Identification and ecological characterisation of *Choristoneura occidentalis* (Lepidoptera: Tortricidae) populations in southwestern Alberta, Canada

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Abstract—The western spruce budworm, *Choristoneura occidentalis* Freeman (Lepidoptera: Tortricidae), is an important pest of western North American coniferous forests, where its principal larval host is Rocky Mountain Douglas-fir, *Pseudotsuga menziesii* subspecies *glauca* (Beissner) Murray (Pinaceae). In southwestern Alberta, Canada, populations were recently discovered feeding on an unconventional host, an Engelmann spruce, *Picea engelmannii* Parry ex. Engelmann × white spruce, *Picea glauca* (Moench) Voss hybrid (Pinaceae), in a transition zone between the two major forest types characterised by these conifer species. We use molecular evidence to verify the species identity of outbreaking *Choristoneura* populations collected from Douglas-fir and hybrid spruces in southwestern Alberta in 2009, and characterise the larval and male moth phenology. Both mitochondrial and microsatellite markers confirmed these populations as *C. occidentalis*, but admixture with *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae) was detected in some individuals. Few differences associated with separate host trees were evident in the phenology of larvae and the flight period of male moths.

Résumé—La tordeuse occidentale de l'épinette, *Choristoneura occidentalis* Freeman (Lepidoptera: Tortricidae) est un ravageur important des forêts de conifères de l'Ouest de l'Amérique du Nord, où son hôte larvaire principal est le sapin bleu de Douglas, *Pseudotsuga menziesii* sous-espèce *glauca* (Beissner) Murray (Pinaceae). Dans le sud-ouest de l'Alberta, Canada, des populations ont récemment été observées en train de se nourrir sur un hôte inusité, un hybride de l'épinette d'Engelmann, *Picea engelmannii* Parry ex. Engelmann, x épinette blanche, *Picea glauca* (Moench) Voss (Pinaceae), dans une zone de transition entre les deux types majeurs de forêt caractérisés par ces espèces de conifères. Des données moléculaires nous ont servi à vérifier l'identité des espèces épidémiques de *Choristoneura* récoltées sur les sapins de Douglas et les épinettes hybrides dans le sud-ouest de l'Alberta en 2009 et à décrire la phénologie des larves et des papillons adultes mâles. Tant les marqueurs mitochondriaux que microsatellites confirment que ces populations sont des *C. occidentalis*, mais un mélange avec *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae) a été décelé chez certains individus. Il y a peu de différences dans la phénologie des larves et la période de vol des adultes en fonction des différents arbres-hôtes.

Introduction

The western spruce budworm (WSBW), *Choristoneura occidentalis* (Freeman) (Lepidoptera: Tortricidae), has become a forest pest species of concern in Alberta, Canada, due to its apparently recent presence within the province and its rapid population increase since initial detection. Defoliation of stands dominated by Douglas-fir, *Pseudotsuga menziesii* subspecies *glauca* (Beissner) Murray (Pinaceae), in the Porcupine Hills of southwestern Alberta was first documented in 2005 and the defoliator responsible was provisionally identified as WSBW (Sustainable Resource

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Development 2005). By 2008, over 20 000 ha of forest in and around the Porcupine Hills had moderate levels of defoliation (Sustainable Resource Development 2009). Populations of WSBW have also become established in neighbouring low elevation regions of Alberta where white spruce, *Picea glauca* (Moench) Voss (Pinaceae), and a recognised hybrid spruce, *Picea englemannii* Parry ex. Engelmann (Pinaceae) × *P. glauca*, are dominant conifers (Strong and Hills 2006). Strong and Hills (2006) referred to this hybrid as *Picea albertiana* Brown subspecies *ogilviei* Strong and Hills. However, it is unknown whether WSBW develops differently on its alternate hosts in this area, or whether hybrid spruce facilitates WSBW movement between Douglas-fir and non-Douglas-fir dominant forests.

The range of WSBW is largely congruent across western North America with that of Douglas-fir, its primary host (Stehr 1967; Harvey 1985). In Alberta, the Porcupine Hills have the most extensive Douglas-fir stands in the province and are the northeastern limit of the historical range of WSBW (Harvey 1985; Shepherd *et al.* 1995). However, southwestern Alberta is a putative hybrid zone between several budworm species (Shepherd *et al.* 1995; Lumley and Sperling 2011a), which puts the species identity of the outbreaking populations into question.

