Climatic determinants of white spruce cone crops in the boreal forest of southwestern Yukon

C.J. Krebs, J.M. LaMontagne, A.J. Kenney, and S. Boutin

Abstract: White spruce (*Picea glauca* (Moench) Voss) cone crops were measured from 1986 to 2011 in the Kluane region of southwestern Yukon to test the hypothesis that the size of cone crops could be predicted from spring and summer temperature and rainfall of years t, $t-1$, and $t-2$. We counted cones in the top 3 m of an average of 700 white spruce trees each year spread over 3–14 sites along 210 km of the Alaska Highway and the Haines Highway. We tested the conventional explanation for white spruce cone crops that implicates summer temperatures and rainfall in years t and $t-1$ and rejected it, since it explained very little of the variation in our 26 years of data. We used exploratory data analysis with robust multiple regressions coupled with Akaike's information criterion corrected (AIC_c) analysis to determine the best statistical model to predict the size of cone crops. We could statistically explain 54% of the variation in cone crops from July and August temperatures of years $t-1$ and $t-2$ and May precipitation of year $t-2$. There was no indication of a periodicity in cone crops, and years of large cone crops were synchronous over the Kluane region with few exceptions. This is the first quantitative model developed for the prediction of white spruce cone crops in the Canadian boreal forest and has the surprising result that weather conditions 2 years prior to the cone crop are the most significant predictors.

Key words: white spruce cone production, Yukon, climate, Kluane, *Picea glauca*.

Résumé : Les auteurs ont émis l'hypothèse à savoir si l'on peut prédire l'importance de la production des cônes chez l'épinette blanche (*Picea glauca* (Moench) Voss) à partir des températures du printemps et de l'automne et des précipitations des années t, $t-1$, et $t-2$. Pour vérifier l'hypothèse, ils ont mesuré la production des cônes de 1986 à 2011 dans la région de Kluane dans le sud-ouest du Yukon. Chaque année, ils ont compté les cônes dans les 3 m supérieurs d'une moyenne de 700 tiges d'épinettes blanches dispersées dans 3–14 sites sur une longueur de 210 km le long des autoroutes de l'Alaska et Haines. Ils ont vérifié l'explication conventionnelle pour la production des cônes chez l'épinette blanche impliquant les températures estivales et les précipitations des années t et $t-1$, et l'ont rejetée puisqu'elle explique très peu de la variation dans leurs données de 26 années. Ils ont utilisé l'analyse exploratoire des données avec des régressions multiples robustes couplées avec l'analyse du critère d'information d'Akaike corrigé (AIC_c) pour déterminer le meilleur modèle statistique permettant de prédire la production de cônes. Ils ont pu ainsi expliquer 54 % de la variation de la production des cônes à partir des températures de juillet et août des années $t-1$ et $t-2$ et la précipitation de mai de l'année $t-2$. Il n'y a aucune indication de périodicité dans la production des cônes, et les années de forte production sont synchrones sur l'ensemble de la région de Kluane avec quelques exceptions. Il s'agit du premier modèle quantitatif développé pour la prédiction des productions de cônes chez l'épinette blanche dans la forêt boréale canadienne avec le résultat surprenant que les conditions climatiques 2 ans avant l'année de production constituent les meilleurs prédicteurs.

Mots-clés : production de cônes de l'épinette blanche, Yukon, climat, Kluane, *Picea glauca*.

[Traduit par la Rédaction]

Introduction

Cone crops of white spruce (*Picea glauca* (Moench) Voss) in the boreal forest region vary dramatically from year to year. A combination of climatic events are usually put forward to explain these variations in plant production (Juday et al. 2003; Messaoud et al. 2007). There are limited data from the Canadian boreal forest on the amount of variation in white spruce cone production from year to year and no quantitative analysis of the climatic factors that might control this variation.

Foresters have recognized for many years that conifers in the boreal forest have years of high seed production. This type of boom–bust seed production, known as mast years, are well studied in perennial plants and particularly in deciduous tree species (Kelly and Sork 2002; Koenig and Knops 2005). For white spruce, Juday et al. (2003) have described a complex sequential model that leads to heavy cone crops (Fig. 1). They list five gateways or thresholds that must be passed to have a successful cone crop in white spruce in year t:

1. Sufficient growth reserves from previous years so there cannot be two large cone crops in a row.

Received 13 April 2011. Accepted 26 September 2011. Published at www.nrcresearchpress.com/cjb on 9 February 2012.

