Cone characteristics and insect predation levels vary across years in mast seeding white spruce

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Abstract (196/200 words)

Populations of many tree species exhibit synchronous and highly temporally variable seed crops across years. This is called mast seeding, and there are two predominant hypotheses for this pattern of reproduction, pollination efficiency and seed-predator satiation. Mast seeding studies typically involve records of population-level reproduction, with less information on the characteristics of reproductive structures. Here, we use data across six years (2012-2017), spanning a range of population-level cone conditions, to characterize i) white spruce (*Picea glauca*) cone lengths and seeds per cone, and ii) levels of seed predation. We quantified population-level cone production and collected 1,399 cones from a total of 38 trees in the Huron Mountains, Michigan, USA. Linear mixed models showed that mean and minimum cone lengths varied significantly across years; both being longest during the greatest cone production year. Larger cones had more seeds and the slopes of the relationships as well as the intercepts varied significantly across years. Generalized linear mixed models and AIC model selected showed that cones with insect predation damage was greatest when population-level reproduction was the lowest, with a mean proportion of cones damaged 0.82 in that year. Our findings show that white spruce cone characteristics and losses to insect seed predation vary temporally, and follow expectations based on mast seeding hypotheses.

Keywords: cone length, mast seeding, pollination efficiency, predator satiation, white spruce

Introduction

Plants display a wide range of reproductive patterns, from low variation in reproduction across years, to ‘mast seeding’ which is the synchronous and highly temporally variable production of seed crops by a population of perennial plants (Janzen 1976; Kelly 1994). Highly temporally variable reproduction is a common pattern seen in numerous plant species around the world (Sork 1993; Koenig and Knops 2000; Kelly and Sork 2002; Kelly et al. 2008; Wang et al. 2017) including deciduous trees (Silvertown 1980; Sork 1993), coniferous trees (Greene and Johnson 2004; LaMontagne and Boutin 2009), as well as grasses and herbs (Kelly et al. 2013). Mast seeding has implications for forest regeneration; for instance, following a disturbance in mixed wood forests (e.g., fire), up to 10 times as many white spruce (*Picea glauca*) seedlings establish following heavy seed crops as opposed to light seeds crops (Purdy et al. 2002). Large reproduction years (often referred to as 'mast-seeding events' or 'mast years') also act as a resource pulse and directly impact populations of seed-predator species including mammals, birds, and insects, and has cascading effects on communities (Ostfeld and Keesing 2000; Clotfelter et al. 2007; Kelly et al. 2008).

There are two predominant evolutionary hypotheses to explain mast seeding, the pollination efficiency hypothesis and the predator satiation hypothesis (Kelly 1994; Kelly and Sork 2002). For both hypotheses, large reproductive efforts should be more efficient than small ones, called an 'economy of scale' (Janzen 1970; Norton and Kelly 1988; Kelly and Sork 2002; Bogdziewicz et al. 2020; Pearse et al. 2020). The pollination efficiency hypothesis states that synchrony in large reproductive efforts increases pollination success for wind pollinated plants (Nilsson and Wästljung 1987) and temporal variability in reproduction is also higher in wind-pollinated species than those with other pollination modes (i.e., animals) (Herrera et al. 1998;

Wang et al. 2017; Bogdziewicz et al. 2020; Pearse et al. 2020) because there are not pollinator species to saturate (Sork 1993; Kelly and Sork 2002). Consequently, the percent of fruit set (a measure of pollination success) is higher when reproduction is higher (Allen and Platt 1990), and in general, seed quality is highest in years of heavy seed production and lowest in years of low seed production (Nienstaedt and Zasada 1990). For instance, larger acorns are produced in years of larger seed crops (Koenig et al. 2009). The predator satiation hypothesis suggests that periods of low reproductive output combined with the sporadic production of large seed crops within a population of plants reduces losses to seed predators (Janzen 1971). Large seed crops satiate seed predators such that a higher proportion of seeds escape consumption, while a lack of seed production keeps predator populations low in the intervening years (Kelly and Sullivan 1997). The change in seed crop level from year to year influences seed predator populations more than seed crop levels in any given year (Kelly and Sullivan 1997). However, for some seed predators, prey-switching at low seed production levels leads to a type-III functional response, as seen in the North American red squirrel (*Tamiasciurus hudsonicus*; Fletcher et al. 2010) where, for non-mast years, the highest proportional predation of cones occurred at intermediate cone production. Diapause in insects can also influence the numerical response of the seed predators to temporal fluctuations in seed production by a plant population (Kelly and Sork 2002).

While there is evidence for spatial and temporal synchrony in mast seeding over large spatial extents (Koenig and Knops 1998; Pearse et al. 2020), variation in reproductive patterns occurs in individuals within populations over a local scale (LaMontagne and Boutin 2007; Mooney et al. 2011; Munilla and Guitián 2014; Bogdziewicz et al. 2020). Data from individuals are important for testing potential costs of individual variation within a population (Ims 1990; Kelly 1994; LaMontagne 2020). For instance, even in low reproduction years, 10-30% of white

spruce trees produced large cone crops (LaMontagne and Boutin 2007). However, there is relatively little data on reproductive characteristics and seed predation based simultaneously on individual trees and population-level data. Recent work by Bogdziewicz et al. (2020) showed that European beech trees (*Fagus sylvatica*) with higher temporal variability and higher synchrony with conspecifics had lower percentage seed losses to predators than trees with low variability and low synchrony. Here we investigated the characteristics of reproductive structures produced by individual trees of a conifer species, white spruce, which produces many seeds per cone, and the intensity of insect predation across a range of population-level mast-seeding conditions.