At least eight species comprise the spruce budworm (SBW), *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae) species complex (Harvey 1985; Volney and Fleming 2007; Lumley and Sperling 2010), and their ranges overlap in transitional regions between major forest types characterised by their coniferous hosts (Stehr 1967; Volney and Fleming 2007). In Alberta, the range of SBW extends across the northern boreal forest, where white spruce is dominant, and southward along the foothills where it contacts WSBW (Lumley and Sperling 2011a). Isolated populations of these two species also occur in the Cypress Hills, on the boundary between Alberta and Saskatchewan (Lumley and Sperling 2011b). A third species, the two-year cycle budworm, *Choristoneura biennis* Freeman (Lepidoptera: Tortricidae), feeds on Engelmann spruce and subalpine fir, *Abies lasiocarpa* (Hooker) Nuttall (Pinaceae). It contacts the ranges of both SBW and WSBW (Stehr 1967), but is separated from them by the

occurrence of its primary hosts at higher elevations and its obligatory second diapause during the fourth larval instar (Harvey 1967; Nealis 2005). At least two pine-feeding species, *Choristoneura pinus* Freeman and *Choristoneura lambertiana* (Busck) (Lepidoptera: Tortricidae) also occur in parts of central and southern Alberta.

Since SBW species display significant phenological synchrony with their hosts (Volney and Cerezke 1992), which is reinforced by selection on extensive variation in the timing of post-diapause larval emergence of overwintered second instar larvae (Volney *et al.* 1983; Thomson *et al.* 1984; Shepherd 1985), developmental differences can be expected to result from any establishment on alternative hosts with different phenological schedules. This may be more pronounced in areas with hybrid populations, where selection on such traits can be elevated relative to pure populations (Volney *et al.* 1983). In our study, we compare the timing of the development on Douglas-fir and hybrid spruce by *Choristoneura* populations responsible for the recent outbreak in southwestern Alberta, and we use a combination of molecular techniques to determine their species identity.

Materials and methods

Study sites and sampling design

Choristoneura larvae, pupae, and adults were sampled at five locations in the Crowsnest Pass region of southwestern Alberta (Fig. 1). Two 45 cm branch tips were pruned from the mid-crown of a single Douglas-fir or hybrid spruce tree at each location, with sampling occurring between 20 May and 8 August 2009 at 8–10-day intervals. Species identity of the trees was determined using seed cone morphology (Farrar 1995; Strong and Hills 2006). All larval instars were collected into 95% ethanol and were delimited by measuring head capsule width to the nearest 10 μm and developing instar separation criteria using the program HCAP (Logan *et al.* 1998). Pupae were collected live and reared to eclosion. Average observed instar ($AI_{obs} = \sum p_{ii}$ where p_i is the proportion of WSBW in each instar i [Lysyk 1988]) was calculated for each site and tree species and sampling date. Adult flight period was monitored between 12 July and 30 September 2009 by
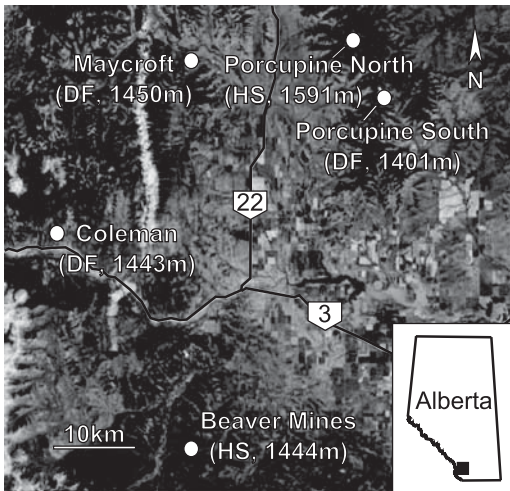
deploying two Multi-Pher I insect traps (Services Bio-Contrôle, Ste-Foy, Québec, Canada) with eastern SBW flex lures (Contech, Victoria, British Columbia, Canada) and Vaportape II[TM] (Hercon, Emigsville, Pennsylvania, United States of America) at each site. Cumulative proportion of male moth trap catch throughout the flight period was arcsine square-root transformed to approach normality. The effects of tree species and site on the relationship between AI_{obs} and day of year, and transformed cumulative proportion of male moths and day of year, were tested using general linear models testing the homogeneity of slopes, *e.g.*, AI_{obs} = day of year + site + day of year × site in R 2.15.1 (R Development Core Team 2012).

