Composition and Seasonal Phenology of a Nonindigenous Root-Feeding Weevil (Coleoptera: Curculionidae) Complex in Northern Hardwood Forests in the Great Lakes Region

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ABSTRACT *Phyllobius oblongus* (L.), *Polydrusus sericeus* (Schaller), and *Sciaphilus asperatus* (Bonsdorff) comprise a complex of nonindigenous root-feeding weevils in northern hardwood forests of the Great Lakes region. Little is known about their detailed biology, seasonality, relative abundance, and distribution patterns. We studied 10 sites over a 2-yr period. Two sites were in northeastern Wisconsin, and eight were in the neighboring southern upper peninsula of Michigan. Larval abundance was estimated by soil sampling, and adult abundance was estimated by sweep netting, emergence trapping, and beating samples. Sweep netting collected the most weevils overall (71.0%), whereas beating and emergence traps collected 22.1 and 6.9%, respectively. *P. sericeus* were the predominant larvae, representing 34.3% of total Curculionidae, whereas *P. oblongus* were the predominant adults, representing 66.4% of Curculionidae. Few *S. asperatus* and *Trachyphloeus aristatus* (Gyllenhal) larvae and adults were collected, with the latter being a new record for Wisconsin. Two additional species, *Barypeithes pellucidus* (Boheman) and an undetermined *Polydrusus* sp., were collected only as larvae. Six species of curculionids were collected overall, with at least five being confirmed as nonindigenous species. *P. oblongus* and *P. sericeus* adults were the most abundant. These did not coincide temporally. Over 63% of *P. oblongus* and *P. sericeus* were collected during single 4-wk intervals in mid-June and mid-July, respectively. Conversely, *S. asperatus* adults overlapped with both other species, occurring sparingly from 4 June through 28 August. One species was predominant at each site and generally accounted for ≥80% of the total weevil population. *P. oblongus* larvae and adults predominated in five and eight sites, respectively, whereas *P. sericeus* and *S. asperatus* larvae and adults predominated in one site each. Adult and larval populations were generally clustered. We evaluated vertical stratification of *P. sericeus* larvae in the soil, and most were located within the top 10 cm.

KEY WORDS *Phyllobius*, *Polydrusus*, *Sciaphilus*, root herbivores, invasive species

INVASIVE NONINDIGENOUS FOREST INSECTS are estimated to cost the United States $2.1 billion annually in losses to forest products, excluding eradication and control expenses (Pimentel et al. 2000). As of 1994, ≈360 nonindigenous insect species were established in North American forests, and 30% of these were serious economic or ecological threats (Mattson et al. 1994, Pimentel et al. 2000). Potential ecological disturbance by invasive species includes loss of native biodiversity, species extinction, interspecific competition, predation, and alteration of ecosystem processes (Vitousek et al. 1996, Wilcove et al. 1998, Mack et al. 2000, Sala et al. 2000). The extent of ecosystem disturbance by nonindigenous species that do not cause commercial losses is particularly poorly characterized (Wilcove et al. 1998, Lodge and Shrader-Frechette 2003).

Past research has focused more heavily on invasive insects in production than natural ecosystems, such as deciduous forests. Of the latter, we know relatively more about the biology and impact of folivores such as the gypsy moth (Lepidoptera: Lymantriidae: *Lymantria dispar* L.) and larch casebearer [Lepidoptera: Coleophoridae: *Coleophora laricella* (Hübner)] (Liebhold et al. 1995), subcortical insects such as the pine shoot beetle (Coleoptera: Scolytinae: *Tomicus piniperda* L.) (Haack and Poland 2001) and Asian longhorned beetle [Coleoptera: Cerambycidae: *Anoplophora glabripennis* (Motschulsky)] (Nowak et al. 2001), and sap feeding insects such as the hemlock woolly adelgid (Hemiptera: Adelgidae: *Adelges tsugae* Annand) (McClure and Cheah 1999) and balsam woolly adelgid [Hemiptera: Adelgidae: *Adelges piceae* (Ratzeburg)] (Hain et al. 1991), than root-feeding insects (Hunter 2001). This is largely because of difficulties in studying root herbivores in general, and because below-ground herbivores exert subtle effects

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that may go unnoticed for substantial periods (Hunter 2001). Potential negative impacts of below-ground herbivores include reduced plant diversity, altered successional processes, altered carbon and nitrogen allocation between roots and foliage, increased susceptibility to other herbivores and pathogens, and reduced total yield (Syvertsen and McCoy 1985, Brown and Gange 1991, 1992, Hunter 2001).

Three root-feeding weevils (Coleoptera: Curculionidae) of European origin are currently established in northern deciduous forests of the Great Lakes region: *Phyllobius oblongus* (L.), *Polydrusus sericeus* (Schaller), and *Sciaphilus asperatus* (Bonsdorff). *P. oblongus* were first collected in New York in 1923 from American elm (*Ulmus americana* L.) (Felt 1928); *S. asperatus* were first collected in Sydney, Nova Scotia, in 1884 (Brown 1940); and *P. sericeus* were first collected near Indianapolis, IN, before 1916 (Blatchley and Leng 1916). All three species occur throughout the northeastern United States and adjacent Canada and as far west as Minnesota (O'Brien and Wibmer 1982, Downie and Arnett 1994, Anderson 2002). *S. asperatus* has also been found in South Dakota, Idaho, Quebec, and British Columbia (Witter and Fields 1977, Levesque and Levesque 1994, Anderson 2002).

