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Impact of the Texas Leaf-Cutting Ant (*Atta texana* (Buckley)) (Order Hymenoptera, Family Formicidae) on a Forested Landscape

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ABSTRACT *Atta texana* (Buckley), the Texas leaf-cutting ant, rapidly expanded in a harvested forested landscape on sandhills characterized by droughty soils, causing mortality of planted loblolly pine (*Pinus taeda* (L.)). The site, composed primarily of Quartzipsamments soils classified as thermic coated Typic Quartzipsamments in the Tonkawa soil series, accounts for approximately 5,000 ha in Nacogdoches, Rusk, Panola, and San Augustine Counties in eastern Texas, USA (Dolezel 1980). These soils are characterized by low fertility, rapid permeability, and extreme acid reaction. These sandhills are resistant to erosion and are considered important ground water recharge areas. The distribution of *A. texana* central nest mounds and foraging areas was examined using aerial photography, digital orthophotographic quarter quadrangles (DOQQ) (scale 1:6000), and global positioning satellite (GPS) data. Plant nutrition of *A. texana* nesting areas was examined. Previous soil texture analysis of the central nest mound and adjacent landscapes is presented.

FROM 1973 TO 1975, approximately 1,400 ha in the Tonkawa soils (Typic Quartzipsamments) were clearcut, followed by extensive site preparation (Tracey et al. 1991). Removal of all organic matter and surface litter from the site exposed the bare mineral soil to the sun and wind, decreasing the moisture holding capacity of the soil and increasing surface temperatures (Kroll et al. 1985). The clearcutting disturbance of the study site quickly resulted in ideal *Atta texana* habitat.

Atta species densities are normally higher in secondary than in primary vegetation (Haines 1978). Nest dimensions are significantly correlated with distances foraged by leafcutters (Fowler and Robinson 1979) and *Atta* species foraging patterns are influenced by the availability and locations of preferred plant species in its territory (Waller 1986). Adaptations in their pattern of nest distribution enable ants to use the food available in the habitat more effectively and reduce the unfavorable results of competition among societies, which limit their reproduction and numbers (Cherrett 1968).

Though long considered serious pests in both natural and plantation ecosystems, the basic biology of leaf-cutting ants is not completely understood. Leaf-cutting ants are exclusively New World species, ranging from Argentina in the south to Texas in the north. The northernmost species is *A. texana*, the Texas leaf-cutting ant (Hölldobler and Wilson 1990).

A. texana shows a decided preference for nesting in sandy or sandy loam soils, but is also capable of nesting in heavy soils and those of limestone origin (Smith 1963). *A. texana* overturns the soil when excavating tunnels and chambers. When building tunnels and chambers, materials transported to the surface by ants are mixed with body fluids to form uniform pellets of soil (Weber 1966). *A. texana* constructs tunnels and chambers in the soil

that are numerous and extend deeper than those of vertebrate animals. The nest area is usually marked by crescent-shaped mounds 15 to 30 cm tall and about 30 cm in diameter.

A. texana shows a decided preference for grasses, weeds, and hardwood leaves. Leaf parts are gathered and used to cultivate their food fungus. They prune the vegetation, stimulate new plant growth, break down vegetable material rapidly, and, in turn, enrich the soil (Hölldobler and Wilson 1990). *A. texana* is a forest pest because it cuts needles from both natural and planted pine seedlings. Though ant foraging occurs year round, the industrial forest impact is felt in the winter months when pines are defoliated in the absence of other forage (Moser 1967). In East Texas, this situation causes considerable loss to timber producers, especially in young plantations on droughty sites.

Methods

A. texana, by overturning the soil when excavating tunnels and chambers, has a profound effect upon organic matter and texture of the Tonkawa soil series. *A. texana* utilized created openings and disturbances to create nesting areas and benefitted from the wintering foraging on pines in their expansion. *A. texana* is found along the FM 1087 road corridor and along the edges of stream side corridors. In regeneration areas, *A. texana* reacted to the monocultural habitat and dispersed in all directions, causing massive destruction to the loblolly plantation.

The study area is located along the FM 1078 road corridor (right of way) and an area of regeneration north of camp Tonkawa, located in northern Nacogdoches and southern Rusk Counties, 10 km west of Garrison, Nacogdoches County, Texas, USA. The distribution of *A. texana* central nest mounds and foraging areas was examined using aerial photography, digital orthophotographic quarter quadrangles (DOQQ) (scale 1:6000), and global positioning satellite (GPS) data. Plant nutrition of *A. texana* nesting areas was examined. Previous soil texture analysis of the central nest mound and adjacent landscapes is presented. This study area encompasses sandy soils and loams capable of sustaining *A. texana* populations.

Results and Discussion

Currently, there are 52 openings found throughout the study area. The total study area was 78 ha, or 78,000 square meters. Total defoliation attributed to *A. texana* accounted for 16,380 square meters (21.5%) of the total study area. The immediate nesting areas or mounds accounted for 1.25% of the total area affected by *A. texana*. Not all disturbance areas contained mounds due to natural mound mortality or chemical treatment with methyl bromide.

Repeated efforts at regeneration and control of *A. texana* in the Tonkawa site have met with limited success. Low site productivity makes intensive forest silvicultural practices marginal. Plantation forestry, particularly involving pines on droughty sites, is adversely affected by *Atta* species defoliation (Cherrett 1968) with the most disastrous outbreaks of *Atta* species occurring in monoculture systems (Hölldobler and Wilson 1990).

The impact of *A. texana* nests is evident following timber harvests as nests become the dominant feature on landscapes with deep sandy soils. *A. texana* is the primary soil-improving organism in the droughty environment of the Typic Quartzsammets or Tonkawa landscape in northern Nacogdoches County, Texas (Cahal 1993, Cahal et al. 1993). Nests extend underground to a depth of 8 m with hundreds of subterranean chambers (Moser

1963) and up to 61 cm of excavated subsoil on the nest's surface (Cahal 1993, Cahal et al. 1993, Kulhavy et al. 1998). *A. texana* significantly increases the percent clay; the percent clay in the pellets of nest mound craters was significantly higher than at the intermound surface and the control surface. When comparing percent clay by depth, the mound surface had a significantly higher percentage of clay (5.6% clay for the pellets of the nest mound crater compared to 3.9% and 3.6% at 50-cm depths and the internest surface, respectively) (Cahal 1993, Cahal et al. 1993, Kulhavy et al. 1998).

Leaf-cutting ants play an important role in soil development (Cherrett 1968, Weber 1972, Haines 1975, Alvarado et al. 1981, Fowler and Haines 1983, Cahal et al. 1993, Kulhavy et al. 1998). Leaf-cutting ants are responsible for pedoturbation, or soil mixing (Hole 1961). The subterranean network of tunnels and galleries reduces soil bulk density and increases the concentrations of soil organic matter. Ants are one of the few species that transport subsoil mineral nutrients to the surface where they can be utilized by plants (Weber 1972, Lockaby and Adams 1985).

Following defoliation and mortality of the pine plantation matrix, the patches are maintained by *A. texana* and eventually become a permanent component of the landscape. These patches can vary in size from a few hundred square meters to 6 hectares.

