

Differential defoliation and mortality of white spruce and balsam fir by Eastern spruce budworm
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Abstract:

Eastern spruce budworm (*Choristoneura fumiferana*) is a native defoliating insect in Canada and the United States that has large impacts on forest health. Balsam fir (*Abies balsamea*) and white spruce (*Picea glauca*) are its primary host trees, where budworm larvae consume buds and needles during larval development. While Eastern spruce budworm consumes both species, it is generally reported to defoliate balsam fir at higher levels. Investigating patterns and conditions that differentiate species' defoliation and mortality is informative for understanding susceptibility. We studied an outbreak of spruce budworm at plantations in northern Wisconsin, USA, with defoliation first detected in 2014 that appeared to have higher impacts on white spruce, which is counter to general expectations. In 2019, we quantified spruce budworm impacts on these two tree species and tested which tree characteristics were most associated with tree defoliation and mortality. We found mortality of 60% and 49% at the sites for white spruce trees, while 0% of the balsam fir trees surveyed were dead. We determined that tree species was the main factor related to spruce budworm defoliation, rather than tree diameter at breast height or canopy class and suggest that different timing of species-specific mast-seeding events were related to defoliation and tree mortality.

Short title: Interspecific tree mortality after spruce budworm outbreak

Keywords

White Spruce, Balsam Fir, Eastern Spruce Budworm, Defoliation, Forest Ecology

1. Introduction

Eastern spruce budworm (*Choristoneura fumiferana*; hereafter ‘spruce budworm’) is a native defoliator of a variety of species of coniferous trees in eastern North America (Bouchard et al., 2017), with historical large-scale outbreaks throughout Canada and the northern states of the United States. The most extensive and destructive outbreaks have occurred in the maritime provinces (New Brunswick, Nova Scotia, Newfoundland), Quebec, Ontario, Maine, and the Great Lakes states (Mattson et al., 1988). Spruce budworm outbreaks last 5 – 25 years and have occurred more or less periodically for at least 200 – 300 years (Boulanger and Arseneault, 2004; Ciesla and Mason, 2005). The impact of spruce budworm on forests can be considerable, including growth loss, cone and seed mortality, and widespread tree mortality (Blais, 1981; Mattson et al., 1988).

Spruce budworm moths lay their eggs on needles of conifer trees in late summer and larva emerge one to two weeks later and immediately enter diapause without feeding (Nealis, 2016; Régnière and Nealis, 2018). Following emergence in the spring after overwintering as larvae, they begin needle mining previous year's needles prior to bud burst in host trees, consuming new growth, and if available, pollen cones (McGugan, 1954). Female moths typically disperse their eggs by laying some of their clutch on one tree, then move onto another tree to lay more eggs (Royama, 1984). While spruce budworm prefers to feed on new (i.e., current-year) needles, multiple years of feeding results in the removal of all needles across age classes (Rahimzadeh-Bajgiran et al., 2018). Mortality resulting from budworm outbreaks in mature stands of host trees usually begins after approximately 4 or 5 years of severe defoliation (Houndode et al., 2021; MacLean, 1984; Solomon et al., 2003).

At the scale of a forest stand, factors contributing to growth loss and tree mortality due to

spruce budworm defoliation include a high composition of mature trees, a large percentage of balsam fir, open stands with tall trees protruding above the forest canopy, extensive and continuous spruce-fir stands, and a downwind position from current outbreaks (Witter et al., 1984). Outbreaks of eastern spruce budworm primarily affect balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), and red spruce (*Picea rubens*) (Boulanger et al., 2012; Hennigar et al., 2008; Schmitt et al., 1984). Spruce budworm larval survival and defoliation is also hypothesized to be positively related to reproduction in host trees (Blais, 1952; Bouchard et al., 2018; Mattson et al., 1991). Many species of conifers undergo mast seeding, the production of highly variably sized seed crops over time (Silvertown, 1980), and during ‘mast-events’ the seed crops are orders of magnitude above that of most years (LaMontagne and Boutin, 2009). The production of reproductive buds (e.g., pollen cones) provides a nutrient-rich food source for spruce budworm, and the allocation of energy to reproduction produces a tradeoff with allocation to growth and defence (Redmond et al., 2019).

