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POPULATION ECOLOGY – ORIGINAL RESEARCH

Plant-available soil nutrients have a limited influence on cone production patterns of individual white spruce trees

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Abstract

The resource budget model for mast seeding hypothesizes that soil nutrients proximately influence reproduction. Plants in high soil nutrient (particularly N) areas are predicted to have lower reproductive variability over time and higher mean reproduction. While often examined theoretically, there are relatively few empirical tests of this hypothesis. We quantified cone production of 110 individual white spruce (*Picea glauca*) trees over seven years and quantified plant-available soil macronutrients (N, Ca, K, Mg, P, S) in natural forest conditions across three years with different cone crop conditions. Each of these plant-available soil nutrients were correlated across years ($r_s = 0.55–0.89$; all > 0.81 for total-N); spatially, total-N availability varied 366-fold across trees. Plant-available soil nutrients did not influence variability or mean annual reproduction, contrary to nutrient perturbation experiments. We examined within-year nutrient and cone-production relationships, and observed significant positive relationships between reproduction and plant-available soil nutrients only in a low-reproduction year preceding a mast event. Both during a mast event and the following year, when overall cone production was very high or very low, there were no relationships. Both external drivers (e.g., weather) and internal resource budgets likely influence soil nutrient-reproduction relationships. These results suggest that plant-available soil nutrients may not be a large factor influencing mast-seeding patterns among individuals in this species.

Keywords Mast seeding · Nitrogen · Nutrient availability · Reproduction · Resource budget

Introduction

Mast seeding is the synchronous production of highly variable seed crops over time by a population of perennial plants (Janzen 1971; Kelly 1994). This reproductive strategy is common in numerous species of deciduous and coniferous trees, grasses, and herbaceous plants in habitats across the world (Sork et al. 1993; Pearse et al. 2017). The predominant evolutionary hypotheses to explain this phenomenon are to increase pollination efficiency (Kelly and Sork 2002) or satiate seed predators (Janzen 1971; Kelly 1994; Kelly and Sork 2002). Proximately, environmental factors such as weather and resource availability influence mast seeding patterns. Weather (i.e., temperature and precipitation) acts as a cue to synchronize mast seeding (Whitehead 1983; Krebs et al. 2012; Roland et al. 2014; Koenig et al. 2015), while resource budgets are hypothesized to be important in the timing and magnitude of reproduction such that resources accumulate over time to a threshold before reproduction occurs (Gysel and Lemmien 1964; Janzen 1974; Isagi et al. 1997; Satake and Iwasa 2000; Crone and Rapp 2014; Pearse et al. 2016; Allen et al. 2017). Plants growing with lower nutrients should take longer to accumulate internal resources and consequently reproduce less frequently and intensely (reviewed in Pearse et al. 2016).

Soil-derived macronutrients [nitrogen (N), potassium (K), calcium (Ca), magnesium (Mg), phosphorous (P), and sulfur (S)] are required for plant growth and reproduction (Maathuis

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2009). Nutrient depletion in plant tissues the year after a mast event indicates the role of macronutrient limitation (Whitehead 1983; Han et al. 2014). N availability and uptake are linked to photosynthetic capacity and carbon gain. Species with lower foliar nutrients (including N) have higher temporal variability (Fernández-Martínez et al. 2019), and experimental macronutrient addition has altered the magnitude and inter-annual variability of plant reproduction. For example, N-fertilization increases stand-level reproduction (Davis et al. 2004; Bogdziewicz et al. 2017), while low fertility soils are associated with less frequent and more intense reproduction events (Tanentzap et al. 2012; Canham et al. 2014). Species vary in their relationship between soil nutrients and reproduction; Ca addition increased seed production of northern hardwoods growing on deficient soils (Long et al. 2011; Halman et al. 2013) and improved allocation to reproduction at higher elevations (Cleavitt and Fahey 2017), while the coniferous species rimu (*Dacrydium cupressinum*) had higher per capita fecundity on less fertile sites (Canham et al. 2014). The relationship between soil nutrients and reproductive patterns in mast seeding species is not well studied empirically, especially in conifers. There is naturally occurring variation in plant-available soil nutrients due to microtopography, soil moisture, soil texture, and microbial activity (Brady and Weil 2002; Paul et al. 2003; Lawrence and Zedler 2011; Pérez-Ramos et al. 2014), even within a seemingly homogenous habitat type. Here, we test the impact of local plant-available soil nutrients on reproductive patterns of white spruce (*Picea glauca*).

White spruce is a mast seeding species dominant throughout the North American boreal forest (LaMontagne and Boutin 2007; Gärtner et al. 2011). While mast seeding is a population-level phenomenon, individuals produce the pattern, and we followed the reproduction of 110 individual white spruce trees across seven years. We also measured plant-available soil nutrient levels at the local (individual tree) scale to test its influence on reproduction. Based on previous findings (Tanentzap et al. 2012; Bogdziewicz et al. 2017), we predicted lower variation in cone production of individual trees over time (CV_i) and increased mean cone production with increased plant-available soil macronutrients, in particular with total-N availability. We also predicted a within-year effect of plant-available soil nutrients on cone production, where trees with higher levels of locally plant-available soil nutrients would have higher cone production in a given year, but that this relationship may be affected by different reproductive conditions (i.e., pre-mast year, mast year, and post-mast year).