C.J. Krebs and A.J. Kenney. Department of Zoology, The University of British Columbia, Vancouver, BC V6T 1Z4, Canada.
J.M. LaMontagne. Department of Biological Sciences, University of Calgary, Calgary, AB T2N 1N4, Canada.
S. Boutin. Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada.

Corresponding author: Charles Krebs (e-mail: krebs@zoology.ubc.ca).

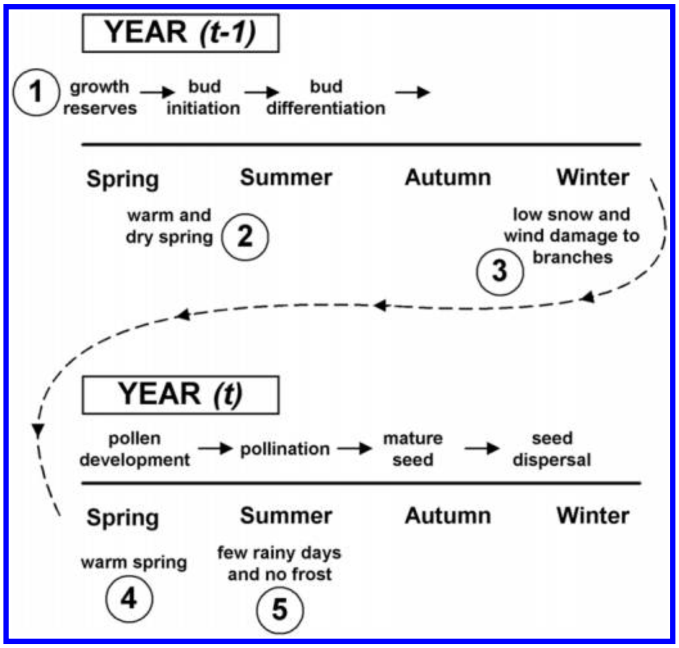
2. Warm temperatures and a drought stress signal in midsummer of year $t - 1$ when bud primordia form. This could be later in the summer at our northern sites.
3. A lack of pruning of reproductive shoots from snow and wind in winter.
4. Warm temperatures in the spring of year t to promote pollen and cone bud maturation. This would be late May–June at our northern sites.
5. Lack of frost and heavy rain in spring of year t to allow pollination.

The anecdotal, less detailed model for good cone crops is warm dry weather in year $t - 1$ to induce the cone crop and again in year t to produce the cone crop (Zasada et al. 1992).

We began measuring white spruce cone production in the Kluane region in 1987. This paper reports on the statistical associations between climatic measurements and white spruce cone production for the interval 1987–2011. We wished to derive a quantitative model for cone crops, and consequently we tested the model of Juday et al. (2003) by specifying the following four quantitative hypotheses with special reference to our northern sites:

> Hypothesis 1: Heavy cone crops cannot occur 2 years in succession.
>
> Hypothesis 2: Low rainfall and warm temperatures in midsummer to late summer of year $t - 1$ are necessary for large cone crops.
>
> Hypothesis 3: Warm temperatures in June of year t assist pollination and increase cone crops.
>
> Hypothesis 4: Lack of frost and heavy rain in May and June of year t increase cone production.

Fig. 1. Conceptual model of the critical gateways (numbered circles) leading to the production of white spruce cones in a 2-year cycle. Start at condition 1 and continue to 5 to visualize the sequence of events required to produce an abundant cone crop. (Adapted from Juday et al. 2003, reproduced with permission of Oxford University Press, *Climate variability and ecosystem response at long-term ecological research sites*, p. 228 © 2003 Oxford University Press.)



We have operationally specified the Juday et al. (2003) model to fit a multiple regression of the form

$$
\begin{aligned}
[1]\quad \text{Mean number of cones per tree} &= f[(\text{June, July, and August precipitation})_{t-1}] \\
&\quad + f[(\text{June, July, and August temperatures})_{t-1}] + f[(\text{May and June temperatures})_{t}] \\
&\quad + f[\text{minimum temperatures May}_{t} \text{ and June}_{t}] + f[(\text{May and June precipitation})_{t}]
\end{aligned}
$$

where $t - 1$ is the summer of the year before the cones are produced and counted, t is the year of cone production, and the functions must have the directionality specified in the four hypotheses stated above. We have tried to adjust the seasons specified in Figure 1 to more closely approximate our Kluane sites, where spring begins later than at more southerly sites.