A single *A. texana* nest is a marvel of engineering and the dimensions are staggering. The central nest mound may be 30 m in diameter, have numerous 0.3-m diameter feeder mounds extending outwards to a radius of 80 m (Moser 1967, Cahal 1993, Kulhavy et al. 1998), and may occupy 30 to 600 square meters (Hölldobler and Wilson 1990, Cahal 1993). Larvae are raised in brood chambers, fungus is cultivated in fungal chambers, and waste material is deposited in detrital chambers. Removal of vegetation covering *A. texana* nests reduces soil moisture. *Atta* species are prodigious foragers and a large colony is capable of gathering several kilograms of leaves per day (Weber 1966).

On the Tonkawa study site, the matrix was composed of pine plantations and post oak savannas. Selective foraging by *A. texana* created patches readily apparent on aerial photography. Nest emigration (new patches) occurs by new-founding queens or translocation of existing colonies (Fowler 1981). Combining GPS and GIS with aerial photography quantifies the impacts these ants have on the forested landscape.

The relationship of *A. texana* to topography and depth above the water table is being examined to develop a landscape model to ascertain the effects of both terrain and location of the ant mounds and the influence of *A. texana* on the forest landscape. Nesting areas (mounds) are most often found on the tops and sides of ridges where the water table is deep and nests can reach depths of 8 meters (Moser 1967, Cahal et al. 1993). Generally, *A. texana* mounds are located between 1.5 m and 8 m from the water table (Moser 1963, Cahal et al. 1993).

Vegetation on active ant mounds in the Tonkawa soils (Typic Quartzipsamments) are species not preferred by *A. texana*. Post oak (*Quercus stellata*), bluejack oak (*Q. incana*), shining sumac (*Rhus capillinum*), yucca (*Yucca louisianensis*), mockernut hickory (*Carya tomentosa*), sassafras (*Sassafras albidum*), muscadine grape (*Vitis rotundifolia*), and dog fennel (*Eupatorium caprifolia*) predominate on *A. texana* nests. This vegetation flourishes following site colonization by *A. texana*. To examine foliar nutrition, samples were collected on *A. texana* central nest mounds and on adjacent non-mound areas, oven dried, and ground with a Wiley mill to prepare the samples for nitric acid digestion (Mills and Jones 1991). Concentrations of a suite of nutrients associated with plant productivity (N, P, K, Ca, Mg, Mn, Cu, S, Na, Fe, As) were determined by ICP (inductively coupled argon plasma emission spectrometry), sensitive to <1 mg kg⁻¹ (Walsh 1983). Each plant species was compared

individually based on location (either on-mound or off-mound), mound size, and ant activity level.

A. texana serves an important ecological function of soil amelioration and increases biodiversity, especially on the very sensitive ecosystem of the Tonkawa study area. Impact of leaf-cutting ants was greatest on planted loblolly pine. Repeated efforts at regeneration and control of *A. texana* in the study area have met with limited success. Regeneration studies on Typic Quartzipsamments indicated the best survival with Terra-Sorb[®]-treated loblolly pine followed by longleaf pine (Tracey et al. 1991).

Currently, the primary land use on Tonkawa soils is pine and wildlife management, although the potential for pine is low due to the droughty and infertile nature of the sand. Watermelons can be grown, but potential is low for any other cultivated crops. Recommendations include (1) encouraging native plants in openings created by *A. texana*, (2) managing for wildlife and limited recreation, (3) allowing *A. texana* to continue its biological function of soil improvement, and (4) utilizing this area for teaching forest pest management and forest entomology (Tracey et al. 1991).

Aerial photography is used to measure landscape impacts, vis-a-vis soil formation of *A. texana* (Cahal 1993, Cahal et al. 1993). Stereoscopic color infrared photographs (1:5000) of a 36- by 36-km area were used to estimate both numbers of mounds present and percentage of area defoliated by *A. texana* in the Tonkawa soil series of the Typic Quartzipsamments. Nest mound location and identification of soils, vegetation associations, and changes in mound size and location were measured and entered into a Geographic Information System using ArcView[®]. Central nest mounds of *A. texana* were located by using the soil survey of Nacogdoches County (Dolezel 1980), aerial observation using fixed-wing aircraft, extensive ground checking, color infrared aerial photography at a scale of 1:6000, and digital orthophotographic quarter quadrangles (DOQQ). Moser (1986) estimated timber losses due to leaf-cutting ants by examining aerial photographs of individual mounds.

For each mound, the center was identified, marked with a sequentially numbered pole, and located with a Trimble[®] TDC-1 GPS receiver. One-meter accuracy was obtained by taking a minimum of 100 locational positions tracking a minimum of four satellites with a positional dilution of precision (PDOP) maximum of 6. Differentially corrected GPS data were transferred to the GIS Laboratory of the Arthur Temple College of Forestry and transferred onto 1996 DOQQ imagery (1:12000). These images were georeferenced, rectified, and parallax and distortion free, which allowed GPS positions to be overlaid with location accuracy. The integration of GPS and DOQQ imagery enhance the investigation of *A. texana* because mound movement can be mapped over time and landscape patterns discerned.

Accurate mapping coupled with an interactive GIS system (ArcView[®]) details the landscape-wide ecological process of patch formation, change in the matrix, and alteration of the structure and function of the forest landscape on Typic Quartzipsamments soils. A thorough investigation of central nest mound changes in size and location, coupled with analysis of the associated vegetation productivity and nutrition, is essential in assessing the ecology of *A. texana* in the forested landscape.

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Insect Defoliators of *Nothofagus obliqua* (Roble) in South Chile: Two Years Monitoring Species and Their Damage

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ABSTRACT *Nothofagus obliqua* (Mirb.) Oerst is one of the most common tree species in Chile. Following severe and early defoliation during the spring and summer of 1996 and 1997, a study was conducted between 39° and 41° south latitude within the range of *N. obliqua*. Permanent plots were established in the Coastal Cordillera, Central Valley, and Andes Cordillera geographic sectors and monthly samples were taken. The main objective of this study was to study the insect defoliator complex of *N. obliqua*, including the types of damage and defoliation levels it produces with respect to space and time. This paper reports on data collected from 1997 to 1998 and from 1998 to 1999.

CHILE HAS A total of 28 million hectares of native forests: 13.5 million hectares of productive forests and 14.5 million hectares of wild, protected areas (Corporación Nacional Forestal 1997, Instituto Forestal 1997). Most of these native forests are temperate forests that are well represented in southern Chile where the soil quality and weather conditions contribute to maintain natural forests.

Nothofagus obliqua (Mirb.) Oerst., commonly called “roble,” is a broadleaf, deciduous member of the Fagaceae family and is the most common tree species in central and southern Chile. Its distribution is between 33° and 41° 30' south in several geographic zones: the Andes Cordillera, the Central Valley, and the Coastal Cordillera (Donoso and Landrum 1973, Hoffman 1982, Donoso 1993). This species is represented in several forest types as roble-hualo (*N. obliqua* - *N. glauca*) (Phil.) Krasser or roble-raulí-coigue (*N. obliqua* - *N. alpina*) (Poepp. et Endl.) Oerst. - *N. dombeyi* (Mirb.) Oerst.). Stands of these species are now mainly second growth forests or renewals (Donoso 1981, 1993; Rodríguez et al. 1983). *N. obliqua* is one of the most exploited species because of the quality of its wood that is used for bridges, wharfs, houses, and furniture (Pérez 1983). The annual growth rate of roble ranges between 8 m³/ha/year under unmanaged conditions to 18 m³/ha/year on good sites and with management. The final rotation age is 60 to 80 years (Instituto Forestal, Corporación Nacional Forestal 1998).

