by insect feeding. Averaging the amount of leaf surface area removed or damaged across all plants showed that defoliation was about 20%. Leaf area losses of this magnitude are quite common in *Populus*, and ought to be expected as the norm. This particular level of injury, although seemingly substantial, may not be anything to worry about because *Populus* is quite defoliation-tolerant, i.e., capable of compensating for low-to-moderate reductions in leaf surface area (Robison and Raffa 1994; Reichenbacher et al. 1996).

Thus, although high-growth traits may often be correlated with low resistance to insects and pathogens, the good news is that some plants, such as *Populus*, may likewise be well equipped for compensating for most leaf damage until it exceeds a moderately high threshold (Herms and Mattson 1992; Reichenbacher et al. 1996). Therefore, growers should think about management strategies for holding pest damage below the limits of the plant's compensation threshold. The thresholds will vary with cultivar and with soil/site, and weather conditions.

Not all insects are equally important

Although folivores, those 200 or so species eating whole leaves or parts of leaves are the most common insects; they as a group are not necessarily the ones of greatest long-term concern because the sum total of their injuries seldom goes beyond normative levels (ca. 30%) of defoliation. Likewise, among the other species that attack other parts of the plant, only a handful are seriously threatening. The poster insects, the ones that need to be kept front and center in our vigilance, are those few species that most seriously impair the optimal functioning of the apical meristems, and the lateral or cambial meristems (Mattson et. al. 1988). The former generates new shoots and buds, and the latter, new phloem and xylem tissues. This is not to dismiss the defoliator class entirely. Growers need to be concerned about just a few folivore species, those that for some reasons have the capacity to generate prodigious outbreaks. These insects are very important because, through their incredible abundance, they not only greatly diminish

photosynthetic area, they also can substantially diminish the generative capacities of the apical and cambial meristem, and hence overall growth. Among the other insects, growers need to be concerned about a half dozen or so that directly damage the young extending shoots, and the main stems.

Selected insect problems

Therefore, rather than present a general overview of the many insects of *Populus*, we will instead address a few species more thoroughly, those perceived to be among the most important insects affecting *Populus* culture (aspens, cottonwoods, hybrid poplars) in North America. Among them are three outbreak defoliators, two shoot feeders, and four stem borers. For each insect species, we will concisely outline their life history and damage, and spell out reasonable management suggestions for them. Other common insects on *Populus* that may sometimes become serious pests are listed in Table 1 along with references to obtain more information about them.

Insects feeding on leaves

Cottonwood leaf beetle

The cottonwood leaf beetle (CLB), *Chrysomela scripta* F. (Coleoptera: Chrysomelidae), is considered to be a major defoliating insect of *Populus* throughout most of the United States and southern Canada, with the exception of the coastal regions of the Pacific Northwest. This native insect is especially damaging to

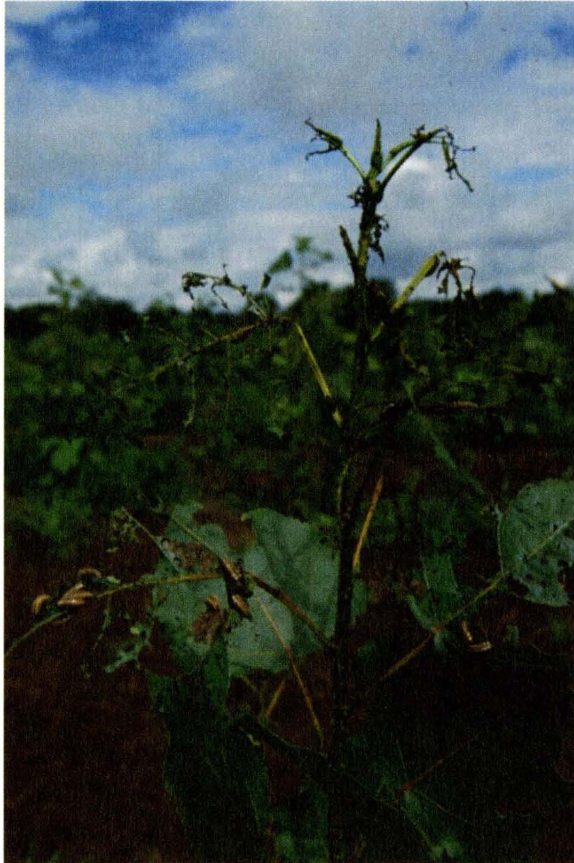
Table 1. Other insects that may be commonly observed in *Populus* plantations, sometimes as significant pests, and an appropriate reference for more information.

Insect common name	Insect Latin name	Plant part attacked	Reference
Poplar tent maker	<i>Clostera inclusa</i>	Leaves	Ostry et al. 1989
Spiny-elm caterpillar	<i>Nymphallis antiopa</i>	Leaves	Ostry et al. 1989
Imported willow leaf beetle	<i>Plagiodera versicolora</i>	Leaves	Ostry et al. 1989
Gypsy moth	<i>Lymantria dispar</i>	Leaves	Delplanque 1998
Aspen blotch leaf miner	<i>Phyllonorycter salicifoliella</i>	Leaves (mining)	Ostry et al. 1989
Pale green weevil	<i>Polydrusus</i> spp.	Leaves, roots	Delplanque 1998
Cottonwood borer	<i>Plectrodera scalator</i>	Roots, base of trunk	Solomon 1995
Agrilus beetles	<i>Agrilus</i> spp.	Roots, trunk	Ostry et al. 1989
Tarnished plant bug	<i>Lygus lineolaris</i>	Shoots	Ostry et al. 1989

species and hybrids of sections *Aigeiros* and *Tacamahaca* (Table 1). For the most part, the CLB is not considered to be a major pest of material with section *Populus* parentage, but recent observations in west-central Minnesota indicate that some hybrids from this section definitely are susceptible under heavy outbreak conditions. Both larvae and adults feed on the foliage (Fig. 1).

