GEOGRAPHICAL DISTRIBUTION OF *CHORISTONEURA* SPECIES (LEPIDOPTERA: TORTRICIDAE) FEEDING ON *ABIES, PICEA*, AND *PSEUDOTSUGA* IN WESTERN CANADA AND ALASKA

R.F. SHEPHERD and T.G. GRAY[1]

Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, 506 West Burnside Road, Victoria, British Columbia, Canada V8Z 1M5

and G.T. HARVEY

Natural Resources Canada, Canadian Forest Service, Great Lakes Forestry Centre, 1219 Queen Street East, Sault Ste. Marie, Ontario, Canada P6A 5M7

Abstract

The Canadian Entomologist **127**: 813–830 (1995)

Male moths of *Choristoneura occidentalis* Freeman, *C. biennis* Freeman, *C. fumiferana* (Clemens), and *C. orae* Freeman were caught in pheromone-baited traps. Ten traps were placed at each site, five baited with an aldehyde lure and five with an acetate lure. This procedure permitted separation of species based on the specific chemical lure and also provided specimens for further study of morphological and isozyme differences. The color of the forewings, presence or absence of spicules on the aedeagus, and a specific allozyme frequency were determined on selected specimens where these characteristics were useful in separating species at a particular site. Distributions of all species were more extensive than previously known, sometimes adding hundreds of kilometres to the recorded range. Areas of sympatry were identified and the fidelity and usefulness of characteristics for separating species in areas of overlap were discussed.

Shepherd, R.F., T.G. Gray et G.T. Harvey. 1995. Répartition géographique des espèces de *Choristoneura* (Lepidoptera: Tortricidae) qui se nourrissent d'*Abies*, *Picea* et *Pseudotsuga* dans l'ouest du Canada et en Alaska. *The Canadian Entomologist* **127**: 813–830.

Résumé

Des mâles de *Choristoneura occidentalis* Freeman, de *C. biennis* Freeman, de *C. fumiferana* (Clemens) et de *C. orae* Freeman ont été capturés dans des pièges à phéromone. Dix pièges ont été placés dans chacun des sites: cinq dont l'appât était un aldéhyde et cinq de l'acétate. Grâce à cette technique, il a été possible de séparer les espèces à l'aide d'un appât chimique spécifique et d'obtenir aussi des spécimens pour poursuivre l'étude sur les différences morphologiques et la constitution des isozymes. La couleur des ailes antérieures, la présence ou l'absence de spicules sur l'édéage, et la fréquence d'une allozyme spécifique ont été établies chez certains spécimens lorsque ces caractéristiques étaient utiles pour séparer les espèces à un endroit donné. L'aire de répartition de toutes les espèces était plus étendue que l'on croyait; elle comportait parfois des centaines de kilomètres de plus que l'aire connue. Des aires de sympatrie sont déterminées; les auteurs traitent de la fidélité et de l'utilité des caractéristiques pour séparer les espèces dans les aires de chevauchement.

Introduction

Many species within the genus *Choristoneura* in northwestern North America are difficult to distinguish taxonomically by morphological characteristics, particularly the Nearctic conifer-feeding species (Dang 1992; Freeman 1967; Harvey 1985; Powell 1980; Stehr 1967). Historically the distribution of these forest species was not well known (Fig. 1) except at locations of population outbreaks where adequate specimens could be obtained for taxonomic studies. The advent of pheromone trapping provided a tool that enabled the collection of specimens at low population densities for morphological and isozyme studies, and also enabled the distinction between species that responded to two different pheromone components, an aldehyde and an acetate. The distribution of selected *Choristoneura* species,

[1] Author to whom correspondence should be addressed.

https://doi.org/10.4039/Ent127813-6 Published online by Cambridge University Press

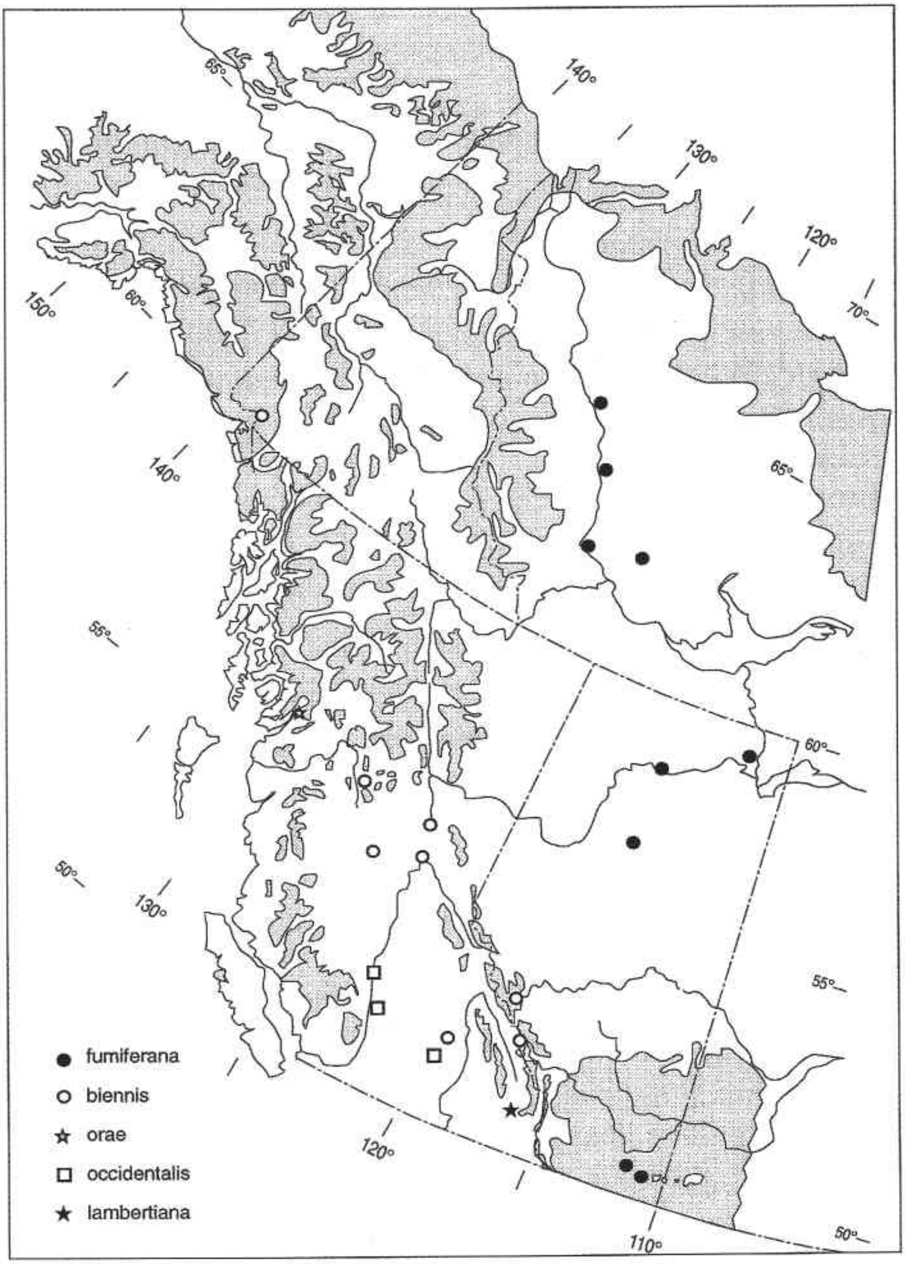

FIG. 1. Distribution of *Choristoneura* species in British Columbia, Alberta, Northwest Territories, Yukon Territory, and Alaska up to and including 1967, after Stehr (1967).

as determined from pheromone trap specimens and augmented by larval collections where possible, was the primary objective of this paper. In addition, the variability of some species characteristics was also discussed where appropriate. The species studied were those that feed primarily on *Abies, Picea*, and *Pseudotsuga* in Alberta, British Columbia, Northwest

https://doi.org/10.4039/Ent127813-6 Published online by Cambridge University Press

TABLE 1. Characteristics used to distinguish four species of western *Choristoneura*

Characteristic	*C. occidentalis*	*C. biennis*	*C. fumiferana*	*C. orae*
Pheromone component	Aldehyde (10% of moths respond to the acetate)	Aldehyde (10% of moths respond to the acetate)	Aldehyde (<3% of moths respond to the acetate)	Acetate (<3% of moths respond to the aldehyde)
Aedeagus	Smooth	Smooth (<3% spic.)	82% spiculed	Smooth
Life history	1 year	2 year	1 year	Variable
Allozyme fr. of AAT-1*	0,0,0,0.02,0.98	0,0,0,0.04,0.96	0,0.01,0.65,0.30,0.05	0,0,0,0.01,0.99
Female and male forewing color	Orange-brown	Dark brownish-grey	Grey	Dark orange-brown
Host	*Pseudotsuga*	*Abies/Picea*	*Abies/Picea*	*Abies/Picea*

*Allozyme frequency for locus 1 of Aspartate aminotransferase (Harvey and Sohi 1985).
† The color is best observed on a comparative basis in a series of adults rather than as individuals (Freeman 1967).