The biggest health threat to roble is the stem borer *Holopterus chilensis* (Coleoptera: Cerambycidae) that frequently attacks the basal stem log. Damage has been observed in 42% of the trees in unmanaged stands, especially in the Central Valley where historically there has been selective thinning (Kruuse 1981, Cabrera 1994, Diaz 1999, Peredo et al. 1999).

Because roble is a deciduous tree, the foliage begins to open in September, fully leafs out from October to November, and begins to decay in February. The folivorous insect

complex has total synchrony with this leaf-out behavior, demonstrating a pattern of optimal utilization of this leaf resource from a temporal perspective.

In the last 5 years, unusually early defoliations have been observed in the X Región (the region with more roble in Chile), probably as a consequence of climatic changes (dry summers) that enhanced population irruptions of defoliators. The impressive impact of these defoliations stimulated some basic studies with the following objectives:

General Objective.

- Evaluate the complex of insect defoliators associated with *Nothofagus obliqua* in the X Región of Chile biologically and physically.

Specific Objectives.

- Identify the species of insect defoliators associated with *Nothofagus obliqua*
- Classify damage from insect defoliators
- Establish the species' seasonal cycles
- Evaluate the degree of defoliation and the cumulative effects on the tree species

Materials and Methods

Study Area. The study area included both adult and renewal stands of *Nothofagus obliqua* in the Valdivia and Osorno provinces in the X Región of Chile. We established three work areas: (1) the northern Valdivia province (North Zone), (2) the central Valdivia province (Central Zone), and (3) the Osorno province (South Zone) (Fig. 1). Each of these three areas was divided into three sectors: the Coastal Cordillera, the Central Valley, and the Andean Cordillera, according to the three geographic zones present in the area. Each sector had two permanent plots.

In the first sampling period (1997 to 1998), 18, 500-m² permanent plots were established and each tree was marked. Geographic coordinates, tree diameter and height, and the health of each tree were recorded. The exact sampling points are shown in Figure 1. Samples were taken every month beginning in September 1997 and ending in March 1998.

In the second sampling period (between August 1998 and April 1999), work was conducted in all three sectors but only in the North Zone; however, visits to all the plots established the first year were made during November 1998 and January 1999. Several sampling results lead to changes in the periodicity of those samples, but financial and human resources were also considered.

In each visit to the permanent plots, we took foliage samples from 6 trees on each plot using a telescopic fork that just reached the intermediate zones of the tree canopy (10 to 15 m in height) (Lowman 1997).

Each sample was taken to the laboratory and maintained in a refrigerated room at 4°C until it was time to count insects and evaluate damage. It was also the best place to conserve fresh foliage for rearing immature insects. For this purpose, the laboratory also had a growth chamber with controlled temperature, humidity, and photoperiod.

Laboratory Work.

Extraction of Insects (eggs, larvae, nymphs, pupae, and adults). Insects were extracted from samples to (1) continue their development in climatic chambers, (2) follow their seasonal cycles, and (3) allow the emergence of parasitoids for mounting and identification. All reared material was placed in our insect collection. Some of these species are still being identified.

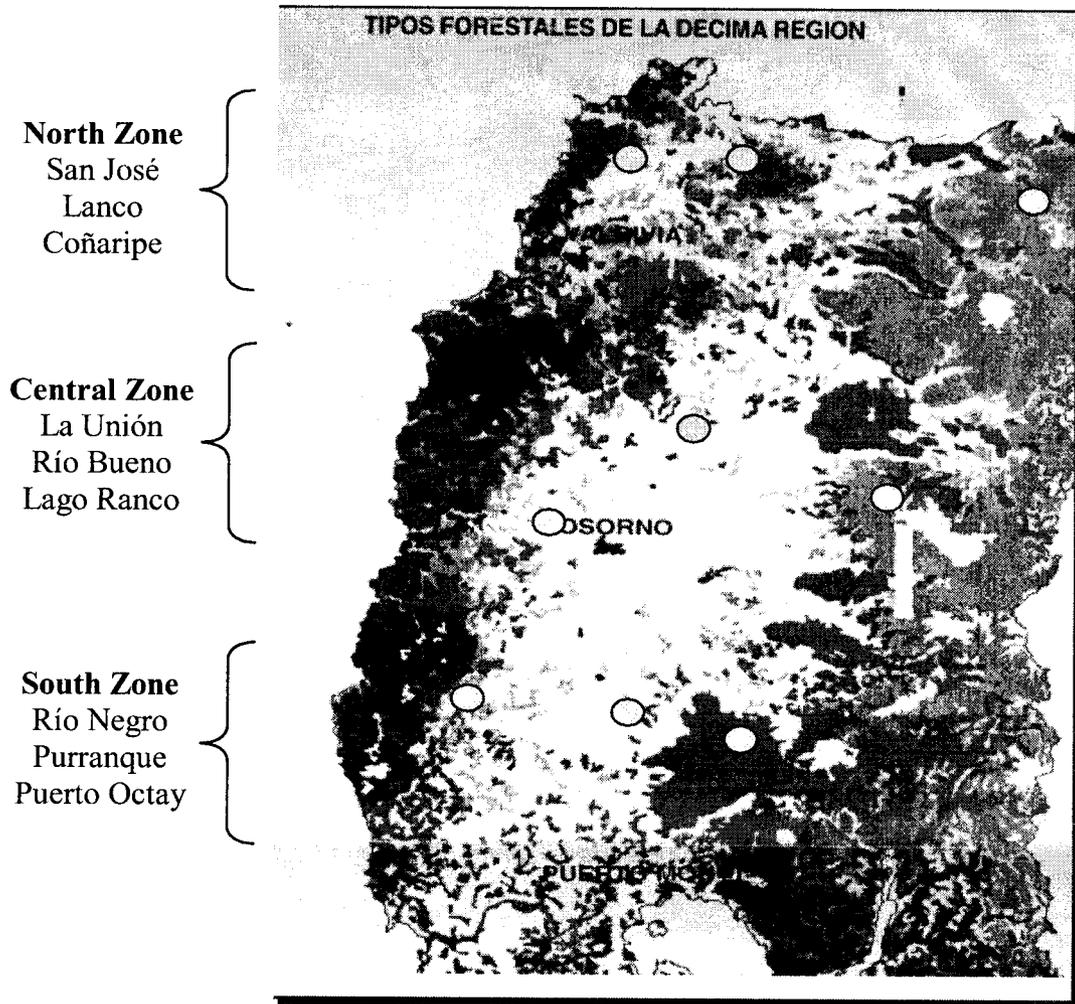


Figure 1. Distribution of the sampling plots (map source: Corporación Nacional Forestal 1997).