The number of generations each year depends upon local climate and weather conditions. In the northern part of its range, the CLB may have only one generation each growing season; in the southern United States, as many as seven generations have been recorded. In central Iowa, three generations per year were noted from 1989 through 1996, but because of warm, extended growing seasons in 1997–1999, four full generations occurred each year. The implication is that if warming trends continue on this continent, additional generations and additional damage also are likely to occur in many areas. The thermal requirements for development from egg to adult are reported to be 230–280 degree days (Burkot and Benjamin 1979; Jarrard 1997).

Fig. 1. Cottonwood leaf beetle damage.



The CLB overwinters as an adult in duff or ground vegetation, and emerges at the same time as native *Populus* buds begin to break in the spring. Following aggregation of both sexes on terminals for feeding and mating, adults disperse and lay eggs in masses of 30–80, preferentially on the underside of immature foliage on a growing terminal (Bingaman and Hart 1992). The younger leaves are preferred for feeding by both larvae and adults; fully expanded, mature leaves usually are non-preferred on most clones. In outbreak populations, all acceptable leaf tissue may be completely devoured and the more succulent stem tissue girdled, causing multiple leaders (Fang and Hart 2000).

The newly-hatched larvae are dark brown to black, feed gregariously, and because of their small size (ca. 1 mm) only graze on the leaf surface. Second and third larval stages are somewhat lighter colored but have large, paired defensive glands on the dorsal surface that when the insect is disturbed emit a defensive chemical. These two stages become progressively less gregarious, and feed on the entire leaf blade, leaving only the midrib and larger veins on the older leaves (Fig. 1). Late third stage larvae wander to various parts of the tree or move to undergrowth, fasten themselves with a posterior adhesive pad, and pupate. Adults are 5.4–9.0 mm long, with longitudinal, ivory-to-gold stripes intermixed with brownish-black stripes on the wing covers (Fig. 2). New emerged adults disperse from the pupation sites, both sexes aggregating, feeding, mating, and then dispersing for egg-laying as did the overwintering adults.

The impact of defoliation is most severe when a high percentage of the foliage on a tree is in a susceptible state of development. There is evidence that trees during the first 1–3 years of growth have the highest percentage of preferred foliage for the first two generations of the CLB (Fang 1997). Studies using artificial defoliation during the first 2 years of growth indicate that growth and biomass losses may surpass one third of the potential when defoliation on LPI 0-8 reaches 75% (Reichenbacher et al. 1996). A recent field study shows that heavy natural defoliation, often approaching 100%, during the first 2 years leads to greater than 50%

Fig. 2. Cottonwood leaf beetle adult.



production loss. Additional studies need to be performed through harvest to determine the economic implications of such natural defoliation over a complete rotation and to determine whether or not it is economically justifiable to consider CLB management after the plantation establishment phase.

Naturally-occurring resistance mechanisms may hold some promise in breeding and selection programs. The role of phenolic glycosides, although important in discouraging feeding by insects that are not closely co-evolved with *Populus*, seems to have limited impact on the preference by the cottonwood leaf beetle (Bingaman & Hart 1993). A combination of chemicals occurring on the leaf surface, however, has been found to affect egg-laying behavior of the insect, and may be useful in breeding and selection for resistance (Lin et al. 1998a, 1998b). Currently, however, no selections with natural resistance to the CLB are commercially available.

Populus selections were among the first trees to be genetically modified for enhanced insect resistance (McCown et al. 1991). These selections included the *Bacillus thuringiensis* (*B.t.*) endotoxin genes and proved to be successful in increasing mortality in Lepidoptera. Transformations that include a Coleoptera-active *B.t.* gene are receiving attention in other programs. Another approach, the inclusion of a novel gene that interferes with the digestive functions of the CLB, has been only marginally successful in affecting CLB biology (Kang et al. 1998), and probably holds little promise as an effective management tool. Other *Populus* selections, transformed with yet a different digestion inhibitor, show promise (Leple et al. 1995) against a related European species, and may warrant additional research in North America.

To date, most CLB management programs in the United States and Canada have depended upon broad-spectrum insecticides applied as ground or aerial sprays. Although they are currently effective, the development of resistance to these chemicals with continued use should be of concern. Recent management efforts have successfully incorporated several commercial *B.t.* formulations (Coyle et al. 1999, 2000). These formulations are effective only against larvae, and particularly the first two larval stages. There are two important considerations for effective use of *B.t.* sprays: (1) applications are effective only during the first one or two generations each year when the development cycle is relatively synchronized and when nearly all of the life stages present are larvae; (2) monitoring activities must be conducted to insure that applications are applied at a time when most of the eggs have hatched or will hatch within a few days. A strict, narrow reliance on *B.t.* as a means of suppression should be avoided because resistance to the *B.t.* toxin can develop (Bauer 1995; James et al. 1999). With a lack of other effective options, as CLB populations become less synchronized through the growing season, broad-spectrum insecticides become the management tool of choice.

The role of natural enemies in CLB suppression has been evaluated in several areas (Head et al. 1977; Burkot and Benjamin 1979; Jarrard 1997). Although there

is evidence of their impact on CLB populations, insufficient information is available at this time to make recommendations beyond using biorational management materials, such as *B.t.*, in a management program to conserve natural enemy populations.

Another leaf-feeding beetle, identified as *Phratora californica*, also native to North America, has emerged as an important problem in the coastal regions of the Pacific Northwest. Limited information is available on the biology and impact of this insect. Host resistance has been observed and is currently under study.

Forest tent caterpillar

The forest tent caterpillar (FTC), *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae), is one of the most widely distributed defoliators in North America. This insect also has a wide host range, severely defoliating water tupelo (*Nyssa aquatica* L.), blackgum (*N. sylvatica* Marsh.), sweetgum (*Liquidambar styraciflua* L.), and oaks (*Quercus* spp.) in the southern U.S. (Fitzgerald 1995). The insect has been recorded as feeding on 29 native forest tree species in the north but seems only to sustain outbreaks in stands where trembling aspen (*P. tremuloides* Michx.) is a principal component (Prentice 1963). Although it also feeds on large tooth aspen (*P. grandidentata* Michx.) and balsam poplar (*P. balsamifera* L.), the FTC does not seem to thrive on these species of *Populus*. Within aspen populations, clones show a variation in susceptibility to feeding by FTC, and this may be indicative of constitutive defenses mediated by levels of proteins and phenolic glycosides in aspen foliage (Lindroth and Bloomer 1991). The basis for these differences in susceptibility might be worth investigating because of the insect's importance in northern areas of poplar culture and the opportunities this research might suggest in producing resistant stock.

