2013

Variation in Cone Production of White Spruce at Two Sites near its Southern Range Limit

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Recommended Citation
Grecco, Allison (2013) "Variation in Cone Production of White Spruce at Two Sites near its Southern Range Limit," DePaul Discoveries: Vol. 2 : Iss. 1 , Article 7.
Available at: https://via.library.depaul.edu/depaul-disc/vol2/iss1/7

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INTRODUCTION

The Boreal forest is the world’s largest biome, containing almost 1/3 of Earth’s forested land, and is a major forest type of the Northern hemisphere. White spruce (Picea glauca) is a dominant coniferous tree species found in the Boreal forest, with a transcontinental range reaching latitudes of 69°N and stretching south into northern Minnesota, Wisconsin, and central Michigan (Sutton, 1969). Many studies on white spruce have been conducted in the northern part of its range (Danby & Hik, 2007; LaMontagne & Boutin, 2007; Krebs et al., 2012), but little is known about this species near the southern range limit of its distribution.

Mast seeding, a phenomenon that occurs synchronously within a plant population, is the production of large quantities of seed on an occasional basis (Kelly, 1994). There are many hypotheses to explain why mast seeding occurs in plant populations. It could be a product of evolutionary processes (e.g., seed-predator satiation, an increase in wind pollination efficiency), or it could be in a direct response to climatic conditions or energy reserves (Kelly, 1994). Spatial and temporal patterns in mast seeding may be synchronous over large geographical areas, even as large as a continental scale. Koenig & Knops (1998) found synchrony in seed production in sites from 500km to 2,500km apart, as well as synchrony in the radial growth of trees between sites of up to 5,000km apart. Others, too, have observed synchrony at a large geographical scale. In a study of seed production patterns in the deciduous Fagus crenata, high levels of synchrony were observed between 11 sites across a geographical area of 80,000km² (Suzuki et al., 2005).

Regional weather patterns of temperature and precipitation can account for some of the observed temporal variation in seed production (Selas et al., 2002). Events such as high temperatures during growing season.
can impact each stage of seed development in *Pinus banksiana*, while warm temperatures and long growing seasons may result in greater resource allocation towards both growth and reproduction (Despland & Houle, 1997). Annual variation in white spruce cone production and mast seeding has been explained by patterns in weather and climate, with strong weather cues (i.e. high late summer temperatures and spring rainfall) 2 years prior to a mast, and resource availability being important for mast seeding (Krebs et al., 2012).

Despite the evidence for synchrony over broad geographical areas, substantial variation in cone production among individuals has been observed. A high level of synchrony among individuals at local scales (<75m apart) decays to only moderate levels of synchrony over a 5km area over 15 years, suggesting that synchrony among individuals is strongest at the local level, but at larger scales (>3km apart) synchrony is much lower (LaMontagne & Boutin, 2007).

Changes in climate may result in changes in population dynamics and seed production patterns of plant species, and the effects of climate change will be most evident at species’ range limits with range shifts occurring (Rizzo & Wiken, 1992). White spruce has shown tree-line expansion at its northern range (Danby & Hik, 2007), indicating that this species’ range is shifting. Understanding the biological characteristics of a species at its range limit is needed to anticipate its potential response to climate change. For instance, higher occurrences of drought could negatively impact the patterns of seed production and the occurrence of mast years. Because seeds are critical components of food webs, the patterns of seed production are crucial for understanding community structure. If changes in seed production patterns occur, the spatial distribution of seed-predator population sizes may be negatively affected over time (Koenig & Knops, 1998).

Here, spatial variation in cone production is examined near the southern range limit for white spruce. We address the question: How variable is cone production in white spruce between two geographical regions, between sites within each region, and between individuals within a site? We expect to see differences in the amount of cone produced between the two regions, as well as large amounts of variation between sites within each region. Because individuals closest to their range limits are most affected by climate change, we expect that cone production in the Kemp region will be more negatively affected by the drought of 2012 because it is closer to the southern range limit of white spruce. This study was conducted on data from a single year, 2012, and is part of a long-term research project observing spatial patterns of seed production in white spruce over time, along with this species’ potential response to climate change.

**METHODS**

**STUDY SITES**

Field work took place during summer 2012 at two field stations near the southern range limit for white spruce: northern Wisconsin (Kemp; 46.0°N, 520m above sea level) and the Upper Peninsula of Michigan (Huron; 46.9°N, 211m above sea level). The Kemp field station is located ~150km south of the Huron field station (Figure 1). The sites at the Kemp region were composed of stands of white spruce plantations. Sites at the Huron region were natural old growth forest and ranged from areas that were almost exclusively white spruce to mixed communities of white spruce, balsam fir, and white pine. We visited the field stations multiple times throughout the summer, with the first visit consisting of identification of focal trees and subsequent visits involving data collection.