The life histories of these weevils have been reported in general terms from their native European ranges. They have similar life cycles, with the exception that *P. oblongus* and *P. sericeus* reproduce sexually, whereas *S. asperatus* is parthenogenic and triploid (Suomalainen et al. 1987). *P. oblongus* and *P. sericeus* are diurnal feeders that disperse by flight, whereas *S. asperatus* is a nocturnal feeder and flightless. Adults emerge from the soil in spring and seem to be relatively polyphagous on foliage of deciduous trees and understory vegetation (Parrott and Glasgow 1916, Hoffman 1950, Massee 1954, Vollman 1954, Fields 1974). It has been speculated that they may also feed on flower buds and blossoms, leaf buds, newly sprouting leaves, and terminal shoots (Massee 1954, Fields 1974). A notch-like wound around the leaf perimeter characterizes adult feeding. Copulation begins immediately on emergence and occurs at the feeding site. Oviposition occurs 10–14 d later, 2–5 cm beneath the soil surface (Vollman 1954). Larvae emerge ≈30 d later and burrow into the soil in search of fine root material. *P. oblongus* has five larval instars (Vollman 1954), but the number for *P. sericeus* and *S. asperatus* is undetermined. Larvae overwinter in the soil as late instars before pupation occurs the following spring. There are also reports of *S. asperatus* completing development by fall and overwintering as adults in leaf litter, thus resulting in two spring emergence peaks (Ministry of Agriculture, Fisheries, and Food 1963, Levesque and Levesque 1994).

Observed host plants of *P. oblongus* in North America include a wide variety of tree and shrub species, particularly maple (*Acer* spp.), birch (*Betula* spp.), hophornbeam [*Ostrya virginiana* (Miller) K. Koch], aspen (*Populus* spp.), willow (*Salix* spp.), American basswood (*Tilia americana* L.), American elm (*Ulmus americana* L.), and several fruit trees, berries, and shrubs (Felt 1928, Carruth 1936, Fields 1974). Host plant records of *P. sericeus* in North America include maple, poplar (*Populus* spp.), and hazel (*Corylus americana* Walter) (Frost 1946). In Europe, they have been observed feeding on alder (*Alnus* spp.), hazel (*Corylus avellana* L.), willow (*Salix americana* Walb.), and a variety of fruit trees and shrubs (Parrott and Glasgow 1916, Morris 1978, Gharadjedaghi 1997, Czerniakowski 1998). *S. asperatus* has been observed feeding primarily on maple, birch, and various fruit trees and shrubs (Henshaw 1888, Witter and Fields 1977, Levesque and Levesque 1994). In general, *P. oblongus* and *S. asperatus* seem to feed more heavily on sugar maple (*Acer saccharum* Marshall), whereas *P. sericeus* has been reported feeding in northern hardwood stands in which maple is not the dominant tree species (Witter and Fields 1977).

There are few reports of damage by these weevils under natural conditions in Europe, but they can be important in commercial settings. Adults of *P. oblongus* are pests of pear (*Pyrus* spp.) and apple (*Malus* spp.) orchards throughout Great Britain and the Netherlands (Massee 1932, Helsen and Blommers 1988); larval *P. sericeus* are considered a serious root-feeding pest in young nursery plantings of oak (*Quercus* spp.) and hazel (*Corylus* spp.) in Belgium (Casteels and De Clercq 1988); larval and adult *S. asperatus* are important pests attacking strawberry (*Fragaria* spp.) roots in Great Britain (Massee 1954, Ministry of Agriculture, Fisheries, and Food 1963) and raspberry (*Rubus* spp.) leaves in Russia (Witter and Fields 1977). Past research in the Great Lakes region has led to speculation that twig scarring and subsequent forked branching of sugar maple resulted from *P. oblongus* and *S. asperatus* feeding (Simmons and Knight 1973, Witter and Fields 1977).

Little research on this nonindigenous weevil complex has been conducted in North America. Thus we have incomplete knowledge of their basic biology, seasonality, relative abundance, and distribution patterns. The objectives of this study were to (1) determine relative abundance of larval and adult *P. oblongus, P. sericeus* and *S. asperatus* populations, (2) determine the seasonal phenologies of larvae and adults, and (3) determine the vertical distribution of *P. sericeus* larvae in the soil.

Materials and Methods

Site Selection. Ten sites were selected in mesic northern hardwood stands throughout northeastern Wisconsin and the Upper Peninsula of Michigan, during autumn 2001 (Table 1). Sites were selected based on previous observations of weevil populations and availability of detailed data on vegetative composition and soil parameters from previous ecosystem studies (Goodburn 1996, Bockheim 1997, Goodburn and Lorimer 1998, 1999). Climate in this region is characterized by an average temperature range of −12 to 19°C, annual frost-free period of 100 d, and 850 mm of precipitation (Goodburn 1996). Soil texture is classified as sandy loam in 8 of the 10 sites and as silt in 2 sites (Bockheim 1997). The sites included a mixture of old growth forests, recently thinned forests, and a

Table 1. Location and description of study sites in northeastern Wisconsin and the upper peninsula in MI

