Sawfly Life History Adaptations to Woody Plants

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19

Life History Patterns of North American Tree-Feeding Sawflies

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I. Introduction

This chapter deals broadly with the North American (NA) sawflies in the two superfamilies Megalodontoidea (Xyelidae and Pamphiliidae, listed phylogenetically) and Tenthredinoidea (Pergidae, Argidae, Cimbicidae, Diprionidae, and Tenthredinidae). The larvae of these sawflies are all phytophagous, and many are significant pests (Smith, 1979; see Smith, Chapter 1 of this volume).

Our aim is to examine various life history attributes of these sawflies and identify general patterns. Whenever possible, we compare sawflies to forest Lepidoptera to underscore differences and similarities between the two groups. First, we determine the degree to which herbs, shrubs, and trees are used as larval food. Then, focusing primarily on the largest group, the tree-feeding sawflies, we examine which plant parts these sawflies consume and how polyphagous they are. Next, we look at various attributes of the host trees to determine whether or not tree genera that support few sawfly species have any life history traits in common with tree genera that support many species. Then we look for patterns among sawflies that are forest pests in the Great Lakes region of North America. We conclude by examining the conifer-feeding Diprionidae and Tenthredinidae of the Great Lakes region, comparing life history attributes of outbreak and nonoutbreak species.

II. North American Sawflies

A. Taxonomic Profile

Smith (1979) recognizes about 1000 North American (NA) sawfly species and subspecies in the seven families Xyelidae, Pamphiliidae, Pergidae, Argidae, Cimbicidae, Diprionidae, and Tenthredinidae (Table 19.1). Tenthredinidae, with about 78% of the taxa, is by far the largest family. Of the remaining NA sawflies, about 0.5% are pergids, 1% cimbicids, 3% xyelids, 5% diprionids, 6% argids, and 7% pamphiliids. About 4% (40 species) of NA sawflies are introduced species and are mostly tenthredinids (83%) and diprionids (10%) (Table 19.1).

B. Preference for Woody Host Plants

Sawfly larvae feed on a wide variety of plants; however, reliable host records are still lacking for nearly 50% of the NA species (Table 19.1). For sawflies with known hosts ($n = 511$), about 68% feed on trees, 13% on

TABLE 19.1 Approximate Number of Native and Introduced Sawfly Species and Subspecies in All of North America and in the Northeastern Quadrant of North America, Sorted by Sawfly Family and Larval Host[a]

		North America							Northeastern North America						
			Larval host[c]							Larval host[c]					
						Tree							Tree		
Sawfly family	Type[b]	Total	?	Hb	Sb	All	Con	Hw	Total	?	Hb	Sb	All	Con	Hw
Xyelidae	All	29	6	0	0	23	20	3	11	2	0	0	9	6	3
	Int	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pamphiliidae	All	72	23	0	9	40	31	9	50	14	0	7	29	20	9
	Int	1	0	0	0	1	1	0	1	0	0	0	1	1	0
Pergidae	All	5	4	0	0	1	0	1	4	3	0	0	1	0	1
	Int	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Argidae	All	59	33	13	6	7	0	7	19	3	7	3	6	0	6
	Int	1	0	0	1	0	0	0	1	0	0	1	0	0	0
Cimbicidae	All	12	5	0	3	4	0	4	7	2	0	3	2	0	2
	Int	1	0	0	1	0	0	0	1	0	0	1	0	0	0
Diprionidae	All	48	6	0	0	42	42	0	24	1	0	0	23	23	0
	Int	4	0	0	0	4	4	0	4	0	0	0	4	4	0
Tenthredinidae	All	789	426	85	49	229	15	214	461	197	63	45	156	6	150
	Int	33	0	9	5	19	1	18	32	0	8	5	19	1	18
Total	All	1014	503	98	67	346	108	238	576	222	70	58	226	55	171
	Int	40	0	9	7	24	6	18	39	0	8	7	24	6	18

[a] Based on Smith (1979).
[b] All, all species, both native and introduced; Int, number of species listed as "introduced" or "probably introduced" as given in Smith (1979) and Drooz (1985).
[c] Larval host ?, Unknown; Hb, herb; Sb, shrub; All, all trees, both conifers and hardwoods; Con, conifers; and Hw, hardwoods. Sawflies recorded as feeding on trees and shrubs or trees and herbs were considered tree feeders.

shrubs, and 19% on herbs. This preference for woody plants is consistent for six of the seven families considered in this chapter (Table 19.1). The exception is the family Argidae, where only 50% are known to feed on woody plants. Each family appears to have specialized on either conifers or broadleaf hardwoods. Of the tree-feeding sawflies, the pergids, argids, and cimbicids feed exclusively on hardwoods, and the tenthredinids feed mostly on hardwoods. Conversely the xyelids and pamphiliids feed mostly on conifers, and the diprionids feed exclusively on conifers.

Just as the NA sawflies show a decided preference for woody plants, so do many Lepidoptera, with one exception being the Papilionoidea (Mattson, 1977; Powell, 1980; Miller, 1992). This should not be too surprising, considering that about 8–10-fold more foliar biomass is produced annually by the woody plant strata than by the herbaceous strata in temperate forest ecosystems (Reichle, 1970).

In Tables 19.1–19.3, we have included host preference data for those sawflies found in the northeastern (NE) quadrant of North America. The number of sawflies assigned to this geographic area (576 species) was based on range data given in Smith (1979). We defined the NE quadrant to include all of Canada east of Manitoba and the United States from Minnesota south to Missouri, east to West Virginia, and north to Maine. About 38% of the NA xyelids are found in the NE quadrant, as well as 69% of the pamphiliids, 80% of the pergids, 32% of the argids, 50% of the cimbicids, 50% of the diprionids, and 58% of the tenthredinids (Table 19.1). The NA argids and xyelids are primarily western species.

C. Feeding Guilds of Tree-Feeding Sawflies

Based on Smith (1979), tree-feeding sawflies can be classified into nine feeding guilds: borers of shoots (1) and fruits (2); gallers of branches (3), buds (4), and leaves (5); chewers of conifer staminate flowers or hardwood catkins (6); external free-feeding chewers of leaves or needles (7); leaf rollers (8); and miners of leaves or leaf petioles (9) (Table 19.2). The vast majority of the NA tree-feeding sawflies are external leaf/needle chewers (68%); the two next largest feeding guilds are branch and leaf gallers (about 7% each). All seven families have members that are leaf/needle chewers; and all members of the families Pamphiliidae, Pergidae, Argidae, Cimbicidae, and Diprionidae belong exclusively to this feeding guild. However, there is one diprionid exception, *Augomonoctenus libocedrii,* which feeds inside cones (Smith, 1979). Although the Tenthredinidae exhibit the widest variety of feeding habits, representing eight of the nine feeding guilds (no shoot borers), most are leaf/needle chewers (61%). In contrast, the majority of xyelids (61%) consume staminate flowers. Of the 24 introduced tree-feeding sawflies in North America, most are either leaf/needle chewers (54%) or leaf miners (33%) (Table 19.2).

D. Diet Breadth of Tree-Feeding Sawflies by Feeding Guild

Considering the data in Smith (1979) for all nine feeding guilds together, the NA tree-feeding sawflies clearly tend toward monophagy. Diet breadth averages 1.26 plant genera and 1.08 plant families per species ($n = 346$ sawflies) (Table 19.2). There is no record of a NA sawfly feeding on both conifers and hardwoods.

Among the nine feeding guilds, however, the hardwood leaf chewers in the families Pergidae, Argidae, and Cimbicidae have marked oligophagous to polyphagous tendencies; diet breadth averages three to four tree genera and two to three families per sawfly species (Table 19.2). The single most polyphagous NA species is the elm sawfly, *Cimbex americana* (Cimbicidae), which feeds on nine tree genera in six plant families (Smith, 1979); it is also the largest NA sawfly. Being large and polyphagous is a well-recognized trend among the Macrolepidoptera (Wassermann and Mitter, 1978; Niemelä *et al.,* 1981). The hardwood leaf-chewing pergids, argids, and cimbicids clearly resemble the Macrolepidoptera in their phagism (Mattson *et al.,* 1988) more than they resemble the sawflies in other feeding guilds, whose diet breadth averages one genera and one families in almost all cases (Table 19.2). The one exception is a leaf-mining tenthredinid, *Profenusa canadensis,* which uses both *Crataegus* and *Prunus* (Smith, 1979; Drooz, 1985).

Unlike the polyphagous hardwood-feeding pergids, argids, and cimbicids, the conifer needle chewers are clearly monophagous; most are restricted to a single genus (91% of 108 species), and all are restricted to a single plant family. The two conifer feeders with the widest host breadth (four genera each) are *Acantholyda balanata* (Pamphiliidae) and *Neodiprion abietis* (Diprionidae), the latter considered a species complex (Smith, 1979). Although the NA pine-feeding sawflies can be technically defined as monophagous, they range from *Neodiprion merkeli,* which feeds on a single host, to *Neodiprion lecontei,* which feeds on more than 20 species of native and introduced species of pine. Overall, the free-feeding conifer sawflies feed on fewer tree genera than not only their counterparts on hardwoods (Table 19.2), but also their lepidopteran counterparts on both conifers and hardwoods (Furniss and Carolin, 1977; Holloway and Hebert, 1979; Drooz, 1985; Björkman and Larsson, 1991a; Hunter, 1991).

Although we classified the redheaded pine sawfly, *N. lecontei* (Diprionidae), as a strict pine feeder, we recognize that it occasionally feeds on *Cedrus, Larix, Picea,* and *Thuja* during outbreaks (Smith, 1979; Wilson *et al.,* 1992). Of the NA conifer sawflies, *N. lecontei* feeds on the most plants within a single genus. It has one of the greatest latitudinal ranges of any NA sawfly, extending from 49° N latitude in Quebec to near 25° N in the Florida Everglades (Wilson *et al.,* 1992). *Neodiprion lecontei* may also be a species complex (Wilson *et al.,* 1992).

TABLE 19.2 Mean Number of Host Plant Families and Genera Used as Larval Food by Tree-Feeding Sawflies in All of North America and in the Northeastern Quadrant of North America, Sorted by Larval Feeding Guild and Sawfly Family[a]

		North America				Northeastern North America			
				No. sawflies[d]				No. sawflies[d]	
Guild[b]	Sawfly families[c]	Host families	Host genera	All	Introduced	Host families	Host genera	All	Introduced
Shoot borer	Xye	1.00	1.00	5	0	1.00	1.00	1	0
	Total	1.00	1.00	5	0	1.00	1.00	1	0
Branch galler	Xye	1.00	1.00	1	0	—	—	0	0
	Ten	1.00	1.00	22	0	1.00	1.00	9	0
	Total	1.00	1.00	23	0	1.00	1.00	9	0
Bud galler	Ten	1.00	1.00	2	0	—	—	0	0
	Total	1.00	1.00	2	0	—	—	0	0
Flower chewer	Xye	1.00	1.00	14	0	1.00	1.00	5	0
	Ten	1.00	1.00	1	0	1.00	1.00	1	0
	Total	1.00	1.00	15	0	1.00	1.00	6	0
Fruit borer	Dip	1.00	1.00	1	0	—	—	0	0
	Ten	1.00	1.00	15	2	1.00	1.00	11	2
	Total	1.00	1.00	16	2	1.00	1.00	11	2
Leaf chewer	Xye	1.00	1.33	3	0	1.00	1.33	3	0
	Pam	1.00	1.27	40	1	1.00	1.21	29	1
	Per	2.00	4.00	1	0	2.00	4.00	1	0
	Arg	2.14	3.14	7	0	2.33	3.50	6	0
	Cim	3.00	4.25	4	0	5.00	7.50	2	0
	Dip	1.00	1.20	41	4	1.00	1.26	23	4
	Ten	1.09	1.27	139	8	1.09	1.29	106	8
	Total	1.12	1.37	235	13	1.16	1.44	170	13
Leaf roller	Ten	1.00	1.00	8	0	1.00	1.00	4	0
	Total	1.00	1.00	8	0	1.00	1.00	4	0
Leaf miner	Ten	1.00	1.06	17	8	1.00	1.07	14	8
	Total	1.00	1.06	17	8	1.00	1.07	14	8
Leaf galler	Ten	1.00	1.00	25	1	1.00	1.00	11	1
	Total	1.00	1.00	25	1	1.00	1.00	11	1
All guilds	Xye	1.00	1.04	23	0	1.00	1.11	9	0
	Pam	1.00	1.27	40	1	1.00	1.21	29	1
	Per	2.00	4.00	1	0	2.00	4.00	1	0
	Arg	2.14	3.14	7	0	2.33	3.50	6	0
	Cim	3.00	4.25	4	0	5.00	7.50	2	0
	Dip	1.00	1.19	42	4	1.00	1.26	23	4
	Ten	1.05	1.17	228	19	1.06	1.21	156	19
	Total	1.08	1.26	346	24	1.12	1.34	226	24

[a] For each mean value, N = number of sawflies listed in the column for "all" sawflies. Based on Smith (1979).
[b] Guild, larval feeding guild as given in Smith (1979). All guilds, mean value for each sawfly family, averaging across all feeding guilds.
[c] Xye, Xyelidae; Pam, Pamphiliidae; Per, Pergidae; Arg, Argidae, Cim, Cimbicidae; Dip, Diprionidae; Ten, Tenthredinidae; Total, mean number of host plant families or genera for all sawflies (native + introduced) within each feeding guild.
[d] All, all native and introduced tree-feeding sawflies with known hosts as given by Smith (1979); introduced, number of introduced species.

