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ORIGINAL ARTICLE

Factors limiting the northern distribution of the blueberry maggot, *Rhagoletis mendax* (Diptera: Tephritidae) in Eastern Canada

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Abstract. Until recently, the Canadian distribution of the blueberry maggot, *Rhagoletis mendax* Curran (Diptera: Tephritidae), was restricted to Nova Scotia, Prince Edward Island and New Brunswick. The insect was first mentioned in southern Quebec in 1996 and, to date, it has not reached the Lac St-Jean region, where 34% of Canadian blueberry acreage is located. Two questions concerning the northern limit of distribution of the blueberry maggot in Quebec were addressed. First, are wild plants suitable hosts for larval development? We collected the fruit of five wild plants, (e.g. *Vaccinium corymbosum*, *Vaccinium angustifolium*, *Vaccinium myrtilloides*, *Gaylussacia baccata*, and *Aronia melanocarpa*) growing in southern Quebec and allowed larvae to complete their development into pupae. Blueberry maggot pupae were recovered from *Vaccinium corymbosum*, *Vaccinium angustifolium*, and *Gaylussacia baccata*, indicating that these plants are suitable for larval development. Second, are harsh winter temperatures a factor limiting the northern distribution of the blueberry maggot? Pupae collected in Quebec and Nova Scotia were put in the soil in the fall and were brought back to the laboratory to determine their supercooling points at different times during winter. The supercooling points of pupae collected in Quebec and Nova Scotia averaged –22.6°C. In natural conditions, air temperatures <–20°C are frequently observed in Quebec in January, February and March. However, due to snow cover, soil temperatures are rarely <–12°C. If –22.6°C constitutes the lower limit for the survival, then winter temperatures are probably not a limiting factor to its northern distribution in Quebec, because blueberry maggot pupae overwinter in the soil.

INTRODUCTION

Native to North America, the blueberry maggot, *Rhagoletis mendax* Curran (Diptera: Tephritidae), is a univoltine insect that attacks the fruit of a number of wild (Smith et al., 2001) and cultivated (Neilson & Wood, 1985; Geddes et al., 1987; Rodriguez-Saona et al., 2015) plants, notably highbush (*Vaccinium corymbosum* L.) and lowbush (*Vaccinium angustifolium* Aiton) blueberries. In Canada, it was found in Nova Scotia, Prince Edward Island and New Brunswick up to the 1990s (Vincent & Lareau, 1989). The insect was first noted in southern Quebec in 1996, and in southern Ontario in 1999 (CFIA, 2012; Yee et al., 2013).

Over the years, the blueberry maggot steadily extended its geographical distribution in Quebec and Ontario (CFIA, 2012). At the time of this writing, it has not yet reached the Lac St-Jean region, where most (ca. 85% of managed surfaces) Quebec lowbush blueberries are produced without insecticide treatment (Ministère de l'Agriculture, des Pêcheries et de l'Alimentation, 2011). As of 2010, Quebec had 34% of blueberry producing areas of Canada (34,277 ha) (Agriculture and Agri-Food Canada, 2012).

Two questions arise regarding the northern limit of the blueberry maggot in Quebec. First, several wild host plants of the blueberry maggot are present from the Quebec/New York State border all the way to the Lac St-Jean region. These wild plants, [e.g. *Vaccinium corymbosum*, *Vaccinium angustifolium*, *Vaccinium myrtilloides* Michaux, *Gaylussacia baccata* (Wangenheim) K. Koch] are suitable hosts in Michigan and southern Ontario (Smith et al., 2001). Here we aim at assessing the suitability of wild plants in Quebec.

Second, in their study using air temperatures to forecast the potential occurrence of pest infestation, Dobesberger & Macdonald (1993) postulated, without experimentation, a lethal temperature of –23°C for overwintering blueberry maggot pupae. However, blueberry maggot overwinters as pupae in the soil, and it is likely that temperatures prevailing in the soil are much different than air temperatures. Experiments were conducted to assess the supercooling point of *R. mendax* of pupae collected in Quebec and Nova Scotia in an attempt to determine if harsh winter conditions could be a limiting factor for blueberry maggot distribution in Quebec.

MATERIALS AND METHODS

Suitability of wild hosts

Mature fruit of five wild plant species growing in Quebec were collected in five locations of southern Quebec (see dates and coordinates in Table S1 – supplemental material) reported to have blueberry maggot presence. For each location, fruit were counted, weighed and laid on fine sand to allow for the development of pupae. After 30 days, the pupae were extracted from the sand and counted.