**FOCAL TREE SELECTION**

Because cone production was our primary factor of interest, we selected trees for this study based on visibility. We needed to be able to completely see at least the top one-third of the tree to determine the number of visible cones the individual produced. We used numbered aluminum tags to mark individual trees for identification. We did not use trees with a dbh (diameter at breast height) of less than 9.3cm in this study, due to...
the difficulty in tagging the trees. We marked a total of 727 individuals across 12 sites (6 sites at Kemp, 6 sites at Huron).

**TREE CHARACTERISTICS**

We measured individual trees for dbh, tree height (m), and crown diameter (m). We used a clinometer to determine tree height and calipers to measure dbh (at 1.3 m above the ground). To calculate the photosynthetic volume (m³), we measured the height from the top of the tree to the lowest branch containing photosynthetic material (h_green) and crown radius (r_crown). We used the formula for the volume of a cone, \( V = \frac{1}{3}\pi (r_{\text{crown}})^2 h_{\text{green}} \) to calculate photosynthetic volume. We also recorded the elevation and location of each tree using a GPS device.

**CONE PRODUCTION**

We quantified cone production following the methods of LaMontagne et al (2005). We conducted counts in late July while the cones were still green and closed but before seed predators (e.g. red squirrels) cached the cones. While in the field, and standing in a single location where the crown of a tree was visible, we used binoculars to count the number of visible cones in the upper one-third of the crown. If the number of cones was greater than 100, we took a photograph and later counted cones using ImageJ software. The number of visible cones on a tree was converted into an estimate of the total number of cones produced by using the following equation: (LaMontagne et al., 2005; Krebs et al., 2012):

\[
\log_e(\text{total number of cones}) = 0.1681 + 1.1891 \log_e(\text{visible cones}) + 0.01
\]

\[
\text{total number of cones} = 1.11568 \times \exp\left(\left[\log_e(\text{total number of cones})\right]\right)
\]

**FOREST DENSITY ANALYSIS**

To calculate the forest density (trees/ha), we used the Point-Centered Quarter Method (PCQM) of Cottam & Curtis (1956). We laid a straight-line transect and placed a central point every 20 meters on that transect. We created four quadrats at each central point from a line perpendicular to the original transect. We determined the distance from each central point to the nearest tree (dbh>15cm) for each quadrat and recorded its species. If no tree in a quadrant was within 20m from the central point, we deemed that quadrant empty and used a distance of 25 meters in calculating the forest density. Although this may slightly overestimate the density of the forest, it is the most feasible means of determining the density of exceedingly open plots.

**STATISTICAL ANALYSIS**

We compared tree characteristics between the Kemp and Huron regions using t-tests, and we used an analysis of covariance (ANCOVA) to compare the dbh and height relationships for trees between the two regions on data that were ln-transformed to linearize the relationship. Because cone production was not normally distributed, a Kruskal-Wallis test was conducted to compare median cone production within regions and between sites within a region.

**RESULTS**

The individual tree characteristics differed between the Kemp and Huron regions (Table 1). We found the mean photosynthetic volume at the Kemp region (64.6m³) to be only 70% that of the mean photosynthetic volume at Huron (93.0m³), but this was not statistically significant (t = -1.8194, df = 9.403, P = 0.101). The mean dbh at Kemp (22.3cm) was slightly smaller than at Huron (25.2cm), but this difference was also not significant (t = -1.4386, df = 9.937, P = 0.181). The tree density at Kemp region (289 trees/ha) was greater than the Huron region (129 trees/ha). Tree density ranged from 41 to 357 trees/ha at Huron sites and from 165 to 588 trees/ha at Kemp sites, with sites H5 and H6 the most open of the Huron sites and K4 the most open at Kemp (Table 1). Tree heights were significantly related to their dbh (F = 769.19, df = 1, 722, P <0.0001) and were significantly different between regions with trees from Huron being taller than trees at Kemp after adjusting for dbh (F = 50.16, df = 1, 722, P <0.0001) (Figure 2). There was no significant difference in the slope of tree height to dbh between regions (F = 1.85, df = 1, 722, P = 0.1738).
In the Huron region, many trees produced many cones, which is a defining characteristic of a mast-year. This is in contrast with the Kemp region where cone production was much lower (Figure 3). We also found significant variation within regions (among sites) during 2012 (Figure 3). Median cone production at the Huron region (199 cones) was significantly greater than the median (0 cones) at Kemp ($\chi^2 = 149.83, df = 1, P = 0.0001$). There were also significant differences in median cone production among the 6 sites within the Huron region (range: 0 - 26,592; Kruskal-Wallis $\chi^2$ approximation = 35.579, df = 5, $P = 0.0001$), and among the 6 sites within the Kemp region (range: 0 – 5030; Kruskal-Wallis $\chi^2$ approximation = 60.38, df = 5, $P = 0.0001$). Even during the mast year at the Huron region, individual cone production within a single site ranged from 0 cones to over 25,000 cones per tree.