In the case of sawflies, we speculate that the suite of adaptations for the external leaf-feeding habit on hardwood trees (e.g., detoxification of plant compounds, defense against natural enemies, oviposition specialization) may have required less exacting plant–insect phenological synchrony, or plant biochemical and anatomical/physical "matching," than did the equivalent suite of adaptations for the external needle-chewing habit on conifers (Mattson *et al.*, 1982, 1988, 1991; Price *et al.*, 1990). For example, if a sawfly uses crypsis or hairiness for defense against natural enemies (as do some hardwood sawflies), it may be less restricted in its potential evolution of host range than if it sequesters particular toxic compounds from its hosts for its defense as do many conifer feeders (Larsson *et al.*, 1986; Björkman *et al.*, 1991; Björkman and Larsson, 1991a,b; Soetens *et al.*, 1991; Miller, 1992). Sequestration as a defense requires highly elaborate behavioral, anatomical, and physiological adaptations that are likely to limit a sawfly's host range (Codella and Raffa, Chapter 10 of this volume). Moreover, sequestering sufficient amounts of such compounds for defense also places crucial time and place (tissue) constraints on the sawfly because the plant's production of such compounds typically follows a distinct phenology—such as terpene and resin acid yield in pines (Bernard-Dagan, 1988).

III. Patterns among North American Woody Host Plants

A. Key Genera and Families of Woody Host Plants

The following NA woody plant genera support the largest number of sawfly species: shrubs—*Rosa* (13 species of sawflies) and *Rubus* (12); conifers—*Abies* (13), *Picea* (14), and *Pinus* (72); and hardwood trees—*Alnus* (18), *Amelanchier* (13), *Betula* (31), *Crataegus* (11), *Populus* (26), *Prunus* (23), *Quercus* (29), and *Salix* (103) (Table 19.3). This list agrees closely with the pattern of sawfly–plant associations in Fennoscandia (Neuvonen and Niemelä, 1983). Because of polyphagy, the total number of sawfly–host associations in any column in Table 19.3 exceeds the number of sawfly species in that same column. For example, the seven woody-plant-feeding cimbicid sawflies have 22 recognized sawfly–host associations (Table 19.3).

Grouping host plants at the family level reveals that about 83% of the NA woody-plant-feeding sawflies are associated with just five plant families: Betulaceae (12%), Fagaceae (6%), Pinaceae (23%), Rosaceae (16%), and Salicaceae (26%). This necessarily means that NA sawflies underuse many north temperate and boreal woody plant families such as Aceraceae, Aquifoliaceae, Ericaceae, Lauraceae, Leguminosae, Magnoliaceae, and Moraceae. We will attempt to explain these patterns in the next few sections.

Microlepidoptera in the Northern Hemisphere are strongly associated with the very same five plant families (Betulaceae, Fagaceae, Pinaceae, Rosaceae, and Salicaceae), although perhaps the Fagaceae (especially oaks, *Quercus*) and Rosaceae may support the most species (Prentice, 1965; Powell, 1980). Likewise, Mattson *et al.* (1991) found that nearly all NA outbreak Lepidoptera (ca. 70 species) were limited to these same plant families. Similarly, the family Aceraceae, which is apparently underused by sawflies, is also relatively underused by forest Lepidoptera (Prentice, 1962, 1965; Rockburn and LaFontaine, 1976; Powell, 1980).

B. Host Plant Attributes Affecting Sawfly Use

A rich body of theory addresses plant–insect associations in relation to physiological, architectural, and ecological properties of plants (Strong *et al.*, 1984; Tahvanainen and Niemelä, 1987) as well as plant phylogenetics (Mitter *et al.*, 1991; Farrell *et al.*, 1992). In brief, this theory argues that insect species richness (number of species) per plant increases with the plant's areal distribution, numerical abundance within its range of distribution, size and architectural complexity, number of close extant relatives, and lack of defenses (Neuvonen and Niemelä, 1981, 1983; Strong *et al.*, 1984; Leather, 1986). In addition, the composition of insect species usually reflects the long-term evolutionary history of each plant's plant–animal community and its unique physical environment (Futuyma, 1991; Farrell *et al.*, 1992). Therefore, we address this question by examining the relationships between numbers of native sawflies using a particular genus of trees and (1) the number of native species within that host genus, (2) the northern latitudinal limits and the latitudinal range of each host genus, (3) the relative abundance of the trees within each genus, and (4) various tree life history characteristics.

Numbers of species within each host genus (pooling shrubs and trees) were taken from Little (1979), who provided data for both the United States and Canada. Latitudinal data were obtained from species range maps given by Little (1971, 1976, 1977) and Viereck and Little (1972). We used latitudinal data for North America north of Mexico because the sawfly data from Smith (1979) cover only NA sawfly species north of Mexico. Tree abundance (net volume and number of live trees) data were generated from computer files of the Forest Inventory & Analysis Project (North Central Forest Experiment Station, USDA Forest Service, St. Paul, Minnesota) for the Lake States of Michigan, Minnesota, and Wisconsin. These three states were chosen because (1) their forest inventory data are complete, detailed, and recent (Michigan in 1980, Minnesota in 1990, and Wisconsin in 1983), and (2) they represent average forest conditions in

TABLE 19.3 Number of Native and Introduced Sawfly Species Using Various Shrub and Tree Genera as Larval Food for All of North America (NA) and for the Northeastern Quadrant of North america (NE), Sorted by Tree Genus and Sawfly Family[a]

	Native and introduced sawfly species (*N*)[b]																Native sawflies only (*N*)	
	Xye		Pam		Per		Arg		Cim		Dip		Ten		Total			
Host genus	NA	NE	NA	NE	NA	NE	NA	NE	NA	NE	NA	NE	NA	NE	NA	NE	NA	NE
Mostly shrubs or small trees																		
Acacia	—	—	—	—	—	—	3	0	—	—	—	—	—	—	3	0	3	0
Azalea	—	—	—	—	—	—	1	1	—	—	—	—	2	2	3	3	3	3
Cephelanthus	—	—	—	—	—	—	—	—	—	—	—	—	2	2	2	2	2	2
Cornus	—	—	2	2	—	—	—	—	—	—	—	—	5	4	7	6	7	6
Corylus	—	—	1	1	—	—	2	2	—	—	—	—	4	4	7	7	7	7
Ligustrum	—	—	—	—	—	—	—	—	—	—	—	—	1[1c]	1[1c]	1[1]	1[1]	0	0
Lonicera	—	—	—	—	—	—	—	—	3[1]	3[1]	—	—	—	—	3[1]	3[1]	2	2
Prosopis	—	—	—	—	—	—	1	0	—	—	—	—	—	—	1	0	1	0
Rhus	—	—	—	—	—	—	2	2	—	—	—	—	—	—	2	2	2	2
Ribes	—	—	—	—	—	—	—	—	—	—	—	—	2[1]	2[1]	2[1]	2[1]	1	1
Rosa	—	—	2	1	—	—	1[1]	1[1]	—	—	—	—	10[4]	9[4]	13[4]	11[4]	9	7
Rubus	—	—	3	2	—	—	—	—	—	—	—	—	9[1]	9[1]	12[1]	11[1]	11	10
Sambucus	—	—	—	—	—	—	—	—	—	—	—	—	5	4	5	4	5	4
Spirea	—	—	—	—	—	—	—	—	—	—	—	—	2	2	2	2	2	2
Symphoricarpos	—	—	—	—	—	—	—	—	2[1]	2[1]	—	—	3	2	5[1]	4[1]	4	3
Vaccinium	—	—	—	—	—	—	—	—	—	—	—	—	7	7	7	7	7	7
Viburnum	—	—	2	2	—	—	—	—	—	—	—	—	4	3	6	5	6	5
Coniferous trees																		
Abies	5	1	5	2	—	—	—	—	—	—	3	1	—	—	13	4	13	4
Cupressus	—	—	—	—	—	—	—	—	—	—	—	—	2	0	2	0	2	0
Juniperus	—	—	—	—	—	—	—	—	—	—	2	2	4	0	6	2	6	2
Larix	—	—	—	—	—	—	—	—	—	—	—	—	6[1]	3[1]	6[1]	3[1]	5	2
Libocedrus	—	—	—	—	—	—	—	—	—	—	1	0	—	—	1	0	1	0
Picea	—	—	7	6	—	—	—	—	—	—	4[1]	3[1]	3	3	14[1]	12[1]	13	11
Pinus	15	5	23[1]	15[1]	—	—	—	—	—	—	34[3]	19[3]	—	—	72[4]	39[4]	68	35
Pseudotsuga	—	—	2	0	—	—	—	—	—	—	2	1	—	—	4	1	4	1
Thuja	—	—	—	—	—	—	—	—	—	—	2	2	—	—	2	2	2	2
Tsuga	—	—	3	1	—	—	—	—	—	—	2	1	—	—	5	2	5	2
Hardwood trees																		
Acer	—	—	—	—	—	—	—	—	1	1	—	—	1[1]	1[1]	2[1]	2[1]	1	1
Alnus	—	—	—	—	—	—	2	2	2	2	—	—	14[3]	12[3]	18[3]	16[3]	15	13
Amelanchier	—	—	2	2	—	—	2	2	—	—	—	—	9	7	13	11	13	11
Betula	—	—	—	—	—	—	3	3	2	2	—	—	26[4]	24[4]	31[4]	29[4]	27	25
Carpinus	—	—	—	—	—	—	1	1	—	—	—	—	1	1	2	2	2	2
Carya	2	2	—	—	1	1	—	—	—	—	—	—	4	4	7	7	7	7
Castanea	—	—	—	—	1	1	—	—	—	—	—	—	4	3	5	4	5	4
Crataegus	—	—	2	2	—	—	2	2	—	—	—	—	7[1]	6[1]	11[1]	10[1]	10	9
Fraxinus	—	—	—	—	—	—	—	—	1	1	—	—	5[1]	5[1]	6[1]	6[1]	5	5
Gleditsia	—	—	—	—	—	—	—	—	—	—	—	—	1	1	1	1	1	1
Juglans	1	1	—	—	1	1	—	—	—	—	—	—	1	1	3	3	3	3
Malus	—	—	1	1	—	—	—	—	—	—	—	—	5[4]	5[4]	6[4]	6[4]	2	2
Nyssa	—	—	—	—	—	—	—	—	—	—	—	—	1	1	1	1	1	1
Ostrya	—	—	—	—	—	—	—	—	1	1	—	—	1	1	2	2	2	2
Platanus	—	—	—	—	—	—	—	—	—	—	—	—	1	0	1	0	1	0
Populus	—	—	1	1	—	—	—	—	2	2	—	—	23[2]	18[2]	26[2]	21[2]	24	19
Prunus	—	—	4	4	—	—	5	4	2	2	—	—	11[1]	9[1]	23[1]	19[1]	22	18
Quercus	—	—	1	1	1	1	1	1	—	—	—	—	26	19	29	22	29	22
Robinia	—	—	—	—	—	—	—	—	—	—	—	—	2	2	2	2	2	2
Salix	—	—	—	—	—	—	2	2	4	2	—	—	96[2]	53[2]	103[2]	57[2]	101	55

