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Insects and other invertebrates in Aspen: Ecology and Management in the Western United States

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INSECTS AND OTHER INVERTEBRATES

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Quaking aspen throughout its range appears to be host to several insect and other invertebrate pests (fig. 1). It is a short-lived species that is palatable to a large variety of animals. Furniss and Carolin (1977) listed 33 insect species that use aspen as a food source. Some are quite damaging and may kill otherwise healthy stands of aspen; others feed on weakened or dying trees; and still others have incidental impacts (fig. 2).

Boss (1972) found that seven species of insects caused major damage to quaking aspen in Colorado: the western tent caterpillar, *Malacosoma californicum* (Packard); the poplar borer, *Saperda calcarata* Say; the poplar twig saperda, *Saperda moesta* Leconte; a flatheaded wood borer, *Poecilonota cyanipes* (Say); and three species of leafhoppers in the genus *Idiocerus* Lewis. Other families, genera, and species also were found associated with aspen during the 2-year survey, although none were found in epidemic numbers.

A more local survey in northern Utah[1] revealed a different array of insects. Most numerous were leafminers (Lepidoptera, Gracillariidae), sawflies (Hymenoptera, Tenthredinidae), and leafhoppers (Homoptera, Cicadellidae). Aphids (Homoptera, Aphididae), thrips (Thysanoptera, Thripidae) and parasites (Hymenoptera, Chalcidoidea) were moderately abundant. Generally, insect abundance varied inversely with tree height.

Defoliating Insects

Tent Caterpillars

The western tent caterpillar, *Malacosoma californicum*, the most prevalent species, has been responsible for periodic defoliation of aspen over widespread areas

[1]*Unpublished data and observations by Diane M. Bowers on file at the Biology Department, Utah State University, Logan.*

Figure 1.—A variety of insects inhabit aspen trees: (center) ants tending aphids; (upper left) an Agromyzid leafminer; (upper right) a leafhopper.

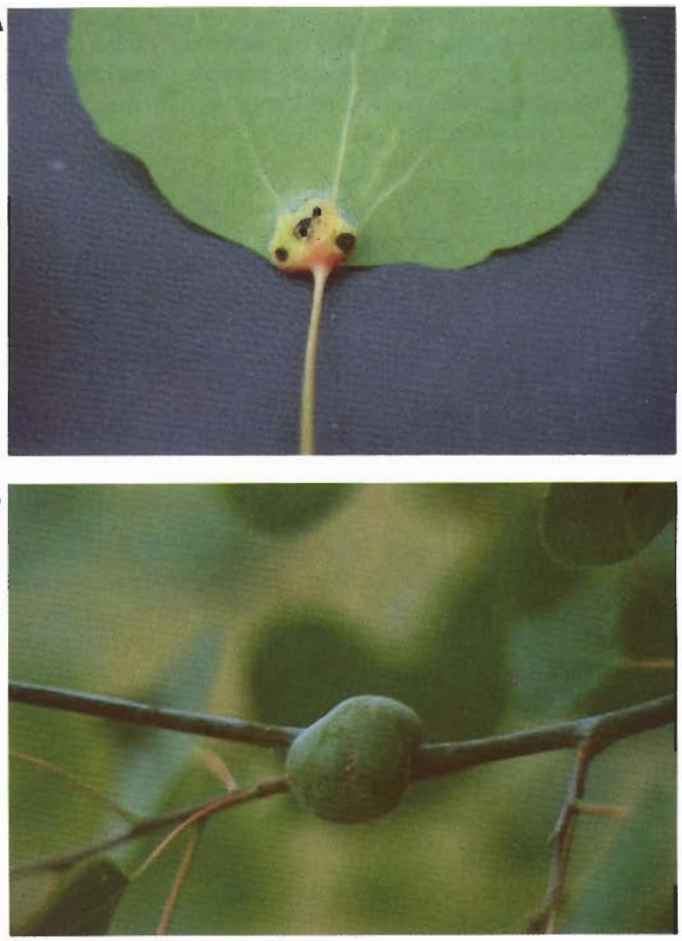

Figure 2.—Some insects leave obvious evidence of their presence. Their feeding causes some abnormal plant growth that results in galls. (A) Leaf gall. (B) Branch gall.

in the West. Its known range extends from Mexico to Washington (fig. 3). This species contains six subspecies (Furniss and Carolin 1977). One of these, *M. c. fragile* (Stretch), which formerly had species status, is commonly known as the Great Basin tent caterpillar. This subspecies is most damaging to aspen in the interior West. Another subspecies, *M. c. pluviale* (Dyar), the northern tent caterpillar, feeds on aspen through much of Canada. It also occurs in northern Idaho and western Montana (Stehr and Cook 1968), but has not been a serious aspen pest in the United States.

A similar insect, the forest tent caterpillar, *Malacosoma disstria* Hubner, is a serious defoliator of aspen in the north central United States (Batzer 1972). For example, an outbreak in 1976-1979, in the Turtle Mountains of North Dakota, defoliated 150,000 acres (61,000 ha) of aspen.[2] This species is found in the East

[2]*Personal communication from Scott Tunnock, Northern Region, USDA Forest Service.*

and in Canada, as well as throughout the interior western mountains as far south as southern New Mexico (Stehr and Cook 1968). The forest tent caterpillar has not been a major threat to aspen stands in the western United States, where it prefers other hosts, most notably common chokecherry (*Prunus virginiana*).[3] However, in a 1963-64 epidemic in northern Idaho, both the aspen and other deciduous trees and shrubs were defoliated (FIDC 1964).[4] Infection by hypoxylon and nectria cankers and attack by borers was shown to increase with increasing severity of defoliation by *M. disstria* of aspen in Minnesota (Churchill et al 1964).