Methods

The study area

The study site is located in southwestern Yukon Territory near Kluane Lake by the Alaska Highway within the Shakwak Trench system (61°01′N, 138°24′W) and lies within the St. Elias Mountains' rain shadow. Mean annual precipitation is ~280 mm and includes a mean annual snowfall of approximately 100 cm. The tree community is dominated by white spruce interspersed with trembling aspen (*Populus tremuloides* Michx.) and balsam poplar (*Populus balsamifera* L.). Fires have been rare in this area, and none have occurred in our study sites for more than 100 years. Nevertheless, forest succession is slow, and consequently the effects of fires can be detected 200–300 years after they occur owing to slow tree growth (Dale et al. 2001).

Weather data

Weather data were obtained from Environment Canada for the Haines Junction and Burwash Airport weather stations. There are systematic differences between these weather stations because Haines Junction is 110 km further south and at a lower elevation than Burwash Airport. But there is a broad correlation between these two stations. For monthly temperature, the correlation is very high ($R^2 = 0.99$, Haines Junction = 0.938 Burwash + 0.871, $n = 180$ months). For monthly rainfall in summer, the correlation between Haines Junction and Burwash is less good ($R^2 = 0.29$, Haines Junction = 0.351 Burwash + 13.85, $n = 64$ months). Rainfall is much more variable spatially in the Kluane region, and in 2000 we began putting automatic weather stations at some of our intensive study sites to improve local precision. Unfortunately, these local weather stations do not cover all the

Table 1. Sample sizes and annual means for white spruce index cone counts from the Kluane Lake area.

Year	No. sites	Total no. trees counted	Mean total no. cones per one side of tree	95% confidence limits	Coefficient of variation (%) among trees
1986	2	186	166.30	143–191	98.2
1987	9	630	44.64	42–47	67.4
1988	8	550	65.86	61–71	85.7
1989	8	697	0.00	0–0	—
1990	9	798	42.59	38–48	173.1
1991	14	867	2.10	1–3	424.9
1992	14	846	91.52	82–101	155.3
1993	14	875	175.34	162–190	119.0
1994	14	874	1.83	1–3	449.7
1995	14	853	111.52	101–123	139.1
1996	5	333	59.00	49–70	164.7
1997	3	230	50.72	43–59	118.9
1998	5	257	458.40	414–506	71.9
1999	6	336	34.20	28–41	200.4
2000	11	818	10.70	9–13	357.6
2001	14	1097	11.90	10–14	360.3
2002	14	1139	75.90	70–82	145.1
2003	14	1149	17.50	15–20	277.6
2004	14	1073	18.10	16–21	270.3
2005	14	1089	162.80	145–182	148.0
2006	14	1087	3.40	2–5	625.0
2007	12	955	49.20	43–55	188.2
2008	7	460	11.10	7–16	389.7
2009	8	564	27.30	23–32	317.8
2010	8	649	552.80	511–595	98.3
2011	7	553	0.30	0.1–0.5	—

Note: These counts are taken from one side of the tree only and are not a total tree count.

areas and years we have studied, so we had to fall back on Environment Canada data. We found that either Burwash Airport data or Haines Junction data could be used in the analysis. We chose the Haines Junction weather data because there were fewer missing data (2 months of rainfall data and 5 months of summer temperature data missing over our period of study). Missing values were replaced with mean values for the particular month.

Cone crop estimation

We measured white spruce cone crops at 14 locations along 210 km of the Alaska Highway and the Haines Road, stretching from St. Elias Lake (60.333°N, 137.049°W) to the Donjek River (61.684°N, 139.774°W). Not all sites were counted in all years, and a core group of six locations were done every year. At each site, 86–100 trees > 5 cm diameter at breast height were individually tagged and counted in early August each year. For our analysis we found that trees having a diameter at breast height of 5–10 cm had many fewer cones than larger trees, so we eliminated them from this analysis. Table 1 gives a summary of the number of sites and trees counted each year. New cones were counted in the top 3 m from one side of each tree with the use of binoculars. If more than 100 cones were present, a photograph was taken and cones were counted later on a computer. These index counts refer to only one side of the tree, and we converted these to whole-tree counts with the equation developed by LaMontagne et al. (2005), who sampled 60 whole trees destructively to develop an equation to transform index counts to total tree counts:

$$[2] \quad \log_{e}(\text{total number of cones}) = 0.1681 + 1.1891[\log_{e}(\text{cone index}) + 0.01]$$

$$\text{total number of cones} = 1.11568 \times \exp\{[\log_{e}(\text{total number of cones})]\}$$

where the second equation transforms the logarithmic estimate to the original scale using the Sprugel (1983) correction, and 0.01 is added to the cone index count to avoid zeros. When we discuss data on cone crops in this paper we are referring to the total number of cones per tree obtained from our index counts by means of the LaMontagne et al. (2005) transformation.

Individual spruce trees to be counted were located systematically at 42 m intervals on snowshoe hare live trapping grids so that for most grid sites 86 trees were counted. For areas without a snowshoe hare grid, we used two parallel lines 100 m apart, with 50 stations in each line, spaced at 15 m intervals, for a sample size of 100 trees. Some trees (<1%) died in a given year or were broken off by wind and a new tree had to be located. We are not interested here in the variance structure of the cone counts on individual trees within a site, or sites within the region, and the mean cone count per tree for each year averaged over all locations was the variable used in the statistical analysis.

Spruce cones were counted while they were still green and before red squirrels (*Tamiasciurus hudsonius*) began to harvest them later in August. Statistical analysis is limited to the 25-year period from 1987 to 2011. All statistical analyses were done in NCSS (Number Crunching Statistical System, Kay, Utah; http://www.ncss.com). Stepwise multiple regressions were used to select four possible candidate regressions of the best climatic variables. We used Akaike information criterion corrected (AIC_c) analysis to determine which of the four had the best evidence ratio (Anderson 2008), followed by robust multiple regression using Huber's method (C = 1.345) to estimate parameters for the regression. Confidence limits for all estimates were estimated by bootstrapping 10 000 samples. We tested all multiple regressions for multicollinearity and found no evidence of this problem in our data.

Results

Climatic variation

One problem with the use of climatic variables in ecological analyses is that there are many possible measures of climate, and thus data-dredging is possible. For white spruce cone production we have the advantage of a clearly specified weather model to isolate the proposed critical weather variables. To measure low rainfall in midsummer, we used total monthly precipitation for June, July, and August (hypothesis 2). To measure early summer temperature, we used mean monthly temperatures in May and June (hypothesis 3). We included in our analysis the minimum temperature for May 16–31 to test for possible frost damage to buds (hypothesis 4), and to estimate heavy rain we used the maximum daily precipitation in May and June.

Cone production and weather

The conventional wisdom is that plants that seed irregularly store energy for 1 or more years and then use that energy to flower and fruit (Vander Kloet and Cabilio 1996; Koenig and Knops 2005). We checked to see whether there was any evidence of inherent rhythms in Yukon white spruce cone crops. We used autocorrelation to test for a periodic rhythm in three time series on fixed sites (Silver, Sulphur, Kloo) that spanned the entire period 1986–2011, but found that only 1 of 24 approached significance for all lags from 1 to 8 years (p = 0.07, Silver, 5-year lag).

Cone crops fluctuated dramatically over the time period from 1987 to 2011 (Fig. 2). The coefficient of variation in mean cone crops among years was 180%, a relatively high value (cf. Kelly and Sork 2002). We tested the four hypotheses with these data as follows:

Hypothesis 1, that heavy cone crops cannot occur 2 years in succession, was confirmed by our data. Figure 2 shows high spruce cone years in 1993, 1998, 2005, and 2010, and each of these high cone years were followed by a year or more of very low cone production.

Hypotheses 2–4 were tested in two ways. First, simple correlations were calculated between cone production and each of the 11 weather variables — May and June temperatures and rainfall of year t; June, July, and August temperatures and rainfall of year t – 1; and May and June minimum temperatures in year t. Table 2 gives these simple correlations. Only 1 of the 11 weather variables correlated significantly with the size of the cone crop — June rainfall of year t. Given that there could be interactions between the weather variables, the critical test of these three hypotheses is whether a multiple regression including all 11 weather variables or a subset of them is significant. We calculated multiple regressions using these 11 weather measures as the independent variables and cone counts, $\log_{10}$ (cone counts), and square root (cone counts) as possible dependent variables. We considered eliminating the three smallest cone crops because of excessive leverage on the regressions line estimates, and we also considered eliminating the data from years following the large cone crops of 1993, 1998, 2005, and 2010. Neither of these eliminations of data made any difference to our conclusions, and we carried out all analyses on the entire data set. We utilized robust multiple regression using Huber's method with C = 1.345 to reduce the impact of outliers in the data, as recommended by Hintze (2007). No multiple regression with these weather variables as defined by the conventional hypothesis was significant ($F_{[11,14]}$ = 0.71, p = 0.71, n = 26, R^2 = 0.36). We could find no subset of the weather variables