Territories, Yukon Territory, and Alaska, namely *C. occidentalis*, *C. biennis*, *C. fumiferana*, and *C. orae*. We followed the taxonomic protocol recommended by Powell and DeBenedictis (1982), i.e. that we "retain the named entities as now conceived until we have a much fuller understanding of the relationships among them."

The pine-feeding *Choristoneura* are a complex of species and subspecies (Powell 1980; Gray and Slessor 1989; Gray and Gries 1993) that have not yet been studied sufficiently in the study area, either taxonomically or in pheromone chemistry, to lend themselves to this type of study. They are only mentioned where they may be confounding acetate trap catches placed out for *C. orae*.

Materials and Methods

The major characteristics used to distinguish these species were derived from Dang (1985, 1992), Gray et al. (1995), Harvey (1996), and Stock and Castrovillo (1981) and are summarized in Table 1. *Choristoneura fumiferana* can be distinguished from the western species because it has a unique allozyme frequency and the aedeagus of most males has spicules. Few males were caught in acetate traps, as compared with *C. occidentalis* or *C. biennis*. *Choristoneura orae* responds to the acetate lure with very few blundering into the aldehyde-baited traps. *Choristoneura occidentalis* and *C. biennis* are similar to each other but their geographic ranges are largely separate and they are best separated on the basis of the presence of a second diapause and the primary feeding host of the larvae. *Choristoneura biennis* is also larger and darker than *C. occidentalis*. With both of these species, if a large number of moths is caught, a few will also be found in the acetate traps. Thus if a relatively low number of *C. orae* males occurred in an *Abies/Picea* forest, mixed with *C. biennis*, they were difficult to detect.

Pheromone traps were used to detect the presence of *Choristoneura* in a stand, determine which pheromone was attractive, and provide moths for morphological and isozyme studies. The specific chemicals used in these lures have been carefully determined: the aldehyde lure consisted of 92% *trans*-11-tetradecenal (*E*11-14:ALD) and 8% *cis*-11-tetradecenal (Z11-14:ALD) (Cory et al. 1982) and the acetate lure consisted of 82% *trans*-11-tetradecenyl *E*11-14:Ac), 9% *cis*-11-tetradecenyl (Z11-14:Ac), and 9% *trans*-11-tetradecenol (*E*11-14:OH) (Gray et al. 1984). The aldehyde lure contained 0.03% (weight/weight) of pheromone in a polyvinyl chloride rod 3 mm diameter by 5 mm in length (Daterman 1974) and the acetate lure contained 5% (weight/weight) of pheromone in polyvinyl chloride, except in 1987 when the acetate lures contained 0.03% and only a few moths were caught at that concentration. The difference in the percentage loading of the lures is important and may be a factor in maintaining species separation.

Ten traps were placed 1.5–2 m above the ground at each location, five baited with an aldehyde lure and five with an acetate lure. New 2-L milk cartons, covered inside with Bird Tanglefoot (The Tanglefoot Company, Grand Rapids, Michigan), were used as traps. Traps were left out to cover the flight period. More than 152 locations were trapped, some for many years, representing a total of over 334 sets of data specific to year and location.

At many locations larval collections were made, hosts were identified, and the larvae were reared to establish the presence or absence of a second diapause and provide series of adults for size and color comparisons. In some cases aedeagi were removed from trapped moths to check for the presence or absence of spicules (Dang 1992).

Trapping to provide moths for isozyme analysis employed Pherocon IC sticky traps (Zoecon Corporation, Palo Alto, California) baited with similar baits (Sanders 1978) and was carried out during the period of 9–21 July in 1986 and 1988. Traps were collected or replaced after one or two nights so that living moths could be obtained for storage in liquid nitrogen (Harvey 1996). Isozyme analyses were carried out using horizontal starch gel electrophoresis (Harvey and Sohi 1985; Harvey 1996). Isozymes at the seven loci (PGI-1, PGM-1, MDH-1, IDH-1, IDH-2, AAT-1, and AAT-2) were measured in moth samples from all locations. Isozymes were measured in 12 loci in larval collections for comparison with moth samples. Special attention was paid to Aspartate aminotransferase (AAT-1) as a differentiating locus. Enzyme characteristics and activity levels for these loci from freshly killed moths were the same as in larvae. No relationship has been demonstrated between any of the isozymes used and other identifying characteristics of the different species. Frequencies of enzymes were analyzed using the software program BIOSYS (Swofford and Selander 1981). A locus was considered polymorphic if the frequency of the most common allele did not exceed 0.95.

Additional collection data by the Forest Insect and Disease Survey and outbreak defoliation maps by Harris et al. (1985) and Unger (1984) were used to supplement the data collected in this study. The point-sample data were compiled and mapped to provide first approximations of species distributions. As more information becomes available in the future, adjustments in these distributions are to be expected.

Results and Discussion

The locations of collection sites are given in Table 2 along with the probable species responding to the two different lures. The incidence of spicules on the male aedeagi is also provided in Table 2 for selected locations where *C. fumiferana* was suspected to occur in sympatry with any western species. In southern Yukon Territory and northern British Columbia separation of *C. fumiferana* from other species was particularly difficult. The identities of moths from these areas, determined by isozyme analysis of short-term moth collections of one to three nights, are also given in Table 2.

Choristoneura fumiferana was previously known to occur through most of the boreal forest of eastern and central Canada (Harvey 1985). In the area south of Fort Nelson, we trapped moths south and west only to Moberly Lake and Pine Pass. This therefore appears to constitute the western limits of this species in northeastern British Columbia (Fig. 5). *Choristoneura fumiferana* moths have been trapped along the Mackenzie River north to Norman Wells, Northwest Territories, and up the Liard River into the Yukon Territory. Through northern Alberta and the Northwest Territories, *C. fumiferana* was the only species collected except at Chinchaga, Alberta, where other *Choristoneura* moths, perhaps from the pine-feeding group, were caught in the acetate-baited traps in 1988. *Choristoneura*

TABLE 2. Probable species of *Choristoneura* collected at various locations in a generally north to south arrangement. Adults were caught using two different lures in separate traps

