

Local-scale synchrony and variability in mast seed production patterns of *Picea glauca*

JALENE M. LAMONTAGNE* and STAN BOUTIN

Department of Biological Sciences, University of Alberta, Edmonton, Alberta, T6G 2E9, Canada

Summary

1. Mast seeding is the synchronous and highly variable production of seed by a population of plants. Mast seeding results from the behaviour of individuals; however, little is known about the synchrony of individuals at local scales.
2. We address two primary questions at a within-population (17–36 ha study plots) and individual level: (i) How variable is seed production between and within years? (ii) How synchronized is seed production between individuals?
3. We monitored annual cone production of 356 *Picea glauca* (white spruce) from 1990 to 2005 within four plots spanning a total distance of 5.3 km in the Yukon Territory, Canada.
4. Spearman correlations (r_s) were conducted to test for synchrony. Overall, the trees were moderately synchronous (mean r_s (\pm SE) of 0.52 ± 0.14), and synchrony was statistically detectable ($r_s > 0$) over all distances. Individuals < 75 m apart were highly synchronous (0.64 ± 0.18), and correlations dropped to 0.33 ± 0.07 for trees > 3 km apart. There was considerable variation in cone production patterns among pairs of individuals.
5. The number of mast years per plot varied from one to three. During a mast year, many individuals within plots produced large cone crops, with more variability between individuals in low mean cone years. Individual trees had dominant endogenous cycles varying from none to 1–5 years. Forty-four per cent of trees had no significant lag, 23% a negative 1-year lag, and 20% a positive 3-year lag. Basal area did not influence lags, but trees with higher mean cone production throughout the study were more likely to have a 3-year lag compared with no lag.
6. The scale of highest synchrony coincided with the scale at which the dominant seed predator in the area, the territorial red squirrel (*Tamiasciurus hudsonicus*), operates. This may be the scale at which selection for synchrony occurs.
7. Based on high synchrony locally, high synchrony within a mast year, and multiple lags in cone production by individuals, both available resources and strong weather cues appear to play roles in the observed patterns.

Key-words: autocorrelation, boreal forest, cone production, individual variability, mast seeding, *Picea glauca*, synchrony, white spruce

Journal of Ecology (2007) **95**, 991–1000

doi: 10.1111/j.1365-2745.2007.01266.x

Introduction

Mast seeding is defined as the synchronous and highly variable production of seed crops by a population of

plants from year to year (Kelly 1994). The critical components of mast seeding are thus both high variability in seed production and high synchrony among individuals. Mast seeding is well documented in a number of plant species, with synchrony detected in seed production between populations over large geographical areas (2500 km for *Pinus* spp.; Koenig & Knops 1998a). Several hypotheses have been proposed to explain synchronous seeding by individuals within populations, with seed predator satiation and increased pollination

*Author to whom correspondence should be addressed. Jalene M. LaMontagne, Ecology Division, Department of Biological Sciences, University of Calgary, 2500 University Drive NW, Calgary, Alberta, T2N 1N4, Canada. E-mail jalene.lamontagne@ualberta.net.

efficiency having the most support (reviewed in Kelly 1994; Kelly & Sork 2002). Mast seeding may satiate seed predators such that individual plants experience higher reproductive success (Janzen 1971; Silvertown 1980; Kelly 1994), or increased individual pollination success (reviewed in Kelly & Sork 2002). As individuals become synchronized, selection should act against asynchronized individuals, thereby enhancing selection for high degrees of synchrony (Janzen 1971).

Although selection for synchrony acts at the level of the individual plant and it is individuals that generate the population-level masting patterns observed, most studies have focused on population rather than individual-level estimates of interannual variability (but see Herrera 1998; Koenig *et al.* 1999; Koenig *et al.* 2003; Liebhold *et al.* 2004). Long-term studies on individual plants and investigations of the local-scale extent of mast seeding have both been suggested as important directions for research on mast seeding (Kelly 1994; Herrera 1998; Herrera *et al.* 1998; DeSteven & Wright 2002; Kelly & Sork 2002; Buonaccorsi *et al.* 2003; Koenig *et al.* 2003; Liebhold *et al.* 2004). Even though the evolution of masting should encourage strong individual synchrony, individual variation in seed production could be maintained because, in addition to regional weather patterns (Selås *et al.* 2002), seed production is influenced by local environmental conditions (Greene *et al.* 2002), or individual attributes such as tree size (Greene & Johnson 1994; Greene *et al.* 2002) and available nutritional reserves (Nienstaedt & Teich 1972). Koenig *et al.* (2003) suggested that the levels of individual variability and synchrony may also be affected by the scale at which various selection pressures operate (e.g. wind vs. animal pollination and dispersal, localized vs. regional seed predators).

Temporal and spatial patterns of variability and synchrony are also relevant to ecosystems because seed-predator population dynamics, and even community-level dynamics, may be affected by seed crop availability (Ostfeld & Keesing 2000; Koenig & Knops 2001). Spatial variation in synchrony of seed production by individual trees over relatively small scales (< 10 km) has been studied in *Quercus* spp. (Koenig *et al.* 1999; Liebhold *et al.* 2004). Synchrony in acorn production between individuals declined with distance for some species and regions, but not others, and the extent of spatial synchrony was correlated with environmental factors influencing acorn production (Koenig *et al.* 1999). Here, we examine the variability and synchrony of seed production by 356 individual *Picea glauca* (Moench) Voss (white spruce) trees separated by distances of 30 m to over 5 km, measured over 16 years. *Picea glauca* is a wind-pollinated and wind-dispersed mast seeding conifer species whose seeds are a food source for many small mammals and birds (Dale *et al.* 2001). We address two questions: (i) How variable is seed production between and within years? (ii) How synchronized are patterns of seed production between individual trees? We determine if synchrony between

individuals varied with distance between individuals and/or whether or not a mast crop was produced. We show considerable variability in the synchrony of cone production patterns of individual trees, and the tendency for synchrony to decline with increased distance between trees. We explore sources of variability that could affect synchrony among individuals, including variation in the occurrence of mast-years at the plot-scale within which individuals are nested, synchrony in the production of large and small cone crops by individuals within years, and endogenous cycles of individual cone production.