We collected data on white spruce reproduction and sampled cones from a set of tagged individual white spruce trees to assess cone characteristics across six years, including very large reproduction years, and seed production and insect predation on cones across four years. White spruce is well-characterized as a mast seeding species that undergoes large fluctuations in population-level reproduction (Nienstaedt and Zasada 1990; LaMontagne and Boutin 2007, 2009; Krebs et al. 2012; LaMontagne 2020) Multiple species of cone and seed insect predators of white spruce (e.g., *Strobilomyia neanthracina*, *Dioryctria reniculelloides*, *Cydia strobilella*) lay eggs in spring between budburst and pollination periods (Turgeon et al. 2005). For instance, female *S, neanthracina* cone maggot flies lay one or a few eggs between conelet scales in spring during the pollination period while female cone strobili are open, and chemically mark cones to discourage other female conspecific flies from laying eggs (FGC Pest Leaflet No. 5). We hypothesized that population-level mast conditions influence the relationship between the number of cones produced by individual trees and cone length (and number of seeds). In white spruce, two seeds are produced at the base of each cone bract, and longer cones have more seeds

(Waldron 1965; Caron and Powell 1989), therefore we predicted that cones would be longer (including mean, minimum, and maximum cones lengths) and have more seeds during mast-seeding events due to an increased investment in reproduction compared to non-mast years. Following the predator satiation hypothesis, we hypothesized that the proportion of insect predated cones would be related to magnitude of population-level reproduction. We predicted the highest proportion of insect predated cones would occur during low years of reproduction and the lowest losses to seed predators would occur during high reproduction 'mast events'.

METHODS

SITE DESCRIPTION

We collected data at four sites within a 14 km^2 area, each consisting of a stand of trees with white spruce present, in the Huron Mountains, Michigan (46.82°N, 87.73°W). The forest tree community is characteristic of the boreal-deciduous forest ecotone and in addition to white spruce there is white pine (*Pinus strobus*), balsam fir (*Abies balsamea*), eastern hemlock (*Tsuga canadensis*), maple (*Acer spp.*), trembling aspen (*Populus tremuloides*), and paper birch (*Betula papyrifera).* This region of the Huron Mountains includes a portion of old-growth forest where fire has been a key natural disturbance (Simpson et al. 1990; Muzika et al. 2015). The closest weather station located 12 km away in Big Bay, MI, had 30-year (1981-2010) monthly mean (± SD) June – August temperatures of 17.8 ºC (± 5.2) (minimum = 11.6 ºC (± 4.4), maximum = 24.0 ºC (± 7.1)); mean total monthly precipitation was 84.8 mm (https://www.nodc.noaa.gov/).

CONE COLLECTION and PROCESSING

Trees included in this study are a part of a larger study of 364 individual white spruce trees; individual trees were larger than 10 cm diameter at breast height, appeared healthy (no insect damage or crown damage), and the top of the crown of the tree was visible, to ensure that cones

129 could be counted by an observe in the field (see below). Over a six-year period (2012-2017) we
130 collected cones opportunistically from beneath a total of 38 individual trees within the study area
131 between late July and early August (n = 1,399 total cones). Seed matures in cones in the summer
132 and red squirrels (*Tamiasciurus hudsonicus*) bite off and drop cones from trees after seed
133 maturity to later cache (Fletcher et al. 2010). This was our data collection method as the trees
134 were too tall to sample and because they are long-term study trees we did not want to collect
135 samples in ways that would damage trees. Mature green cones have to be physically broken off
136 from the branchlets to fall from trees, accordingly, seeing a number of green cones on the ground
137 under a tree is attributed to red squirrels. Otherwise, white spruce cones stay on trees well into
138 the autumn (Garcia et al. 2021), and fall off at some point after the cones dry and open to release
139 seed. All cones used in the study were not deformed in any way, to avoid if there were other
140 reasons for cones to drop. Cones used in this study were collected from the surface of the ground
141 under the crown of focal trees with either no nearby neighboring white spruce trees or
142 neighboring trees with no cone production. Only new cones which were green and closed were
143 collected and the goal was to collect approximately 40 cones per tree. As opposed to sampling a
144 few cones from many trees, we focused on a smaller sample of trees and having more data per
145 tree to address our research questions of cone size-seed number relationships due to variability in
146 cone size, and the proportion of cones with insect predation. Upon collection, cones were
147 wrapped in burlap and placed in the refrigerator until returning to the lab where cones were dried
148 at room-temperature (23˚C). Cone lengths were measured and cones were dissected to count the
149 total number of seeds. The relationship between green cone length (before opening) and dry cone
150 length was correlated using cones in 2015 and 2016, and the correlation was highly positive and
151 significant ($r = 0.97$, $df = 421$, $p < 0.001$). Dry length, hereafter referred to as ‘cone length’ is

used in the analysis across years.