Budworm species identity

To verify the species identity of budworms at each site, we used two types of molecular markers: mitochondrial (mt) DNA and microsatellites. We sequenced a 470 bp region of the cytochrome oxidase I (*coI*) mt gene in 41 adults (eight to nine specimens per location) using the methods of Sperling and Hickey (1994) and Lumley and Sperling (2010). Four adults collected at pheromone traps and four to five reared from larvae were used. Their *coI* sequences were

then related to 169 previously published *coI* haplotypes (Sperling and Hickey 1994; Roe and Sperling 2007; Lumley and Sperling 2010, 2011a, 2011b), using maximum parsimony and likelihood as in Lumley and Sperling (2011a).

For microsatellites, we genotyped each of the 41 individuals at eight previously published loci (Lumley *et al.* 2009) and analysed the data as in Lumley and Sperling (2011a, 2011b) using *structure* v2.3.2 (Pritchard *et al.* 2000). Data for the 1135 specimens of Lumley and Sperling (2011a), encompassing all known North American SBW species, was used to train the admixture model with locations. Genotypes for the 41 new southwestern Alberta specimens were then used to infer assignment probabilities for each of six previously defined populations, corresponding to *C. fumiferana*, Western A, Western B, *C. lambertiana*, *C. pinus*, and *Choristoneura retiniana* genetic clusters (Lumley and Sperling 2011a).

Results

A total of 698 larvae, 149 pupae, and 7189 male moths were collected over 132 days (18 sampling times; Table 1). Larval abundance was highest at Beaver Mines and lowest at Porcupine South, Alberta with 239 and 104 larvae/pupae collected in total from each site, respectively (Table 1). The average observed instar (AI_{obs}) at each sampling time and site is shown in Figure 2 along with the cumulative proportion of male moths throughout the flight period at each location. The relationship between AI_{obs} and ordinal date did not differ significantly among sites ($F_{4,32} = 0.2856$; $P = 0.8851$) or hosts ($F_{1,38} = 1.223$; $P = 0.2758$).

Male moth abundance was highest at Coleman (2553 moths) and lowest at Porcupine South (870 moths; Table 1). However, when abundance is represented as the cumulative proportion of moths relative to the total caught per site to account for potential differences in population size (Fig. 2), there are no significant differences in the relationship between male moth flight phenology and ordinal date between sites ($F_{4,35} = 0.3981$; $P = 0.8086$) or hosts ($F_{1,41} = 0.3533$; $P = 0.5555$).

Species identity

Maximum parsimony and likelihood analyses of new mtDNA sequences combined with

Table 1. Sample size of larval/pupal and adult (male) *Choristoneura* collections by ordinal date.

Day	Beaver Mines	Coleman	Maycroft	Porcupine North	Porcupine South
140/141	0	2	0	0	0
148	14	9	9	0	6
157	10	14	33	0	1
166	78	17	19	15	12
175	47	12	30	24	12
184	23	19	51	24	16
193	29	21	25	20	19
201/202	22 (42)	31 (107)	28 (29)	25 (12)	18 (9)
211	16 (115)	17 (249)	26 (100)	14 (116)	14 (63)
220	350	5 (548)	8 (248)	6 (193)	6 (105)
229	478	624	261	161	253
238	351	845	265	447	345
246	46	103	53	371	79
255	13	47	6	53	4
264	5	11	27	10	8
273	0	9	23	1	4
Immatures	239	147	229	128	104
Adults	1400	2543	1012	1364	870
Total	1639	2690	1241	1492	974

Note: Parentheses denote adult collections that occurred concurrently with larval collections.

