Reproductive Trade-Offs in a Mast Seeding Species (*Picea glauca*)

Abigail C. Leeper
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Jalene M. LaMontagne, PhD, Biological Sciences

Windsor E. Aguirre, PhD, Biological Sciences

Abstract

Individuals have limited resources, typically leading to trade-offs in the size and number of offspring produced. However, evolutionary pressures may alter this relationship. For instance, many perennial plant species exhibit a reproductive pattern known as mast seeding. During mast seeding events, individuals produce very large seed crops. One hypothesis associates these events with increased pollination efficiency during synchronous reproduction, where there is expected to be higher reproductive success during mast conditions. Thus, during a mast event, this trade-off may not exist. Using white spruce (*Picea glauca*) as a focal species, we investigated the relationship between mast seeding and the offspring size and number trade-off. Between 2012 and 2016, ~40 cones were collected from 38 trees at a site in northern Michigan. We found the relationship between cone length (hence seed number) and the total number of cones produced varied across years, but was not strongly negative. Understanding this relationship can provide insight into how the phenomenon of mast seeding influences life-history traits for reproduction.

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INTRODUCTION

Life history traits are described as investments in growth, reproduction, and survival that impact the fitness of individuals (Stearns 1989). Life history theory suggests parental organism's evolutionary adaptations maximize fitness depending on a variety of conditions. Due to a limitation in available resources, there are trade-offs among these traits that have been measured through field observations, experimental manipulations as well as phenotypic and genetic correlations (Guinness & Albon 1983; Partridge & Farquhar 1981; Rose & Charlesworth 1981). A well-known life history tradeoff involves the number and size of offspring produced that has been documented in both animals and plants (Lalonde 1989; Sinervo et al. 1992; D. Ebert 1993; Olsson & Shine 1997).

In general, given a constant investment in reproduction, an individual with a large reproductive output (many offspring) is expected to produce offspring of a smaller size while an individual with a small reproductive output (fewer offspring) would have larger offspring. This theory can be applied to plants and animals alike; plants are expected to produce fewer, larger seeds or many, small seeds. However, many perennial plants species are characterized by a pattern of reproduction called "mast seeding", the synchronous but highly temporally sporadic production of large seed crops (Kelly 1994). While there is evidence for spatial and temporal synchrony in mast events over the size of a continent, variation in production has been documented in individuals over a local scale (Koenig & Knops 1998; LaMontagne & Boutin 2007). Despite a vast amount of research on mast seeding species, there is a lack of information on how the offspring size and number life history trait holds during mast and non-mast conditions.

There are several evolutionary hypotheses used to explain mast seeding including the predator satiation hypothesis, which states that sporadic production of large seed crop reduces losses to seed predators (Janzen 1971), resource matching hypothesis and weather-driven hypothesis which claim variable seed production is best explained by variable resource availability and variable weather conditions, respectively (Kelly & Sork 2002). Finally, the pollination efficiency hypothesis which states that synchrony in flowering increases pollination success for wind pollinated plants (Nilsson & Wastljung 1987).

While a closer examination into any of the evolutionary hypotheses may provide insight into the relationship between offspring size-number and seed production, the pollination efficiency hypothesis is focused on in this study. As described, individuals within a population will synchronously produce an over-abundance of pollen, therefore increasing their potential seed crop. The possibility of increased pollination efficiency is an ultimate evolutionary hypothesis as masting would be strongly selected in species able to achieve greater pollination efficiency through synchronous and increased flowering (Kelly & Sork 2002).

When considering the offspring size and number trade-off in relation to this evolutionary hypothesis, it is important to note the increase in resources, in the form of pollen, available to nearby individuals in mast conditions. This abundance of pollen in tandem with an individual's increased allocation of resources (e.g. energy, nutrients) to reproduction could lead to the production of a larger seed crop comprised of seeds of a larger mass or size. If this is true it would violate the typical offspring size and number trade-off, where an increase in potential offspring would lead to a decrease in their size (i.e. many, small seeds). During non-mast conditions, individuals would not be exposed to an over-abundance of pollen as the population is no longer funneling their resources towards reproduction and smaller seed crops would ensue.

To better understand the relationship between seed size and number and mast seeding, an assessment of the quantity and physical size of reproductive structures must be made. To do this, white spruce (*Picea glauca*), a dominant species in the boreal forest, has been selected as a focal species. White spruce is found in the United States along its southern ranging limit reaching into northeastern Minnesota, northern Wisconsin, northeastern New York, northern New Hampshire, Vermont and Maine (Thompson et al. 1999; Appendix I – Figure 1). Characterized as a mast seeding species, the time between mast years for white spruce has been found to be greater at northern latitudes than southern latitudes; however, mast events for white spruce have been found to occur roughly every 2 to 7 years (Nienstaedt & Zasada 1990; Kelly 1994; LaMontagne & Boutin 2007; Gärtner et al. 2011).

