

Density has more influence than drought on spruce budworm (*Choristoneura fumiferana*) performance under outbreak conditions



Eric R.D. Moise*, Michael B. Lavigne, Rob C. Johns

Natural Resources Canada, Canadian Forest Service, Atlantic Forestry Centre, P.O. Box 4000, Fredericton, NB E3B 5P7, Canada

ARTICLE INFO

Keywords:

Climate change
Defoliation
Mass
Performance
Survival
Wing length

ABSTRACT

Eruptive insect pests have significant impacts on the structure and function of forest ecosystems. Outbreaks of spruce budworm (*Choristoneura fumiferana*) (Clem.), for instance, occur approximately every 35–40 years, resulting in the loss of millions of hectares of spruce–fir forests in eastern North America. In addition to the density-dependent relationships that drive insect outbreaks, rising populations often coincide with drought events, which are expected to increase in both frequency and intensity in response to climate change. However, as populations approach the eruptive phase, consequences of intraspecific competition may outweigh the benefit of host water stress. The objective of our study was to quantify defoliation and insect performance responses to the interactive effects of drought and density of spruce budworm. To test for these interactions, we established a manipulative field experiment in a mature, balsam fir-dominated forest stand using a combination of single-tree rainout shelters and sleeve-caged insect larvae at four different densities: 0, 25, 50, or 100 individuals.

Defoliation of 1-year old shoots, but not current-year shoots, significantly increased in response to higher insect densities. Density also had a significant, negative effect on budworm percent survival, although the total number of recovered adults remained highest in the high density treatment. Adult female body mass was significantly reduced in response to increased density, but only on droughted trees. Lastly, male wing length was significantly decreased in response to increased density. Overall, our results demonstrate that across a broad range of outbreak densities, rain exclusion had a minor impact. Accordingly, we anticipate that as insect pest populations approach epidemic levels, the influence of density on defoliation, insect survival, and body condition is likely to outweigh the impact of moderate drought stress.

1. Introduction

Eruptive insect pests have significant impacts on the structure and function of forest ecosystems (Cooke et al., 2007). In the case of defoliators, for instance, increased feeding damage may initially inhibit tree growth and productivity (Blais, 1958a), and after multiple years, can cause tree mortality (Blais, 1958b; Batzer, 1972) or leave trees more susceptible to secondary pests (Wallin and Raffa, 2001). In addition to the downstream impacts on associated biota and ecosystem services (Belyea, 1952; Stadler et al., 2006), timber losses impose economic consequences on the forestry sector (Elliott, 1960; MacLean et al., 2002). Further complicating outbreak impacts are the potential consequences of climate change on pest–tree interactions (Logan et al., 2003; Bréda et al., 2006). Accordingly, understanding the biotic and abiotic drivers of eruptive pest populations is important for effective forest management under both current and future environmental

scenarios.

Although density-dependent interactions are often a key force driving insect outbreak cycles, density-independent factors may also play a role in determining the timing and intensity of outbreaks. For example, outbreaks for many insects often coincide with warm, dry periods (Rouault et al., 2006; Raffa et al., 2008), suggesting that insect–host interactions are further influenced by tree water status. Indeed, moisture stress can alter foliage quality through changes in nutrients, defense compounds, and toughness (Mattson and Haack, 1987; Huberty and Denno, 2004; McDowell et al., 2011). Because climate change is expected to increase the severity and frequency of drought events, there are likely to be important interactions between moisture stress and insect attack (Anderegg et al., 2015). Current evidence suggests that drought increases defoliator damage while decreasing damage from wood feeders (Jactel et al., 2011). Additionally, both the direction and magnitude of drought impacts on insect fitness are highly

* Corresponding author at: Natural Resources Canada, Canadian Forest Service, Atlantic Forestry Centre, P.O. Box 960, Corner Brook, Newfoundland A2H 6J3, Canada.

E-mail addresses: eric.moise@canada.ca (E.R.D. Moise), mike.lavigne@canada.ca (M.B. Lavigne), rob.johns@canada.ca (R.C. Johns).

<https://doi.org/10.1016/j.foreco.2018.10.031>

Received 31 May 2018; Received in revised form 11 October 2018; Accepted 13 October 2018

0378-1127/ Crown Copyright © 2018 Published by Elsevier B.V. All rights reserved.

guild specific (Koricheva et al., 1998; Huberty and Denno, 2004). However, much of these data have been generated under laboratory conditions or at low population densities, and little is known about drought effects when populations reach the eruptive phase of an outbreak.

The spruce budworm, *Choristoneura fumiferana* (Clem.), is the most destructive insect pest of spruce–fir forests in eastern North America (MacLean and Ostaff, 1989; Hennigar et al., 2008). During outbreaks, population densities increase several orders of magnitude and can begin to kill trees after 4–5 years of severe defoliation (MacLean, 1980; Pureswaran et al., 2016). Budworm outbreaks are cyclical, exhibiting a periodicity of approximately 35–40 years, and are driven by a combination of natural enemies, weather, resource depletion, and migration (Pureswaran et al., 2016). Climate change is already impacting spruce budworm population dynamics (Pureswaran et al., 2015), and the economic and ecological consequences of outbreaks may be magnified in the coming decades (Gray, 2008; Régnière et al., 2012). Even with this past work on the relationship between budworm population dynamics and climate change, there are few field experiments examining how budworm might respond under different drought conditions or whether these responses vary at different population densities. Such interactions have already been reported for grassland systems (Branson, 2016), and are likely to further extend to pest–tree dynamics.