Materials and methods

Site description

Our research was conducted in the Huron Mountains (46.82°N, 87.73°W), Michigan, USA. Tree communities are characteristic of the boreal-deciduous forest ecotone, with white spruce, white pine (*Pinus strobus*), balsam fir (*Abies balsamea*), eastern hemlock (*Tsuga canadensis*), striped maple (*Acer pensylvanicum*), red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), northern white cedar (*Thuja occidentalis*), trembling aspen (*Populus tremuloides*), and paper birch (*Betula papyrifera*). This region of the Huron Mountains includes a portion of the old-growth forest where fire has been a key natural disturbance (Simpson et al. 1990; Muzika et al. 2015). Bedrock of the study region is Pre-Cambrian granite, gneiss, and sandstones (Dorr and Eschmann 1970). Soils are thin and acidic, with more humus overlying sandy surface horizons. The Big Bay, MI, weather station had 30-year (1981–2010) monthly mean (± SD) June–August temperatures of 17.8 °C (± 5.2) [minimum = 11.6 °C (± 4.4), maximum = 24.0 °C (± 7.1)]; mean total monthly precipitation was 84.8 mm (https://www.nodc.noaa.gov/). While summer temperatures in the region are generally warm, there is variability across years (Hinkel and Nelson 2012). During our study, mean summer soil moisture was 0.25 (± 0.03) $m^3 \cdot m^{-3}$ Surface soils in the study area were ~ 90% sand with moderate organic matter levels (5.40% carbon) and low bulk density (0.85 $g \cdot cm^{-3}$; see Online Resource 1).

We quantified cone production and soil nutrient availability around 110 focal individual white spruce trees distributed across four sites within a 21-km^2 area. These trees were randomly selected from a larger set of trees with cone production recorded annually from 2012 to 2015. All trees included in the study reproduced at least once during the seven years of observation and ranged in size from 13.6 to 64.3 cm diameter at breast height in 2012. White spruce is wind pollinated and seeds are wind dispersed (Nienstaedt and Zasada 1990). Reproductive buds differentiate in summer the year prior to pollination and seed dispersal (Eis 1967; Owens and Molder 1977), with weather during bud differentiation influencing the reproductive output (Nienstaedt and Zasada 1990; Krebs et al. 2012).

Cone production

Reproduction was quantified as cone production per tree, a measure commonly used in conifers (Zasada and Viereck 1970; LaMontagne et al. 2005; LaMontagne and Boutin 2007; Krebs et al. 2012; Pearse et al. 2017). We collected cone production data from 2012 to 2018 on dominant and co-dominant trees with visible and undamaged crowns. Cones were counted following the methods derived for white spruce by LaMontagne et al. (2005); briefly, a stationary observer on the ground uses binoculars to count all visible cones on individually tagged trees each year in late July or early August. Trees with more than 100–200 visible cones were photographed and cone counts were done in ImageJ. From visible cones, we used an established relationship to estimate total cones produced per tree (LaMontagne et al. 2005). For patterns across all years, we calculated mean cones per basal area (Greene et al. 2002) using the basal area of trees recorded in 2012, and we used the coefficient of variation (CV_i) for each tree to examine variability in reproduction. Mean cones per basal area was not correlated to the basal area ($r = 0.14$, $p = 0.14$) whereas cones per tree were highly correlated with tree basal area ($r = 0.69$, $p < 0.001$).

Soil nutrient availability

We measured plant-available soil nutrients around 110 trees in 2016 and a random subset of 45 of these trees in both 2017 and 2018. Nutrient supply rates adjacent to each tree were quantified using Plant Root Simulator® probes (PRS probes; Western Ag Innovations), which have strong positive relationships with extractable N in spruce soils (Harrison and Maynard 2014), and are used in a variety of habitats to assess plant-available soil nutrients (Hueso et al. 2019; Johnson et al. 2019; Kurth et al. 2019; Norby et al. 2019). Each PRS® probe consists of an ion exchange membrane pre-treated chemically to mimic characteristics of plant root surfaces. PRS® probes continuously adsorb charged ionic species over the burial period, providing an index of soil nutrient availability including N (NO_3-N, NH_4-N), phosphorous (P), and other macronutrients (Ca, K, Mg, and S). The resin membrane mimics root-exchange properties in soils (Qian and Schoenau 2005) and has high utility because they cause minimal disturbance, allow resampling in the same location over time, and have high soil-resin contact. Edaphic factors, such as soil moisture, that influence plant root uptake are similarly reflected by measurements obtained through PRS® probes (Qian and Schoenau 2002) and they integrate nutrient availability over time (deployment period), therefore, they are more likely than static measures of nutrient concentrations to correlate with plant nutrient uptake rates (Norby et al. 2019). Foliar nutrients are considered good indicators of soil nutrient availability to plants (Fernández-Martínez et al. 2017). We corroborated this relationship between PRS plant-available total N with %N content of new growth needles collected from 23 trees in July 2017 to confirm that PRS data provided appropriate indices of plant-available soil nutrients in this ecosystem. Needles were dried at 60°C for 48 h, pulverized in a ball mill, and analyzed for C and N content (See methods in Online Resource 1). A Pearson correlation between 2017 total plant-available N and 2017 foliar % N was significant ($r = 0.68$, $p < 0.001$).