**DISCUSSION**

We observed significant variation in cone production across multiple spatial scales during 2012. At the regional level, a cone mast occurred at the Huron region but not at the Kemp region. This does not support the idea of high levels of spatial synchrony in mast-seeding over large geographical areas, especially since the Huron region is only 150km north of the Kemp region. Since climate determines a plant’s investment toward growth and reproduction and is critical in cone development (Despland & Houle, 1997; Selas et al., 2002), the failure of white spruce to produce mast crops in Kemp could be caused by its sensitivity to weather patterns due to its proximity to the southern range limit.

In Wisconsin, summer 2012 was the second warmest on record and precipitation was below normal levels (NOAA, 2012). Summer temperatures at Wausau, WI (~98 km S of Kemp) were above average and total summer precipitation was 6.9 cm below average (Kapela et al., NOAA, 2013). In contrast, annual precipitation in Michigan was near normal despite temperatures being the third highest on record (NOAA, 2012). Total summer precipitation in Marquette, MI (~41km SE of Huron), was 0.6 cm above average, and temperatures were 1.7 °C above average (Local Climatological Data, Marquette, MI, 2012). The prolonged drought in Wisconsin, coupled with the Kemp region being nearer the southern range limit of white spruce, may have resulted in the cone failure at Kemp. Since mast-seeding is thought to be synchronous, perhaps a cone mast would have occurred at Kemp during 2012 had more normal weather conditions persisted. Furthermore, since species near their range limits are more sensitive to changes in climate (Rizzo & Wiken, 1992), the effects of the 2012 drought could have been more pronounced at the Kemp region, causing some of the variation in cone production.

Differences in the amount of cone produced were seen between sites within a region and between individuals within a site and these differences were often pronounced. Resource availability, such as the availability of light, affects cone production (Greene et al., 2002) and competition for resources among individuals may be responsible for some of the variation seen in this study. That the sites in Huron that yielded higher median cones per individual (H2, H5, and H6) also had the lowest forest densities could indicate that competition for resources is lower at these sites leading to more energy allocation toward cone production. Competition for resources may explain the differences in median cone production at the H1 and H2 sites, 36 and 728 cones per individual respectively, despite the two sites having similar community densities. The mean white spruce dbh at the H1 site (19.4cm) was much smaller than the mean of trees in the community (31.8cm), relative to the difference in the mean white spruce dbh at the H2 site (24.1cm) compared to the mean dbh of trees in the community (30.6cm). Competition for light among white spruce trees may be greater at the H1 site because white spruce trees may not reach the top of the canopy, since trees in the community are larger. Average white spruce tree height also supports this, as white spruce trees at the H1 site were, on average, much shorter (11.4m) than those at the H2 site (15.7m). White spruce trees at the H2 site may reach the top of the canopy and have greater access to light than trees at the H1 site, which provides more energy for cone production.
The pattern of high cone yield at lower forest densities was also seen at Kemp with the K4 site, which had the lowest forest density but produced the highest mean number of cones. In contrast, the K1 site, which was the densest of the Kemp sites, showed little variation among individuals and had the lowest mean cones produced. Overall, there was more cone production at the Huron region with a cone mast occurring during 2012 at the Huron region and not at the Kemp region. The Huron region was ~160 trees/ha less dense than the Kemp region. We may expect that in non-mast years, the higher density of trees in Kemp would suggest that cone production may still be lower because of an increase in competition. Because significantly fewer cones were produced in Kemp, which had a greater number of trees/ha, it is plausible that a combination of differences in weather patterns and competition for resources contribute to the variation seen in cone production.