Supercooling point (SCP) of pupae

Blueberry maggot material

Wild berries were collected in August 2004 and 2005 near the Ecological Reserve Pin Rigide, St-Chrysostome (45°05.603´N; 73°52.117´W), Qc, Canada. In the laboratory, they were put at ca. 22°C (14L : 10D) and laid on moist sand (ca. 85% sand and 15% water, by volume) where blueberry maggot pupated. Several weeks later, the sand was sifted to extract pupae. The extracted pupae were randomly assigned to groups, each approximately corresponding to a winter month (Table 2). In November 2004 and 2005, the groups of pupae were each placed in metallic sieves (8 cm diameter, 3 cm deep, 16 mesh size) that were buried ca. 3 cm in the soil of a commercial blueberry field (located at St-Chrysostome: 45°06.878´N; 73°49.980´W) documented to be infested by the blueberry maggot. Electronic temperature loggers (Optic Stowaway® Temp., Onset computer Corporation, Pocasset, MA, USA) were positioned at a depth of 3 cm in the soil nearby the sieves containing the pupae to monitor (one temperature measurement per hour) soil temperatures from November to May. As previously described, electronic temperature loggers were also positioned in non-infested commercial blueberry fields located in L'Épiphanie (45°49.130´N; 73°31.562´W), Frelighsburg (45°08.190´N; 72°51.707´W), Saint-Eugène (49°00.228´N; 72°19.904´W), Normandin (48°46.754´N; 72°33.272´W) and Labrecque (48°39.670´N; 71°31.734´W), Qc, Canada.

Air temperatures at 1.5 m from ground level were obtained from weather stations belonging to the Quebec cooperative weather network (Lepage & Bourgeois, 2011). Stations located at Frelighsburg and Normandin provided data on site. Weather stations of Franklin (45°01.983´N; 73°55.000´W) and L'Assomption (45°49.002´N; 73°25.999´W) provided approximations of air temperatures for the nearby localities of St-Chrysostome and L'Épiphanie respectively. Air temperatures from 2003 to 2013 were extracted from a database with the software CIPRA (Bourgeois et al., 2008).

To determine if SCPs of blueberry maggot pupae in Quebec are similar to those of another region where blueberry maggot overwinters, fruit samples were collected in Nova Scotia from heavily infested commercial blueberry fields and processed as described previously. Pupae were stored at 2°C for several weeks, and shipped to the Horticultural Research and Development Centre at Saint-Jean-sur-Richelieu when needed for experiments.

Determination of SCP

Each month, a sieve containing one group of pupae was extracted from the field (St-Chrysostome, Qc) and brought to the laboratory. Their SCP, i.e. exotherms caused by the release of heat of crystallization (Denlinger & Lee, 1998), was determined within ca. 24 h. In order to have a slow decrease of temperature, the following set-up was developed. Blueberry maggot pupae were introduced individually in cavities of a microtube storage box (15 × 10 × 6.5 cm) in which a thermocouple (type T, size 36) allowed to maintain one pupa against a wall of a cavity (Fig. 1A). The thermocouple was connected to a data acquisition unit (model 34970A, Agilent Technologies®, Loveland, Colorado, USA) driven by the software Benchlink® (Agilent Technologies®, Loveland, Colorado, USA) to take one temperature measurement per second. Cotton wool was placed in the lid of the storage box for thermal insulation. To further insulate the set-up, the storage box was placed in a styrofoam box (30 × 20 × 13 cm) (Fig. 1A), and the empty space between the two boxes was filled with vermiculite. The styrofoam box was put in a freezer set at –80°C until the SCP occurred (Fig. 1B, C). The set-up allowed to determine the SCPs of 15 blueberry maggot pupae at a time. Comparison of SCPs was done with an unpaired t-test with the software XLSTAT (Addinsoft, 2011).