Despite the vast amount of research on cone production and mast seeding events in white spruce, variation in seed production and cone size during mast and non-mast conditions is not well understood. The relationship between offspring size and number has been analyzed for Valley Oak (*Quercus lobata*), where trees were found to produce larger acorns in years of larger seed crops (Koenig et al. 2009), but there is a lack of research in this area yet. Estimates of cone production by individual white spruce trees can be made from the ground using methods described by LaMontagne et al. (2005), and cones collected from these trees can provide information on the relationship between cone size and seed production in the context of overall cone production. This study explored the reproductive patterns of white spruce as they relate to the offspring size and number trade-off. During mast conditions, indicated by a substantial increase in the number of cones produced, the offspring size and number trade-off was predicted to be violated as trees are allocating resources towards producing more, large cones with the potential to hold many seeds.

METHODS

SITE DESCRIPTION

Data was collected in the Huron Mountains (46.82°N, 87.73°W), near Big Bay, Michigan, USA, over a five-year period (2012-2016). The study area has a mean summer (June – August) high and low temperature of 24.0 ˚C and 11.6 ˚C, respectively. Mean precipitation in this region during the summer months is 85 mm, falling as rain. Study sites were comprised of white spruce (*Picea glauca*) stands, with some other coniferous species such as white pine (*Pinus strobus*), balsam fir (*Abies balsamea*), and eastern hemlock (*Tsuga canadensis*) found in the region.

CONE PRODUCTION

Estimates of total cone production by trees were based on an index of cone production of 364 trees from visual counts from the ground each year between June and August following the methodology of LaMontagne et al. (2005). Counts were performed from one side of a tree with binoculars. Trees having more than 200 visible cones were photographed and counts were performed in ImageJ. From the index of production, total cone production by individual trees was estimated. It was from a sample of these trees that cones were collected.

CONE COLLECTION and PROCESSING

Cones were collected opportunistically from beneath 38 individual trees at six sites across the five years between July and August. Only cones which were green and closed (hereafter referred to as “wet”) were collected. In total, 1484 cones were collected (between 19 and 56 cones per individual tree) over the five years. Upon collection, cones were wrapped tightly in canvas and placed in the refrigerator until processed in the lab. Cones were placed in paper cups in a window sill until they opened. In 2015 and 2016, cones were measured before opening for a 'wet length' measurement. Upon their opening, cone lengths were re-measured (referred to as 'dry length') and dissected to count the total number of seeds. To determine if there was a difference in 'wet' vs 'dry' length measurements, the relationship between wet cone length and dry cone length for 2015 and 2016 white spruce cones was determined using a Pearson product moment correlation. Wet cone length and dry cone length is highly positively correlated (r=0.97, df=421, p<0.0001), so dry length, hereafter referred to as 'cone length', is used in the analysis across years. During measurements, cones were separated into groups based on insect damage ('undamaged' vs 'damaged').

INSECT DAMAGE

Information on insect damage was recorded from 2014 to 2016. This included the presence of frass, insect holes, bract damage due to insects, and the presence of spruce maggots (*Strobilomyia neanthracina*). Cones were categorized as damaged and undamaged while seeds were categorized as intact and not-intact. Seeds considered intact and not-intact were counted separately. Seeds identified as not-intact seeds were those which were damaged by insect predation. All analysis involving seed data uses only the last three years of data and includes only undamaged cones. To ensure insect damage did not impact the length of the cones, a generalized linear mixed effects model was performed. It was determined that insect damage did not impact the length of cones (χ^2 (1) = 0.66 p=0.415). Because of this, analysis involving cone length is completed using all data collected, regardless of insect damage.

STATISTICAL ANALYSIS

All analyses were run using R-statistical software 3.1.2. R (R Core Team, 2014). The values for total cones on trees were log-transformed. To calculate log-total seeds per tree, the average number of seeds per tree was determined and then multiplied by the total number of cones on the individual tree. This value was then log-transformed. A Pearson product-moment correlation analysis was performed to examine the relationship between wet cone length and dry cone length for the last two years of data collection. An unpaired t-test was used to compare the mean cone length between two years of the same individual. The *lme4* package (Bates et al. 2012) was used to perform linear mixed effects (lme) analyses, with year, site, and individual tree ID entered as random effects for each lme model. We examined the relationship between insect damage and cone length, with cone length as a continuous fixed effect. To determine the relationship between cone length and total cones on trees, an lme was performed using total cones as a continuous fixed effect. A linear model was used to determine the relationship between log total seeds per tree and log total cones on tree. Inspection of residual plots did not indicate deviations from homoscedasticity or normality. P values were obtained using the Likelihood Ratio test.

RESULTS

CONE PRODUCTION AND CONE LENGTH

Mean cone production for the site was highest in 2013, indicative of a mast year, and lowest in 2016 (Figure 1). Overall, the mean cone length within populations of trees varied across years; with 2013 having the largest mean cone length, and 2014 having the shortest mean cone length (Table 1). A linear mixed effects model showed significant variation between years (χ^2 (4) = 252.4, p<0.0001). There was a significant difference in cone length for all years except between 2012 and 2014 (F (4) = 135.8, p<0.0001). Variation in cone length within individuals for each year (represented as the mean difference in minimum and maximum cone length) was the largest in 2012 while 2016 had the least variation (Table 1).