Site	GPS coordinate	County	Ownership	Percentage dominant tree species[b]	Percentage other host tree species[b]			Canopy structure
					Acer saccharum	*Betula alleghaniensis*	*Ostrya virginiana*	
Butternut North[a]	N 45°54.133′ W 089°01.498′	Forest County, WI	Nicolet National Forest	74.31% *Acer saccharum*	74.31%	0.28%	5.70%	Uneven-aged
Sucker Lake 1	N 46°18.164′ W 089°14.001′	Gogebic County, MI	Ottawa National Forest	33.42% *Acer rubrum*	29.18%	7.65%	0.00%	Uneven-aged
Taylor Lake 1	N 46°15.617′ W 089°02.994′	Gogebic County, MI	Ottawa National Forest	96.31% *Acer saccharum*	96.31%	0.05%	2.04%	Uneven-aged
Sylvania 2	N 46°13.349′ W 089°18.104′	Gogebic County, MI	Sylvania Wilderness Area	60.80% *Acer saccharum*	60.80%	9.75%	1.17%	Old growth
Sylvania 6	N 46°12.451′ W 089°15.842′	Gogebic County, MI	Sylvania Wilderness Area	98.25% *Acer saccharum*	98.25%	0.00%	1.04%	Old growth
Imp Lake 2	N 46°11.706′ W 089°04.759′	Gogebic County, MI	Ottawa National Forest	61.56% *Acer saccharum*	61.56%	10.56%	1.61%	Even-aged
Sucker Lake 2	N 46°19.279′ W 089°13.514′	Gogebic County, MI	Ottawa National Forest	86.91% *Acer saccharum*	86.91%	0.00%	0.44%	Even-aged
Tamarack Lake 2[a]	N 46°11.897′ W 088°59.849′	Gogebic County, MI	Ottawa National Forest	67.36% *Acer saccharum*	67.36%	0.00%	0.00%	Even-aged
Taylor Lake 2[a]	N 46°15.588′ W 089°03.101′	Gogebic County, MI	Ottawa National Forest	49.00% *Acer saccharum*	49.00%	13.76%	0.15%	Even-aged
Rhinelander[a]	N 45°40.891′ W 089°37.590′	Oneida County, WI	USDA-FS Research	100.00% *Populus* spp.	0.00%	0.00%	0.00%	Plantation

[a] Plots selected for intensive study.

[b] Additional information on tree species composition and site characteristics are in Goodburn (1996).

hybrid poplar plantation (Table 1). Sugar maple is the predominant tree species in 8 of the 10 sites; red maple (*Acer rubrum* L.) and hybrid poplar (*Populus* spp.) are each predominant in 1 site (Table 1). Other common trees include yellow birch (*Betula alleghaniensis* Britton), paper birch (*Betula papyrifera* Marshall), American basswood (*Tilia americana* L.), northern red oak (*Quercus rubra* L.), white ash (*Fraxinus americana* L.), black Ash (*Fraxinus nigra* Marshall), ironwood [*Ostrya virginiana* (Miller) K. Koch], black cherry (*Prunus serotina* Ehrhart), and trembling aspen (*Populus tremuloides* Michaux).

One 1,600-m^2 main plot was established at each site and was divided into four quadrants for sampling purposes. Each main plot was marked at the center, and its GPS coordinates were recorded. Four of the 10 study sites, hereafter termed intensive, were chosen for more frequent sampling and detailed observations (Table 1). These were the locations with the highest population density of each weevil species, based on preliminary data collected during summer 2001. Two intensive sites were chosen for *P. sericeus* because it was most abundant in the hybrid poplar plantation, but it was also desirable to have a more natural forest habitat.

Larval Sampling. The occurrence and density of larvae were estimated by sampling soil with an auger (8.2 cm diameter by 16 cm deep, 845 cm^3). Surface leaf litter was removed before taking samples. Soil samples were collected 29 September and 10 November 2001 and 3 May and 2 November 2002. In 2001, all 10 sites were sampled, eight samples at each site, two randomly selected from each of the quadrants. Because of the apparent clustered distribution of larvae, the number of study sites was decreased to allow an increased number of soil samples per plot in 2002. In 2002, only the four intensive sites were sampled, and there were 40 samples per site, with 10 per quadrant.

Stratified soil samples were collected as above, with the exception of taking samples at each of three depths. For each sample, the top 0–10 cm, the next 10–20 cm, and the next 20–30 cm of soil were collected. Stratified samples were collected 10 November 2001 and 3 May and 2 November 2002. Two intensive sites were sampled in 2001 with six samples per site. All four intensive sites were sampled in May 2002, with 20 samples per site, including five randomly selected per quadrant. Few larvae were present in all but one site, so only the latter was sampled in November 2002.

Each soil sample was placed in a self-sealing plastic bag in the field. Samples were stored in a walk-in cooler (5.5°C) within 4 d of collection. Samples were generally stored for 2–3 wk, with a maximum of 8 wk before larval extraction. Each sample was sifted through two sieves having 2.38- and 0.98-mm mesh, respectively. The larger mesh opening collected root debris, leaf litter, and large larvae, whereas the smaller passed fine soil but collected small larvae. The contents of each screen and the collection pan were examined for 5 min. All larvae and other macro-soil dwelling insects were collected and fixed in boiling water before preservation in 70% ethanol. The number of earthworms in each sample was also recorded, and a representative sample was retained. Voucher specimens were deposited in the University of Wisconsin-Madison, Department of Entomology, Insect Research Collection.

Identification to family was determined using Lawrence (1991). Curculionidae were further identified to genus using van Emden (1952). Identification of *P. oblongus* and *S. asperatus* were based on van Emden (1952), Vollman (1954), and Axelsson et al. (1973), and the status of *S. asperatus* as the only *Sciaphilus* in North America (O'Brien and Wibmer 1982, Downie and Arnett 1994, Anderson 2002). Identification of *P. sericeus* was validated by comparison between larvae collected in the field and those reared in the laboratory from adults.