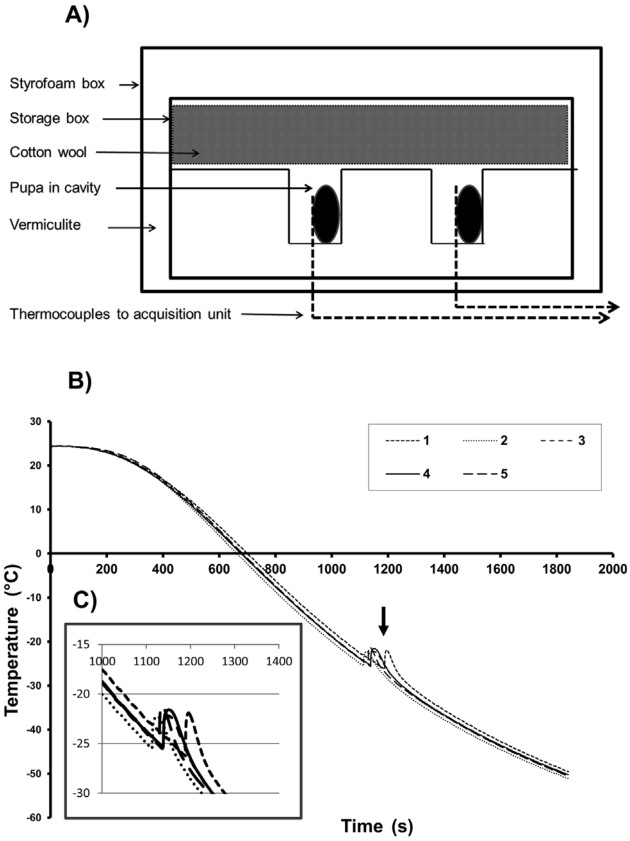

Fig. 1. A – set-up to determine the SCP of blueberry maggot pupae in the laboratory; B – determination of SCPs of blueberry maggot pupae occurred when a slight elevation of temperature (example shown by arrow) was measured. In the five selected examples (extracted from the dataset 26 January 2006, Quebec; Table 2), SCPs occurred at ca. 1100–1200 seconds and around –23.37°C; C – detailed view of temperatures determined between 1000 and 1400 s.

RESULTS AND DISCUSSION

The number of pupae retrieved from fruit collected from five wild plant species was highly variable. Assuming one larva per fruit, the percentage of fruit infested ranged from 0 to 18.4% in *G. baccata* (i.e., black huckleberry), 0 to 4.31% in *V. angustifolium*, 0 to 11.9% in *V. corymbosum*, and from 0 to 0.16% (2 pupae) in *V. myrtilloides* (i.e. velvet-leaved blueberry) (Table S1). Smith et al. (2001) found that *G. baccata* is a suitable host as indicated by high fruit infestation. They found highly variable % fruit

Table 1. Number of frost-free days and mean annual temperature in 6 locations infested with blueberry maggot and 2 non-infested localities of north eastern North America.

Locations, State or Province	Status*	Site # **	No. days frost-free****	Mean annual temperature (°C)****
Pellston, MI	I	5	154a	8.6g
Allegan, MI	I	1	170b	6.1g
Watseka, IL	NI	19	172c	10.2h
Wheatfield, IN	I	21	176d	10.1i
Wainfleet Bog, ONT	I	36	182f	9.2f
Akron, OH	I	23	179e	9.9j
Ormstown, QC	I	NA***	151f	6.7f
Normandin, QC	NI	NA	130f	2.6f

*I – infested with blueberry maggot; NI – non-infested; **from Table 1 in Smith et al. (2001); ***NA – non-applicable, this study; ****a–e – average of data from 1951 to 2010 (Benning et al., 2011a–e, respectively); f – average of data from 1981 to 2010 (Canadian Climate Normals, 1981–2010); g – average of data from 1981 to 2010 (Michigan State Climatologist's Office, 2016); h – average of data from 1981 to 2010 (Illinois State Water Survey, 2016); i – average of data from 1981 to 2010 (Indiana State Climate Office, 2016); j – average of data from 1981 to 2010 (National Climatic Data Center, 2011).

infestation for *V. corymbosum* collected in Michigan (0–28.8%). In southern Ontario, wild *V. corymbosum* fruit had no infestation 11 times out of 14, while they had 0.1, 0.2 and 15.2% infestation in three occasions. Directive D-02-04 of the CFIA (2014, 5th revision) states that the following plants are regulated as hosts of the blueberry maggot: lowbush blueberry (*V. angustifolium*, including *V. pennsylvanicum*); sourtop blueberry (*V. myrtilloides*, including *V. canadense*); highbush blueberry (*V. corymbosum*, including, *V. ashei* and *V. atrococcum*); small cranberry (*V. oxycoccus*); deerberry (*V. stamineum*); lingonberry (*V. vitis-idaea*); black huckleberry (*G. baccata*); dangleberry (*G. frondosa*); dwarf huckleberry (*G. dumosa*) and hillside blueberry (*V. pallidum*, including *V. vacillans*). This means that wild or protected areas, such as the Ecological Reserve Pin Rigide, can be major sources of blueberry maggot populations once they become infested.

