NRC Research Press

ARTICLE

Predicting white spruce cone crops in the boreal forests of southern and central Yukon

C.J. Krebs, M. O'Donoghue, Shawn Taylor, A.J. Kenney, E.J. Hofer, and S. Boutin

Abstract: White spruce (*Picea glauca* (Moench) Voss) cone crops were measured at five regional centers in southern and central Yukon for 30 years at one site from 1986 to 2015 and at four other sites during 9 to 11 years to select the best climatic model that uses cues from growing season temperature and rainfall to predict the size of cone crops. We evaluated six climatic models that use summer temperature and rainfall of years $t-1$ and $t-2$ to predict cone crops in year t. July temperatures provided the best predictors of white spruce cone crops, and no rainfall variable was related to the size of cone crops. We explored three variants of July temperatures: mean temperature, degree-days > 5 °C, and maximum temperatures. For each of these, we used the ΔT model that uses the difference in the July temperature measures of years $t-1$ and $t-2$. We compared the resulting six models with corrected Akaike's information criterion (AIC_c) to determine their relative predictive performance. The best model combined ΔT measures of degree-days > 5 °C and the four highest daily maximum July temperatures with $R^2 = 0.65$. By comparison, the ΔT model involving only mean July temperatures was less successful ($R^2 = 0.49$). There was good regional synchrony ($r_p = 0.7$ to 0.8) in high cone crops over southern and central Yukon during 1986 to 2015.

Key words: white spruce cone production, Yukon, climate, *Picea glauca*, delta-*T* model, mast seeding.

Résumé : La production de cônes d'épinette blanche (*Picea glauca* (Moench) Voss) a été mesurée dans cinq centres régionaux au Yukon pendant 30 ans à un endroit, de 1986 à 2015, et à quatre autres endroits pendant 9–11 ans pour choisir le meilleur modèle climatique qui utilise des signaux de la température et des précipitations durant la saison de croissance pour prédire la production de cônes. Nous avons évalué six modèles climatiques qui utilisent la température estivale et la précipitation des années $t-1$ et $t-2$ pour prédire la production de cônes durant l'année t. Les températures de juillet ont fourni les meilleurs prédicteurs de la production de cônes d'épinette blanche et aucune variable reliée à la précipitation n'était associée à la quantité de cônes récoltés. Nous avons exploré trois variantes de la température de juillet : la température moyenne, les degrés-jours > 5 °C et les températures maximum. Pour chacune de ces variantes, nous avons appliqué le modèle ΔT qui utilise les différences dans les mesures de température de juillet entre les années $t-1$ et $t-2$. Nous avons comparé les six modèles que nous avons obtenus à l'aide du critère d'information d'Akaike (AIC_c) pour déterminer leur performance prédictive relative. Le meilleur modèle combinait les mesures de ΔT des degrés-jours > 5 °C et les quatre températures journalières maximum les plus élevées de juillet avec un $R^2 = 0{,}65$. Par comparaison, le modèle ΔT qui utilisait seulement les températures moyennes de juillet était moins performant ($R^2 = 0{,}49$). Les années de forte production de cônes étaient bien synchronisées ($r_p = 0{,}7$ à 0,8) à l'échelle régionale dans le centre et le sud du Yukon de 1986 à 2015. [Traduit par la Rédaction]

Mots-clés : production de cônes d'épinette blanche, Yukon, climat, *Picea glauca*, modèle delta-*T*, bonne année semencière.

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 is usually put forward to explain these variations in plant production (Juday et al. 2003; Messaoud et al. 2007; Allen et al. 2014; Pearse et al. 2016). In 2012, we produced a quantitative model for the prediction of white spruce cone crops in the Yukon from climatic factors 1 and 2 years prior to the crop (Krebs et al. 2012). After our analysis, a new model, the ΔT model, for cone crops was proposed by Kelly et al. (2013). This model is based solely on temperature in the growing season of the previous 2 years and is thus a conceptually simple model suggesting the cues for the response of masting trees to temperature variations.

The new ΔT model is particularly attractive as an alternative model because of its simplicity, involving only summer temperatures, and because as Kelly et al. (2013) show, the ΔT model fits a variety of masting records from many plant species and thus achieves a level of generality often lacking in climatic models of biological events. Climatic models are particularly difficult to construct because of the plethora of variables possible, so that development of models can too often turn into a fishing expedition.