Mean cone length was highest in 2013 and lowest in 2015 (Figure 1). In 2012, cone length and log-total cone production reflected a trade-off between offspring size and number (Figure 2), where increased log-cone production led to a decrease in cone length ($\chi^2(1)$ =8.93, p=0.0028). No trade-off between offspring size and number was observed in 2013 or 2014 ($\chi^2(1)$ =0.0904, p=0.764 and ($\chi^2(1)$ =1.39, p=0.2381, respectively). In 2015, there is a non-significant negative trend, where individuals producing more cones tend to have smaller ones ($\chi^2(1)$ =1.95, p=0.163). However, a significant trend, opposite to that seen in 2012, is observed in 2016, where increased cone production lead to the production of longer, hence larger, cones ($\chi^2(1)$ =6.46, p=0.011). Overall, there was no significant effect of total cone production on cone length ($\chi^2(1)$ =3.05, p=0.081).

SEED PRODUCTION

For the years when seed quantity data was available (Appendix I – Table 1), total seeds produced per tree was calculated. Cone length and total number of seeds per cone across years were highly positively related to one another (Figure 3). Cone length positively affected the total number of seeds per cone over the three years (Linear Mixed Effects Model, $\chi^2(1)$ =106.7, p<0.0001). Across all years of data, increased cone production led to an increased production of seeds per tree. There was significant increase in total seeds produced by trees with increases in log-total cone production (F (21) =990.2, p<0.0001). There was a strong positive relationship between log-total seeds produced per tree and log-total cones produced (Figure 4; r^2=0.9782).

VARIATION IN INDIVIDUALS ACROSS YEARS

Over the 5 years of collection, cones were collected twice from 7 different trees. (Table 3). Of the 7 trees sampled more than once, the mean length of the cones was significantly different on 5 occasions. Mean dry cone length did not decrease with increased cone production between the two years nor did it consistently increase with increased cone production. Two trees, identified as trees 337 and 361, were collected during the year of highest cone production and then again during a later year. For tree 361, the cone length in 2013 was nearly a full 10 mm larger than in 2015; however, total cone production was nearly the same for this tree between the two years. For tree 337, cone production during the mast year was not very different than cone production during the non-mast year, but mean cone length for this tree was statistically different. For tree number 292, cone production between the two years was drastically different. In 2014, this tree produced nearly 15,000 cones and only 228 cones in 2016. Despite this large difference in cone production between 2014 and 2016, the mean cone length between the two years was not statistically different, differing by only 0.46 mm. The amount of variation within trees between two years indicates no consistent trade-off in size and number of potential offspring.

INSECT DAMAGE

During 2014-2016, 874 cones were collected with 36% marked as damaged and 64% as undamaged. The percent of insect damaged cones varied significantly over the three years of data ($\chi^2(1) = 133.11$, $p < 0.0001$). In 2014, the mean (SD) percent damage by insects of the cones collected from individuals was 18 (28) %. However, in 2015, 20 (17) % of the cones collected were damaged by insects, and in 2016 the largest number of damaged cones 59 (35) % were collected. A mixed effects multiple logistic regression analysis showed no preference by insects for larger cones. No significant relationship between cone length and insect presence was found ($\chi^2(1) = 0.0433$, $p = 0.835$), indicating insects showed no preference for larger cones, hence the potential for more seeds.

DISCUSSION

Variation in cone length was observed within and between years, and within individuals. If the offspring size and number life history tradeoff were being adhered to, cone length should decrease in years of high production and increase in years of low production. Meanwhile, the pollination efficiency suggests synchrony in the flowering of individuals within a population will lead to larger seed crops for perennial plants species whose pollen is wind dispersed (Kelly & Sork 2002). Based on this hypothesis, a mast year in white spruce is predicted to produce larger cones due to the increased allocation of resources toward reproduction. During the year of highest cone production across the site (2013) cones were significantly longer than all other years. This violation of the offspring size and number trade-off provides support for the pollination efficiency hypothesis used to explain the evolutionary merit of mast seeding as a reproductive strategy.

In non-mast years, increased cone production was predicted to lead to a decrease in cone length. In 2012, trees with greater cone production tended to have smaller cones, adhering to the life history trait of offspring size and number. This finding aligns with the hypothesis made about non-mast years, as individuals are not allocating as much of their resources to reproduction and therefore are producing smaller cones. However, 2016 showed the opposite trend, where trees with greater cone production had larger cones. Cone production in this year was lowest among all years on record, however these conflicting results may in part be due to differences in sample size. In 2012, a total of 210 cones from 7 trees were collected and measured; whereas, in 2016, only 59 cones were collected and measured from 4 trees. A larger sample of cone lengths from 2016 may lead to a different observation in the relationship between cone length and total cones per tree. A study on Valley Oak, (*Quercus lobata*), in California no trade-off between offspring size and number was observed (Koenig et al. 2009). Suggesting the lack of evidence for the relationship between the offspring size-number trade-off and annual seed production has been seen in another mast seeding species, though few studies have been done.