In northern Quebec the suitability of wild plants as hosts can be questioned because climatic conditions prevailing in that region are much harsher than those prevailing in Michigan, southern Ontario or southern Quebec (Table 1). For example, there are 130 frost-free days in Normandin, a locality of the Lac St-Jean region, while there are > 154 frost-free days in most of the localities sampled by Smith et al. (2001) (Table 1). In the fall at Normandin, the earliest and latest frosts occurred on 13 August and 25 September, respectively; on 10 September there is 50% probability that frost occurred (Ouellet & Laporte, 1963). In the fall at Saint-Clotilde (a site located ca. 10 km from St-Chrysostome), the earliest and latest frosts occurred on 25 August and 7 October, respectively; on 13 September there is 50% probability that frost occurred (Ouellet & Laporte, 1963). Furthermore, the annual average temperature in Normandin is 2.6°C, while it is > 6.1°C in most of the localities

Table 2. Supercooling points (°C) of blueberry maggot pupae collected in Quebec and Nova Scotia in 2004 and 2005; n = number of pupae used.

Date of determination	Quebec		Nova Scotia	
	Average (± s.e.)	n	Average (± s.e.)	n
7–8, 20–21 October 2004	–22.7 (2.72)	58	–20.6 (1.93)	15
25–26 November 2004			–24.6 (1.37)	60
16–17, 20 December 2004			–22.5 (3.44)	65
20–21 December 2004	–22.2 (3.50)	58		
24–26 January 2005			–23.1 (1.68)	78
27–28 January 2005	–21.4 (5.27)	55		
15–16 March 2005			–22.6 (5.70)	76
21 March 2005	–22.3 (6.25)	57		
27–29 April 2005			–23.9 (4.75)	59
4–5 May 2005	–23.9 (3.71)	60		
25 November 2005	–23.5 (3.62)	45		
13–14 December 2005			–20.3 (7.08)	38
20 December 2005	–22.7 (4.50)	37		
26 January 2006	–23.4 (4.71)	14		
27 January 2006			–22.2 (3.71)	51
20 February 2006	–22.5 (3.41)	20		
17 March 2006	–21.5 (6.29)	39		
17 March 2006			–22.6 (3.71)	55
21 April 2006	–22.7 (2.75)	43		
4 May 2006			–20.8 (6.51)	43
Average	–22.6 (4.12)		–22.6 (4.29)	

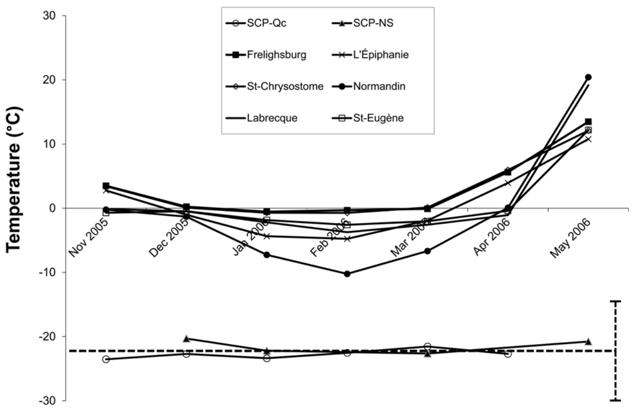

Fig. 2. Soil temperatures measured at 3 cm depth in several localities of Quebec during winter 2005 and 2006. The dotted horizontal line represents the average SCP of pupae, i.e. –22.6°C. The two lines hovering around the dotted horizontal line are SCPs determined for blueberry maggot pupae of Quebec (empty bullets) and Nova Scotia (black triangles), as reported in Table 2. The dotted vertical line represent the maximal value of the standard error associated with SCP of pupae, i.e. 7.08 (see Table 2).

sampled by Smith et al. (2001) in Michigan. Under colder conditions in the North, it is likely that the blueberry maggot larvae will have less time to complete their larval development, not only because lower temperatures directly slows developmental duration in poikilotherms, but also because lower temperatures indirectly decrease the duration of availability of suitable fruit to complete larval development.