(continued)

TABLE 19.3 (*Continued*)

Host genus	Xye		Pam		Per		Arg		Cim		Dip		Ten		Total		Native sawflies only (N)	
	Native and introduced sawfly species (N)[b]																	
	NA	NE	NA	NE	NA	NE	NA	NE	NA	NE	NA	NE	NA	NE	NA	NE	NA	NE
Sorbus	—	—	—	—	—	—	—	—	—	—	—	—	3^2	3^2	3^2	3^2	1	1
Tilia	—	—	—	—	—	—	—	—	1	1	—	—	0	0	1	1	1	1
Ulmus	1	1	—	—	—	—	1	1	1	1	—	—	1^1	1^1	4^1	4^1	3	3
Number of sawfly–woody plant associations																		
Shrub	0	0	10	8	0	0	10	6	5	5	0	0	56	51	81	70	72	61
Tree	24	10	51	35	4	4	19	18	17	15	50	29	258	183	425	294	397	266
Conifers	20	6	40	24	0	0	0	0	0	0	50	29	15	6	125	65	119	59
Hardwoods	4	4	11	11	4	4	19	18	17	15	0	0	243	177	300	229	278	207
Total	24	10	61	43	4	4	29	24	22	20	50	29	313	234	506	364	469	327
Number of sawfly species																		
Shrub	0	0	9	7	0	0	6	3	3	3	0	0	49	45	67	58	60	51
Tree	23	9	40	29	1	1	7	6	4	2	42	23	229	156	346	226	322	202
Conifers	20	6	31	20	0	0	0	0	0	0	42	23	15	6	108	55	102	49
Hardwoods	3	3	9	9	1	1	7	6	4	2	0	0	214	150	238	171	220	153
Total	23	9	49	36	1	1	13	9	7	5	42	23	278	201	413	284	382	253

[a] Based on Smith (1979).
[b] Family abbreviations as in Table 19.2. Total, total number of native and introduced sawfly species feeding on a particular host, summing across all seven sawfly families.
[c] Superscripts reflect the number of introduced species present in each case. If no superscript occurs, all species are native.

the NE quadrant because the boreal-temperate ecotone divides these states and, thus, tree species from both ecosystems are represented. Net volume was measured in cubic feet based on all live trees ≥5 in. dbh on commercial forest land. Similarly, number of live trees was based on all live trees ≥1 in. dbh. The commercial forest land represents more than 97% of all forest land in the Lake States.

1. Sawfly Richness Linked to Size of Host Plant Genus

Considering only NA tree genera that host sawflies (Table 19.3), we found a strong positive linear relation ($P < 0.0001$, $R^2 = 0.66$, $n = 33$ tree genera) between the number of native sawflies feeding on a genus of woody plants (sawfly richness) and the number of native tree and shrub species within that genus (Fig. 19.1). Neuvonen and Niemelä (1983) found a similar relationship in Fennoscandia. We found similar positive relationships when only the number of trees ($P < 0.004$) or shrubs ($P < 0.0001$) in each host genus was used in the regression analyses. *Salix* was the pivotal genus in that it consists of 27 species of trees and 60 species of shrubs in North America (Little, 1979) and supports the greatest number of sawfly species (103). Likewise, *Salix* supports the highest number of sawflies (ca.

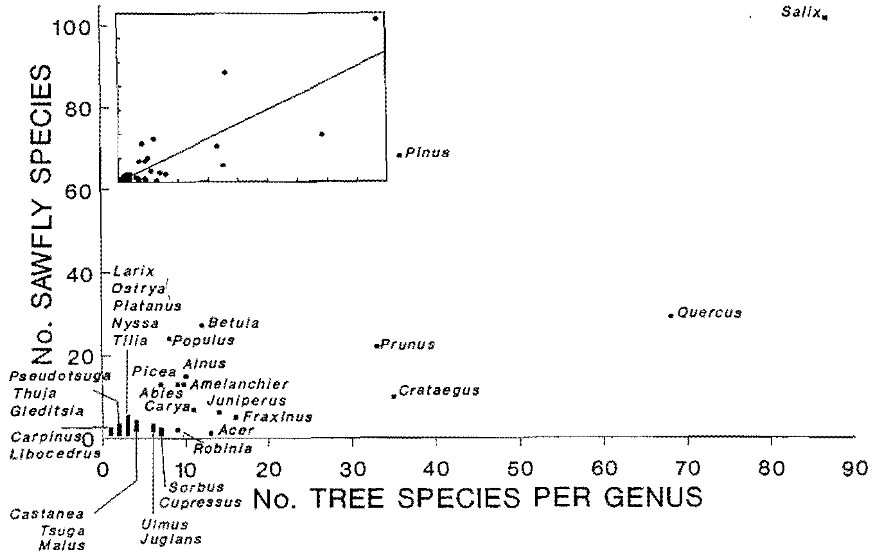

FIGURE 19.1 Relation between the number of native sawfly species that use a particular tree genus as larval food in North America and the number of North American shrub and tree species within that genus. Only tree genera that support at least one species of sawfly were included. All values are for North America, north of Mexico. A linear model (see insert) gave the best fit to the data: $P<0.0001, R^2=0.66, n=33$.

90) in Fennoscandia, although on fewer willow species (ca. 20) (Neuvonen and Niemelä, 1983). Another key genus was *Pinus*, the third largest genus of NA woody plants (36), after *Quercus*, and supporting the second highest number of sawflies (72). Similar positive trends would have existed had we included the NA tree genera that do not support sawflies because even the three largest of these tree genera have relatively few members: *Ilex* (13 woody species), *Magnolia* (8), and *Aesculus* (6) (Little, 1979).

2. Sawfly Richness Linked to Plant Latitudinal Limits

Smith (1979) states that the sawflies in general, but especially members of the Diprionidae and Tenthredinidae, increase in dominance relative to other groups of insects when going northward from temperate to boreal forests in the Northern Hemisphere. The most northern record of a sawfly is 83° N latitude, on Ward Hunt Island in Canada (Smith, 1979). Given the increasing commonness of sawflies in boreal ecosystems, we hypothesized that the northern latitudinal limits of the NA tree genera may be linked to the number of native sawfly species supported by each tree genus. Using species range maps, we estimated both the southernmost and northernmost extent of each tree genus that supports sawflies. We used 25° N latitude as the southern cutoff, equating to the Florida Keys, even though some NA tree species range southward to southern Mexico (<15° N latitude). We considered the difference between the northern and southern latitudinal extremes of all species within each genus to be the latitudinal range of a particular tree genus.

Considering only the tree genera that support sawflies, we found positive nonlinear relationships between sawfly richness on a particular tree genus and both the northern latitudinal limits ($P < 0.001$, $R^2 = 0.40$, $n = 33$; Fig. 19.2) and the latitudinal range ($P < 0.0001$, $R^2 = 0.49$, $n = 33$; Fig. 19.3) of the tree genus, but not its southern latitudinal limit ($P > 0.16$). If we had included Mexico to extend the possible southern latitudinal limit of each tree genus, the relationship of sawfly richness to latitudinal range would have remained highly significant ($P < 0.001$).

3. Sawfly Richness Linked to Numerical Dominance of Tree Genera

Plotting NE sawfly richness per tree genus (for both host and nonhost tree genera) against the log value of net volume of that genus in the forests of the Great Lakes States revealed a significant, but weak, linear relationship ($P < 0.01$, $R^2 = 0.16$, $n = 37$; Fig. 19.4A). The same was true when plotting against the log value of total live stems, but the relationship was still weaker ($P < 0.05$, $R^2 = 0.10$, $n = 37$, Fig. 19.4B). In other words, there is a trend for species richness of sawflies to increase with increasing tree abundance, especially with several of the more abundant tree genera (*Betula, Pinus, Populus,* and *Quercus*). However, some tree species were clearly deviant—for example, *Salix,* which was clearly overused by

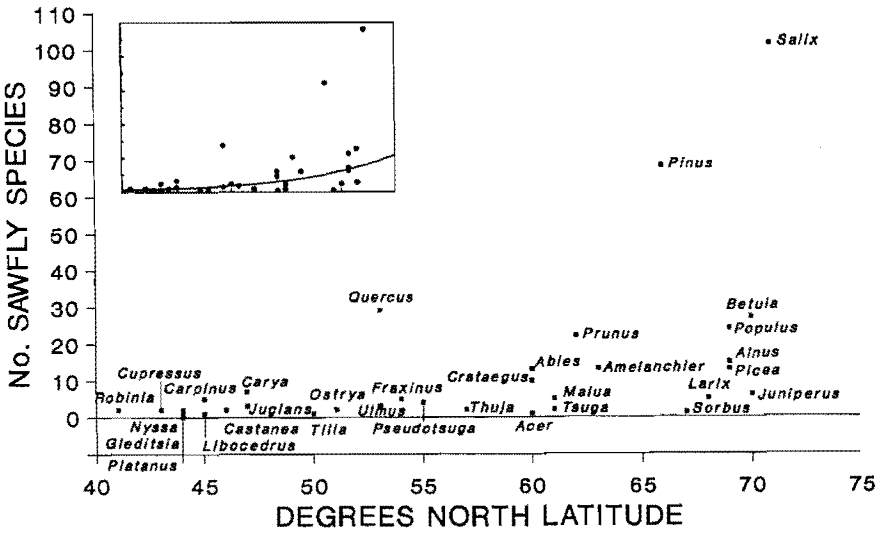

FIGURE 19.2 Relation between the number of native sawfly species that use a particular tree genus as larval food in North America and the northern latitudinal limit of that tree genus in North America. Only tree genera that support at least one species of sawfly were included. All values are for North America, north of Mexico. A nonlinear model (see insert) gave the best fit to the data: $P < 0.001$, $R^2 = 0.40$, $n = 33$.

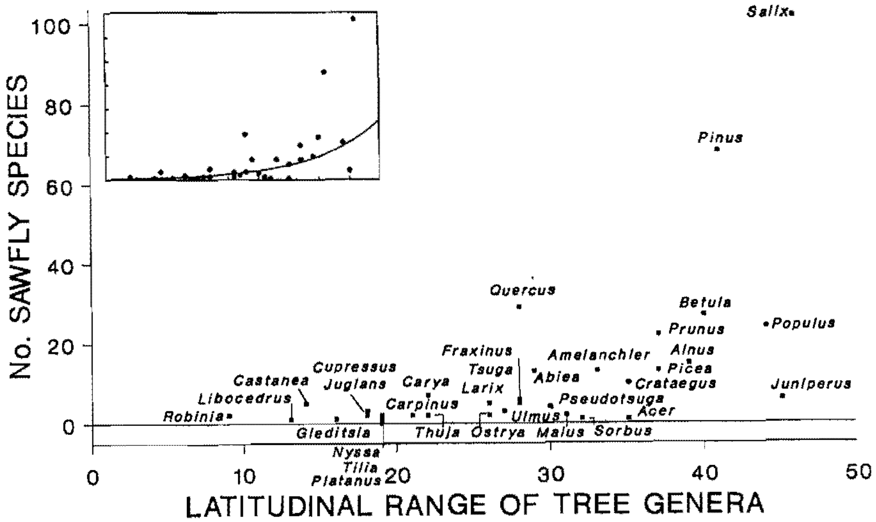

FIGURE 19.3 Relation between the number of native sawfly species that use a particular tree genus as larval food in North America and the north–south latitudinal range (°N latitude) of that tree genus in North America. Only tree genera that support at least one species of sawfly were included. All values are for North America, north of Mexico. A nonlinear model (see insert) gave the best fit to the data: $P < 0.001$, $R^2 = 0.49$, $n = 33$.