Larger cones are expected to hold more seeds as they have an increased number of scales available to hold seeds. The relationship between cone length and seed production reflects that larger cones tend to hold more seeds such that larger cones have significantly more seeds then smaller cones. An analysis of how this relationship holds during a mast event is unavailable now due to limitations in the dataset; however, continued collection of cones over the next years, may provide more insight into this trend. Given the strong relationship between log-total seeds produced per tree and log-total cones produced by the tree, increased cone production leads to increased seed production by the tree. This relationship was observed in years of both high and low cone production, suggesting individuals producing more cones do produce more seeds, and this is consistent regardless of the mast conditions. This information suggests cone production is a legitimate proxy for seed production in white spruce.

Variation in cone length can be seen when comparing individual trees which have been sampled more than once. Cone length varied significantly within each tree, except one, between the two years of collection. This suggests high variation in length of cones produced by individuals from year to year, regardless of cone production. However, when considering the pollination efficiency hypothesis, cone production across the site as a whole must be considered, as individual variation may be attributed to a number of confounding factors.

In addition to pollination efficiency hypothesis, mast seeding is thought to be the result of climatic cues and resource availability. Annual white spruce seed, hence cone production, is influenced by regional climate. Mast seeding events in white spruce tend to be associated with warmer, dry weather during the previous growing season (Zasada et al. 1969; Zasada et al. 1992; Roland et al. 2014), including a study in the Yukon indicating the production of large seed crops are preceded by summers of warm temperatures (Krebs et al. 2012). The study site in this project, near the southern shore of Lake Superior in the upper peninsula of Michigan, is located from the shore to 10 km inland. Temperature near the lake and further inland in this area has been found to vary by as much as 11˚C (Hinkel & Nelson 2012). This climatic variation may impact synchrony in the output of large cone crops across the site, influencing the reproductive patterns of individuals and local sites within the study region.

The predator satiation hypothesis suggests seed predators cause selection for mast seeding when larger seed crops among a population experience lower seed predation (Janzen 1971). Mast seeding is selected for by species of perennial plant when large variation of seed crop size will satiate seed predators during years of high production (Kelly & Sork 2002). Red squirrels are a specialized seed predator of white spruce (*Picea glauca*), caching cones before they open. A single red squirrel may cut and cache up to 16,000 cones per year (Smith 1968). Seed-eating birds are also thought to be impacted by seed crop variation, where years of low production in boreal trees may potentially cause birds to move outside of their range to find food. While eruptions in bird density can be explained by a few hypotheses, the ‘seed-failure’ hypothesis has been supported at a species-specific level in the white-winged crossbill (Koenig 2001). However, spruce maggots are also responsible for a large portion of pre-dispersal seed predation. A study in Alaska found spruce cone maggots frequently eat up to 50% of seeds per cone, potentially eating 90% of seeds in low cone crop years (Holsten et al. 2008; Sweeney & Quiring 1998). During the years of cone production and collection where insect damage was recorded, the year of lowest total cone production saw the highest percent predation of seeds by spruce maggots. Although 2014, the highest year of production, saw more percent predation than 2015, this may be attributed to location of cone collection as well as time of year collected. While notes on insect damage are not available for 2013, determination of the percent damage to seed crops during a mast year may support this trend.

Caveats to the study include that variation in fitness of individuals may contribute to inconsistencies in results. Trees sampled were assumed and appear to be healthy; however, some trees may have higher production than other individuals due to other confounding variables. Size and age of the individual as well as available soil nutrients, temperature and rainfall may impact the reproduction of individuals. Koenig et al. (2009) notes that underlying offspring size-number trade-offs can be distorted by variation in resources. Given this variation, a trade-off is more likely observable during low production years in individuals for which resources are a limiting factor (Koenig et al. 2009). This would likely result in a stronger negative correlation between offspring size and number. To correct for the dissimilarity in resources use across individuals, the most desirable study to analyze this relationship would be one in which resources can be controlled.

An understanding of the relationship between cone length, cone production and seed crop during mast and non-mast years can provide insight into small mammal population dynamics and the reproductive strategies of mast seeding perennial plants. While several factors impact white spruce regeneration, variation in cone production significantly impacts white spruce regeneration and population dynamics. Additionally, an increased knowledge of the relationship between cone production and cone length, hence seed production, will provide silviculturalists with a better understanding of tree reproductive yield and life history traits.