CONE PRODUCTION

White spruce cone production was quantified using visual counts from the ground each year in late July or early August that were then converted to an estimate of total cones per tree (following LaMontagne et al. 2005). Briefly, cone counts were performed by a stationary observer, using binoculars, standing in a constant location on one side of a tree. All visible new cones were counted. Trees having more than 200 visible cones were photographed and counts of visible cones were performed in ImageJ. From this index of cone production, total cone production by individual trees was estimated using an established relationship (LaMontagne et al. 2005). Population-level cone production was based on a collection of the same 364 individually tagged trees in the study area; it was from a sample of these trees that reproductive cones were collected.

INSECT DAMAGE AND SEED DATA

We collected information on seed counts per cone and insect damage for four years (2014 to 2017). Only seeds considered whole and intact and from undamaged cones are used in the analysis of seed data. “Intact” seeds were whole seeds that had no visible external damage. Seeds categorized as “not-intact” were visually damaged or had been damaged by insects. Insect presence for cones was determined by the presence of a larvae and/or the presence of frass. Many cones that had insects also possessed a very large amount of insect frass and were significantly damaged due to insect predation. We also examined the exterior of cones for insect holes. Individual cones were considered as damaged based on the presence of frass, insect emergence holes, bract damage due to insects, and the presence of insect larvae within the cone (Turgeon et al. 2005). We did not differentiate between insect predators in assessing cone

damage, thus the data on insect predation is combined across species. Cones were categorized as damaged and undamaged while seeds were categorized as intact and not-intact. Insect damage did not impact cone length (χ^2 (1) = 16.87, p=0.42), therefore analysis involving cone length is completed using all data collected regardless of insect damage.

STATISTICAL ANALYSIS

To compare mean cone lengths across years, we used a linear mixed effects model, with year as a categorical fixed effect and tree ID and stand as random effects using the *lme4* package (Bates et al. 2012), obtained P-values using likelihood-ratio tests, comparing to a null model (without year in the model), and performed post-hoc Tukey comparisons across groups using 'glht' in the *multcomp* package (Hothorn et al. 2008) following significant likelihood-ratio tests. We included random effects of individual tree ID because some trees were sampled in more than one year and stand to account for variation within the study area. The same model structure was used to compare minimum and mean maximum cone lengths across years, and the mean number of undamaged seeds per cone across years. We also ran a linear mixed effects model with cones lengths as the response variable and log(annual population-level cone production) as a continuous fixed effect with random effects of tree ID and stand, and compared this model to a null model without annual population-level cone production using a likelihood-ratio test. To test whether the relationship between cone length and the number of intact seeds per cone varies with year, we ran an ANCOVA, with year as a covariate and tree ID and site as random effects and ran likelihood ratio tests to test for a significant cone length with year interaction on seeds per cone, and for a significant effect of year.

For analyses related to seed predator satiation, we used a generalized linear mixed model to test for a relationship between a binary variable for insect damage (absence, presence) with

198 log_{10}-transformed mean annual population cones, log_{10}-transformed individual cones, tree height,
199 and an interaction between log-population cones and log-individual cones as continuous fixed
200 effects, and tree ID and stand as random effects. We used Akaike's Information Criterion (AIC_c)
201 and AIC_c weights (w_i) to determine the model and variables that best described insect presence
202 from the candidate model set that included all combinations of the variables above. We assessed
203 statistical significance based on $\alpha = 0.05$. Plots were made using *ggplot2* (Wickham 2016). All
204 analyses were run using R-statistical software 3.5.1 (Team 2018).

205 **RESULTS**

206 *CONE PRODUCTION AND CONE LENGTH*

207 Population-level white spruce cone production varied greatly across years, it peaked in 2013 with
208 a mean of 2,742 cones per tree, with 2017 being another peak year with 2,408cones and dropped
209 to a low of 216 cones per tree in 2016 (Fig. 1). The total of 1,399 cones that we collected
210 represented a mean of 37 cones per tree (range per tree: 15 to 56 cones) and between 136 and
211 349 cones per year (Table 1). Additionally, cone lengths differed significantly among years (χ^2
212 $(5) = 126.93$, $p < 0.001$); 2013 had significantly longer mean cones compared to all other years,
213 and while 2017, the other peak reproduction year had the second highest cone lengths, they were
214 not significantly different to other years (Fig. 2a). Cone lengths were significantly positively
215 related to log(annual population-level cone production) (χ^2 $(1) = 23.07$, $p < 0.001$). Minimum
216 cone lengths per tree varied significantly across years (χ^2 $(5) = 14.97$, $p = 0.01$; Fig. 2b), with
217 2013 and 2015 being significantly longer than 2012, while maximum cone lengths did not differ
218 significantly across years (χ^2 $(5) = 9.91$, $p = 0.08$; Fig 2c).