Classification and Quantification of Insect Damage. For this purpose, we obtained a subsample of 3 shoots on 3 trees per plot, counted all the leaves, and recorded leaf condition (damaged or undamaged) as well as the type of damage following a field guide prepared from preliminary samples. Some observations were directed to feeding behavior. We distinguished the following types of damage agents: *leaf chewers* (Type 1 consumes the entire leaf, Type 2 makes holes, and Type 3 sometimes feeds just on the leaf margin); *leaf skeletonizers*; and *leaf miners* (distinguished by the leaf mining pattern: blotch or linear).

Data Analysis. The families and species of sampled insects were analyzed and their presence in different zones and sectors was recorded. The following were also either observed or calculated: the type of damage they produced, insect stages, biological cycles, damage consistency and dominance of the species, and their temporal importance in different zones and sectors (Saiz et al. 1981). A nonparametric analysis was done using Statgraphics 2.0 Plus.

Results and Discussion

About the Species and Their Participation. The species detected in both sampling periods in all zones and sectors are listed in Tables 1 and 2. From 1997 to 1998, 9 families and 23 species were collected, whereas from 1998 to 1999, a total of 12 families and 22 species were collected.

The most common species were *Hornius grandis* (Philippi & Philippi), *Polydrossus nothofagi* Kuschel, *Omaguacua longibursae* Parra & Beèche, *Lagynopterix botulata* (Felder & Rogenhofer), and one species of Oecophoridae and Tenthredinidae (Parra and Beèche 1986, Beèche et al. 1987, Jerez and Cerda 1988, Jerez and Ibarra-Vidal 1992). The percentages of relative importance of the species for both years of sampling are illustrated in Figures 2 and 3.

Table 1. Presence of the families and species of insect defoliators for the first sampling period (1997 to 1998) by geographic zone and sector^a

Family	Species	North Zone			Central Zone			South Zone		
		C.C.	C.V.	A.C.	C.C.	C.V.	A.C.	C.C.	C.V.	A.C.
Tettigonidae	sp. 1 ^b		X	X			X			
Scarabaeidae	<i>Hylamorpha elegans</i>								X	
Chrysomelidae	<i>Crepidodera notata</i>	X	X	X	X			X	X	X
	<i>Hornius grandis</i>	X	X	X	X	X	X	X	X	X
	sp. 3 ^b	X	X		X			X	X	X
Curculionidae	<i>Polydrossus nothofagi</i>	X	X	X	X	X	X	X	X	X
	<i>Apion</i> sp.	X	X		X	X	X			X
Geometridae	<i>Omaguacua longibursae</i>	X	X	X	X	X	X	X	X	X
	sp. 2 ^b	X	X	X	X	X	X	X	X	X
	sp. 3 ^b	X	X	X	X	X	X	X	X	X
	sp. 4 ^b	X				X			X	
	sp. 5 ^b	X	X	X						
	<i>Lagynopterix botulata</i>	X	X	X	X	X	X	X	X	X
	sp. 7									
	<i>Mycroclysia pristopera</i>	X	X					X	X	
Saturniidae	<i>Ormiscodes</i> spp.							X		
	sp. 2 ^b		X	X						
	sp. 3 ^b		X	X	X					
	sp. 4 ^b	X								
Oecophoridae	sp. 1 ^b	X	X	X	X	X	X	X	X	X
	sp. 2 ^b				X	X	X			
Cynipidae	sp. 1 ^b								X	
Tenthredinidae	sp. 1 ^b	X	X	X	X	X	X	X	X	X

^a C.C. = Coastal Cordillera sector; C.V. = Central Valley sector; A.C. = Andean Cordillera sector

^b In the identification process

Table 2. Presence of the families and species of insect defoliators for the second sampling period (1998 to 1999) by geographic zone and sector^a

Family	Species	North Zone			Central Zone			South Zone			
		C.C.	C.V.	A.C.	C.C.	C.V.	A.C.	C.C.	C.V.	A.C.	
Tettigonidae	sp. 1 ^b	X	X	X							
Scarabaeidae	<i>Hylamorpha elegans</i>	X		X							
Chrysomelidae	<i>Crepidodera notata</i>	X					X	X			
	<i>Hornius grandis</i>	X	X	X	X		X	X	X	X	
	sp. 3 ^b	X									
Curculionidae	<i>Polydrossus nothofagi</i>	X	X	X			X			X	
Geometridae	<i>Omaguacua longibursae</i>	X	X	X		X	X	X	X	X	
	sp. 2 ^b	X	X	X							
	sp. 3 ^b									X	
	sp. 5 ^b	X									
	<i>Lagynopteryx botulata</i>	X	X	X	X	X	X	X	X	X	
	<i>Mycroclysia pristopera</i>	X	X	X		X	X				
	sp. 9 ^b		X								
	sp. 10 ^b	X		X						X	
	Saturniidae	sp. 2 ^b	X		X						
		sp. 4 ^b	X	X	X						
Oecophoridae	sp. 1 ^b	X	X	X	X	X	X	X	X	X	
Lasiocampidae	sp. 1 ^b			X							
Lepidoptera	sp. 1 ^b	X	X				X				
Cynipidae	sp. 1 ^b			X							
Tenthredinidae	sp. 1 ^b	X	X	X					X	X	
Cecidomyiidae	sp. 1 ^b		X								

^a C.C. = Coastal Cordillera sector; C.V. = Central Valley sector; A.C. = Andean Cordillera sector

^b In the identification process

Because the insect species were the same in all of the permanent plots established, work was concentrated only in the northern Valdivia zone (all sectors) for the second sampling period despite significant differences in defoliation intensity. This permitted us to refine rearing methodologies and clarify the biological cycles of the most frequent species, which was one of the objectives of the second sampling period.

Bauerle et al. (1997) recorded 16 species associated with roble in a bibliographic review. Some of them did not appear in our samples, such as *Cerospastus volupis* Konow, traditionally indicated as an important defoliator of this tree. Another defoliator that was never captured during our sampling periods was *Doina clarkei* Parra and Ibarra-Vidal (Parra and Ibarra-Vidal 1991).

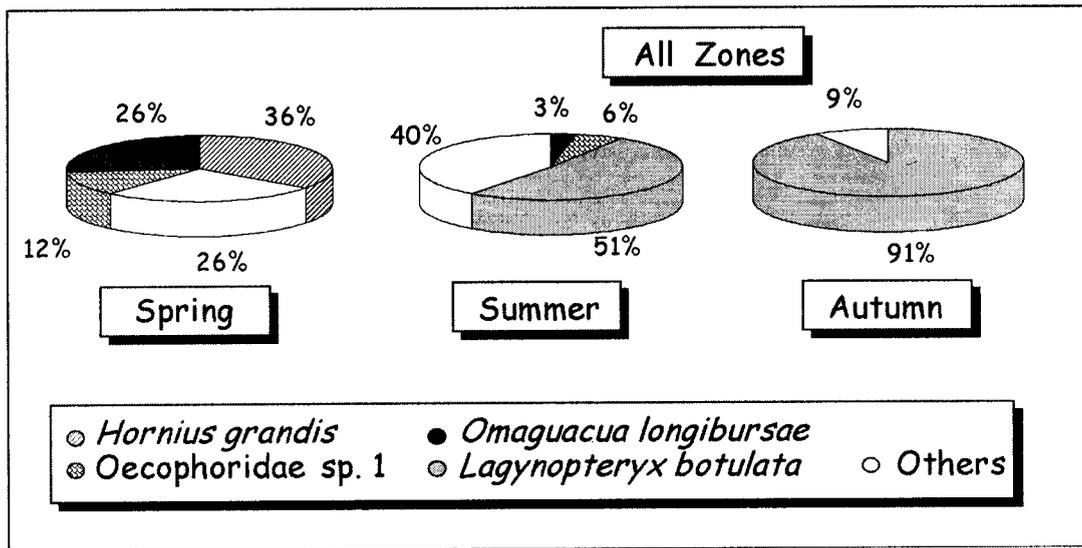


Figure 2. Percentage of relative importance of the most common species collected during the first sampling period (1997 to 1998) in all zones surveyed.