To assess the effects of larval density and drought on defoliation and spruce budworm performance, we conducted a manipulative field experiment using a combination of sleeve-caged insects and individual tree rainout shelters. We predicted that, in addition to individual effects of drought and density on defoliation, insect survival, and body condition, these factors would interact such that effects of drought would be moderated with increasing insect density.

2. Methods

2.1. Study area

The experiment was established as a split plot design, with each of nine blocks consisting of two balsam fir trees; one droughted and one receiving ambient precipitation (Fig. 1). Two additional control trees were also included in the experiment. Four spruce budworm density treatments (Control, Low, Medium, High) were randomly assigned to branches on each tree. The field site was located in the Dunbar Resource Area near Taymouth, New Brunswick, Canada (N 46°09′41.59″, W 66°41′36.82″). The forest stand was mixed conifer, dominated by balsam fir (*Abies balsamea* (L.) Mill.) (approximately 80%) with a smaller contingent of white spruce (*Picea glauca* (Moench) Voss). The stand was closed-canopy and approximately 35 years old.

2.2. Herbivory and drought treatments

We obtained second-instar spruce budworm larvae from the Great

Lakes Forestry Centre Insect Production Services (Sault Ste. Marie, ON). Spruce budworm were placed in the lab to emerge from hibernacula, put in plastic containers in groups of five or ten, then transferred to the field, and sleeve caged on mid-crown branches of drought and control trees between 28 and 29 May 2015. Each tree received four sleeve cages (sleeve dimensions 1 m × 0.5 m) corresponding to the four density treatments; 100 spruce budworm (High), 50 spruce budworm (Medium), 25 spruce budworm (Low), and 0 spruce budworm (Control). Bioassays were initiated approximately 2 weeks prior to local budburst, which reflects the approximate timing that budworm begin feeding on hosts such as white spruce (Lawrence et al., 1997).

After setting up and enclosing larvae in sleeve cages, rainout shelters were built around the bole of each drought tree using transparent, UV-resistant tarp (design modified from Olesinski et al. (2011)). Tarps were positioned in a tent shape with a peak 2 m above the ground at the tree bole and sloped to 0.5 m above the ground at their periphery to allow for water runoff. A drip collar was attached around the tree bole above each shelter to exclude stem flow. Tarp radius ranged from 4 to 6 m and was standardized as 2X crown radius. Standing vegetation within the shelter area was either removed (stems < 10 cm dbh) or accommodated by slitting and re-taping the tarp (stems ≥ 10 cm dbh). Similar removals were performed surrounding control trees to standardize disturbances.

To quantify the drought effect on soil moisture, volumetric water content (0–30 cm soil depth) was measured twice weekly (Fieldscout TDR 300, Spectrum Technologies, Plainfield, IL, USA). Soil moisture was recorded as the average of four measurements, one at each cardinal direction, collected at approximately 1 m from the bole of the tree. To explicitly determine drought effects on tree hydrology, shoot predawn moisture potential was quantified on 13 August 2015 by collecting branches using a pole pruner and measuring the force required to expel water from the cut end of a shoot placed in a pressure chamber (Plant Moisture Instrument, Model 615, PMS, Albany, OR, USA). Finally, to determine whether the presence of the tarp produced any experimental artifacts on microclimate, Hobo data loggers were fastened to the tree bole beneath the tarp of five drought trees and at an equivalent height on five control trees. Additionally, a PAR (photosynthetically active radiation) sensor was used to quantify potential tarp effects on sunlight penetration.

2.3. Insect performance and defoliation

Sleeve cages were checked twice weekly beginning 13 July 2015 to collect spruce budworm pupae. Pupae were transported to the laboratory and placed individually in plastic containers to allow eclosion. Adults were frozen at −18 °C, placed in an oven (70 °C for 48 h) to record dry weight, and measured under a microscope to record sex and wing length. Insect survival was recorded for each sleeve cage as:

$$\text{Number of adult moths recovered} / \text{Number of L2 larvae originally}$$

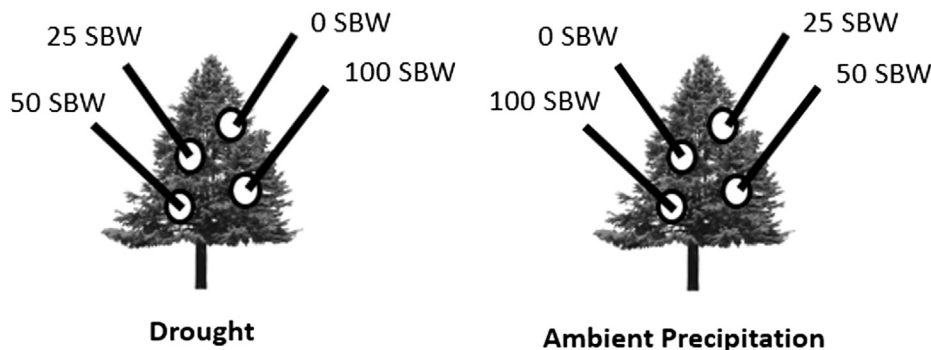


Fig. 1. Diagram of an experimental block. Within-block drought treatments as well as within-tree placement of density treatments were randomly assigned.

placed on the sleeve-caged branch

Following pupa removal, branch defoliation was recorded for new shoots as well as for 1-year-old shoots (C and C1, respectively) using a modified version of the Fettes method (Fettes, 1950). Briefly, shoot defoliation was scored in 5% increments and averaged over age class for each branch.