The average SCPs of blueberry maggot pupae collected in Quebec (–22.6°C) and Nova Scotia (–22.6°C) were not significantly different ($t = -0.118$, $df = 1023$, $p = 0.906$), while average standard errors were 4.12 ($n = 11$) and 4.29 ($n = 10$), respectively, and the maximal standard error was 7.08 (Table 2). In his review on insect cold hardiness, Bale (1996) stated that the SCP is simply the physical process of supercooling, but possibly the lower limit of survival in an overwintering insect. The determination of the lower limit requires formal experimentation. Partial determination has been done by Vincent et al. (2014) who found that exposure of blueberry maggot larvae and pupae at –20°C for > 2 days caused 100% mortality in laboratory conditions, while exposure at –20°C for 2 days did not cause 100% mortality.

Soil temperatures measured at a depth of 3 cm were frequently > –10°C during the winter months of 2005 and 2006 (Fig. 2). In our data set, soil temperature was lower than –20°C only once (–21.8°C) in 2003 at l'Epiphanie when snow cover was exceptionally rare. This is consistent with the data produced by Ouellet et al. (1975), who reported average monthly temperatures (taken at 1 cm in the soil) for 15 localities of the Lac St-Jean region. These average temperatures ranged from –1.1 to –6.9°C in January, the coldest month of the year. In contrast, from 2003 to 2013, minimum air temperatures measured at 1m above the soil in L'Assomption (locality near l'Epiphanie) were < –20°C 111 times in January, 70 times in February and 24 times in March (Table S2). Likewise, from 2003 to 2013, minimum air temperatures measured at 1m above the soil in Normandin were < –20°C 230 times in January, 173 times in February and 97 times in March (Table S2). Air temperature, used as input variables for the model of Dobesberger & Macdonald (1993), is a poor predictor of the temperature that the pupae might experience in the soil, where the temperature is moderated by the soil and snow cover in Quebec.

CONCLUSIONS

Two conclusions emerge from our study. First, several wild plant species are suitable hosts in southern Quebec (e.g. Ormstown, Qc), where the number of frost-free days and average temperature is comparable (Table 1) to those of several localities reported in Smith et al. (2001). It remains to be seen if these wild plants will be suitable hosts in the Lac St-Jean region. Other species can also be suitable host plants, including cultivated highbush and lowbush blueberry. In their study, Smith et al. (2001) found that *G. dumosa* is a valid host allowing pupation of the blueberry maggot, while no pupae were retrieved from *Vaccinium pallidum* Aiton. Second, the supercooling point of blueberry maggot pupae is –22.6°C. In natural conditions, soil temperature < –20°C is a rare mortality factor for blueberry maggot pupae because there is frequently snow cover that has insulating effect against air temperatures. Therefore, if –22.6°C constitutes the lower limit for the survival, then winter air temperatures probably do not represent a limiting factor to blueberry maggot northern distribution.

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Table S1. Suitability of wild fruit collected in Southern Quebec for larval development of the blueberry maggot. All locatities were at altitude ranging from 161 to 341 m from sea level.