			Characteristics*				
Trap location	Lat. and long.	Probable species	Pheromone	Aedeagi	Isozymes	Hosts	Life cycle
			Northwest Territories				
Fort Smith	60°00′N 111°55′N	*fumiferana*	Ald	—	—	*Abies*/*Picea*	
Hay River	61°50′N 115°49′W	*fumiferana*	Ald	—	—	*Abies*/*Picea*	
Fort Simpson	61°48′N 121°35′W	*fumiferana*	Ald	—	—	*Abies*/*Picea*	
Norman Wells	65°18′N 125°30′W	*fumiferana*	Ald	—	—	*Abies*/*Picea*	
			Yukon Territory				
Dawson City	64°7′N 139°18′W	*fumiferana* & *orae*	Ald	—	—	*Abies*/*Picea*	
			Ac	—	—	*Abies*/*Picea*	
Carmacks	62°6′N 136°18′W	*fumiferana* & *orae*	Ald	Sp	fum	*Abies*/*Picea*	
			Ac	—	west	*Abies*/*Picea*	
Beaver Creek	62°20′N 140°40′W	*orae*	Ac	—	west	*Abies*/*Picea*	
Haines Jct.	60°49′N 137°33′W	*biennis* & *orae*	Ald	Sp	west	*Abies*/*Picea*	
			Ac	Sp	west	*Abies*/*Picea*	
Whitehorse	60°43′N 135°04′W	*orae*	Ac	Sm	west	*Abies*/*Picea*	
Teslin	60°04′N 133°45′W	*orae*	Ac	Sm	west	*Abies*/*Picea*	
Ross River	62°01′N 132°25′W	*fumiferana* & *orae*	Ald	—	west	*Abies*/*Picea*	
			Ac	—	west	*Abies*/*Picea*	
Frances Lake	61°18′N 129°10′W	*fumiferana* & *orae*	Ald	—	—	*Abies*/*Picea*	
			Ac	—	—	*Abies*/*Picea*	
Swift River	60°01′N 131°15′W	*fumiferana* & *orae*	Ald	Sp	fum	*Abies*/*Picea*	
			Ac	Sm	west	*Abies*/*Picea*	
Watson Lake	60°02′N 128°45′W	*fumiferana* & *orae*	Ald	Sp	fum	*Abies*/*Picea*	
			Ac	Sm	west	*Abies*/*Picea*	
			Alaska				
Fairbanks	64°40′N 147°55′W	*fumiferana* & *orae*	Ald	—	—	*Abies*/*Picea*	
			Ac	—	—	*Abies*/*Picea*	
Salcha River	64°30′N 147°30′W	*fumiferana*	Ald	—	—	*Abies*/*Picea*	
Moon Lake	64°00′N 145°00′W	*fumiferana* & *orae*	Ald	—	—	*Abies*/*Picea*	
			Ac	—	—	*Abies*/*Picea*	
Tok	63°18′N 142°40′W	*fumiferana* & *orae*	Ald	Sp	fum	*Abies*/*Picea*	
			Ac	Sm	west	*Abies*/*Picea*	

TABLE 2. (*continued*)

Trap location	Lat. and long.	Probable species	Characteristics*				
			Pheromone	Aedeagi	Isozymes	Hosts	Life cycle
Tetlin	63°17′N 142°40′W	*fumiferana & orae*	Ald	—	—	*Abies*/*Picea*	
			Ac	—	—	*Abies*/*Picea*	
Honolulu Creek	63°00′N 149°30′W	*orae*	Ac	—	—	*Abies*/*Picea*	
Trapper Creek	62°15′N 150°15′W	*orae*	Ac	—	—	*Abies*/*Picea*	
Copper Center	61°58′N 145°24′W	*orae*	Ac	—	—	*Abies*/*Picea*	Some 2 year
Tiekel	61°10′N 145°09′W	*orae*	Ac	—	—	*Abies*/*Picea*	
Valdez	61°15′N 146°10′W	—	No *Choristoneura* caught				
Cordova	60°26′N 145°50′W	—	No *Choristoneura* caught				
Seward	60°06′N 149°28′W	*orae*	Ac	—	—	*Abies*/*Picea*	
Ninilchik	60°04′N 151°42′W	*orae*	Ac	—	—	*Abies*/*Picea*	
Homer	59°45′N 151°27′W	*orae*	Ac	—	—	*Abies*/*Picea*	
Skagway	59°30′N 138°18′W	*biennis*	Ald	Sm	—	*Abies*/*Picea*	
Juneau	58°18′N 134°20′W	*biennis*	Ald	Sm	—	*Abies*/*Picea*	
Petersburg	56°48′N 131°00′W	*biennis*	Ald	—	—	*Abies*/*Picea*	
Ketchikan	55°24′N 131°20′W	*biennis & orae*	Ald	Sm	—	*Abies*/*Picea*	
			Ac	—	—	*Abies*/*Picea*	
			Alberta				
Steen River	59°40′N 117°07′W	*fumiferana*	Ald	—	—	*Abies*/*Picea*	
Hutch Lake	58°43′N 117°13′W	*fumiferana*	Ald	—	—	*Abies*/*Picea*	
Chinchaga	58°42′N 118°41′W	*fumiferana* +?†	Ald	—	—	*Abies*/*Picea*	
			Ac	—	—	Lodgepole pine	
Fort McKay	57°12′N 111°66′W	*fumiferana*	Ald	—	—	*Abies*/*Picea*	
Fort McMurray	56°40′N 111°30′W	*fumiferana*	Ald	—	—	*Abies*/*Picea*	
Saddle Hills	55°22′N 119°30′W	*fumiferana*	Ald	—	—	*Abies*/*Picea*	
Grovedale	55°00′N 118°52′W	*fumiferana*	Ald	—	—	*Abies*/*Picea*	
Edmonton	53°33′N 113°13′W	*fumiferana*	Ald	—	—	*Abies*/*Picea*	
Lacombe	52°28′N 113°40′W	*fumiferana*	Ald	—	—	*Abies*/*Picea*	
Fiddle River	53°12′N 117°51′W	*biennis* &/or	Ald	—	—	*Abies*/*Picea*/*Pseudotsuga*	
		occidentalis &?	Ac	—	—	Lodgepole pine	
Sask. R. Crossing	52°12′N 117°10′W	*biennis* &?	Ald	—	—	*Abies*/*Picea*/*Pseudotsuga*	2 year
			Ac	—	—	Lodgepole pine	

TABLE 2. (*continued*)

Trap location	Lat. and long.	Probable species	Characteristics*				
			Pheromone	Aedeagi	Isozymes	Hosts	Life cycle
Canmore	51°05′N 115°20′W	*biennis* &/or	Ald	—	—	*Abies/Picea/Pseudotsuga*	
		occidentalis &?	Ac	—	—	Lodgepole pine	
Porcupine Hills	50°28′N 114°45′W	*biennis* &/or	Ald	—	—	*Abies/Picea/Pseudotsuga*	
		occidentalis &? or *lambertiana*	Ac	—	—	Lodgepole pine	
British Columbia							
Chilkat Pass	59°56′N 136°19′W	*biennis*	Ald	—	—	*Abies/Picea*	
Tutshi Lk.	60°12′N 134°20′W	*biennis* & *orae*	Ald	—	west	*Abies/Picea*	
			Ac	Sm	west	*Abies/Picea*	
Atlin	59°36′N 131°38′W	*biennis* & *orae*	Ald	—	—	*Abies/Picea*	
			Ac	Sm	—	*Abies/Picea*	
Boya Lake	59°23′N 129°05′W	*fumiferana* & *orae*	Ald	—	—	*Abies/Picea*	
			Ac	Sm	—	*Abies/Picea*	
Dease Lake	58°24′N 130°02′W	*fumiferana* & *orae*	Ald	—	—	*Abies/Picea*	
			Ac	—	—	*Abies/Picea*	
Stikine River	58°02′N 129°55′W	*biennis* &/or	Ald	—	—	*Abies/Picea*	
		fumiferana & *orae*	Ac	—	—	*Abies/Picea*	
Kinaskin Lake	57°32′N 130°17′W	*biennis* & *orae*	Ald	—	—	*Abies/Picea*	
			Ac	—	—	*Abies/Picea*	
Bell Irving II	56°49′N 129°42′W	*biennis* & *orae*	Ald	—	—	*Abies/Picea*	
			Ac	—	—	*Abies/Picea*	
Bell Irving I	56°24′N 129°15′W	*biennis* & *orae*	Ald	Sm	—	*Abies/Picea*	
			Ac	—	—	*Abies/Picea*	
Meziadin Lake	56°02′N 129°20′W	*biennis* & *orae*	Ald	—	—	*Abies/Picea*	
			Ac	—	—	*Abies/Picea*	
Stewart	55°54′N 130°00′W	*biennis* & *orae*	Ald	Sm	—	*Abies/Picea*	
			Ac	—	—	*Abies/Picea*	
Kispiox River	55°24′N 127°40′W	*biennis* & *orae*	Ald	—	—	*Abies/Picea*	
			Ac	—	—	*Abies/Picea*	
Terrace	54°24′N 128°28′W	*biennis* & *orae*	Ald	—	—	*Abies/Picea*	
			Ac	—	—	*Abies/Picea*	

TABLE 2. (*continued*)

