The balsam bark weevil, *Pissodes striatulus* (Coleoptera: Curculionidae): life history and occurrence in southern British Columbia

L.E. MACLAUCHLAN[1] AND J.E. BROOKS[2]

ABSTRACT

Subalpine fir (*Abies lasiocarpa* (Pinaceae)) forests in British Columbia (B.C.) are increasingly climate-stressed and vulnerable to pest damage. Following a drought in southern B.C., the balsam bark weevil, *Pissodes striatulus* (Coleoptera: Curculionidae), was observed attacking and killing mature subalpine fir trees. This study documents *P. striatulus* as a tree-killing insect, often associated with western balsam bark beetle (Coleoptera: Curculionidae), which is considered the most destructive insect pest of subalpine fir. In B.C., this weevil displays a one-year life history, overwintering as late-instar larvae in the bark and as newly emerged or older adults in the duff at the base of attacked trees. Attacked trees are difficult to identify until the tree becomes chlorotic and dies. Larvae may excavate diagnostic chip cocoons in the sapwood before pupating, but most complete their development in the phloem where their galleries quickly become obscured by woodborer activity and other insects. *Pissodes striatulus* was found at 71% of sites surveyed, and 19% of trees sampled were killed by the weevil acting as the primary invader. The weevil uses downed trees, slash, and susceptible live trees, is long lived, and can switch from primary to secondary attacker, demonstrating its capacity to adapt to available and changing conditions.

Key words: balsam bark weevil, *Pissodes striatulus*, subalpine fir, climate stress

INTRODUCTION

Over the past two decades, subalpine fir *Abies lasiocarpa* (Hook.) Nutt. (Pinaceae) mortality in British Columbia (B.C.) has increased due to insect attack, root disease, and climatic stress (Maclauchlan 2016). Much of this mortality is attributed to the western balsam bark beetle (WBBB), *Dryocoetes confusus* Swaine (Coleoptera: Curculionidae), largely considered the most destructive insect pest of subalpine fir and causing scattered mortality over large areas of high-elevation forests (Furniss and Carolin 1977; Stock 1991; Garbutt 1992; McMillin *et al.* 2003; Lalande *et al.* 2020). Although the primary mortality agent may be WBBB, there is little ground survey information on the incidence and impact of WBBB and other damaging agents in these sensitive and often remote high-elevation forests.

Subalpine fir ecosystems are threatened by climate extremes, pests, and increased harvesting (Reich *et al.* 2016; Lalande *et al.* 2020). These are extremely valuable forests due to their inherent hydrologic contribution (Winkler *et al.* 2017), carbon sequestration, and habitat attributes. Subalpine fir grows well at high elevations, from 600 to 2 250 metres, throughout most of the B.C. interior (Parish and Thomson 1994). In the mountains and plateaus of interior B.C., subalpine fir is often associated with spruce (Pinaceae) and is a major component of the interior high-elevation forests from Yukon, Canada, to Arizona, United States of America. Cool summers, cold winters, and a deep

[1] Ministry of Forests, Lands and Natural Resource Operations and Rural Development, 441 Columbia Street, Kamloops, B.C. V2C 2T3; Lorraine.maclauchlan@gov.bc.ca

[2] Forest Health Management, 466 Central Ave., Gibsons, B.C. V0N 1V1

snowpack are important in determining where subalpine fir grows well (Parish and Thomson 1994).

As more non-native insects establish and expand in B.C. and climate change increases in intensity, many forest insects and fungal pathogens, both native and non-native, are expected to expand their ranges northwards and to higher elevations and, with this expansion, bring more severe impacts to newly invaded areas (Bentz *et al.* 2010; Woods *et al.* 2010, 2017; Haughian *et al.* 2012). The expansion of mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae), well beyond its historic range into northern B.C., Yukon, and Northwest Territories (Safranyik *et al.* 2010), coupled with the beetle's extensive attack in young lodgepole pine (Maclauchlan *et al.* 2015), is a well-documented example of a native insect responding to the effects of climate change on both insect and host.

Another recent example of insect range expansion in B.C. is that of the balsam woolly adelgid, *Adelges piceae* (Ratzeburg) (Hemiptera: Adelgidae), an introduced insect from Europe. It was thought to be contained in a provincial quarantine zone on the B.C. coast until recent surveys (Zilahi-Balogh *et al.* 2016; Maclauchlan and Buxton 2018) confirmed its presence outside the pre-2014 quarantine zone, affecting subalpine fir throughout the southern interior and as far north as Horsefly in the B.C. Cariboo Region.

While conducting studies on WBBB in subalpine fir forests (Maclauchlan and Buxton 2016, 2017; Maclauchlan 2020), a weevil was observed attacking and killing live, mature subalpine fir trees, acting as a primary invader, much like tree-killing bark beetle species. The weevil was identified as the balsam bark weevil, *Pissodes striatulus* (Fabricius) (Coleoptera; Curculionidae) (Randall 1838; O'Brien and Thompson 1986). Most published records of this weevil are from eastern Canada, primarily Ontario, Quebec, and New Brunswick, and the northeastern United States of America, where reports have noted it infesting balsam fir, *Abies balsamea* (L.) Mill. (Pinaceae) that has been severely defoliated or killed by eastern spruce budworm, *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae) (Swaine *et al.* 1924; Craighead 1950; Belyea 1952a). In B.C., there are very few published records for *P. striatulus,* and it has typically been observed in association with WBBB. Little is known of the life history, host selection parameters, and habits of this weevil in B.C.

Swaine *et al.* (1924) considered *P. striatulus* to be the most aggressive of the insects that attacked dead and dying trees following eastern spruce budworm defoliation. According to his studies, the larvae were reported never to develop to maturity unless the tree was almost dead, and two or three successive attacks could be made on the same tree before the tree's resistance was low enough that weevil larvae could survive and mature to adulthood. Most observations from eastern forests describe *P. striatulus* as essentially a secondary insect (Craighead 1950). Secondary insects usually select hosts that have impaired defenses and avoid vigourous trees, whereas primary invaders attack and kill apparently vigourous trees through pheromone-mediated mass attacks. Early observations on the seasonal history of this weevil differ somewhat depending upon location (Swaine *et al.* 1924; Belyea 1952a, 1952b), suggesting it has a plastic life history and is able to adapt to local and seasonal climate. Belyea (1952a) observed full-grown larvae and pupae under the bark of infested trees in the Lake Nipigon area of Ontario, Canada, in late June, with adults emerging from late June through the middle of August, and the majority emerging in the last three weeks of July. They estimated development time to be just less than 12 months from egg to emergent adult in this area. Swaine *et al.* (1924), however, suggested a two-year life cycle, with the insects overwintering as adults and emerging from the duff in the spring to mate and lay their eggs. All studies found that the weevils preferred to oviposit on the lower fifth to lower half of their balsam fir host.

Other *Pissodes* species have similar host selection parameters to *P. striatulus*. *Pissodes nemorensis* Germar and *Pissodes schwarzi* Hopk., are attracted to boles, slash, and root collars of weakened, stressed, or dying trees (Finnegan 1958; United States Department of Agriculture Forest Service 1985; Atkinson *et al.* 1988; Maclauchlan *et al.*

1993). Host selection by *P. nemorensis* and *P. schwarzi* has been shown to be pheromone mediated (Fontaine and Foltz 1982; Maclauchlan *et al.* 1993), with *P. nemorensis* producing grandisol (cis-2-isopropenyl-l-methy1cyclobutaneethanol) and its corresponding aldehyde, grandisal, which act together as aggregation pheromones (Booth *et al.* 1983; Phillips *et al.* 1984; Phillips and Lanier 1986). *P. striatulus* may also use these pheromones and the smell of stressed trees to attract mates and aggregate on potential host trees.

The objectives of this study were to describe the occurrence, life history, and host preference of *P. striatulus* in susceptible stands of subalpine fir in southern British Columbia. Additionally, we aimed to determine the prevalence of *P. striatulus* attack in low-elevation, climate-stressed subalpine fir stands and its interaction with WBBB.