We began measuring white spruce cone production in the Kluane region in 1986 because of the ecological implications of highly variable seed crops for seed-eating mammals and birds. We have added data here from the Yukon Community Ecological Monitoring Program (CEMP) for sites at Faro (2007–2015) and Mayo, Whitehorse, and Watson Lake (all 2005–2015). The utility of a model of masting is that natural resource managers and government seed collection agencies can use it to anticipate years of high and low seed production, particularly if the model predictions can be generalized over large spatial areas.

Received 1 June 2016. Accepted 7 September 2016.

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 Published at www.nrcresearchpress.com/cjfr on 14 September 2016.

Fig. 1. Location of the five major sites at which spruce cones were counted. Table 1 provides the average climatic variables for each site. [This figure is available in colour online.]

This paper reports on the statistical associations between climatic measurements and white spruce cone production for all of these CEMP regions in southern and central Yukon.

In a broader context, we wish to determine if temperature, rainfall, or both are the best predictors of the size of future white spruce cone crops and to estimate which monthly variables are the best predictors. We focus on Δ models measuring the difference in any particular climatic variable 1 and 2 years before the observed cone crop. We emphasize here that we view growing season temperature and rainfall as possible cues to subsequent cone production and we do not know for this system how temperature and rainfall might relate to the proximate physiological drivers that have a direct, mechanistic relationship with cone production.

Methods

The study areas

The study regions are all in southern and central Yukon and all contain tree communities with abundant white spruce. Figure 1 shows the locations of the five regions, and Table 1 provides the average summer temperature and rainfall for each region for the last 30 years. The climate in all regions is continental, and as a consequence, tree growth and forest succession are slow. The effects of climate change in these regions in the last 50 years are significant but not large (Conway and Danby 2014). From 1980 to 2014, the change of July summer temperature at the Haines Junction weather station has been an increase of 0.021 °C per year, a slight but significant change ($p = 0.04$). Summer rainfall trends for the June and July time period are also nonsignificant ($p = 0.53$). The five regions are spread across about 390 km north–south and 550 km east–west, covering a boreal forest area of about 200 000 km².

Weather data

Weather data were obtained from Environment Canada for weather stations at each of the five regions. The Kluane Lake study areas are located between the Haines Junction and Burwash Airport weather stations. For these five regional areas, Mayo is the warmest in summer along with Watson Lake, and Kluane is the coldest (Burwash and Haines Junction area). Rainfall is highly variable, with Watson Lake being the wettest and Whitehorse being the driest. We found that either Burwash Airport data or Haines Junction data could be used for analysis of white spruce cone production at Kluane Lake. We chose the Haines Junction weather data because they had less missing data and are slightly closer to most of our Kluane study sites.

Cone crop estimation

We measured white spruce cone crops of individual tagged trees at all locations with the same methods. Only trees > 10 cm diameter at breast height were used. New cones were counted in the top 3 m from one side of each tree by the use of binoculars. If more than 100 cones were present, a photograph was taken and the 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 cone counts with the equation developed by LaMontagne et al. (2005), who destructively sampled 60 whole trees to develop an equation to transform index counts to total-tree counts of cones. Not all regions were counted in all years. Table 2 provides a summary of the number of trees counted at each region in each year. 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.

At Kluane Lake, individual spruce trees to be counted were located systematically at 42 m intervals on checkerboard 36 ha snowshoe hare live-trapping grids (Krebs et al. 2001) so that 86 trees were counted for most grid sites. For the other four regions, we used two (or four) parallel lines 100 m apart, with 50 (or 25) stations in each line, spaced at 15 m intervals, for a minimum sample size of about 100 trees per region (Table 2). All trees were tagged. Some trees (<1%) died in a given year or were broken off by wind and a new tree had to be located. Data were pooled at all sampling sites within each of the five regions. The mean cone count per tree for each year averaged over all sampling sites within each of the five regions was the dependent variable used in statistical analyses. Over all of the years, a total of 71 region-years of data were available, with the longest time series being 30 years at Kluane Lake.

Spruce cones were counted in late July or early August while they were still green and before red squirrels (*Tamiasciurus hudsonius*) began to harvest them in late August (early boreal autumn; Fletcher et al. 2013).