While white spruce and balsam fir are similarly susceptible throughout the spruce budworm life cycle (Nealis and Régnière, 2004), balsam fir defoliation and mortality has been reported to be higher than white spruce (Blais, 1981; Hennigar et al., 2008; Nealis and Régnière, 2004). Balsam fir is thought to be the main host for spruce budworm because its spring budburst is synchronous with spruce budworm instar development (Hennigar et al., 2008). Studies have reported over 80% of trees being dead in mature balsam fir stands versus less than 50% mortality in white spruce stands (MacLean, 1980; Nealis and Régnière, 2004). Rapid early season growth in white spruce compared to balsam fir may reduce budworm defoliation in white spruce (Nealis and Régnière, 2004). However, Berthiaume et al. (2020) found that white spruce was a better host for spruce budworm than balsam fir, having produced heavier pupae and heavier

overwintering larvae.

A spruce budworm outbreak began in northern Wisconsin, USA, in 2012 (WI DNR, 2015) and we detected moderate levels of defoliation of some white spruce trees at study sites in Vilas County in summer 2014. Prior to 2011, spruce budworm was not mentioned in annual forest health reports for northern Wisconsin (WI DNR, 2010); however, by 2012 spruce budworm was detected in neighbouring counties (WI DNR, 2012), and reports of spruce budworm defoliation have persisted over multiple years (WI DNR, 2019). At our study sites, we noticed that white spruce trees appeared to have greater levels of defoliation and mortality rather than balsam fir since 2014 (LaMontagne and Leeper, personal observations), contrary to reports from the literature of higher levels of defoliation and mortality in balsam fir. Therefore, during summer 2019, we assessed the status of trees belonging to each species. Our main objectives were to 1) quantify mortality of white spruce and balsam fir following this spruce budworm outbreak, and 2) to examine the relationships between tree status (alive or dead) in 2019 and tree characteristics (diameter at breast height, proximity to dead trees, and crown class). We hypothesized that tree species will determine defoliation and the subsequent tree status in 2019 (alive or dead) five years after budworm activity was first detected at the sites. We tested predictions from the literature that that spruce budworm defoliated both species equally or that balsam fir would experience higher levels of defoliation. We also hypothesized that the 2019 tree status was dependent on tree characteristics; we predicted that the dead trees would have a larger diameter at breast height (DBH) and be taller than the canopy or in an open growth crown class. We also discuss the findings in the context of reproduction in each conifer species.

2. Material and methods

2.1. Study area

Our study took place in Vilas County, Wisconsin, USA (45.98° N, 89.46° W), a region within the distribution range of eastern spruce budworm, and we focus on two study sites (KDD and KPE) separated by 10.5 km. These sites are plantations, and were comprised of mixed wood forests with predominantly white spruce, balsam fir, and some eastern white pine (*Pinus strobus*), maple (*Acer* spp.), and birch (*Betula* spp.). A spruce budworm outbreak was reported in neighbouring counties of northern Wisconsin in 2012 (WI DNR, 2015) and in July 2014 we observed evidence of defoliation at these sites consistent with spruce budworm and identified spruce budworm pupal casings within the trees (Fig. 1). These observation were consistent with state-level forest health reports of “light to moderate defoliation” in the area (WI DNR, 2014).

2.2. Tree mortality by species

We assessed site-level tree mortality of white spruce and balsam fir in July 2019 using modified 'point count' visual surveys. For these surveys, an observer stood at point locations in an open area (e.g., a clearing or a meadow) to count the number of ‘alive’ and ‘dead’ trees seen within 360° or 180° of points (modified from Freemark and Rogers, 1995; Mitchell et al., 1995). At each point, surveys were performed over the same area for both white spruce and balsam fir. We classified trees as alive if they had some green needles, even if there was some defoliation, and classified as dead if trees were completely defoliated. While mortality does not necessarily occur at the same time as severe defoliation, we checked the status of all white spruce trees in the study annually between 2014 and 2021, and we observed no regrowth of needles on any trees that were classified as dead in 2019. At KDD, these surveys were done at four points along a road that intersected the site with the observer conducting 180° visual surveys at two-point locations and 360° visual surveys at two-point locations. At KPE, we used three-point locations and conducted 360° visual surveys at each location.