Bands that consist of as many as 200 eggs are deposited, encircling twigs by mated FTC female moths in July. The neonate larvae overwinter within the egg band and emerge at about budbreak of the earliest flushing clones of trembling aspen. Delays in hatching relative to budbreak decreases the survival of larvae (Parry et al. 1998). Larvae are able to mine developing trembling aspen buds (Ives and Wong 1988) and are thus able to survive on ramets of later flushing clones. Larvae feed gregariously for the first instars, returning to a silken mat between feeding bouts. They eventually become solitary and often wander off the host tree in the final instar, especially if most of the foliage on the host trees has been consumed (Fig. 3). Cocoons are spun between aspen leaves if defoliation is not severe. In high populations, cocoons can be found in any available crevice.

Reasons for population changes in FTC have not been determined definitively (Fitzgerald 1995). There is a suggestion that cold winters and warm springs favor population increases and that unfavourable weather during the larval stage can cause populations to collapse. Although diseases and starvation of larvae may play a role in the collapse of some outbreaks, it would appear, based on a large

Fig. 3. Forest tent caterpillar late instar larvae.



number of reports, that pupal parasitoids are typically correlated with the decline of populations (Fitzgerald 1995). At endemic levels, experiments suggest that predation of pupae by the northern oriole (*Icterus galbula* L.) may be the factor responsible for maintaining low densities (Parry et al. 1997a). The mechanisms of release of endemic populations from control by predation remain unexplained.

Large areas of northern aspen-dominated forests are completely defoliated by FTC when its populations erupt. Records dating from the early years of the last century suggest that outbreaks have been a constant problem somewhere in the

range. In the last series of Canadian outbreaks, the size of the areas involved peaked at 10.0, 12.8, and 13.0 million ha in Manitoba, Saskatchewan, and Alberta, respectively (Cerezke and Volney 1995). Outbreaks seem to recur at 10–12 year intervals and may last from 2 to 5 years in individual stands. These particular outbreaks were located on the southern margin of the boreal forest and the grassland/forest ecotone. Thus, their ubiquity in the region likely to support intensive poplar culture and the ability of the moths to disperse over several kilometers make the risk of damage from FTC a constant threat to investments in intensively managed stands.

The damage caused by severe defoliation results in an immediate reduction in growth and is reflected in a suppression of radial increment throughout the stem. There is a corresponding increase in mortality of stems in subsequent years that can be attributed directly to FTC defoliation. However, secondary pests further contribute to the reduction in stand yield in the years following outbreaks. In simulating the impacts of FTC defoliation on young aspen stands, Mattson and Addy (1975) suggest that in addition to a yield loss of 25% at age 40 years, one severe FTC outbreak lasting 3 years affected the stand's productive capacity for a decade following population decline. The decline of stands following defoliation may be further exacerbated by diseases such as hypoxylon canker, and climatic conditions that include late frosts and drought (Witter et al. 1975).

Management of FTC populations has included attempts at direct control through the use of insecticides and microorganisms (Fitzgerald 1995). This approach is a reactive strategy that may be viewed as a stopgap method to protect valuable stands with established populations that erupt. Maintenance of a healthy natural enemy complex that includes the preservation and enhancement of oriole populations may be a significant element in the protection of intensively managed *Populus* stands that risk being damaged by FTC. The development and management of resistance to FTC in genetically modified planting stock warrants serious examination. If the benefits from these technologies are not to be squandered, given the evolutionary potential of most pest species to swamp resistance mechanism bred into planting stock, then the spatial and temporal arrangement of resistant, susceptible and native stands must be designed to mitigate this contingency. The concerns regarding the use of resistant stock range from the evolution of resistant target insect populations, the extirpation of non-target populations that harbor important natural enemies, the depletion of genetic diversity within intensively managed stands, reducing future opportunities for genetic gain, and the susceptibility of the stock to other insect species that are presently not considered pests.

Large aspen tortrix

The large aspen tortrix (LAT), *Choristoneura conflictana* (Walker) (Lepidoptera: Tortricidae), feeds primarily on aspen, with only 3, 2, and 1% of the collections made by the Forest Insect Survey of Canada being recovered from willow (*Salix* spp.), balsam poplar, and bigtooth aspen, respectively (Prentice 1965). There is

one generation per year. Females lay eggs in masses containing up to 450 eggs on the upper surfaces of leaves (Prentice 1955). Eggs hatch in mid to late July, and first instars feed on the leaf epidermis before dispersing and finding suitable overwintering sites to spin hibernacula. Larvae moult to the second instar and overwinter in this condition. In spring, second instars emerge to feed on developing aspen buds. There are five instars; the later instars (Fig. 4) web developing aspen leaves together and feed within the shelter thus created. Pupation also occurs within these shelters. Moths emerge in late June to early July, often leaving pupal cases protruding from the shelters. There is some variability in many of these traits, depending on stand conditions and geographical location. Eggs may be laid on a variety of available surfaces in severely defoliated stands and overwintering larvae may be found throughout the crown in mild climates. Prentice (1955) reports that eggs are found on leaves and overwintering larvae are restricted to lower tree boles. Presumably overwintering larvae are thus protected from extreme winter conditions or predation below the snow line.