Weather variables

We used standard weather data from nearby meteorological stations (Table 1) to estimate the mean July temperature for each potential cone crop year for each region and used that as the ΔT measure suggested by Kelly et al. (2013), which is one measure of the difference in warmth between the two previous growing seasons. We estimated ΔT from mean daily temperature from mid-June to mid-August and for July only. There was a very high correlation between these measures from 16 June to 15 August and the same measures in July ($r > 0.97$), so we used the simplest July-only measures of the temperature of the growing season. ΔT is defined here as

$$(1) \qquad \Delta T = \text{mean July temperature (year } t-1) - \text{mean July temperature (year } t-2)$$

Growing degree-days (GDDs) might provide a more precise measure of summer warmth for spruce trees. For each region, we calculated GDDs for each July from daily mean temperatures by subtracting 5 from each day in which the mean temperature was above 5 °C and then summing these for July. We then calculated ΔGDDs by the following equations:

Table 1. Locations of the five main Yukon regions at which white spruce cone crops have been measured.

Site	Location of meteorological station	Mean summer temperature (°C)	Total summer precipitation (mm)	Mean annual temperature (°C)	Mean total annual precipitation (mm)
Haines Junction	60.7528°N, 137.5067°W	11.83	111.4	–2.1	340.2
Burwash Airport	61.3706°N, 139.0400°W	11.70	158.9	–3.2	274.7
Mayo	63.5931°N, 135.8956°W	14.57	133.8	–2.4	313.5
Faro	62.2331°N, 133.3331°W	13.53	141.0	–2.0	319.7
Whitehorse	60.7167°N, 135.0500°W	13.07	106.3	–0.1	262.3
Watson Lake	60.1167°N, 128.8000°W	13.83	162.0	–2.4	416.4

Note: Weather data are from Environment Canada weather stations in each location. Kluane Lake data are gathered in the area between the Haines Junction weather station and the Burwash Airport weather station. Summer is June through August. Data are averages from 1981 to 2010.

Table 2. Sample sizes for each year for white spruce cone counts for each of the five Yukon regions.

	Number of spruce trees counted for cones				
Year	Kluane Lake	Mayo	Faro	Whitehorse	Watson Lake
1986	172	—	—	—	—
1987	916	—	—	—	—
1988	700	—	—	—	—
1989	697	—	—	—	—
1990	834	—	—	—	—
1991	553	—	—	—	—
1992	539	—	—	—	—
1993	553	—	—	—	—
1994	560	—	—	—	—
1995	559	—	—	—	—
1996	377	—	—	—	—
1997	333	—	—	—	—
1998	257	—	—	—	—
1999	336	—	—	—	—
2000	818	—	—	—	—
2001	1097	—	—	—	—
2002	1139	—	—	—	—
2003	1149	—	—	—	—
2004	1073	—	—	—	—
2005	1089	125	0	65	85
2006	1087	125	0	0	84
2007	955	125	93	93	85
2008	460	125	96	100	80
2009	564	125	96	100	80
2010	649	125	96	99	84
2011	553	125	96	99	84
2012	520	125	96	100	85
2013	496	125	95	100	83
2014	489	125	96	100	85
2015	495	125	96	100	85

$$\text{(2)} \qquad \text{GDDs for day } X = \text{mean daily temperature for day } X - 5 (= 0 \text{ if mean daily temperature was below } 5\ ^\circ\text{C})$$

$$\text{(3)} \qquad \Delta\text{GDDs} = \text{total GDDs (July } t - 1) - \text{total GDDs (July } t - 2)$$

We used degree-days above 5 °C but would get the exact same results with degree-days above 0 °C because virtually all July temperatures are above 5 °C.

There are many other measures of temperature that could be used, and we added one more, the mean of the four highest daily temperatures in July, to determine if cone crops were influenced by extreme values of summer temperature rather than mean values.

In addition to temperature data, we looked for correlations with rainfall in each of the summer growing-season months from May to August in years $t - 1$ and $t - 2$. We checked all of these weather variables from year $t - 3$ and found no significant correlations, so we have gone back only to year $t - 2$ for weather variables.