Abundance of *P. sericeus* at various soil depths was analyzed at the hybrid poplar plantation site according to a split plot design with subsampling (PROC GLM; SAS Institute 1999). The mean number of larvae was compared among depths and as an interaction of depth and time. Time was treated as the whole plot factor, depth as the subplot factor, and sample locations within quadrants as subsamples. If F was significant ($P < 0.05$), means were separated using Fisher protected least significant difference (LSD) test with a Bonferroni correction. A square-root transformation was applied to fulfill the assumption of equal variance.

Adult Sampling. Adult occurrence in the forest understory was estimated primarily by sweep net sampling. Sampling was conducted during 25 May through 28 August 2002 and 4 June through 1 August 2003. During 2002, extensive sites were sampled approximately monthly, and intensive sites were sampled biweekly. During 2003, both intensive and extensive sites were sampled biweekly during peak populations of all three species. Two randomly chosen points were selected from each quadrant in each site (total = 192, 224, and 400 for extensive and intensive sites in 2002 and all sites in 2003, respectively). A sample consisting of 10 sweeps of vegetation within 1 m of the forest floor was collected at each point. Goodburn (1996) provides a complete description of understory vegetation. Data collected during 2002 included coleopterans only; in 2003, all insects except Culicidae were included.

The occurrence of adults higher in the canopy was estimated by branch-beating samples. Beating samples were collected biweekly at intensive sites. Two randomly chosen trees were selected from each quadrant per site (total = 224 and 160 for 2002 and 2003, respectively). One limb from each tree was sampled. A 1-m^2 ground cloth was placed under the limb before beating. Limb height and tree species were recorded for each sample, with limb height never exceeding 3.5 m. In 2002, only Coleoptera were recorded from samples; in 2003, all insects were recorded.

Emergence traps consisting of inverted 18.9-liter buckets were deployed at two intensive study sites during 2002 and at one during 2003. Two glass jars containing tissue paper were fastened to each bucket through holes cut into the sides. There were two randomly placed traps per quadrant at each site (total = 16 and 8 for 2002 and 2003, respectively). Emergence traps were checked biweekly June to August 2002 and 2003.

Insects were brought to the laboratory and stored in the freezer (−10°C) until identification. Generic and species-level identifications of weevils were conducted using Sleeper (1957), Brown (1965), Downie and Arnett (1994), and Morris (1997). Familial identification for all other insects was performed by S. J. Krauth (Curator, University of Wisconsin-Madison, Department of Entomology, Insect Research Collection) or using Borror et al. (1989).

The variation of adult *P. oblongus* abundance between quadrants within a site was analyzed by a χ^2 test ($P < 0.05$), which compared an expected uniform distribution to the observed results. Abundance within quadrants, instead of individual samples, was used for data analysis because samples within quadrants were randomly located. We limited statistical analyses to the 19 June sampling date when the *P. oblongus* population was at its peak. The remaining weevil species were not analyzed because of large numbers of zeroes.

Results

Relative Abundance of Weevils. Curculionid larvae comprised 55.2% (74.0% when the four samples containing all of the Formicidae are omitted from Hymenoptera) of the macro-soil insect fauna in both single and stratified soil samples collected in 2001 and 2002 (Table 2). The remainder included 25.7% Hymenoptera, 11.1% Diptera, 7.6% other Coleoptera, and 0.4% other. In addition to insect larvae, 153 Annelida and untabulated Chilopoda and Diplopoda were collected.

The average number of weevil larvae collected per 845-cm^3 soil core sample among all sites was 0.23 ± 0.05 ($n = 160$; range, 0–4) in 2001 and 0.50 ± 0.06 ($n = 320$; range, 0–10) in 2002. Of the 268 weevil larvae collected, 17.2% were unidentifiable to species because of physical condition or discrepancies from the identification key (Table 3). The composition of the remaining weevils was 34.3% *P. sericeus*, 15.7% *Barypeithes pellucidus* (Boheman), 15.3% *P. oblongus*, 9.3% *S. asperatus*, 7.1% *Polydrusus* sp., and 1.1% *Trachyphloeus* sp. (Table 3). The *Trachyphloeus* sp. larvae are most likely *T. aristatus* (Gyllenhal), because adults were collected from the site in which they were found. *Polydrusus* sp. larvae could not be validated to species, but other than *P. sericeus*, *P. impressifrons* (Gyllenhal) and *P. americanus* (Gyllenhal) are the only *Polydrusus* known to be prevalent throughout the Great Lakes region (O'Brien and Wibmer 1982, Downie and Arnett 1994, Anderson 2002). All identified curculionid larvae collected were exotic species.

The diversity and abundance of all insects collected from foliage are grouped by order (except for Curculionidae, which are separated from other beetles) in Table 2. All insects on foliage were adult, except for

Table 2. Total numbers of insects collected from experimental sites in northeastern Wisconsin and the upper peninsula of Michigan

Order/family	Soil samples[a]		Foliar samples			
			Sweeping[b]		Beating[c]	
	2001 ($n = 10$)	2002 ($n = 4$)	2002 ($n = 10$)	2003 ($n = 10$)	2002 ($n = 4$)	2003 ($n = 4$)
Curculionidae	40	228	245	66	56	41
Coleoptera	12	25	13	19	5	12
Diptera	0	54	—	29	—	0
Hemiptera	0	1	—	56	—	8
Hymenoptera	0	125	—	9	—	1
Lepidoptera	0	0	—	21	—	5
Mecoptera	1	0	—	1	—	0
Psocoptera	0	0	—	1	—	2

n = number of sites sampled.