Fig. 2. White spruce cone counts from 1986 to 2011 in the Kluane region of Yukon. Counts are total tree counts as defined by LaMontagne et al. (2005). Error bars are 95% confidence limits.

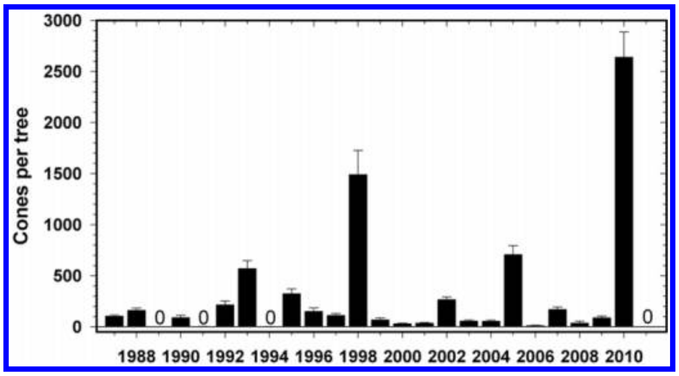


Table 2. Spearman rank correlations (r_s) among the 11 climatic variables considered as possible drivers of white spruce cone crops based on the current literature model for 1986–2011.

Weather variable	r_s with white spruce cone crop
May temperature of year t	0.19
June temperature of year t	0.11
May precipitation of year t	–0.10
June precipitation of year t	**–0.43**
June temperature of year t – 1	0.00
July temperature of year t – 1	0.31
August temperature of year t – 1	0.06
June precipitation of year t – 1	–0.06
July precipitation of year t – 1	0.15
August precipitation of year t – 1	–0.01
May 16–31 and June minimum temperatures of year t	0.15

Note: Only one of these correlations (in bold) is significant (p = 0.03). n = 26 years.

Table 3. Pearson correlations (r) among the climatic variables selected by exploratory data analysis and subsequent $\mathrm{AIC_c}$ analysis as drivers of white spruce cone crops in the Kluane region for 1986–2011.

	July and August mean temperatures in year t – 1	July and August mean temperatures in year t – 2	May rainfall in year t – 2	Mean no. of cones per tree
July and August mean temperatures in year t – 1	—	–0.13 (0.11)	0.13 (0.23)	0.29 (0.20)
July and August mean temperatures in year t – 2		—	–0.22 (–0.33)	**–0.44** (**–0.49**)
May rainfall in year t – 2			—	–0.19 (–0.33)

Note: Bold values indicate correlations that are significant at $p < 0.05$. Values in parentheses are partial correlations of the four variables.

that was significant, and consequently we rejected hypotheses 2–4 for our data.

Nevertheless, the general belief that weather variables in past and current years determine the size of conifer cone crops is well established in the literature, and consequently we continued to carry out exploratory data analysis to see whether another weather model might be predictive. For this analysis we used weather data from summer temperature and rainfall for years t, t – 1, and t – 2. We found only one significant pairwise correlation among the climatic variables and the cone counts (Table 3), and that was from midsummer temperatures of year t – 2. We used stepwise regression to select the best candidates of predictors for cone crops and then conducted robust multiple regressions. When we had a choice of several weather variables that produced multiple regressions of similar fit to the data (measured by R^2 values), we used $\mathrm{AIC_c}$ analysis to select the model with the highest weight (Anderson 2008). We arrived at this statistical model as the best model with the highest evidence ratio:

$$[3] \quad \log_{10}(\text{cone crop}) = 4.3801 + 0.2220[(\text{July and August mean temperatures})_{t-1}] - 0.3797[(\text{July and August mean temperatures})_{t-2}] - 0.0293[(\text{May total rainfall})_{t-2}]$$

with $R^2 = 0.54$, $n = 26$, $p = 0.0006$. Note that this is a statistical model chosen on the basis of best fit, and it contains only some of the variables suggested in Figure 1. The major deviation from the expected model for spruce cone crops (Fig. 1) is that temperatures in the late summers of years t – 1 and t – 2 were the most significant predictors, along with rainfall in spring of year t – 2. Figure 3 illustrates the observed and predicted estimates for cone crops and shows the considerable scatter that remains to be explained.