Statistical analysis

Statistical analysis is limited to data from the 30-year period from 1986 to 2015. All statistical analyses were done in NCSS 10 (NCSS Statistical Software, Kaysville, Utah, www.ncss.com). Multiple regressions for all of the models were computed by the use of robust regression following Huber's method ($C = 1.345$) to reduce the impact of outliers in the data, as suggested by Kutner et al. (2005) and Huber and Ronchetti (2009). Confidence limits for all estimates were estimated by bootstrapping 10 000 samples. Synchrony among areas was quantified using methods suggested by Koenig et al. (2003). All cone count and temperature data are given in the Supplementary Table S1[1].

Results

Testing temperature and rainfall variables

We carried out an extensive exploratory data analysis on all monthly summer (May to September) temperature and rainfall variables from the two years prior to cone production. We found no monthly rainfall variables that were correlated with spruce cone counts either as individual months or as the analogue to the ΔT method, using rainfall instead of temperature. The only significant correlations were obtained from midsummer temperatures of both of the two years before the cone crop. We calculated five possible measures of midsummer temperatures for July: mean temperature, total degree-days > 5 °C, total degree-days > 10 °C, average of the four maximum temperatures, and average of the eight maximum temperatures. We deleted total degree-days > 10 °C and the average of the eight maximum temperatures from the analysis because they were poorly correlated with cone crops. We explored the best measure for cone crops and found that square root transformation was the preferred transformation for the assumption of normality in the cone data (Shapiro–Wilk $W = 0.976$, $p = 0.22$). Table 3 provides the correlations between the cone counts and the temperature variables used in our analysis.

We calculated robust multiple regressions for each combination of temperature variables possible, with the results given in Table 4. The best model (eq. 4) for predicting cone crops included two July weather variables (expressed as Δ year $t - 1$ – year $t - 2$): degree-days > 5 °C and the average of four maximum July temperatures. This regression is given by

$$\text{(4)} \qquad \sqrt{\text{total cones per tree}} = 12.5798 + 0.0812\ (\Delta \text{ degree-days July}) + 2.1408\ (\Delta \text{ four maximum July temperatures})$$

The second best model (eq. 5) included three July weather variables (all in Δ format): degree-days > 5 °C, mean temperature, and the average of four highest July temperatures. The second best

[1]Supplementary Table S1 is available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2016-0180.

Table 3. Pearson correlations between climate variables related to spruce cone counts.

	Total cones	Square root total cones	Log_{10} total cones	July mean temperature of t – 1 year	July mean temperature of t – 2 year	ΔT July	ΔT four highest July temperatures	Δ June degree-days > 5 °C	Δ July degree-days > 5 °C
Total cones	1.000	0.945	0.639	0.223	–0.455	0.585	0.653	0.433	0.651
Square root total cones		1.000	0.828	0.247	–0.493	0.635	0.728	0.496	0.696
Log_{10} total cones			1.000	0.217	–0.504	0.620	0.694	0.503	0.645
July mean temperature of t – 1 year				1.000	0.314	0.557	0.321	0.551	0.557
July mean temperature of t – 2 year					1.000	–0.613	–0.545	–0.300	–0.575
ΔT July						1.000	0.752	0.705	0.949
ΔT four highest July temperatures							1.000	0.392	0.714
Δ June degree-days > 5 °C								1.000	0.725
Δ July degree-days > 5 °C									1.000

Note: All Δ variables are the difference of year (t – 1) minus year (t – 2) for that variable. Sample size is 71 region-years.

Table 4. AIC_c evaluation of six possible regressions of weather variables as predictors of white spruce cone crops.

Model	Error sum of squares	No. of observations	No. of variables	Log likelihood	AIC_c	ΔAIC_c	Evidence ratio*	R^2
Square root (cones) predicted by Δ degree-days July and Δ four maximum July temperatures (eq. 4)	3644.113	67	4	–133.872	276.39	0.00	1.00	0.65
Square root (cones) predicted by Δ degree-days July, ΔT July, and Δ four maximum July temperatures (eq. 5)	3630.225	67	5	–133.744	278.47	2.08	2.83	0.65
Square root (cones) predicted by ΔT July and Δ four maximum July temperatures (eq. 6)	3616.283	68	4	–135.106	278.85	2.46	3.42	0.64
Square root (cones) predicted by Δ four maximum July temperatures, July mean temperature in year t – 1, and July mean temperature in year t – 2 (eq. 7)	3621.906	68	5	–135.1584	281.28	4.90	11.56	0.64
Square root (cones) predicted by mean temperature in July (t – 1), mean temperature in July (t – 2), and May rainfall (t – 2) from Krebs et al. (2012)	5131.033	72	5	–153.590	318.09	41.70	>1000	0.53
Square root (cones) predicted by ΔT July (eq. 8)	5679.689	72	3	–157.247	320.85	44.46	>2000	0.49