2.4. Statistical analyses

The effects of drought, spruce budworm density, and their interaction (all as fixed effects factors) were assessed for all feeding and insect performance responses. Given the split plot design, tree was included as a random effect to account for the use of multiple branches per individual. Defoliation results for the C and C1 shoot age classes approximated gamma and negative binomial distributions, respectively, and were analyzed using generalized linear mixed effects models. For insect performance responses, we used linear mixed effects models to assess male mass and female wing length responses. Generalized linear mixed effects models were used to analyze insect percent survival and total number of adult moth recovered (data for both responses approximated negative binomial distributions), as well as male wing length and female mass (gamma data distributions). Finally, we used a series of one-way ANOVAs to test for the effects of the rainout shelter on soil moisture, shoot predawn moisture potential, and air temperature. Relative humidity and PAR results approximated gamma and negative binomial data distributions, respectively, and were analyzed using generalized linear models. Where significant main or interactive effects were present, we used a Tukey's test to identify significantly different pairwise comparisons. All statistical analyses were conducted using the R platform (v. 3.5.1, "Feather Spray"), implementing the 'lme4' package (v. 1.1-18.1) to construct linear mixed effects models, the 'MASS' package (v. 7.3–50) to construct generalized linear models and the 'emmeans' package (v. 1.2.4) for post hoc Tukey's HSD tests.

3. Results

3.1. Hydrology and rainout shelter microenvironment

Shoot predawn moisture potential and soil volumetric water content (Fig. 2) were both significantly reduced under the drought treatment ($P < 0.001$ for each response; statistical results for all main and interactive effects presented in Table 1). The rainout shelter significantly increased air temperature ($P = 0.001$), but only by 0.1 °C. There was no effect of the rainout shelter on humidity or PAR.

3.2. Defoliation and insect survival

The 0 budworm treatment artificially inflated the significance of the density effect on defoliation and was therefore removed from the model and analyzed separately to quantify the effect of drought on foliage loss in the absence of budworm. When budworm were absent, drought significantly increased %foliage loss in current-year shoots (9.57 ± 3.38 vs. 1.22 ± 0.31 ; $P < 0.001$) but not in 1-year-old shoots (3.72 ± 0.94 vs. 2.09 ± 0.55 ; $P = 0.1$). Analysis of the remaining treatment levels indicated that density had a significant, positive effect on the defoliation of 1-year-old shoots ($P = 0.011$) but had no effect on the defoliation of current-year shoots (Fig. 3). Density had a significant, negative effect on spruce budworm survival ($P = 0.008$; Fig. 4a), but the total number of recovered adults was positively related to density ($P < 0.001$; Fig. 4b).

3.3. Insect body condition

Density had a negative, marginally significant effect on adult female mass ($P = 0.067$; Fig. 5a), and a significant interaction between density

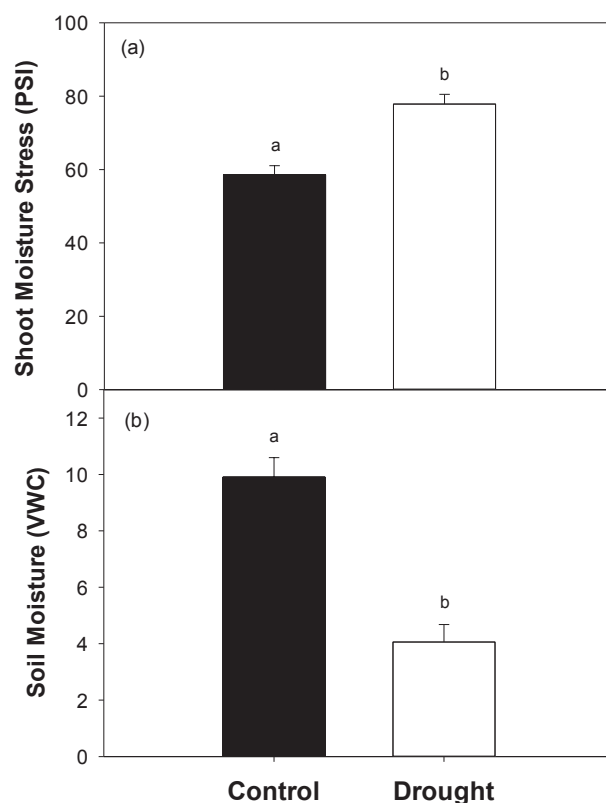


Fig. 2. Effects of drought on (a) balsam fir shoot moisture stress, and (b) soil moisture. Values represent means \pm SE. Different lowercase letters denote statistically significant pairwise differences ($P < 0.05$) in moisture content based on a post hoc Tukey's HSD test.

and drought ($P < 0.001$) indicated that this response was restricted to droughted trees. Neither drought, density, nor their interaction had a significant effect on female wing length or adult male mass (Fig. 5b, c), whereas increased density significantly decreased male wing length ($P = 0.001$; Fig. 5d).