METHODS

Life history sampling and field observations. Three field sites were selected to study the life history of *P. striatulus* in southern B.C. A site located off the Spahats Creek Forest Service Road (51° 46' 25.18" N, 119° 45' 26.77" W; elevation: 1 600 m) northeast of Clearwater, B.C. in the Engelmann–Spruce–Subalpine Fir–Wet–Cold biogeoclimatic zone (ESSFwc) (Lloyd *et al.* 1990; Meidinger and Pojar 1991), and predominantly subalpine fir, was selected to collect observational data during the summers of 2015–2016. The other two sites, Watching Creek (50° 54' 23.64" N, 120° 26' 32.78" W; elevation: 1 375 m) and Antler Road (50° 52' 54.12" N, 120° 24' 39.96" W; elevation: 1 260 m) were located about 30 km northwest of Kamloops, B.C., on the west side of the North Thompson River. Both sites are situated in the Montane–Spruce–Dry–Mild biogeoclimatic subzone (MSdm). The Watching Creek site is composed of spruce, Douglas-fir, and subalpine fir. The Antler Road site is a mix of spruce and subalpine fir. From 2015 through 2017, both the Watching Creek and Antler Road sites had a high population of *P. striatulus*, and the sites were accessible throughout most of the year.

In 2016 through 2018, a total of 15 live, green subalpine fir trees that were newly mass attacked by *P. striatulus* at the Watching Creek and Antler Road sites were selected for twice-weekly life-stage sampling and observation (March–November). During field sampling, a ladder was used to access higher portions of the trees to collect bark samples, which were approximately 20 cm × 20 cm. Larvae and other life stages that were easily visible when the bark was removed were collected and placed into vials containing 70% ethanol (EtOH). Each remaining bark sample was placed in a sealable bag, labelled, and brought into the laboratory, where it was dissected to expose remaining life stages within one day of collection. All specimens were preserved in 70% EtOH for future measurement. Ten live adult weevils were collected and sent to L. Humble, Canadian Forest Service, Victoria, B.C., Canada, to confirm species identification. The following information was recorded at each field sampling: life stage(s) present; gallery description; timing of attack and oviposition; presence–absence of chip cocoons or exit holes; timing of adult emergence; and, bole and foliar symptoms of attacked trees. Adults collected during field sampling were frozen until measured. All life stage and field observations were compiled along a timeline to produce a lifetable for *P. striatulus* in southern B.C.

A Hobo™ U23-003 Pro v2 Temperature Data Logger, with 2 exterior sensors and a Hobo™ RSI Solar Radiation Shield (Onset Computer Corporation, Bourne, Massachussetts, United States of America; https://www.onsetcomp.com/) were set up at the Watching Creek and Antler Road sites to monitor daily minimum and maximum temperatures over a full year (January–December 2017). One temperature sensor was placed at ground level, and the second sensor was placed at 2.5 m on the north side of a tree situated inside the stand. Temperature records were downloaded to a laptop computer every two to three weeks. At the Watching Creek site, four 8-funnel Lindgren multiple-funnel traps (Lindgren 1983) were placed at 25-metre intervals throughout the stand. Two traps were baited with (±)-*exo*-brevicomin to monitor WBBB flight times, and two were baited with grandisal and grandisol (supplied by Synergy Semiochemicals Corp., Delta, British Columbia, Canada), to monitor the onset of *P. striatulus* flight. The traps were checked when life-stage sampling was conducted at the sites. Average daily maximum and minimum temperatures were compared to trap catches and life stage sampling data.

In addition to the periodic sampling of trees, five additional live, green subalpine fir trees mass attacked by *P. striatulus* at the Watching Creek and Antler Road sites were felled to assess attack over the entire length of the trees, to collect life stages, and to quantify successful weevil emergence (Table 1). Each time an emergence hole was counted, an X was marked over the hole in indelible marker to ensure a single count. Felled trees were cut into one-metre sections, with the cardinal direction marked and labelled according to position in the bole, and then transported to the laboratory, where the final count of emergence holes was done. The cut ends of all sample sections were sealed with paraffin wax to prevent desiccation; each section was covered in mesh screening and placed in a 20 °C environment chamber to allow any further emergence. The diameter of each one-metre tree section was measured and the bark surface area calculated. The length and position of each section was converted to reflect height on individual trees. The diameter of a sub-sample of exit holes was measured. The data were converted to the number of emergence holes per square metre of bark surface, and the frequency distribution of emergence density by tree height was calculated.

Table 1. List of subalpine fir trees felled to assess emergence and extent of attack on trees, noting year of attack, date felled, site (Watching Creek: 50° 54' 23.64" N, 120° 26' 32.78" W; elevation: 1 375 m; Antler Road: 50° 52' 54.12" N, 120° 24' 39.96" W; elevation: 1 260 m), and dates each tree was field sampled.

Attack year	Date felled	Site	Field sampling dates
2015	16 Sep. 2016	Watching Creek	Sep. – 1 Nov. 2016
2016	16 Nov. 2016	Watching Creek	No field sampling
2015	26 Apr. 2017	Watching Creek	6 Jun. – 6 Sep. 2016
2017	18 Jun. 2018	Antler Road	5 Jul. – 22 Nov. 2017[a]
2017	24 Aug. 2018	Antler Road	15 May – 24 Aug. 2018

[a] Observed undergoing mass attack by *P. striatulus* on 5 July 2017.

The head-capsule widths of each collected larva were measured at the widest point using a Meiji binocular microscope (Meiji Techno, San Jose, California, United States of America) equipped with a micrometer to determine the number and size range of larval instars (Stark and Wood 1964; Langor and Williams 1998; Logan *et al.* 1998; Panzavolta 2007). The head-capsule width data were analyzed using the Hcap program developed by Logan *et al.* (1998). Adult weevils collected during field or laboratory sampling were measured at their widest and longest points to determine size range.

Eleven longterm installations previously established to monitor WBBB attack and stand succession in subalpine fir forests in southern B.C. (Maclauchlan and Buxton 2017; Maclauchlan 2020) had occasional records of *P. striatulus* colonising trees within these plots. Plots were located in three ESSF subzones: three in the ESSFxc (very dry, cold); six in the ESSFwc (wet, cold); and two in the ESSFmw (moist, warm) (Lloyd *et al.* 1990; Meidinger and Pojar 1991). The weevil was observed colonising mature subalpine fir alone and in association with WBBB. We summarised all records of *P. striatulus* from these 11 plots.

Field surveys. The objective of the field survey was to ascertain presence or absence of *P. striatulus* in randomly selected low- to mid-elevation subalpine fir stands by examining recently dead subalpine fir trees. Using Aerial Overview Survey spatial data (Ministry of Forests, Lands, Natural Resource Operations and Rural Development 2016), low- to mid-elevation stands containing subalpine fir and current WBBB attack (red trees) were identified. From the air, red subalpine fir is typically labelled as mortality caused by WBBB. Geo-referenced PDF maps were created for candidate areas, loaded onto a tablet. and using Avenza Systems Inc.® (2017; Toronto, Ontario, Canada) were located in the field. Survey sites were chosen based upon road access and visible red or fading subalpine fir near mapped areas of 2016 WBBB. Elevation and GPS coordinates were recorded for each site that was surveyed. Recently dead subalpine firs (displaying chlorotic to bright red foliage) were assessed for *P. striatulus* and other mortality factors. Occasionally, if older attack (displaying dull red foliage) or green trees undergoing current attack were present, they were also assessed. The number of trees assessed in each stand varied, based on the abundance of recently killed trees in the stand. Each tree was thoroughly checked by first examining the outer bark for exit holes and signs of oviposition or resin, and then peeling back the bark to look for weevil galleries, chip cocoons, and life stages. The foliage colour was recorded as green or chlorotic (new attack), bright red (prior year attack) and dull red (older attack). Western balsam bark beetle, woodborers, and any other insects or pathogens found under the bark were noted. All *P. striatulus* life stages were collected, labelled, and stored in 70% alcohol. For each sampled tree, existence of evidence of only *P. striatulus* attack, only WBBB attack, or whether both species were observed was recorded.