The western tent caterpillar feeds on the leaves of many deciduous trees and shrubs; but, from New Mexico north to southern Idaho, aspen is preferred. Farther north it occasionally feeds on aspen but appears to prefer other, more prevalent species (FIDC,[4] Stehr and Cook 1968). Sustained outbreaks in aspen have been reported from the Pikes Peak area of central Colorado, the Chuska Mountains of northeastern Arizona, and the San Juan and Sangre de Cristo Mountains of northern New Mexico and bordering districts of Colorado (Boss 1972, Clark 1958, FIDC,[4] Gardner 1905, Stelzer 1968).

Four successive years of complete defoliation killed entire trees and top killed others in many aspen stands in New Mexico and southern Colorado, during the 1950s and 1960s (fig. 4). Stands lightly defoliated or defoliated only 1 or 2 years in sequence had minor damage (Boss 1972, Stelzer 1968). Typically, an outbreak persists in a locale for several years, flaring up in one stand and then another without repeated stripping of the same stand.[5]

Diameter growth is markedly affected by tent caterpillar defoliation. Stelzer (1968) reported that during 3 years of complete defoliation, ring widths of surviving stems in New Mexico were less than the average of the six preceding years by 2.4%, 52.2%, and 74.6%, respectively. In Minnesota, aspen defoliated for as little as 1 year by *M. disstria* grew much less in diameter than normal during that year and the next year (Churchill et al. 1964, Duncan and Hodson 1958). Pollard (1972b) studied a mature Ontario stand after a 3-year outbreak of *M. disstria*, and found that growth scarcely improved at all during the first post-outbreak year, and to only about 50% of their pre-outbreak level by the third year.

Diameter growth was assessed on plots in the western tent caterpillar outbreak area of New Mexico and southern Colorado, after the population collapsed.[6] Very narrow growth rings were found in the upper boles; but none could be found at stump height or breast height. Considering that the sampled aspen stands had not been conspicuously damaged, these observations suggest surprisingly severe growth reduction from tent caterpillar defoliation. There is a possibility, however, that the small "extra" rings in the upper boles might be false rings.[7] Perhaps a small amount of growth occurred in spring from stored carbohydrates and initial photosynthates; then defoliation stopped diameter growth until the trees releafed in mid-summer; then another spurt of growth occurred in late summer. Thus, two narrow growth rings could have developed in each year of defoliation.

Defoliation by western tent caterpillar is extensive by the time cambial cells begin to divide (Stelzer 1968, 1971). Because the buds and young leaves are sources of growth-regulating compounds (Wilcox 1962), cambial growth is strongly inhibited in defoliated trees by a lack of regulatory compounds (Kozlowski 1969). Thus, this defoliation drastically reduces photosynthesis and upsets the growth regulating processes in the tree, both of which inhibit growth (see the GROWTH and the VEGETATIVE REGENERATION chapters).

The western tent caterpillar overwinters as eggs. The larvae emerge and begin to feed when aspen leaf buds begin to open. Trees may be stripped of leaves by the end of June. The larvae mature in 30 to 40 days, then pupate (Stelzer 1968, 1971). Later in the summer, the trees put out new leaves (FIDC 1974).[4] In New Mexico, the moths emerge mostly in July, mate, and lay their eggs (Stelzer 1968).

During heavy infestations, all leaves may be eaten before most larvae are mature; many larvae then starve (Stelzer 1968). Also, newly hatched larvae may starve in the spring, if cold weather delays leaf emergence or if a late freeze kills emerging leaves. However, it is doubtful if starvation collapses many tent caterpillar outbreaks

[3] *Personal communication from Mark McGregor, Northern Region, and William Klein, formerly with the Intermountain Region, USDA Forest Service.*

[4] *"Forest Insect Conditions in the United States" was published by the USDA Forest Service from 1951 to 1970. It was expanded to "Forest Insect and Disease Conditions in the United States" in 1971. It presents the status of known significant outbreaks in all regions of the country.*

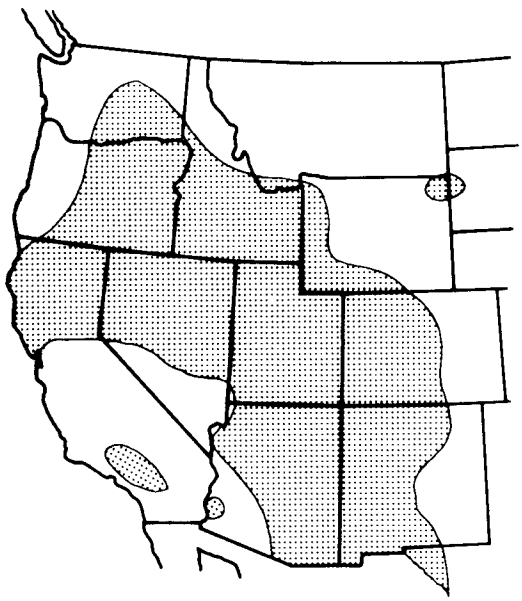

Figure 3.—Distribution of western tent caterpillar in the United States (adapted from Stehr and Cook 1968).