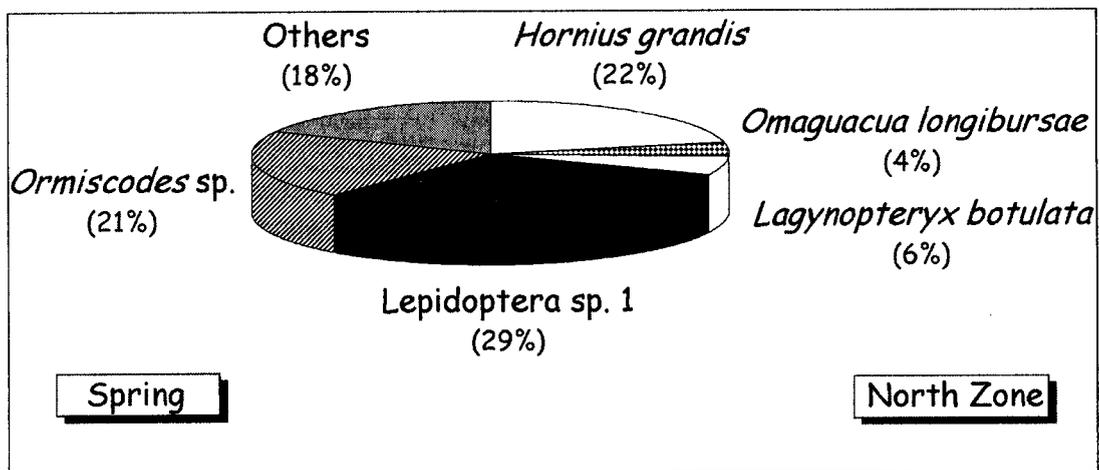


Figure 3. Representation of the main species in the second spring sampling period (1999) in the northern Valdivia (North) zone.

About the Species and Their Type of Damage. To evaluate the impact of the species, leaf damage type was recorded from 1997 to 1998 and from 1998 to 1999, respectively (Tables 3 and 4, Figs. 4 and 5). The complex of insect defoliators consumed part or all of the leaves. The insect feeding behavior, along with the insect's development, could change; sometimes they never ate all of the leaf surface. Field and laboratory observations were very time consuming and most behavioral patterns were new, especially for those species that are new or little known. Other observations relative to different life stages or instars were new for Chile.

Table 3. Types of damage and families/species involved for the first sampling period (1997 to 1998)

Types of Damage	Family	Species	Stage and Instar ^a
All-leaf Chewers (1)	Scarabaeidae	<i>Phytoloema mutabilis</i>	Adults
	Saturniidae	<i>Ormiscodes</i> sp.	Larvae ³
		sp. 4	Larvae ³
	Geometridae	<i>Omaguacua longibursae</i>	Larvae ³
		sp. 2	Larvae ³
		<i>Lagynopteryx botulata</i>	Larvae ³
	<i>Mycroclysia pristopera</i>	Larvae ³	
Hole Makers (2)	Tettigonidae	sp. 1	Nimphae
	Chrysomelidae	<i>Hornius grandis</i>	Adults
		<i>Crepidodera notata</i>	Adults
		sp. 3	Adults
	Curculionidae	<i>Polydrossus nothofagi</i>	Adults
		<i>Apion</i> sp.	Adults
	Geometridae	<i>Omaguacua longibursae</i>	Larvae ¹
		sp. 2	Larvae ¹
		sp. 3	Larvae ¹
		sp. 4	Larvae ¹
		sp. 5	Larvae ¹
		<i>Lagynopteryx botulata</i>	Larvae ¹
		sp. 7	Larvae ¹
	<i>Mycroclysia pristopera</i>	Larvae ¹	
Tenthredinidae	sp. 1	Larvae ¹	
Border-leaf Chewers (3)	Chrysomelidae	<i>Hornius grandis</i>	Larvae ^{2,3}
	Geometridae	<i>Omaguacua longibursae</i>	Larvae ²
		sp. 2	Larvae ²
		sp. 3	Larvae ²
		sp. 4	Larvae ²
		sp. 5	Larvae ²
		<i>Lagynopteryx botulata</i>	Larvae ²
		sp. 7	Larvae ²
	<i>Mycroclysia pristopera</i>	Larvae ²	
Tenthredinidae	sp. 1	Larvae ²	
Skeletonizers (4)	Oecophoridae	sp. 1	Larvae ^{1,2,3}
		sp. 2	Larvae ^{1,2,3}
Leaf Miners (5)	Chrysomelidae	sp. 1	Larvae ^{1,2,3}
Leaf-gall Makers (6)	Cecidomyiidae	sp. 1	Larvae ^{1,2,3}
	Cynipidae	sp. 1	Larvae ^{1,2,3}

^a 1 = First instars; 2 = Intermediate instars; 3 = Last instars

Table 4. Types of damage and families/species involved for the second sampling period (1998 to 1999)

Types of Damage	Family	Species	Stage and Instar ^a
All-leaf Chewers (1)	Scarabaeidae	<i>Hylamorpha elegans</i>	Adults
	Saturniidae	sp. 2	Larvae ³
	Geometridae	<i>Omaguacua longibursae</i>	Larvae ³
		sp. 2	Larvae ³
		<i>Lagynopteryx botulata</i>	Larvae ³
	<i>Mycroclysia pristopera</i>	Larvae ³	
Hole Makers (2)	Tettigonidae	sp. 1	Nymphae
	Chrysomelidae	<i>Hornius grandis</i>	Larvae ¹
		<i>Crepidodera notata</i>	Adults
		sp. 3	Adults
	Curculionidae	<i>Polydrossus nothofagi</i>	Adults
	Geometridae	<i>Omaguacua longibursae</i>	Larvae ¹
		sp. 2	Larvae ¹
		<i>Lagynopteryx botulata</i>	Larvae ¹
		<i>Mycroclysia pristopera</i>	Larvae ¹
Tenthredinidae	sp. 1	Larvae ¹	
Border-leaf Chewers (3)	Chrysomelidae	<i>Hornius grandis</i>	Larvae ^{2,3}
	Geometridae	<i>Omaguacua longibursae</i>	Larvae ²
		sp. 2	Larvae ²
		sp. 5	Larvae ²
		<i>Lagynopteryx botulata</i>	Larvae ²
		<i>Mycroclysia pristopera</i>	Larvae ²
		sp. 9	Larvae ²
		sp. 10	Larvae ²
Lasiocampidae?	sp. 1	Larvae ^{1,2}	
Tenthredinidae	sp. 1	Larvae ²	
Skeletonizers (4)	Oecophoridae	sp. 1	Larvae ^{1,2,3}
	? ^b	sp. 1	Larvae ^{1,2,3}
Leaf Miners (5)	Chrysomelidae	sp. 1	Larvae ^{1,2,3}
Leaf-gall Makers (6)	Cecidomyiidae	sp. 1	Larvae ^{1,2,3}
	Cynipidae	sp. 1	Larvae ^{1,2,3}