Fig. 1: Evidence of spruce budworm defoliation on white spruce included a) characteristic patterns of defoliation of needles (shown here in 2014), and b) presence of pupal casings on trees. c) By 2019, many trees at the study sites had been completely defoliated. (Photos by LaMontagne).

2.3. *Tree characteristics related to tree mortality*

We assessed the characteristics of a total of 113 individual white spruce and balsam fir trees across the two sites to determine if they were related to individual-level tree mortality (KDD: n = 34 white spruce, n = 26 balsam fir; KPE: n = 26 white spruce, n = 27 balsam fir). Trees were selected throughout the sites. For white spruce trees this included every third numerically tagged tree (as trees had been previously tagged for a long-term study on cone production) and included all dead tagged trees when encountered. Balsam fir trees were selected throughout the same area of the sites as the white spruce trees, at approximately the same spacing as white spruce in order to obtain similar sample sizes. For each tree, we recorded its status (alive or dead), measured its diameter at breast height (DBH; with a minimum DBH cutoff for inclusion being 10 cm), and its crown class. We adapted crown classes (DeYoung and Sutton 2016) as an assessment of tree height relative to other trees in the stand, based on access to sunlight. Open grown (OP) trees either grew separated from other trees or had a crown that substantially surpassed (in height) the trees that surrounded it. Dominant (DO) were trees that were able to intercept more sunlight from the top and sides of the tree for most of the day than surrounding trees. Codominant (CO) trees were similar in height to surrounding trees and intercepted sunlight via the top of the crown for most of the day. Intermediate (IN) trees gather little sunlight through small gaps within the canopies of CO and DO trees in their respective populations. Overtopped (OV) were subcanopy trees that had little to no direct sunlight.

2.4. *Potential relationship with cone production*

We have cone production data on white spruce trees based at each of the two sites (n = 60 trees per site) in 2012, 2013, and 2014. To quantify cone production, an observer stood in a

location where the top crown of an individual tree was in full view and the total number of visible cones were counted or a photograph was taken if there were more than approximately 200 cones (LaMontagne et al., 2005) to be counted using ImageJ software (Schneider et al. 2012). Estimation of total cones was determined following LaMontagne et al. (2005). Balsam fir cone production is from photos taken of balsam fir trees in 2014. Based on the high level of cone production in 2014 (see results), tree reproduction was inferred to be low in 2013 because mast-seeding trees do not show mast events in consecutive years (Holland and James, 2014; LaMontagne et al., 2020; LaMontagne and Boutin, 2009). Due to differences in the level of detailed sampling for white spruce and balsam fir cone production, reproduction was not included explicitly in statistical analyses, however it was a species-specific difference.

2.5. Statistical Analyses

To test the hypothesis that tree species influenced tree defoliation and mortality following the spruce budworm outbreak (objective 1) we used the Cochran–Mantel–Haenszel test. This is an inferential test for the association between two binary variables, while controlling for a third confounding nominal variable (Cochran, 1954; Mantel and Haenszel, 1959). Our test of association used data on alive and dead trees for each species from point-count sampling data, tree species, and accounted for the two sites. To test the hypothesis that individual tree characteristics were related to tree mortality (objective 2), we fit generalized linear mixed effects models, with tree status (alive, dead) as a binary response variable, and independent variables of tree species, DBH, the interaction between species and DBH, crown class, and site as a random effect using the *lme4* package (Bates et al., 2015). From this global model, we used AICc model selection to find the best model(s) based on Δ AICc values and AICc weights (Burnham and Anderson, 2002) using the *MuMIn* package (Bartoń, 2018). For inferential statistical tests we

used an α value of 0.05 for statistical significance. R studio 1.2.1335 was used to conduct analyses.