CONCLUSIONS

While individual trees may produce large cone crops, mast conditions overall varied. The mean cone length of white spruce during the year of highest production was significantly longer than during non-mast years. However, variation within individuals and in the study population exists, making trade-offs inconsistent across mast conditions. Additionally, the relationship between seed production and cone production did not remain consistent across non-mast years. Sample size for analysis using seed production was limited to intact seeds. For trees sampled more than once, the relationship between cone production and cone length was not consistent as some trees had similar reproductive output but the mean cone length between the two years was significantly different. To better assess the relationship between cone size, seed production and cone production, further sampling of cones and collection of data would be beneficial and may provide a more conclusive finding. Quantifying viable versus non-viable seeds produced during mast and non-mast years would also provide insight into the energy expenditure and allocation of resources by these individuals during years of high reproductive output.

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Table 1. Variations in 1073 White Spruce Cone Length Across Years

Year	Mean Cone Production (SD)	Mean Cone Length (mm; SD)	Mean Minimum Cone Length (mm; SD)	Mean Maximum Cone Length (mm; SD)
2012	1704 (651)	33.83 (7.15)	22.32 (6.02)	45.49 (5.40)
2013	2742 (1821)	41.99 (5.97)	29.98 (4.94)	51.46 (4.22)
2014	1409 (716)	33.18 (5.94)	22.74 (4.96)	42.29 (4.32)
2015	542 (422)	39.35 (4.68)	29.59 (3.22)	47.74 (3.96)
2016	220 (196)	36.71 (5.13)	27.85 (5.64)	45.17 (5.55)

Table 2. Number of cones collected across years (2012-2016), the undamaged cones, and the mean number of seeds per cone. Note that cone damage and seed numbers are not available for 2012-2013.

Year	Total Number of Cones Collected	Total Number of Undamaged Cones	Mean Number of Seeds Per Cone (SD)
2012	210	NA	NA
2013	349	NA	NA
2014	461	225	61.63 (31.47)
2015	287	230	70.98 (15.16)
2016	177	59	76.32 (17.06)

Table 3. Relationship between Mean Cone Length (mm) and Total Cone Production for Individual White Spruce Trees between Two Years

	1st Year Collected				2nd Year Collected			
Tree ID	Year	Total Cones on Tree	Number of Cones Collected	Mean Length (mm; SD)	Year	Total Cones on Tree	Number of Cones Collected	Mean Length (mm; SD)
222*	2012	9526	22	28.49 (3.63)	2014	8675	42	34.55 (3.93)
244*	2012	3810	27	33.44 (5.10)	2016	5065	18	42.81 (4.20)
275*	2012	2102	32	42.85 (3.39)	2014	17406	42	31.60 (3.35)
287	2015	4164	41	39.73 (3.80)	2016	1036	37	39.61 (4.07)
292	2014	14648	44	33.56 (4.15)	2016	228	41	33.10 (3.82)
337*	2013	9237	44	43.85 (3.61)	2015	6774	41	35.23 (3.15)
361*	2013	14111	40	48.21 (4.08)	2015	14152	42	39.28 (4.77)

*Indicates significant difference in cone length between years ($P<0.0001$)