^a 1 = First instars; 2 = Intermediate instars; 3 = Last instars

^b ? = Lepidoptera; family and species in identification

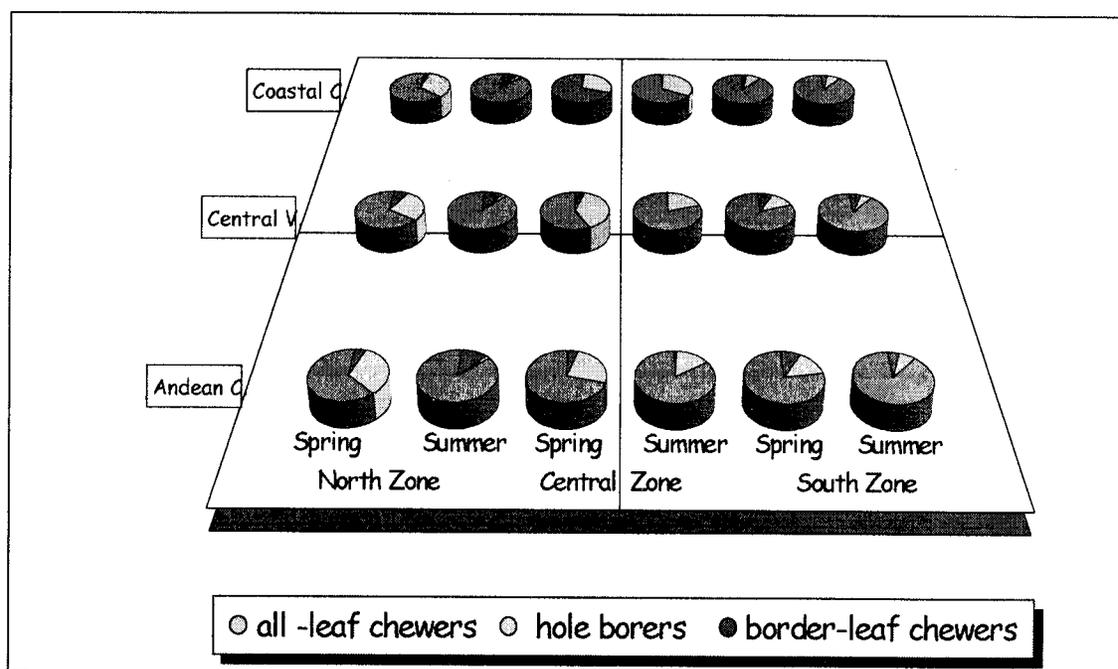


Figure 4. Types of damage during spring and summer (1997 to 1998) in all zones and sectors. Coastal C. = Coastal Cordillera sector; Central V. = Central Valley sector; Andean C. = Andean Cordillera sector

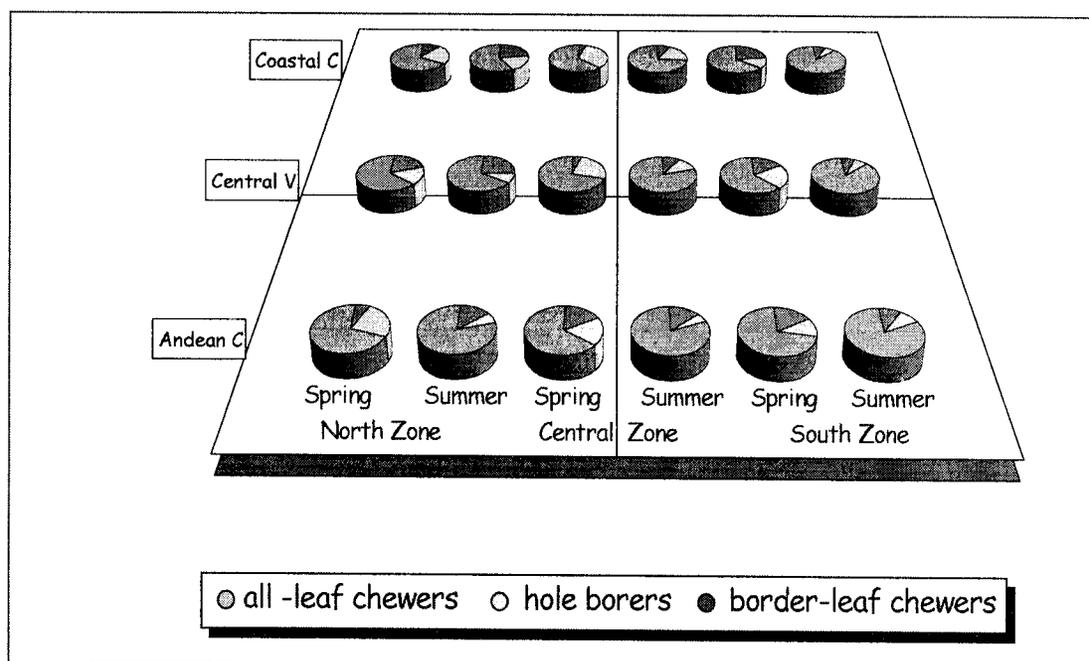


Figure 5. Types of damage during spring and summer (1998 to 1999) in all zones and sectors. Coastal C. = Coastal Cordillera sector; Central V. = Central Valley sector; Andean C. = Andean Cordillera sector

Levels of Defoliation. Figures 6 and 7 illustrate the relationship between undamaged and damaged foliage for both sampling periods. The North Zone exhibited the highest levels of defoliation that increased up to 90% in December. Peak defoliation occurred in the other zones at the end of the foliage period during March, although defoliation levels were not as high as those measured in the North Zone.

There was a decrease in defoliation in the Coastal Cordillera sector from north to south, but no trends were clear in the other sectors. This is reinforced by the significant differences between sectors and zones.

Defoliation levels were lower in the second sampling period (around 40% or less) and defoliation near 80% was observed only in the Andes Cordillera sector plots during February.

To summarize the relationship between undamaged and damaged foliage, there is a dynamic that involves (1) the feeding habits of the damage agents (insects), (2) insect population levels, and (3) foliage characteristics, influenced by climatic changes and their (insects) own temporal changes. It seemed that for each nutritional condition of the leaves, there were one or more species that exploited this resource.