Trap location	Lat. and long.	Probable species	Characteristics*				
			Pheromone	Aedeagi	Isozymes	Hosts	Life cycle
Onion Lake	54°20′N 128°25′W	*biennis* & *orae*	Ald	—	—	*Abies*/*Picea*	
			Ac	—	—	*Abies*/*Picea*	
Kitimat	54°02′N 128°37′W	*biennis* & *orae*	Ald	—	—	*Abies*/*Picea*	
			Ac	—	—	*Abies*/*Picea*	
Prince Rupert	54°21′N 130°15′W	*biennis* & *orae*	Ald	Sm	—	*Abies*/*Picea*	
			Ac	—	—	*Abies*/*Picea*	
Port Clements (QCI)	53°40′N 132°07′W	*biennis*	Ald	Sm	—	*Abies*/*Picea*	
Telkwa River	54°42′N 127°02′W	*biennis* & *orae*	Ald	—	—	*Abies*/*Picea*	
			Ac	—	—	*Abies*/*Picea*	
Morrice River	54°13′N 125°48′W	*biennis* & *orae*	Ald	—	—	*Abies*/*Picea*	
			Ac	—	—	*Abies*/*Picea*	
Burns Lake	54°13′N 125°47′W	*biennis* & *orae*	Ald	—	—	*Abies*/*Picea*	
			Ac	—	—	*Abies*/*Picea*	
Smith River	59°54′N 126°15′W	*fumiferana* &?	Ald	Sm	fum	*Abies*/*Picea*	
			Ac	—	—	Lodgepole pine	
Fort Nelson	58°48′N 122°40′W	*fumiferana* &?	Ald	Sm	fum	*Abies*/*Picea*	
			Ac	—	west	Lodgepole pine	
Trutch	57°40′N 123°00′W	*fumiferana*	Ald	Sp	—	*Abies*/*Picea*	
Buckinghorse River	57°23′N 122°15′W	*fumiferana* &?	Ald	—	—	*Abies*/*Picea*	
			Ac	—	—	Lodgepole pine	
Moberly Lake	55°50′N 121°45′W	*fumiferana* &?	Ald	—	fum	*Abies*/*Picea*	
			Ac	—	west	Lodgepole pine	
Tumbler Ridge	55°08′N 121°00′W	*fumiferana* &?	Ald	Sp	—	*Abies*/*Picea*	
			Ac	—	—	Lodgepole pine	
Pine Pass	55°18′N 122°36′W	*biennis* & CPG‡	Ald	—	fum	*Abies*/*Picea*	
			Ac	—	west	Lodgepole pine	
Tudyah Lake	55°04′N 123°00′W	*biennis* & CPG	Ald	Sm	West	*Abies*/*Picea*	
			Ac	Sm	—	Lodgepole pine	
Bear Lake	54°29′N 122°38′W	*biennis* & CPG	Ald	Sm	—	*Abies*/*Picea*	
			Ac	Sm	west	Lodgepole pine	
Fort St. James	54°24′N 124°16′W	*biennis* & CPG	Ald	—	—	*Abies*/*Picea*	
		or *orae*	Ac	Sm	—	Lodgepole pine	
Purden Lake	54°05′N 122°19′W	*biennis*	Ald	—	—	*Abies*/*Picea*	

TABLE 2. *(continued)*

Trap location	Lat. and long.	Probable species	Characteristics*				
			Pheromone	Aedeagi	Isozymes	Hosts	Life cycle
Prince George	53°55′N 122°48′W	*biennis* & CPG	Ald	—	—	*Abies/Picea*	2 year
			Ac	—	—	Lodgepole pine	
Bowron River	53°47′N 121°55′W	*biennis*	Ald	—	—	*Abies/Picea*	2 year
Blackwater River	53°17′N 122°59′W	*biennis*	Ald	—	—	*Abies/Picea*	
Quesnel	52°58′N 122°29′W	*biennis* &/or *occidentalis*	Ald	—	—	*Abies/Picea/Pseudotsuga*	
Kleena Kleen	51°59′N 124°55′W	*occidentalis* &/or *biennis* &?	Ald	—	—	*Abies/Picea/Pseudotsuga*	
			Ac	—	—	Lodgepole pine	
Alexis Cr.	52°05′N 123°15′W	*occidentalis* &/or *biennis* &?	Ald	—	—	*Abies/Picea/Pseudotsuga*	
			Ac	—	—	Lodgepole pine	
Canim Lake	51°46′N 120°53′W	*biennis* &/or *occidentalis*	Ald	—	—	*Abies/Picea/Pseudotsuga*	2 year
Lac La Hache	51°50′N 121°28′W	*biennis* &/or *occidentalis*	Ald	—	—	*Abies/Picea/Pseudotsuga*	
Tete Jaune	52°55′N 119°30′W	*biennis* &/or *occidentalis* & CPG	Ald	Sm	—	*Abies/Picea/Pseudotsuga*	
			Ac	Sm	—	Lodgepole pine	
Adolph Cr.	52°33′N 119°25′W	*biennis*	Ald	—	—	*Abies/Picea*	2 year
Blue River	52°06′N 119°19′W	*biennis* &/or *occidentalis*	Ald	—	—	*Abies/Picea/Pseudotsuga*	
Clearwater	51°40′N 120°03′W	*occidentalis*	Ald	—	—	*Pseudotsuga*	
Barriere	51°11′N 120°04′W	*occidentalis*	Ald	—	—	*Pseudotsuga*	
Kamloops	50°39′N 120°17′W	*occidentalis*	Ald	—	—	*Pseudotsuga*	
Barnes lake	50°40′N 121°11′W	*occidentalis*	Ald	Sm	—	*Pseudotsuga*	
Pemberton	50°19′N 122°48′W	*occidentalis*	Ald	—	—	*Pseudotsuga*	
Port Hardy	50°43′N 127°30′W	—	No *Choristoneura* caught				
Campbell River	50°00′N 125°15′W	*occidentalis*	Ald	—	—	*Pseudotsuga*	
Gold River	49°41′N 126°07′W	*occidentalis*	Ald	—	—	*Pseudotsuga*	
Horne lake	49°34′N 124°36′W	?	Ac	Sm	—	Lodgepole pine	
Parksville	49°19′N 124°30′W	*occidentalis*	Ald	—	—	*Pseudotsuga*	
Jordon River	48°26′N 124°04′W	*occidentalis*	Ald	—	—	*Pseudotsuga*	
Vernon	50°16′N 119°15′W	*occidentalis*	Ald	—	—	*Pseudotsuga*	
Summerland	49°36′N 119°39′W	*occidentalis*	Ald	—	—	*Pseudotsuga*	

TABLE 2. *(concluded)*

Trap location	Lat. and long.	Probable species	Characteristics*				
			Pheromone	Aedeagi	Isozymes	Hosts	Life cycle
Oliver	49°11′N 119°31′W	*occidentalis* &	Ald	—	—	*Pseudotsuga*	
		lambertiana	Ac	—	—	Lodgepole pine	
Princeton	49°27′N 120°29′W	*occidentalis*	Ald	—	—	*Pseudotsuga*	
Greenwood	49°06′N 118°41′W	*occidentalis* &	Ald	—	—	*Pseudotsuga*	
		lambertiana	Ac	—	—	Lodgepole pine	
Grand Forks	49°02′N 118°26′W	*occidentalis* &	Ald	—	—	*Pseudotsuga*	
		lambertiana	Ac	—	—	Lodgepole pine	
Castlegar	49°19′N 117°40′W	*occidentalis* &	Ald	—	—	*Pseudotsuga*	
		lambertiana	Ac	—	—	Lodgepole pine	
Fruitvale	49°06′N 117°32′W	*occidentalis* &	Ald	—	—	*Pseudotsuga*	
		lambertiana	Ac	—	—	Lodgepole pine	
Burton	49°58′N 117°51′W	*occidentalis*	Ald	—	—	*Pseudotsuga*	
Creston	49°06′N 116°30′W	*occidentalis* &	Ald	—	—	*Pseudotsuga*	
		lambertiana	Ac	—	—	Lodgepole pine	
Yahk	49°04′N 116°02′W	*occidentalis* &	Ald	—	—	*Pseudotsuga*	
		lambertiana	Ac	—	—	Lodgepole pine	
Grassmere	49°06′N 115°03′W	*occidentalis*	Ald	—	—	*Pseudotsuga*	
Sparwood	49°40′N 114°46′W	*occidentalis*	Ald	—	—	*Pseudotsuga*	
Wasa	49°48′N 115°44′W	*occidentalis*	Ald	—	—	*Pseudotsuga*	
Invermere	50°30′N 116°02′W	*occidentalis* &	Ald	—	—	*Pseudotsuga*	
		lambertiana	Ac	—	—	Lodgepole pine	
N. White River	50°37′N 115°12′W	*biennis*	Ald	—	—	*Abies*/*Picea*	2 year
Golden	51°14′N 116°58′W	*occidentalis* or	Ald	—	—	*Abies*/*Picea*/*Pseudotsuga*	2 year
		biennis					
Revelstoke	51°00′N 118°20′W	*occidentalis*	Ald	—	—	*Pseudotsuga*	

*Characteristics: pheromone — (Ald) aldehyde, (Ac) acetate; aedeagus — (Sm) smooth, (Sp) spiculed; isoenzyme frequency characteristics of — (fum) *C. fumiferana* and (west) western species; hosts present in the area — (*Abies*) true firs, (*Picea*) spruce, (*Pseudotsuga*) Douglas-fir, lodgepole pine; life cycle — two-year life cycle (2 year) determined by rearing young larvae.