RESULTS

Life history sampling and field observations. The 10 weevil specimens sent to L. Humble were confirmed as *P. striatulus,* the balsam bark weevil (pers. comm.). The life table shown in Figure 1 was constructed by combining all field observations and life-stage sampling gathered in 2015 through 2017. On 2 July 2015, at the Spahats Creek site, numerous adult *P. striatulus* were observed mating and ovipositing on the freshly cut surface of a subalpine fir stump at the phloem–cambium interface and on the boles of standing live subalpine fir. Oviposition was distinguished by small feeding punctures made by the weevil in the outer bark, where it had laid one to several eggs and then had capped the puncture with a frass plug. At the oviposition site, a droplet of cloudy, red pitch (Fig. 2) usually was present, and the tree characteristically produced streams of resin. In late September, the bark was peeled from the attacked stumps, and the galleries originating from the cut surface were clearly visible radiating downwards to the root collar (Fig. 2). The larvae created straight or sometimes winding serpentine-like galleries downwards from the point of oviposition; as the larvae grew, they often veered off at right angles and mined around the circumference of the tree. By 25 September, larvae were large, late instar, and presumably in the overwintering stage. At that time, *P. striatulus* larvae (same life stage as in the stump) were also found in standing subalpine fir attacked by WBBB in 2014. Weevil attack occurred on the lower bole where there was available phloem not used by WBBB.

In October 2015, the Watching Creek site was first located by field-checking a fading subalpine fir that displayed a slightly different fade pattern than is normally associated with trees attacked and killed by WBBB, which typically fade to a bright red the summer following attack. This tree had dull red foliage with remnants of green on some branch tips (Fig. 2). Under the bark, galleries around the entire circumference of the tree, like those at the Spahats Creek site, and late-instar weevil larvae were found, indicating that attack had likely occurred that summer. The outer bark showed no sign of attack by WBBB, nor was frass or sawdust present around the bole, as is usually the case with WBBB attack.

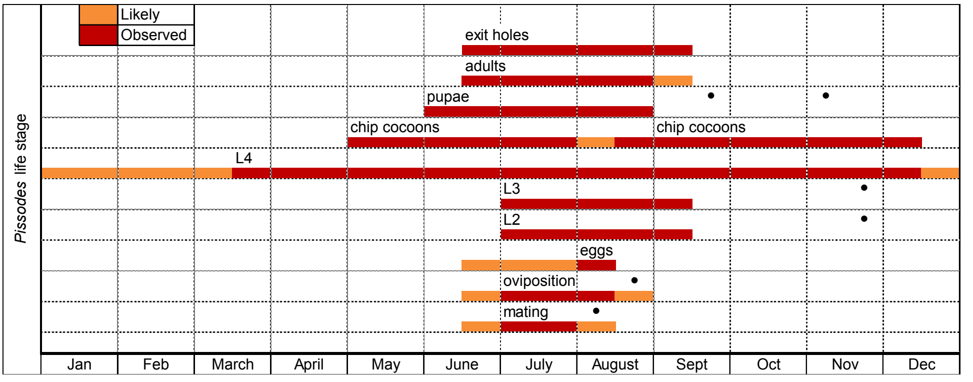

Figure 1. Timing of behaviour and life stages of *P. striatulus* from first to last observation (data from 2015–2017). Outliers are represented by ●.

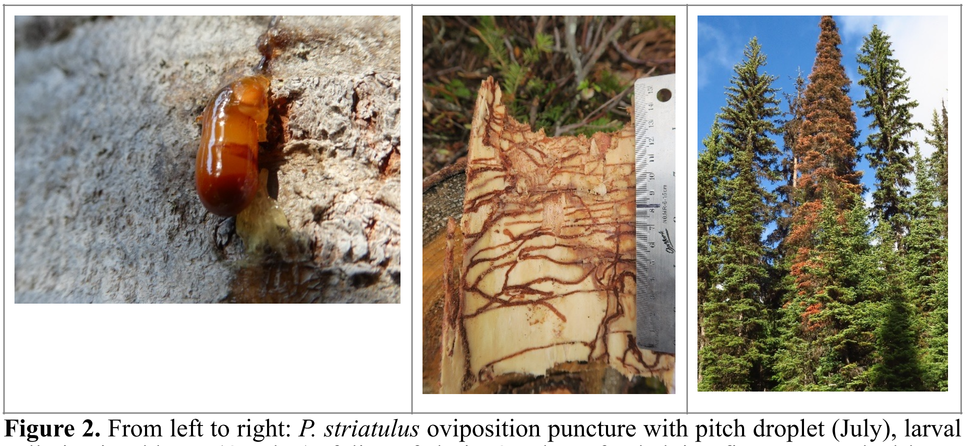

Figure 2. From left to right: *P. striatulus* oviposition puncture with pitch droplet (July), larval galleries in phloem (October), foliage fade in October of subalpine fir trees attacked by *P. striatulus* earlier in the summer.

Observations and field sampling in 2016–2017 at the Watching Creek and Antler Road sites revealed that larvae were active under the bark by late April or early May from attack the previous summer. Larvae present near the phloem–sapwood interface were beginning to construct chip cocoons at that time. Sampling found that the majority of larvae within the bark layer did not score the sapwood. Slower development was noted on the north aspect of trees, near the ground, and in trees located well within the stand, where conditions were cooler and less sunlight could penetrate the canopy. Overwintering adults were found in the duff layer at the base of trees throughout May during the periodic field assessments. By mid-June, late-instar (large) larvae and pupae were most predominant under the bark, and adults were observed on tree boles, cut stumps, and in recent axe cuts on trees. From late June through mid-July, pupae and late-instar larvae (Fig. 3) were predominant, and through July, teneral and mature adults were found. Emergence peaked from late July into early September on trees that were attacked the previous summer, although some larvae and a few pupae could still be found.

Emergence holes were abundant on the southeast aspect (warmer side) of many trees (Fig. 3). By October, all trees attacked by *P. striatulus* earlier in the year contained large larvae (presumably third or fourth instar).

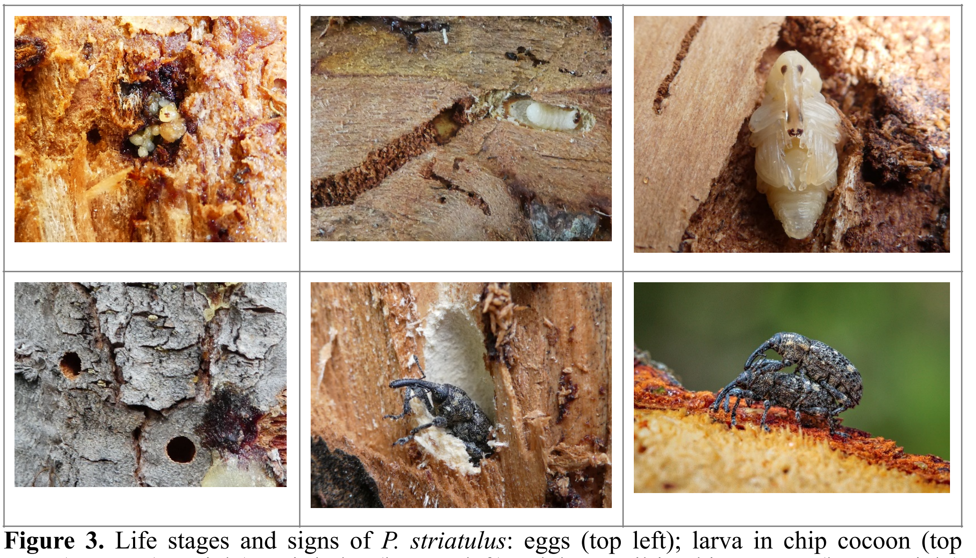

Figure 3. Life stages and signs of *P. striatulus*: eggs (top left); larva in chip cocoon (top centre); pupa (top right); exit holes (bottom left); adult weevil in chip cocoon (bottom right) prior to emergence; and mating adults.

Some trees attacked by *P. striatulus* in 2015 were subsequently attacked by WBBB in 2016. Trees were already fading, but some available phloem remained for WBBB to colonise. From late June through July, adult *P. striatulus* were observed mating and ovipositing on the boles of mature, live, outwardly healthy-looking subalpine firs at the Watching Creek and Antler Road sites. The first adult emergence at the Watching Creek site was observed on 11 July 2016. Therefore, weevils seen ovipositing could presumably both be overwintered and newly emerged adults. By 20 July, many small larval galleries were observed under the bark of newly attacked trees. On 5 July 2017, a large, live healthy subalpine fir at the Antler Road site was observed undergoing mass attack, with many adult weevils on the bole mating and ovipositing.