4. Discussion

Despite this experiment having consisted of a single season of rain exclusion, we observed significant drought effects on both soil volumetric water content and shoot moisture potential (Fig. 2), although the lack of any obvious signs of severe tree water stress (e.g., brittle needles, extensive shoot dieback) suggests that the drought was likely moderate. Overall, our data revealed that across the wide range of outbreak population scenarios employed in this study, the effects of density (e.g., crowding and resource depletion) had greater influence than tree water stress in driving spruce budworm defoliation and performance. The absence of a defoliation response to water stress was somewhat surprising given the results of a recent meta-analysis revealed that defoliator damage generally increased in response to drought (Jactel et al., 2011). However, results for chewing insects were equivocal and the net effect only marginally significant. Also, the lack of a spruce budworm performance response to drought is consistent with a review published by Huberty and Denno (2004), although negative effects on chewing insects have been reported elsewhere (Koricheva et al., 1998).

4.1. Defoliation and survival

In the absence of budworm, needle loss in current-year shoots was approximately 8 times greater for droughted trees than for control trees

Table 1

Resultant *P* values for (a) the effects of drought, density, and their interaction on spruce budworm performance and defoliation, and (b) the effect of drought on hydrology and rainout shelter microenvironment. C and C1 denote current year, and one-year-old, foliage, respectively.

(A)	Insect survival	Total No. adults	Males		Females		Defoliation	
			Wing length	Body mass	Wing length	Body mass	C	C1
Drought	0.581	0.603	0.27	0.517	0.947	0.11	0.672	0.223
Density	0.008	< 0.001	0.001	0.901	0.169	0.067*	0.347	0.011
Drought × Density	0.164	0.164	0.207	0.823	0.905	< 0.001	0.983	0.288
(B)								
Shoot moisture								
Stress		Soil moisture	Temperature	Humidity	PAR			
< 0.001		< 0.001	0.001	0.125	0.585			

Bold numbering denotes a statistically significant effect.

* Denotes marginal significance.

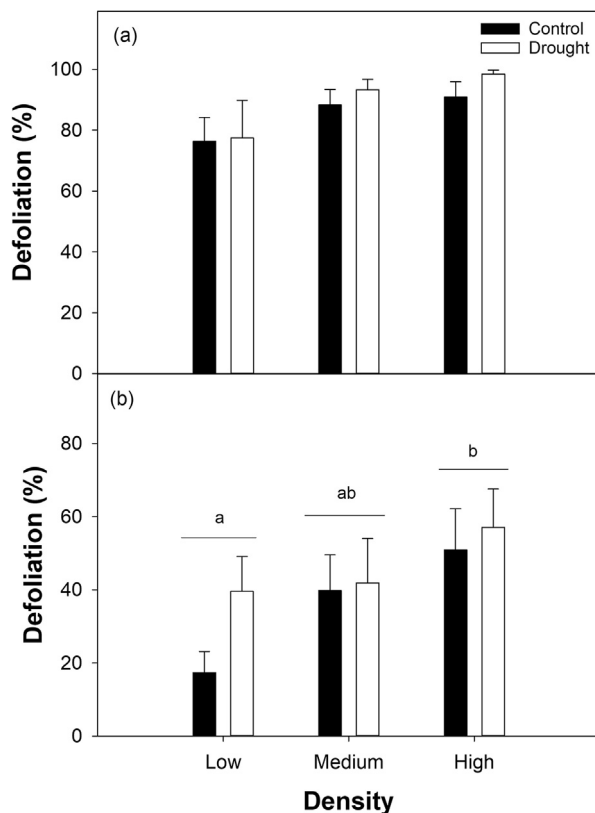


Fig. 3. Effects of drought and density on the defoliation of (a) current, and (b) 1-year-old balsam fir shoots. Values represent means \pm SE. Different lowercase letters denote statistically significant pairwise (pooled over drought) differences ($P < 0.05$) in defoliation based on a post hoc Tukey's HSD test.

(9.6 vs. 1.2%). However, when budworm were present, drought had no effect on feeding damage, and defoliation of current-year foliage was consistently high across all budworm densities (Fig. 3a), which reflects previous reports of extensive feeding by spruce budworm on balsam fir (MacLean and Ostaff, 1989; Hennigar et al., 2008). However, despite a general positive relationship there were no significant differences among treatment groups. Much of the defoliation can be attributed to bud damage prior to bud burst, which is common in spruce budworm (Miller, 1977; pers. obs.) and other Lepidopteran defoliators, including autumnal moth (*Epirrita autumnata* Borkhausen; Kaitaniemi et al., 1997). However, we did not observe complete defoliation even under the highest density treatment. Instead, feeding damage extended to older foliage, where defoliation of 1-year-old shoots increased significantly with density (Fig. 3b). Despite the negative consequences of feeding on older foliage (Blais, 1953; Delisle and Hardy, 1997), this back feeding can occur during spruce budworm outbreaks even if new