219 *SEED PRODUCTION*

220 Across 2014-2017, there was a significant difference in the number of intact seeds produced

from undamaged cones between years (χ^2 (3) = 50.20. p < 0.01; Fig. 2d). Longer white spruce cones contained more seeds, and there was a significant influence of the covariate of year on the slope of the relationship (Fig. 3; $\chi^2(3) = 14.68$, p = 0.002) and the intercept varied significantly across years (Fig. 3; $\chi^2(3) = 58.605$, p < 0.001). The peak cone year of 2017 had significantly more mean intact seeds produced per cone compared the other years per cone at almost 100 seeds per cone and was lower in years population-level cone production decreased to a low of about 33 seeds per cone in 2015.

INSECT DAMAGE

During 2014-2017, 1,141 cones were collected from a total of 27 trees to assess insect damage to cones. Across these years, the overall proportion of insect damaged cones was 0.32, with the remaining 0.68 undamaged. There was a significant effect of year on the prevalence of insect-damaged cones ($\chi^2(3) = 91.60$, p < 0.001; Fig. 4a). In 2016, the year of the lowest population-level cone production, the mean (sd) proportion of cones damaged by insects (0.82 (0.16)) was approximately three times greater than other years with higher cone production.

We used AIC_c analysis to identify the best model(s) to describe the prevalence of cones damage by insects, and we found that the best overall model included only log_{10}-population-level cone production ($w_i = 0.404$). The second-best model included both log_{10}-population-level and tree height ($\Delta AIC_c = 1.03$, $w_i = 0.242$) and the third-best model included both log_{10}-population-level cone production and log_{10}-individual-level cone production ($\Delta AIC_c = 1.93$, $w_i = 0.154$); Table 2). All other models had ΔAIC_c values >2, and AIC_c weights less than 0.100. Across all candidate models, log_{10}-population-level cone production was in all top models and had a summed weight of 1.000, while log_{10}-individual cones and tree height had summed weights across all models of 0.355 and 0.373, respectively. The interaction between population-level and

individual-level cone production contributed very little to the model weights (0.110) and no models with the interaction had a model weight higher than 0.070. To visualize the effects of the terms in the top two models, individual trees with fewer cones had a higher prevalence of insect damage (Fig. 4b) and taller trees had more insect presence per cone (Fig. 4c).

DISCUSSION

We showed that cone length varied significantly across years, with the peak cone production year, 2013, having significantly longer cones; we also showed positive relationships between cone lengths and intact seeds. Consistent with this is other research that larger white spruce cones contain more and larger sound seed than small cones (Waldron 1965). Across years, mean cone lengths varied more than minimum cone lengths, while maximum cone lengths did not differ significantly across years. The incidence of insect predation on white spruce cones (and therefore the seeds within) was highest when the fewest cones were produced, and lower when cone production was higher. There was little variation in insect predation among years that were not the lowest cone production year, suggesting that mast-level conditions are not required to reduce incidences of insect predation on spruce cones and seeds.

The pollination efficiency hypothesis suggests that synchronized high levels of reproductive investment by individuals within a population will lead to larger seed crops (Kelly and Sork 2002). Based on this hypothesis, high reproduction years in white spruce is predicted to produce larger cones (which contain more seeds, Waldron 1965; Caron and Powell 1989) due to the increased allocation of resources toward reproduction; our findings were consistent with this hypothesis. With population-level cones as a predictor variable there was a positive relationship between log(population cones) and cone length. Mean cone lengths were significantly smaller in the year before and the year following the 2013 mast year, and resource depletion could play a

role in lower reproductive investment in the number and size of cones following a mast year. Weather cues have been linked to white spruce reproduction (Krebs et al. 2012; Roland et al. 2014) and warmer conditions during the time of bud differentiation may positively influence not only the number of reproductive buds produced but also the size of the female strobili . At the base of each cone scale there is space for a pair of seeds, and longer cones have more cone scales, which directly influences the number of potential seeds. Among the 2014-2017 data, there were significantly more intact seeds per cone in 2017 compared to other lower cone production years, with a positive relationship between cone length and intact seeds.

Regarding insect damage, the year of lowest population-level cone production had the highest proportion of cones with insect damage. These data show support the predator satiation hypothesis and suggest seed predators select for mast seeding when larger seed crops among a population experience lower seed predation (Janzen 1971; Kelly and Sork 2002; Bogdziewicz et al. 2020). However, here was not a substantial difference in the proportion of insect-damaged cones on trees in years that were not the lowest cone year regardless of population-level cone production; it did not take a large reproductive event in white spruce to reduce proportional losses to insects. Model selection showed that insect damage to white spruce cones was greater in taller trees but is negatively impacted by population-level cones. The interaction between individual and population-level reproduction was not in the top models for cone losses to insect attack. Seed predation, both pre- and post- dispersal, on conifers can be large (Castro et al. 1999). Silvertown (1980) examined seed crop size and predispersal seed predation in 25 tree species, and large mast crops decreased seed predation in 16 species.