Temperature data were recorded throughout 2017 except for an 18-day period (25 May–12 June) when there was a malfunction, after which the temperature-recording device was replaced. Mating, oviposition, eggs, and early instar larvae were first observed when average daily minimum temperatures ranged from 5 °C to above 10 °C and average daily maximum temperatures ranged from 15 °C to above 25 °C. Pupae occurred when the average daily maximum temperature was from above 10 °C to the mid-20 degrees Celsius (Fig. 1; Fig. 4). Little or no development was noted after average daily minimum temperature was at or below 0 °C in late September to early October.

Based on trap catches at the Watching Creek site, two distinct flights by WBBB occurred. one in late June and the other in mid-August to mid-September. The later flight period was more prolonged. A few *P. striatulus* adults were caught in pheromone-baited traps on 5 July and 13 July 2017. Weevils were caught at the end of WBBB's first flight period. Western balsam bark beetle were caught in traps once the average daily minimum temperature rose above 0 °C and the average daily maximum temperature surpassed 10 °C, while *P. striatulus* were caught in traps once the average daily minimum temperature surpassed 10 °C and the average daily maximum temperature was above 20 °C.

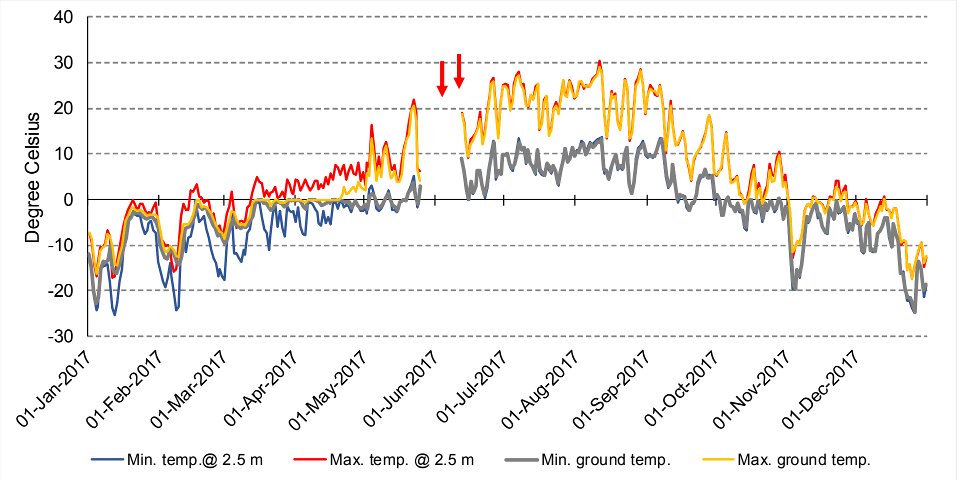

Figure 4. Average daily minimum and maximum temperatures at Watching Creek in 2017 taken at ground level and 2.5 metres on the north side of a tree. The two red arrows indicate when *P. striatulus* were caught in pheromone traps.

The three felled subalpine firs were just over 120 years old, and diameter at stump height ranged from 21.0 cm to 43.0 cm. Tree 2, the largest tree, was attacked from the base of the tree up to 21.0 m high and had the highest density of successful emergence, with a maximum of over 100 exit holes per metre of^2 bark area at 6.5 metres height (Fig. 5). The average number of exit holes along the bole between 4.0 to 15.0 metres was 70 exit holes per metre of^2 bark area. The smallest felled tree (Tree 1), at 21.0 cm diameter at stump height, had emergence from the stump end to 8.0 metres, ranging from 10 to 30 exit holes per metre of^2 bark area. In Tree 3 (31.0 cm stump diameter), most emergence occurred from 2.0 to 10.0 metres height, ranging from 4 to 28 exit holes per metre of^2 bark area (Fig. 5). Attack was found well into the crown area of all trees. The diameter of the top section from each tree ranged from 9.0 cm to 18.5 cm.

A total of 1 202 larval head-capsule widths were measured, with widths ranging from 0.4 mm to 2.2 mm (Table 2). The Hcap program (Logan *et al.* 1998) was used to determine instar classification (Fig. 6). Hcap did not produce a clear separation of instars; however, there appear to be four. The number of larvae within a range of head-capsule widths was plotted, and four probable instar delineations were identified (Fig. 6). Based on these delineations, the average head-capsule width (± S.E.) and range were calculated (Table 2). No clear demarcation occurred between second and third or third and fourth instars, but the average size of fourth-instar head capsules was 1.6 ± 0.15 mm (Table 2).

The length and width of 54 adult weevils and the width of 66 exit holes were measured. The average length and width (± S.E.) of *P. striatulus* was 6.7 ± 0.1 mm and 2.6 ± 0.05 mm, respectively. Exit holes were very circular and easily recognised, with an average width (± S.E.) of 3.3 ± 0.1 mm (Fig. 3).

Pissodes striatulus was recorded in all 11 permanent sample plots previously established to monitor mortality caused by WBBB and other damaging agents. Stems per hectare of subalpine fir affected by the weevil ranged from 2 to 69, and tree mortality ranged from <1% to 6%. The weevil was found both alone in trees and in combination with WBBB. Incidence of the weevil varied by year and location, with two plots in the ESSFxc and one plot in the ESSFwc having the highest recorded incidence of *P. striatulus* attack.

Field surveys. Fourteen geographic areas were surveyed for a total of 58 sites and 235 trees (Table 3) in the summer of 2017. Site elevation ranged from 1 257 m to 1 800

m. One to eleven subalpine fir trees were assessed at each site, for an average of 4.1 ± 0.3 (± S.E.) trees per site. Western balsam bark beetle attack was recorded at 69% of the sites, and 60% of subalpine fir showed evidence of WBBB attack. *Pissodes striatulus* attack was confirmed at 71% of sites, and of all subalpine fir assessed, 29% had some level of weevil attack (Table 3). Nineteen per cent (45 trees) of the trees sampled were colonised only by *P. striatulus,* and in the absence of any other potential mortality agent (*e.g.*, root disease), it was apparent that the weevil killed these trees.

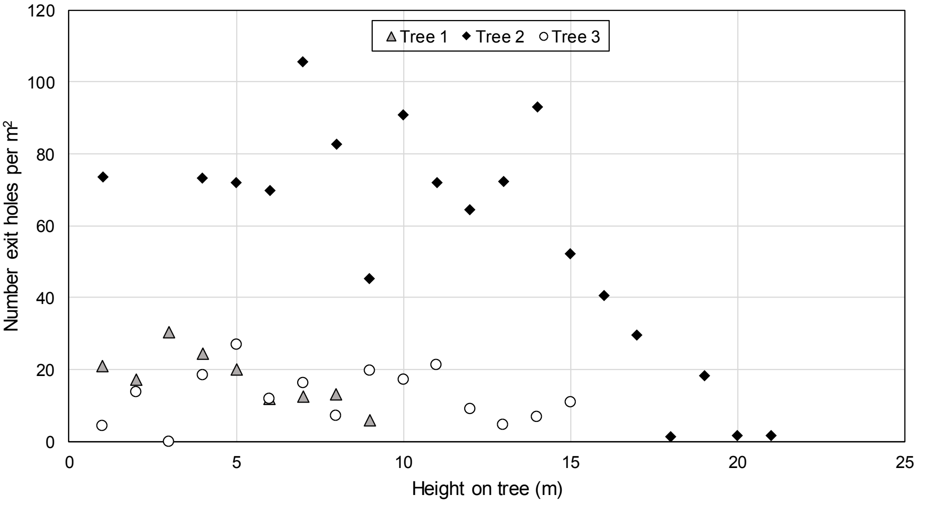

Figure 5. Number of *P. striatulus* exit holes (per square metre of bark) along the bole of three mass-attacked subalpine fir trees.