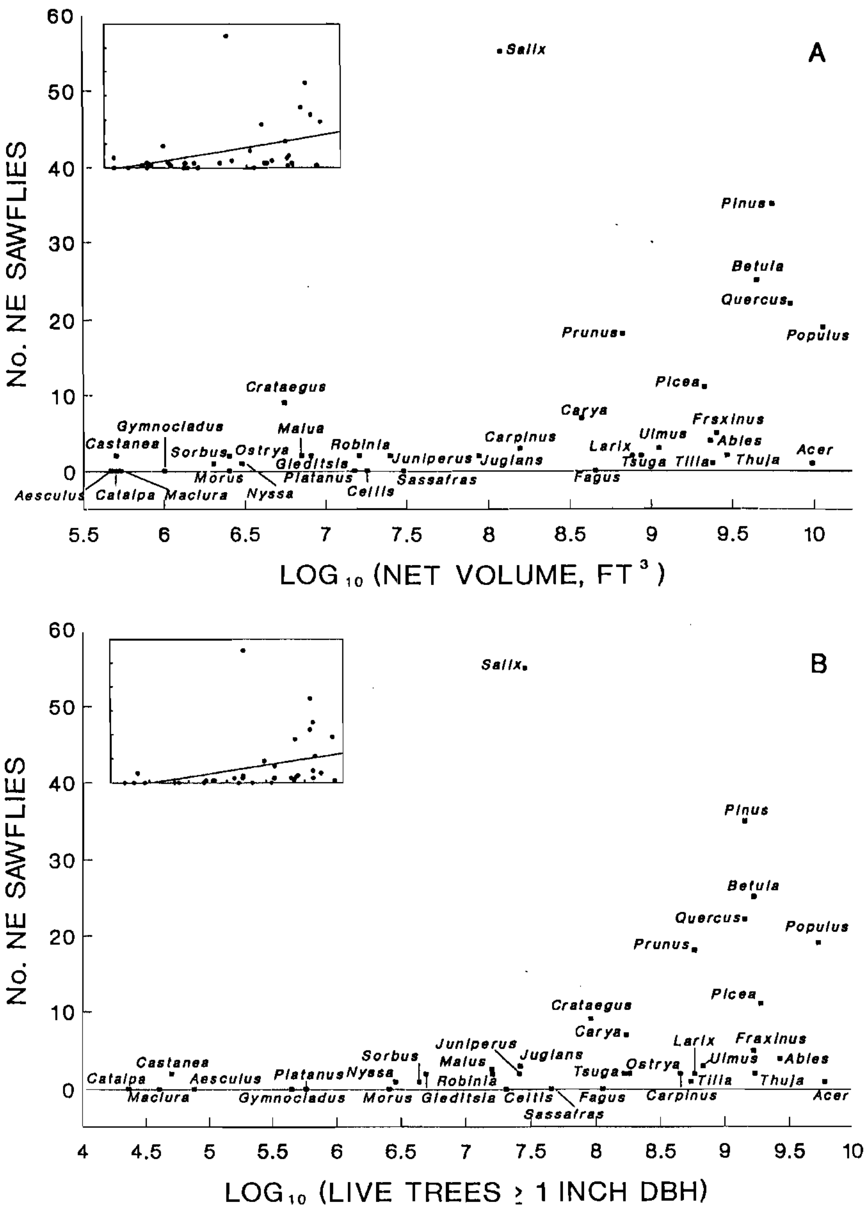

FIGURE 19.4 Relation between the number of native sawfly species that use a particular tree genus as larval food in the northeastern quadrant of North America and the $\log_{10}$ value of total net volume (cubic feet) of all live trees ≥5 in. dbh (A) and the $\log_{10}$ value of total live trees ≥1 in. dbh (B) on commercial forest land in Michigan, Minnesota, and Wisconsin by tree genus. All tree genera found on official forest survey plots were included. Linear models (see inserts) were fit to the data: $P<0.01$, $R^2=0.16$, $n=37$, for (A); $P<0.05$, $R^2=0.10$, $n=37$, for (B). Forest inventories were conducted in 1980 in Michigan, in 1990 in Minnesota, and in 1983 in Wisconsin.

sawflies, and *Acer,* which was underused, relative to their abundances. Simple abundance of a plant genus does not satisfactorily explain its use as a host by sawflies.

4. Sawfly Richness Linked to Tree Life History Traits

To look for patterns in the life history attributes of trees that may affect their sawfly richness, we focused on the plant's environmental indices or synecological coordinates (moisture, nutrients, heat, and light requirements), growth rate, longevity, and relative abundance (Brand, 1985; Loehle, 1988; Mattson *et al.,* 1991). Because these values vary among species within a tree genus, and across the geographical range within species, we arbitrarily used values for Michigan trees based on Barnes and Wagner (1981) and Brand (1985). For tree genera with more than one species, we used life history attributes of the tree species that hosted the most NE sawflies (Smith, 1979). For example, *Pinus banksiana* was chosen to represent the genus *Pinus, Betula papyrifera* was chosen for *Betula,* and *Populus tremuloides* was chosen for *Populus.* A complete set of data was available for 27 of Michigan's 42 tree genera. Of the 27 tree genera, 25 support sawflies in North America and 2 do not (*Fagus* and *Hamamelis*).

We used principal components ordination analysis to examine the relationships between sawfly richness and tree life history traits. We assigned each genus to one of five classes (values 1–5) of shade tolerance, moisture, nutrients, and heat requirements. Values of 1 signify shady, dry, poor, and cool, respectively, as assigned by Brand (1985). We also gave each tree genus a growth rate and longevity classification, with values of 1–4, after Barnes and Wagner (1981). Growth rate was defined as the rate of height growth of young to middle-aged trees growing on their representative forest sites in Michigan: slow-growing (<30 cm/year), moderately slow-growing (30–60 cm/year), moderately fast-growing (61–90 cm/year), and fast-growing (>90 cm/year). Longevity for trees in their natural habitat was divided into four categories: short-lived (<100 years), moderately short-lived (100–150 years), moderately long-lived (151–250 years), and long-lived (>250 years).

Figure 19.5 shows the spatial arrangement for 27 of Michigan's tree genera plotted along the axes of principal components 1 and 2. The first two principal components accounted for 82% of the total variation. The two variables most strongly associated with the first principal component were nutrients (coefficient = 0.52) and shade tolerance (0.50); heat (0.66) and height growth rate (0.58) were most strongly associated with the second principal component. Tree longevity was most strongly associated with the third principal component (0.82).

In general, average sawfly loading (number of native sawfly species using a particular genus of plants per number of native tree and shrub species within that same genus) declines sharply going from the left-hand cluster of seven genera in Fig. 19.5 (*Alnus, Betula, Larix, Pinus, Populus,*

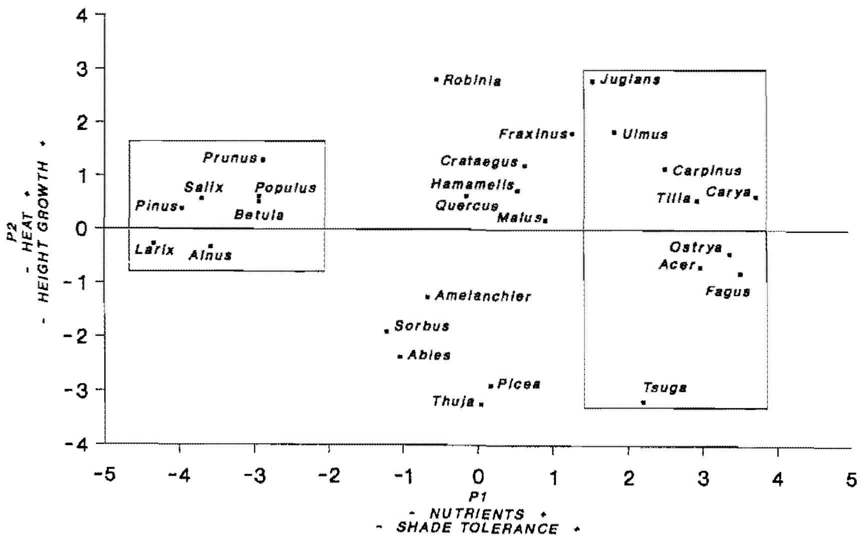

FIGURE 19.5 Spatial array (ordination) of 27 Michigan tree genera along principal component one (P1; soil nutrient status and shade tolerance) and principal component two (P2; heat requirements and height growth). Values range from low (−) to high (+) along each axis.

Prunus, and *Salix;* sawfly loading = 1.73 sawflies/plant species) to the right-hand cluster of nine genera (0.77). Overall, the seven genera on the far left host about 66% of all NA woody-plant-feeding sawflies, whereas those nine genera on the far right host only about 6%. The life history traits that separate these two plant groups are primarily shade tolerance and nutrient requirements. Overall, the seven genera to the left are very light-demanding (shade intolerant), fast-growing, and short-lived; have high shoot : root ratios; and form dense, usually monospecific to oligospecific, even-aged stands where competition is largely conspecific. These traits are common to pioneer tree species, or colonizers (Marks, 1975; Mattson *et al.*, 1991). In addition, each of these genera extends deeply into the boreal forests, and is quite species-rich—averaging 27 species per genus, except for *Larix,* which has only 3 species. According to Stebbins (1974), intermediate-type, marginal environments that present climatically and biologically volatile challenges to plants will promote plant speciation.

On the other hand, trees in the nine genera that cluster on the far right of Fig. 19.5 are largely temperate genera whose life history traits contrast sharply with those of the more boreal plants on the far left of the figure. These nine genera are specialized for existence in more mesic, stable, late successional environments. They are very shade-tolerant,

slow-growing, and long-lived; have low shoot : root ratios; and are adapted for growing in polydominant, mixed-age communities where competition is both intra- and interspecific. None of these nine tree genera extend north beyond the southern edges of the true boreal ecosystem (Fig. 19.2), and compared to the seven genera on the left they are relatively species-poor, averaging six species per genus.

Another important physiological trait separating these two general groups is their tendency toward either indeterminate or determinate growth. *Alnus, Betula, Larix, Populus, Salix,* and some *Prunus* exhibit *free,* or indeterminate, growth (Kozlowski, 1964; Marks, 1975), which is defined as the continuous expansion of shoots and leaves throughout much of the growing season. In contrast, all of the shade-tolerant genera on the far right exhibit mostly *fixed,* or determinate, growth, which is characterized by a predetermined number of stem units in the buds that expand over a relatively short period early in the growing season. This trait has an important bearing on insect species richness per plant (Niemelä and Haukioja, 1982). Plants that exhibit free growth have much broader spectra of leaf age and quality classes available for insect colonization because new foliage is produced continuously throughout much of the growing season. In contrast, plants with determinate growth produce only a single cohort of leaves, thereby providing a more synchronized and more uniform set of leaf resources. The net result is that plants with indeterminate growth provide much broader phenological windows for herbivores—especially for those that have particular requirements for immature leaves. Such fundamental differences in growth patterns ought to be correlated with differences in plant defenses and leaf nutritional quality (Mattson, 1980), and this in turn ought to promote differences in herbivore species richness (Niemelä and Haukioja, 1982).