*The evidence ratio gives the likelihood that the current statistical model is as good as the best of the existing models. For example, an evidence ratio of 2.83 means that the best model is more than twice as likely to be better than the current model, given the current data.

model showed only slightly poorer fit than the best model (Table 4) with a corrected Akaike's information criterion (AIC_c) 2.08 likelihood units below the best model, and an evidence ratio of 2.83.

$$\sqrt{\text{total cones per tree}} = 12.6095 + 0.06197\,(\Delta\ \text{degree-days July}) + 2.0800\,(\Delta\ \text{four maximum July temperatures}) + 0.7071\,(\Delta T\ \text{July}) \tag{5}$$

The third best model (eq. 6) was 2.46 likelihood units below the best model, with an evidence ratio of 3.42.

$$\sqrt{\text{total cones per tree}} = 12.5056 + 2.0648 \times (\Delta\ \text{four maximum July temperatures}) + 2.4616\,(\Delta T\ \text{July}) \tag{6}$$

The fourth best model (eq. 7) with a low evidence ratio was a model using the mean July temperature of year (t – 1), the mean July temperature of year (t – 2), and the ΔT of the mean of the four highest temperatures in July for the previous 2 years:

$$\sqrt{\text{total cones per tree}} = 23.2543 + 1.9532 \times (\Delta\ \text{four maximum July temperatures}) + 2.2732\,(\text{mean July temperature} \times (t - 1)) - 3.0210\,(\text{mean July temperature}\ (t - 2)) \tag{7}$$

The fifth best model was the Krebs et al. (2012) model, and the sixth best model (eq. 8), the simple ΔT model on July mean temperatures, had much less support.

$$\sqrt{\text{total cones per tree}} = 0.1024 + 5.1310\,(\Delta T\ \text{July}) \tag{8}$$

The weather variable with the highest standardized coefficient for both the first and second models was the ΔT of the mean of the four highest temperatures in July (0.53), compared with the ΔT of degree-days in July (0.33). One additional reason for not preferring the second (eq. 5) and third (eq. 6) models (in addition to the AIC_c analysis) is that they both fail the normality assumption of multiple regression as measured by the Shapiro–Wilk test.

Figure 2 shows the observed cone counts and the predicted counts from the best statistical model (eq. 4) listed in Table 4. A curious but unexplained aspect of this graph is that the predicted counts tend to be too large when small cone crops occur but too small when the major masting years occur with very large cone crops. Simple one-variable scatterplots of the two most important variables in the multiple regression are shown as ΔT variables in Fig. 3 (four maximum July temperatures) and Fig. 4 (degree-days > 5 °C in July). The most interesting aspect of Fig. 3 is that there appears to be a threshold in Δ July maximum temperatures around –2 °C below which there is virtually no cone production. The correlation shown here is not improved by fitting a threshold model and truncating the observed data at –2 °C.

Figure 2 suggests visually that all of the data from the five regions fit a single line. We tested this hypothesis with an analysis of covariance (ANCOVA) (NCSS 10) and accepted a common slope assumption ($F_{[4,47]} = 1.07$, $p = 0.38$, $n = 66$) and no significant difference among adjusted means ($F_{[4,60]} = 1.13$, $p = 0.35$). The covariance test is weakened somewhat by sample sizes, which are much higher for Kluane Lake ($n = 30$) than for the other four regions (n from 9 to 11). However, from the present data, we have no statistical indication that we can reject the assumption that one regression fits all five regions of the Yukon.

Fig. 2. Observed white spruce cone crops for the five Yukon regions in relation to the predicted cone crop estimated from eq. 4, the best multiple regression. (R^2 = 0.65, n = 67). All data are plotted on a square root scale. [This figure is available in colour online.]