Methods

STUDY SPECIES

We studied *P. glauca* in the boreal forest region of the south-western Yukon Territory, Canada (61°N, 138°W). Here, cone production by *P. glauca* ranges from years with complete cone failure, when virtually all trees produce no cones, to mast years (Dale *et al.* 2001). The study area (maximum extent *c.* 5.3 km) ranges from 850 to 950 m elevation and experiences low precipitation (annual mean = 230 mm) falling primarily as rain during summer; mean snowfall is 100 cm (Krebs & Boonstra 2001). Vegetation is dominated by *P. glauca*, the only conifer species in the area, with small patches of *Populus tremuloides* Michx (trembling aspen; see Krebs *et al.* 2001 for a detailed description). The dominant *P. glauca* vertebrate seed predator in the area is red squirrel (*Tamiasciurus hudsonicus*), caching thousands of cones annually (Smith 1968). Other vertebrate seed predators are boreal red-backed voles (*Clethrionomys rutilus*), white-winged crossbills (*Loxia leucoptera*), boreal chickadees (*Parus hudsonicus*), and bohemian waxwings (*Bombycilla garrulus*) (Smith & Folkard 2001).

DATA COLLECTION

We measured the annual cone production of *P. glauca* trees at 371 locations from 1990 to 2005. Tree locations were distributed over four study plots established to study ecosystem dynamics of the boreal forest (Krebs *et al.* 2001) and the plots were assumed to be representative of the boreal forest in the study region; plot A was 17 ha, and plots B, C and D were each 36 ha (Fig. 1). Grid patterns (30 m) were established over each plot and sampled trees were selected based on the closest tree to a specified grid location. A minimum distance of 30 m, and a maximum distance of approximately 5.3 km, separated sampled trees. All trees sampled had a diameter at breast height > 5 cm, the size at which *P. glauca* may produce cones in this area (J. M. LaMontagne & S. Boutin, unpublished data). Cone production for each tree was estimated by counting the number of cones visible to an observer standing on one side of the tree in late July to early August of each year,

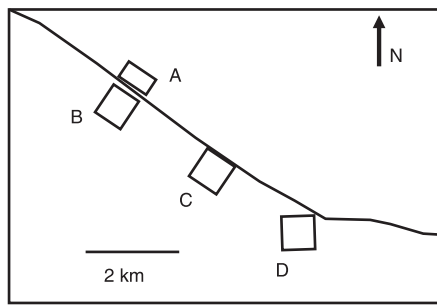


Fig. 1 Study plot locations for *P. glauca* synchrony in cone production, Yukon, Canada. The line in the map represents the Alaska Highway.

prior to cone harvesting by red squirrels (Peters *et al.* 2003). This was converted to 'total' cones using: total cones = $10^{(0.073 + 1.189 \cdot \log(\text{visible cones}))}$ (LaMontagne *et al.* 2005). Total cones were used in analyses. If a marked tree died it was replaced by the next closest live tree. Only one tree per location, the one monitored for the most years, was used in our analyses (range 5–16 years; mean 11.8 years; median 13 years). This avoided pseudoreplication with respect to the correlation and distance classes. No cone data were available for plot D in 1996 and 1997, and some locations in this plot were not sampled after 1995. Fifteen locations (trees) were excluded from analyses, having never reproduced (following Koenig *et al.* 2003); the total number of individual trees used in our analyses was 356.

VARIABILITY IN CONE PRODUCTION

To confirm that *P. glauca* was undergoing mast seeding we calculated the mean annual total cone production plus the standard deviation, and the coefficient of variation of the annual means as measured over all years of the study for each plot ($CV_p = \text{Overall plot SD} / \text{Overall plot mean}$). We also measured individual variability by calculating the mean coefficient of variation of all individuals within a plot using the average and standard deviation of cones produced by an individual tree across all years (mean CV_i ; Herrera 1998).

INDIVIDUAL SYNCHRONY IN CONE PRODUCTION

Tests of synchrony in cone production of individual trees over years were conducted based on a modified correlogram (Koenig 1999). First, cone production patterns of all pairs of individual trees over time were correlated to each other using Spearman rank correlations (r_s). Previous studies have used Pearson correlations to test for synchrony (e.g. Schaubert *et al.* 2002; Buonaccorsi *et al.* 2003; Koenig *et al.* 2003), but our data were not bivariate normal distributed (in 332 of 356 cases; Shapiro-Wilk test) and in many cases also violated the linearity assumption of Pearson correlations (Zar 1999). Under these circumstances Spearman

correlation is a more robust test (Quinn & Keough 2002). We refer to the Spearman coefficients as levels of synchrony. We examined spatial synchrony of cone production patterns within distance classes between trees (< 75 m, 76–150 m, 151–300 m, 301–500 m, 501–1000 m, 1001–2000 m, 2001–3000 m, 3001–4400 m, 4401–5316 m) using bootstrap samples. We calculated the mean correlation (mean r_s) and standard error for each distance class based on 5000 iterations. For each iteration, correlations between pairs were chosen from the pool of all pairs such that each individual was only used once (Koenig & Knops 1998b).

Within each distance class, we tested synchrony in cone production patterns between individuals against values selected to represent two dichotomies of synchrony: no synchrony, if the mean correlation coefficient was not significantly greater than zero; and perfect synchrony, defined as counts over time for different individuals being piecewise parallel (Buonaccorsi *et al.* 2003) or the mean correlation coefficient being not significantly less than 1.0 (one-sided single sample *t*-tests and an $\alpha = 0.05$). Although we conduct these baseline tests, we are less concerned with testing for statistically detectable synchrony, and are more interested in the levels of synchrony of cone production patterns with distance. This is because individuals may be statistically synchronous even if the mean correlation coefficient is very low (Koenig & Knops 1998b).

SYNCHRONY IN MAST AND LOW CONE PRODUCTION YEARS

Asynchrony between individuals could arise because different trees produce their largest cone crops in different years or because trees in mast years are highly synchronous but highly asynchronous in intervening years. In addition, the local plots may have different levels of productivity (Greene *et al.* 2002) that may be reflected in the occurrence of mast years.