IV. Outbreak Sawflies in the Great Lakes Region

To search for ecological/life history patterns among sawflies commonly reported as forest pests, we will focus on the Great Lakes region and, in particular, the states of (from west to east) Minnesota, Wisconsin, and Michigan and the province of Ontario. For these states and province, we attempted to locate and review all annual reports of forest pest conditions covering the years 1950–1990. Overall, we obtained 22 annual reports from Minnesota, 37 from Wisconsin, 38 from Michigan, and 29 from Ontario. For each sawfly listed in them, we recorded the year, host, area involved, and damage level (degree of defoliation). Damage levels were categorized as light, medium, heavy, or severe, following the typical adjectives used in the pest reports. When defoliation was described as medium to heavy, for example, we recorded the outbreak as heavy, using the worse situation reported. To simplify the data, we later pooled reports of "light" with "medium" and "heavy" with "severe." Because the area of defoliation was not always given, we required no minimum acreage for inclusion in our data set. Despite the difficulties, we consider the data to be a good assessment of the most pestiferous tree-feeding sawflies in the Great Lakes region during the past few decades.

A. Diprionids Cause Most Outbreaks

There were 52 different sawflies reported in the 126 annual reports from the Great Lakes region (Table 19.4). These 52 species represent about 23% of the 226 potential tree-feeding sawflies in the NE quadrant (Table 19.1). We recognize that not all 226 NE tree-feeding sawflies occur in the Great Lakes region, but we will use the NE values from Tables 19.1–19.3 as approximate values in the discussions to follow.

Of the 52 pest sawflies, there was 1 xyelid, 1 argid, 1 cimbicid, 3 pamphiliids, 17 diprionids, and 29 tenthredinids; 96% (50 of 52) were leaf/needle chewers or leaf/petiole miners (Table 19.4). The number of species reported as pests within each sawfly family was not proportional to the number of NE tree-feeding sawflies in those families ($P < 0.002$, Chi-square). The most overrepresented family in the pest category is Diprionidae, comprising about 10% of the tree-feeding NE sawflies (Table 19.1) but accounting for nearly 33% of the pest species reported in the Great Lakes region (Table 19.4). This value would have been even more disproportionate had we included four other diprionids that are occasionally pests in the NE quadrant but are not found in the Great Lakes region: *Neodiprion excitans, N. pinusrigidae, N. pratti pratti,* and *N. taedae linearis.* Based on the annual forest pest reports, the diprionids are the most outbreak-prone family of sawflies in the Great Lakes region (Table 19.4). However, it is plausible that other sawflies reach "outbreak" levels but go unnoticed because of their more innocuous feeding activities (e.g., leaf galling, leaf rolling, flower chewing).

B. Pines Support Most Sawfly Outbreaks

The host plants most commonly used by pest sawflies (Table 19.4) differed significantly from the overall pattern of host usage by NE sawflies (Table 19.3) ($P < 0.001$, Chi-square). In absolute terms, *Pinus* was the most deviant because it accounted for 52% of the pest sawfly–tree associations (614 of the 1175 outbreaks listed in Table 19.4, summing across all states and the one province) but only 12% of the NE sawfly–tree associations in Table 19.3. Other host plant genera that supported disproportionately high numbers of pest sawflies were *Abies* (5.5 versus 1.4%, respectively), *Larix* (9.2 versus 1.0%), *Picea* (7.7 versus 4.1%), *Sorbus* (4.3 versus 1.0%), and *Ulmus* (3.0 versus 1.4%). Of these six genera, all are relatively common in the Lake States, except for *Sorbus* (Fig. 19.4). Nevertheless, absolute raw abundance does not ensure that sawfly outbreaks will follow. For example, although *Populus* and *Acer* are the most abundant tree species in the Lake States (Fig. 19.4), they hosted fewer than 2% of sawfly outbreaks noted in Table 19.4.

C. Pine Plantation Monocultures Contribute to Outbreaks

Reforestation practices during the early 1900s seem to have influenced the propensity of certain sawflies to reach outbreak levels. To develop an historical account of tree-planting efforts, we (1) examined the original 1903–1980 planting maps for the state forests in the northern half of Michigan's lower peninsula and (2) obtained the stand history data for the Huron–Manistee National Forest, located in the same geographic region of Michigan. We considered the reforestation history of Michigan to be representative of the Great Lakes region. While compiling the data, we found that pine was used in nearly all reforestation efforts on these state and federal lands in Michigan. Therefore, we calculated the total acreage planted to jack pine (*Pinus banksiana*), red pine (*P. resinosa*), or white pine (*P. strobus*) by year. All acreages listed for state forest land represent plantations that were planted by hand or machine; however, the National Forest data did not distinguish between hand/machine-planted plantations and those that were established naturally (e.g., naturally seeded land following a fire). Nevertheless, managers on the Huron–Manistee National Forest state that the vast majority of their pine plantations—especially red pine—were planted by hand or machine.

Major reforestation efforts in Michigan began in the 1920s and then peaked in the late 1920s on state forest land and in the 1930s on federal land (Fig. 19.6). The bulk of the plantations were planted to red pine. Most plantations established during the 1930s were planted by members of the Civilian Conservation Corps, a large national program established by President Franklin Roosevelt that spanned the period 1933–1942 (Merrill, 1981). Reforestation efforts dropped dramatically during World War II but then resumed aggressively in the late 1940s (Fig. 19.6).

Not surprisingly, many "new" species of pine-feeding sawflies had been observed by the mid-1920s (Graham, 1925). Shortly thereafter, six new species of jack pine- and red pine-feeding sawflies were described in the Great Lakes region: *Neodiprion pratti banksianae* in 1925; *N. swainei* in 1931; and *N. dubiosus, N. nanulus nanulus, N. nigroscutum,* and *N. rugifrons* in 1933 (Smith, 1979). Similarly, *N. merkeli* was identified by Ross (1961) as a new species and pest of slash pine, *Pinus elliottii,* soon after the wide-scale planting of slash pine in the southeastern United States (Deneve, 1968).

TABLE 19.4 Summary Data for All Sawfly Species Listed in Recent Annual Forest Pest Reports for Minnesota, Wisconsin, Michigan, and Ontario[a]

	Outbreak history (years)[b]								Larval habits		
	MN 22 YR		WI 37 YR		MI 38 YR		ONT 29 YR				
Sawfly family and species	LM	HS	LM	HS	LM	HS	LM	HS	Host	Feeding guild[c]	Native[d]
Xyelidae											
Pleroneura brunneicornis	—	—	—	—	—	—	6	5	*Abies*	S	N
Pamphiliidae											
Acantholyda erythrocephala	2	0	4	0	—	—	1	9	*Pinus*	L	I
Acantholyda zappei	1	0	—	—	—	—	—	—	*Pinus*	L	N
Cephalcia frontalis	—	—	—	—	—	—	1	2	*Pinus*	L	N
Argidae											
Arge pectoralis	1	2	—	—	—	—	—	—	*Betula*	L	N
Cimbicidae											
Cimbex americana	—	—	5	0	—	—	1	0	*Ulmus*	L	N
Diprionidae											
Diprion similis	6	10	23	10	7	2	10	10	*Pinus*	L	I
Gilpinia frutetorum	—	—	3	0	—	—	9	0	*Pinus*	L	I
Gilpinia hercyniae	—	—	1	0	—	—	13	0	*Picea*	L	I
Monoctenus spp.	—	—	—	—	—	—	1	0	*Thuja*	L	N
Neodiprion abbotii	—	—	—	—	—	—	1	0	*Pinus*	L	N
Neodiprion abietis	9	3	8	2	0	5	8	19	*Abies/Picea*	L	N
Neodiprion compar	—	—	—	—	—	—	2	0	*Pinus*	L	N
Neodiprion lecontei	13	3	17	20	12	24	7	20	*Pinus*	L	N
Neodiprion maurus	5	0	1	0	2	0	4	1	*Pinus*	L	N
Neodiprion nigroscutum	—	—	—	—	—	—	1	0	*Pinus*	L	N
Neodiprion nanulus nanulus	6	1	20	11	2	3	16	8	*Pinus*	L	N
Neodiprion pinetum	1	0	13	8	0	1	1	3	*Pinus*	L	N
Neodiprion pratti banksianae	12	1	16	5	8	12	18	11	*Pinus*	L	N
Neodiprion pratti paradioxicus	—	—	—	—	—	—	10	18	*Pinus*	L	N
Neodiprion rugifrons[e]	7	2	5	3	3	1	13	15	*Pinus*	L	N
Neodiprion sertifer	0	1	9	12	7	22	12	15	*Pinus*	L	I
Neodiprion swainei	2	0	4	3	—	—	16	12	*Pinus*	L	N
Tenthredinidae											
Caliroa cerasi	1	0	—	—	—	—	0	1	*Malus/Sorbus*	L	I
Caliroa fasciata	—	—	—	—	—	—	2	3	*Quercus*	L	N
Caliroa quercuscoccinae	2	0	—	—	—	—	—	—	*Quercus*	L	N
Caulocampus acericaulis	3	0	4	0	5	0	—	—	*Acer*	PM	I
Croesus latitarsus	—	—	8	0	—	—	—	—	*Betula*	L	N
Dimorphopteryx melanognathus	—	—	—	—	—	—	2	4	*Betula*	L	N
Dimorphopteryx pinguis	—	—	—	—	—	—	0	1	*Alnus/Betula*	L	N
Eriocampa ovata	—	—	—	—	—	—	1	3	*Alnus*	L	I
Eupareophora parca	—	—	—	—	—	—	3	3	*Fraxinus*	L	I
Fenusa dohrnii	—	—	—	—	—	—	0	5	*Alnus*	LM	I
Fenusa pusilla	5	10	7	16	4	17	2	26	*Betula*	LM	I
Fenusa ulmi	9	5	1	4	—	—	1	9	*Ulmus*	LM	I
Hemichroa crocea	1	0	1	3	—	—	0	4	*Alnus*	L	N
Messa nana	—	—	—	—	—	—	5	8	*Betula*	LM	I
Messa populifoliella	—	—	—	—	—	—	0	2	*Populus*	LM	N
Nematus limbatus	—	—	—	—	—	—	1	1	*Salix*	L	N
Nematus salicisodoratus	2	0	1	0	—	—	—	—	*Salix*	L	I
Nematus ventralis	1	0	—	—	—	—	1	0	*Populus/Salix*	L	N

(continued)

TABLE 19.4 (Continued)

Sawfly family and species	Outbreak history (years)[b] MN 22 YR LM	MN HS	WI 37 YR LM	WI HS	MI 38 YR LM	MI HS	ONT 29 YR LM	ONT HS	Larval habits Host	Feeding guild[c]	Native[d]
Nematus spp.	—	—	—	—	—	—	0	5	*Populus/Salix*	L	N
Pikonema alaskensis	7	13	10	6	3	5	2	28	*Picea*	L	N
Pikonema dimockii	—	—	—	—	—	—	2	0	*Picea*	L	N
Pontania spp.	1	0	—	—	—	—	—	—	*Salix*	LG	N
Pristiphora erichsonii	7	12	8	26	5	21	6	23	*Larix*	L	I
Pristiphora geniculata	5	5	1	5	5	1	5	22	*Sorbus*	L	I
Pristophora lena	—	—	—	—	—	—	1	0	*Picea*	L	N
Profenusa lucifex	—	—	—	—	—	—	2	6	*Quercus*	LM	N
Profenusa thomsoni	—	—	—	—	—	—	3	17	*Betula*	LM	I
Tethida cordigera	1	0	1	1	—	—	—	—	*Fraxinus*	L	N
Tomostethus multicinctus	2	0	1	0	—	—	—	—	*Fraxinus*	L	N

[a] Pest reports covered the years 1968–1990 for Minnesota (missing 1973; total of 22 annual reports), 1953–1990 for Wisconsin (missing 1956; total of 37 reports), 1950–1990 for Michigan (missing 1951, 1973, 1988; total of 38 reports), and 1960–1988 for Ontario (none missing; total of 29 reports). The most severe outbreak condition was reported from each annual report.

[b] Number of years out of a total of 22 for Minnesota (MN), 37 for Wisconsin (WI), 38 for Michigan (MI), and 29 for Ontario (ONT) that each sawfly was reported as causing "light to medium" (LM) or "heavy to severe" (HS) defoliation or damage. A dash signifies that the insect was not reported during the years examined.