The LAT is an occasional defoliator of aspen without any apparent defined periodicity to their outbreaks. The reliance on defoliation surveys and the confusion with FTC defoliation may have resulted in under-reporting of LAT outbreaks (Volney and Cerezke 1995). Outbreaks that have been observed last for 2–3 years. Declines in population densities of the LAT have been associated with starvation

Fig. 4. Large aspen tortrix late instar larva.



and subsequent reduced fecundity. Numerous parasitoid species have been reared from LAT, with the tachinid *Omotoma fumiferanae* Toth., accounting for as much as 64% mortality in one case. Disease caused by *Beauveria bassiana* (Bals.) Vuill. seemed to be an important contributor to overwintering larval mortality (Prentice 1955). Ants (*Formica fusca* L. and *F. sanguinea subnuda* Emery) also are known to prey on larvae emerging from hibernacula. Ives (1981) associated an increased chickadee population in decreasing populations of LAT.

The locations most severely affected by LAT tend to be north of those affected by FTC. The areas affected can be as large as the 1.3 million ha outbreak near Fairbanks, Alaska (Beckwith 1968). Because of the sporadic nature of outbreaks and their short duration, damage to trees seems to be restricted to losses of radial increment and twig mortality rather than outright tree mortality (Cerezke and Volney 1995). No studies have reported secondary pest effects following severe defoliation by LAT. Temperatures as low as -40°C do not seem to hinder survival of overwintering larvae (Beckwith 1968), and Prentice's (1955) observation that the overwintering sites are on the lower bole may reflect the effect of chickadees on these populations. In analyzing long-term Forest Insect Survey data, Ives (1981) concluded that cold weather with heavy precipitation early in the winter followed by mild weather with light precipitation enhanced survival and was associated with periods of LAT population increases. Late spring frosts also adversely affect populations if the developing foliage is severely damaged. Extremely hot weather, by elevating temperatures within the larval feeding shelter, has been considered a factor in larval mortality (Criddle quoted by Ives 1981).

Management of LAT has not been necessary in the extensive northern aspen forests. The increasing importance of the resource and a commitment to intensive culture may make intervention increasingly necessary, however. The likelihood that world climate change will alter the risk of outbreaks and thus increase the need for management intervention is uncertain. Indications are that winter and spring temperatures have increased more than the summer and fall temperatures over the past century in Canada. Although this risk is mitigated somewhat by slightly warmer summer temperatures decreasing survival, this is not completely compensated for by the positive effects that the fewer late spring frosts and the increasing winter and spring temperatures will have on elevating survival of LAT larvae.

Direct control agents such as *B.t.* may be problematical for use against this insect in the spring because the shelter makes it difficult to deliver a sufficiently toxic deposit on the feeding surfaces efficiently. Alternatives such as applications of *Beauveria bassiana* or *B.t.* could be developed for treating first instars when they feed on the upper surfaces of fully developed leaves. Such a strategy may also augment the mortality of overwintering larvae from the diseases caused by these organisms. Other natural enemy populations, such as ants, downy woodpeckers, red-eyed vireos (Prentice 1955), and chickadees (Ives 1981), should also be investigated for their potential in reducing or maintaining low LAT populations

through cultural practices. Options here include retention of residual forest structure to provide shelter, nesting opportunities, and alternate food sources in stumps, snags, and standing live and dead trees on harvested sites. Late flushing clones of aspen pose some problems for newly emerged LAT larvae establishing feeding sites in spring (Parry et al. 1997b). Although larvae are able to compensate by spinning an additional hibernaculum on developing buds, their survival suffers because of the increased exposure to the elements, dispersal losses, and natural enemies.

Insects feeding on elongating shoots

Spotted poplar aphid

The spotted poplar aphid (SPA), *Aphis maculatae* Oestlund (Homoptera: Aphididae), a dark aphid having powdery patches along the sides of its body (Fig. 5), is primarily a pest of very young plantings, having greatest impact during the first three summers of development. During the summer months, they feed on the tips of the young, long shoots and the expanding leaves of *Populus*. In the fall, they transfer to dogwoods, where they overwinter. Populations of the SPA can enlarge substantially over the summer because the aphid is incredibly prolific, capable of producing many generations, weather permitting. Consequently, one may see dense clusters containing hundreds to thousands of aphids, infesting all of the expanding long shoots and immature leaves of susceptible trees. When aphid populations attain such high levels, they can significantly reduce *Populus* canopy enlargement because their feeding diminishes long shoot geometric growth, which in turn determines how much photosynthetic area the plant produces during a growing season. Overall growth of the trees is directly correlated with canopy architecture and size.

Management of the SPA can be done by, first of all, planting less susceptible *Populus* clones (Table 1). Next, growers should encourage populations of aphid natural enemies (ladybird beetles, parasitic wasps, lacewings, hover flies, etc.) by avoiding the application of any broad spectrum pesticides. Coupled with plant resistance, natural enemies are the main line of natural defense against aphid outbreaks. When all else fails, aphicides would be the first choice.

Cottonwood twig borer

The cottonwood twig borer (CTB), *Gypsonoma haimbachiana* (Kearfott) (Lepidoptera: Tortricidae), a small caterpillar in the bellmoth family, is native to the eastern United States and infests *Populus* species and hybrids throughout the range of its hosts. In southern U.S., where there is higher probability of high populations, the CTB may be a limiting factor on the success of commercial *Populus* plantings (Payne et al. 1972). Overwintering is passed in an early larval stage under bark scales or leaf scars; in spring these larvae move to the growing shoots,

Fig. 5. White spotted poplar aphids.



bore in, and tunnel and feed to complete development. The pupal stage is completed in bark crevices or in litter beneath trees. Eggs of the next generation are deposited on leaves, and the first larval stage mines into the leaf veins. The second larval stage moves to the tender shoot, and larval development is completed inside the shoot. Infested tips often die back, resulting in multiple leaders, which may in turn be attacked by the next generation of CTB, leading to stunted growth and malformed stems. Multiple infestations in each shoot are quite common in the southern United States, and may lead to heavy shoot mortality (Stewart and Payne 1975).

There are two generations each year in central Iowa (McMillin et al. 1998) and as many as five in Mississippi. Generations per year and population levels seem to be related to climate and to weather conditions.