DISCUSSION

This study reveals that *P. striatulus* is a commonly found insect in subalpine ecosystems and that it regularly attacks and occasionally kills subalpine fir in lower-elevation, more climatically stressed stands in southern B.C. The weevil is likely ubiquitous throughout all subalpine fir ecosystems in B.C.; it is recorded in this study's 11 permanent sample plots, which are distributed throughout southern B.C., and in northern B.C. (J. Robert, Ministry of Forests, Lands, Natural Resource Operations and Rural Development, Omineca Region, B.C. personal communication), as well as from Waterton north to near Grande Cache, Alberta (D. Langor, Canadian Forest Service, Northern Forestry Centre, Edmonton, Alberta, Canada, personal communication). *Pissodes striatulus* may act both as a primary attacker, killing live subalpine firs, and as a secondary attacker, usually associated with WBBB. Both insects are known to colonise trees exhibiting reduced vigour (Craighead 1950; Belyea 1952a; Bleiker *et al.* 2003) caused by age (senescence), climate stress such as drought, or pre-existing stressors such as defoliation or disease. This study's observations show that *P. striatulus* and WBBB can both initiate attack on apparently healthy, live subalpine firs, with one or the other following in the secondary attacker role; both insects will attack freshly down trees or stumps (L. Maclauchlan personal observation.; Stock 1991; McMillin *et al.* 2003, 2017). The ability of the weevil to use downed trees and slash material and to switch roles between secondary invader colonising highly stressed or dead trees and primary invader attacking live, green trees demonstrates its capacity to adapt to changing and available conditions. The live, green subalpine firs observed being attacked by *P. striatulus* did not exhibit any outwards signs of stress or decline. Drought conditions may have predisposed trees to attack by one or both insects; however, no obvious drought mortality was observed.

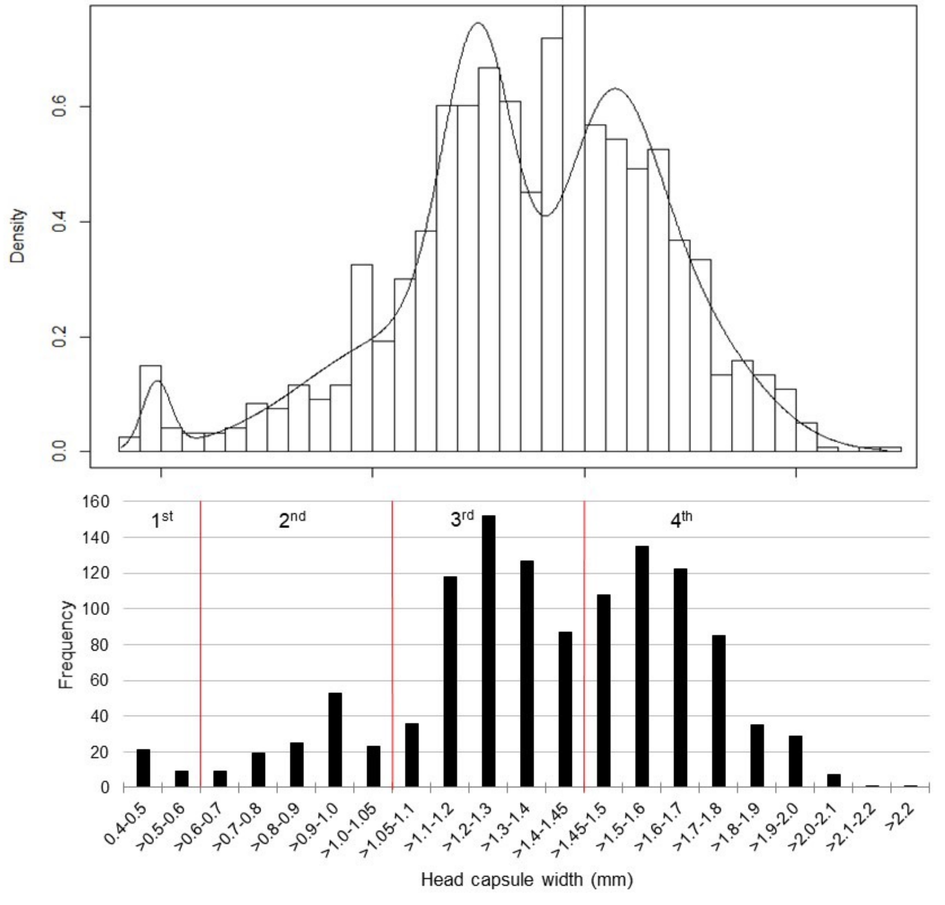

Figure 6. Head-capsule width distribution of *P. striatulus*. The line in the upper graph represents possible instar distribution (graph generated using Hcap; Logan *et al.* 1998). The lower graph shows frequency over a range of head-capsule widths and possible instar separation.

Table 2. Delineation of *P. striatulus* larval instars by head-capsule width.

Instar	N	Average width (mm) (± S.E.)	Size range (mm)
1	30	0.5 ± 0.01	0.4-0.6
2	129	0.9 ± 0.01	0.6-1.0
3	520	1.3 ± 0.01	1.1-1.4
4	523	1.6 ± 0.01	1.5-2.2

Evidence that *P. striatulus* has killed or colonised trees may be difficult to detect. Unlike WBBB, which leaves diagnostic gallery traces etched into the sapwood, *P. striatulus* rarely does so. The weevil often spends its entire development period within the phloem–cork portion of the bark, where the traces of its galleries are quickly obscured by those made by woodborers and other insects (L. Maclauchlan, personal observation), that arrive after the weevil has initiated attack. Belyea (1952a, 1952b) reported that *P. striatulus* was sometimes associated with the woodborer, *Monochamus* spp. Dejean (Coleoptera: Cerambycidae) in balsam fir trees sampled in New Brunswick and Quebec, Canada. and Minnesota, United States of America, after the severe eastern spruce budworm outbreaks of the early 1900s. He suggested that *P. striatulus* could kill weakened balsam fir trees that had survived severe budworm defoliation, up to four years following the budworm outbreak. This supports the current study's observations of *P. striatulus* contributing to the death of subalpine fir in ecosystems affected by disease or defoliation or in years following drought events. *Pissodes* spp. Germar may live up to four years (McMullen and Condrashoff 1973; Maclauchlan 1992; Langor and Williams 1998; Lewis *et al.* 2002), and this study records the presence of overwintered adults, suggesting that *P. striatulus* populations could potentially build up when stressed trees are abundant.

Trees attacked by *P. striatulus* alone have distinctive foliage-fade symptoms. Treetops fade rapidly during the summer and begin to shed foliage, while the lower branches of affected trees may turn red and lose foliage or they may retain some green foliage. Crowns are generally characterised by browning and dropping of needles. By the end of the summer, much of the foliage has dropped, and the attacked trees are a mix of red and grey. This differs from the foliar-fade symptoms observed after WBBB attack, which include the rapid, bright red colouration of foliage in the year following attack by WBBB. Mortality associated with WBBB is caused by a beetle–fungus complex, WBBB and *Ophiostoma dryocoetidis* (Kendrick and Molnar) de Hoog & Scheffer (Ophiostomataceae) (Molnar 1965; Garbutt 1992; Bleiker *et al.* 2005), and the fungus plays a vital role in the death of the host tree. There is no indication that *P. striatulus* has a fungal associate, which could in part account for the different symptoms displayed by the foliage of trees attacked only by the weevil.

Adult weevils are active from mid-June through to at least late August, showing a long biological window for finding suitable hosts, mating, and oviposition. Adults were found mating and ovipositing on trees before and throughout the emergence period of new weevils from attacked trees. Therefore, both overwintered (older) weevils and new adults could attack trees in mid-summer. The timing of attack can overlap with that of WBBB, highlighting the possibility that either insect can be the first coloniser. Lewis *et al.* (2002) demonstrated that *P. strobi* (Peck), a significant pest of young Sitka spruce, was capable of oviposition in the spring without needing to mate, if prior mating had occurred the previous autumn and the females were fecund. This may explain, in part, the long biological window. If long-lived adults are already fecund, synchronised emergence is less necessary to find mates and colonise novel habitats. It may also explain why pheromone-trap catches tend to be low in number for many species of *Pissodes* (Fontaine and Foltz 1982; Phillips and Lanier 1986; Nevill and Alexander 1992; Miller and Heppner 1999). Perhaps mating in this species occurs more frequently due to random encounters rather than sexual attraction through pheromone release.

Pissodes striatulus will mass attack a tree from ground level to the upper crown of trees. It prefers mature, large trees but, within a stand, can attack trees across a range of sizes. Successful weevil emergence was noted from upper tree sections as small as 9.0 cm in diameter. *Pissodes striatulus*, like many *Pissodes* spp., displays a very plastic life cycle, and development time can vary based on position of attack on the tree and annual weather conditions. Development near the root collar was slower than it was on the main bole and the warmer, east-facing aspects of attacked trees. Mating, oviposition, and larval development progressed rapidly during the warmest summer period, when average daily minimum temperatures exceeded 0 °C and average daily maximum temperatures ranged from above 10 °C to 30 °C.