3. Results

3.1. Tree mortality by species

We found a significant difference in tree mortality following the spruce budworm outbreak in white spruce-balsam fir forest stands, based on tree species ($\chi^2 = 73.61$, $df = 1$, $P < 0.001$). By 2019, only white spruce trees had been completely defoliated and were classified as dead. At the KDD site, 65% of white spruce trees in point counts were dead (62 of 95 trees) and 0% of balsam fir trees were dead (0 of 22 trees). Similarly, at the KPE site, 53% of white spruce tree in point counts were dead (73 of 139 trees) and 0% of the balsam fir trees (0 of 55 trees).

3.2. Tree characteristics related to mortality

Similar to the point-count data, the subset of focal trees sampled to assess tree characteristics at each site were comprised of 56% dead white spruce trees and 0% of balsam fir trees at KDD, and 42% dead white spruce trees and 0% of dead balsam fir trees at KPE. Based on these trees, the best model to describe patterns of tree mortality in 2019 following the 2014 spruce budworm outbreak included only tree species (AICc weight = 0.69; Table 1) with white spruce trees more likely to be dead than balsam fir trees. The next best model included tree species and DBH, with larger trees more likely to be dead; however, this model had a $\Delta AICc$ value >2 compared to the best model and an AICc weight of 0.24. Terms not included in the best model included DBH (Fig. 2), the interaction between species and DBH, and crown class of trees (Fig. 3).

Table 1: Model selection results for white spruce and balsam fir tree mortality in 2019 following a 2014 spruce budworm outbreak in northern Wisconsin, USA. Models with AICc weights <0.01 are not shown. 'k' represents the number of parameters in each model, 'LL' is the log-likelihood.

Model terms	k	LL	ΔAICc	AICc weight
Species	4	-40.17	0.00	0.69
Species + DBH	5	-40.16	2.13	0.24
Species + Crown class	8	-38.41	5.35	0.05
Species + DBH + Crown class	9	-38.26	7.38	0.02

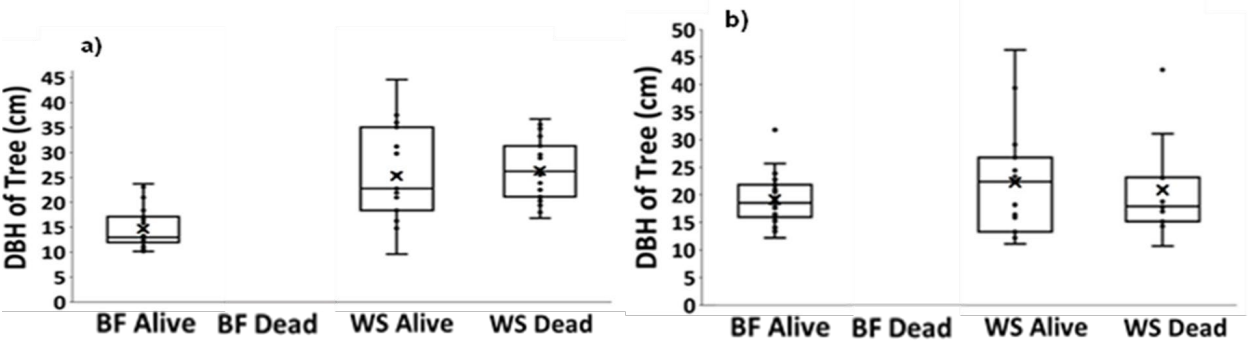


Fig. 2: Characteristics of trees classified as alive and dead in northern Wisconsin, USA, in 2019 following a spruce budworm outbreak detected in 2014. Data include diameter at breast height (DBH; cm) of balsam fir (BF; alive (n = 52 trees), dead (n = 0 trees)) and white spruce (WS; alive (n = 30 trees), dead (n = 30 trees)) in 2019 at two sites, a) KDD, b) KPE. Points represent values for individual trees, 'x' is the mean, and notes that the BF Dead category was included because it is a potential state the balsam fir trees could exhibit, although there were none.