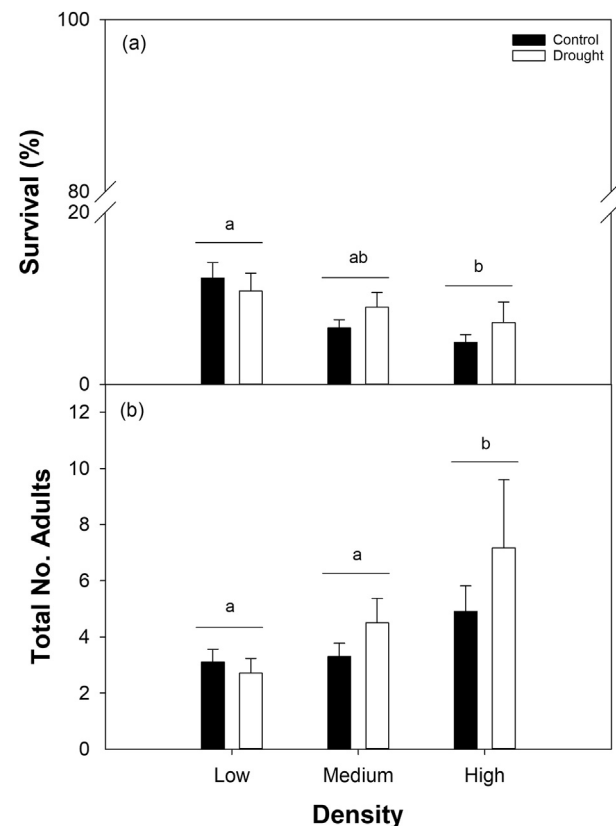


Fig. 4. Effects of drought and density on (a) spruce budworm percent survival, and (b) total number of adult spruce budworm recovered. Values represent means \pm SE. Different lowercase letters denote statistically significant pairwise (pooled over drought) differences ($P < 0.05$) based on a post hoc Tukey's HSD test.

shoots are not entirely exhausted (Royama, 1984).

Spruce budworm survival was negatively impacted by density (Fig. 4a), which contrasts with responses for other forest pests such as autumnal moth (Klemola et al., 2004). However, spruce budworm exhibits density-dependent mortality driven by a combination of natural enemies, disease, and competition (Royama, 1984). For instance, at outbreak densities, defoliation significantly decreased the survival of late-instar spruce budworm larvae (Régnière and Nealis, 2007). This self-limitation would have also contributed to the lack of complete defoliation we observed for current-year foliage. Despite this density effect on mortality, the total number of spruce budworm that survived to adulthood remained highest in the high density treatment, and was more than double the number collected from the low density treatment (6.4 vs. 2.6; Fig. 4b). Unsurprisingly, late-instar spruce budworm

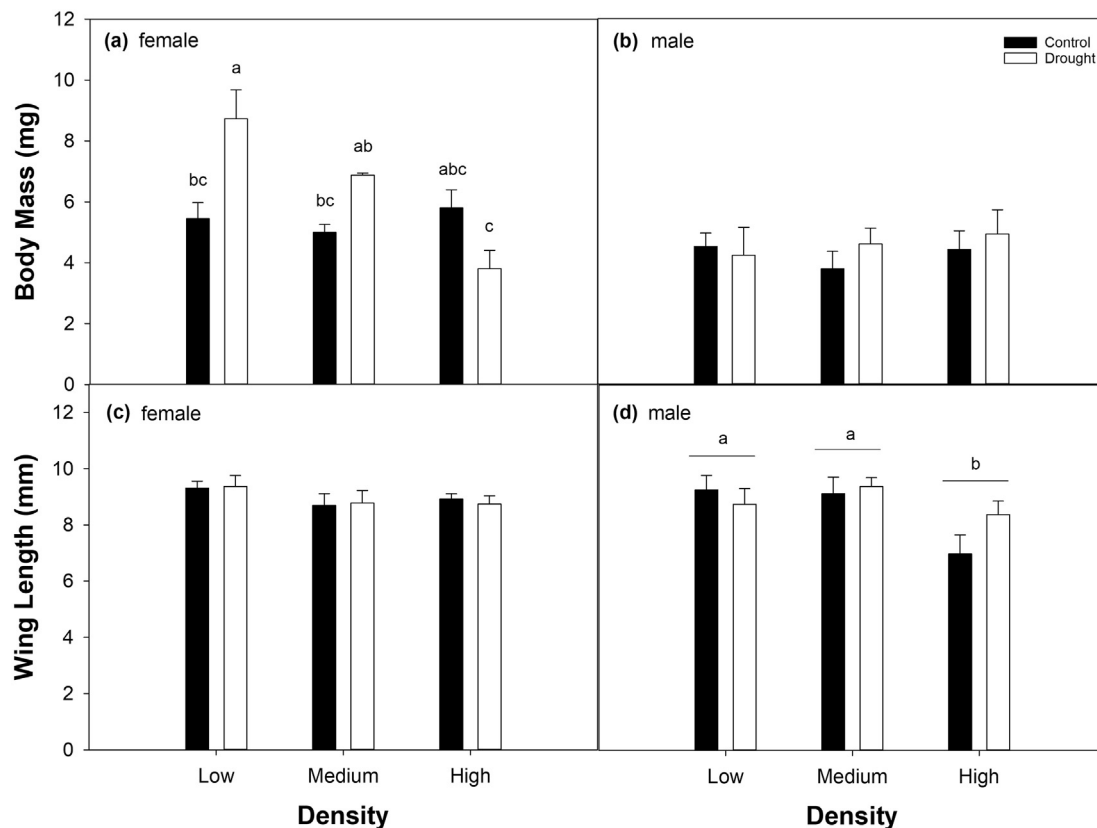


Fig. 5. Effects of drought and density on (a) adult female mass, (b) adult male mass, (c) adult female wing length, and (d) adult male wing length. Values represent means \pm SE. Different lowercase letters denote statistically significant pairwise (pooled over drought in panel d) differences ($P < 0.05$) based on a post hoc Tukey's HSD test.