† Undescribed species responding to the acetate lure.

‡ Population of undetermined relationship to *C. pinus* and *C. lambertiana*.

fumiferana was also found westward onto the Liard Plain (Watson Lake, Yukon Territory), and the Cassiar Mountains (Swift River, British Columbia), northwest to Frances Lake and the Pelly and lower Yukon River valleys of the Yukon Territory and in the Tanana Valley of east-central Alaska. Isozyme studies confirmed its presence at many of these locations (Table 2). It was not found in the southwestern Yukon Territory around Whitehorse, Teslin, or Haines Junction, or south of the Alaska Range of mountains which runs east–west through central Alaska. Large numbers of moths were caught in traps over a wide area in northern British Columbia in 1989, indicating possible widespread dispersal from an outbreak around Fort Nelson, British Columbia, and the lower Laird River Valley. No defoliation was evident and no moths were recovered in subsequent years in the areas where these dispersed moths were trapped.

At Smith River, Liard River, Fort Nelson, Moberly Lake, Fisher Creek, and Link Creek in northeastern British Columbia, *C. fumiferana* was probably the most common species present, as demonstrated by the isozyme characteristics of larval collections and by an average 62% of moths with one or more spicules which were caught in aldehyde-baited traps. The identity of moths caught in acetate traps is less clear. Most individuals of both eastern species (*C. fumiferana* and *C. pinus*) have spicules. Therefore the absence of spicules on the aedeagus of 76% of the moths and the isozyme patterns indicated that moths from acetate traps were not *C. pinus*. Their light and ochreous-colored forewings indicated that they were not *C. orae* but were more closely related to the pine-feeding populations in the area (Gray and Gries 1993).

Originally *C. orae* had only been found around Terrace and Kitimat, British Columbia, but through pheromone trapping and isozyme studies we have determined that this species occurs from Telkwa to Prince Rupert and north through the passes in the rain shadow east of the Coast Mountains to Dease and Boya lakes, British Columbia, and then into the Yukon Territory and Alaska (Fig. 2). The capability of a second diapause probably enables this species to survive in these cool passes (Harvey 1985; Harvey and Stehr 1967). Short-term trapping over a period of 2 weeks in 1987 indicated the flight of *C. orae* at Carmacks and several other locations was earlier than that of *C. fumiferana*. At Whitehorse, Beaver Creek, and Teslin, Yukon Territory, the acetate-responding *C. orae* was the only species collected. No evidence of this species was found east of Watson Lake, Yukon Territory. No trapping was carried out in the Alaska portion of the Yukon River Valley but both *C. orae* and *C. fumiferana* would be expected to be present because of the continuity of forests with the Tanana River Valley and because these species were trapped in the Yukon River Valley further eastward in the Yukon Territory. No trapping has been carried out west of Fairbanks, Alaska. *Choristoneura orae* was the only species found south of the Alaska Range and an intense outbreak has occurred in the Copper River Valley (U.S. Forest Service 1983). No moths of any species were trapped from Valdez to Cordova in the coastal forest south of the Chugach Mountains, probably indicating that there are no *Choristoneura* population connections along the intermittent coastal forest extending to southeast Alaska. Large numbers of *C. orae* moths were caught in the Copper River Valley in 1987 and at various places in 1989 but not in 1988 or 1990, indicating that a 2-year cycle may be involved. Larval rearings from this area confirmed the species as *C. orae*.

Choristoneura biennis occurs in ecologically specific high-elevation stands in southeastern British Columbia (Shepherd 1959) and is known to occur in the Rocky Mountains from Jasper National Park south to the Canada–USA border (Fig. 3). It was widespread in the *Abies*/*Picea* forests from Prince George to Prince Rupert. East of the Coast Mountains it has been found north as far as the Stikine River. West of these mountains it has been found at Ketchikan, Juneau, and Skagway and in the Chilkoot and White passes leading north from southeast Alaska to Haines Junction, Yukon Territory. Identifications at most of these locations have been confirmed through aedeagi studies. This species may occur on the

https://doi.org/10.4039/Ent127813-6 Published online by Cambridge University Press

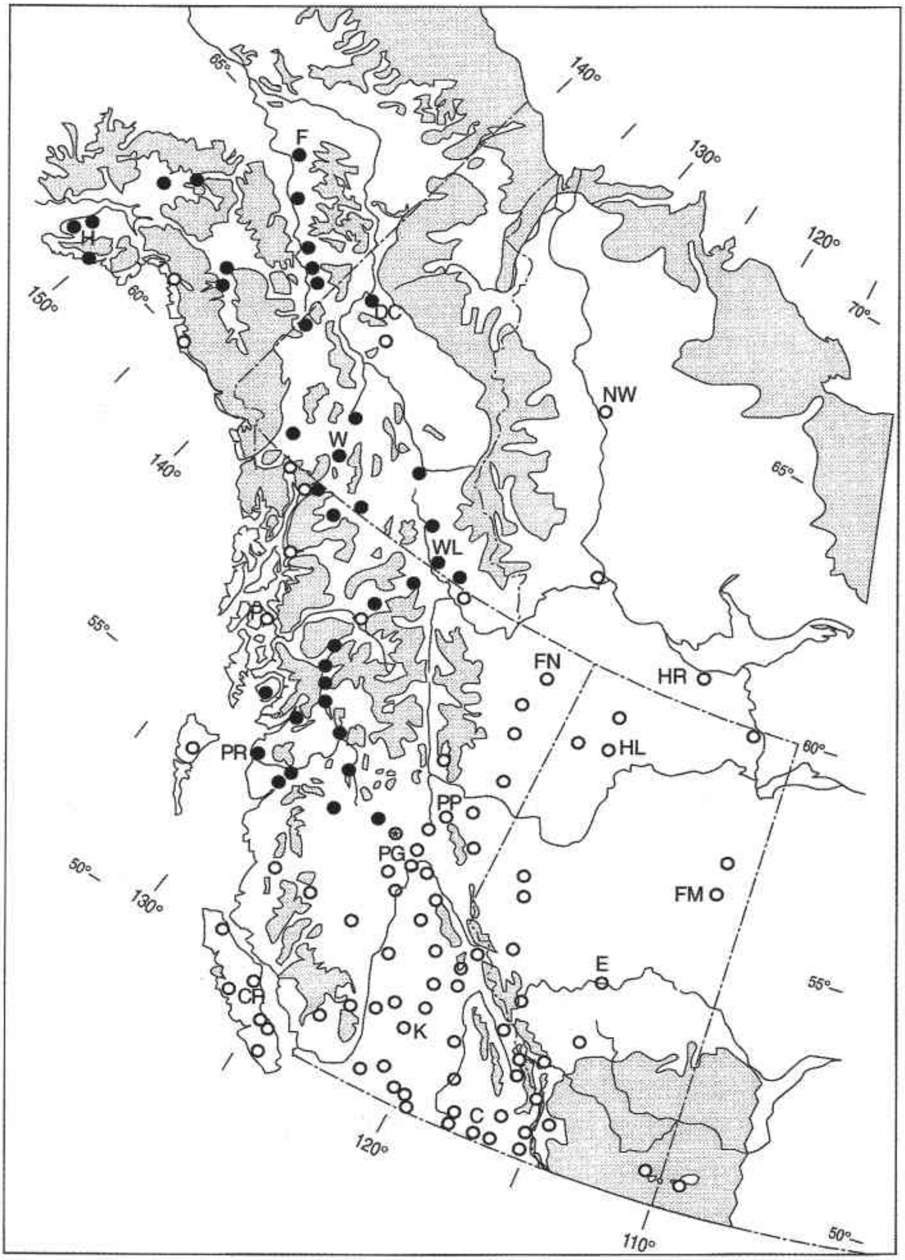

FIG. 2. Distribution of *Choristoneura orae* as determined from pheromone trap catches, larval collections and rearings, and isozyme analyses. Locations of positive collections are indicated by black dots and locations of negative collections by open circles. Areas lacking suitable conifer hosts are indicated by stippling. Selected locations are indicated by first letters: C, Creston; CR, Campbell River; DC, Dawson Creek; E, Edmonton; F, Fairbanks; FM, Fort McMurray; FN, Fort Nelson; H, Homer; HL, High Level; HR, Hay River; K, Kamloops; NW, Norman Wells; P, Petersburg; PG, Prince George; PP, Pine Pass; PR, Prince Rupert; W, Whitehorse; WL, Watson Lake.