While there are a variety of insects that feed upon spruce cones, two principal cone insects include *S. neanthracina* and *D. reniculelloides* (Turgeon et al. 2005). *S. neanthracina* are

responsible for a large portion of pre-dispersal seed predation, eating up to 65% of the seeds in a cone, and 90% of seeds in low cone crop years (Sweeney and Quiring 1998; Holsten 2001; Turgeon et al. 2005). In years of low cone production, *S. neanthracina* and *C. strobilella* are capable of destroying ~60% and ~34% of potentially sound seed crop, respectively (Tripp and Hedlin 1956). Conversely, in a year of high cone production, roughly 25% and 15% of sound seed is destroyed by *S. neanthracina* and *C. strobilella*, respectively (Tripp and Hedlin 1956). Extended diapause in some of the seed predator insects of white spruce may influence the patterns of seed predation, since they may emerge at different times. Extended diapause in seed-predating insects and mast seeding are coevolutionary traits (Tachiki and Iwasa 2013). In times of low cone availability, insects can also use cones of nearby suitable species if available (Smith and Balda 1979). This is functionally similar to prey-switching seen in other seed predators, such as red squirrels, who switch to alternate food sources in low reproduction years (Fletcher et al. 2010). It is the proportional impact on reproductive structures by seed predators that is predicted to fluctuate across the temporal variability in tree reproduction, with the highest proportional losses in the lowest reproduction years. Despite the dilution effect of higher cone production on the proportion of cones damaged by insects, in raw numbers there are more cone losses at higher levels of reproduction. While we can infer consequences for evolutionary hypotheses for mast seeding, it is important to note that evidence supporting the benefits of the predator-satiation hypothesis is not necessarily evidence against the benefits of synchronous pollination and the pollination efficiency hypothesis (Monks and Kelly 2006; Linhart et al. 2014) and vice-versa (Moreira et al. 2014).

Because we opportunistically collected cones from beneath trees, we were dependent on trees producing cone crops across a variety of population-level conditions. Our results show that

313 individual trees investing in reproduction during low-reproduction years are not as efficient as in
314 a high reproduction year based on intact seeds per cone. These trees may be producing cone
315 crops, but the cones tend to be smaller, and therefore hold fewer seeds. Self-pollination in white
316 spruce leads to very low seed set (Fowler and Park 1983; Lee 1988), which is an advantage to
317 investing in high levels of reproduction with other individuals in the population. Individual
318 variation in mast seeding patterns across years have been detected in white spruce (LaMontagne
319 and Boutin 2007), and microsite characteristics including local light availability (Greene et al.
320 2002) and temperature (Koenig et al. 2015) could impact annual reproduction by individuals.
321 Our goal was to characterize white spruce cones and seed numbers across years. Plants
322 have a range of patterns in the relationship between seed size and number, but few of these
323 studies have been done with trees (Koenig et al. 2009). Our sample size of the number of
324 individual trees studied was limited by the ability to opportunistically collect cones, and with
325 1,399 cones examined across six years of study, we report on relationships of cone lengths, seed
326 production, insect damage, and cone production across multiple years. Further studies on mast
327 seeding patterns across years and individual trees related to pollination efficiency and seed
328 quality could examine seed germination, which could be influenced by pollen source where self-
329 pollination tends to reduce germination success (Lee 1988). Quantifying viable versus non-viable
330 seeds produced during high and low reproduction years would also provide insight into the
331 energy expenditure and allocation of resources by individuals during years of high reproductive
332 output. Future work could also include identification of the insects involved in seed and cone
333 predation to gain further insight into the relationship between mast seeding species and seed
334 predator diapause. Furthermore, tree age and size, weather conditions, as well as available soil
335 nutrients, and temperature and rainfall microclimates may also impact patterns of reproduction

by individuals (Koenig et al. 2015; Leeper et al. 2020). The causes and consequences of highly temporally variable patterns of plant reproduction (mast seeding) has long been a focus of interest because of the many roles that plants play in ecosystems, from community dynamics to forest regeneration (Ostfeld and Keesing 2000; Moreira et al. 2014). Our findings contribute that large reproductive events in white spruce not only result in more cones (which is known) but that these cones are longer and contain more intact seeds than in other years; these seeds form the basis of the food web and forest regeneration.

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TABLES AND FIGURES

Table 1. Summary data on annual white spruce cone sample sizes (2012-2017; n = 1,399 total cones) and sampled trees (n=38).

Year	Number of cones collected	Number of trees sampled
2012	210	7
2013	349	9
2014	264	6
2015	287	7
2016	136	4
2017	153	5

Table 2. AICc model selection for insect damage (as a binary variable) as influenced by population-level $\log_{10}$-cone production (PC), individual-level $\log_{10}$-cone production (IC) and their interaction, and tree height (TH).

Model Terms	K	Log-likelihood	ΔAICc	Weight
PC	4	- 368.93	0.00	0.404
PC + TH	5	- 368.43	1.03	0.242
PC + IC	5	- 368.88	1.93	0.154
PC + IC + TH	6	- 368.40	2.99	0.091
PC + IC + PC*IC	6	- 368.66	3.52	0.070
PC + IC + TH + PC*IC	7	- 368.20	4.63	0.040
IC	4	- 380.03	22.21	< 0.001
IC + TH	5	- 379.76	23.68	< 0.001
Intercept Only	3	- 413.89	87.90	< 0.001
TH	4	- 413.58	89.31	< 0.001

Figure Captions

Figure 1. Mean annual population-level (n = 364) white spruce cone production between 2012 and 2018 in the Huron Mountains, MI, USA. Cone length data spans 2012-2017 and the horizontal line under the x-axis highlights the years (2014-2017) when seed counts and insect predation were quantified.