In summary, we found a significant amount of variation in white spruce cone production across all spatial scales during 2012. The most pronounced variation occurred between the two regions, with a cone mast in the Huron region but not in Kemp. It is possible that variation in cone production between the two regions is a result of differences in precipitation that occurred during cone development in 2012. We also saw significant variation among sites within each region, and competition for available resources may help to explain this between-site variation. However, there is still a considerable amount of individual variation within sites which challenges the evolutionary hypotheses for synchronous mast seeding events within populations.
FIGURE 1
Map of Wisconsin and Michigan with symbols denoting the relative locations of the Huron (Black) and Kemp (Grey) field stations.

FIGURE 2
The relationship of ln(tree height) as a function of ln(dbh). Each symbol represents an individual tree. Kemp is represented by the solid symbols and solid line. Huron is represented by the open symbols and dashed line. (Kemp \(y = 0.57x + 0.84, R^2 = 0.53\) and Huron \(y = 0.63x + 0.53, R^2 = 0.53\)).

FIGURE 3
Boxplots of each region showing median number of cones produced (shown as middle bar in boxplot) and variation in the total number of cones produced by individual white spruce trees at each site during 2012 for the Huron region and Kemp region. Note the difference in range of y-axis values between plots.
### TABLE 1

Mean tree characteristics (± standard deviation) of the Huron (H) and Kemp (K) regions and site means of the 6 sites located within each region. n represents the number of individuals at each site or region.

<table>
<thead>
<tr>
<th>Region</th>
<th>n</th>
<th>Mean Height (m)</th>
<th>Mean white spruce dbh (cm)</th>
<th>Mean Photosynthetic Volume (m³)</th>
<th>Median Cone Production</th>
<th>Forest Density (trees/ha)</th>
<th>Mean Community dbh (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Huron region overall</td>
<td>364</td>
<td>13.4 (5.3)</td>
<td>25.2 (11.4)</td>
<td>93 (30)</td>
<td>199</td>
<td>129</td>
<td>30.4 (12.4)</td>
</tr>
<tr>
<td>Kemp region overall</td>
<td>363</td>
<td>13.7 (4.2)</td>
<td>22.3 (9.8)</td>
<td>65 (23)</td>
<td>0</td>
<td>289</td>
<td>26.5 (13.7)</td>
</tr>
<tr>
<td>H1</td>
<td>36</td>
<td>11.4 (5.6)</td>
<td>19.4 (10.8)</td>
<td>47 (45)</td>
<td>36</td>
<td>307</td>
<td>31.8 (12.5)</td>
</tr>
<tr>
<td>H2</td>
<td>60</td>
<td>15.7 (5.2)</td>
<td>24.1 (10.1)</td>
<td>72 (77)</td>
<td>728</td>
<td>305</td>
<td>30.6 (14.9)</td>
</tr>
<tr>
<td>H3</td>
<td>77</td>
<td>14.5 (6.1)</td>
<td>23.5 (12.2)</td>
<td>99 (98)</td>
<td>3</td>
<td>346</td>
<td>29.3 (11.5)</td>
</tr>
<tr>
<td>H4</td>
<td>50</td>
<td>15.3 (4.5)</td>
<td>27.3 (13.3)</td>
<td>129 (114)</td>
<td>84</td>
<td>357</td>
<td>30.7 (14.1)</td>
</tr>
<tr>
<td>H5</td>
<td>53</td>
<td>12.5 (4.3)</td>
<td>29.2 (12.0)</td>
<td>119 (88)</td>
<td>519</td>
<td>41</td>
<td>29 (11.8)</td>
</tr>
<tr>
<td>H6</td>
<td>88</td>
<td>10.9 (3.7)</td>
<td>27.6 (8.7)</td>
<td>94 (71)</td>
<td>964</td>
<td>60</td>
<td>30.5 (7.9)</td>
</tr>
<tr>
<td>K1</td>
<td>57</td>
<td>14.9 (4.2)</td>
<td>19.4 (6.1)</td>
<td>42 (32)</td>
<td>0</td>
<td>588</td>
<td>26.6 (13.3)</td>
</tr>
<tr>
<td>K2</td>
<td>61</td>
<td>17.6 (4.3)</td>
<td>25.5 (7.1)</td>
<td>67 (45)</td>
<td>0</td>
<td>301</td>
<td>27.4 (17.7)</td>
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<td>18.0 (5.0)</td>
<td>35 (23)</td>
<td>1</td>
<td>414</td>
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<td>165</td>
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<td>K5</td>
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<td>23.2 (12.4)</td>
<td>86 (81)</td>
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<td>0</td>
<td>241</td>
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REFERENCES