During deployment, probes were inserted vertically into the uppermost soil layer, to approximately 10-cm depth. Each year, pairs of anion/cation probes were deployed in each of the four cardinal directions 1-m from the trunk of each focal tree for 44 days (mid-June to early-August). Our 44 day probe deployment was used to both ensure that plant-available soil nutrient data would be recorded across trees given the sandy soils at our sites and to avoid probe saturation; in a mixed-conifer forest, PRS® probes have been deployed for 8-weeks (Bengtson et al. 2007) while Harrison and Maynard (2014) studied PRS® probe use in spruce soils and found saturation of probes in fertilized soils beginning at week eight of their study. After extraction in the field, PRS® probes were cleaned, transferred to Ziplock® bags (probes surrounding an individual tree were combined together), and shipped to the Western Ag Innovations Inc. laboratory in Saskatoon, Saskatchewan where they were analyzed for nutrients. The PRS probes were eluted with 0.5 N HCl for one hour to desorb ions from the ion-exchange membrane; the eluent was analyzed for NH_4-N and NO_3-N using calorimetry (Skalar Continuous Flow Analyzer), and analyses of other ions were completed using inductively coupled plasma optical emission spectrometry (Perkin Elmer ICP-OES 8300) (Western Ag pers comm.). Ion supply rates were averaged across the four pairs of probes deployed around each tree; units for nutrients are μg per 10 cm^2 per burial length (44 days). Following other studies, we combined N ions to estimate total plant-available N (Tanentzap et al. 2012; Bogdziewicz et al. 2017). Plant-available soil macronutrients sampled during 2016, 2017, and 2018 ($n = 45$ trees) were significantly and positively correlated between years ($r_s = 0.55$–0.89; all > 0.81 for total-N, data not shown). Because of these significant correlations, we used the 2016 plant-available soil macronutrient data to test hypotheses related to patterns in variability and mean reproduction across all years (the CV and mean cones per tree calculated from 2012–2018; $n = 110$ trees). To test hypotheses for within-year relationships between plant-available soil nutrients and cone production for each of 2016–2018 we used the plant-available soil measurements for the respective year.

Statistical analysis

To examine how plant-available soil nutrient levels influenced mast seeding patterns across years (2012–2018), including both reproductive variability (CV_i) and mean cone production, we used linear mixed-effects models (*lme4* package in R; Bates et al. 2012) with linear combinations of each nutrient as main effects and site as a random effect to account for unquantified variation in site characteristics. We compared models using AICc analysis and AICc weights (Burnham and Anderson 2002). For each plant-available soil nutrient main effect, we used likelihood-ratio tests to compare the relationship to a null model to test for significance. We tested model residuals for normality using a Shapiro-Wilks test, and data not fitting a normal distribution were ln-transformed to better fit assumptions.

To examine relationships between each plant-available soil nutrient and individual tree cone production under different reproductive conditions (2016 and 2018 were low cone years, 2017 was a high reproduction 'mast' year), we used a zero-inflated negative binomial mixed-effects model using the *glmmTMB* package in R (Brooks et al. 2017). Cones per tree were used as the response variable, with predictor variables being plant-available soil nutrient and year, and the interaction between the nutrient and year in the model, and the year was used in the zero-inflated portion of the model. Individual treeID was used as a random effect, and an offset term of the basal area was used to account for tree size. We used *ggpredict* to generate the best-fit curve for each model (Lüdecke 2018). For analysis of S, we omitted three data points with plant-available soil nutrient values > 100 because they were almost double the magnitude of the next highest S value, and led to predicted values of cones that were an impossibly high magnitude. We assessed statistical significance using α = 0.05. All analyses were run using RStudio version 1.2.1335.

Results

Mean annual cone production per individual tree peaked in 2013 and 2017, and was lowest in 2018 (Fig. 1). Cone production varied across individual trees, and overall mean cones per basal area (SD) during 2012–2018 was 2.37 (2.03) cones · cm^{-2}, ranging from 0.002 to 10.81 cones · cm^{-2}. Mean CV$_i$ (SD) was 1.69 (0.51), ranging from 0.72 to 2.65 (Table 1). During years when we deployed nutrient probes, mean cones per tree were 222 in 2016, 4099 in 2017, and 7 in 2018; mean cones per basal area were 0.24, 4.42, and 0.02 cones · cm^{-2} per year, respectively.

There was considerable spatial variation in plant-available soil nutrients around trees, with maximum available total-N being 366 times higher than the minimum (Table 1). Variability in the availability of other soil nutrients included some trees having 47 times more K and 93 times more P than other trees; overall, variation in other soil nutrients was less than that of N availability (Table 1, see Online Resource 1 Table S1 for summaries of plant-available soil nutrients in 2017 and 2018).

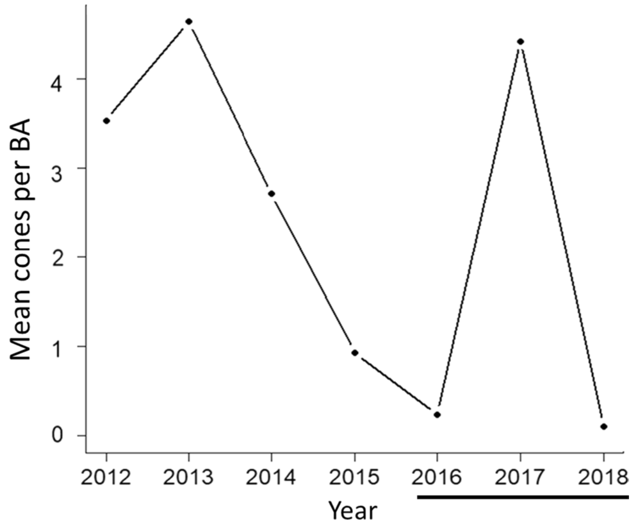

Fig. 1 Mean annual cone production per basal area (BA; cones · cm^{-2}) for 110 white spruce trees between 2012 and 2018 in the Huron Mountains, MI, USA. The horizontal line under the *x* axis highlights the years when plant-available soil nutrients were measured