[5] *Personal communication from Robert Acciavatti, formerly with the Southwestern Region, USDA Forest Service.*

[6] *Personal observation by John R. Jones.*

[7] *Personal communication from Gene Lessard, formerly with the Southwestern Region, USDA Forest Service.*

Figure 4.—Deteriorating aspen stand 1 year after collapse of a western tent caterpillar infestation. The stand had been completely defoliated for three consecutive years (Stelzer 1968).

(Smith and Raske 1968). Also, parasitic and predatory insects kill eggs, larvae, and pupae of the western tent caterpillar; but heavy parasitism has not been reported (Stelzer 1968) and, therefore, does not appear to be an effective control either. Instead, buildup of a nuclear polyhedrosis virus, specific to tent caterpillars, appears to be the key factor responsible for collapsing outbreaks (Clark 1955, 1958; Stelzer 1965, 1968). In each reported instance, it took several years for this virus to naturally reach effective levels in the major outbreak areas.

Stelzer (1965, 1967, 1968) demonstrated that new outbreaks of western tent caterpillar could be quickly aborted on a practical field scale by aerial spraying with a water suspension of the virus mixed with *Bacillus thuringiensis*. The virus persists on the trees for at least 1 year after collapse of the caterpillar population (Clark 1958). That persistence should drive the insect population to extremely low levels and prevent quick new buildups on the site.

Large Aspen Tortrix

The larvae of the large aspen tortrix, *Choristoneura conflictana* (Walker), first mine the buds and later roll the leaves into feeding shelters. This moth is found through much of the range of aspen in the West (Beckwith 1973). Extensive outbreaks have occurred in Alaska, Manitoba, and Minnesota (Batzer 1972, FIDC[4]). Occasional local outbreaks of varying severity have been reported in the western United States.[4] Apparently, these have not caused heavy tree losses (Davidson and Prentice 1968, FIDC 1972[4]). A substantial outbreak of the large aspen tortrix persisted for 3 years on the Kaibab Plateau, in northern Arizona. Limited branch mortality but no conspicuous tree mortality was noted.[5] Beckwith (1973) reviewed the factors that tend to keep tortrix populations in check: birds, predatory and parasitic insects, a fungus which kills larvae in winter, and spring freezing. He doubted, however, that any of these mortality factors cause major declines when populations are high. Perhaps starvation is important (Furniss and Carolin 1977).

Aspen Leaftier

The larvae of the aspen leaftier, *Sciaphila duplex* (Walsingham), skeletonize, roll, and then tie the rolled leaves together as they feed (Furniss and Carolin 1977). Heavy feeding may completely defoliate a tree in one season. This moth is widespread; it occurs in the western Canadian Provinces, and in California, Idaho, Nevada, Utah, and Wyoming. In the 1960s a large outbreak occurred in Idaho, Utah, and Wyoming (McGregor 1967). This outbreak, as well as other leaftier outbreaks, sometimes are associated with aspen tortrix outbreaks.[4]

Geometrid Moths

The caterpillars of five species of geometrid moths feed upon the leaves of aspen in the West (Furniss and Carolin 1977). These larvae are commonly known as loopers, spanworms, or inchworms. The fall canker-worm, *Alsophila pometaria* (Harris), is very widespread and attacks many deciduous trees and shrubs, including aspen. The pepper-and-salt moth, *Biston cognataria* (Guenee), occurs across the northern States and Canada. This large larva (7.5 cm long) is a solitary feeder, commonly on aspen. In British Columbia and Oregon, a third species, *Erannis vancouverensis* Hulst, sometimes severely defoliates aspen. *Itame loricaria* (Eversmann) is a common species, at least in Alberta,

where it causes light defoliation of aspen from mid-May through June. The Bruce spanworm, *Operophtera bruceata* (Hulst), occurs across Canada, where it prefers aspen and willow as hosts (Furniss and Carolin 1977). In the U.S., it heavily defoliated some aspen stands in northern Idaho in the late 1960s; and, in 1973 it infested thousands of acres in the Turtle Mountains of North Dakota.[2]

Leafrollers

Four species of leafrollers have been noted on western aspen (Furniss and Carolin 1977). A solitary leafroller, *Epinotia criddleana* (Kearfott), feeds primarily on aspen and occurs from Alberta eastward in Canada. Another, *Pandemis canadana* Kearfott, is transcontinental and quite prevalent from Alberta to Manitoba. It feeds largely upon aspen, willow, birch, and poplar. A third solitary leafroller, *Pseudexentera oregonana* (Walsingham), is common on aspen in Oregon and in western Canada. A fourth leafroller, *Anacampsis* [*Compsolechia*] *niveopulvella* (Chambers), is a transcontinental species that is common in the North. It was credited with causing considerable defoliation in an Arizona locale, too (FIDC 1974).[4]

Other Defoliators

Larvae of several other western moths defoliate aspen. Within Noctuidae, the cottonwood dagger moth, *Acronicta lepusculina* Guenee, larvae feed most of the summer on leaves of several genera within Salicaceae, with aspen its favorite host (Furniss and Carolin 1977). A second member, *Orthosia hibisci* (Guenee), is a common moth on aspen in the Pacific Northwest, Alberta, Manitoba, and Saskatchewan. A member of the Notodontidae family, the redhumped caterpillar, *Schizura concinna* (J.E. Smith), is a leaf skeletonizer that occurs throughout the West, and is an occasional pest of forest, fruit, and shade trees. It has severely defoliated aspen in British Columbia and Saskatchewan (Furniss and Carolin 1977).