Fig. 2. Developmental progression of *Choristoneura* populations at five sites in southwestern Alberta, Canada. Left side shows observed average instar for each site and the regression line for all sites combined, with two to six for larval instars and seven for pupae. Right side shows arcsine square-root transformed cumulative proportion of male moth abundance per collection date at each site with the regression line for all sites combined. The right axis is presented back-transformed. Horizontal axis shows ordinal date.
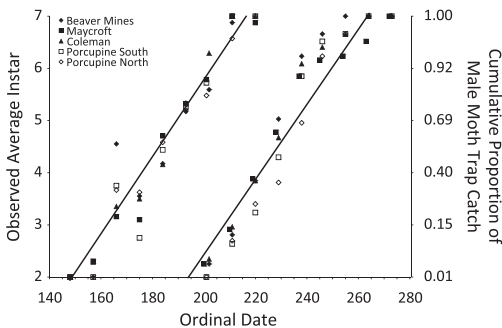
previously published haplotypes gave trees with very similar topologies and the same major lineages as in previous studies (Sperling and Hickey 1994; Lumley and Sperling 2010, 2011a, 2011b). Thirty-nine *o*-lineage and two *o*β-lineage *coI* haplotypes

were found among the 41 specimens from southwestern Alberta (Table 2). Three new haplotypes (o94, o95, and o96; GenBank accession numbers KC172836:KC172838) differed by at least 1 bp from known haplotypes. No *f*-lineage haplotypes, characteristic of *C. fumiferana*, were sampled at the five locations.

Microsatellite analyses were also congruent with previous work (Lumley and Sperling 2011a, 2011b). Each of the 41 specimens from southwestern Alberta was assigned to the previously known genetic clusters (Table 2). Most were assigned to Population 2 (Western A, $n = 26$) or Population 3 (Western B, $n = 12$) genetic clusters, with approximately equal numbers of reared and pheromone-trapped specimens included in each cluster. The three remaining individuals were assigned to Population 1 (*C. fumiferana*, $n = 3$), with two from Coleman (one reared on Douglas-fir and one pheromone-trapped) and one from Maycroft (pheromone-trapped). However, each of these three individuals had *o*-lineage mtDNA, and assignment probabilities to the Population 1 microsatellite cluster were not high (44%, 61%, and 72%). Although the Western A and B genetic clusters defined by Lumley and Sperling (2011a)

Table 2. *Choristoneura* collection site, method of collection (adult reared from larva or pheromone trapped), and combined genetic profile (microsatellite population/mtDNA *co1* haplotype (sample size)).

Site	Collection method	Combined genetic profile
Beaver Mines	Reared	2/b1(1), 2/o2(3), 3/o2(1)
Beaver Mines	Trapped	2/b1(1), 2/o5(1), 3/o1(1), 3/o2(1)
Coleman	Reared	1/b1(1), 2/b1(1), 2/o2(1), 2/o3(1),
Coleman	Trapped	1/o2(1), 2/oβ(1), 3/o2(2)
Maycroft	Reared	2/o1(1), 2/o2(1), 2/o94(1)*, 3/o11(1)
Maycroft	Trapped	1/o2(1), 2/o2(2), 2/o28(1)
Porcupine North	Reared	2/o2(1), 2/o95(1)*, 3/o2(2)
Porcupine North	Trapped	2/o1(1), 2/o5(1), 2/o41(1), 3/o11(1)
Porcupine South	Reared	2/oβ(1), 2/b1(1), 3/o2(2)
Porcupine South	Trapped	2/o1(1), 2/o2(1), 2/o28(1), 3/o96(1)*

Note: Previously named haplotypes are as in Sperling and Hickey (1994) and Lumley and Sperling (2010, 2011a, 2011b).

*New mtDNA *co1* haplotypes, Genbank accession numbers KC172836:KC172838.

mtDNA, mitochondrial DNA; *coI*, cytochrome oxidase I.

contained species in addition to *C. occidentalis* that are potentially present in southwestern Alberta, none of our larval specimens exhibited the second diapause characteristic of *C. biennis*, nor were any larvae taken from pines or adults from the pheromone lures normally associated with *C. lambertiana* (Harvey 1985).

Discussion

DNA evidence as well as life history traits (lack of second diapause and type of pheromone attraction), indicate that the *Choristoneura* populations responsible for severe defoliation of coniferous forests in southwestern Alberta are best identified as WSBW. Although the presence of this species in Alberta is not new (Harvey 1985; Shepherd *et al.* 1995), it does represent the first major outbreak of WSBW in the province (Sustainable Resource Development 2007). Aerial surveys conducted concurrently with the work described in this study estimated more than 30 000 ha of forest with moderate to severe levels of defoliation in the Porcupine Hills and surrounding areas (Sustainable Resource Development 2010). This outbreak declined precipitously to just 2900 ha in 2010 (Sustainable Resource Development 2011), but larval populations remain high in restricted areas on Douglas-fir and hybrid spruce.