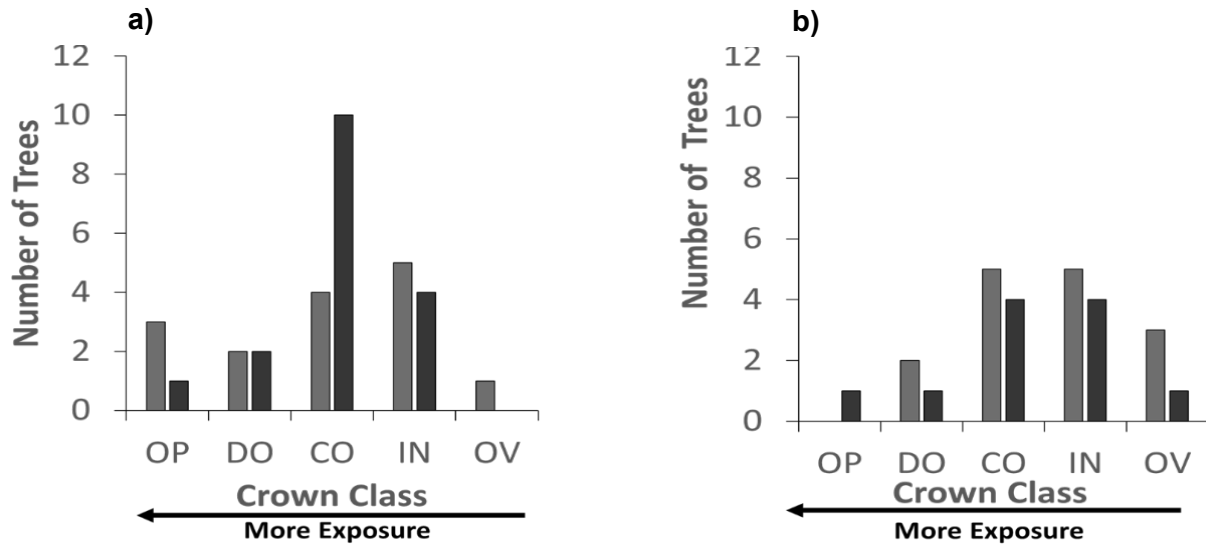


Fig. 3: Frequency distributions of the crown class of alive (gray) and dead (black) white spruce trees assessed in summer 2019 at two sites, a) KDD, b) KPE. OP = open growth, DO = Dominant, CO = Codominant, IN = Intermediate, OV = Overtopped.

3.3. Cone Production

In the two years prior to the observation of spruce budworm defoliation at these sites, mean white spruce cone production was 186 cones per tree in 2012, 691 cones per tree in 2013, and 6 cones per tree in 2014. For balsam fir, there were not abundant cones observed on trees in 2012 or 2013 (LaMontagne, personal observation), while in 2014 balsam fir cone production was high (Fig. 4 shows a tree with 230 cones counted using ImageJ), also suggesting that balsam fir cone production was low in 2013 (the high cone production year for white spruce).



Fig. 4: Balsam fir trees in the study area produced large cone crops in 2014, as shown here with 230 visible cones (photo taken on 8 August 2014, by LaMontagne).

4. Discussion

4.1. Summary of results

Our data showed white spruce trees experienced higher mortality than balsam fir at our sites following a spruce budworm outbreak, contrary to expectations based on previous literature

(Blais, 1981; Hennigar et al., 2008). By 2019, five years after we first observed defoliation, white spruce trees had experienced 60% and 49% mortality at the sites, whereas balsam fir trees had experienced 0% mortality. Neither tree size (DBH), nor canopy class were factors included in the best model explaining tree mortality. The only factor included that explained patterns of mortality following the initial observation of spruce budworm defoliation in 2014 at these sites was tree species. We expected trees that stood above the canopy may intercept more flying females and therefore have more eggs deposited and therefore have higher levels of defoliation and mortality, but that was not the case. In addition, spruce budworm defoliate trees of a range of sizes including those with smaller DBH (Russell and Albers 2018), however smaller trees are less vulnerable to mortality (Miller 1975), but we did not find this during our study.