We examined the occurrence of mast years among plots and the synchrony of individuals producing their largest 'x' cone crops, where 'x' is the number of designated mast years at the plot level (see below). The percentage of trees in each plot within each year producing one of their 'x' largest cone crops was calculated, for example if a plot displayed three mast years we determined the proportion of trees that produced one of their top three cone crops in each of the mast years. Only trees in the data set for 13–16 years were included in this analysis ($n = 196$). In order to do this we needed to identify mast years.

Within the definition of 'mast seeding' given by Kelly (1994), 'mast years' are those years when heavy seed crop is produced (Norton & Kelly 1988). We defined mast years at the plot scale in the following manner (LaMontagne 2007; J. M. LaMontagne & S. Boutin, unpublished manuscript). For each plot we first expressed yearly cone production as a standardized deviate of the annual mean cone production to the long-term

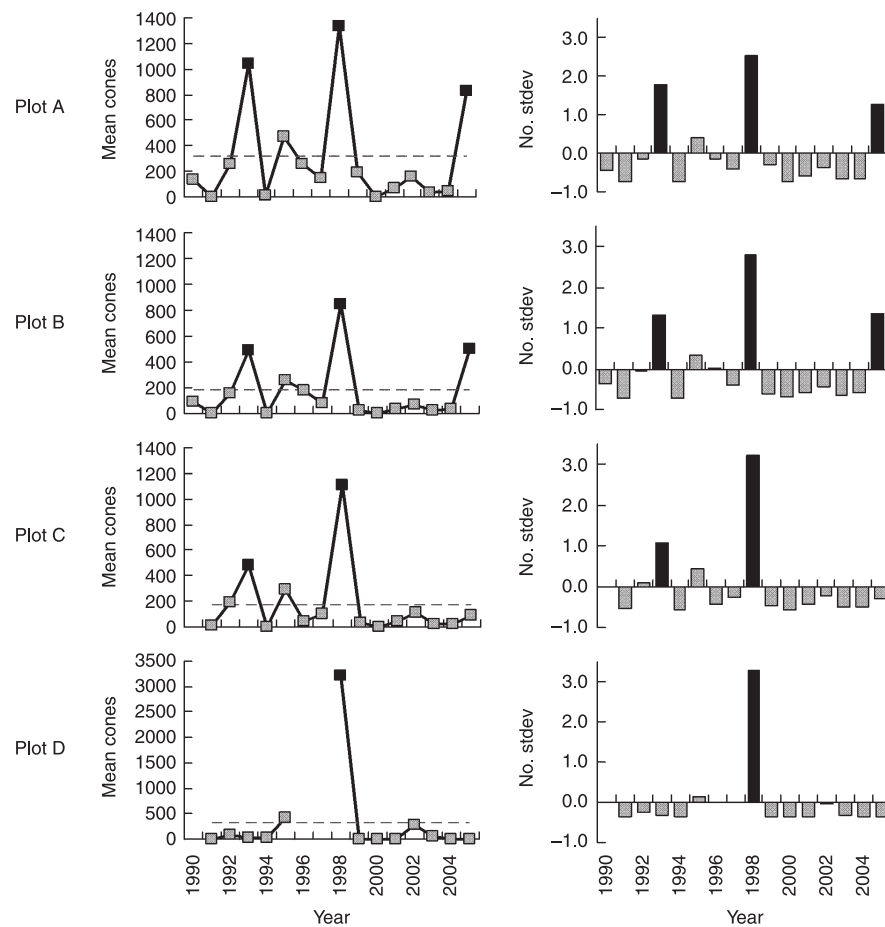


Fig. 2 Mean annual *P. glauca* cone production for each study plot: A, B, C, and D from 1990 (or 1991) to 2005 in the Yukon, Canada (left panels). The dashed line represents the long-term mean cone production during the study. Right panels show the number of standardized deviations the annual cone production mean was from the long-term mean. Filled symbols/bars represent mast years based on deviations in cone production from the long-term mean.

plot mean calculated over all years (i.e. (mean cones in year 't' - long-term mean cones)/SD calculated over all years). We defined 'mast years' as years in which the annual standardized deviate of cone production was greater than the absolute magnitude of the variation below the mean. We suggest that years with cones close to the mean abundance will be close to 0 standardized deviates from the mean, low cone years will have standardized deviates that are negative, and high cone 'mast years' will be positive and beyond the range of the negative standardized deviates (Fig. 2). Our approach uses the long-term variation in cone productivity occurring within a plot to dictate which years are mast years, as opposed to a theoretical distribution, allowing comparisons between sites having different productivity. Synchrony in low cone production by individual trees was based on the percentage of trees within a plot that had their lowest cone production observed in a year.

ENDOGENOUS CYCLES OF INDIVIDUAL CONE PRODUCTION

Variation in synchrony of cone production among individuals may result from endogenous cycles within individuals. To examine this we calculated autocorre-

lation functions (ACF_t , where 't' represents the lag) for individuals in the data set for at least 13 years. Data were log-transformed and differenced to the mean annual total cones per tree, to fit assumptions of normality and stationarity (Berryman 1999) for each tree. Gaps in the data were not interpolated and were not included in ACF analysis. No lags greater than 5 years were examined due to the length of the data. Patterns of the dominant ACF lag for each tree were coded, from no significant lag to a maximum 5-year lag, and as either positive or negative. Variation in the dominant cone production lag was analysed with multinomial logistic regression and the modelling approach of Hosmer & Lemeshow (1989). Univariate multinomial logistic regressions were conducted with individual tree attributes, including maximum basal area (cm^2) over the study and mean log-transformed cone abundance. Both predictors had $P < 0.2$, so were included in a multivariate model, with non-significant terms ($P > 0.05$) removed in a stepwise procedure, until remaining terms were significant.

Results

All four plots underwent mast seeding (all $CV_p > 1$; Table 1; Liebhold *et al.* 2004) with mean annual cone

Table 1 Plot-level information on variability and synchrony of cone production by *P. glauca*. For each plot, the coefficient of variation (CV_p), the mean Spearman correlation for synchrony of all pairs of trees (mean r_s), and the mean CV_i for each plot, are shown. Number of years of cone production data for each of the study plots is shown by 'n'. See text for number of individuals in plots

Plot	CV_p	Mean r_s	Mean CV_i	n
A	1.31	0.59	1.84	16
B	1.40	0.59	2.07	16
C	1.71	0.50	2.10	15
D	2.74	0.63	2.15	13

crops typically being the highest on plot A, followed by plots B, C and D (Fig. 2). For each plot, mean CV_i ranged from 1.84 to 2.15 (Table 1).