Figure 2. White spruce cone attributes of individual trees (2012-2017) including (a) all cone lengths (n = 1399 cones, 38 trees), (b) minimum cone lengths per tree (n = 38 trees), (c) maximum cone lengths (n = 38 trees), (d) number of intact seeds per cone (2014 – 2017; n = 449 cones, 20 trees). Note that the y-axis varies among panels, and for panels b and c that open circles represent values for each tree sampled. Mean values are shown as triangles in each panel.

Figure 3. Relationships between *P. glauca* total intact seeds per cone and cone length (mm) for undamaged cones across years in the Huron Mountains, Michigan, USA. Each symbol represents an undamaged cone.

Figure 4. Insect damage on white spruce cones, showing relationships between (a) the proportion of insect damaged cones per individual tree and mean annual population-level cones (mean cones per tree) across years (2014-2017). The mean proportion of cones damaged each year and box-plots of the relationship between insect damage (presence or absence) per cone and (b) individual cone production, (c) individual tree height (m).

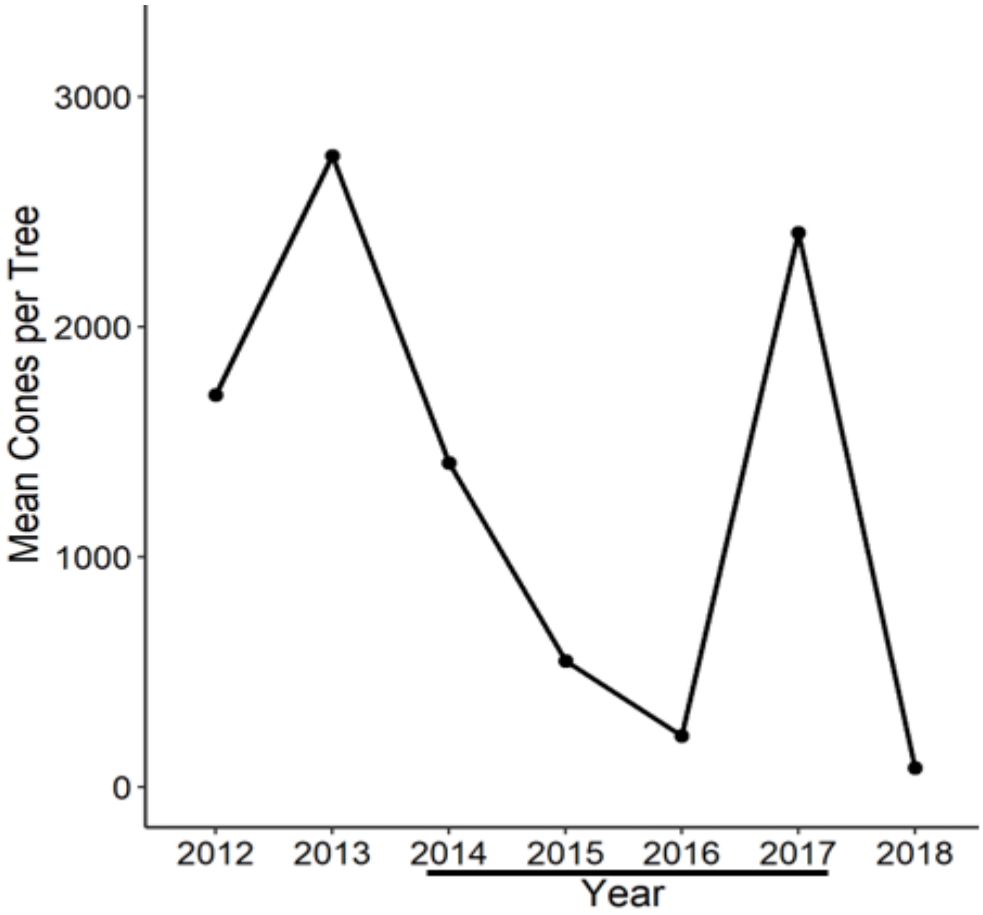
3000
2000
1000
0
Mean Cones per Tree
2012
2013
2014
2015
2016
2017
2018
Year

Figure 1.