Some indication of host plant resistance has been noted in Texas (Woessner and Payne 1971), but the role that it may play in management of the insect is uncertain. Management with broad-spectrum insecticides can be accomplished (Morris

1986), but whether or not it is economically or ecologically feasible is uncertain as well.

Insects feeding within woody stems

Poplar borer

The poplar borer, *Saperda calcarata* Say (Coleoptera: Cerambycidae), a large beetle, roughly 30 mm long, is a pest of both young and older stands, living primarily at and below the root collar zone in young trees and throughout the bole on larger trees (Solomon 1995). Damage is invariably more common in open than in dense stands, and often along the edges of stands, owing to the beetle's apparent preference for higher light conditions for oviposition. Egg-laying begins typically in late June to early July when the females cut crescent-shaped slits in the bark and insert their eggs into the phloem. About three weeks later, the eggs hatch and young larvae begin tunneling at the inner bark – sapwood interface. The next season, the larvae leave this interface area and tunnel into the sapwood and heartwood where they eventually weaken the stems and predispose them to storm breakage (Fig. 6). After feeding for 2–3 years, the larvae attain a length of 40–50 mm, and pupate inside the stem behind a plug of wood chips. Adults emerge in late June. Besides the damage done by the borer itself, woodpeckers exacerbate the problem as they create even larger wounds while trying to find the poplar borer larvae. These wounds may become important infection courts for fungi.

Management of the poplar borer is best done by maintaining dense, thrifty stands. Nothing is presently known about resistant cultivars, but such selections could eventually be very important in minimizing damage by this species. Highly infested trees should be rogued from the stand and cut into small pieces, chipped, or burned to cause rapid desiccation and death of the larvae.

Poplar gall saperda and the poplar branch borer

The poplar gall saperda (PGS), *Saperda inornata* Say (Coleoptera: Cerambycidae), in contrast to the poplar borer, is a smaller beetle, about 12 mm long (Fig. 7), and is mainly a problem in young stands, less than 5 years old (Nord et al. 1972a). As does its larger relative, it bores into the stems of young trees; in older trees, it bores mainly into the branches where its injuries are mostly insignificant, unless they facilitate fungal invasion of the tree. Adults seem to prefer higher light conditions and thus their damage is more common in low-density stands and on edges. Also, there is a correlation of high PGS incidence on poor sites (Nord et al. 1972a). In mid-late June, females deposit their eggs under horseshoe-shaped egg niches cut into the bark of small stems or branches. Often a female will cut 2–3 egg niches at about the same relative height but spaced around the stem. The larvae, when they hatch, begin feeding at the inner bark – wood

Fig. 6. Poplar borer adult, larvae, and damage.



interface, and stimulate the growth of a globose or spindle-shaped gall (Fig. 8). As they grow for the next 1–2 years, larvae bore into the wood, creating winding tunnels that weaken the stem and often predispose them to storm breakage. Not only the beetles galleries but also woodpeckers can seriously damage the stem when they hammer into the saperda galls in search of larvae. Both beetles and woodpeckers also create infection courts for the highly damaging and typically lethal fungus, hypoxylon canker (Nord and Knight 1972; Ostry and Anderson 1998), especially in the aspens, and hybrid poplars in section *Populus* (Ostry et al. 1989).

The poplar branch borer (PBB), *Oberia schaumii* LeConte (Coleoptera: Cerambycidae), is also a small beetle, similar in size to the PGS (Solomon 1995). Just as for the PGS, PBB preferentially attacks stems of young saplings and branches on older trees, and is most prevalent in low-density stands (Myers et al. 1968; Nord et al. 1972b). In mid–late June, the female gnaws an elongate, rectangular egg niche in the outer bark and inserts her eggs into the inner bark. Larvae bore downward (15–30 cm) from this point and eventually tunnel into the wood. They do not trigger an obvious swelling of the wood, and thus no gall develops as it does for the PGS. Their hidden tunneling and feeding is often revealed by either bleeding sap or golden sawdust-like frass emanating from the egg niche or 1–3 small shot

Fig. 7. Poplar gall saperda adult.



Fig. 8. Poplar gall sawfly larva in a stem.



holes in the stem 10–30 cm below the oviposition scar. It typically takes 3 years to complete their life cycle. In young trees, their wounds can likewise predispose trees to storm breakage. Similarly, the wounds may also enhance hypoxylon infections. This could be much more important than their direct damage by tunneling in the wood.

Management of both the PGS and PBB is best done by maintaining dense plantings on good sites. Stocking levels of less than 20 000 stems/ha are highly suitable for beetle infestation (Myers et al. 1968). Sanitation is recommended along with employing resistant clones when they are known. Slow-growing trees on poor soils may be more susceptible to these beetles because the trees' induced defenses, such as rapid callus formation and strong hypersensitive reactions to eggs and young larvae, may be debilitated. Fast-growing individuals have more potent rapid inducible defenses, which are effective against poorly mobile, invasive herbivores such as the small, young larvae of these beetles (Herms and Mattson 1992).

Poplar–willow borer

The poplar–willow borer (PWB), *Cryptorhynchus lapathi* (L.) (Coleoptera: Curculionidae), introduced from Europe, is a robust weevil about 10 mm long that attacks cottonwoods, poplars, willows, and alders (Solomon 1995; Schoene 1907). They seem to prefer stems that are more than 2 years old, and greater than 25 mm basal diameter. They may also attack branches as do the PGS and PBB. Adults emerge from infested stems during the late summer and early fall. After a week or so of feeding and mating, gravid females chew slits in the corky bark, often in lenticels, scar tissue, branch bases, and injured areas, typically within 40 mm from the root collar, and insert eggs therein. The developing larvae feed at the inner bark – sapwood interface and only later bore into the wood itself as they mature. The tree is thus weakened by their excavations and may break during wind, snow, or ice storms, or die from stem girdling (Fig. 9). Development from egg to sexually mature adult takes 1–2 years, but adults may overwinter (in the duff) and live up to 2 years. These carryover adults will emerge as warm weather arrives the next spring and quickly begin egg-laying (Furniss 1972).