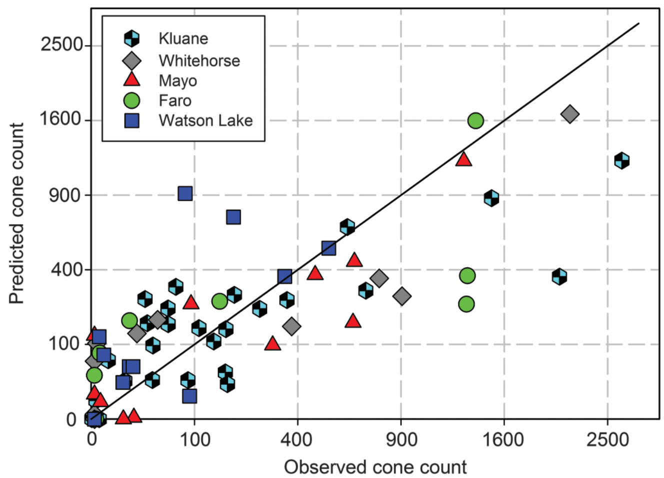


Fig. 3. Relationship between observed square root transformed white spruce cone counts per tree and observed ΔT measured as the mean of the four maximum temperatures in July. All data from all regions, n = 66, Spearman's r = 0.78. This is the best single variable correlation in our data set. [This figure is available in colour online.]

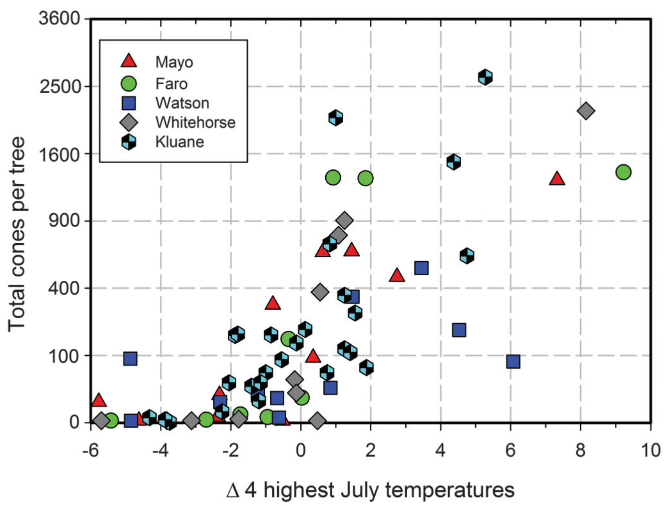
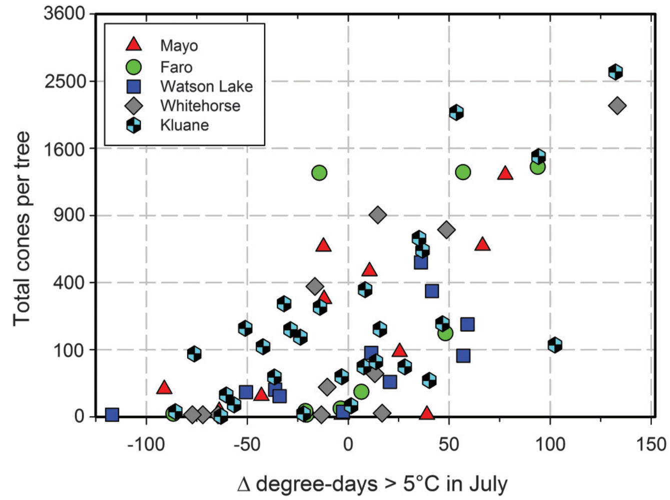


Fig. 4. Relationship between observed square root transformed white spruce cone counts per tree and Δ degree-days > 5 °C in July, one of the two key variables specified in eq. 2. All data from all regions, n = 68, Spearman's r = 0.67. This is the second best single variable in our data set. [This figure is available in colour online.]



Discussion

Plants that seed irregularly store energy for one or more years and then use that energy to flower and fruit (Koenig and Knops 2005; Vander Kloet and Cabilio 1996; Pearse et al. 2014). For white spruce at these five Yukon regions, summer temperature in the two years prior to the cone crop seems to be a cue that can be used to estimate the predicted size of the cone crop before it occurs. A similar result highlighting temperature rather than rainfall as the best predictor was reported by Norton and Kelly (1988). We do not know if temperature is the proximate driver for the cone crop because we do not know the mechanism by which temperature acts in this ecosystem (see discussion in Pearse et al. 2014). For Yukon white spruce, we checked to see if there was any evidence of inherent cyclic rhythms in the cone crops (spectral analysis in NCSS 10), and there is no regular cycle visible in the data that we have covering 30 years at Kluane Lake. There is also no inherent cyclic rhythm in July temperatures for the last 30 years at Haines Junction (spectral analysis).