Table 1 2016 Plant-available soil nutrients (μg · 10 cm^{-2} · 44 days) associated with individual white spruce trees, and cone production characteristics for 110 trees in the Huron Mountains, Michigan (USA)

Characteristic	Mean	SD	Min	Max
Plant-available soil nutrients				
TN	64.0	116.2	1.5	564.1
Ca	1447.0	691.0	247.2	2717.4
K	235.2	182.4	17.0	804.1
P	12.1	9.1	0.5	42.3
S	21.5	12.6	5.4	104.6
Mg	199.3	59.7	51.0	320.3
Cone production				
Mean cones per BA	2.37	2.03	0.002	10.81
CV$_i$	1.69	0.51	0.72	2.65

Mean cones per basal area (BA, cones · cm^{-2}) is the mean of annual cone production across each individual from 2012 to 2018. Coefficient of variation for individual trees (CV$_i$) is based on the coefficient of variation (CV) of each tree calculated across years (2012–2018)

Total N and cone production

There was no significant relationship between ln-interannual variation in cone production (ln-CV$_i$) and ln-plant-available soil-N ($\chi^2(1) = 0.012$, $p = 0.91$; Fig. 2a). There was also no significant effect of ln-plant-available soil-N on mean cones per basal area across years for individual trees (Fig. 2b; $\chi^2(1) = 0.001$, $p = 0.97$). In AIC model comparisons, for both ln-CV$_i$ and mean cones per basal area, none of the top models with nutrients (that combined up

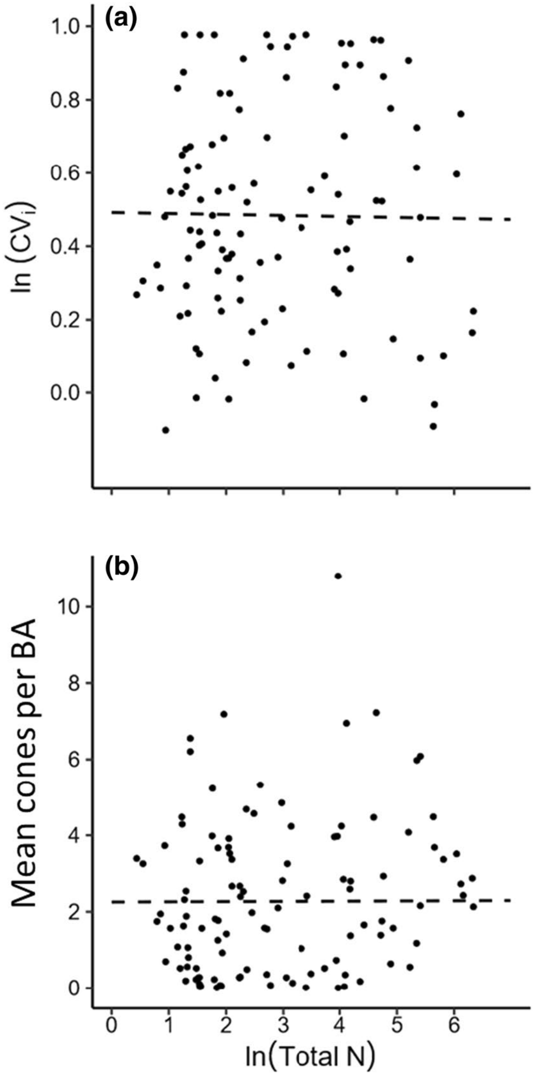

Fig. 2 Relationships between plant-available soil total N [ln(Total N_{2016}), $\mu g \cdot 10 cm^{-2} \cdot 44$ days] and cone production dynamics (2012–2018; $n = 110$ trees) including (**a**) variability in cone production over time [ln CV_i] ($p = 0.91$); and (**b**) mean cones per basal area [$cones \cdot cm^{-2}$] ($p = 0.97$). Each point represents data for an individual tree (dashed lines are not statistically significant relationships)

Table 2 Effects of 2016 soil macronutrients on variation in white spruce cone production, ln CV_i, from 2012 to 2018 ($n = 110$ trees) using AICc model comparison in the Huron Mountains, MI, USA

Model	*k*	LL	ΔAICc	AICc weight
Ca, Mg	5	− 21.62	0.00	0.07
Ca, ln Total N, Mg	6	− 20.91	0.82	0.05
ln S, Mg	5	− 22.04	0.84	0.05
Ca, ln S, Mg	6	− 20.97	0.94	0.05
Ca, ln S, ln Total N, Mg	7	− 20.03	1.33	0.04
(Null)	3	− 24.82	2.04	0.03

Site was included as a random effect in both the full and null models. '*k*' is the number of model parameters, and 'LL' is the log-likelihood. Models up to ΔAICc of two are shown

to 90% of the top AICc weights) were a better fit than the null model (ΔAICc values were ≤ 2.0 from the null model and AICc weights were very low; Tables 2 and 3). See Online Resource 1—Fig. S1 for the relationship between plant-available soil-N with CV_i.