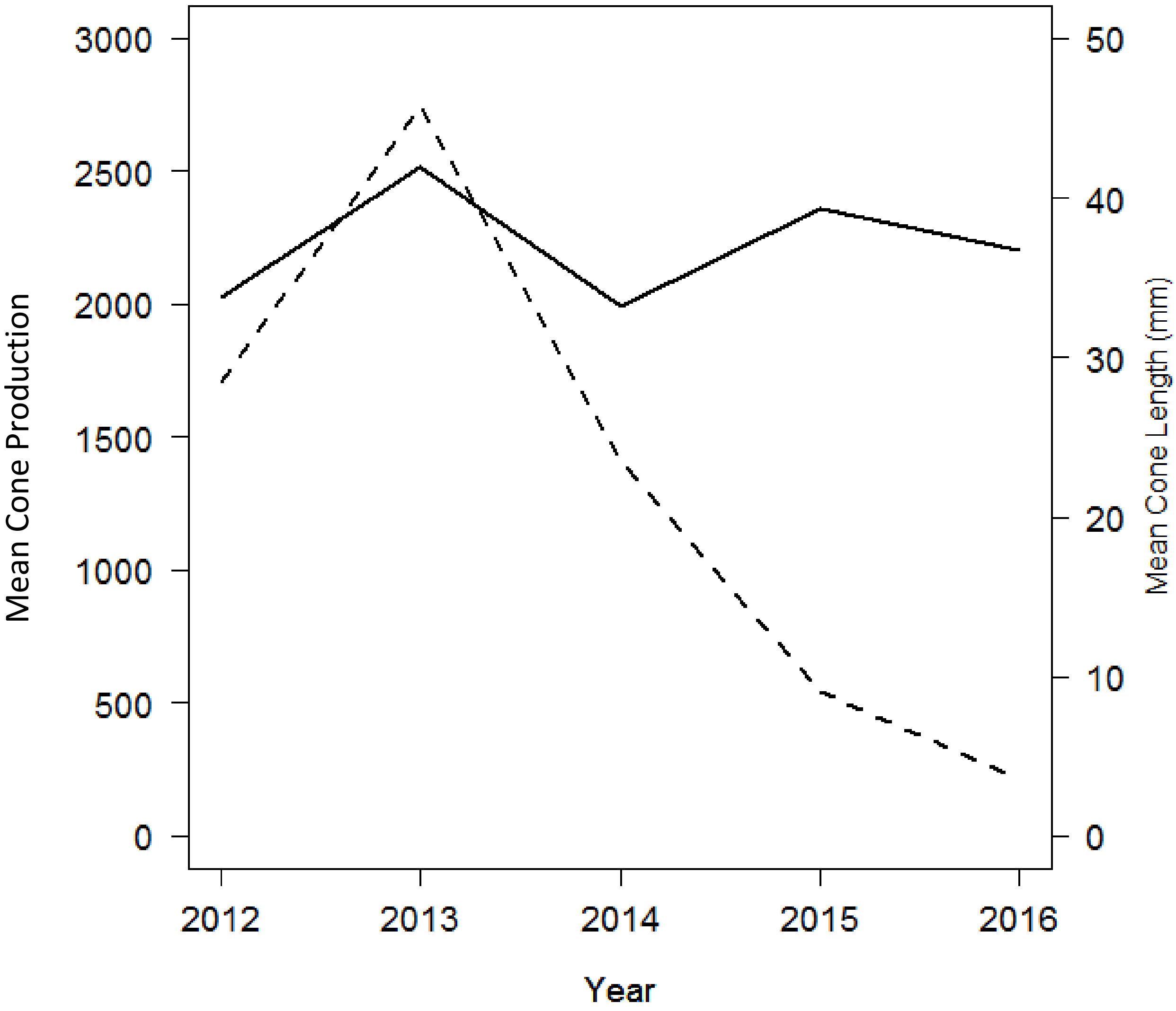

Figure 1. Mean Cone Production for Tagged white spruce (*Picea glauca*) Trees (black-hashed, n=364) and Mean Cone Length for Sample of white spruce (black-solid, n=38) Over 5 Years; letters indicate significant difference.