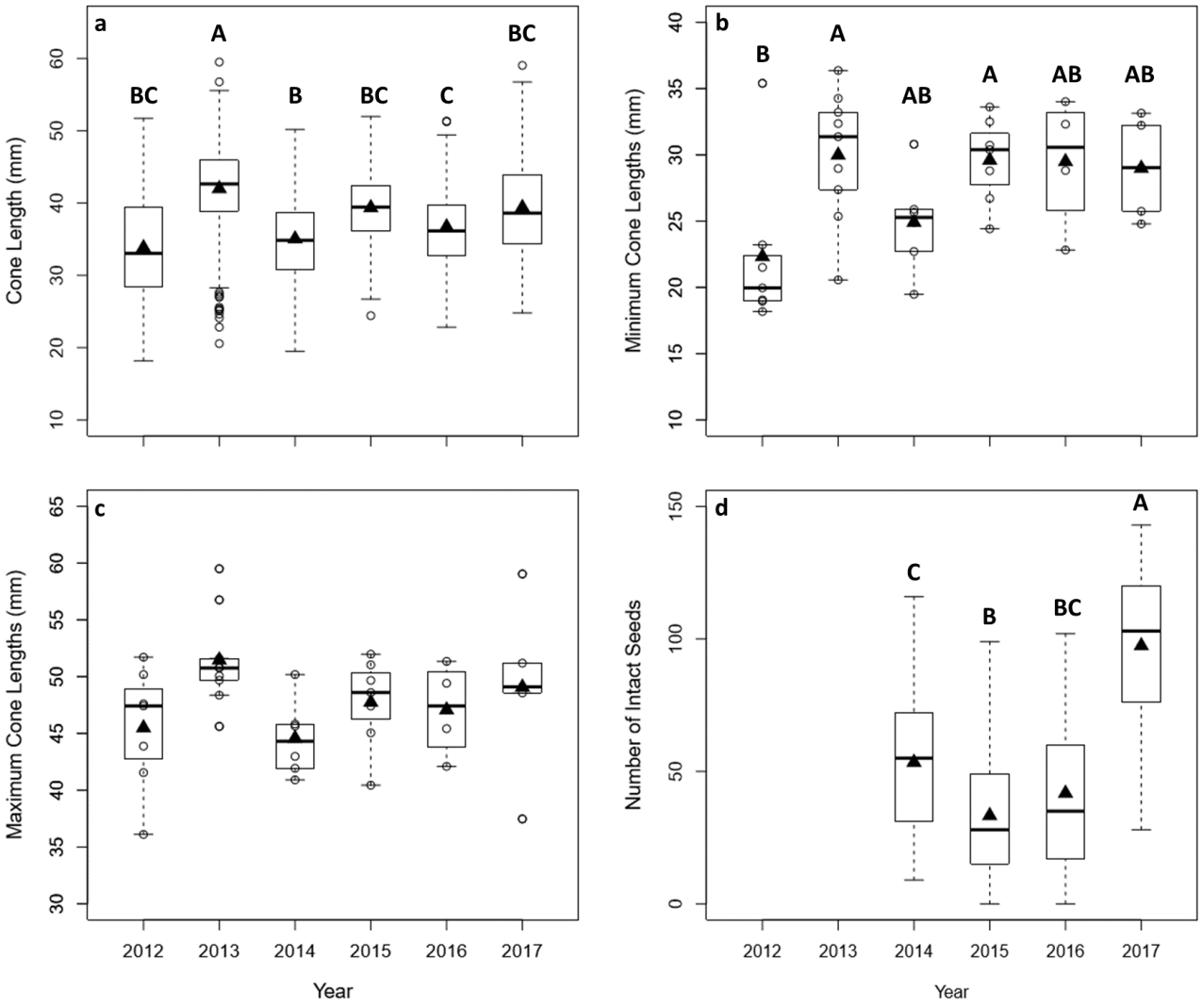
a
BC
A
B
BC
C
BC
Cone Length (mm)
b
B
A
AB
A
AB
AB
Minimum Cone Lengths (mm)
c
Maximum Cone Lengths (mm)
d
C
B
BC
A
Number of Intact Seeds
2012
2013
2014
2015
2016
2017
Year

Figure 2.

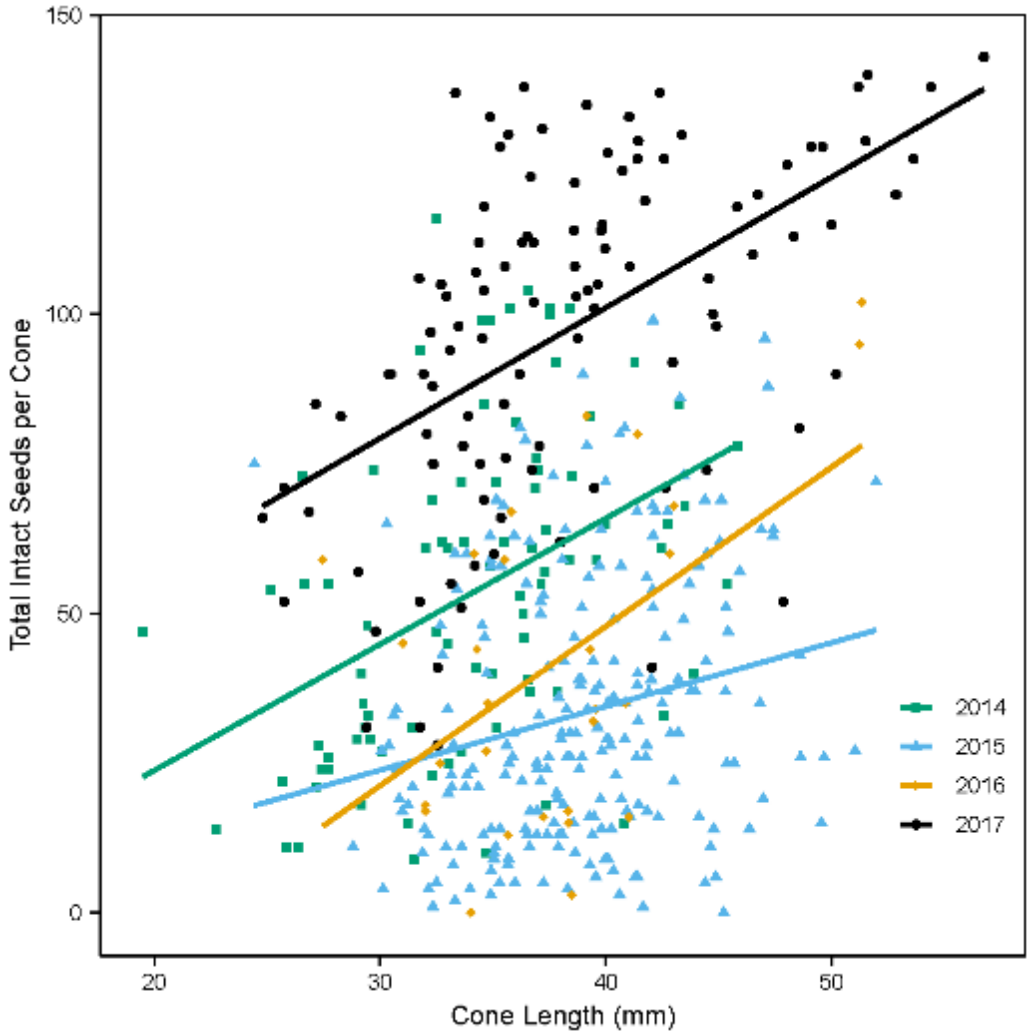
150
100
50
0
Total Intact Seeds per Cone
20
30
40
50
Cone Length (mm)
2014
2015
2016
2017