For the within-year analysis, there was a significant interaction between cones per tree and year. In 2016, cones per tree were significantly and positively related to plant-available soil N, the low cone production year preceding a mast year ($p = 0.04$; Fig. 3a), but this relationship between plant-available soil nutrients and cone production was not significant in 2017, the high-reproduction 'mast' year ($p = 0.63$; Fig. 3b), or in 2018, the low cone year following the mast year ($p = 0.89$; Fig. 3c).

Other nutrients (Ca, K, P, S, Mg)

There were no significant relationships found between plant-available soil Ca, K, P, S, or Mg with ln-CV_i (all $p > 0.05$; Fig. 4a–e) or with mean annual cone production (Fig. 4f–j). Also similar to N, there was a significant interaction between year and four of the five other plant-available soil nutrients. There were significant relationships of Ca, K, P, and S with 2016 cone production ($p < 0.01$, $p < 0.01$, $p = 0.01$, and $p = 0.03$, respectively); this was not the case for Mg ($p = 0.79$; Fig. 5a–e). During the mast year (2017) and the post-mast year (2018), there were no significant relationships between nutrient availability and cone production (all $p > 0.10$; Fig. 5f–j, Fig. 5k–o, respectively).

Discussion

Plant-available soil-N availability did not predict either mean reproduction or variability in white spruce cone production over time, despite the large amount of variation in levels of naturally occurring soil-N. Within years,

Table 3 Effects of 2016 soil macronutrients on mean cones produced per basal area (2012–2018) of white spruce using AICc model comparison in the Huron Mountains, MI, USA

Model	*k*	LL	ΔAICc	AICc weight
(Null)	3	− 101.27	0.00	0.16
Mg	4	− 100.69	1.27	0.08
K	4	− 100.90	1.69	0.07
Ca	4	− 101.13	2.14	0.05

Site was included as a random effect in both the full and null models. '*k*' is the number of model parameters, and 'LL' is the log-likelihood. Models up to ΔAICc of two are shown

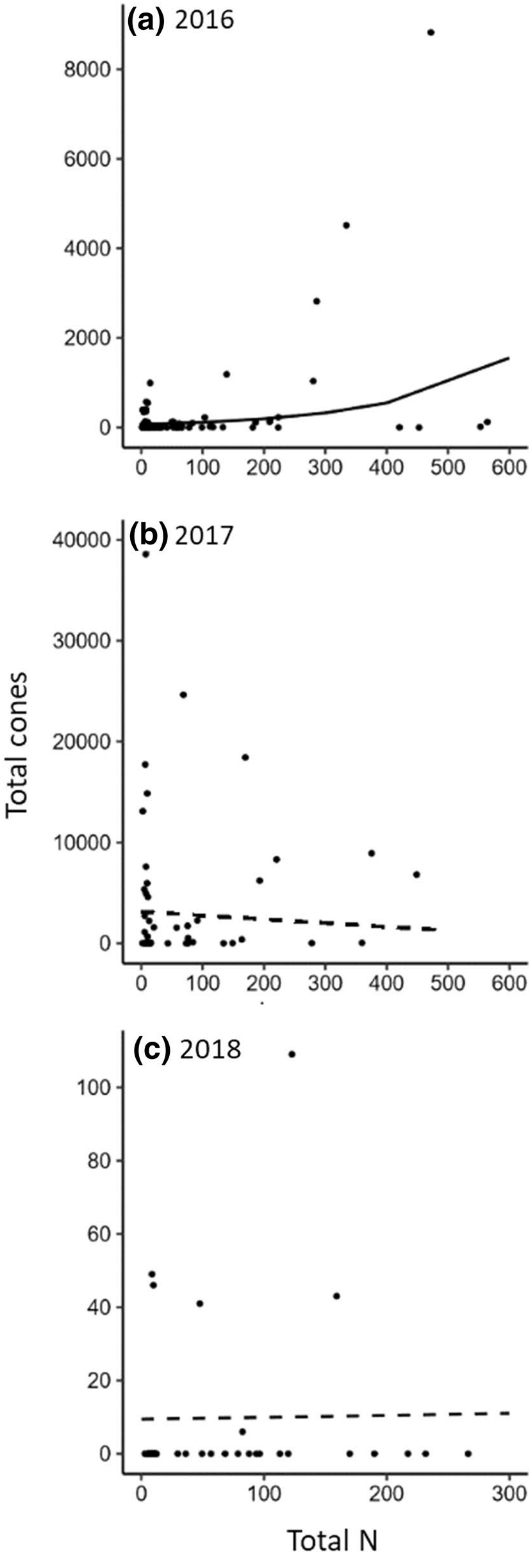

Fig. 3 Plant-available soil Total N [μg · 10 cm^{-2} · 44 days] and annual white spruce cone production in each of (**a**) 2016 (n = 110 trees), (**b**) 2017 (n = 45 trees), and (**c**) 2018 (n = 45 trees). Each point represents data for an individual tree each year, and lines are zero-inflated negative binomial model predictions (dashed lines are not statistically significant relationships). Note difference in scale in **c**

plant-available soil-N (as well as Ca, S) was positively related to cone production only in a year of low reproductive output 4 years after the previous high-reproduction mast year and prior to a mast event. However, this plant-available soil nutrient-reproduction relationship did not hold either during or following the mast year. These relationships were generally consistent across other soil macronutrients. These data suggest that plant-available soil-N influences white spruce cone production in limited circumstances.