In every year there were some individual trees that were out of synchrony with all the others. For example, in 2006 there was a nearly complete cone failure. Of the 1087 trees counted, 95% had zero cones, and 98% had fewer than 120 cones. Only 1.8% of the trees had more than 120 cones, and one tree had 1500 cones. By contrast, in the high cone year of 2010, of the 649 trees counted, 17 had zero cones (2.6%), and 10% of the trees had fewer than 140 cones. The maximum cone count in 2010 was 4700 cones on one tree.

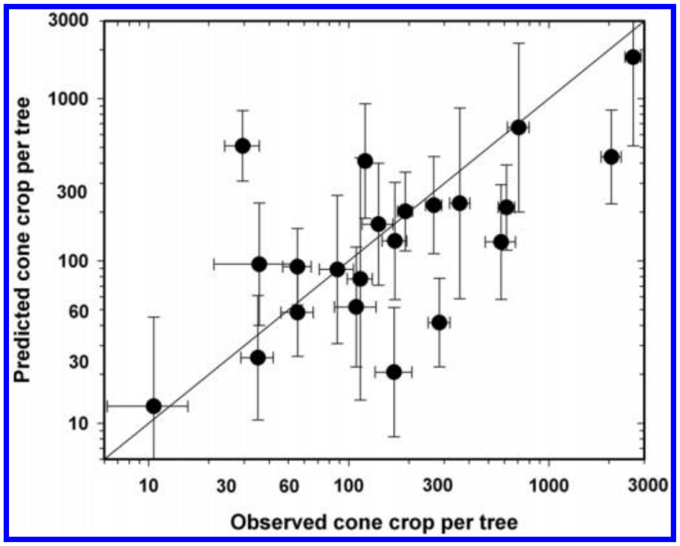
Discussion

There were several constraints to this study. The measurement of spruce cone crops was robust, and we pooled all the data from the 14 locations because there was general synchrony among sites — good cone crop years are generally good across the boreal forest area of Kluane. But we had only 26 years of data with which to do exploratory data analysis. Our exploratory analysis had 33 possible independent variables (temperature and rainfall for May–September for years t, t – 1, and t – 2, and May–June minimum temperatures). By combining these into 2–3 month blocks, we could reduce this analysis to 15 variables. Multiple regression is notoriously fickle when the number of possible explanatory variables approaches the number of degrees of freedom, and the conventional wisdom is to have a sample size at least 5 times the number of predictor variables (Sokal and Rohlf 1995, p. 655). We did not have enough data to subdivide it for prediction, so the test of these regression models will have to come from further work to determine their level of predictive precision.

Our data showed that, on average, one can explain statistically about 54% of the observed variation in the size of the spruce cone crop in a given year. Figure 3 shows the strength of this predictive ability for the regression we developed. We do not know what factors might operate to explain the other 46% of the variation in cone crops in this region. Allocation of energy to growth and away from cone production could contribute variation here. Koenig and Knops (1998) found synchrony in tree-ring growth over large spatial areas and an inverse relationship between tree growth and reproduction. Tree-ring growth patterns are also generally correlated with temperature or rainfall. Alternatively, energy reserves could interact with weather conditions, such that hot, dry summers could give rise to mast conditions, but only if the current and preceding cone crops have been poor (Nienstaedt and Zasada 1990). It is possible that short-term, one-off events like a severe wind or frost could affect cone crops, and these are not easy to quantify. In particular, if short episodes of frost or heavy rain in spring affect cone crops, it will be almost impossible to recognize this type of effect with current weather data. We assume that when large cone crops are regional in extent, small local storms or frosts are unlikely to explain the variations we have observed.