Baker (1925) reported that the tiny larvae of unspecified Chrysomelid beetles strip aspen in some locales; but the outbreaks normally last just one season. He listed the cottonwood leaf beetle, *Chrysomela scripta* F., as an aspen defoliator in Montana; however, Furniss and Carolin (1977) specifically stated that this species does not feed on aspen. However, they listed two leaf beetles that do: the aspen leaf beetle, *C. crotchi* Brown, feeds on aspen, and occurs in the West from New Mexico to Alaska; and the American aspen beetle, *Gonioctena americana* (Schaeffer), periodically defoliates aspen in Canada. An unidentified *Chrysomela* heavily defoliated stands of aspen and paper birch for two consecutive years, in the Black Hills of South Dakota (FIDC 1963, 1964).[4] Baker (1925) also reported defoliation by a small leaf weevil, *Thricolepis inornata* Horn.

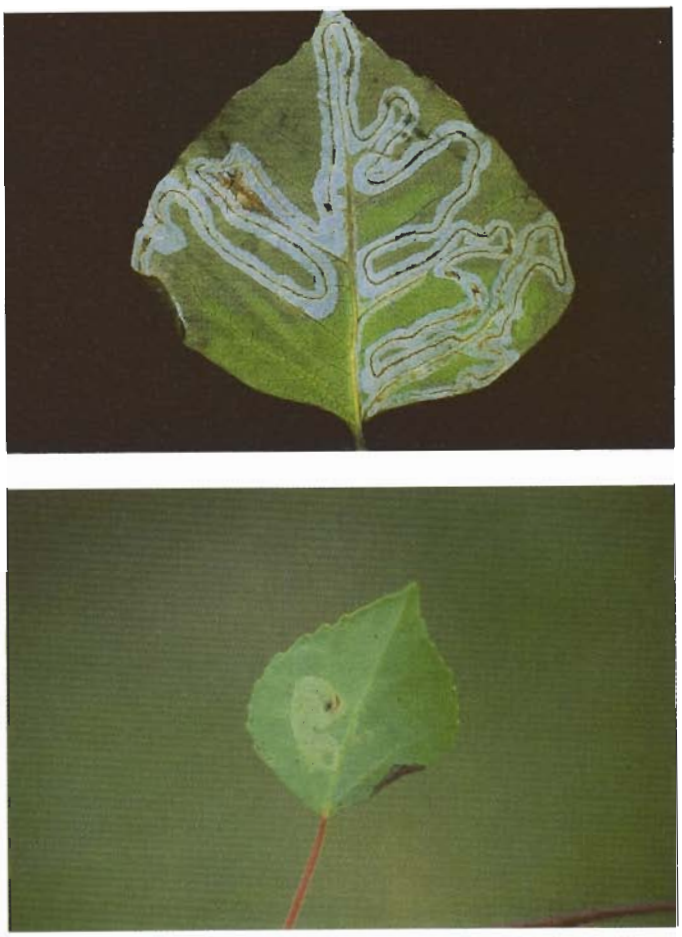

Figure 5.—(A) The aspen leafminer has a very serpentine mine. Note the folded edge of the leaf in the upper right, where the pupa is located. (B) The aspen blotchminer gets its name from the rounded mining activity.

Other Leaf and Branch Insects

Aspen Leafminer

To the casual observer, the aspen leafminer, *Phyllocnistis populiella* Chambers, is one of the most common and visually significant insects on aspen throughout much of the West (fig. 5A). During most years, however, leafminer infestations are not severe enough to significantly affect the well-being of aspen trees. There are exceptions. Considerable tree deformity and some mortality resulted from an outbreak lasting at least 15 years in western Wyoming and southeastern Idaho (FIDC 1959 et seq.).[4] Canadian infestations of this insect have caused some mortality and a considerable reduction in height growth (Conrashoff 1962, Davidson and Prentice 1968). Attempts to rear leafminers from northern Utah were unsuccessful because of parasitism, which indicated that a variety of Hymenoptera parasites attack this insect.[1]

Agromyzid flies also mine aspen leaves. This mining easily can be overlooked, especially early in the season,

because of its similarity to the pattern of the aspen leafminer. Comparison of the mines makes field distinction relatively easy. The mines of Agromyzid flies are distinctly narrower, shorter, and more jagged (fig. 1) than those of the leafminer.