density closely mirrors defoliation in balsam fir (Régnière and Nealis, 2007), and reflected the relationship between overall survivorship and defoliation present in our study.

4.2. Body condition

Larval density has important consequences for fitness in many insect groups (Peters and Barbosa, 1977; Harrison, 1980; Fescemyer and Hammond, 1986; Brent, 2010) and is reflected in the results from our study (Fig. 5). Furthermore, we observed a clear sexual dichotomy in responses. Increasing larval density had a significant, negative effect on the size of male wings, resulting in a 20% decrease in length (Fig. 5d). Similar results have been reported for gypsy moth (*Lymantria dispar* (L.)) when population outbreaks result in extensive defoliation (i.e., > 40%; Carter et al., 1991). Likewise, high larval densities reduced wing size in male autumnal moths (Ruohomäki, 1992). In turn, reduced wing size could influence dispersal capacity of male spruce budworm. Wing load, for example, could be increased during outbreaks because male body mass was insensitive to density (Fig. 5b). However, overall impacts on mating success would likely be minimal given that spruce budworm exhibits protandry (Nealis and Régnière, 2004), with females being mated immediately following eclosion and therefore prior to any significant dispersal event.

For the purposes of reproduction, a positive relationship between density and wing size is highly beneficial for female insects, given that local resources for offspring may become depleted as populations increase. Indeed, for many insect groups increasing density promotes the development of wings (i.e. alate or macropterous morphs) to facilitate dispersal to a more favorable environment (Harrison, 1980; Applebaum and Heifetz, 1999). Despite this benefit, female spruce budworm wing length was unaffected by density (range 8.85–9.33 mm; Fig. 5c),

although net dispersal capacity may still increase with population size because female body mass decreased with increasing density (Fig. 5a). However, this effect was only significant on water-stressed trees, possibly because it depended on insect performance in later stages, when impacts of drought on trees would have likely been most pronounced. This response is consistent with the negative effects of drought on insect mass reported elsewhere (Koricheva et al., 1998), and represents the only significant insect performance response to drought observed in our study. Additionally, because insect body size is correlated with fecundity (Honěk, 1993), any dispersal benefit arising from mass reduction would likely be offset by a loss in reproductive potential.

5. Conclusion

The outbreak of insect forest pests often coincides with warm, dry periods (Rouault et al., 2006; Raffa et al., 2008), intuitively suggesting that drought and density function in tandem to the benefit of insect performance. As with many other ecological relationships, however, the nature of the mechanisms that drive insect epidemics are highly complicated given the interspecific variation in insect life history and developmental plasticity. Additionally, despite our current knowledge of drought effects on plant–insect interactions, the extent to which water stress matters once populations reach epidemic levels is poorly understood (Jactel et al., 2011). Our results demonstrated that, across a broad range of outbreak densities, drought had a minor impact. The only significant insect response to rain exclusion was restricted to the performance of female moths, and given that drought can influence phytochemistry (McDowell et al., 2011), this may reflect higher sensitivity female insects tend to have to variations in host quality (e.g. Johns et al., 2010). Moreover, because larvae emerge early in the growing season, coupled with a potential lag period prior to trees exhibiting a

water stress response, spruce budworm may temporally escape much of the drought effect during the early part of their development. Despite evidence that climate change could fundamentally alter spruce budworm outbreak dynamics (Gray, 2008; Régnière et al., 2012), our results suggest that once populations approach epidemic levels, the influence of density on defoliation, insect survival and body condition may outweigh impacts of (moderate) drought stress.

Declarations of interest

None.

Acknowledgements

This project was supported by funding from the Canadian Forest Service. Additional support for technicians was provided by the Natural Resources Canada Science Internship Program. ERDM was supported by the NSERC Visiting Fellowships in Canadian Government Laboratories program. We are grateful to Lauren Stead, Garrett Brodersen, Rodney Foster and Zach Sylvain for field assistance, and are thankful for valuable reviewer feedback on a previous version of this manuscript.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2018.10.031>.