The length of the 54 *P. striatulus* adults that were measured ranged from 4.9 mm to 8.3 mm, exactly comparable to the range of length of weevils described attacking stressed balsam fir and spruce in eastern Canada (5.0–8.0 mm) (Swaine *et al.* 1924). In the east, oviposition is confined to the base or lower sections of the bole (Swaine *et al.* 1924; Belyea 1952a), whereas in the current study observations indicate that attack can occur higher and along much of the length of the tree bole. The seasonal history and timing of emergence vary in the literature (Swaine *et al.* 1924; Belyea 1952a), as they do in this study, with adults emerging from June through August. Observations of this weevil in eastern spruce–balsam fir forests suggest that the insect mainly breeds in severely defoliated and nearly dead trees but are also able to attack trees that have recovered from defoliation events (Belyea 1952b). Host selection parameters appear to be similar on subalpine fir in B.C.; however, the stress level of trees and causal agents of that stress are less obvious.

Pissodes striatulus is a large *Pissodes*, with adults averaging 2.6 mm × 6.7 mm (width × length). Late-instar weevil larvae are larger than are bark beetle larvae associated with the phloem of dying subalpine fir and so are easily distinguished. The measurement of *P. striatulus* larval head-capsule widths did not clearly delineate instar separation. There appeared to be four instars, averaging in size from 0.5 mm (first instar) to 1.6 mm (fourth instar). Finding and collecting early instar larvae of this weevil was difficult due to the cryptic nature of attack and oviposition by adults. Adult weevils are difficult to see on tree bark, and the only visible sign of oviposition is a minute resin droplet. Our frequent and rigourous field assessments allowed us to locate several trees undergoing mass attack. However, dissecting out eggs and early instar larvae was difficult. Therefore, early instars were underrepresented in our sampling. Some size distinction occurred among later-instar head-capsule measurements, with a large range in size. Much variation in the size of weevils and their brood occurred, due to parental characteristics (large *vs.* small mothers), oviposition location on tree bole, age and size of host tree, physiological condition of tree, and other biotic and abiotic influences; thus, the size range of head capsules of successive instars overlaps. Most terminal-infesting *Pissodes* have been reported as having four larval instars (Wallace and Sullivan 1985; Park and Byun 1988; Langor and Williams 1998). Zhang *et al.* (2004) describe *Pissodes yunnanensis* Langor *et* Zhang, a weevil that attacks boles of young Yunnan pine, *Pinus yunnanensis* Franchet (Pinaceae), in southwestern China, as having four instars and the head capsule width of the fourth instar averaging 6.1 mm. Finnegan (1958) reported that *P. approximatus* (subsequently shown to be a synonym of *P. nemorensis*) (Godwin *et al.* 1982; Williams and Langor 2002) has four larval instars with head capsule widths ranging in size from just over 0.3 mm to over 1.4 mm. Reports differ on the number of larval instars of *P. strobi*; Harman (1970) describes five larval instars, with the average head-capsule width ranging from 0.3 mm to 1.2 mm, whereas McIntosh *et al.* (1996) report four larval instars, with a similar range in average head-capsule width as Harman (1970) from first through final instar.

In summary, *P. striatulus* is capable of mass attacking and killing large, mature subalpine fir trees. Due to its abundance in lower-elevation subalpine fir stands, which experience more frequent and severe drought events, we hypothesise that this abiotic stress on the host tree attracts the weevil. Our findings show that adult weevils overwinter, are likely long-lived, and are capable of oviposition over multiple years, similar to other *Pissodes* species (McMullen and Condrashoff 1973; Furniss and Carolin 1977; Maclauchlan 1992). This would enable *P. striatulus* to take advantage of periodic stressor events such as drought to build up populations rapidly. As moisture stress and higher annual temperatures become prevalent in subalpine fir forests in B.C., the presence and tree-killing habit of *P. striatulus* are likely to increase.

Table 3. Survey results for *P. striatulus* showing geographic locations with general latitude and longitude (Lat, Long); elevation; number of sites sampled per location; number of subalpine fir trees (Bl) assessed; number of trees with WBBB attack; number of trees where *P. striatulus* was the sole (1°) coloniser or co-occurred with WBBB (2°); and total number of trees containing *P. striatulus*.

Geographic Location	Lat/Long	Elevation (m)	No. sites sampled	No. Bl sampled	No. Bl with WBBB	No. Bl with weevil attack		
						1° attack	2° attack	Total
Sunset Main	49.8597° N, -120.1362° W	1,678	1	5	5	0	1	1
Whiterocks	50.0326° N, -119.6752° W	1,360	1	5	5	0	1	1
Apex Road	49.3865° N, -119.9458° W	1,800	1	9	9	0	1	1
Antler Road	50.8831° N, -120.4131° W	1,260	2	5	3	1	3	4
Crystal Mountain	49.8942° N, -119.8155° W	1,314	2	8	3	2	2	4
Sullivan	50.9843° N, -120.0796° W	1,357	2	6	4	2	3	5
Community	50.9250° N, -120.0691° W	1,350	2	11	10	2	2	4
Esperon Road	50.0527° N, -119.6576° W	1,343	3	11	7	3	2	5
Badger Lake	51.0361° N, -120.1080° W	1,317	3	13	10	2	0	2
Peachland Main	49.8090° N, -119.9985° W	1,469	4	9	5	3	2	5
Whiteman Creek	50.2476° N, -119.7161° W	1,378	7	36	5	6	4	10
Watching Creek	50.9084° N, -120.4392° W	1,274	9	30	14	11	0	11
T.F.L. 18	51.7612° N, -120.0852° W	1,257	10	55	42	7	1	8
Hyas Lake	50.7798° N, -119.9543° W	1,258	11	32	22	6	2	8
Total			58	235	144	45	24	69

Pissodes striatulus is also found in trees under attack by WBBB, where it may encounter less host resistance. Common tree defence mechanisms such as increased resin flow and the production of defensive chemicals due to insect attack (Berryman and Ashraf 1970; Alfaro *et al.* 2002) would be reduced if WBBB has already mass attacked the tree, making it easier for the weevil to colonise unused portions of the bole. The ability of *P. striatulus* to switch from secondary to primary invader depending upon climate and the host conditions available makes it well suited to adapt to warmer and more severe climate conditions. Subalpine fir is intolerant of high temperatures or moisture deficits (Alexander 1987); therefore, as changes in climate continue, elevated stress levels will continue in these outlying populations of subalpine fir, and potentially in northern and high-elevation forests throughout B.C. Changing climatic conditions, coupled with the fact that adult weevils are long-lived and may have multiple broods, could allow the weevil to proliferate, colonise, and kill an increasing number of trees throughout the range of subalpine fir, accelerating mortality and rates of succession. This study emphasises the need for additional monitoring of and research into high-elevation forests, their insect complexes, and how climate change can impact these fragile relationships.

ACKNOWLEDGEMENTS

We thank K. Buxton and B. Zimonick for field assistance and Kamloops Fire Centre Initial Attack Crew for felling trees. B. Zimonick also provided a photograph (Fig. 3. mating adults) for inclusion in the manuscript. We also thank S. Neufeld, T. Griffin, and K. Streichert for laboratory work. K. White and B. Bains provided thoughtful reviews of the manuscript. We thank B. Bentz for her time analysing head-capsule data using the Hcap model. Many thanks to the three reviewers for their thoughtful and meticulous reviews of our paper. Their comments greatly improved our submission. The project was supported in part by funding from the British Columbia Ministry of Forests, Lands and Natural Resource Operations and Rural Development Forests Sciences Program.

REFERENCES

Alexander, R.R. 1987. Ecology, silviculture, and management of the Engelmann spruce – subalpine fir type in the central and southern Rocky Mountains. Agriculture Handbook No. 659. United States Department of Agriculture Forest Service, Washington, D.C., United States of America.

Alfaro, R.I., Borden, J.H., King, J.N., Tomlin, E.S., McIntosh, R.L., and Bohlmann, J. 2002. Mechanisms of resistance in conifers against shoot infesting insects. *In* Mechanisms and deployment of resistance in trees to insects. *Edited by* M.R. Wagner, K.M. Clancy, F. Lieutier, and T.D. Paine. Springer, Dordrecht, The Netherlands. doi:10.1007/0-306-47596-0_4.