Aspen Blotchminer

The aspen blotchminer, *Lithocolletis* [*Phyllonorycter*] *tremuloidiella* Braun, sometimes destroys most of the leaves in the lower portion of tree canopies. Its common name is derived from the circular blotch shape of the mine (fig. 5B). This insect has been reported from California, Idaho, Utah, and western Canada (Furniss and Carolin 1977, FIDC 1961,[4] Keen 1952). In northern Utah, the aspen blotchminer was much rarer than the aspen leafminer; but sometimes both species were found in the same leaf.[1]

Sawflies

Larvae of common sawflies (Tenthredinidae) frequently were found feeding on aspen leaves in northern Utah.[1] While not always obvious, these caterpillar-like insects or evidence of their skeletonizing activity can be found in rolled and folded leaves (fig. 6). These larvae readily can be distinguished from Lepidoptera caterpillars by their more than five pairs of fleshy legs.

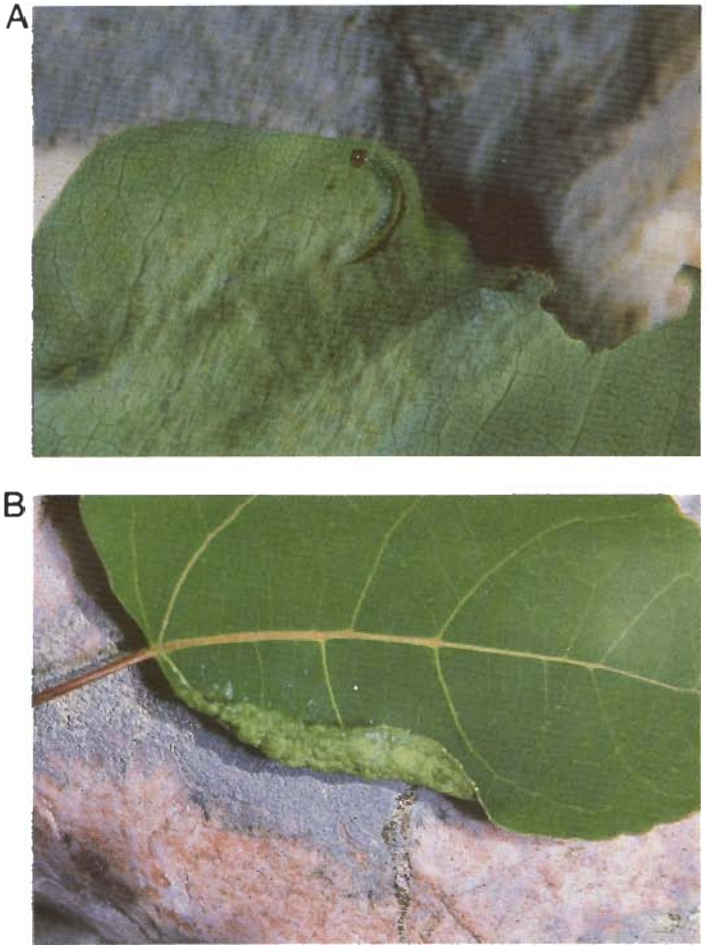

Figure 6.—Common sawfly larvae (A) are not always readily visible because (B) they commonly are found in folded leaf edges.

Figure 7.—*Idocerus* probably is the most common leafhopper on aspen.

Leafhoppers

The leafhoppers, all in the Cicadellidae family, are small insects that suck juices from leaves and succulent twigs (fig. 7). They lay their eggs in slits cut into new twigs. Leafhopper feeding may be severe enough to cause aspen leaves to curl, wither, or turn brown. In Michigan, they are likely to be involved in early thinning of sucker stands at about 5 years of age (Graham et al. 1963). No literature was found on the impact of leafhopper feeding on aspen in the West. However, Bowers[1] noted that leafhopper nymphs were so numerous on young aspen in northern Utah in 1978, that their feeding had bleached leaves to a pale greenish yellow (fig. 8).

Boss (1972) listed three species of leafhoppers on aspen in Colorado: *Idiocerus formosus* Ball, *I. lachrymalis* Fitch, and *I. suturalis* Fitch. He found several fungi associated with the egg slits of these leafhoppers, including *Cytospora* sp. and *Dothiorella* sp. In northern Utah, in addition to *Idiocerus*, Bowers[1] found leafhopper species in the subfamilies Deltocephalinae,

Macropsinae, and Typhlocybinae on aspen. Her observations suggest that some leafhopper species restrict feeding to specific areas on aspen trees, such as twigs or petioles. These species were cryptically colored to match their location and were not apparent by casual observation.