SYNCHRONY IN CONE PRODUCTION WITH DISTANCE

While pairs of trees over all distance classes were significantly correlated (mean $r_s > 0$; all $P < 0.001$), all distance classes showed less than perfect synchrony (all $P < 0.02$). The overall mean correlation coefficient was 0.52 ± 0.14 (mean \pm SE), and levels of synchrony ranged from a high of 0.64 ± 0.18 for trees < 75 m apart, to a low of 0.33 ± 0.07 with > 3 km between pairs of trees (Fig. 3). There was no significant decrease in average synchrony between pairs of individuals in closest and farthest distance classes (one sided t -test, $t_{623} = 1.213$, $P = 0.113$).

SYNCHRONY IN MAST AND LOW CONE PRODUCTION YEARS

The occurrence of mast years varied between plots. The two plots closest to each other, A and B (Fig. 1), had

three mast years (1993, 1998, 2005); plot C had two (1993, 1998); and plot D had one mast year (1998). All four plots had their largest mean cone crop in 1998 when they all had a cone mast. While plots A and B produced a mast in 2005, plot C produced below average cones (mean = 87 cones per tree), and plot D had almost no cones (mean = 0.1 cones per tree).

In 1998, the year with the highest annual mean cones and when all plots produced a mast crop, 84–100% of the trees in each plot produced large cone crops (Fig. 4). In 1993, 36–77% of the trees in plots A, B and C produced large cone crops, and in 2005, 38% and 50% of trees in plots A and B, respectively, produced one of their largest three cone crops. In years when the mean cone production was relatively low, 10–30% of trees within plots still produced one of their large cone crops. No trees produced a top cone crop in 1991 or 1994, when 65–95% of trees within plots did not produce cones (Fig. 5). The annual percentage of trees producing low cones varied substantially, with less variation between plots within a year (Fig. 5). A notable exception was 2005 when plots A and B showed a mast year, while plot C had 50% and plot D $> 90\%$ of trees producing low cones. In mast years on a plot, few trees failed to produce cones (on average 5.8%). There was only one complete cone failure observed (plot D in 2000). In the post-mast years of 1994 and 1999, 75–79% and 30–50% of trees in plots that masted the previous year, produced low cones, respectively.

TEMPORAL PATTERNS OF INDIVIDUAL CONE PRODUCTION

Three patterns of temporal autocorrelation in cone production for individuals were commonly detected (Table 2). These included trees with no significant lag (86 of 196 trees or 44%), a negative correlation in cone production at 1 year (23%), or a positive correlation at

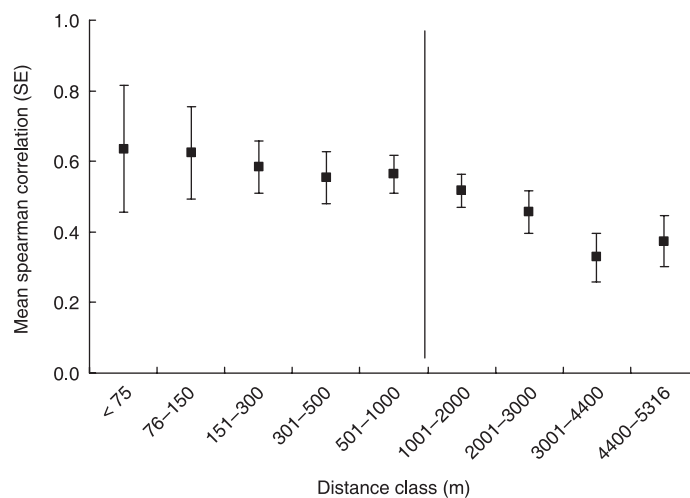


Fig. 3 Spatial variation in synchrony of cone production by *P. glauca* pairs of individuals. The vertical line is where distances between tree pairs generally move from within to between study plots. All mean correlations for each distance class were significantly greater than zero and less than one.

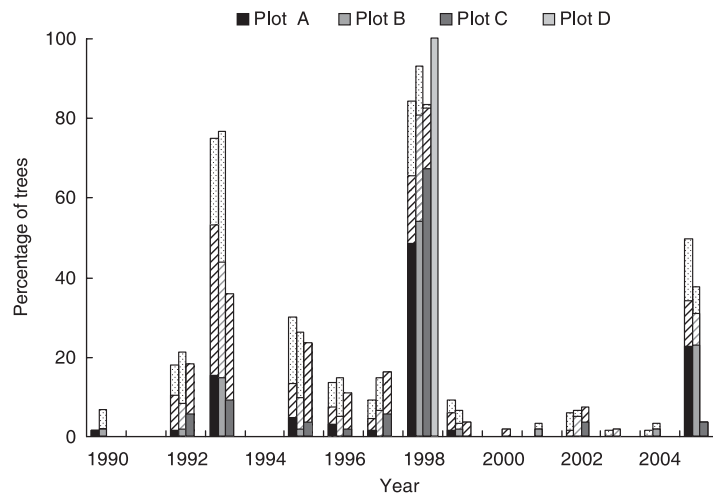


Fig. 4 Percentage of *P. glauca* trees that produced large cone crops within each year. Only trees in the data set for at least 13 years were included in the analysis. Plot A ($n = 66$) and plot B ($n = 61$) have their top 3, plot C ($n = 55$) has its top 2, and plot D ($n = 14$) has the single top cone year shown, based on the number of high cones years in Fig. 2. Solid bars represent the top cone year, angled lines represent the second most cones, and dotted bars represent years with the third most cones, when shown. Recall that data for plots C and D span 1991–2005 only, and no data are available for plot D in 1996 and 1997.