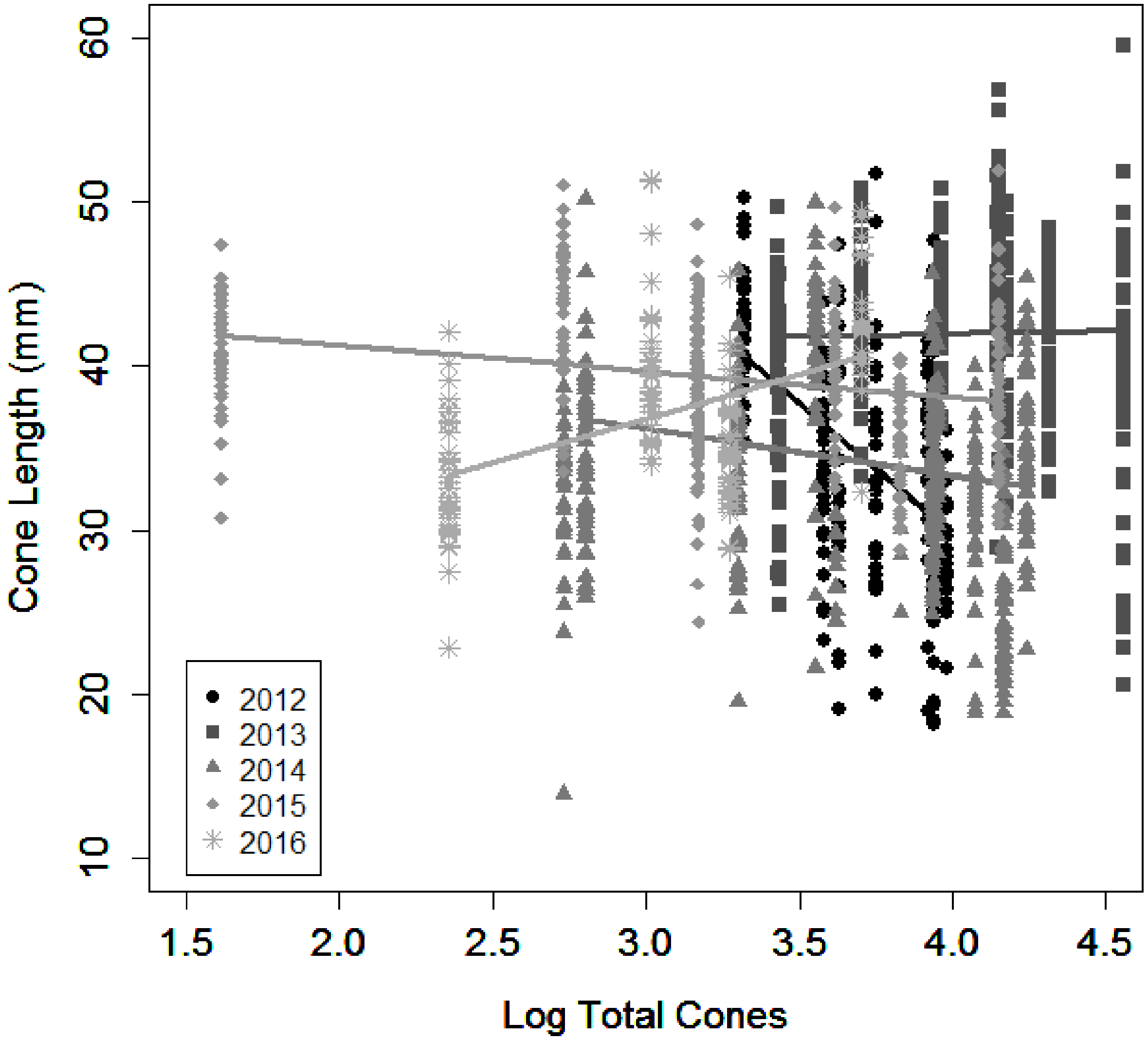

Figure 2. Relationship between white spruce (*Picea glauca*) cone length (mm) and log-total cones (n=210 Cones) for individual trees (n=38 trees) across years in Northern Michigan.

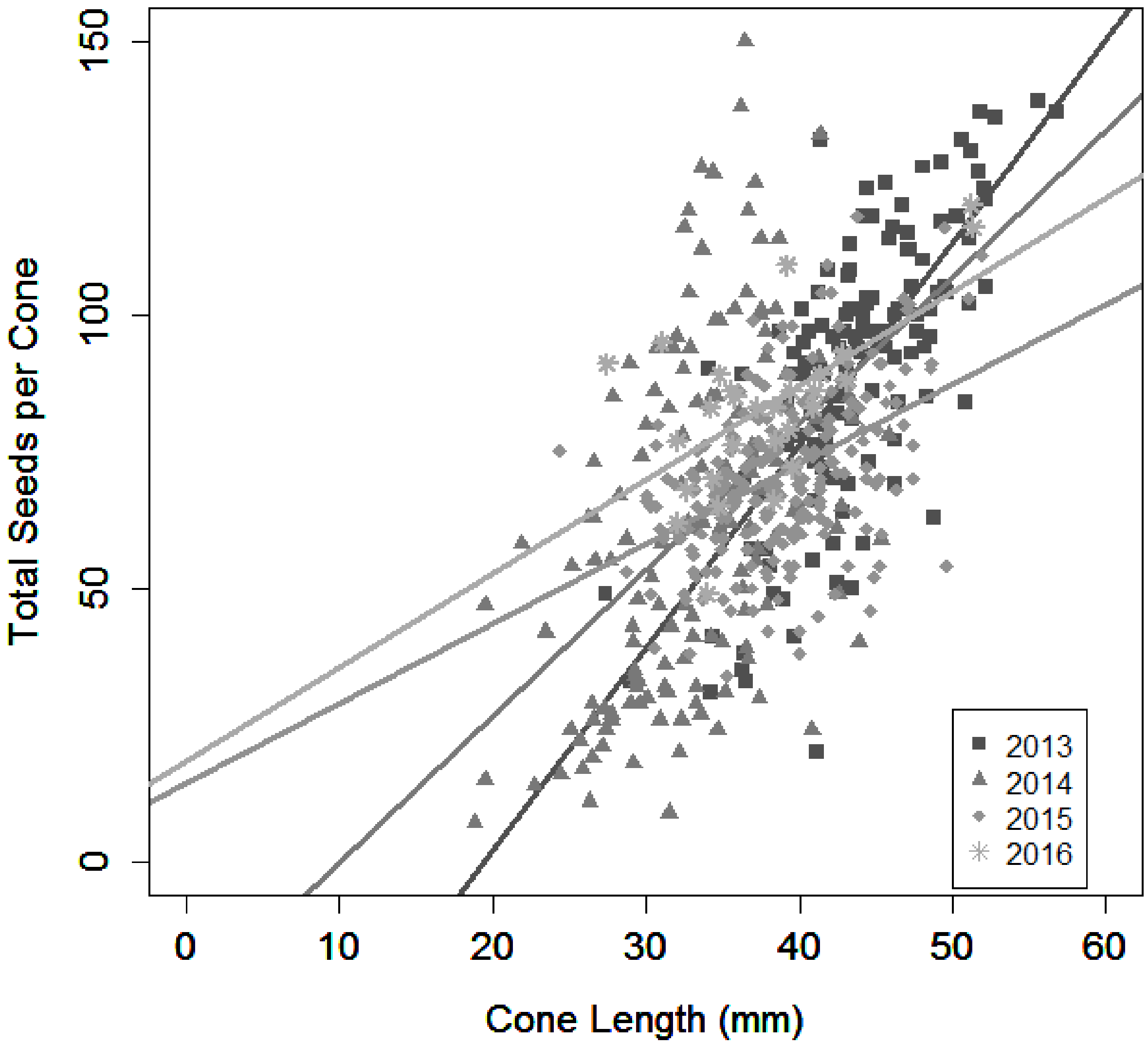

Figure 3. Relationship between Cone Length (n=1132 cones) and Total Seeds per Cone Across Years.