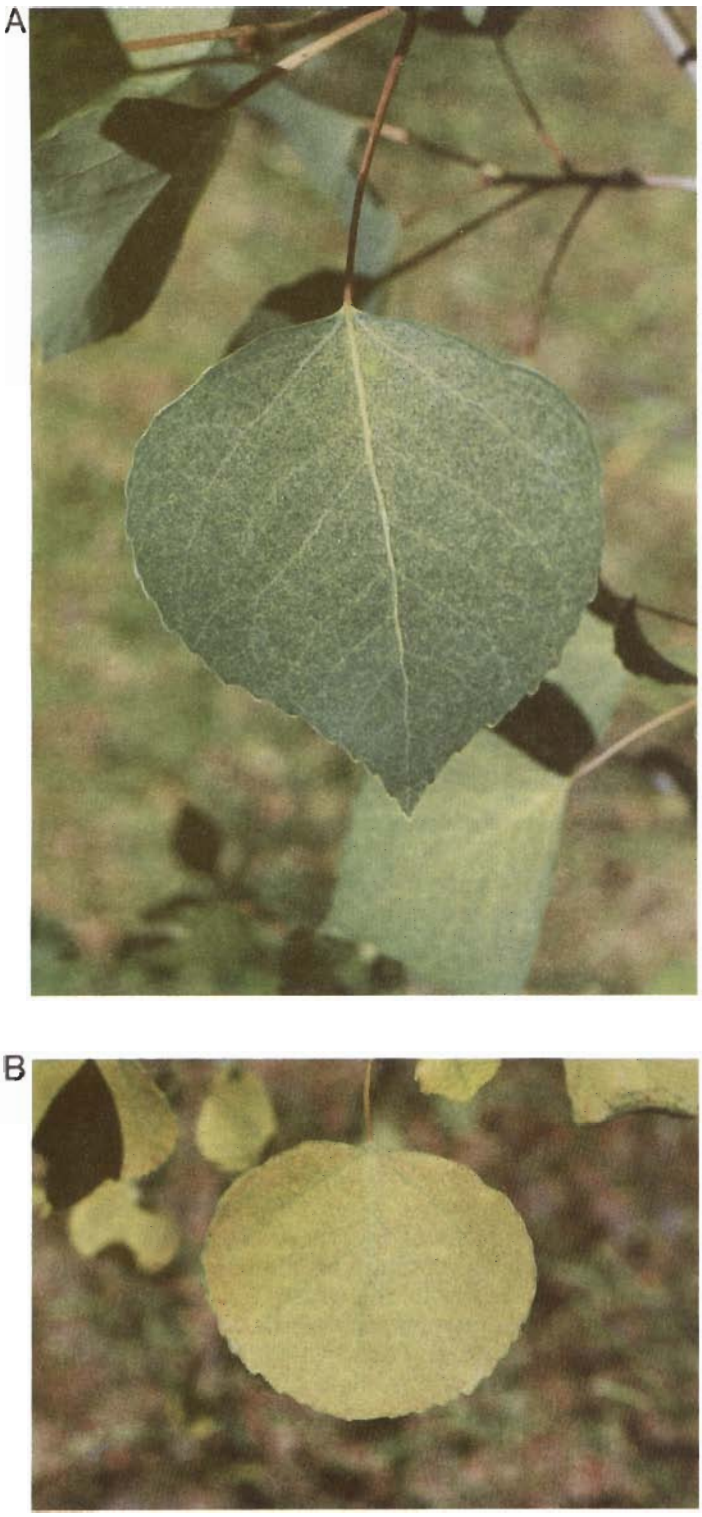

Figure 8.—Yellow spots on aspen leaves (A) are caused by sucking insects. If leafhopper nymphs extensively feed on aspen, the entire leaf may turn yellow (B).

Aphids

The poplar leaf aphid, *Chaitophorus populicola* Thomas, occurs in western Canada and at least in Colorado and Utah. It sometimes causes leaf drop in aspen by feeding on the apical twigs and developing leaves (Furniss and Carolin 1977). Aphid abundance may be positively affected by ants. Some ant species protect aphids and "milk" them for the excess sugars (honeydew) they secrete. Aphids can be most readily located by looking first for concentrations of ants on aspen trees (fig. 9).[1]

Oyster Scale

The oyster scale, *Lepidosaphes ulmi* (L.), attacks aspen in the West. These insects congregate as solid crusts on limbs and twigs. Heavy infestations often kill infested trees (Keen 1952). Survivors show areas of roughened bark (Graham et al. 1963).

Others

A variety of bugs (Hemiptera) were found on aspen in northern Utah.[1] They were in the families Anthocoridae, Lygaeidae, and Miridae. None were numerous. Their effects are unknown. Also, occasionally unidentified species of weevils (Curculionidae) and click beetles (Elateridae) were found on these northern Utah aspen.

Boring Insects

Insects that bore into the bark and wood directly injure aspen trees, and also act as vectors for diseases, such as canker and trunk rot (Bird 1930, Graham and Harrison 1954, Graham et al. 1963, Hinds 1972b, Hofer 1920, Sandberg 1951). In an extensive sample of mature and overmature aspen stands in Colorado, bark injuries by boring insects were found on more than 3% of the trunks and on 52% of the plots (Hinds 1964). In some cases, *Cytospora* also was present, indicating active infection of the recent wound by a canker fungus. Bark injuries by borers were most frequent on good sites and at upper elevations.

Poplar Borer

The adult beetles of the poplar borer, *Saperda calcarata*, are elongate, gray, and 20-30 mm long. Early surveys throughout the Rocky Mountains listed this roundheaded borer as one of the main insects attacking aspen (Baker 1925). Hofer (1920) credited the poplar borer with killing many aspen in the Pikes Peak area between 6,500 and 8,000 feet (2,000 m and 2,500 m) elevation.

The poplar borer may prefer certain aspen associations. At least, in the aspen grovelands east of the Rocky

Mountains in northern Montana, Lynch (1955) found infestations restricted to the *Populus-Symphoricarpos* association, where impacts often were severe; whereas the borer was nonexistent in the *Populus-Osmorrhiza* and *Populus-Aster* associations.