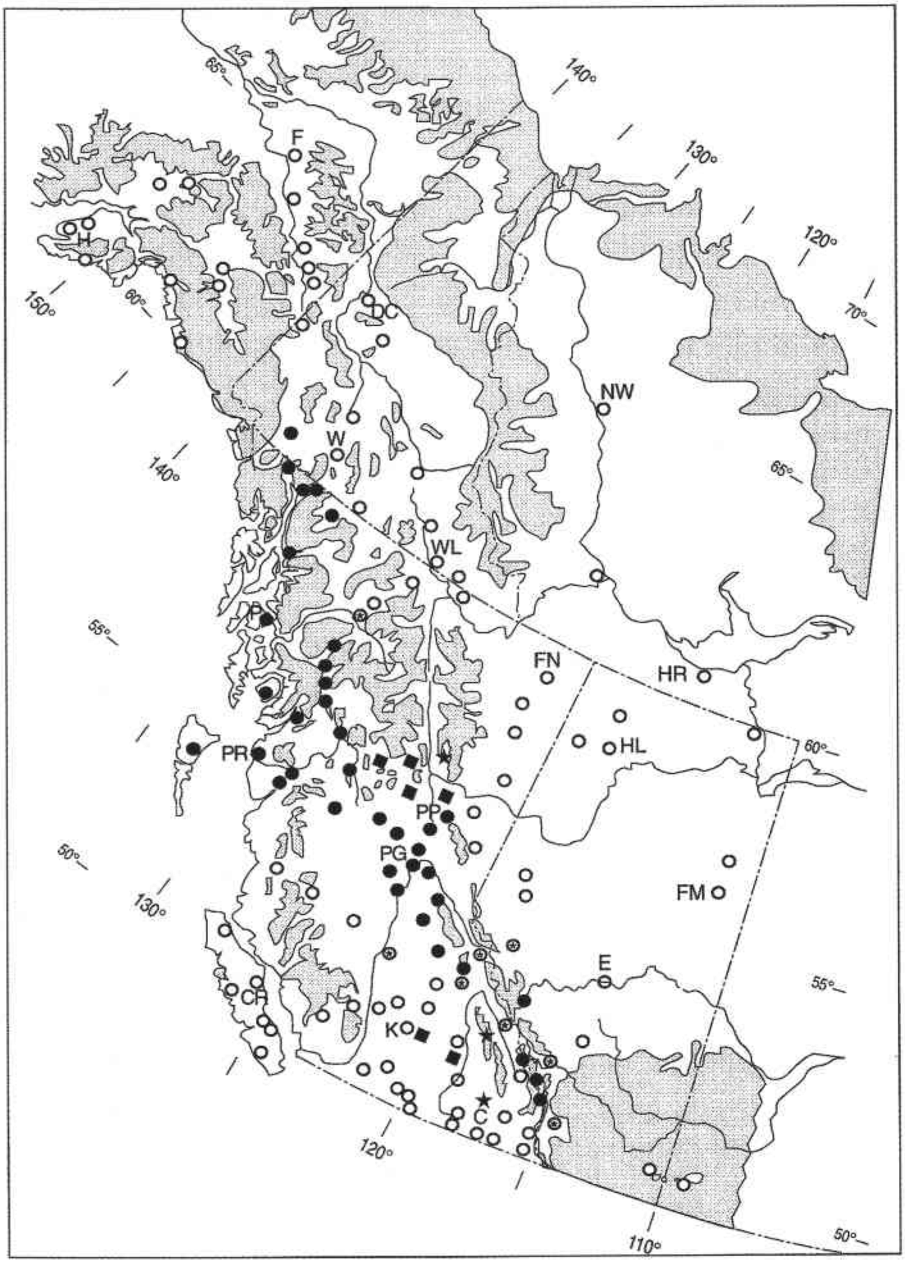

FIG. 3. Distribution of *Choristoneura biennis* as determined from pheromone trap catches, larval collections and rearings, and isozyme analyses. The locations of positive collections where the majority of adults emerged on even-numbered years are indicated by black dots, those where the majority of adults emerged on odd-numbered years are indicated by black stars, and locations of negative collections are indicated by open circles. Additional areas where pheromone traps have not been used but the species is known because outbreaks have occurred and larvae were reared for identification (Unger 1984) are identified by black squares. Areas where *C. occidentalis* could not be distinguished from *C. biennis* are indicated by an asterisk inside a circle. Areas lacking suitable coniferous hosts are indicated by stippling. Locality symbols are explained in the caption for Fig. 2.

islands of southeast Alaska as well, because it has been trapped on the Queen Charlotte Islands of British Columbia. Presumably the presence of a second diapause allows this species to survive in this cool climate.

Within a watershed, the 2-year cycle populations of *C. biennis* are synchronized, with most adults appearing in 1 year and only a few in the 2nd year. Throughout most of its range, *C. biennis* adults emerge in the even-numbered years, but in the Selkirk Mountains between the Columbia Trench and the Duncan-Kootenay Lakes Valley, adults emerge in the odd-numbered years. In addition, a population has been reported in the Ospika Valley northeast of Williston Lake, British Columbia, with adults appearing in the odd-numbered years (Turnquist and Ferris 1989); this is the only population found to do so within the Rocky Mountains. At Juneau, Alaska, a moderate number of moths of *C. biennis* was trapped every year from 1981 to 1986 indicating possible overlapping generations, but no larvae have been collected.

Choristoneura occidentalis has been found throughout the range of Douglas-fir east of the Coast Mountains (Fig. 4). This may include populations found in remnant Douglas-fir forests east of the Rocky Mountains but separation from *C. biennis* is difficult. On Vancouver Island it was found as far north as Campbell River and Gold River and to a similar latitude on the mainland coast.

Isozyme characteristics indicated the presence of two species of males in aldehyde traps at Link Creek, British Columbia. This result suggested a small area of sympatry of *C. fumiferana* and *C. biennis* east of Pine Pass, British Columbia, where the ranges are known to be close. Alternatively, the results at Link Creek could be explained by a flight of one or both species into the trapping area. Nevertheless, at Link Creek the presence of rare AAT-1 genotypes, and of higher frequencies of some other alleles than occurred in the samples of *C. fumiferana* from two nearby locations (Fisher Creek and Moberly Lake, British Columbia), suggests possible hybridization. Little is known of the extent of the area of sympatry or the degree of failure of reproductive isolation between the two species. However, there were no deviations from expected isozyme frequencies (AAT-1) among all the other collections, either in areas of possible sympatry or in areas where species were clearly separated; hence we must conclude that between these two species, hybridization, if it occurs, is not common. *Choristoneura fumiferana* and *C. biennis* both respond to the aldehyde lure so their reproductive isolation cannot be explained on that basis; the phenological and genetically fixed diapause differences probably contribute to their continued separation.