[c] L, external leaf or needle chewer; LG, leaf galler; LM, leaf miner; PM, petiole miner; S, shoot borer.

[d] I, listed by Smith (1979) or Drooz (1985) as "introduced" or "probably introduced;" N, native to North America.

[e] *Neodiprion rugifrons* is often reported as the *N. virginianus* complex and, at times, may include *N. dubiosus*.

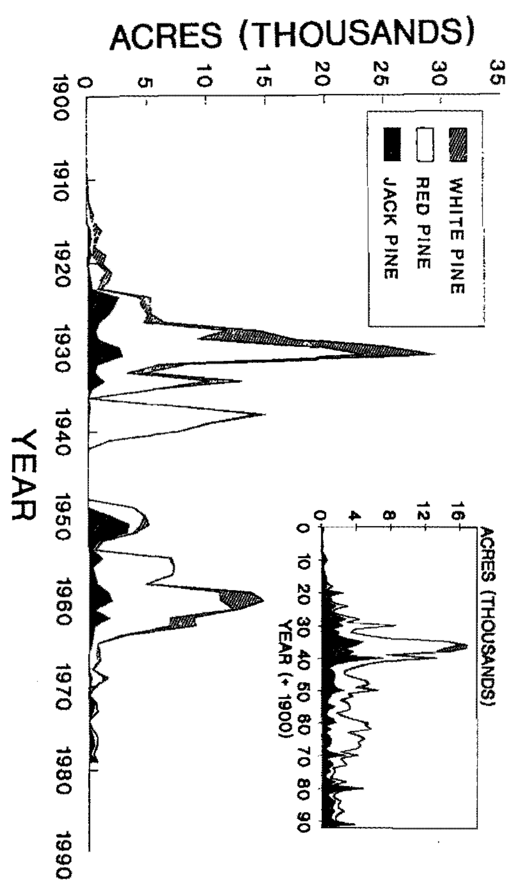

FIGURE 19.6 Number of acres of pine plantations by year of origin during the period 1903–1980 on state forest land in the northern lower peninsula of Michigan (Region II), and the period 1900–1991 on the Huron–Manistee National Forest (see insert) in the same general region of Michigan. Each year is divided into the number of acres planted to white pine, red pine, and jack pine. For example, in 1931, about 29,435 acres of pine plantations were established on state forests in Michigan's Region II: 2896 acres of jack pine, 20,221 acres of red pine, and 6318 acres of white pine.

Graham's 1925 prediction—that the creation of vast, even-age monocultures of pine will allow some typically innocuous insects to rise to outbreak status—seems to have come true. We believe that the near-complete reliance on pine in reforestation projects, done in large, continuous single-species blocks totaling millions of acres, is the principal reason that pine sawflies (Diprionidae) are the leading group of pest sawflies in the Great Lakes region (Table 19.5).

Another contributing factor is that the Great Lakes region has been and continues to be the leading producer of Christmas trees in the United States (Leefers *et al.*, 1988; Snider, 1992). In fact, many of the sawfly outbreaks reported in Table 19.4 occurred in Christmas tree plantations of *Abies, Picea,* and *Pinus.* With the Christmas tree industry now moving from *Pinus* toward *Abies* and *Pseudotsuga* in the Great Lakes region, we confidently predict an upsurge in outbreaks of *N. abietis,* which feeds on trees in both of these genera.

TABLE 19.5 Life History Attributes of Outbreak and Nonoutbreak Conifer-Feeding Sawflies of the Great Lakes Region

		Sawfly parameters[a]																		
Species	Host	Outbreak	Native	Site	Stage	Egg site	Fecundity	Maximum egg/N	Month	Voltinism	Food	Kill host	Colony	Head	Body	Pattern	Larval length	Female length	Male length	Instars	References[b]
Diprionidae																					
Diprion similis	*Pinus*	O	I	ST	C	N	160	19	M2	2	ONT	1	G	B	Y	P	28	9	8	6	4, 13, 14, 18, 31, 42, 45, 51
Gilpinia frutetorum	*Pinus*	N	I	ST	C	N	96	1	J1	2	ON	0	S	R	G	T	22	9.5	8	—	2, 15, 18, 27, 31, 37, 42, 43, 52
Gilpinia hercyniae	*Picea*	N	I	S	C	N	35	1	M2	2	ON	1	S	B	Y	T	20	9	7	5	1, 2, 15, 18, 27, 31, 38, 42, 52
Monoctenus fulvus	*Juniperus* and *Thuja*	N	N	S	C	N	—	—	J1	1	—	0	S	R	—	T	18	8	—	—	31, 34, 39, 46
Monoctenus melliceps	*Juniperus* and *Thuja*	N	N	S	C	N	—	—	J1	1	—	0	S	W	G	T	18	8	—	—	16, 31, 39, 46, 52
Monoctenus suffusus	*Juniperus* and *Thuja*	N	N	S	C	N	—	—	J1	1	—	0	S	R	Y	T	18	8	—	—	24, 30, 31, 39, 46, 52
Neodiprion abbotii	*Pinus*	N	N	S	C	N	64	20	J2	1	—	0	G	B	G	T	22	8	—	5	1, 2, 4, 13, 16, 18, 24, 52
Neodiprion abietis	*Abies*	O	N	N	E	N	100	1	M2	1	ON	2	G	B	G	T	25	8	5	6	1, 2, 4, 11, 15, 18, 27, 31, 32, 38, 42, 45
Neodiprion compar	*Pinus*	N	N	S	C	N	—	5	J2	1	—	0	S	W	G	T	—	8	7	—	2, 3, 16, 18, 31, 52
Neodiprion dubiosus	*Pinus*	N	N	S	C	N	—	—	J2	1	—	0	G	R	Y	S	18	9	5	6	7, 18, 31, 44, 52
Neodiprion lecontei	*Pinus*	O	N	S	C	N	218	38	J2	2	ONT	1	G	R	Y	P	30	10	7	6	8, 15, 18, 31, 32, 42, 45, 52, 53, 54
Neodiprion maurus	*Pinus*	N	N	S	C	N	—	6	M2	1	ON	0	G	B	G	S	—	5.5	4.5	—	2, 3, 6, 36, 37, 52
Neodiprion nigroscutiom	*Pinus*	N	N	S	C	N	134	8	M2	2	ON	0	S	R	G	T	22	10.2	7	6	2, 3, 6, 52
Neodiprion nanulus nanulus	*Pinus*	O	N	N	E	N	68	15	M1	1	O	2	G	B	G	T	22	8	6.3	6	1, 2, 3, 4, 13, 15, 18, 26, 45, 52
Neodiprion pinetum	*Pinus*	O	N	S	C	N	161	5	J1	2	ON	1	G	B	Y	P	25	8.1	7.1	6	1–4, 31, 35, 42, 45, 52
Neodiprion pratti banksianae	*Pinus*	O	N	N	E	N	150	6	M1	1	O	2	G	B	G	T	25	8	6	6	1–4, 18, 20, 21, 31, 32, 42, 45, 48, 52
Neodiprion pratti paradoxicus	*Pinus*	O	N	N	E	N	113	10	M2	1	O	2	G	B	G	S	23	8	—	6	18, 31
Neodiprion rugifrons	*Pinus*	O	N	S	C	N	150	28	J1	2	ON	1	G	R	W	S	20	10	6	6	3, 13, 18, 31, 47, 52
Neodiprion sertifer	*Pinus*	O	I	N	E	N	200	19	M1	1	OT	2	G	B	G	T	25	9	7	6	1, 2, 9, 10, 15, 18, 22, 28, 29, 45, 50, 52
Neodiprion swainei	*Pinus*	O	N	S	C	N	140	4	J2	1	ON	2	G	W	G	S	25	8	6	7	1, 2, 5, 18, 31, 37, 45, 52
Tenthredinidae																					
Pikonemea alaskensis	*Picea*	O	N	S	C	NT	95	3	J1	1	ON	1	G	W	G	T	20	10	8	6	18, 19, 25, 31, 33, 38, 42, 45, 49, 52
Pikonema dimockii	*Picea*	N	N	S	C	NT	50	3	J1	1	ON	0	G	G	G	T	20	10	8	6	1, 18, 27, 31, 38, 40, 49, 52
Pristiphora erichsonii	*Larix*	O	I	S	C	T	206	—	J1	2	N	2	G	B	G	O	25	10	7	5	4, 17, 18, 31, 32, 39, 42, 45, 52
Pristiphora leva	*Picea*	N	N	S	C	—	—	—	J1	1	N	0	G	R	—	—	10	—	—	—	31, 38
Anoplonyx canadensis	*Larix*	N	N	S	C	N	—	1	U2	1	—	0	S	W	G	T	15	5	4.5	5	12, 31
Anoplonyx luteipes	*Larix*	N	N	S	C	N	—	1	J2	1	N	0	S	W	G	T	15	5	4.5	5	12, 31, 39, 46

[a] Outbreak: sawfly classified as an outbreak (O) or nonoutbreak (N) species. Native: a native (N) or introduced (I) species to North america. Site: overwintering site in soil (S), in needle (N), on tree (T), or a combination of these. Stage: overwintering stage is an egg (E) or a prepupa in a cocoon (C). Egg site: oviposition site is in needle (N), twig (T), or both (NT). Fecundity: maximal reported fecundity (eggs/female). Maximum eggs/N: maximum number of eggs reported within a single needle. Month: time when larval feeding is generally initiated in the Lake States (i.e., early May [M1], late May [M2], early June [J1], late June [J2], and late July [U2]). Voltinism: number of generations per year that may occur in the Lake States region. Food: larval consumption of 1-year-old or older foliage (O), current-year foliage (N), twig bark

(footnote continued on page 530)

D. Introduced Sawflies Are More Outbreak-Prone

Another important factor in the pattern of outbreak sawflies is the great number that are introduced species, most of which seem to have volatile populations in North America (Tables 19.1 and 19.4). Of the 226 NE tree-feeding sawflies, significantly more of the introduced species have been reported as pests in the Great Lakes region than have native species (63% vs. 17%, respectively; $P < 0.0001$, Chi-square) (Tables 19.1 and 19.4). This same pattern holds at the family level for the three sawfly families with introduced tree-feeding sawflies: Pamphiliidae (100% of the introduced species into the NE quadrant vs. 7% of the native NE species), Diprionidae (100 versus 68%), and Tenthredinidae (53 versus 12%).

Most, and in some cases all, of the sawfly outbreaks in the Great Lakes region on *Acer, Betula, Larix, Sorbus,* and *Ulmus* have been caused by introduced species: *Caulocampus acericaulis* on *Acer, Fenusa pusilla* and *Profenusa thomsoni* on *Betula, Fenusa ulmi* on *Ulmus, Pristiphora erichsonii* on *Larix,* and *Pristiphora geniculata* on *Sorbus.* Likewise, the introduced *Acantholyda erythrocephala, Diprion similis, Gilpinia frutetorum,* and *Neodiprion sertifer* accounted for nearly 32% of the reported outbreaks on *Pinus,* and *Gilpinia hercyniae* accounted for 10% of the outbreaks on *Picea* (Table 19.4).

(T), or a combination of these. Kill host: host death due to larval feeding can result after 1 year of feeding (1), after several years (2), or seldom/never occurs (0). Colony: larval feeding behavior as mostly gregarious (G) or solitary (S). Head: head capsule color of last-instar larvae mostly black (B), red (R), brown (W), or green (G). Body: body color of last-instar larvae mostly brown (W), green (G), or yellow (Y). Pattern: dorsal pattern of last-instar larvae spotted (P), striped (T), striped and spotted (S), or solid (O). Larval length: maximal larval length reported in millimeters. Female length: maximal length reported for adult female in millimeters. Male length: maximal length reported for adult male in millimeters. Instars: maximal reported number of instars for female larvae.