The poplar borer infests aspen from saplings to mature trees (Hofer 1920). Large trees are attacked anywhere on the stem. Many attacks are abortive. Eggs usually are laid after an egg niche is cut. After hatching, the larvae may not always successfully mine away from the vicinity of the niche. According to Graham et al. (1963), fungi and bacteria invariably invade the egg niche; and, if fungal growth is rapid, the larvae die because they are deprived of the living wood cells required for food.

The larvae feed in the sapwood and heartwood for 2 or 3 years, expelling coarse fibrous frass through slits in the bark. Borer activity is marked by accumulations of ejected frass and by streaks of varnish-like dried sap on the bark beneath the opening. Callus growth and rough bark around these openings, and secondary attacks by callus borers and fungi, give a rough appearance to heavily attacked trees (Graham et al. 1963). Successful attacks result in extensive staining of the wood. Even unsuccessful attacks cause staining. Stain from an unsuccessful attack by *Saperda calcarata* may extend as much as 10 feet (3 m) below the attack site (Graham et al. 1963).

In Canada, Michigan, and Colorado, the mines of the poplar borer have been described as important sites for infection and rapid growth of the trunk rot fungus, *Phellinus tremulae* (Bird 1930, Graham et al. 1963, Hofer 1920). In Lower Michigan, most hypoxylon cankers on the boles of aspen started in poplar borer wounds (Graham and Harrison 1954).

In Colorado, Hofer (1920) found attacks by *S. calcarata* concentrated in certain trees, which he called "brood" trees. Brood trees develop because adult beetles tend to lay eggs in the same tree from which they emerged.[8] Hofer (1920) noted that fungi often develop rapidly in brood trees, destroying many larvae. Brood trees often break in the wind because of extensive mining of the wood; and many larvae in these windbroken trees fail to mature and emerge.

Successful attacks by the poplar borer in the Lake States are concentrated in larger trees; and infestations are greater in poorly stocked stands (Ewan 1960). Graham and Harrison (1954) noted that the beetles cut many holes but did not lay eggs in the more vigorous trees. Riley and Hildahl (1963) reported that drought stricken Canadian aspen were heavily attacked by *S. calcarata*. Colorado aspen defoliated by the western tent caterpillar were selected by the borer.[8] Hinds (1976a) found that Colorado aspen exposed to the sun by construction of roads and campgrounds suffered increased attacks by unidentified borers. Attacks also increased markedly in stands that had been selectively logged.[9]

[8]*U.S. Department of Agriculture, Forest Service. 1962. Timber management guide for aspen. 14 p. U.S. Department of Agriculture, Forest Service, Rocky Mountain Region, Denver, Colo.*

Figure 9.—Ants often are found tending aphids on aspen.

Poplar Twig Borer

The poplar twig borer, *Saperda moesta*, is related to the poplar borer but the adult beetle is somewhat smaller (about 12 mm long), and colored dark gray to black. It infests and forms galls in aspen twigs and small suckers. The infested branch or sucker is not directly killed; but it becomes weakened and breaks easily from snow or wind (Boss 1972, Graham et al. 1963). Boss (1972) considered damage caused by *S. moesta* to be significant in Colorado. The egg slit is distinctive; a U-shaped flap is formed that opens downward, and the eggs are laid beneath it.

Poplar Branch Borer

The poplar branch borer, *Oberea schaumii* LeConte, is a widespread species that mines and sometimes kills the branches of *Populus* trees; but it is not considered a serious pest (Furniss and Carolin 1977).

Poplar Butt Borer

The poplar butt borer, *Xylotrechus obliteratus* LeConte, has killed large areas of aspen above 7,000 feet (2,100 m) in Colorado and Utah (Keen 1952). This beetle, about 15 mm long, is somewhat smaller than *S. calcarata*, is dark colored, and is marked with three yellow bands across the wing covers. Unlike the adults of most other roundheaded borers (also called longhorned beetles because their antennae are at least as long as their bodies), the antennae of the poplar butt borer are only slightly longer than the head. Tree bases are most heavily attacked (Hofer 1920, Keen 1952). Attacks are repeated until the heartwood is completely honeycombed and the trees break off during wind or snow storms (Furniss and Carolin 1977, Keen 1952).

[9]*Personal communication from T. E. Hinds, Rocky Mountain Forest and Range Experiment Station, USDA Forest Service.*

Poecilonota cyanipes (Say)

A flatheaded borer, *P. cyanipes*, also has been reported in aspen in the West. In Colorado, Boss (1972) found it attacking only the bases of trees, and only trees with bark already damaged, perhaps by sunscald. On exposed aspen boles, borer attacks were found on all sides except the north. They were not found in any tree whose base was shaded. Attacks were common on poor sites and in sparsely stocked stands. *P. cyanipes* also was common along sun-facing margins of dense stands. In the Lake States, *P. cyanipes* is not restricted to the bases of trees; there Graham et al. (1963) found it most common near branch stubs.

Bronze Poplar Borer

The bronze poplar borer, *Agrilus liragus* Barter and Brown, is a flatheaded borer that attacks weakened aspen. Trees whose phloem has been partially girdled, such as by gnawing by elk, are most commonly attacked. Aspen in campgrounds, carved by tourists, often are attacked, too. Symptoms of *A. liragus* infestation include subnormal leaf size, fading leaf color, and early leaf fall (Boss 1972). A related species, the bronze birch borer (*A. anxius* Gory), also girdles and kills aspen twigs (Keen 1952).