These studies indicated that a substantial area of sympatry of two *Choristoneura* species, *C. fumiferana* and *C. orae*, exists in the Yukon Territory and Alaska. Similarly, on the west slopes of the Cariboo Mountains, *C. occidentalis* and *C. biennis* merge in a mixed forest of *Abies*, *Picea*, and *Pseudotsuga*; generally these two species are separated by their biology, host, and habitat. It is not known if intermediates occur in these areas of convergence, but there was no evidence in the isozyme frequencies of any hybridization. Evidence is also presented for the sympatry of *C. orae* and *C. biennis* in west-central British Columbia and in southwestern Yukon Territory, and of both *C. fumiferana* and *C. biennis* with undescribed acetate-responding populations from Fort Nelson to south of Prince George. Reproductive isolation between *C. fumiferana* and *C. orae* and between *C. biennis* and *C. orae* in the areas of sympatry can be explained by pheromone differences.

Acetate-responding *Choristoneura*, distinct from *C. orae*, that resemble *C. lambertiana* (Bsk.) are found over most of British Columbia east of the Coast Mountains, through the lower Fraser Valley, and on eastern Vancouver Island. Two new entities have been discovered on *Pinus* sp. (Gray and Slessor 1989; Gray and Gries 1993) as well as *C. lambertiana* which occurs on *Pinus contorta*. The species interrelationships and distributions of this group have yet to be determined.

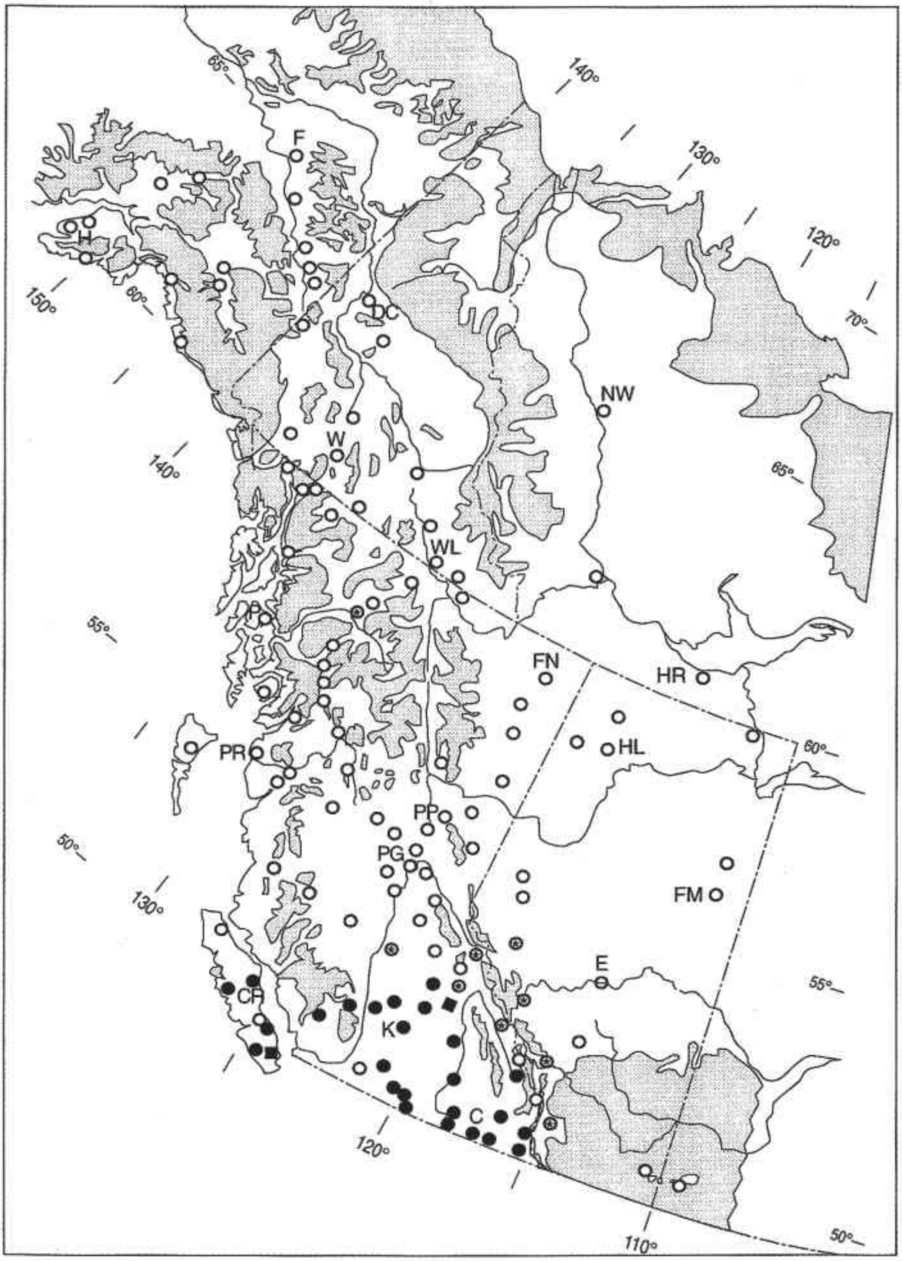

FIG. 4. Distribution of *Choristoneura occidentalis* as determined from pheromone trap catches, larval collections and rearings, and isozyme analyses. Locations of positive collections are indicated by black dots and locations of negative collections by open circles. Additional areas where pheromone traps have not been used but the species is known because outbreaks have occurred and larvae were reared for identification (Harris et al. 1985) are indicated by black squares. Areas where *C. occidentalis* could not be distinguished from *C. biennis* are indicated by an asterisk inside a circle. Areas lacking suitable coniferous hosts are indicated by stippling. Locality symbols are explained in the caption for Fig. 2.

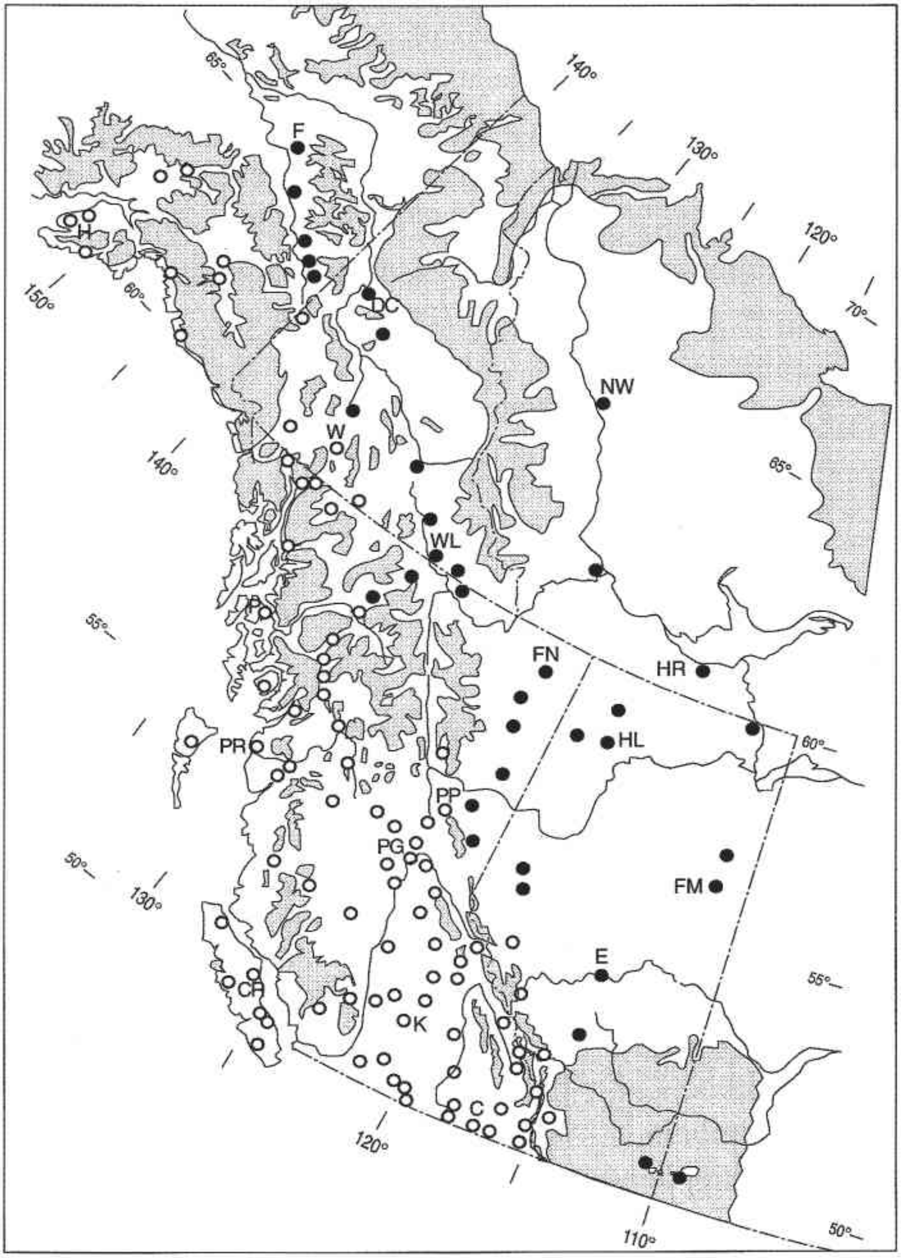

FIG. 5. Distribution of *Choristoneura fumiferana* as determined from pheromone trap catches, larval collections and rearings, and isozyme analyses. Locations of positive collections are indicated by black dots and locations of negative collections by open circles. Areas lacking suitable conifer hosts are indicated by stippling. Locality symbols are explained in the caption for Fig. 2.