[a] Soil samples were collected September and November 2001 and May and November 2002. Data include both single auger and stratified depth samples. The number of single auger samples per date per site was 8 in 2001 and 40 in 2002. The number of stratified depth samples collected per site was 6 in 2001 and 20 in 2002.

[b] Data include sweep net samples collected mid-May through August: approximately monthly at $n = 6$ sites and biweekly at $n = 4$ sites during 2002, and biweekly at all 10 sites during 2003.

[c] Beating samples were collected approximately biweekly at $n = 4$ sites mid-May through August of 2002 and 2003.

Lepidoptera and some Hemiptera, and most insects in soil were immature. Additional information on the breakdown of these orders by family can be found in Pinski (2004). Curculionids comprised 94.1% of the total coleopterans collected by sweep netting and beating in 2002. Curculionids comprised 39.5% of the total insect fauna in 2003. The remaining insects collected by sweep net and beating (complete sampling in 2003 only) were 22.1% Hemiptera, 12.9% other Coleoptera, 10.7% Diptera, 9.6% larval Lepidoptera, 3.7% Hymenoptera, and 1.5% other.

Phyllobius oblongus was the predominant species collected from foliage, representing 66.4% of all curculionids (Table 3). The remaining composition of weevils was 21.9% *P. sericeus*, 6.2% *S. asperatus*, and 5.5% *T. aristatus*. As with soil samples, all curculionids collected with sweep net, emergence trap, and beating techniques in stands having a predominantly sugar maple understory were exotic species. Fewer species were collected as adults; *B. pellucidus* and the undetermined *Polydrusus* sp. occurred in soil samples, but not sweep net, emergence trap, or beating samples.

Sweep net sampling collected the most weevils overall (71.0%), whereas beating and emergence traps collected 22.1 and 6.9%, respectively. Sweep net sampling accounted for almost all *P. oblongus* (82.1%) and *S. asperatus* (100%) obtained. In contrast, sweep net sampling accounted for only 45.8% of the total *P. sericeus* and beating techniques accounted for

Table 3. Numbers and species of Curculionidae collected from experimental sites in northeastern Wisconsin and the upper peninsula of Michigan

Species	Larvae		Adults					
	2001	2002	2002			2003		
	Soil[a] ($n = 10$)	Soil ($n = 4$)	Sweeping[b] ($n = 10$)	Beating[c] ($n = 4$)	Emergence[d] ($n = 2$)	Sweeping ($n = 10$)	Beating ($n = 4$)	Emergence ($n = 1$)
Barypeithes pellucidus[e]	6	36	0	0	0	0	0	0
Phyllobius oblongus[e]	22	19	190	33	0	49	19	0
Polydrusus sericeus[e]	5	87	33	23	5	11	22	2
Polydrusus sp.	0	19	0	0	0	0	0	0
Sciaphilus asperatus[e]	2	23	21	0	0	6	0	0
Trachyphloeus sp.[e]	0	3	0	0	0	0	0	0
Trachyphloeus aristatus[e]	0	0	1	0	15	0	0	8
Unidentified *spp.* morphospecies 1	0	2	0	0	0	0	0	0
Rearing specimens	0	29	0	0	0	0	0	0
Physically deformed	5	10	0	0	0	0	0	0
Total	40	228	245	56	20	66	41	10

n = number of sites sampled.

[a] Soil samples were collected September and November 2001 and May and November 2002, and include both single auger and stratified depth samples. The number of single soil samples collected per date per site was 8 in 2001 and 40 in 2002. The number of stratified depth samples collected per site per date was 6 in 2001 and 20 in 2002.

[b] Sweep net samples were collected mid-May through August: approximately monthly at $n = 6$ sites and biweekly at $n = 4$ sites during 2002, and biweekly at all 10 sites during 2003.

[c] Beating samples were collected approximately biweekly at $n = 4$ sites mid-May through August of 2002 and 2003.

[d] Emergence trap samples were collected approximately biweekly at $n = 2$ and $n = 1$ sites mid-May through August of 2002 and 2003, respectively.

[e] Nonindigenous species.

Table 4. Temporal phenology and mean number of weevil larvae collected per 845-cm^3 sample

Species	Date			
	29 September 2001	10 November 2001	3 May 2002[a]	2 November 2002
Phyllobius oblongus	0.08 ± 0.03	0.20 ± 0.05	0.01 ± 0.01	0.11 ± 0.03
Polydrusus sericeus	0.03 ± 0.02	0.01 ± 0.01	0.20 ± 0.04	0.19 ± 0.05
Sciaphilus asperatus	0	0.01 ± 0.01	0.03 ± 0.01	0.09 ± 0.05

Samples were collected from all 10 experimental sites during 2001 and from four intensive-study sites during 2002.
n (single auger soil samples) = 80 for 2001 and 160 for 2002.
[a] An additional two unidentified pupae were obtained.

46.9%. Emergence traps collected only 7.3% of the total *P. sericeus* and no *P. oblongus* or *S. asperatus*. However, they accounted for 95.8% of *T. aristatus*.