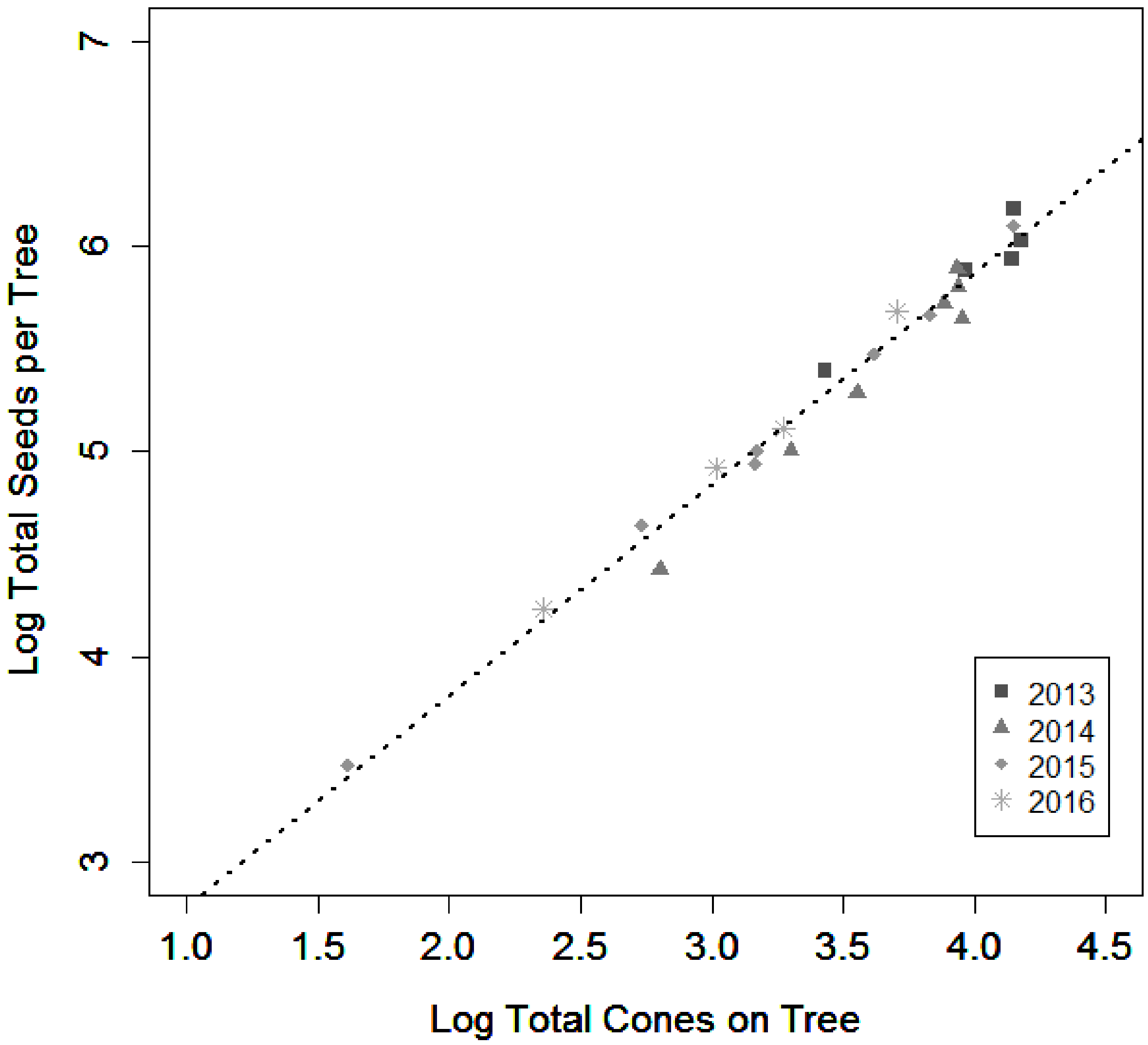

Figure 4. Relationship between Log Total Seeds per Tree and Log Total Cone Production in white spruce (*Picea glauca*) varies across years.

APPENDIX I

Table 1. Summary Table of Available Cone Length and Seed Quantity Data

Year of Collection	Mean Cones Collected per Tree	Range of Cones Collected (Min-Max)	Total Trees	Cone Length Data Available (# Trees)	Seed Quantity Data (# Trees)
2012	30	20 – 56	7	7	0
2013	39	19 – 44	9	4	5
2014	42	31 – 46	11	10	9
2015	41	39 – 42	7	7	7
2016	35	18 – 41	4	4	4

Figure 1. White spruce distribution. Map from USGS: 1971 USDA.