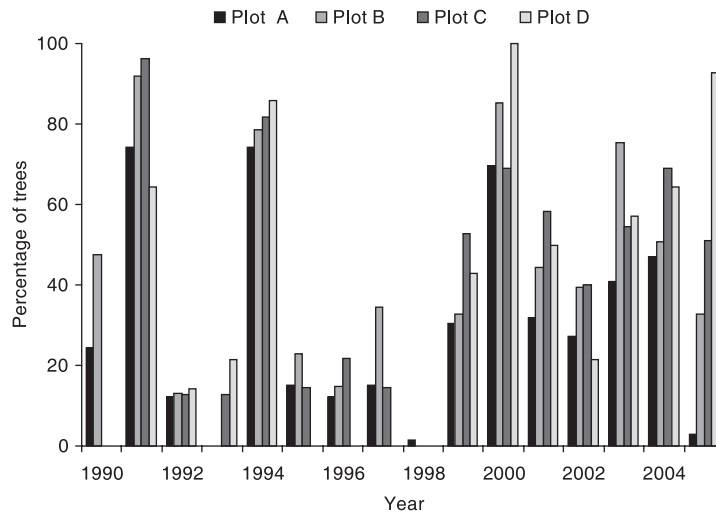


Fig. 5 Percentage of *P. glauca* trees producing their lowest cone crop within each year for each of the four study plots. Only trees in the data set for a minimum of 13 years were included in the analysis. The lowest cones may occur in more than one year for each tree. Sample sizes are the same as in Fig. 4. Note that plots C and D span 1991–2005 only, and no data were available for plot D in 1996 and 1997.

3 years (20%). Other lags included a negative correlation at 2 (6%) and 4 years (3%), and a positive correlation at 5 years (4%). There was no significant relationship between basal area and temporal patterns of cone production. Mean individual cone production influenced the lag patterns of cone production (Table 2); individuals with higher cone production were more likely to have a 3-year lag, compared with no significant lag (Table 2).

Discussion

Overall, individual trees were moderately synchronous in their pattern of cone production, with a mean correlation of 0.52, but this varied with distance between trees. This correlation value is in keeping with ‘moder-

ate synchrony’ used previously to describe mean Spearman and Pearson correlations of 0.53 (Buonaccorsi *et al.* 2001; Koenig *et al.* 2003, respectively). Individuals were highly synchronous at the most local spatial scale, and they showed low synchrony at distances over 3000 m. Some of this variation was due to differences detected at the plot-scale, specifically with respect to the occurrence of mast years. Our results suggest that regional mast years can vary in intensity locally, and can affect synchrony of individuals. In 1998 ‘masting’ occurred over all study plots. In 1993, all but one of the plots masted, while in 2005 only half of the plots had a mast cone crop.

Variability among individuals was also detected in the level of synchrony in the production of large cone

Table 2 Final model from multinomial logistic regression for dominant ACF lags. Individual trees with a negative lag at 1 year, or a positive lag at 3 years, were compared with trees with no significant lag. 'n' is the number of individuals with each pattern. Trees with dominant lags of 2, 4 and 5 years were omitted from this analysis; they comprised only 10% of individuals sampled

ACF _t	n	Parameter	b (SE)	P	Odds ratio (95% CI)	Mean log(cones) (SE)	Mean basal area cm ² (SE)
No lag significant	86					2.46 (0.13)	246.7 (20.2)
Lag 1 negative	46	Intercept	-0.112 (0.390)	0.774	0.799 (0.592, 1.079)	2.13 (0.18)	194.6 (23.8)
		Mean log(cones)	-0.224 (0.153)	0.143			
Lag 3 positive	40	Intercept	-2.329 (0.552)	< 0.001	1.729 (1.235, 2.420)	3.24 (0.18)	283.4 (30.1)
		Mean log(cones)	0.548 (0.171)	0.001			

crops by trees, and in different lags of cone production. The degree of synchrony within a year at the plot level appeared to vary with the magnitude of cone production. Many trees produced large cone crops during mast events. During the 1998 mast, synchrony in the production of large cone crops by individuals was especially high; only 10% of all trees sampled did not produce one of their large cone crops. In the other mast years (1993, 2005) the extent of masting was not as strong, with the percentage of trees within a masting plot that produced large cone crops varying from 36 to 75%. In low cone years, some individuals produced large cone crops that would contribute to the moderate level of overall synchrony. Variability in the number of cones produced among individuals within a year tended to be inversely related to mean cone abundance within the year.

Variation in synchrony among individuals could also be influenced by persistent individual differences in temporal cone production patterns. We detected three dominant patterns of cone production by trees. Some individuals showed no lag in cone production over the years (i.e. each year was independent of those preceding it). Other individuals showed a significant negative effect of cone production in one year on the cones produced the next year; third, those trees producing more mean cones over the study than those in the other groups tended to have a positive autocorrelation at 3-year intervals. *P. glauca* cones develop over 2 years, with bud differentiation occurring in summer of one year and the cones produced the next year (Nienstaedt & Zasada 1990). Greene & Johnson (2004), in a study of North American tree species, reported 31% of the data sets in their study had significant lag 1 autocorrelations, suggesting it was related to resource depletion, but provided no explanation for variation among trees. Local habitat quality (e.g. basal light availability) influences cone production (Greene *et al.* 2002), and energy reserve dynamics of individuals could affect their seed production patterns (Satake & Iwasa 2000). In high quality areas trees may have more resources, resulting in both high cone production within a year and allowing trees to produce cones over successive years (Nienstaedt & Teich 1972) and in a multiyear lag in cone production. Habitat variability within sites could be a factor in the variation in synchrony in *Quercus* spp. mentioned previously (Liebhold *et al.*

2004). A tendency for a small proportion of trees to produce a large proportion of seed in a population has been shown in *Quercus* spp. (Healy *et al.* 1999). Here, the dominant 3-year lag for the high mean cone producing trees coincided with the significant plot-level lag in cone production (for plots A and B; analysis not shown).

While we reported correlation coefficients statistically greater than zero at all distance classes, we focused more on the patterns and relative amounts of synchrony among individuals rather than simply the statistical detection of synchrony. Previous studies have inferred synchrony from a statistically significant positive correlation among individuals (i.e. significantly > 0), regardless of how small and close to zero (Koenig & Knops 1998b, e.g. a correlation of 0.12 ± 0.03 (95% CI); Crone & Lesica 2004). Further information on the amount of variability explained could be attained by squaring the correlation coefficients, while preserving the sign of the Spearman correlation, to generate 'correlation index' (r^2) values, representing the proportion of variability in the cone production pattern of a tree explained by correlating it with another tree (Zar 1999). The correlation index may be useful for quantifying and interpreting the relative importance of correlations of different magnitudes compared with the correlation coefficient (r_s), especially when correlations are not very strong (not close to 1 or -1), nor very weak (not close to 0) (Sokal & Rohlf 1995).