Our study is also the first report of WSBW feeding freely as larvae on an unconventional conifer host, hybrid spruce, within the province. However, feeding on this alternative host to Douglas-fir had no apparent impact on rate of development. We failed to find any significant effect of site or host on the relationship between AI_{obs} and ordinal date. Second instar larvae were first observed in late May (day 140). Late instar larvae and pupae were found up to the date of the last larval collection at the beginning of August (day 220). Similarly, the cumulative proportion of male moths caught throughout the sampling period did not differ between sites or hosts. Male moths were first observed on 21 July (day 201), but may have been present as early as 12 July (day 193) when the pheromone traps were first deployed and pupae were first observed. Peak densities of male moths were observed between 17 and 26 August (days 229–238) and moths were still present in low densities at four of the five sites at the end of September (day 273).

The use of hybrid spruce as a larval host by WSBW is not unexpected, since the patchy landscape of the cordilleran region of western North America may predispose WSBW populations to tolerate variation in host-tree species (Volney 1985). In fact, WSBW are known to feed on firs, Douglas-fir and spruces (Fellin and Dewey 1982; Sanders 1991), in addition to one other white spruce × Engelmann spruce hybrid, which has long been identified as a host for budworms located in the hybrid zone between white spruce and Engelmann spruce (Stehr 1967).

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However, oviposition preferences by gravid females suggest that firs and Douglas-fir are the favoured hosts (Leyva *et al.* 2000, 2003).

The relatively labile feeding behavior of WSBW raises the possibility that hybrid stands may facilitate budworm movement between stands of more favourable hosts. The "hybrid-bridge" hypothesis, for instance, proposes that hybrid host trees may act as physiological intermediates between parental plant species and allow sustained host-shifts by herbivores (Floate and Whitman 1993). A current example is the expansion of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae), onto Jack pine, *Pinus banksiana* Lambert (Pinaceae), in Alberta via hybrids between Jack pine and the closely related lodgepole pine, *Pinus contorta* Douglas (Pinaceae) (Cullingham *et al.* 2011). Although there is no evidence that WSBW is experiencing a similar host shift in southwest Alberta, it is noteworthy that its populations are surviving on hybrid spruces that not only bridge the region between boreal and montane forests along the eastern slopes of the Rocky Mountains, but also range far into Canada's interior (Strong and Hills 2006).

We also found evidence for hybridisation among WSBW and SBW in the populations surveyed. Although all 41 individuals analysed for microsatellite characteristics had some degree of admixture between the six predefined genetic clusters, three individuals were not assigned to genetic clusters associated with WSBW. Instead these three individuals were assigned to the genetic cluster associated with SBW. All individuals also had *o*- or *o*β-lineage haplotypes, indicating that hybridisation between these two species would have resulted from matings between male SBW and female WSBW. These results are highly concordant with recent reports of genetic introgression among budworm species whose ranges overlap in Alberta (Lumley and Sperling 2011a, 2011b). They are also supported by mating experiments that suggest introgression between WSBW and SBW may be most likely to occur via a male SBW, since egg weights from that combination are greater than the reciprocal cross (Harvey 1997). Previous studies have shown that hybrid populations can rapidly adapt to divergent developmental patterns of different host species (Volney *et al.* 1983; Volney 1999);

however, the survival rates of hybrids have not been examined for southwestern Alberta.

In summary, WSBW is successfully establishing itself at the edge of its range in southwestern Alberta. Populations on Douglas-fir and hybrid spruce in the Porcupine Hills and surrounding areas do not differ developmentally, at least at the scale of this study. Fine-scaled phenology models and within-site comparisons would shed light on the developmental consequences of different host associations, and should eventually benefit the management of these populations. Moreover, investigation of the genetic structure of the hybrid zone between WSBW and SBW, and any correlations with hybridisation between white spruce and Engelmann spruce, may provide useful insight into the evolutionary and ecological characteristics of the SBW species complex.

Acknowledgements

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