Despite the positive relationship between plant-available soil nutrients and foliar nutrient concentrations (Harrison and Maynard 2014), we found support for our hypotheses only in a limited context. Resource budget models suggest that plants accumulate resources to produce a large seed crop over multiple years (Isagi et al. 1997; Satake and Iwasa 2000; Pearse et al. 2016; Allen et al. 2017). Only in 2016 do our results suggest that trees with high soil nutrients may have achieved a threshold for reproduction following the previous mast event (in 2013) and invested some resources at that time. There was no negative effect of 2016 reproduction on reproduction during the 2017 mast event. We found a significant positive relationship between cone production and Ca in 2016, and in northern hardwoods, Ca addition has positively influenced seed production (Long et al. 2011; Halman et al. 2013; Cleavitt and Fahey 2017). Across the years, however, the impact of Ca on mean cone production and temporal variability in our data was quite weak. While we saw negative within-year relationships for plant-available soil K and P with cone production in 2016, it is unclear why. Wang and Klinka (1997) reported negative relationships between foliar K and P with stand age; we did not have data on tree ages in the study. Fernández-Martínez et al. (2017) found allocation to fruit production (NPP$_f$) was positively associated with foliar P concentrations during their analysis of 126 European forests, but we did not see similar relationships with P in our study; while our measure of cone production is appropriate for assessing the magnitude and variation of reproduction over time, it does not address patterns of allocation. While some of the macronutrients we investigated are not directly associated with plant reproduction, each plays a functional role in plant cells and structure (Holman and Robbins 1937; Ge et al. 2007). Negative relationships could be associated with stoichiometric requirements or co-limitation by multiple nutrients (Agren et al. 2012; Marleau et al. 2015), and examining N:P:K ratios of vegetation may indicate whether the species experiences co-limitation (Wang and Moore 2014). A recent paper found that masting intensity is higher in species with low foliar N and P concentrations (Fernández-Martínez et al. 2019); our findings suggest that this interspecific variation may not translate to intraspecific variation in plant-available soil nutrients relationships with reproductive patterns.

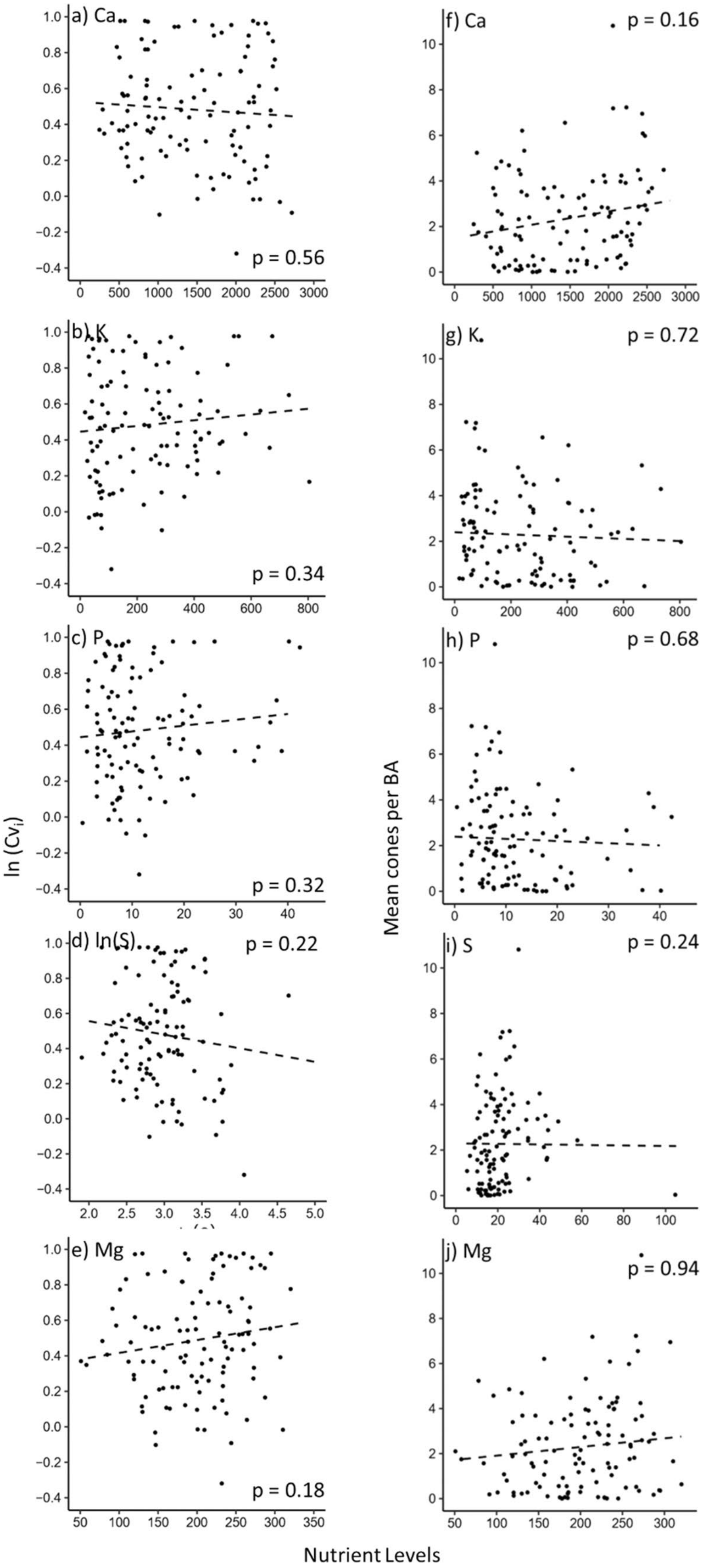

Fig. 4 Relationships between other soil macronutrients (Ca, K, P, S, and Mg, $\mu g \cdot 10\,cm^{-2} \cdot 44$ days) and (**a**–**e**) cone production variability [ln(CV$_i$)] and **f**–**j**) mean cone production [mean cones per basal area (BA); cones $\cdot$ cm^{-2}] between 2012 and 2018 ($n = 110$ trees). Lines represent model fits (dashed lines represent non-significant relationships)