References

- Anderegg, W.R.L., Hicke, J.A., Fisher, R.A., Allen, C.D., Aukema, J., Bentz, B., Hood, S., Lichstein, J.W., Macalady, A.K., McDowell, N., Pan, Y., Raffa, K., Sala, A., Shaw, J.D., Stephenson, N.L., Tague, C., Zeppel, M., 2015. Tree mortality from drought, insects, and their interactions in a changing climate. *New Phytol.* 208, 674–683. <https://doi.org/10.1111/nph.13477>.
- Applebaum, S.W., Heifetz, Y., 1999. Density-dependent physiological phase in insects. *Annu. Rev. Entomol.* 44, 317–341. <https://doi.org/10.1146/annurev.ento.44.1.317>.
- Batzler, H.O., 1972. Net effect of spruce budworm defoliation on mortality and growth of balsam fir. *J. For.* 71, 34–37.
- Belyea, R.M., 1952. 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. *Can. Entomol.* 84, 325–335.
- Blais, J.R., 1953. Effects of the destruction of the current year's foliage of balsam fir on the fecundity and habits of flight of the spruce budworm. *Can. Entomol.* 85, 446–448. <https://doi.org/10.4039/Ent85446-12>.
- Blais, J.R., 1958a. Effects of defoliation by spruce budworm (*Choristoneura fumiferana* Clem.) on radial growth at breast height of balsam fir (*Abies balsamea* (L.) Mill.) and white spruce (*Picea glauca* (Moench) Voss.). *For. Chron.* 34, 39–47. <https://doi.org/10.5558/tfc34039-1>.
- Blais, J.R., 1958b. The vulnerability of balsam fir to spruce budworm attack in north-western Ontario, with special reference to the physiological age of the tree. *For. Chron.* 34, 405–422.
- Branson, D.H., 2016. Drought impacts on competition in *Pheoaltetes nebrascensis* (Orthoptera: Acrididae) in a northern mixed grassland. *Environ. Entomol.* 45, 492–499. <https://doi.org/10.1093/ee/nvv225>.
- Bréda, N., Huc, R., Granier, A., Dreyer, E., 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Ann. For. Sci.* 63, 625–644. <https://doi.org/10.1051/forest:2006042>.
- Brent, C.S., 2010. Stage-specific effects of population density on the development and fertility of the western tarnished plant bug, *Lygus hesperus*. *J. Insect Sci.* 10, 49. <https://doi.org/10.1673/031.010.4901>.
- Carter, M.R., Ravlin, F.W., McManus, M.L., 1991. Changes in gypsy moth (Lepidoptera: Lymantriidae) fecundity and male wing length resulting from defoliation. *Environ. Entomol.* 20, 1042–1047.
- Cooke, B.J., Nealis, V.G., Régnière, J., 2007. Insect defoliators as periodic disturbances in northern forest ecosystems. In: Johnson, E.A., Miyanishi, K. (Eds.), *Plant Disturbance Ecology: The Process and the Response*. Elsevier, Amsterdam, Netherlands, pp. 487–525.
- Delisle, J., Hardy, M., 1997. Male larval nutrition influences the reproductive success of both sexes of the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). *Funct. Ecol.* 11, 451–463. <https://doi.org/10.1046/j.1365-2435.1997.00114.x>.
- Elliott, K.R., 1960. A history of recent infestations of the spruce budworm in northwestern Ontario, and an estimate of resultant timber losses. *For. Chron.* 36, 61–82.
- Fescemyer, H.W., Hammond, A.M., 1986. Effect of density and plant age on color phase variation and development of larval velvetbean caterpillar, *Anticarsia gemmatilis* Hübner (Lepidoptera: Noctuidae). *Environ. Entomol.* 15, 784–789.
- Fettes, J.J., 1950. Investigations of sampling techniques for population studies of the spruce budworm on balsam fir in Ontario. *For. Insect Lab. Sault Ste. Marie, Annu. Tech. Rep.* 4, 163–401.
- Gray, D.R., 2008. The relationship between climate and outbreak characteristics of the spruce budworm in eastern Canada. *Clim. Change* 87, 361–383. <https://doi.org/10.1007/s10584-007-9317-5>.
- Harrison, R.G., 1980. Dispersal polymorphisms in insects. *Annu. Rev. Ecol. Syst.* 11, 95–118.
- Hennigar, C.R., MacLean, D.A., Quiring, D.T., Kershaw, J.A., 2008. Differences in spruce budworm defoliation among balsam fir and white, red, and black spruce. *For. Sci.* 54, 158–166.
- Honěk, A., 1993. Intraspecific variation in body size and fecundity in insects: a general relationship. *Oikos* 66, 483–492.
- Huberty, A.F., Denno, R.F., 2004. Plant water stress and its consequences for herbivorous insects: a new synthesis. *Ecology* 85, 1383–1398.
- Jactel, H., Petit, J., Desprez-Loustau, M.L., Delzon, S., Piou, D., Battisti, A., Koricheva, J., 2011. Drought effects on damage by forest insects and pathogens: a meta-analysis. *Glob. Chang. Biol.* 18, 267–276. <https://doi.org/10.1111/j.1365-2486.2011.02512.x>.
- Johns, R., Quiring, D., Ostaff, D., Baucé, É., 2010. Intra-tree variation in foliage quality drives the adaptive sex-biased foraging behaviors of a specialist herbivore. *Oecologia* 163, 935–947. <https://doi.org/10.1007/s00442-010-1632-2>.