Figure 3.

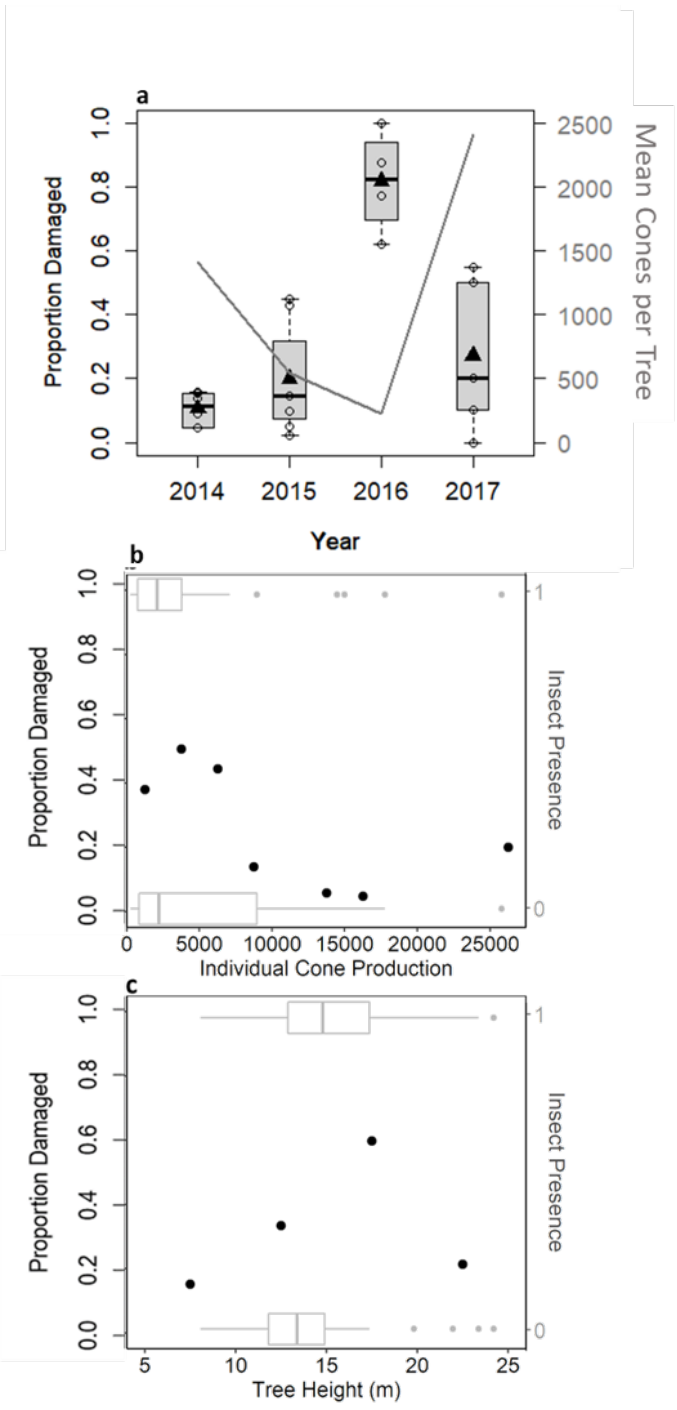
a
Proportion Damaged
0.0
0.2
0.4
0.6
0.8
1.0
Mean Cones per Tree
0
500
1000
1500
2000
2500
2014
2015
2016
2017
Year
b
Proportion Damaged
Insect Presence
0
1
0
5000
10000
15000
20000
25000
Individual Cone Production
c
Proportion Damaged
Insect Presence
0
1
5
10
15
20
25
Tree Height (m)

Figure 4.