With the correlation index approach, the mean proportion of variation explained for the 356 trees was 0.35 ± 0.12 . The spatial pattern of the proportion of variability explained in cone production patterns between pairs of individuals had the same trend as the Spearman correlation (i.e. a decline with distance). The mean proportion of the variation explained ranged from a high of 0.47 ± 0.18 to a low of 0.21 ± 0.06 (see Figure S1 in Supplementary Material). Similar to the Spearman correlation for measuring synchrony, there was no significant reduction in the mean correlation index between pairs of trees in the closest and furthest distance classes (one sided *t*-test, $t_{623} = 0.981$, $P = 0.164$). The variability in cone production patterns explained by pairs of trees over all distance classes was statistically greater than 0, and there was considerable variation in the cone production patterns of individual trees.

Analyses of 43 *Quercus* spp. acorn production data sets using mean Pearson correlation coefficients

among individuals as measures of synchrony, ranged widely from 0.18 to 0.82 (Koenig *et al.* 2003). Our mean Spearman correlation was in the middle of this range at 0.52. Spatial synchrony in acorn production between individuals of three *Quercus* spp. based on Pearson correlations were in the range of 0.60 to 0.35 over distances up to 5 km (Koenig *et al.* 1999). Although we found no statistical difference in the synchrony of *P. glauca* trees at 75 m compared with 4 km apart, synchrony did decline with distance to a low of 0.33. Whether synchrony in cone production by *P. glauca* individuals over larger distances declines further is unknown. Using population means, Koenig & Knops (1998a) found detectable levels of synchrony for *Picea* spp. populations up to 2500 km apart. Because we focused on the synchrony between individual plants, and not population means, the overall mean correlation based on individuals (0.52) was lower than that based on *P. glauca* means for populations less than 10 km apart (0.73 here, based on plot means; *c.* 0.70 from Koenig & Knops 1998a). This occurs at least in part because taking the mean ignores the individual variation by combining individuals in an area into a single value, and suggests that considerable variation may remain undetected when population means, not individual values, are used in the analysis of synchrony.

WEATHER AS A CUE FOR SYNCHRONY

Broad-scale weather has been suggested as a cue ensuring the majority of trees are synchronous seed producers (Norton & Kelly 1988). Koenig *et al.* (1999) proposed that the synchronizing effect of weather over large areas, known as the Moran effect (Moran 1953), could be responsible for synchrony in acorn production by *Quercus* spp. over hundreds of kilometres. Also, abnormally high temperatures in the summer before seedfall, consistent with the La Niña phase of the El Niño Southern Oscillation, has been associated with synchronous fruiting in multiple species across New Zealand (Schauber *et al.* 2002). Broad weather patterns may also play a role in the detectable levels of synchrony in *Picea* spp. seeding occurring over large spatial scales (Koenig & Knops 1998a). Bud development in many conifer species occurs a year prior to cone formation, triggered by hot dry conditions during the period of differentiation into vegetative or sexual buds (Owens & Molder 1977; Nienstaedt & Zasada 1990), with a high correlation to the number of pollen cones and seed cones on individual trees (Caron 1995).

Janzen (1971) postulated that for weather to be a synchronizing factor over a large area it must be of a sufficient intensity to override differences due to local conditions. Over the relatively small spatial extent of the current study area we expected that the general climatic conditions favouring the formation of reproductive buds would not differ. However, tree growth and seed output are also affected by soil moisture and competition for resources (Greene *et al.* 2002), and

these are likely to be correlated for individuals close together, leading to patterns of local high synchrony. Perhaps local microsite conditions were such that, if the synchronizing effect of weather must achieve some threshold to override local microsite variation (as per Janzen 1971), the conditions leading up to the 1998 mast were well above the threshold (so all areas had a cone mast), whereas weather conditions in 1993 and 2005 were nearer the threshold, such that the occurrence of cone masting was more variable between plots. Accordingly, no mast years occurred in other years perhaps because the large-scale cue was not present. The spatial variation in mast years among plots, and variability in individual synchrony, could reflect the variation in habitat conditions (Liebhold *et al.* 2004) when these conditions are not overridden by weather for mast seeding. We do not know the cause of the variation in mast occurrence among plots. Local moisture or frost conditions during the very short time of pollen shedding (3–5 days; Nienstaedt & Zasada 1990) could negatively affect synchronization of masting. We did not have climatological data to pursue this further. The broad scale patterns showing some detectable level of synchrony in population means observed over very large distances (e.g. Koenig & Knops 1998a) could result from large-scale climatic conditions that trigger a mast year across sites over large distances, with considerable variation in the other years.

POLLINATION EFFICIENCY AND PREDATOR SATIATION

It was not our goal to differentiate between evolutionary hypotheses for mast seeding, so we only briefly comment on pollination efficiency and predator satiation in light of our results on variability and synchrony. The high CV_p and mean CV_i , along with high local mean r_s , could be the response to selection due to local pollination efficiency and localized seed predators (Koenig *et al.* 2003). *Picea glauca* pollen is wind dispersed; most pollen from wind-dispersed conifers has been shown to fall closer to the source tree (Robledo-Arnuncio & Gil 2005), and could result in individuals closer together being more synchronous. This could reinforce via heritability the different patterns of lags observed in cone production, perhaps reflecting different seed production strategies or abilities. Genetics may also play a role in the mast seeding behaviour of *P. glauca* individuals (Nienstaedt & Zasada 1990), but we do not have the data to test this idea further. As the only conifer in our study area, *P. glauca* should experience strong selection to be synchronous due to predation pressure. However, this selection is likely to be influenced by the attributes of predator species. If the dominant seed predator was highly mobile, then very high synchrony in seed production may occur over the range of the seed predator. Red squirrels are territorial and thus do not roam in search of food, unlike birds such as crossbills (Holimon