[b] 1, Anderson (1960); 2, Atwood (1961); 3, Atwood and Peck (1943); 4, Baker (1972); 5, Becker and Benjamin (1964); 6, Becker and Benjamin (1967); 7, Becker *et al.* (1966); 8, Benjamin (1955); 9, Benjamin *et al.* (1955); 10, Benjamin *et al.* (1973); 11, Bird (1929); 12, Bracken (1961); 13, Coppel and Benjamin (1965); 14, Coppel *et al.* (1974); 15, Craighead (1950); 16, Cresson (1880); 17, Drooz (1960); 18, Drooz (1985); 19, Eidt (1969); 20, Ghent (1955); 21, Ghent (1960); 22, Griffiths (1959); 23, Heron (1966); 24, Hetrick (1956); 25, Houseweart and Kulman (1976); 26, Kapler and Benjamin (1960); 27, Knerer and Atwood (1973); 28, Kraemer and Coppel (1977); 29, Lyons (1964); 30, MacGillivray (1894); 31, Martineau (1984); 32, McDaniel (1932); 33, Nash (1939); 34, Norton (1872); 35, Rauf and Benjamin (1980); 36, Rohwer (1918); 37, Rose and Lindquist (1973); 38, Rose and Lindquist (1977); 39, Rose and Lindquist (1980); 40, Ross (1938); 41, Ross (1955); 42, Schaffner (1943); 43, Shaffner (1944); 44, Schedl (1933); 45, Shenefelt and Benjamin (1955); 46, Smith (1974); 47, Wilkinson *et al.* (1966); 48, Wilson (1971a); 49, Wilson (1971b); 50, Wilson (1971c); 51, Wilson (1971d); 52, Wilson (1977); 53, Wilson and Averill (1979); 54, Wilson *et al.* (1992); 55, Wong (1955).

The European spruce sawfly, *G. hercyniae,* was first found in North America in 1922 (Martineau, 1984). For the next 15–20 years, this sawfly caused widespread defoliation and mortality of spruce trees in eastern Canada. However, after the accidental introduction of a virus in the 1930s, the pest status of this sawfly in North America rapidly diminished; note that *G. hercyniae* caused no heavy to severe defoliation in Ontario in recent decades (Table 19.4).

V. Comparing Outbreak and Nonoutbreak Sawfly Species

We conclude our discussion by comparing life history attributes of outbreak and nonoutbreak species of sawflies, focusing on all 26 conifer needle-feeding diprionids and tenthredinids of the Great Lakes region. We chose these sawflies because many reach outbreak levels, all are external needle chewers, and most have been well studied (Table 19.5). In this section, we arbitrarily classified a sawfly as an outbreak species if it was reported as having caused heavy to severe defoliation at least five times in the 126 annual forest pest reports discussed in Table 19.4. Using this criterion, we classified 12 sawflies as outbreak species and 14 as nonoutbreak species.

Based on several studies of outbreak insects (McNamee *et al.,* 1981; Nothnagle and Schultz, 1987; Hunter, 1991), we sought traits for each sawfly that might explain its pest status: overwintering site and life stage, oviposition site, maximal fecundity, timing of larval feeding, voltinism pattern, type of foliage consumed and likelihood of causing host death, gregarious or solitary feeding behavior, larval head capsule and body coloration, number of larval instars, and maximal length of larvae and adults (Table 19.5). General textbooks and the primary literature were consulted to amass the needed data. However, we were unable to obtain complete data for all species, especially for several of the less studied nonoutbreak species. Contingency tables (Chi-square and Fisher's Exact tests) and *t* tests were used to test for differences between outbreak and nonoutbreak species.

A. Overwintering Site and Life Stage

Overwintering behavior differed significantly between outbreak and nonoutbreak sawflies ($P < 0.012$, Fisher's Exact test, $n = 26$ sawflies). Outbreak species overwintered either as eggs in needles (42%) or as prepupae in cocoons in the soil (58%), whereas all (100%) nonoutbreak species overwintered as prepupae in soil (Table 19.5). Some sawflies such as *D. similis* and *G. frutetorum* spin cocoons in the soil as well as on host trees. McNamee *et al.* (1981) emphasized the crucial importance of pupating in the soil/litter on the fundamental pattern of insect population dynamics because this behavior exposes insects to the powerful regulatory potential of ground-dwelling predators. For hardwood-feeding Macrolepidoptera, Hunter (1991) found that more outbreak species (37%) overwinter as eggs than do nonoutbreak species (16%).

B. Oviposition Site

Oviposition behavior did not differ between outbreak and nonoutbreak sawflies ($P > 0.72$, Fisher's Exact test, $n = 25$). Practically all conifer-feeding sawflies oviposit in needles (Table 19.5). The major exception is the larch sawfly, *P. erichsonii,* which lays eggs in tender new twigs on *Larix*. Two other sawflies that at times oviposit in the bark between needles are two *Picea* feeders: the yellowheaded spruce sawfly, *Pikonema alaskensis,* and the greenheaded spruce sawfly, *Pikonema dimockii.*

C. Maximal Fecundity

Outbreak species had greater maximal fecundity than nonoutbreak species, averaging 150 versus 76 eggs/female, respectively ($P < 0.01$, *t* test, $n = 16$). A similar relationship was noted when the maximal reported values of mean fecundity were analyzed: 103 versus 62 eggs/female, respectively ($P < 0.02$, *t* test $n = 16$). We prefer maximal fecundity over mean fecundity because at times only the range of fecundity values was reported. Another potential problem with mean fecundity is that it can decrease during the course of an outbreak, as documented for *P. erichsonii* (Drooz, 1960; Heron, 1966).

The greatest reported maximal fecundity was 218 eggs/female for *N. lecontei* (Wilson *et al.,* 1992; Table 19.5). Two others having maximal fecundity of 200 eggs/female or greater were *P. erichsonii* (Drooz, 1960) and *N. sertifer* (Griffiths, 1959). There was a significant positive linear relation between maximal fecundity and the number of times a sawfly was listed in the 126 pest reports described in Table 19.4 ($P < 0.003$, $R^2 = 0.48$, $n = 16$). Similarly, Hunter (1991) found that outbreak Macrolepidoptera had greater maximal fecundity (226 eggs/female) than nonoutbreak species (122).

D. Timing of Larval Feeding and Voltinism Patterns

A very comprehensive attempt at monitoring sawfly phenology was reported by Becker and Benjamin (1967) for jack pine sawflies in Wisconsin.

Using their results as a foundation and other data from the primary literature and the forest pest reports noted in Table 19.4, we estimated the time at which larvae typically initiate feeding in the Lake States (Table 19.5). Overall, outbreak sawflies initiated larval feeding earlier (67% in May) than nonoutbreak sawflies (21% in May) ($P < 0.04$, Fisher's Exact test, $n = 26$). This difference resulted largely from the five outbreak sawflies that overwinter as eggs and whose larvae initiate feeding typically in early May. In contrast, all nonoutbreak sawflies overwinter as prepupae and must complete all steps from pupation through oviposition before larval feeding can occur. If we analyze only sawflies that overwinter as prepupae, then no significant difference in the initiation time of larval feeding occurred between outbreak and nonoutbreak sawflies ($P > 0.74$, Fisher's Exact test, $n = 21$). For hardwood-feeding Macrolepidoptera, Hunter (1991) concluded that outbreak species tended to initiate larval feeding earlier than nonoutbreak species.

The proportion of outbreak and nonoutbreak sawflies reported as multivoltine was similar: 42 vs. 29%, respectively ($P > 0.40$, Fisher's Exact test, $n = 26$). When segregated by overwintering life stage, none of the five sawflies that overwinter as eggs were multivoltine, but 43% of the sawflies that overwinter as prepupae were multivoltine (Table 19.5). Similarly, Hunter (1991) reported that all outbreak Macrolepidoptera that overwintered as eggs were univoltine. Perhaps overwintering as eggs is less likely to lead to multivoltinism, given that second-generation larvae would be less able to complete development, pupate, mate, and oviposit if temperatures were to fall suddenly late in the year. However, for sawflies that overwinter as prepupae, cooler weather would perhaps only prolong feeding of second-generation larvae further into autumn, and at worse they would spin cocoons before reaching their maximal size.

E. Type of Foliage Consumed and Likelihood of Causing Host Death

Larvae of needle-feeding conifer sawflies feed either on current-year needles, foliage that is 1 or more years of age, or both (Table 19.5). We did not analyze this trait statistically because information on foliage use was lacking for several nonoutbreak species. Nevertheless, the general pattern for sawflies that overwinter as eggs is that they feed exclusively on old foliage. Similarly, for the first generation of pine-feeding sawflies that overwinter as prepupae, feeding occurs primarily on old foliage. However, if the old foliage is exhausted, larvae will finish development on current-year foliage. For multivoltine pine-feeding sawflies, larvae of the second or subsequent generations feed preferentially on the then fully expanded, mature current-year foliage. In the spruce-feeding sawflies, *G. hercyniae* prefers old foliage, but the two *Pikonema* species prefer mid- to late-season current-year foliage. The larch-feeding sawflies feed only on current-year foliage, given that *Larix* is a deciduous conifer. The initial preference for older foliage by most pine-feeding sawflies contrasts sharply with the marked preference for current-year foliage by external needle-feeding Lepidoptera (Drooz, 1985). Such variation in feeding behavior would apparently allow greater resource partitioning.

As would be expected, outbreak sawflies are more likely to kill their host than nonoutbreak sawflies are (92 versus 7%, respectively; $P < 0.0001$, Chi-square). *Gilpinia hercyniae* was the only nonoutbreak sawfly listed as being able to kill its host (Table 19.5). However, this capacity was based on its past behavior in North America because it has seldom reached outbreak status in recent history (Martineau, 1984; Table 19.4). For sawflies that overwinter as eggs, several years of consecutive defoliation are required to kill their host. This occurs because these sawflies are all univoltine and consume only old foliage. In contrast, sawflies that overwinter as prepupae—especially the multivoltine species—can kill their host in a single season because they consume both old and current-year foliage. Evergreen conifers generally die if completely defoliated in a single season (Kulman, 1971). However, deciduous conifers such as *Larix* typically require 6–9 years of consecutive severe defoliation before they die (Drooz, 1960).

F. Gregarious or Solitary Feeding Behavior

Larval feeding behavior differed significantly between outbreak and nonoutbreak sawflies ($P < 0.001$, Fisher's Exact test, $n = 26$). All outbreak sawflies feed gregariously, or at least do so initially, whereas only 36% of the nonoutbreak sawflies are gregarious (Table 19.5). Similarly, Hanski (1987) noted colonialism as the main difference between outbreak and nonoutbreak pine-feeding sawflies in Europe. We classified *Neodiprion compar* and *N. nigroscutum* as solitary feeders even though they can be found in colonies of 4–5 larvae (Atwood, 1961) and 3–10 larvae (Becker and Benjamin, 1967), respectively. Most other *Neodiprion* sawflies feed in colonies of 50–200 larvae. Larvae of the genera *Anoplonyx, Gilpinia,* and *Monoctenus* all exhibit solitary feeding. Eggs are laid singly in needles for most solitary feeders, whereas up to 38 eggs have been found in a single needle for gregarious conifer sawflies (Wilson *et al.*, 1992; Table 19.5). Considering hardwood Macrolepidoptera, Hunter (1991) reported that more outbreak species (51%) were gregarious as larvae than were nonoutbreak species (7%).

Gregariousness may have several advantages over solitary feeding (see also Knerer, Chapter 2, and Codella and Raffa, Chapter 10, of this volume). For example, gregarious larvae have less mortality from predation in both sawflies (Ghent, 1960; Lyons, 1962) and Lepidoptera

(Lawrence, 1990). Moreover, gregarious feeding may allow for better thermoregulation (Porter, 1984; Mattson and Scriber, 1987) and easier consumption of tougher materials than would be possible by solitary feeders (Ghent, 1960). When isolated, normally gregarious larvae wander for long periods of time, resulting in slower growth and greater mortality (Kalin and Knerer, 1977; Stamp and Bowers, 1990).