Few seem to doubt the general hypothesis that climatic conditions 1 or 2 years prior have a strong influence on the size of conifer cone crops (Alden 1985; Zasada 1986; Zasada et al. 1992). The specific model proposed by Juday et al. (2003; Fig. 1) does not fit our data, and the anecdotal model

Fig. 3. Observed and predicted white spruce cone crops for the Kluane region in Yukon. Predicted counts are from the multiple regression $\log_{10}$ (total cone count) = 4.3801 + 0.2220 (late summer temperature year $t - 1$) – 0.3797 (late summer temperature year $t - 2$) – 0.0293 (May precipitation year $t - 2$); $R^2 = 0.54$, $n = 26$. Error bars are 95% confidence limits.



that warm weather in the growing seasons of year t and $t - 1$ are sufficient to generate a good cone crop is only partly supported. We could find no correlates of our cone crops to any weather variable in the current season, although warm weather in year $t - 1$ was highly significant. The deviation of our empirical model from the Juday model is probably explained by the difference in growing conditions in northern parts of the boreal zone, so that events 2 years ago may partly determine present cone crops.

We can find no explicit quantitative model in the literature for the prediction of white spruce cone crops. It is possible that the exact quantitative relationships given here may not be general across the boreal forests of northern Canada and Alaska. We would prefer to specify this model and then to follow cone crops in the Kluane regions for several years to test its validity at least for that particular region, and then to determine whether global climatic changes affect cone production.

Cone production in white spruce occurs in near absolute synchrony in the Kluane region of Yukon, reflecting general patterns seen in *Picea* (Koenig and Knops 1998). High cone crops in a good year like 2010 occur over thousands of square kilometres. There is some variation among individual trees in all years, but in general trees that deviate from the general trend are few (2%–3%). Kelly and Sork (2002) reviewed the extent of seed masting in plants. For white spruce the conventional explanation for masting is that of predator satiation (Fletcher et al. 2010). Red squirrels hoard cones of white spruce to tide them over years of low cone production.

Of the four hypotheses we specified in the introduction, hypothesis 1 is supported in general by our data because cone crops after large mast years were very close to zero. This implies at least a partial energy limitation on masting in white spruce in this part of the boreal forest. Hypothesis 2 is partly supported by warm temperatures in year $t - 1$, which was associated with higher cone crops. Hypotheses 3 and 4 could not be supported by our data, but this could be caused by short-term or even single-day events that are difficult to measure with standard meteorological data. Simple weather measurements in the spring of year t did not help to statistically predict cone crops.

We have not discussed a set of alternative models for cone crop production that depend on single-day events like a late frost in spring or an early snowfall in autumn. It is impossible at present to specify these single-event models in quantitative ways that are testable because they tend to be ad hoc explanations that occur after the fact. We attempted to look for these effects by using minimum May temperature of the current year as a predictor, but it was of limited use. But spring frosts may be a critical weather event. In 2005, high cone crops at most of our sites were in contrast to nearly no cones in two areas (CC and LL grids) in the center of our study area. If these two areas were storing energy for a high cone crop, we might expect them to have higher cone counts in subsequent years and in particular to have high cone counts in the next mast year (2010). Neither of these predictions was confirmed, and one possible reason is that the cone crop of 2005 was relatively low (about 700 cones per tree) compared with the larger mast years of 1998 and 2010 (>2000 cones per tree). In 2010, the CC and LL sites had cone counts 10%–20% below the mean of all 2010 sites, so there was no evidence of the trees at these sites overcompensating for the missed 2005 cone mast year. We do not have any detailed weather data to associate with the 2005 cone crop failure on these two grids, which for the other 25 years of our study had cone crops that followed the regional pattern of highs and lows. We do not know, for example, the critical thermal limits for flower bud loss, and we do not have the detailed temperature measurements that would record the relevant data. Progress in developing these very specific models will come only when these details of plant physiology are better known.

We suggest that future efforts focus on testing the relationships shown in Figure 3 with further studies in the Kluane region of Yukon and that the general hypotheses of climatic control of white spruce cone crops be tested with specific quantitative models in other sites of the boreal forest where the forest composition and climatic patterns vary. Our experience is that at least 10 years of data will be required to specify quantitative relationships for other regions. Given the rapid pace of climate change in northern Canada, more information on the climatic controls of spruce cone production would provide advance warning of expected changes.