4.2. Balsam fir vs white spruce defoliation patterns

We expected at a minimum for balsam fir and white spruce to be defoliated equally. However, our observations reported here showed that equal defoliation or a bias towards more balsam fir defoliation was not the case. Differential mortality in white spruce and balsam fir followed differences in defoliation observed in 2014; while there were high levels of defoliation on white spruce (e.g., Fig. 1a), balsam fir trees showed minimal needle loss (e.g., Fig. 4). Over time, substantial tree mortality after five years of defoliation has been shown (Houndode et al., 2021), and consistent with this we saw low white spruce mortality in 2015 and cumulative mortality increased over time to 2019 (Leeper 2020). While the literature tends to report higher defoliation and mortality in balsam fir compared to white spruce, some studies have revealed instances where white spruce is the better host tree. Nealis and Régnière (2004) showed superior foliar quality of white spruce for larval development and Berthiaume et al. (2020) found significantly heavier spruce budworm pupae and significantly heavier overwintering larvae were

associated with feeding on white spruce compared to balsam fir or black spruce. It has been suggested that balsam fir is the main host species due to its earlier flush of buds that is synchronized with larval development in spring, and that defoliation of balsam fir is greater than white spruce (Hennigar et al., 2008). However, defoliation by spruce budworm advances white spruce bud-burst the subsequent year, by 3.5 days (Deslauriers et al., 2019), making up the interspecific difference in bud-burst timing with balsam fir, which may also contribute to future increased defoliation of budworm on white spruce.

Supporting our findings of spruce budworm related mortality in white spruce, the presence of spruce budworm has been a significant decline factor for white spruce and a predictor of tree mortality in the Wisconsin, Michigan, and Minnesota region of the United States (Brewster, 2009). At field sites in nearby Oneida County, WI (to the south of the Vilas County area of the present study), where spruce budworm defoliation had not been observed, only 4% of white spruce trees were dead in 2019 (Leeper et al., in review), vastly fewer than the mortality at sites in this study, and no balsam fir trees were dead. This lack of balsam fir mortality both at sites with and without spruce budworm activity is interesting, and somewhat unexpected if tree reproduction were to play a role in defoliation (see 4.3), as while balsam fir did not have high reproduction in 2013, it did in 2014. The weakened state of white spruce following the 2013 mast-seeding event made these trees more susceptible to defoliation and mortality due to issues related to resource allocation (see 4.3). It could be that white spruce is the better host and consequently females in the region of study preferentially laid eggs on white spruce, using monoterpenes to identify host trees (Ennis et al., 2017), or some combination of the above. The mechanisms driving differential mortality between host species is an area for future research.

4.3. *Tree reproduction, allocation, and impacts of defoliation*

A link between high levels of reproduction in host conifer species and the timing of spruce budworm outbreaks has been hypothesized (Bouchard et al. 2017). The host conifer species for spruce budworm undergo mast seeding. Mast-seeding events occur in years when a population of trees produces a superabundance of reproductive structures (Kelly 1994), and this could be important for spruce budworm preferentially feeds on pollen cones (Régnière and Nealis 2018). Our cone production data reveal a high level of reproduction for white spruce at these sites and region-wide in 2013 (Leeper, 2020), the year prior to our first detecting defoliation at these sites. High white spruce reproduction could have led to higher spruce budworm larval survival and greater mass, so they consumed more foliage, and the larger females who weighed more may lay most of her eggs on the white spruce, so the balsam fir would not be impacted as severely. For spruce budworm, females producing a large number of eggs have had access to high quality food resources and lay half of their eggs on their natal tree before dispersing (Miller, 1975), leading to higher defoliation of individual white spruce trees.