Locality	GPS coordinates	Date (dd-mm-yy)	Host plant	No. of fruit collected	Weight of fruit (average fruit weight) in g	No. of pupae	% fruit infested [1]
Carrière, Qc	45°06.770´N; 73°52.569´W	08-08-03	*Vaccinium angustifolium*	818	125.0 (0.153)	9	1.1
		08-08-03	*Gaylussacia baccata*	883	232.5 (0.263)	78	8.83
		08-08-03	*Aronia melanocarpa*	704	157.6 (0.224)	0	0
Carrière, Qc	45°06.770´N; 73°52.569´W	18-08-03	*Gaylussacia baccata*	295	54.8 (0.186)	4	1.36
		18-08-03	*Aronia melanocarpa*	1186	372.9 (0.314)	0	0
Ormstown, Qc	45°04.558´N; 73°55.891´W	20-08-03	*Vaccinium angustifolium*	2185	412.2 (0.189)	1	0.05
		20-08-03	*Vaccinium myrtilloides*	317	55.7 (0.176)	0	0
Ormstown, Qc	45°04.558´N; 73°55.891´W	25-08-03	*Vaccinium corymbosum*	1111	199.0 (0.179)	0	0
		25-08-03	*Vaccinium myrtilloides*	1235	218.8 (0.177)	2	0.16
Réserve du Pin Rigide, Qc	45°05.603´N; 73°52.117´W	26-08-03	*Vaccinium corymbosum*	36	4.3 (0.119)	0	0
		26-08-03	*Gaylussacia baccata*	545	75.9 (0.139)	29	5.32
Carrière, Qc	45°06.770´N; 73°52.569´W	29-08-03	*Gaylussacia baccata*	387	52.7 (0.136)	13	3.36
Réserve du Pin Rigide, Qc	45°05.603´N; 73°52.117´W	19-08-04	*Gaylussacia baccata*	2821	751.1 (0.266)	241	8.54
Carrière, Qc	45°06.770´N; 73°52.569´W	20-08-04	*Vaccinium corymbosum*	1802	390.8 (0.294)	2	0.11
Carrière, Qc	45°06.770´N; 73°52.569´W	20-08-04	*Vaccinium angustifolium*	4493	1885.3 (0.217)	102	2.27
Carrière, Qc	45°06.770´N; 73°52.569´W	31-08-04	*Gaylussacia baccata*	2132	1100.9 (0.516)	58	2.72
Réserve du Pin Rigide, Qc	45°05.603´N; 73°52.117´W	20-07-05	*Vaccinium corymbosum*	1195	491.6 (0.411)	0	0
		20-07-05	*Vaccinium angustifolium*	1305	469.1 (0.359)	0	0
Ormstown, Qc	45°04.558´N; 73°55.891´W	21-07-05	*Vaccinium corymbosum*	1355	522.3 (0.385)	1	0.07
		21-07-05	*Vaccinium angustifolium*	1516	469.3 (0.310)	5	0.33
		21-07-05	*Vaccinium myrtilloides*	36	8.1 (0.225)	0	0
Carrière, Qc	45°06.770´N; 73°52.569´W	28-07-05	*Vaccinium corymbosum*	1344	482.7 (0.359)	11	0.89
		28-07-05	*Vaccinium angustifolium*	2313	691.4 (0.299)	2	0.09
		28-07-05	*Gaylussacia baccata*	1088	397.8 (0.366)	75	6.89
Ste-Sabine, Qc	45°14.682´N; 73°02.413´W	04-08-05	*Vaccinium corymbosum*	1514	543.9 (0.359)	0	0
Cairnside, Qc	45°05 802´N; 73°51 582´W	10-08-05	*Vaccinium corymbosum*	1976	601.2 (0.304)	0	0
		10-08-05	*Vaccinium angustifolium*	218	29.3 (0.134)	0	0
		10-08-05	*Gaylussacia baccata*	2105	553.5 (0.263)	0	0
Cairnside, Qc	45°05.802´N; 73°51.582´W	11-08-05	*Vaccinium corymbosum*	1793	519.2 (0.290)	215	11.9
		11-08-05	*Vaccinium angustifolium*	1119	270.5 (0.242)	7	0.63
		11-08-05	*Gaylussacia baccata*	3212	715,3 (0.223)	192	5.98
Réserve du Pin Rigide, Qc	45°05.603´N; 73°52.117´W	17-08-05	*Vaccinium corymbosum*	673	187.1 (0.278)	0	0
		17-08-05	*Vaccinium angustifolium*	928	258.3 (0.278)	40	4.31
		17-08-05	*Gaylussacia baccata*	734	232.1 (0.316)	135	18.4
Carrière, Qc	45°06.770´N; 73°52.569´W	19-08-05	*Vaccinium corymbosum*	169	44.2 (0.262)	0	0
		19-08-05	*Vaccinium angustifolium*	1012	259.2 (0.256)	0	0
		19-08-05	*Gaylussacia baccata*	1530	376.7 (0.246)	97	6.34

[1] Assuming one larva per fruit.

Table S2. Number of days during January, February and March 2003 to 2013 where minimum air temperature was < –20°C in four localities in Quebec, Canada. (Extracted with the software CIPRA; Bourgeois et al., 2008.)

Year	Frelighsburg Jan-Feb-Mar	Franklin Jan-Feb-Mar	L'Assomption Jan-Feb-Mar	Normandin Jan-Feb-Mar
2003	12-9-5	11-10-2	16-11-7	26-18-15
2004	14-5-0	14-4-0	15-9-0	24-14-13
2005	12-4-0	10-6-2	10-6-2	29-11-5
2006	1-1-0	2-4-0	0-4-0	17-20-5
2007	8-3-6	10-5-4	10-6-5	16-21-12
2008	5-3-0	4-3-0	8-9-4	19-21-17
2009	13-3-3	6-1-0	18-6-2	27-14-14
2010	6-1-0	3-0-0	6-0-0	13-4-3
2011	7-0-1	1-0-0	8-7-2	18-17-7
2012	6-3-0	4-0-0	8-7-2	20-16-4
2013	5-5-2	7-3-0	12-5-0	21-17-2
Total	89-37-17	72-36-8	111-70-24	230-173-97