Management of the PWB is best done by maintaining well-stocked, thrifty stands. Planting young trees near older trees that may be infested is not recommended. The use of resistant clones would be desirable if they were known. Finally, sanitation, i.e., complete removal and chipping or burning of infested trees parts, is recommended.

What to plant? Choosing low-susceptibility clones

With such a large number of insect and mite species that are capable of feeding upon *Populus*, and the dangers inherent in ramping up to large acreage, it

Fig. 9. Poplar–willow borer damage.



behooves growers to make careful selections of the cultivars. It is especially important to match the clones to the climate and soils (Dickmann and Isebrands 1998). Unfortunately, there has not yet been a comprehensive, in-depth study of the insect-resistance traits of most *Populus* clones. As a result, the available data on insect resistance remains quite spotty, and none has been fully and unequivocally confirmed by repeated trials over many different environments. And to

make matters worse, there are only a few cases where insect resistance has been linked to pathogen resistance or to other desirable traits such as high plant growth rates and high wood quality. Therefore, we are walking on thin ice with respect to cultivar selection and the challenges that insects and diseases are likely to throw at us. But, we cannot wait to obtain all this desired information. Instead, we need to proceed with what knowledge we have and make creative adjustments, i.e., adaptive management, as we encounter problems. Anything that is learned about resistance/susceptibility to insects from first-hand experience in the field should be duly and carefully recorded and brought to the attention of specialists in the genetics and pests of *Populus*. In other words, learning by doing is one of the best options.

Table 2 compiles what has been learned so far about hybrid poplar insect resistance to many different insects, each species usually studied at only one locality. Because growers need to consider the simultaneous impacts of many different insect pests, it is not yet obvious if any clone will have the needed traits to render them of moderate to high resistance to all of the major insect problems. However, at least one hybrid poplar clone looks broadly interesting, NC5339. Several others, NC4872, 5270, 5271, and 5272, may exhibit low susceptibility to defoliators. Growers should be advised, however, that few of the clones listed in Table 2 are commercially available, and none has received extensive evaluation for field performance under a wide range of conditions. Nor are any of the mechanisms of resistance or tolerance sufficiently well understood to use in breeding and selection programs. Other traits such as plant resistance to pathogens, adaptations to prevailing climatic and site conditions as well as growth characteristics must also be considered.

Landscape considerations: how to plant, knowing that more plants means more insects

It may be a law of nature that as crop acreage increases so does the likelihood of more serious insect and pathogen damage. Ecological literature has long reported on the positive correlations that exist between the numbers of species of insects occurring on a plant and the geographic area covered by the plant. It might be called the target hypothesis; the bigger the target area, the more insect species from the surrounding environment are eventually capable of finding and thus "hitting" the target plant. An important corollary of the target hypothesis is that as the number of close relatives of said target plant increases in its surrounding environment, the more insects (coming from nearby relatives) will find and colonize the target plant.

Foresters, farmers, and others have long known that large monocultures of any kind of plant are somehow inevitably linked to outbreaks of pests. In fact, Mattson et al. (1991) analyzed the character of natural North American forests

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Table 2. Ranking of tested hybrid poplar clones according to their relative susceptibility (high, medium, low) to different insect pests, and tolerance to defoliation in the Great Lakes region, N.A.

Clone numbers	Clone parentage ^a	Spotted aphid rank ^b	Tarnished plant bug rank ^c	Forest tent caterpillar rank ^d	Cottonwood leaf beetle rank ^e	Defoliation tolerance rank ^d
D38	<i>deltoides</i>	Low				
DBJ21	× <i>jackii</i>	High				
DBJ22	× <i>jackii</i>	High				
DN1	× <i>canadensis</i>		Med.			
DN17	× <i>canadensis</i>	Low				
DN18	× <i>canadensis</i>	Low	Low			
DN19	× <i>canadensis</i>	Low				
DN21	× <i>canadensis</i>		High			
DN22	× <i>canadensis</i>	Med.	Low			
DN31	× <i>canadensis</i>		High			
DN55	× <i>canadensis</i>	Low	High			
DN9	× <i>canadensis</i>		Low			
DN96	× <i>canadensis</i>	Low				
DTAC2	<i>deltoides</i> var. <i>angulata</i> × <i>berolinensis</i>			Med.		Med.
ELJ14	× <i>jackii</i>	High				
FRS1	Unidentified (Fry nursery)		Low			
FRS2	Unidentified (Fry nursery)		High			
GRJ6	× <i>jackii</i>	Med.				
I4551	× <i>canadensis</i>	Low	Med.			
LJ14	× <i>jackii</i>	High				
LUJ7	× <i>jackii</i>	High				
NC11004	<i>deltoides</i>			High		Med.
NC11382	<i>nigra</i> var. <i>charkowiensis</i> × <i>berolinensis</i>			Med.		High
NC11396	<i>maximowiczii</i> × <i>berolinensis</i>			High		Med.
NC11432	<i>deltoides</i> var. <i>angulata</i> × <i>trichocarpa</i>			Med.		High

Table 2 (continued).