et al. 1998). Red squirrels feed primarily on *P. glauca* seed (Smith 1968) and individuals cache upwards of 12 000 cones prior to seedfall (Hurly & Lourie 1997), preferentially selecting cones from trees with larger cone crops (Peters *et al.* 2003). Seeds lose their viability after 1–2 years in a red squirrel cache (Nienstaedt & Zasada 1990). Therefore, while selection should act against individual trees producing large cone crops asynchronously, this may only be important in a local area, for example within a red squirrel territory (0.25 ha, or a diameter of about 60 m; J. M. LaMontagne & S. Boutin, unpublished data). This may contribute to the high level of synchrony among individuals in the closest proximity (< 75 m). Increased asynchrony with distance, resulting in areas where trees produce many cones when other trees produce small cone crops, may promote seed predator persistence, especially in low seed years. However, mobile generalist seed predators may show the opposite of predator satiation (i.e. higher proportion of the seed crop consumed in high seed years or for high-seed trees), as shown for *Betula allegheniensis* (Kelly *et al.* 2001). Under the latter conditions it might be more favourable for individual plants to be highly variable (high mean CV_i) with lower spatial synchrony to tailor the amount of variation and its spatial scale to the characteristics of its seed predator(s), as outlined by Koenig *et al.* (2003).

Although statistically detectable synchrony in seed production by plant populations may extend over very large spatial extents, individual variation in cone production patterns may be considerable. Different species and even different populations of a common species will experience different local environmental conditions and selection pressures via the characteristics of seed predator populations and developmental times (e.g. promoting asynchrony between different species of *Quercus* spp. in a common area; Liebhold *et al.* 2004). Based on high local synchrony, high synchrony within a mast year, and multiple lags in cone production by individuals, both available resources and strong weather cues appear to play roles in the observed patterns. Spatial variation in the occurrence of mast years can have an effect on the population dynamics of seed predators and local community dynamics (Ostfeld & Keesing 2000). There is much opportunity to investigate further the causes and consequences of individual variation in synchrony, and individual lags in seed production, with a view to increasing our understanding of seeding patterns within plant populations.

Acknowledgements

We thank all field assistants involved in this study. A. Sykes, E. Anderson and E. Hofer maintained data bases. The manuscript was improved by comments from Craig Aumann, Diane Haughland, and anonymous reviewers. Research support was provided by the Natural Sciences and Engineering Research Council

of Canada (NSERC), Circumpolar/Boreal Alberta Research, and Northern Scientific Training Program grants. A NSERC Postgraduate Scholarship and an Izaak Walton Killam Graduate Scholarship provided personal support to J.M.L. This is paper number 35 of the Kluane Red Squirrel Project.

References

- Berryman, A.A. (1999) *Principles of Population Dynamics and Their Application*. Stanley Thornes Publishers, Cheltenham.
- Buonaccorsi, J.P., Elkinton, J.S., Evans, S.R. & Liebhold, A.M. (2001) Measuring and testing for spatial synchrony. *Ecology*, **82**, 1668–1679.
- Buonaccorsi, J.P., Elkinton, J., Koenig, W., Duncan, R.P., Kelly, D. & Sork, V. (2003) Measuring mast seeding behavior: relationships among population variation, individual variation and synchrony. *Journal of Theoretical Biology*, **224**, 107–114.
- Caron, G.E. (1995) Seed-cone and pollen-cone production models for young black spruce seedling seed orchards: a first approximation. *Canadian Journal of Forest Research*, **25**, 921–928.
- Crone, E.E. & Lesica, P. (2004) Causes of synchronous flowering in *Astragalus scaphoides*, an iteroparous perennial plant. *Ecology*, **85**, 1944–1954.
- Dale, M.R.T., Francis, S., Krebs, C.J. & Nils, V.O. (2001) Trees. *Ecosystem Dynamics of the Boreal Forest* (eds C.J. Krebs, S. Boutin & R. Boonstra), pp. 116–137. Oxford University Press, New York.
- DeSteven, D. & Wright, S.J. (2002) Consequences of variable reproduction for seedling recruitment in three neotropical tree species. *Ecology*, **83**, 2315–2327.
- Greene, D.F. & Johnson, E.A. (1994) Estimating the mean annual seed production of trees. *Ecology*, **75**, 642–647.
- Greene, D.F. & Johnson, E.A. (2004) Modelling the temporal variation in the seed production of North American trees. *Canadian Journal of Forest Research*, **34**, 65–75.
- Greene, D.F., Messier, C., Asselin, H. & Fortin, M.-J. (2002) The effect of light availability and basal areas on cone production in *Abies balsamea* and *Picea glauca*. *Canadian Journal of Botany*, **80**, 370–377.
- Healy, W.M., Lewis, A.M. & Emery, F.B. (1999) Variation of red oak acorn production. *Forest Ecology and Management*, **116**, 1–11.
- Herrera, C.M. (1998) Population-level estimates of inter-annual variability in seed production: what do they actually tell us? *Oikos*, **82**, 612–616.
- Herrera, C.M., Jordano, P., Guitián, J. & Traveset, A. (1998) Annual variability in seed production by woody plants and the masting concept: reassessment of principles and relationship to pollination and seed dispersal. *American Naturalist*, **152**, 576–594.
- Holimon, W.C., Benkman, C.W. & Willson, M.F. (1998) The importance of mature conifers to red crossbills in southeast Alaska. *Forest Ecology and Management*, **102**, 167–172.
- Hosmer, D.W. & Lemeshow, S. (1989) *Applied Logistic Regression*. John Wiley, New York.
- Hurly, T.A. & Lourie, S.A. (1997) Scatterhoarding and larderhoarding by red squirrels: size, dispersion, and allocation of hoards. *Journal of Mammalogy*, **78**, 529–537.
- Janzen, D.H. (1971) Seed predation by animals. *Annual Review of Ecology and Systematics*, **2**, 465–492.
- Kelly, D. (1994) The evolutionary ecology of mast seeding. *Trends in Ecology and Evolution*, **9**, 465–470.
- Kelly, D., Hart, D.E. & Allen, R.B. (2001) Evaluating the wind pollination benefits of mast seeding. *Ecology*, **82**, 117–126.