Aspen Root Girdler

The root girdler, *Agrilus horni* Kerremans, has been collected in Arizona and South Dakota (Nord et al. 1965) and probably occurs elsewhere in the West. The larvae form spiral galleries in young suckers and often girdle the main roots and lower stems. In Wisconsin and Michigan, the girdled suckers died before normal leaf abscission. These suckers kept their dead brown leaves over winter and were readily recognized when the rest of the stand was bare. Damage has been of little consequence in heavily stocked regeneration but may be serious in lightly stocked sucker stands (Nord et al. 1965). Root damage in aspen plantations in Wisconsin also has been reported (Benson and Einspahr 1967). With increased efforts to regenerate aspen in the West, *A. horni* may significantly impact young sucker stands in the West, too.

Bark Beetles

Three species of bark beetles are listed by Furniss and Carolin (1977) as infesting aspen trees in the West: *Procryphalus mucronatus* (LeConte), *Trypophloeus populi* (Hopkins), and *T. thatcheri* Wood. These and other species of these two genera mine the bark on the bole and large branches of living hardwood trees. The adults of all species are small (1.5-2.0 mm long) and brown to black. In central Utah, Petty (1977) found that *P. mucronatus* favored dead bark of aspen and had little affect on the tree, whereas *T. populi* used the green bark of unhealthy aspen and hastened the death of trees.

Other Boring Insects

The ambrosia beetle, *Typodendron retusum* (LeConte), invades the sapwood of living but declining aspen throughout the West (Hinds and Davidson 1972). Species of *Ceratocystis* and other fungi are associated with these pinhole galleries and with young adult beetles.

Keen (1952) listed two species of flatheaded borers, *Chrysobothris femorata* (Oliver) and *C. mali* (Horn), as attacking aspen twigs. Two others, *Buprestis confluenta* Say and *Dicerca tenebrica* (Kirby) (= *D. prolongata* LeConte), mine aspen logs.

A powderpost beetle, *Ptilinus basalis* LeConte, attacks dead and cured wood of aspen and other hardwoods from California to British Columbia (Hatch 1962 cited by Furniss and Carolin 1977).

In western Canada, the ghost moth, *Sthenopis quadriguttatus* Grote, larvae bore into the roots of aspen and other members of the family Salicaceae (Furniss and Carolin 1977).

Miscellaneous Insects and Other Invertebrates

Several species of beetles have been found by Hinds (1972b) to carry the fungus *Ceratocystis fimbriata* Ell. & Halst., which causes black cankers on aspen. Two of these vectors are sap beetles (Nitidulidae)—*Epurea* sp. and *Colopterus truncatus* Randall; two are rove beetles—*Nudobius corticalis* Casey and *Quedius raevigatus* Gyllenhal; and one is the root eating *Rhizophagus brunneus* (Horn). Nitidulid beetles are attracted by fresh wounds on aspen and are believed to be the principal vector of black canker in Colorado (Davidson and Hinds 1968, Hinds 1972b).

Nematodes of several genera, all associates or parasites of nitidulid beetles, have been recovered from black and sooty-bark cankers in Colorado and New Mexico. These small worms may influence the establishment and development of cankers (Massey and Hinds 1970).

Cutworms, larvae of moths in the family Noctuidae, kill succulent new suckers by cutting them off at the ground line. At least in Michigan, this mortality source is significant (Graham et al. 1963).

The larvae of a moth in the family Olethreutidae (which includes the aspen leaftier), *Laspeyresia populana* Busck, feeds on the cambium of aspen. It has been reported from both Montana and Alberta (Furniss and Carolin 1977).

Eriophyid mites feed on a wide variety of plants, including broad-leaved trees. Some cause galls. Probably most noticeable on aspen is the one that causes pimple-like galls on leaves. Feeding by *Eriophyes parapopuli* Keifer results in woody gall formation around the buds of aspen and poplars in the West. It also stunts tree growth. Another species, *E. neoessigi* Keifer, occurs from Alberta to California, and forms galls in the catkins of *Populus* trees (Furniss and Carolin 1977).

Insect ecology is the scientific study of how insects, individually or as a community, interact with the surrounding environment or ecosystem. Insects play significant roles in the ecology of the world due to their vast diversity of form, function and lifestyle; their considerable biomass; and their interaction with plant life, other organisms and the environment. Since they are the major contributor to biodiversity in the majority of habitats, except in the sea, they accordingly play a variety of Aspen: Ecology and Management in the Western United States Norbert V. DeByle and Robert P. Winokur, editors INTRODUCTION DeByle and Winokur I. THE TREE Taxonomy Distribution Morphology Growth Sexual Reproduction, Seeds, and Seedlings Vegetative Regeneration Genetics and Variation Harper, Shane, and Jones Jones Jones and DeByle Jones and Schier McDonough Schier, Jones, and Winokur Jones and DeByle 11. ECOLOGY Vegetation Associations Climates Soils Effects of Water and Temperature Fire Other Physical Factors Diseases Insects and Other Invertebrates Animal Impacts Mueggler Jones and DeByle Jones