Clone numbers	Clone parentage ^a	Spotted aphid rank ^b	Tarnished plant bug rank ^c	Forest tent caterpillar rank ^d	Cottonwood leaf beetle rank ^e	Defoliation tolerance rank ^d
NC11445	<i>nigra</i> × <i>laurifolia</i>			High		High
NC11505	<i>maximowiczii</i> × <i>trichocarpa</i>	Med.	Low	Med.		High
NC238	<i>deltoides</i> × <i>nigra</i> Volga		Low			
NC4877	<i>alba</i>				Low	
NC4878	× <i>canadensis</i>				High	
NC4879	× <i>canadensis</i>		Low		Med.	
NC5258	<i>Populus</i> sp.	Low	Low		Med.	
NC5260	<i>tristis</i> × <i>balsamifera</i>		Low	Med.	Med.	
NC5261	<i>deltoides</i> × <i>balsamifera</i>				Med.	
NC5262	<i>balsamifera</i> var. <i>candicans</i> × <i>berolinensis</i>	Med.	High	Med.	Med.	High
NC5263	<i>balsamifera</i> var. <i>candicans</i> × <i>berolinensis</i>	High	High		High	
NC5264	<i>deltoides</i> var. <i>angulata</i> × <i>nigra</i> var. <i>plantierensis</i>	Low	Low		High	
NC5265	<i>deltoides</i> var. <i>angulata</i> × <i>trichocarpa</i>				Med.	
NC5266	<i>deltoides</i> var. <i>angulata</i> × <i>trichocarpa</i>		Low		Med.	
NC5267	<i>deltoides</i> × <i>nigra</i> var. <i>caudina</i>				Med.	
NC5268	<i>deltoides</i> × <i>trichocarpa</i>				Med.	
NC5270	<i>deltoides</i> × <i>trichocarpa</i>				Low	

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Table 2 (continued).

Clone numbers	Clone parentage ^a	Spotted aphid rank ^b	Tarnished plant bug rank ^c	Forest tent caterpillar rank ^d	Cottonwood leaf beetle rank ^e	Defoliation tolerance rank ^d
NC5271	<i>nigra</i> var. <i>charkowiensis</i> × <i>nigra</i> var. <i>caudina</i>			Med.	Low	High
NC5272	<i>nigra</i> × <i>laurifolia</i> Strathglass	Med.	Med.		Low	
NC5273	<i>deltooides</i>				High	
NC5277	× <i>canadensis</i>		Med.			
NC5318	<i>deltooides</i>				Med.	
NC5319	<i>deltooides</i>				High	
NC5321	× <i>canadensis</i>				Med.	
NC5322	× <i>canadensis</i>				Med.	
NC5323	× <i>canadensis</i>	Low	Low		High	
NC5324	× <i>canadensis</i>				Med.	
NC5325	× <i>canadensis</i>	Med.	Low		High	
NC5326	× <i>canadensis</i>	Low	High		Med.	
NC5327	× <i>canadensis</i>				High	
NC5328	× <i>canadensis</i>				Med.	
NC5331	<i>nigra</i> var. <i>betulifolia</i> × <i>trichocarpa</i>	Low	Low	Med.	Med.	Med.
NC5332	<i>nigra</i> var. <i>betulifolia</i> × <i>trichocarpa</i>	High	High		Med.	
NC5334	<i>deltooides</i> var. <i>angulata</i> × <i>trichocarpa</i>	Med.	Low		High	
NC5335	<i>deltooides</i> × <i>trichocarpa</i>				High	
NC5339	<i>alba</i> × <i>grandidentata</i>		Low	Low	Low	
NC5351	<i>Populus</i> sp.		Med.			
NC5377	× <i>canadensis</i>			Med.	High	Med.
NC9921	<i>Populus</i> sp.		High			
NC9922	<i>Populus</i> sp.		Low			
NE10	<i>nigra</i> × <i>trichocarpa</i>	Med.				

Table 2. (continued).

Clone numbers	Clone parentage ^a	Spotted aphid rank ^b	Tarnished plant bug rank ^c	Forest tent caterpillar rank ^d	Cottonwood leaf beetle rank ^e	Defoliation tolerance rank ^d
NE19	<i>nigra</i> var. <i>charkowiensis</i> × <i>nigra</i> var. <i>caudina</i>	Low	Low			
NE20	<i>nigra</i> var. <i>charkowiensis</i> × <i>nigra</i> var. <i>caudina</i>	Low	Low			
NE206	<i>deltoides</i> × <i>trichocarpa</i>	Low				
NE207	<i>deltoides</i> × <i>trichocarpa</i>	Low				
NE209	<i>deltoides</i> × <i>trichocarpa</i>	High				
NE214	<i>deltoides</i> × <i>trichocarpa</i>	Low				
NE224	<i>deltoides</i> × <i>nigra</i> var. <i>caudina</i>	Low				
NE225	<i>deltoides</i> × <i>nigra</i> var. <i>caudina</i>	Med.				
NE238	<i>deltoides</i> × <i>nigra</i> Volga	Low				
NE255	<i>deltoides</i> var. <i>angulata</i> × <i>trichocarpa</i>	Low				
NE264	<i>deltoides</i> var. <i>angulata</i> × <i>nigra</i> Volga	Med.				
NE265	<i>deltoides</i> var. <i>angulata</i> × <i>nigra</i> Volga	Med.				
NE300	<i>nigra</i> var. <i>betulifolia</i> × <i>trichocarpa</i>	Low				
NE308	<i>nigra</i> var. <i>charkowiensis</i> × <i>nigra</i> var. <i>incrassata</i>	Low	Low			

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Table 2 (concluded).

Clone numbers	Clone parentage ^a	Spotted aphid rank ^b	Tarnished plant bug rank ^c	Forest tent caterpillar rank ^d	Cottonwood leaf beetle rank ^e	Defoliation tolerance rank ^d
NE318	<i>deltoides</i> var. <i>charkowiensis</i> × <i>deltoides</i>	Low				
NE332	<i>simonii</i> × <i>berolinensis</i>			Med.		
NE346	<i>deltoides</i> × <i>trichocarpa</i>	Low				
NE351	<i>deltoides</i> × <i>nigra</i> var. <i>caudina</i>	Low				
NE359	<i>deltoides</i> × <i>nigra</i> var. <i>caudina</i>	Med.	Low			
NE360	<i>deltoides</i> × <i>nigra</i> var. <i>caudina</i>	High				
NE373	<i>deltoides</i> var. <i>angulata</i> × <i>trichocarpa</i>	Low				
NE374	<i>deltoides</i> var. <i>angulata</i> × <i>trichocarpa</i>	Low				
NE41	<i>maximowiczii</i> × <i>trichocarpa</i> Androscoggin	Med.				
NM6	<i>nigra</i> × <i>maximowiczii</i>			Med.		High
RAV	× <i>canadensis</i>	Low	Med.			