Seasonal Phenology of Weevils. Weevil larvae were found in the soil from 29 September through 3 May (Table 4). The mean number of *P. oblongus* larvae collected per sample was 20 and 10 times, respectively, greater during the two Novembers preceding and following the May sampling date. Conversely, the mean number of *P. sericeus* larvae collected per sample did not vary temporally at equal sampling intensities. Few *S. asperatus* larvae were collected overall, but their collection increased with successive sampling periods. Two curculionid pupae were collected during the May sampling period.

Based on combined sweep net data from 2002 (excluding times when only intensive sites were sampled) and 2003, 66.5% of *P. oblongus* adults were obtained on 19 June, and all were obtained from 4 June through 16 July (Fig. 1). Sixty-three percent of *P. sericeus* were obtained on 12 July, and all were obtained from 12 July through 28 August. In contrast, only 34.6% of *S. asperatus* were obtained within the peak sampling period, 12 July, and others were obtained from 4 June through 28 August.

Thus, all three of these species spend most of their life cycles as larvae in the soil (Witter and Fields 1977), but their peaks of adult activity differ. There was little overlap between *P. oblongus* and *P. sericeus* adults, although emergence traps indicate that *P. seri-*

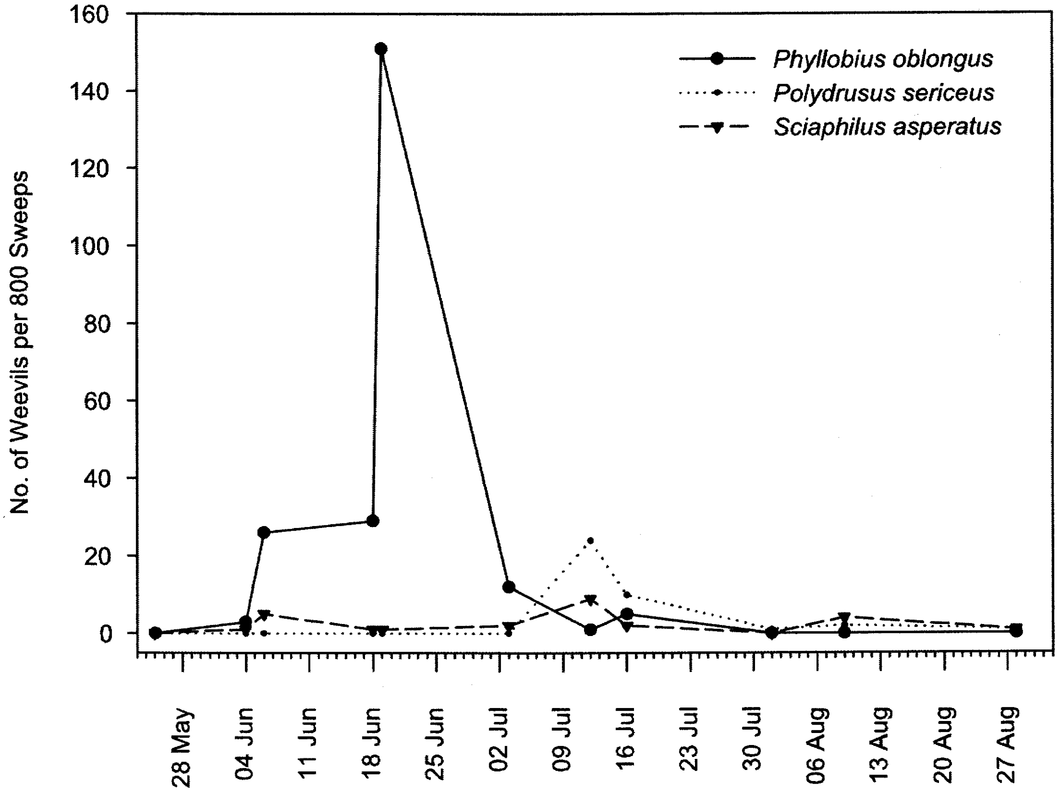

Fig. 1. Seasonal phenology of adult weevils collected from northern hardwood forests in northeastern Wisconsin and the upper peninsula of Michigan. Data based on sweep net samples from 10 sites collected monthly and biweekly, mid-May through August 2002 and 2003, respectively.