Atkinson, H.A., Foltz, J.L., and Connor, M.D. 1988. Bionomics of *Pissodes nemorensis* Germar (Coleoptera: Curculionidae) in Northern Florida. Annals of the Entomological Society of America, 81: 255-261. doi: 10.1093/aesa/81.2.255.

Avenza Systems Inc. 2017. Avenza Maps Pro. [software]. Available from https://www.avenza.com/ avenza maps/ [accessed 31 August 2020].

Belyea, R.M. 1952a. Death and deterioration of balsam fir weakened by spruce budworm defoliation in Ontario. Part I. Notes on the seasonal history and habits of insects breeding in severely weakened and dead trees. The Canadian Entomologist, 11: 325–335. doi:10.4039/ent84325-11.

Belyea, R.M. 1952b. Death and deterioration of balsam fir weakened by spruce budworm defoliation in Ontario. Part II. An assessment of the role of associated species in the death of severely weakened trees. Journal of Forestry, 50: 729–738. doi:10.1093/jof/50.10.z1.

Bentz, B.J., Régnière, J., Fettig, C.J., Matthew, E., Hayes, J.L., Hicke, J.A., Kelsey, R.G., Negrón, J.F., and Seybold, S.J. 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. BioScience, 60: 602–613. doi:10.1525/bio.2010.60.8.6.

Berryman, A.A. and Ashraf, M. 1970. Effects of *Abies grandis* resin on the attack behaviour and brood survival of *Scolytus ventralis* (Coleoptera: Scolytidae). The Canadian Entomologist, 102: 1229–1236. doi:10.4039/ent1021229-10.

Bleiker, K.P., Lindgren, B.S., and Maclauchlan, L.E. 2003. Characteristics of subalpine fir susceptible to attack by western balsam bark beetle (Coleoptera: Scolytidae). Canadian Journal of Forest Research, 33: 1538-1543. doi:10.1139/x03-071.

Bleiker, K.P., Lindgren, B.S., and Maclauchlan, L.E. 2005. Resistance of fast- and slow-growing subalpine fir to pheromone-induced attack by western balsam bark beetle (Coleoptera: Scolytinae). Agricultural and Forest Entomology, 7: 237–244. doi:10.1111/j.1461-9555.2005.00266.x.

Booth, D.C., Phillips, T.W., Claesson, A., Silverstein, R.M., Lanier, G.N., and West, J.R. 1983. Aggregation pheromone components of two species of *Pissodes* weevils (Coleoptera: Curculionidae): isolation, identification, and field activity. Journal of Chemical Ecology, 9: 1–12. doi:10.1007/bf00987766.

Craighead, F.C. 1950. Insect enemies of eastern forests. Miscellaneous Publication Number 657. United States Department of Agriculture, National Agricultural Library, Washington, D.C., United States of America. doi:10.5962/bhl.title.65598.

Finnegan, R.J. 1958. The pine weevil, *Pissodes approximatus* Hopk., in southern Ontario. The Canadian Entomologist, 90: 348–354. doi:10.4039/Ent90348-6.

Fontaine, M.S. and Foltz, J.L. 1982. Field studies of a male-released aggregation pheromone in *Pissodes nemorensis*. Environmental Entomology, 11: 881–883. doi:10.1093/ee/11.4.881.

Furniss, R.L. and Carolin, V.M. 1977. Western forest insects. Miscellaneous Publication Number 1339. United States Department of Agriculture Forest Service, Washington, D.C. United States of America. doi:10.5962/bhl.title.131875.

Garbutt, R. 1992. Western balsam bark beetle. Forest Pest Leaflet 64. Canadian Forest Service, Pacific Forestry Research Centre, Victoria, British Columbia, Canada.

Godwin, P.A., Valentine, H.T., and Odell, T.M. 1982. Identification of *Pissodes strobi, P. approximatus*, and *P. nemorensis* (Coleoptera: Curculionidae) using discriminant analysis. Annals of the Entomological Society of America, 75: 599–604. doi:10.1093/aesa/75.6.599.

Harman, D.M. 1970. Determination of larval instars of the white-pine weevil by head-capsule measurements. Annals of the Entomological Society of America, 63: 1573–1575. doi:10.1093/aesa/63.6.1573.

Haughian, S.R., Burton, P.J., Taylor, S.W., and Curry, C.L. 2012. Expected effects of climate change on forest disturbance regimes in British Columbia. British Columbia Journal of Ecosystems and Management, 13: 1–24 [online]. Available from jem.forrex.org/index.php/jem/article/viewFile/152/107 [accessed 31 August 2020].

Lalande, B.M., Hughes, K., Jacobi, W.R., Tinkham, W.T., Reich, R., and Stewart, J.E. 2020. Subalpine fir mortality in Colorado is associated with stand density, warming climates and interactions among fungal diseases and the western balsam bark beetle. Forest Ecology and Management, 466: 118–133. doi:10.1016/j.foreco.2020.118133.

Langor, D.W. and Williams, D.J.M. 1998. Lifecycle and mortality of *Pissodes terminalis* (Coleoptera: Curculionidae) in lodgepole pine. The Canadian Entomologist, 130: 387–397. doi:10.4039/ent130387-4.

Lewis, K.G., Liewlaksaneeyanawin, C., Alfaro, R.I., Ritland, C., Ritland, K., and El-Kassaby, Y.A. 2002. Sexual reproduction in the white pine weevil (*Pissodes strobi* [Peck] Coleoptera: Curculionidae): implications for population genetic diversity. The Journal of Heredity, 93: 165–169. doi:10.1093/jhered/93.3.165.

Lindgren, B.S. 1983. A multiple funnel trap for scolytid beetles (Coleoptera). The Canadian Entomologist, 115: 299–302. doi:10.4039/Ent115299-3.

Lloyd, D., Angove, K., Hope, G., and Thompson, C. 1990. A guide to site identification and interpretation for the Kamloops Forest Region. Land Management Handbook No. 23. British Columbia Ministry of Forests, Victoria, British Columbia, Canada.

Logan, J., Bentz, B., Vandygriff, J., and Turner, D.L. 1998. General program for determining instar distributions from head capsule widths: example analysis of mountain pine beetle (Coleoptera: Scolytidae) data. Environmental Entomology, 27: 555–563. doi:10.1093/ee/27.3.555.

Maclauchlan, L.E. 1992. Attack dynamics, impact and biology of *Pissodes terminalis* Hopping in regenerating lodgepole pine stands. PhD. thesis, Simon Fraser University, Burnaby, British Columbia, Canada.

Maclauchlan, L.E. 2016. Quantification of *Dryocoetes confusus* caused mortality in subalpine fir forests of southern British Columbia. Forest Ecology and Management, 359: 210–220. doi:10.1016/j.foreco.2015.10.013.

Maclauchlan, L.E. 2020. 2019 Overview of forest health conditions in southern British Columbia. B.C. Ministry of Forests, Range and Natural Resource Operations and Rural Development, Thompson Okanagan Region, Kamloops, British Columbia, Canada [online]. Available from https://www2.gov.bc.ca/gov/content/industry/forestry/managing-our-forest-resources/forest-health/aerial-overview-surveys/summary-reports [accessed 31 August 2020].

Maclauchlan, L.E. and Buxton, K. 2016. 2015 Overview of Forest Health Conditions in Southern British Columbia. B.C. Ministry of Forests, Range and Natural Resource Operations and Rural Development, Thompson Okanagan Region, Kamloops, British Columbia, Canada [online]. Available from https://www2.gov.bc.ca/gov/content/industry/forestry/managing-our-forest-resources/forest-health/aerial-overview-surveys/summary-reports [accessed 31 August 2020].

Maclauchlan, L.E. and Buxton, K. 2017. 2016 Overview of Forest Health Conditions in Southern British Columbia. B.C. Ministry of Forests, Range and Natural Resource Operations and Rural Development, Thompson Okanagan Region, Kamloops, British Columbia, Canada [online]. Available from https://www2.gov.bc.ca/gov/content/industry/forestry/managing-our-forest-resources/forest-health/aerial-overview-surveys/summary-reports [accessed 31 August 2020].