^aSeveral Latin names in this column do not reflect current taxonomic priority. See Chap. 1, especially Tables 1–3, for correct synonyms.

^bSource: Wilson and Moore 1986.

^cSource: Wilson and Moore 1985; Sapio et al. 1982.

^dSource: Robison and Raffa 1994.

^eSource: Harrell et al. 1981; Caldbeck et al. 1978.

that are notorious for expansive, severe outbreaks by insects, and concluded that virtually all such forests are typically dominated ($\geq 50\%$ composition) by one or a few tree species, the commonest ones being the primary hosts of the outbreak insects. Outbreaks refer to insect or pathogen populations that are so abundant that they cause plant injuries to vastly overshoot the plant's natural compensation threshold. In the case of trembling aspen, for example, during outbreak peaks of the forest tent caterpillar and the large aspen tortrix, the caterpillar populations can reach millions per hectare and typically remove all of the foliage from the tree canopies with the result that wood growth is nearly negligible. This commonly continues for 2–3 consecutive years, causing substantial losses in wood yield.

Polycultures are in; monocultures are out

The particular cultivars used and their spatial deployment are obviously important, if not crucial, considerations in trying to minimize the development of future pest problems. Yet, there are few hard rules to live by. Because forest crops are likely to be in the ground for 10+ years, it makes sense to select several of the most resistant lines known. However, they should not be planted in monocultures, but in polycultures. Polyculture stands ought to be constructed of several clones, varying in their susceptibility to the major pests anticipated (Gould 1991). Three clones is probably the minimum. Using polycultures is desirable because there will be heightened within-stand heterogeneity, causing a multiplicity of plant selection factors to influence the growth and survival of the insect populations. The goal is to prevent insects from responding uniformly to the resistance traits of the most resistant plants and in so doing developing counter-adaptations (Gould 1991). By employing some clones with only low-moderate resistance, there also will likely be enough insects around to sustain the highly valuable populations of natural enemies (e.g., predators, and parasitic wasps and flies) in the stands to enable them to take part in keeping pests in check, i.e., below the damage thresholds.

Checkerboarding: keeping “islands” small and difficult to find increases pest extinction

Based on the theories of island biogeography and metapopulation dynamics, stand size and patterns across the landscape are another important level of consideration in pest management. When possible, small stands, relatively isolated from one another, will work to minimize pest issues. Small remains to be defined, but perhaps keeping stands in the 10–20 ha range is a reasonable consideration. Likewise, keeping the small stands distant or separated (by non-host crops, forests) from one another will help to minimize outbreaks and to increase the pests' extinction rates within each individual stand. All insect populations are prone to

fluctuate, but small populations are more prone to fluctuate to extinction or near extinction, caused by random mortality factors such as unfavorable weather. When and if this happens, the stand is at least temporarily free from the impact of the pest species until an immigrant female from a surrounding similar stand happens to discover the empty island. This is why it is important that each island be difficult to find, owing either to its long distance from the pest inoculum, or its concealing surroundings of non-host trees. As yet, this is not an exact science, and hard knowledge will only come from trial and error.

Managing natural enemies to encourage presence, persistence, and efficacy

Although it is desirable to make the pest populations prone to extinction and unlikely to discover the crop stands, the opposite is true for their natural enemies. To promote natural enemy abundance and their efficacy in finding the pests, one needs special, detailed information about which natural enemies are important for each and every significant pest (for example, the nine listed above) and what factors limit natural enemy abundance and searching capacity. This detail is beyond the scope of this article, but nevertheless the principles will be addressed here in at least a cursory fashion. Planting poplars next to another crop that will not share its pests but will share its natural enemies is one approach. For example, some generalist parasitoids coming from defoliators in a spruce-fir forest might very likely search for pest defoliators in a neighboring poplar stand. The same might be true for natural enemies derived from an adjacent pine stand, maple stand, or even a marsh. Mattson et al. (1968) reported, for example, that blackbirds that nested in marshes adjacent to a several hundred hectare jack pine forest flocked in hundreds to prey for several weeks on jack pine budworms, *Choristoneura pinus* Freeman, which were abundant in the jack pines. In the same vein, fostering birds by conserving patches of their habitat or certain limiting resources that they need for nesting may provide a measure of resistance to stands at risk to attack by defoliators such as FTC and LAT.

The nutrition of adult parasitoids is often limiting, and hence their capacity for searching for and parasitizing pests is likewise limited (Cappuccino et al. 1999). Because many parasitic flies and wasps require plant nectar and (or) honeydew from aphids and scales to bolster their energy demands while egg-laying, enhancing the abundance of nectar and honeydew sources could pay dividends in pest management. For example, fresh honeydew and dried honeydew on the leaves of a nominal number of aphid-susceptible trees, purposely planted within poplar stands, might significantly aid parasites. Likewise, border trees, and plants that are honeydew and (or) nectar producers might substantially enhance parasitism rates.

Concluding remarks

Insect and disease problems are inevitable and can be severe when growing *Populus*. Therefore, growers must be prepared for their appearance. First and foremost, selecting several clones that have some evidence of resistance to the main insect and disease problems must be the first line of preparation. Next, at the stand level, growing polycultures (mixtures) of many clones rather than monocultures or near monocultures of few clones is strongly advised. Hopefully, both disease and insect resistance will be incorporated into the best clones. Mixtures of several carefully selected clones may actually have higher yields per hectare than equivalent stands of monocultures. At the landscape level, whenever feasible, arranging stands so that there will be minimal movement of pests among them and minimal immigration of pests into them from natural stands is recommended. Encouraging populations of natural enemies of insect pests is also highly advised. This may be accomplished through many means: providing nesting sites for important birds, encouraging wild flowers, and weeds that offer nutrition for parasitic flies and wasps, and establishing poplar plantations close to plant communities that are natural sources of predators and parasites, but not pests. There are no simple, guaranteed recipes for success. Instead, employing common sense and adaptive management are the key principles for achieving success.

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