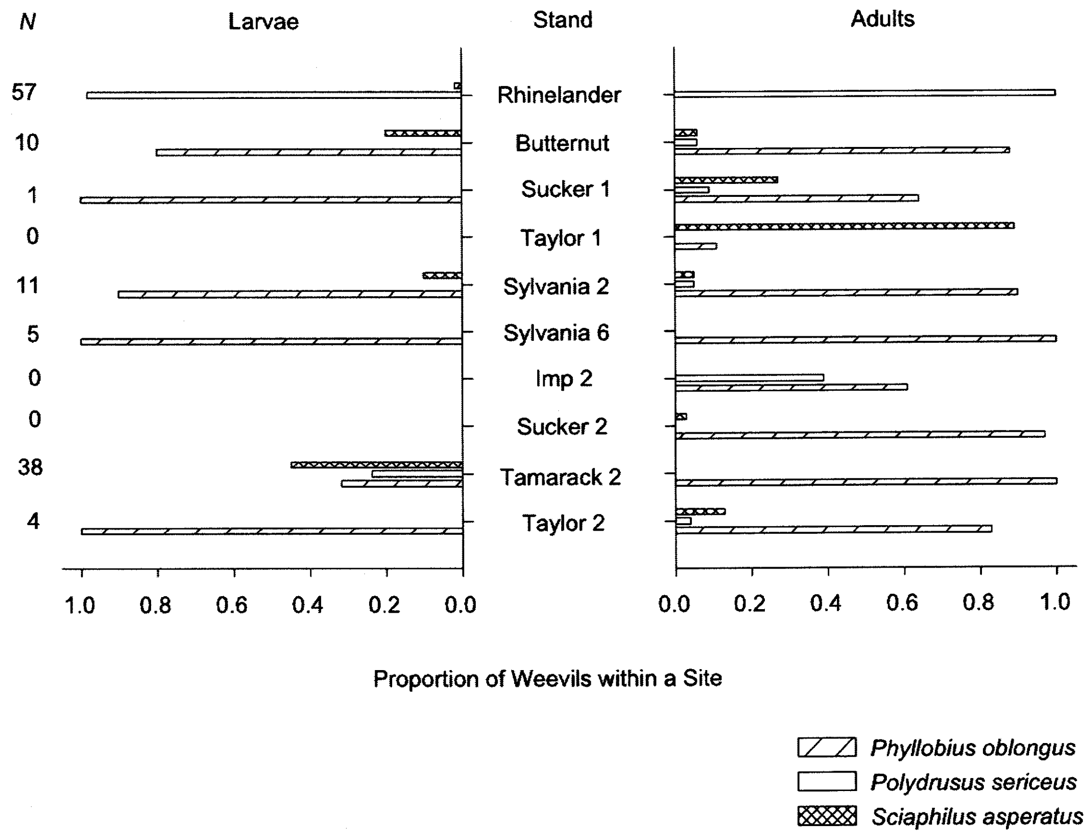

Fig. 2. Species distribution of larvae and adult weevils among northern hardwood forest sites. Proportion of species within a site is displayed, and the total number of weevils is listed after each bar grouping. Larval data are based on single auger soil samples collected from 10 sites 29 September and 10 November 2001 and from 4 intensive-study sites 3 May and 2 November 2002. Adults based on sweep net samples from 10 sites collected approximately once monthly, mid-May through August 2002.

ceus begins to emerge in late June. In contrast, there was only a slight peak for *S. asperatus* adults, whose populations were more evenly distributed 4 June through 28 August, and coincided with both *P. oblongus* and *P. sericeus*.

Distribution of Weevil Larvae Within and Between Sites. The average number of *P. sericeus* larvae (0.41 ± 0.10) within the top 10 cm of the soil surface was significantly greater than at depths of 10–20 (0.15 ± 0.05) and 20–30 cm (0.02 ± 0.02) ($F_{2,120} = 7.07$, $P = 0.0013$). The latter two depths did not differ. The mean proportion of larvae recovered at each depth was similar during May, September, and November collections ($F_{4,120} = 1.47$, $P = 0.2150$).

In six of the seven sites, one species accounted for ≥80% of total larvae, and one species accounted for >44% of the total in all seven sites (Fig. 2). *P. oblongus* dominated weevil larval composition in five sites. However, the number of *P. oblongus* varied greatly, with just three sites providing 75% of their total. *P. sericeus* and *S. asperatus* were predominant in one site each. These sites comprised 86.2% of the total *P. sericeus* and 81% of the total *S. asperatus* collected.

Overall, larval populations appeared to be clustered. The percentage of samples that yielded zeroes on 29 September 2001, 10 November 2001, 3 May 2002, and 2 November 2002 were 91.3, 75.0, 70.0, and 73.8%, respectively. Of those samples in which larvae were found, their numbers averaged 1.14 ± 0.14, 1.45 ± 0.19, 1.63 ± 0.14, and 1.98 ± 0.31 larvae/845 cm^3. Even in the hybrid poplar plantation, the most homogeneous of all habitats sampled, 42.5 and 62.5%, respectively, of the 3 May and 2 November 2002 samples yielded no *P. sericeus* larvae, yet 7.5 and 12.5% of these samples yielded 31 and 58.3% of the total (Appendix 1 of Pinski 2004). There is some evidence that increasing the sampling intensity may raise the overall mean of larvae collected per sample because of their aggregated distribution. Overall, the estimates of mean larval density were 44 and 95/m^2 with 8 and 40 samples per site, respectively. At the hybrid poplar plantation, for example, the average number of weevil larvae per soil auger sample was 0.44 ± 0.16 ($n = 16$; range, 0–2) in 2001 and 1.08 ± 0.14 ($n = 80$; range, 0–7) in 2002. However, we cannot distinguish whether this trend is caused by sampling intensity or between-year differences.

Distribution of Weevil Adults Between Sites. Adult weevil species composition was dominated by *P. oblongus* in 8 of the 10 sites (Fig. 2). Their numbers varied greatly among sites, however, with 80.9% of the total collected in just five sites. *P. sericeus* and *S. asperatus* were predominant in one site each; 70.4% of the total *P. sericeus* were collected in just one site, and 70% of the total *S. asperatus* were collected in just two sites. Thus, 8 of the 10 sites were dominated by one species, accounting for >80% of the total, and all 10 sites were dominated by one species, accounting for >60% of the total. Graphical analysis of sweep net sampling data indicated that the predominant weevil species within each site did not vary between 2002 and 2003 (Pinski 2004). However, populations were substantially lower in 2003 compared with 2002 (Table 3). Therefore, only sweep net data from 2002 are displayed to portray between-site species distributions (Fig. 2).