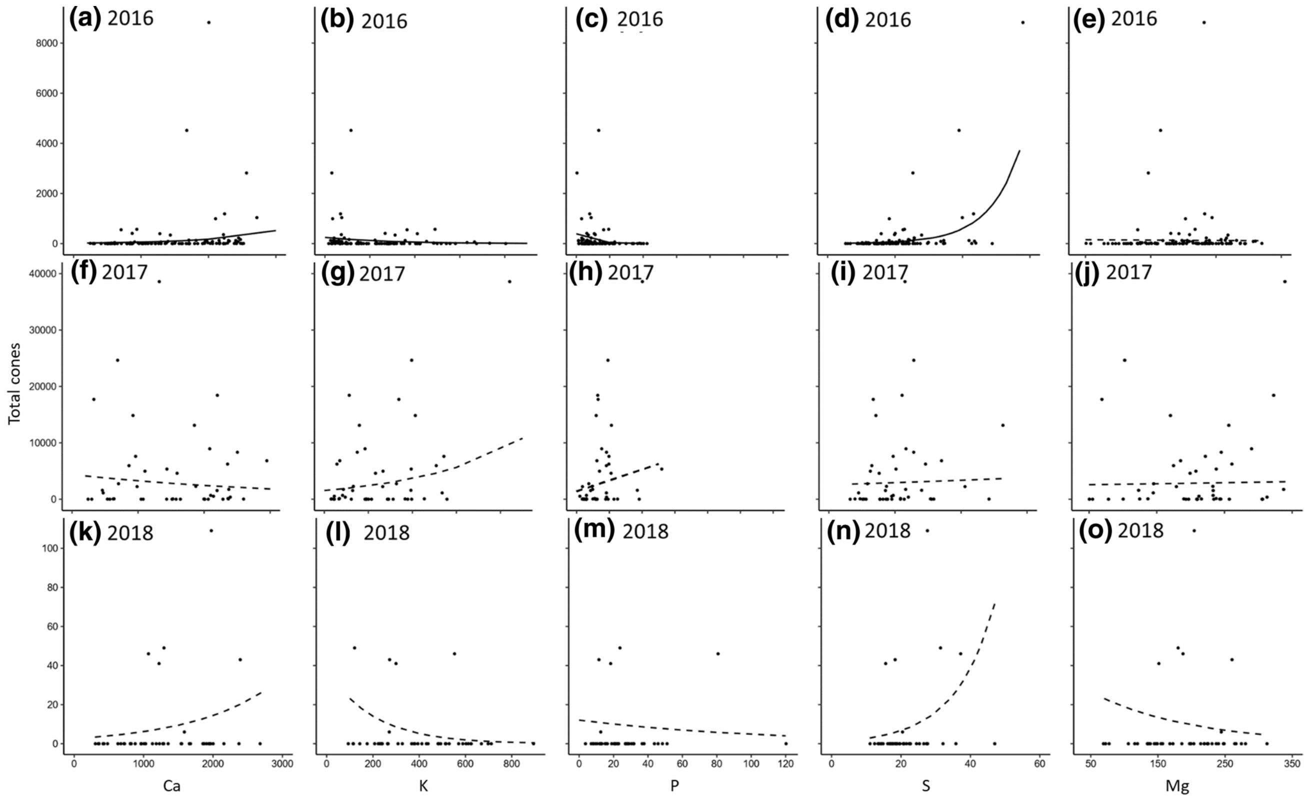

Fig. 5 Plant-available soil nutrients [$\mu g \cdot 10\,cm^{-2} \cdot 44$ days] and cone production by individual white spruce trees in **a**–**e** 2016 ($n = 110$), and **f**–**j** 2017 ($n = 45$), and **k**–**o** 2018 ($n = 45$) in the Huron Mountains, MI, USA. Lines represent fits from zero-inflated negative binomial mixed-effects models; lines are solid when significant, and dashed when not statistically significant. Points represent data from individual trees

Our findings also contrast those of experimental N fertilization increasing average reproductive output (Davis et al. 2004; Bogdziewicz et al. 2017) and predictions of less frequent and more intense reproduction on N-poor soils (Tanentzap et al. 2012). However, similar to our findings, a long-term N-fertilization study of oak reproduction showed that the impact of fertilization on annual acorn production relative to controlled conditions varied by year (Bogdziewicz et al. 2017). Fertilization studies add large amounts of nutrients to treatment plots (Smaill et al. 2011; Bogdziewicz et al. 2017) and data on natural soil nutrient levels in experimental studies prior to treatment, or comparisons of plant-available soil nutrients in treatment and control plots are generally not available. Therefore, we cannot compare the ranges observed across trees in our naturally observed nutrient values to that induced from experiments. Reporting impacts of fertilization on plant-available nutrient levels would allow experimental results to be put in the context of naturally occurring nutrient levels. Recent work has shown that mast seeding patterns are unrelated to stored carbon in multiple mast seeding tree species, suggesting that recent and current carbon is more important to reproduction (Hoch et al. 2013; Igarashi et al. 2019). Research on soil nutrients suggests that while N appears to be more limiting than carbon in temperate tree species, relatively few species have been studied (Han and Kabeya 2017).