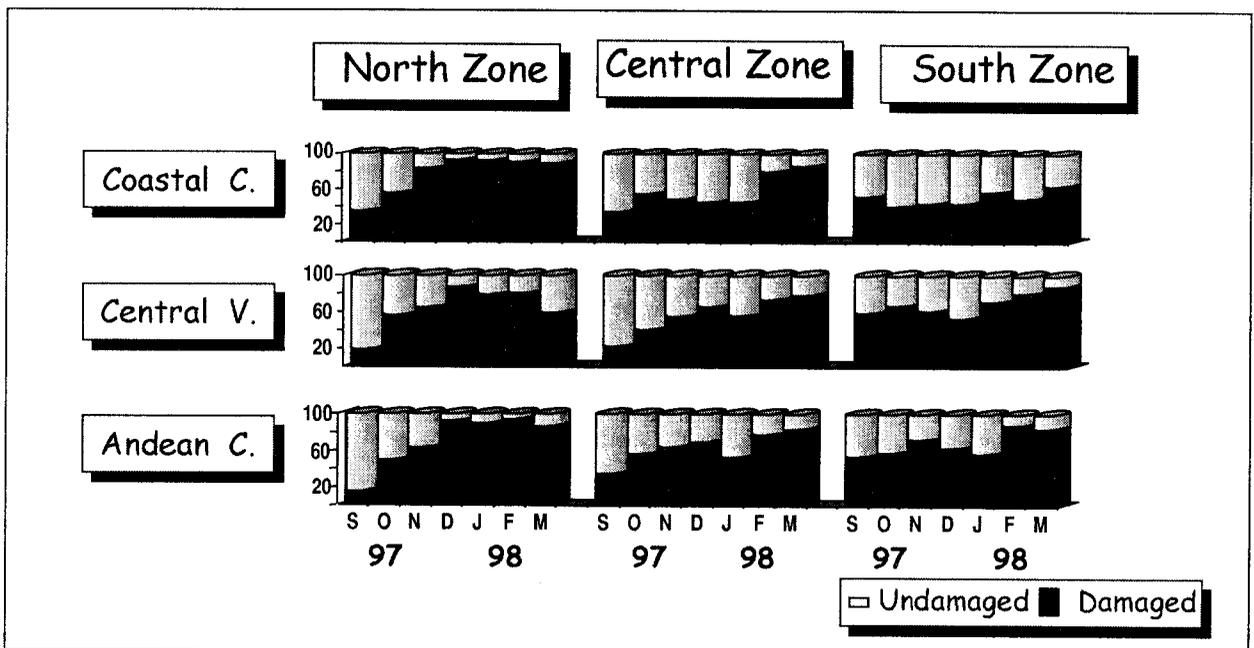


Figure 6. Relationship between undamaged and damaged foliage in the first sampling period (1997 to 1998) in all zones and sectors. Coastal C. = Coastal Cordillera sector; Central V. = Central Valley sector; Andean C. = Andean Cordillera sector

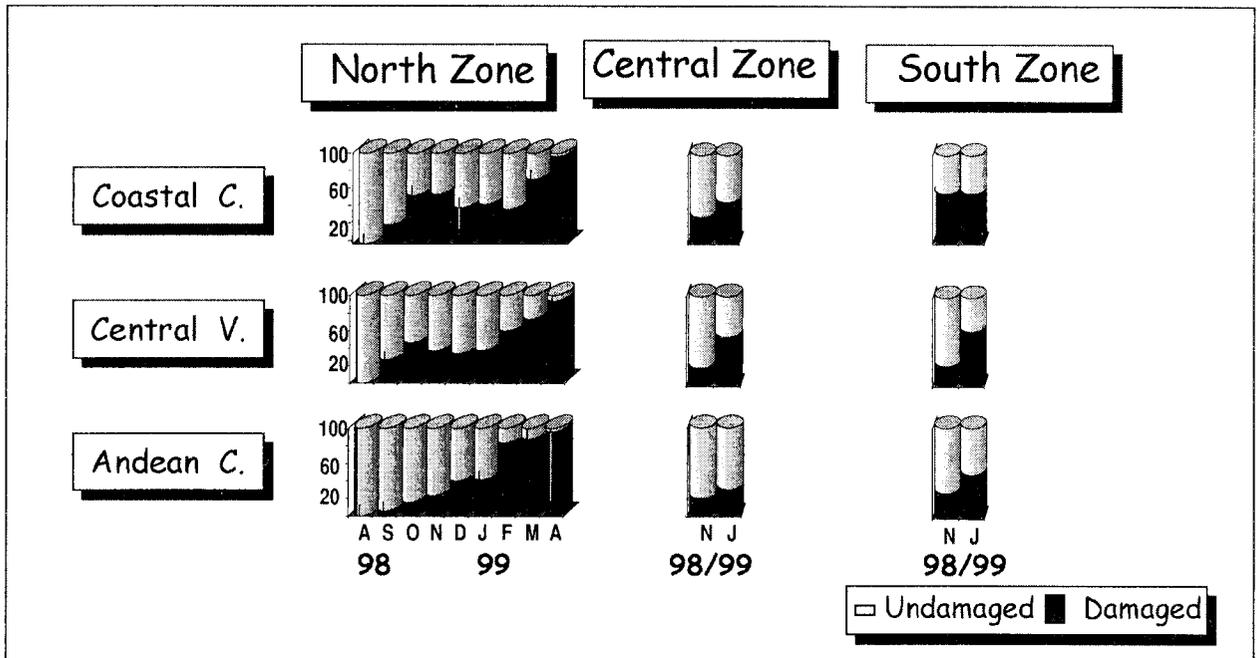


Figure 7. Relationship between undamaged and damaged foliage in the second sampling period (1998 to 1999). All sectors were sampled; however, sectors in the Central and South zones were sampled only two times: November 1998 and January 1999. Coastal C. = Coastal Cordillera sector; Central V. = Central Valley sector; Andean C. = Andean Cordillera sector

Conclusions

- No tree mortality was detected after two consecutive years of severe defoliation.
- Refoliation occurred in zones and sectors with more defoliation damage.
- All of the associated insect species were native and some were new.
- Twenty three species were collected, but only six were dominants and shared the foliage resource.
- Dominant species were present in all study areas.
- Most damage was produced by all-leaf chewers, hole borers, and border-leaf chewers.
- The study increased our knowledge of the biological cycles, life strategies, and natural enemies of roble insect defoliators.
- Defoliation increased during the study period (August to April) in synchrony with tree phenology and climatic conditions.
- There were no significant differences in leaf damage between zones and their sectors in spring and summer of the first sampling period.
- There were significant differences in leaf damage among the two sampling periods for zones, sectors, and seasons.

Future Studies

In a third study period, several new approaches are being implemented:

- Collecting monthly canopy samples using a new methodology to compare the insect fauna and their distribution at different tree heights
- Documenting foliar nutritional changes and how these affect leaf quality and therefore associated insects
- Dendrochronological studies to document historical defoliation events

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Outbreak of *Cephalcia arvensis* (s.l.) (Hymenoptera, Pamphiliidae) in Czechia from 1997 to 1999

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ABSTRACT In 1997, a local outbreak of the spruce web-spinning sawfly (*Cephalcia arvensis* (s.l.)) appeared in Czechia. The total infested area of Norway spruce (*Picea abies* (L.) Karst.) stands covered about 650 ha. Because the stands were seriously endangered by heavy defoliation, it was decided to protect them with an aerial treatment of diflubenzuron in 1998 and, to a lesser extent, in 1999. Observations of the insect's biology obtained during the outbreak are briefly summarized in this paper.