Adult weevil populations appeared to be clustered. The abundance of *P. oblongus* varied significantly among quadrants during the 19 June 2002 sampling at Sucker 2 ($\chi^2 = 29.6$; df = 3; $P < 0.0001$), Taylor 2 ($\chi^2 = 15.8$; df = 3; $P = 0.0012$), and Imp 2 ($\chi^2 = 10.8$; df = 3; $P = 0.0129$) sites. The remaining sites were not analyzed statistically because of the low number of *P. oblongus* collected, but again, trends suggest a clustered distribution. The mean number of *P. oblongus* collected per sweep net sample across all sites on 19 June was 1.9 ± 0.3 ($n = 80$; range, 0–15). Forty-five percent of the samples collected no *P. oblongus*, whereas just 10% returned 51.7% (Appendix 2 of Pinski 2004). Sixty-four percent of the samples that contained weevils had at least two weevils.

Overall, the predominant species at sites were similar between larvae and adults (Fig. 2). This correspondence held, for example, at three of the four intensive study sites. However, species compositions of weevil larvae and adults collected within sites did not always coincide. For example, *S. asperatus* and *P. sericeus* were collected from Tamarack 2 as larvae and from Taylor 2 as adults, but not as adults or larvae from these sites, respectively. Additionally, *P. sericeus* was collected as adults from Butternut, but not as larvae, and *S. asperatus* was collected as larvae from Rhinelander, but not as adults.

Discussion

Exotic curculionids dominated the insect fauna in both the soil and on the understory foliage, and there was a surprising lack of native weevils in these habitats (Table 2). Each site was dominated by a single weevil species, in both larval and adult samples (Fig. 2). Overall, the two predominant species as both larvae and adults were *P. sericeus* and *P. oblongus*, respectively (Table 3).

Despite the added labor, soil sampling is a valuable component of assessing overall weevil species composition. For example, the unidentified *Polydrusus* sp. and *B. pellucidus* were obtained only by larval sampling (Table 3), although *B. pellucidus* have also been collected in pitfall traps at these and similar sites (Werner and Raffa 2000). All identified weevil larvae are considered soil inhabitants and external rhizophagous feeders (Kerr 1949, van Emden 1950, 1952, Vollman 1954, Brandt et al. 1996). Larval sampling broadened the known composition of the nonindigenous soil weevil complex in this region, which now totals a minimum of five species (Table 3). Our results indicate that a relatively large number of soil samples are required to accurately estimate weevil abundance within a site. Increasing the number of samples from 8 to 40 may partially address difficulties associated with clustered larval distributions.

Adult sampling methods varied in their applicability among different weevil species. Sweep netting alone was adequate for obtaining *P. oblongus*, whereas sweep netting and beating were equally effective at obtaining *P. sericeus* (Table 3). Sweep netting accounted for all *S. asperatus* adults, but few were collected overall (Table 3). In contrast, this nocturnal species comprised 50.7% of all Curculionidae collected in pitfall traps at these and similar sites, whereas *P. oblongus* and *P. sericeus* comprised only 13.5 and 0.2%, respectively (Werner and Raffa 2000). Hence comparisons of species abundance based on different methods should be interpreted with caution. Emergence traps provided the most effective method for collecting *T. aristatus*, a nocturnal ground-dwelling, flightless, parthenogenic weevil native to Europe (Table 3) (Brown 1965, Suomalainen et al. 1987, Morris 1997). The only prior North American records were near Ottawa, Ontario (Brown 1965, O'Brien and Wibmer 1982)

Sweep net results may not only be affected by weevil behavior but also by canopy structure. The average number of weevils collected per sweep net sample from even-aged stands was nearly three times greater than from uneven-aged stands in 2002 (Pinski 2004), suggesting multilayer understories may draw adult weevils higher into the canopy. Hence, if ground cover is scarce, the value of branch beating increases. For example, most *P. sericeus* at the hybrid poplar plantation, where ground cover was minimal, were obtained by beating (Table 3).

Further research should concentrate on refining sampling protocols to employ multiple techniques (Table 3), standardization among different methods, and stratified subsampling to account for the effects of varying vegetation patterns (Table 1). Two important considerations are time of day when each species is most active and its method of dispersal. *P. oblongus* and *P. sericeus* are diurnally active and disperse by flight, thus sweep netting and branch-beating (Table 3) seem more effective than pitfall traps, which collected 114 *P. oblongus* and only 2 *P. sericeus* among 23 northern hardwood study sites during 1996 (Werner and Raffa 2000). Conversely, *S. asperatus*, *B. pellucidus*, and *T. aristatus* are nocturnally active, flightless, leaf-litter inhabiting weevils (Brown 1965, Galford 1987, Suomalainen et al. 1987, Morris 1997), so they were less commonly collected in our sweep net samples (Table 3) than previous pitfall trap samples, which yielded 428 *S. asperatus* and 225 *B. pellucidus* (Werner and Raffa 2000).

The absence of native weevil species in both understory vegetation and forest soils throughout this region is surprising, given the frequency, distribution, and intensity of our sampling efforts. Moreover, observations by Witter and Fields (1977) report similar findings. The most likely explanation is competitive displacement by these five nonindigenous weevils, particularly *P. oblongus* and *P. sericeus*. However, it is difficult to resolve such discrepancies or document competitive displacement without baseline biodiversity inventories (Kremen et al. 1993, Kremen 1994, Sharkey 2001).

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