Mast-seeding events depress tree resources preventing large reproductive events from occurring in consecutive years (LaMontagne et al., 2020; LaMontagne and Boutin, 2009) and impacting tradeoffs in allocation. Resource allocation to high levels of reproduction in trees has created tradeoffs with growth (Hacket-Pain et al., 2015) and defence (Redmond et al., 2019). This reallocation of resources, combined with defoliation and the loss of needles required for photosynthesis, and reduced radial growth, negatively impacts the carbon balance of defoliated trees (Deslauriers et al., 2019). Thus, while the flushing of epicormic buds can be a response of conifer trees (including white spruce and balsam fir) to defoliation (Nealis and Régnière, 2004) allowing trees to compensate and recover from lost needles (Piene, 1989; Piene and Eveleigh,

1996; Poirier, 2017), the development of buds requires resources. Perhaps due to mast seeding in white spruce and trade-offs in resource allocation, the trees did not have the reserves to use to produce epicormic buds.

4.4. *Alternative explanations of observed results*

Alternative explanations for our observed outcome, although less likely, include that other insects, such as spruce bark beetle (*Dendroctonus rufipennis*) could lead to differential mortality in white spruce and balsam fir, however only a single tree at our site has been killed following spruce bark beetle attack (LaMontagne, pers. obs.). *Rhizosphaera* needle cast (*Rhizosphaera kalkhoffi*) had been detected to cause needle loss for some spruce trees in Wisconsin as of 2019, but this was primarily affecting blue spruce (*P. pungens*) (WI DNR, 2019), so was also not likely responsible for our findings. Maybe late new growth budding in the balsam fir, which normally would occur prior to white spruce, thus made spruce preferable to spruce budworm larvae (Albert and Jerrett, 1981); we do not have data on the timing of budburst in the population we studied or spruce budworm densities on individual trees. This information could help understand spruce budworm preferences for different host species; however, it has been reported that balsam fir is more susceptible to spruce budworm defoliation (Hennigar et al., 2008; MacLean, 1980; Nealis and Régnière, 2004). Drought could be another factor, however while summer 2012 was ‘abnormally dry’ in the county our research was done, there were not drought conditions in the area during our study (US Drought Monitor, 2021), and white spruce is known to be quite drought tolerant (Nienstaedt and Zasada, 1990).

4.5. *Conclusion and future research*

Mast-seeding patterns are influenced by weather conditions (Kelly and Sork, 2002; Koenig and Knops, 2000; LaMontagne et al., 2020), and some species have similar cues related

to temperature and precipitation (LaMontagne et al., 2021; Wang et al., 2017). The development time for white spruce and balsam fir seed is similar, and similar patterns of seed production over time have been seen (Rossi et al., 2012). Bouchard et al. (2017) connected spruce budworm outbreaks to mast-seeding events over time, linking white spruce mast seeding and spruce budworm captures in balsam fir forest. However, the timeframe between large seed crops in balsam fir and white spruce vary (Frank, 1990; Nienstaedt and Zasada, 1990), and there can be variation in mast-seeding patterns over time across species (LaMontagne et al., 2021; Wang et al., 2017), therefore mast events for these two species will not always coincide. Overall, there have been relatively few community-level mast-seeding studies of trees conducted (Wang et al., 2017). Our results show an instance in which white spruce experienced higher levels of defoliation compared to balsam fir in a mixed stand of mature individuals. Tree species was the determining factor of defoliation by eastern spruce budworm and timing of a mast-seeding event and species-specific asynchrony in mast-event timing may impact future tree survival, and is an area for more future research.

CRedit author contribution statement – **Cristian Corona:** Methodology, Formal analysis, Investigation, Writing- Original draft preparation. **Abigail Leeper:** Methodology, Formal analysis, Writing- Reviewing and Editing. **Jalene LaMontagne:** Conceptualization, Writing- Reviewing and Editing, Supervision, Funding acquisition.

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