THE SPRUCE WEB-SPINNING sawfly (*Cephalcia arvensis* (s.l.)) is one of three economically important species of the genus *Cephalcia* living on Norway spruce (*Picea abies* (L.) Karst.) in Czechia. In the 1980s, *C. arvensis* caused heavy defoliation of the spruce stands in an area of several hundreds of hectares in northeastern Bohemia. A further outbreak followed here at the end of the 1990s.

Materials and Methods

The outbreak was located near the village of Česká Čermná in northeastern Bohemia (Longitude 16°14', Latitude 50°23'). It occurred mostly in older, artificially established pure Norway spruce stands situated on slopes and plateaus at an altitude of about 500 to 650 m. The main climax tree species here is European beech (*Fagus sylvatica* L.). Characteristics of the locality are summarized in Table 1.

An increase in the web-spinning sawfly population was first detected in 1996; the following year (1997) was considered the beginning of the outbreak. The infested area almost precisely coincides with an outbreak that occurred from 1982 to 1988 (Martinek 1991). Thus, the present epidemic may be regarded as a local repeated outbreak.

In 1998 and 1999, observations in the outbreak area focused on the following problems: (1) identifying the spectrum of spruce web-spinning sawfly species involved in the infestation (with emphasis on the epidemic taxon), (2) life activities of the epidemic population, and (3) questions connected with the importance of the outbreak to forestry, including control efforts.

Voucher specimens of the examined material are deposited in the collection of the first author.

Results and Discussion

Taxonomic Identity of the Epidemic Population. In the 1980s, two outbreaks of *Cephalcia arvensis* (s.l.) were first recorded in Czechia. Because populations in single outbreak areas had different adult emergence times, they have been called the spring and summer forms, respectively, of *Cephalcia arvensis* (Panzer, 1805). Detailed information on these forms is given by Křístek and Švestka 1986, Martinek 1991, and Battisti 1993.

Table 1. Characteristics of a *Cephalcia arvensis* (s.l.) outbreak in Czechia from 1997 to 1999

Locality:	Česká Čermná environment (Long. 16°14', Lat. 50°23')	
Habitat:	hill country at an altitude of 480 to 640 m	
Area infested:	600 to 700 ha	
Age of stand:	60 to 80 years	
Major tree species in the area:	<i>Picea abies</i> (L.) Karst. (predominant), <i>Larix decidua</i> Mill., <i>Pinus sylvestris</i> L., <i>Fagus sylvatica</i> L.	
Tree species infested:	<i>Picea abies</i> (L.) Karst.	
Population of <i>Cephalcia arvensis</i> (s.l.)		
Density of larvae in the soil (total number of eonymphs and pronymphs per m ²):	average	200 to 300
	max. 1998	1,300
	max. 1999	570
Percentage of potential swarmers:	1998	72.6%
	1999	67.6%
Main swarming period of adults:	1998	April 14 to 18
	1999	April 20 to 25
Occurrence of males and females:	moderate protandry (several days)	
Fecundity:	17 eggs on average (n = 21)	
Egg laying:	on older (stiff, brush-like) needles in a row from 1 to 4 eggs (most frequently 2 to 3: 67.6% of cases)	
Hatching of larvae:	1998	end of May to beginning of June
	1999	end of May to beginning of June
Larval feeding:	end of May to mid July older needles (they avoid young shoots) gregarious (1 to 4 larvae)	
Falling period of larvae:	end of June to mid July	
Depth of hibernation in the soil:	1997/98	3 to 5 cm (n = 172)
	1998/99	5 to 8 cm (n = 76)
Voltinism:	prevalence of one-year generation (60 to 70%)	
Occurrence of accompanying species of the genus <i>Cephalcia</i> Panzer in the outbreak area		
<i>Cephalcia abietis</i> (L.)	numerous	
<i>Cephalcia annulicornis</i> (Hartig)	single	
<i>Cephalcia alpina</i> (Klug) (= <i>fallenii</i> (Dalman))	Sporadic	

The population in the outbreak area near Česká Čermná from 1982 to 1988 and from 1997 to 1999 represents the spring phenological form according to the literature cited above. Morphological features of the adults conform to the diagnosis of the species *Cephalcia arvensis* (Panzer, 1805) as described in the revision by Beneš (1976) and van Achterberg and van Aartsen (1986). This species, however, appears to be a complex of several closely related species (Battisti and Zanocco 1994) so that the taxonomic status of the *C. arvensis* population in the outbreak area remains open.

Species Spectrum of the Genus *Cephalcia* Panzer. Besides the predominant species *C. arvensis*, an additional three species of spruce web-spinning sawfly were found in the outbreak area. They were, in decreasing order of abundance, *Cephalcia abietis* (Linnaeus, 1758), *Cephalcia annulicornis* (Hartig, 1837), and *Cephalcia alpina* (Klug, 1808). The total percentage of these three species did not exceed 1 to 2% in either year.

Notes on Bionomics. Some biological attributes of the *C. arvensis* epidemic population in northeastern Bohemia are summarized in Table 1. Some attributes differ from the data obtained from other localities in Europe where epidemic populations of *C. arvensis* have been studied (Pschorn-Walcher 1982; Křístek and Švestka 1986; Battisti 1993, 1994). These differences are undoubtedly due to a different taxonomic identity of the Bohemian population.

On the other hand, data received by Martinek (1991) from the same locality from 1982 to 1988 have been confirmed and provided the following observations:

- swarming began very early (second half of April)
- 1 to 3 (4) eggs were laid in one row on a needle
- the preferred egg laying site was older, stiff brush-like needles in the upper, sun-exposed parts of the crowns
- larvae fed exclusively on older needles
- larvae from the same egg mass were gregarious
- larvae hibernated in the upper layer of the soil, out of the mineral horizon
- one-year generation was prevalent, regardless of prevailing weather conditions during the year

Economic Importance of the Outbreak. In places where population densities of swarmers exceeded an average of 300 specimens per m², the number of eggs laid in tree crowns was higher than the critical number (indicating severe defoliation). There were more than 50 (critical number) and not infrequently up to 100 to 200 eggs per 1-m section of a branch. When sample trees were felled (n = 30), it was found that a high density of eggs occurred relatively evenly throughout the stand. For *C. abietis*, on the other hand, the uneven, mosaic character of an infestation is typical, and only a portion of the trees in a stand is severely defoliated. Therefore, it may be concluded that outbreaks of *C. arvensis* can be more dangerous than those of *C. abietis*, a well-known species infesting large areas in central Europe.

The area infested with *C. arvensis* was treated with a ULV spray containing 0.2 litres of Dimilin 48 SC (active ingredient diflubenzuron) per hectare. On May 25, 1998, 600 ha were treated; on May 26th of the following year (1999), only 120 ha were treated. The treatment resulted in larval mortality between 80 and 90%. A comparable effectiveness was obtained when this preparation was used against *C. abietis*.

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