- Kelly, D. & Sork, V. (2002) Mast seeding in perennial plants: why, how, where? *Annual Review of Ecology and Systematics*, **33**, 427–447.
- Koenig, W.D. (1999) Spatial autocorrelation of ecological phenomena. *Trends in Ecology and Evolution*, **14**, 22–26.
- Koenig, W.D., Kelly, D., Sork, V.L., Duncan, R.P., Elkinton, J.S., Peltonen, M.S. & Westfall, R.D. (2003) Dissecting components of population-level variation in seed production and the evolution of masting behavior. *Oikos*, **102**, 581–591.
- Koenig, W.D. & Knops, J.M.H. (1998a) Scale of mast-seeding and tree-ring growth. *Nature*, **396**, 225–226.
- Koenig, W.D. & Knops, J.M.H. (1998b) Testing for spatial autocorrelation in ecological studies. *Ecography*, **21**, 423–429.
- Koenig, W.D. & Knops, J.M.H. (2001) Seed-crop size and eruptions of North American boreal seed-eating birds. *Journal of Animal Ecology*, **70**, 609–620.
- Koenig, W.D., Knops, J.M.H., Carmen, W.J. & Stanback, M.T. (1999) Spatial dynamics in the absence of dispersal: acorn production by oaks in central coastal California. *Ecography*, **22**, 499–506.
- Krebs, C.J. & Boonstra, R. (2001) The Kluane Region. *Ecosystem Dynamics of the Boreal Forest* (eds C.J. Krebs, S. Boutin & R. Boonstra), pp. 9–24. Oxford University Press, New York.
- Krebs, C.J., Boutin, S. & Boonstra, R. (2001) *Ecosystem Dynamics of the Boreal Forest*. Oxford University Press, New York.
- LaMontagne, J.M. (2007) *Spatial and temporal variation in white spruce (Picea glauca) cone production: individual and population responses of North American red squirrels (Tamiasciurus hudsonicus)*. PhD thesis, University of Alberta, Edmonton, Alberta, Canada.
- LaMontagne, J.M., Peters, S. & Boutin, S. (2005) A visual index for estimating cone production for individual white spruce trees. *Canadian Journal of Forest Research*, **35**, 3020–3026.
- Liebhold, A., Sork, V., Peltonen, M., Koenig, W., Bjornstad, O.N., Westfall, R., Elkinton, J. & Knops, J.H.M. (2004) Within-population spatial synchrony in mast seeding of North American oaks. *Oikos*, **104**, 156–164.
- Moran, P.A.P. (1953) The statistical analysis of the Canadian lynx cycle. II. Synchronization and meteorology. *Australian Journal of Zoology*, **1**, 291–298.
- Nienstaedt, H. & Teich, A. (1972) *Genetics of White Spruce*. Research Paper WO-15. United States Department of Agriculture and Forest Service, Washington, DC.
- Nienstaedt, H. & Zasada, J.C. (1990) *Picea glauca* (Moench) Voss White Spruce. *Silvics of North America, Volume 1, Conifers* (eds R.M. Burns & B.H. Honkala), pp. 204–226. Agricultural Handbook 654. United States Department of Agriculture and Forest Service, Washington, DC.
- Norton, D.A. & Kelly, D. (1988) Mast seeding over 33 years by *Dacrydium cupressinum* Lamb. (rimu) (Podocarpaceae) in New Zealand: the importance of economies of scale. *Functional Ecology*, **2**, 399–408.
- Ostfeld, R.S. & Keesing, F. (2000) Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends in Ecology and Evolution*, **15**, 232–237.
- Owens, J.N. & Molder, M. (1977) Bud development in *Picea glauca*. II. Cone differentiation and early development. *Canadian Journal of Botany*, **55**, 2746–2760.
- Peters, S., Boutin, S. & Macdonald, E. (2003) Pre-dispersal seed predation of white spruce cones in logged boreal mixedwood forest. *Canadian Journal of Forest Research*, **33**, 33–40.
- Quinn, G.P. & Keough, M.J. (2002) *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge.
- Robledo-Arnuncio, J.J. & Gil, L. (2005) Patterns of pollen dispersal in a small population of *Pinus sylvestris* L. revealed by total-exclusion paternity analysis. *Heredity*, **94**, 13–22.
- Satake, A. & Iwasa, Y. (2000) Pollen-coupling of forest trees: forming synchronized and periodic reproduction out of chaos. *Journal of Theoretical Biology*, **203**, 63–84.
- Schauber, E.M., Kelly, D., Turchin, P., Simon, C., Lee, W.G., Allen, R.B., Payton, I.J., Wilson, P.R., Cowan, P.E. & Brockie, R.E. (2002) Masting by eighteen New Zealand plant species: the role of temperature as a synchronizing cue. *Ecology*, **83**, 1214–1225.
- Selås, V., Piovesan, G., Adams, J.M. & Bernabei, M. (2002) Climatic factors controlling reproduction and growth of Norway spruce in southern Norway. *Canadian Journal of Forest Research*, **32**, 217–225.
- Silvertown, J.W. (1980) The evolutionary ecology of mast seeding in trees. *Biological Journal of the Linnean Society*, **14**, 235–250.
- Smith, M.C. (1968) Red squirrel responses to spruce cone failure in interior Alaska. *Journal of Wildlife Management*, **32**, 305–316.
- Smith, J.N.M. & Folkard, N.F.G. (2001) Other herbivores and small predators: arthropods, birds and mammals. *Ecosystem Dynamics of the Boreal Forest* (eds C.J. Krebs, S. Boutin & R. Boonstra), pp. 261–272. Oxford University Press, New York.
- Sokal, R.R. & Rohlf, F.J. (1995) *Biometry*, 3rd edn. W.H. Freeman Co., New York.
- Zar, J.H. (1999) *Biostatistical Analysis*, 4th edn. Prentice Hall, New Jersey.

Received 24 October 2006; revision accepted 25 April 2007
Handling Editor: John Pannell

Supplementary material

The following supplementary material is available for this article:

Figure S1 Correlation index for *Picea glauca* cone production between pairs of individuals at various distance classes.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2745.2007.01266.x>

Please note: Blackwell Publishing are not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.