Acknowledgements

We thank Liz Hofer, David Henry, Sylvie Mitford, and Parks Canada staff for assistance with field work. Comments by Jim Hone and three reviewers helped us to sharpen the presentation. Research funding was provided by the Natural Sciences and Engineering Research Council of Canada (NSERC) (R.B., C.K.), Northern Studies grants, and the EJLB Foundation. The facilities of the Kluane Lake Research Station of the Arctic Institute of North America were essential to this long-term research program, and we thank Andy and Carole Williams and Lance Goodwin and Sian Williams for their assistance.

References

Alden, J. 1985. Biology and management of white spruce seed crops for reforestation in Subarctic Taiga Forests. University of Alaska Agricultural and Forestry Experiment Station, School of Agriculture and Land Management. Bulletin No. 69. pp. 1–51.

Anderson, D.R. 2008. Model based inference in the life sciences: a primer on evidence. Springer, New York.

Dale, M.R.T., Francis, S., Krebs, C.J., and Nams, V.O. 2001. Trees. *In* Ecosystem dynamics of the boreal forest. *Edited by* C.J. Krebs, S. Boutin, and R. Boonstra. Oxford University Press, New York. pp. 116–137.

▶Fletcher, Q.E., Boutin, S., Lane, J.E., LaMontagne, J.M., McAdam, A.G., Krebs, C.J., and Humphries, M.M. 2010. The functional response of a hoarding seed predator to mast seeding. Ecology, **91** (9): 2673–2683. doi:10.1890/09-1816.1. PMID:20957961.

Hintze, J.L. 2007. NCSS Help System. NCSS, Kaysville, Utah.

Juday, G.P., Barber, V., Rupp, S., Zasada, J.C., and Wilmking, M. 2003. A 200-year perspective of climate variability and the response of white spruce in interior Alaska. *In* Climate variability and ecosystem response at long-term ecological research sites. *Edited by* D. Greenland, D.G. Goodin, and R.C. Smith. Oxford University Press, Oxford. pp. 226–250.

▶Kelly, D., and Sork, V.L. 2002. Mast seeding in perennial plants: why, how, where? Annu. Rev. Ecol. Syst. **33**(1): 427–447. doi:10.1146/annurev.ecolsys.33.020602.095433.

▶Koenig, W.D., and Knops, J.M.H. 1998. Scale of mast-seeding and tree-ring growth. Nature (Lond.), **396**(6708): 225–226. doi:10.1038/24293.

▶Koenig, W.D., and Knops, J.M.H. 2005. The mystery of masting in trees. Am. Sci. **93**(July–August): 340–347.

▶LaMontagne, J.M., Peters, S., and Boutin, S. 2005. A visual index for estimating cone production for individual white spruce trees. Can. J. For. Res. **35**(12): 3020–3026. doi:10.1139/x05-210.

▶Messaoud, Y., Bergeron, Y., and Asselin, H. 2007. Reproductive potential of balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), and black spruce (*P. mariana*) at the ecotone between mixedwood and coniferous forests in the boreal zone of western Quebec. Am. J. Bot. **94**(5): 746–754. doi:10.3732/ajb.94.5.746. PMID:21636443.

Nienstaedt, H., and Zasada, J.C. 1990. *Picea glauca* (Moench) Voss White Spruce. *In* Silvics of North America. Vol. 1. Conifers. *Edited by* R.M. Burns and B.H. Honkala. USDA For. Serv. Agric. Handb. 654. pp. 204–226.

Sokal, R.R., and Rohlf, F.J. 1995. Biometry. W.H. Freeman, New York.

▶Sprugel, D.G. 1983. Correcting for bias in log-transformed allometric equations. Ecology, **64**(1): 209–210. doi:10.2307/1937343.

▶Vander Kloet, S.P., and Cabilio, P. 1996. Ten year study of the annual variation in berry and seed production in a population of *Vaccinium corymbosum* L. Am. Midl. Nat. **135**(2): 349–356. doi:10.2307/2426718.

Zasada, J.C. 1986. Natural regeneration of trees and tall shrubs on forest sites in interior Alaska. *In* Forest ecosystems in the Alaskan taiga: a synthesis of structure and function. *Edited by* F.S. Chapin III, P.W. Flanagan, L.A. Viereck, and K. Van Cleve. Springer-Verlag, New York. pp. 44–73.

Zasada, J.C., Sharik, T.L., and Nygren, M. 1992. The reproductive process in boreal forest trees. *In* A systems analysis of the global boreal forest. *Edited by* H.H. Shugart, R. Leemans, and G.B. Bonan. pp. 85–125.