- Kaitaniemi, P., Ruohomäki, K., Haukioja, E., 1997. Consumption of apical buds as a mechanism of alleviating host plant resistance for *Epirrita autumnata* larvae. *Oikos* 78, 230–238.
- Klemola, T., Ruohomäki, K., Andersson, T., Neuvonen, S., 2004. Reduction in size and fecundity of the autumnal moth, *Epirrita autumnata*, in the increase phase of a population cycle. *Oecologia* 141, 47–56. <https://doi.org/10.1007/s00442-004-1642-z>.
- Koricheva, J., Larsson, S., Haukioja, E., 1998. Insect performance on experimentally stressed woody plants: a meta-analysis. *Annu. Rev. Entomol.* 43, 195–216. <https://doi.org/10.1146/annurev.ento.43.1.195>.
- Lawrence, R.K., Mattson, W.J., Haack, R.A., 1997. White spruce and the spruce budworm: defining the phenological window of susceptibility. *Can. Entomol.* 129, 291–318. <https://doi.org/10.4039/Ent129291-2>.
- Logan, J.A., Régnière, J., Powell, J.A., 2003. Assessing the impacts of global warming on forest pest dynamics. *Front. Ecol. Environ.* 1, 130–137.
- MacLean, D.A., 1980. Vulnerability of fir-spruce stands during uncontrolled spruce budworm outbreaks: a review and discussion. *For. Chron.* 56, 213–221.
- MacLean, D.A., Beaton, K.P., Porter, K.B., MacKinnon, W.E., Budd, M.G., 2002. Potential wood supply losses to spruce budworm in New Brunswick estimated using the Spruce Budworm Decision Support System. *For. Chron.* 78, 739–750. <https://doi.org/10.5558/tfc78739-5>.
- MacLean, D.A., Ostaff, D.P., 1989. Patterns of balsam fir mortality caused by and uncontrolled spruce budworm outbreak. *Can. J. For. Res.* 19, 1087–1095.
- Mattson, W.J., Haack, R.A., 1987. The role of drought in outbreaks of plant-eating insects. *Bioscience* 37, 110–118. <https://doi.org/10.2307/1310365>.
- McDowell, N.G., Beerling, D.J., Breshears, D.D., Fisher, R.A., Raffa, K.F., Stitt, M., 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends Ecol. Evol.* 26, 523–532. <https://doi.org/10.1016/j.tree.2011.06.003>.
- Miller, C.A., 1977. The feeding impact of spruce budworm on balsam fir. *Can. J. For. Res.* 7, 76–84.
- Nealis, V.G., Régnière, J., 2004. Fecundity and recruitment of eggs during outbreaks of the spruce budworm. *Can. Entomol.* 136, 591–604. <https://doi.org/10.4039/n03-089>.
- Olesinski, J., Lavigne, M.B., Krasowski, M.J., 2011. Effects of soil moisture manipulations on fine root dynamics in a mature balsam fir (*Abies balsamea* L. Mill.) forest. *Tree Physiol.* 31, 339–348. <https://doi.org/10.1093/treephys/tpq006>.
- Peters, T.M., Barbosa, P., 1977. Influence of population density on size, fecundity, and development rate of insects in culture. *Annu. Rev. Entomol.* 22, 431–450.
- Pureswaran, D.S., De Grandpré, L., Paré, D., Taylor, A., Barrette, M., Morin, H., Régnière, J., Kneeshaw, D.D., 2015. Climate-induced changes in host tree — insect phenology may drive ecological state-shift in boreal forests. *Ecology* 96, 1480–1491.
- Pureswaran, D.S., Johns, R., Heard, S.B., Quiring, D., 2016. Paradigms in eastern spruce budworm (Lepidoptera: Tortricidae) population ecology: a century of debate. *Environ. Entomol.* 45, 1333–1342. <https://doi.org/10.1093/ee/nvv103>.
- Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., Romme, W.H., 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *Bioscience* 58, 501–517. <https://doi.org/10.1641/B580607>.
- Régnière, J., Nealis, V.G., 2007. Ecological mechanisms of population change during outbreaks of the spruce budworm. *Ecol. Entomol.* 32, 461–477. <https://doi.org/10.1111/j.1365-2311.2007.00888.x>.
- Régnière, J., St-Amant, R., Duval, P., 2012. Predicting insect distributions under climate change from physiological responses: spruce budworm as an example. *Biol. Invasions* 14, 1571–1586. <https://doi.org/10.1007/s10530-010-9918-1>.
- Rouault, G., Candau, J.-N., Lieutier, F., Nageleisen, L.-M., Martin, J.-C., Warzée, N., 2006. Effects of drought and heat on forest insect populations in relation to the 2003 drought in Western Europe. *Ann. For. Sci.* 63, 613–624. <https://doi.org/10.1051/forest:2006044>.
- Royama, T., 1984. Population dynamics of the spruce budworm *Choristoneura fumiferana*. *Ecol. Monogr.* 54, 429–462.
- Ruohomäki, K., 1992. Wing size variation in *Epirrita autumnata* (Lep., Geometridae) in relation to larval density. *Oikos* 63, 260–266.
- Stadler, B., Müller, T., Orwig, D., 2006. The ecology of energy and nutrient fluxes in hemlock forests invaded by hemlock woolly adelgid. *Ecology* 87, 1792–1804.
- Wallin, K.F., Raffa, K.F., 2001. Effects of folivory on subcortical plant defenses: can defense theories predict interguild processes? *Ecology* 82, 1387–1400.