Maclauchlan, L.E. and Buxton, K. 2018. 2017 Overview of Forest Health Conditions in Southern British Columbia. B.C. Ministry of Forests, Range and Natural Resource Operations and Rural Development, Thompson Okanagan Region, Kamloops, British Columbia, Canada [online]. Available from https://www2.gov.bc.ca/gov/content/industry/forestry/managing-our-forest-resources/forest-health/aerial-overview-surveys/summary-reports [accessed 31 August 2020].

Maclauchlan, L.E., Borden, J.H., and Price, I. 1993. Life history and pheromone response in *Pissodes schwarzi* Hopk. (Coleoptera: Curculionidae). Journal of the Entomological Society of British Columbia, 90: 30–35.

Maclauchlan, L.E., Brooks, J.E., and White, K.J. 2015. Impacts and susceptibility of young pine stands to the mountain pine beetle, *Dendroctonus ponderosae*, in British Columbia. Journal of Ecosystems and Management, 15: 1–18. Available from jemonline.org/index.php/jem/article/viewFile/580/505 [accessed 31 August 2020].

McIntosh, R.L, McLean, J.A., Alfaro, R.I, and Kiss, G.K. 1996. Dispersal of *Pissodes strobi* in putatively resistant white spruce in Vernon, B.C. The Forestry Chronicle, 72: 381–387. doi:10.5558/tfc72381-4.

McMillin, J.D., Allen, K.K., Long, D., Harris, J.L., and Negrón, J.F. 2003. Effects of western balsam bark beetle on spruce-fir forests of north-central Wyoming. Western Journal of Applied Forestry, 184: 259–266. doi:10.1093/wjaf/18.4.259.

McMillin, J., Malesky, D., Kegley, S., and Munson, A.S. 2017. Western balsam bark beetle. Forest Insect and Disease Leaflet Number 184. United States of America Forest Service, Pacific Northwest Region, Portland, Oregon, United States of America.

McMullen, L.H. and Condrashoff, S.F. 1973. Notes on dispersal and longevity, and overwintering of adult *Pissodes strobi* (Peck) (Coleoptera: Curculionidae) on Vancouver Island. Journal of the Entomological Society of British Columbia, 70: 22–26.

Meidinger, D. and Pojar, J. 1991. Ecosystems of British Columbia. Special Report Series 6. British Columbia Ministry of Forests, Victoria, British Columbia, Canada.

Miller, D.R. and Heppner, D. 1999. Attraction of *Pissodes affinis* and *P. fasciatus* (Coleoptera: Curculionidae) to pityol and α-pinene in a coastal stand of western white pine and Douglas-fir. Journal of the Entomological Society of British Columbia, 96: 73–76.

Ministry of Forests, Lands, Natural Resource Operations and Rural Development. 2016. Aerial overview survey spatial data [online]. Available from https://www2.gov.bc.ca/gov/content/industry/forestry/managing-our-forest-resources/forest-health/aerial-overview-surveys/data-files [accessed 31 August 2020].

Molnar, A.C. 1965. Pathogenic fungi associated with a bark beetle on alpine fir. Canadian Journal of Botany, 43: 563–570. doi:10.1139/b65-062.

Nevill, R.J. and Alexander, S.A. 1992. Distribution of *Hylobius pales* and *Pissodes nemorensis* (Coleoptera: Curculionidae) within Christmas tree plantations with Procerum root disease. Environmental Entomology, 21: 1077–1085. doi:10.1093/ee/21.5.1077.

O'Brien, C.W. and Thompson, R.T. 1986. *Curculio striatulus*, a North American *Pissodes* (Coleoptera: Curculionidae). Entomological News, 97: 198–200.

Panzavolta, T. 2007. Instar determination for *Pissodes castaneus* (Coleoptera: Curculionidae) using head capsule widths and lengths. Environmental Entomology, 36: 1054–1058. doi:10.1603/0046-225x(2007)36[1054:idfpcc]2.0.co;2.

Parish, R. and Thomson, S. 1994. Tree book: learning to recognize trees of British Columbia. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia, and British Columbia Ministry of Forests, Victoria, British Columbia, Canada.

Park, J.D. and Byun, B.H. 1988. Bionomics of the yellow-spotted pine weevil, *Pissodes nitidus* Roelofs (Coleoptera: Curculionidae). Research Reports of the Forestry Research Institute (Seoul), 36: 120–125.

Phillips, T.W. and Lanier, G.N. 1986. Interspecific activity of semiochemicals among sibling species of *Pissodes* (Coleoptera: Curculionidae). Journal of Chemical Ecology, 12:1587–1601. doi:10.1007/bf01020266.

Phillips, T.W., West, J.R., Foltz, J.L., Silverstein, R.M, and Lanier, G.N. 1984. Aggregation pheromone of the deodar weevil, *Pissodes nemorensis* (Coleoptera: Curculionidae): isolation and activity of grandisol and grandisal. Journal of Chemical Ecology, 10: 1417–1423. doi:10.1007/bf00990312.

Randall, J.W. 1838. Descriptions of new species of coleopterous insects inhabiting the state of Maine. Boston Journal of Natural History, 2: 1–33.

Reich, R.M., Lundquist, J.E., and Hughes, K. 2016. Host-environment mismatches associated with subalpine fir decline in Colorado. Journal of Forest Research, 27: 1177–1189. doi:10.1007/s11676-016-0234-1.

Safranyik, L., Carroll, A.L., Régnière, J., Langor, D.W., Riel, W.G., Shore, T.L., Peter, B. Cooke, B.J., Nealis, V.G., and Taylor, S.W. 2010. Potential for range expansion of mountain pine beetle into the boreal forest of North America. The Canadian Entomologist, 142: 415–442. doi:10.4039/n08-cpa01.

Stark, R. and Wood, D.L. 1964. The biology of *Pissodes terminalis* Hopping (Coleoptera: Curculionidae) in California. The Canadian Entomologist, 96: 1208–1218. doi:10.4039/ent961208-9.

Stock, A.J. 1991. The western balsam bark beetle, *Dryocoetes confusus* Swaine: impact and semiochemical-based management. Ph.D. thesis, Simon Fraser University, Burnaby, British Columbia, Canada.

Swaine, J.M., Craighead, F.C., and Bailey, I.W. 1924. Studies on the spruce budworm [*Cacoecia fumiferana* Clem.] Technical Bulletin 37. Dominion of Canada, Department of Agriculture, Ottawa, Ontario, Canada. doi:10.5962/bhl.title.63095.

United States Department of Agriculture Forest Service. 1985. Insects of eastern forests. Miscellaneous Publication Number 1426. United States Department of Agriculture Forest Service, National Agricultural Library, Washington, D.C., United States of America. doi:10.5962/bhl.title.65300.

Wallace, D.R. and Sullivan, C.R. 1985. The white pine weevil, *Pissodes strobi* (Coleoptera: Curculionidae): A review emphasizing behaviour and development in relation to physical factors. White Pine Symposium, Supplemental Proceedings of the Entomological Society of Ontario, 116: 39–62.

Williams, D.J.M. and Langor, D.W. 2002. Morphometric study of the *Pissodes strobi* complex (Coleoptera: Curculionidae). The Canadian Entomologist, 134: 447–466. doi:10.4039/ent134447-4.

Winkler, R., Spittlehouse, D., and Boon, S. 2017. Streamflow response to clear-cut logging on British Columbia's Okanagan Plateau. Ecohydrology, 10: 1836. doi:10.1002/eco.1836.

Woods, A.J., Heppner, D., Kope, H.H., Burleigh J., and Maclauchlan, L. 2010. Forest health and climate change: a British Columbia perspective. The Forestry Chronicle, 86: 412–422. doi:10.5558/tfc86412-4.

Woods, A.J., Coates, K.D., Watts, M., Foord, V., and Holtzman, E.I. 2017. Warning signals of adverse interactions between climate change and native stressors in British Columbia Forests. Forests 8, 280. doi:10.3390/f8080280.

Zhang, H., Ye, H., Haack, R.A., and Langor, D.W. 2004. Biology of *Pissodes yunnanensis* (Coleoptera: Curculionidae), a pest of Yunnan pine in southwestern China. The Canadian Entomologist, 136: 719–726. doi:10.4039/n04-019.

Zilahi-Balogh, G., Humble, L., Foottit, R., Burleigh, J., and Stock, A. 2016. History of the balsam woolly adelgid, *Adelges piceae* (Ratzeburg), in British Columbia, with notes on a recent range expansion. Journal of the Entomological Society of British Columbia, 113: 21–38.