The species distributions indicated by the results of this study represent large extensions of range to those previously known (Fig. 1) (Stehr 1967) and give considerably more detail of occurrence in many areas. Although these results improve our understanding of the distribution, ecology, and interrelationships among the *Choristoneura*, there are still important questions that will require further study. The techniques and findings of Harvey (1996) and Sperling and Hickey (1995) are an attempt to further identify populations and their DNA characteristics to enable us to understand the dynamics of gene flow and divergence and/or coalescence of *Choristoneura* populations. It appears that the *Choristoneura* in northwestern North America are highly variable and mobile and the speciation process is rapidly proceeding. The resolution and understanding of this process would be of great significance for science and the management of our forests.

Acknowledgments

Many people aided in the collection of data through pheromone trapping and larval collections. The Forest Insect and Disease Survey of the Canadian Forest Service in the Pacific and Yukon Region, Northwest Region, and Ontario Region contributed greatly. Similarly, R.A. Werner, E.H. Holsten, and A. Eglitis, USDA Forest Service, Alaska, provided trapping data and larval collections. P. Roden, Canadian Forest Service, Ontario Region, carried out the electrophoresis analysis.

References

Cory, H.T., G.E. Daterman, G.D. Daves, Jr., L.L. Sower, R.F. Shepherd, and C.J. Sanders. 1982. Chemistry and field evaluation of the sex pheromone of western spruce budworm, *Choristoneura occidentalis*, Freeman. *Journal of Chemical Ecology* **8**: 339–350.

Dang, P.T. 1985. Key to adult males of conifer-feeding species of *Choristoneura* Lederer (Lepidoptera: Tortricidae) in Canada and Alaska. *The Canadian Entomologist* **117**: 1–5.

——— 1992. Morphological study of male genitalia with phylogenetic inference of *Choristoneura* Lederer (Lepidoptera: Tortricidae). *The Canadian Entomologist* **124**: 7–48.

Daterman, G.E. 1974. Synthetic Sex Pheromones for Detection Survey of European Pine Shoot Moth. *USDA Forest Service Research Paper* **PNW-180**: 12 pp.

Freeman, T.N. 1967. On coniferophagous species of *Choristoneura* (Lepidoptera: Tortricidae) in North America. I. Some new forms of *Choristoneura* allied to *C. fumiferana*. *The Canadian Entomologist* **99**: 449–455.

Gray, T.G., and G. Gries. 1993. Sex pheromone components of an undescribed *Choristoneura* species (Lepidoptera: Tortricidae) on lodgepole pine in British Columbia. *Journal of the Entomological Society of British Columbia* **90**: 13–18.

Gray, T.G., R.F. Shepherd, and G.T. Harvey. 1995. Incidence of spicules on the aedeagi of *Choristoneura fumiferana*, *C. biennis* and *C.* unidentified species (Lepidoptera: Tortricidae). *The Canadian Entomologist* **127**: 161–166.

Gray, T.G., and K.N. Slessor. 1989. Morphology, life history and identification of sex pheromone components of an undescribed species of *Choristoneura* (Lepidoptera: Tortricidae) on Scots pine in British Columbia. *Journal of the Entomological Society of British Columbia* **86**: 39–47.

Gray, T.G., K.N. Slessor, G.G. Grant, R.F. Shepherd, E.H. Holsten, and A.S. Tracey. 1984. Identification and field testing of pheromone components of *Choristoneura orae* (Lepidoptera: Tortricidae). *The Canadian Entomologist* **116**: 51–56.

Harris, J.W.E., R.I. Alfaro, A.F. Dawson, and R.G. Brown. 1985. The Western Spruce Budworm in British Columbia 1909–1983. *Canadian Forestry Service, Pacific Forest Research Centre, Information Report* **BC-X-257**: 32 pp.

Harvey, G.T. 1985. The taxonomy of coniferophagous *Choristoneura* (Lepidoptera: Tortricidae): A review. pp. 16–59 *in* Sanders, C.J., R.W. Stark, E.J. Mullins, and J. Murphy (Eds.), Recent Advances in Spruce Budworm Research: Proceedings of the CANUSA Research Symposium, Bangor, Maine, Sept. 16–20, 1984.

——— 1996. Population genetics of the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae), in relation to geographical and population density differences. *The Canadian Entomologist* **128**. In press.

Harvey, G.T., and S.S. Sohi. 1985. Isozyme characterization of 28 cell lines from five insect species. *Canadian Journal of Zoology* **63**: 2270–2276.

Harvey, G.T., and G. Stehr. 1967. On coniferophagous species of *Choristoneura* (Lepidoptera: Tortricidae) in North America. III. Some characters of immature forms helpful in the identification of species. *The Canadian Entomologist* **99**: 464–481.

Powell, J.A. 1980. Nomenclature of Neararctic Conifer-Feeding *Choristoneura* (Lepidoptera: Tortricidae): Historical Review and Present Status. *USDA Forest Service General Technical Report* **PNW-100**: 18 pp.

Powell, J.A., and J.A. DeBenedictis. 1982. Taxonomic Relationships and Pheromone Isolations among Western Spruce Budworm Populations. Canada/US Spruce Budworms Program-West, Portland, OR. Final Report. 40 pp.

Sanders, C.J. 1978. Evaluation of sex attractant traps for monitoring spruce budworm populations (Lepidoptera: Tortricidae). *The Canadian Entomologist* **110**: 43–50.

Shepherd, R.F. 1959. Phytosociological and environmental characteristics of outbreak and non-outbreak areas of the two-year cycle spruce budworm, *Choristoneura fumiferana*. *Ecology* **40**(4): 608–620.

Sperling, F.A.H., and D.A. Hickey. 1995. Amplified mitochondrial DNA as a diagnostic marker for species of conifer-feeding *Choristoneura* (Lepidoptera: Tortricidae). *The Canadian Entomologist* **127**: 277–288.

Stehr, G.W. 1967. On coniferophagous species of *Choristoneura* (Lepidoptera: Tortricidae) in North America. II. Geographic distribution in accordance with forest regions. *The Canadian Entomologist* **99**: 456–463.

Stock, M.W., and P.J. Castrovillo. 1981. Genetic relationships among representative populations of five *Choristoneura* species: *C. occidentalis*, *C. retiniana*, *C. biennis*, *C. lambertiana* and *C. fumiferana* (Lepidoptera: Tortricidae). *The Canadian Entomologist* **113**: 857–865.

Swofford, D.L., and R.B. Selander. 1981. BIOSYS-1: A Fortran program for the comprehensive analysis of electrophoretic data in population genetics and systematics. *Journal of Heredity* **72**: 281–283.

Turnquist, R., and R. Ferris. 1989. Forest Insect and Disease Conditions, Prince George Region 1989. Forestry Canada, Pacific and Yukon Region, Victoria, B.C. 26 pp.

Unger, L.S. 1984. Two-year Cycle Spruce Budworm in British Columbia 1914–1982. *Canadian Forestry Service, Pacific Forest Research Centre, FIDS Report* **84-1**: 26 pp.

U.S. Forest Service. 1983. Forest Insect and Disease Conditions in Alaska (R-10), 1981–1982. *USDA Forest Service, Alaska Region, Anchorage, Report* **173**: 20 pp.

(Date received: 11 August 1994; date accepted: 30 May 1995)