Our study in the southern region of the boreal forest, overlapped with cold temperate needleleaf forests; residence time for soil-N in this type of habitat is 33–138 years (Vogt et al. 1986). Here, soil-N availability was positively correlated across years suggesting that spatial variation in soil-N persists over time. Soil fertility requirements vary across species, and white spruce grow on a variety of soils. Impacts of fertilizer on reproduction are unknown for natural stands of white spruce; increased growth has been found in populations with nutrient deficiencies when fertilizer is applied but reproduction was not examined (Wilde 1966; Stiell 1976). Another conifer species, rimu, was more fecund on less fertile marine terrace sites than on alluvial surfaces when compared to angiosperms (Canham et al. 2014), which contrasts with the idea that mast seeding species are less fecund on less productive soils (Kelly and Sork 2002). While Pérez-Ramos et al. (2014), reported that trees inhabiting more fertile sites had a higher CV_i in seed production, and impacts on mean reproduction varied between the two species studied (one had a positive effect of soil fertility, the other saw no effect).

Mast-seeding events are promoted evolutionarily as an economy of scale, but this interacts with resources and weather cues to impact reproductive output (Pearse et al. 2016). Tanentzap et al. (2012) observed that soil-N availability increased with late-spring air temperatures and was associated with less variable flowering frequency in species across latitudinal bioclimatic zones. In this study, all of our trees were within the same bioclimatic zone and we suggest that weather cues may be key to driving mast seeding patterns particularly as recent and current carbon has been shown to be used for reproduction (Han and Kabeya 2017). There are a number of documented relationships between weather cues, particularly related to summer temperatures and precipitation, linked to tree reproduction the following year and promoting mast events (Whitehead 1983; Krebs et al. 2012; Pearse et al. 2014; Roland et al. 2014; LaMontagne et al. 2020). During a mast event, high levels of reproduction occur across many individual trees and may contribute to a lack of a within-year plant-available soil nutrient–reproduction relationship, and similarly the year after a mast event reproduction is low across most individuals (LaMontagne and Boutin 2007). In post-mast conditions, nutrient resources are thought to be exhausted, potentially prohibiting a plant-available soil nutrient–reproduction relationship.

The influence of plant-available soil nutrients on reproduction between mast years may inform us how long recovery from nutrient depletion lasts and explain observed individual variation in mast seeding patterns (e.g., LaMontagne and Boutin 2007). We suggest that only after a number of low cone years that trees growing in areas with higher plant-available soil nutrients, including nitrogen, calcium and sulphur, showed a positive relationship with cone production. This was not seen in the mast year or the post-mast year and may be due to the ability of plants in those higher nutrient areas to have more stored nutrients. This could explain why, after several low reproduction years following the 2013 mast event that in 2016 (the year preceding another mast event) there was a significant relationship with these plant-available soil nutrients. While quantifying nutrient storage in trees was beyond the scope of this study, we recommend future analyses of mast seeding patterns in individual trees investigate linkages between soil nutrient availability, nutrient storage within the trees, and reproductive patterns. Resource addition experiments could be valuable for investigating drivers of mast seeding in future studies related to nutrients through controlled experiments, over multiple years, and involving more species (Bogdziewicz et al. 2020). In addition, genetic factors may influence intraspecific variability in nutrient uptake by trees.

Our goal was to characterize soil nutrient availability and test its influence on the variability and magnitude of reproduction in the mast seeding species, white spruce. To further understand the role of nutrient resources in mast seeding, it has been suggested that species in different habitats and individual trees should be studied during both mast and non-mast years (Han and Kabeya 2017). Increased N deposition is associated with climate change (Hole and Engardt 2008) and makes understanding the influence of nutrients on plant reproduction an area of particular interest (Kelly et al. 2013; Pearse et al. 2017). N deposition is predicted to reduce the occurrence of mast events, impacting seed predator population dynamics and decreasing the recruitment of mast seeding trees (Bogdziewicz et al. 2017). Despite the large spatial variation in the availability of total-N and other macronutrients across trees, we found little effect of soil nutrients on mast-seeding dynamics. Our study site is in an area with relatively long growing seasons relative to other parts of the white spruce range, and studies of soil nutrients and mast seeding patterns in other areas, and on other conifer species, would be valuable. Mast seeding has been of interest because of its implications ranging from forest regeneration to community dynamics. By focusing on individual-level resources and patterns, we gain additional insight to test drivers of mast seeding patterns. In addition, further studies could examine nutrient content in cones and seeds and its relationship with soil and plant tissue nutrients (Hay et al. 2008; Han et al. 2014).

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Author contribution statement ACL, BAL, and JML contributed to experimental design and writing the manuscript. ACL and JML performed fieldwork and BAL conducted laboratory work on soil characteristics and foliar nutrients. ACL, BAL, and JML contributed to statistical approaches and ACL conducted the statistical analysis.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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