G. Larval Head Capsule and Body Coloration

We collected information on head capsule color (black, green, or red to brown), body background color (green, white, or yellow), and dorsal body markings (solid, striped, or spotted) for last-instar larvae (Table 19.5). Overall, more outbreak sawflies tended to have larvae with black head capsules (67 vs. 21%, $P < 0.04$, Fisher's Exact test, $n = 26$) and solid or spotted dorsal markings (33 vs. 0%, $P < 0.04$, Fisher's Exact test, $n = 26$). Background coloration was similar in outbreak and nonoutbreak sawflies ($P = 1.00$, Fisher's Exact test, $n = 24$). All sawflies that overwinter as eggs have black head capsules as well as do most gregarious sawflies (Table 19.5). Perhaps black head capsules allow for greater heat absorption, which may be especially important for spring-feeding sawflies (i.e., those that overwinter as eggs).

H. Number of Larval Instars

Female sawfly larvae typically have five or six instars; however, some *N. swainei* females have seven instars (Becker and Benjamin, 1964). We found instar data for all outbreak sawflies but only 50% of the nonoutbreak sawflies (Table 19.5). Still, for this restricted data set, females of all outbreak species had six or seven instars; only 43% of the nonoutbreak species had six instars and none had seven ($P < 0.02$, Fisher's Exact test, $n = 20$). Having more instars may allow larvae to grow larger (see Section V.I) and, thus, cause greater defoliation.

I. Maximal Length of Larvae and Adults

The maximal reported length of larvae and adults was recorded for each sawfly (Table 19.5). We used maximal reported length because several papers gave only a single value or a range of values. Overall, larvae of outbreak species attained greater length than nonoutbreak larvae (24.5 versus 18.2 mm, respectively; $P < 0.0001$, t test, $n = 23$). *Neodiprion lecontei* larvae attained the greatest length (30 mm; Wilson *et al.*, 1992), whereas *Pristiphora lena* larvae were the shortest (10 mm; Rose and Lindquist, 1977). Maximal adult length, however, was not significantly different between outbreak and nonoutbreak sawflies, neither for females (8.8 versus 7.9 mm, respectively; $P > 0.13$, t test, $n = 25$) nor for males (6.7 versus 6.3 mm; $P > 0.47$, t test, $n = 20$). Differences in length of mature larvae between outbreak and nonoutbreak sawflies probably reflect in part the greater number of instars that outbreak sawflies typically have. Likewise, differences in larval length may help explain the greater fecundity of outbreak sawflies (see Section V.C), even though average adult female lengths were similar. Perhaps average body width or volume (data not obtained) is significantly different between outbreak and nonoutbreak sawflies. For hardwood-feeding Macrolepidoptera, Hunter (1991) found no significant difference ($P = 0.11$) in larval length between outbreak and nonoutbreak species.

VI. Conclusions

A. General Patterns

Many patterns have been observed in sawfly life history traits as we have moved from a wide continental view of NA sawflies to the conifer-feeding diprionids and tenthredinids of the Great Lakes region. In telegraph form, the major findings are that most sawflies (1) feed on woody plants; (2) are external leaf/needle feeders; (3) are relatively monophagous; (4) are more numerous on tree genera that contain many species, have a broad latitudinal range, extend well northward into the boreal forest, and dominate the landscape; (5) are most numerous within the plant families (in decreasing order) Salicaceae, Pinaceae, Betulaceae, Rosaceae, and Fagaceae, and (6) are most numerous on trees that are relatively shade-intolerant, low in nutrient demands, fast-growing, short-lived, and high in heat demands. The tree-feeding sawflies most often reported as pests in the Great Lakes region tended to be (7) diprionids, (8) external leaf/needle feeders, (9) pine feeders, and (10) introduced species. Of the conifer-feeding diprionids and tenthredinids of the Great Lakes region, the most outbreak-prone sawfly species tended to (11) be more fecund, (12) initiate larval feeding earlier in the year, (13) have black head capsules as larvae, (14) feed gregariously, (15) have more larval instars, (16) attain greater larval length, and (17) be more likely to cause tree death.

B. Sawfly Radiation on North American Woody Plants

The trend for sawfly richness to be linearly related to the number of species per plant genus (Fig. 19.1) implies that over evolutionary time each

new plant species permitted on average the evolution of another new sawfly species because the slope of the regression (0.90) was nearly 1.0. This is approximately true for *Salix* and many other genera but not for *Betula, Pinus,* and *Populus,* which have two or more native sawflies per species. It is also not true for *Acer, Crataegus,* or *Quercus,* which have fewer than 0.5 sawflies per species. The tendency for some plant genera to depart from the 1:1 average seemed to vary with their phylogeny. Therefore, we plotted the residuals from a linear regression ANOVA that included all tree genera and most shrub genera from Table 19.3 against the mean number of native sawfly species per plant species (sawfly loading) in related NA genera (i.e., within the same plant order) (Fig. 19.7); *Ribes, Rosa,* and *Rubus* were not included because of uncertainty in the number of native NA species in each genus.

In the order Sapindales, for example, two genera support sawflies: *Acer,* averaging 0.14 sawfly species/species of *Acer,* and *Rhus,* averaging 0.08 sawfly species/species of *Rhus.* Therefore, *Acer*'s average species loading for related genera is 0.08, and the comparable figure for *Rhus* is 0.14. The result was that average sawfly loading in related genera was linearly related to and explained about 21% of the variation in the residuals (Fig. 19.7). This value is surprisingly high and biologically meaningful given the rather crude grouping of "related genera" (Cronquist, 1968; Little, 1979). All genera within an order are not equally close phylogenetically, and many are as distant as genera in different orders. In the order Fagales, for example, the birches, alders, and hazels appear very similar to one another, but much less similar to the oaks and beeches in the number of sawflies that each supports. Likewise, in the Coniferales, the many genera in the Pinaceae seem very similar to one another but are substantially distant from the related genera in the Cupressaceae. In fact, two substantial outliers were *Quercus* and *Pinus* (Fig. 19.7): *Quercus* due to its low sawfly species richness even though other members of the Fagales (i.e., Betulaceae) had abundant sawflies, and *Pinus* due to its very high richness relative to the average for its order (Table 19.3).

Regressing both sawfly loading in related genera and the number of plant species per plant genus accounted for about 70% of the variation in sawfly richness per plant genus. In other words, sawfly radiation in a given plant genus is related to both the number of species in that plant genus and the level of sawfly radiation on related NA plant genera.

In Fennoscandia, there is a similar linear relationship to that found in North America between sawfly richness and numbers of species of plants per genus (Fig. 19.1), but the slope is fivefold greater (4.6 versus 0.9, respectively; Neuvonen and Niemelä, 1983), indicating substantially greater sawfly loading in Fennoscandia. Given Finland's more northerly latitude and the trend for sawfly richness to increase toward the north in the

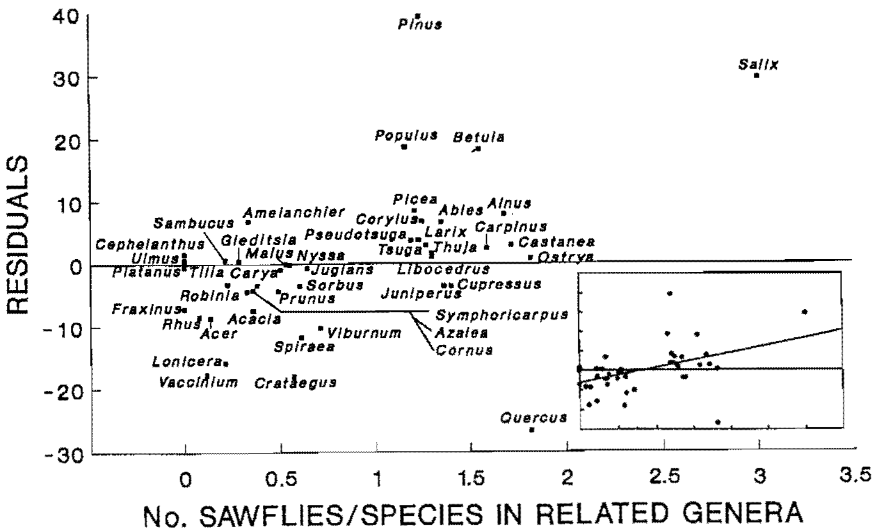

FIGURE 19.7 Relation between the residuals from an ANOVA similar to that used in Fig. 19.1 and mean sawfly loading (number of native sawfly species per plant species) on related North American woody plant genera (same plant order). A linear model (see insert) gave the best fit to the data: $P<0.002$, $R^2=0.21$, $n=45$.

Northern Hemisphere (Smith, 1979; Schwenke, 1982), we might expect sawfly richness to be higher on Fennoscandian boreal and subarctic woody plants.

The tendency for most NA sawflies to be associated with short-lived, sun-loving trees and shrubs that have low to medium nutrient requirements and that tend to form monodominant to oligodominant plant communities (the left-hand cluster of genera in Fig. 19.5) suggests that sawflies are particularly well adapted to (1) the physical/spatial features of such environments (Eastop, 1973; Futyuma, 1991) and (2) the special physiological, biochemical, and morphological traits of the plants occurring therein (Mattson *et al.*, 1991; Herms and Mattson, 1992). NA sawflies have obviously radiated abundantly on such plants (which are themselves quite speciose) because sawfly loading averages 1.73 sawflies/plant species in the left-hand cluster of seven genera in Fig. 19.5.

At the other extreme, fewer sawflies are associated with the more strictly temperate, long-lived plants that have low light and high nutrient requirements and that form polydominant, mixed species communities (the right-hand cluster of genera in Fig. 19.5). For these nine woody plant

genera, sawfly loading averages only 0.77 sawflies/plant species. Apparently, neither their physical/spatial environment nor their special plant properties have been very conducive to sawfly colonization and radiation over evolutionary time despite their current abundance in NA forests (Fig. 19.4). However, some individual genera within this group (e.g., *Tsuga, Carpinus,* and *Ostrya*) average more than 1 sawfly/plant species.

Among the central cluster of woody plants in Fig. 19.5, which have intermediate light and nutrient requirements, some are largely boreal/cool temperate and some are strictly temperate genera. Sawfly loading averages 0.76 sawflies/plant species. Among these, *Quercus* is the largest genus (68 species) and supports the most sawfly species (29). The oaks have obviously provided a suitable platform for sawfly radiation in North America, but nothing like the more ruderal, boreal genera that average almost twice as many sawflies per plant species. Because the distribution of oaks is far south of the boreal regions of North America, and because oaks often grow in more mixed species communities under xeric, nutrient-poor conditions (Abrams, 1992), we speculate that oaks offer only a mediocre environment for sawflies and that other insects such as Lepidoptera may be better adapted to oaks and, hence, more competitive.

It would be interesting to know whether or not sawflies have displaced other insect herbivores in the colder, simpler ecosystems of the world and vice versa in the warmer, more diverse ones. In some respects sawflies are like aphids in that both are poorly represented in the warm Tropics (Schwenke, 1982; Eastop, 1973); perhaps because both groups tend toward monophagy, which may be maladaptive in richly diverse ecosystems where host finding may become a limiting factor (Eastop, 1973; Dixon, 1985). Not surprisingly, aphids and sawflies have radiated richly on many of the same woody plant families: Betulaceae, Fagaceae, Pinaceae, and Salicaceae. However, aphids differ in having also adopted the Aceraceae and Juglandaceae as major hosts (Eastop, 1973; Dixon, 1985), perhaps reflecting the greater propensity of aphids to inhabit the north temperate ecosystems of the world.

C. Caveat: Incomplete Knowledge of North American Sawflies

We conclude by reminding the reader that our analyses and conclusions are based on rather incomplete knowledge of the NA sawflies. Only about 50% of the NA sawflies were included in our analyses because of incomplete larval host data (Table 19.1). Therefore, as more life history data accumulate, many of the preceding particulars and some of the generalities will surely change. We hope, however, that this chapter provides a framework for organizing newly acquired knowledge.

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