There are many variables that could affect the success of a masting event such as failure of pollination, insect attacks, snowstorms, or other singular bad weather events. The ability of simple statistical models to capture the main factors quantitatively predicting successful masting events has been limited, and this could be because the time series of data on masting is shorter than needed for a good statistical model or that the best model has not yet been articulated.

Two important points are shown by our analyses. The best weather model in our analysis was a robust predictor for all regions and achieved an accuracy of prediction similar to or better than that obtained from many other weather models from other masting plant species (Kelly et al. 2013). The cue to masting events is the difference in temperature of the growing seasons one and two years previously. The key weather parameters for white spruce in our region were all some measure of midsummer temperatures, and the resulting model (eq. 4) produced a good fit that was robust in applying to five different regions scattered across southern and central Yukon. We could find no evidence that variation in summer rainfall was associated with variation in cone crops.

There were several constraints to this study. The measurement of spruce cone crops was robust, and we pooled all of the data from each of the five regional locations to produce an average cone crop estimate for each year because there was general synchrony within regions — good cone crop years are generally good across large areas of the boreal forest areas in the Yukon (average r_p among all areas = 0.66; omitting Watson Lake, average r_p = 0.81). However, we have climate data only for the nearest Environment Canada meteorological station to each region. For all regions except those at Kluane Lake, the meteorological stations are quite close to the field sites, but for Kluane Lake sites (situated about 40 km from Burwash Station and Haines Junction Station), it would be more useful to have site-specific weather data to see if predictions could be improved with on-site temperature records. The test of the current model will have to come from better temperature data and further cone counts to determine the model's predictive precision.

Our data show that, on average, with the current model, one can explain statistically about 65% of the observed variation in the size of the spruce cone crop in a given year. The general belief that large cone crops will reduce ring widths in trees such as white spruce has been validated for our Kluane Lake site ($r = -0.48$, $n =$ 25 years, $p = 0.01$) but not for our other sites. We do not know what factors might operate to explain the other 35% of the variation in cone crops in this region. Energy reserves could interact with weather conditions (Pearse et al. 2016) 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). For white spruce, we suggest that part of the 35% variation in cone crops left to be explained is caused by variation in the effectiveness of wind pollination due to heavy rain or strong winds. It is also possible that short-term, one-off events such as 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 that we have observed.

Our objective has been to test the simplest explicit quantitative weather model for the prediction of white spruce cone crops. We did not use the 14 parameter complex model suggested by Roland et al. (2014) because it violates the principles of overfitting models outlined in Ginzburg and Jensen (2004). It is possible that the exact quantitative relationships given here may not be general across the boreal forests of northern Canada and Alaska and this requires testing. Cone production in white spruce occurs in nearly absolute synchrony in the Kluane region of the Yukon, reflecting general patterns seen in *Picea* (Koenig and Knops 1998). High cone crops in a good year such as 2014 occur over thousands of square kilometres. There is some variation in cone counts among individual trees in all years (CV among individual trees within sites averages 2.48), but trees that deviate from the general trend in cone numbers are few (2%–3%).

Being able to predict masting years is useful in a wider ecosystem context than simply recording spruce tree dynamics. Red squirrels, northern red-backed voles (*Myodes rutilus*), and a variety of seed-eating birds such as crossbills respond dramatically to an abundance of spruce seeds (Krebs et al. 2001). Changing climate may or may not affect masting frequency and result in changes in food chain dynamics. A graphic example of ecosystem impacts of masting can be seen in New Zealand forests (Holland et al. 2015).

We suggest that future efforts focus on testing the relationships shown in Fig. 2 with further studies in climatically variable areas of northwestern Canada. Our experience is that at least 10 years of data will be required to specify quantitative relationships for other regions, and consequently, the accumulation of data for testing models can proceed only slowly. Given the pace of climate change in northern Canada (Gauthier et al. 2014), more information on the climatic controls of spruce cone production would provide advance warning of expected changes. High cone crops affect the breeding success of a variety of birds and small mammals and advance knowledge of their timing would give managers insights into potential effects of climate change on tree regeneration and animal populations.

Acknowledgements

We thank David Henry, Todd Heakes, many students who counted cones, and Parks Canada staff for assistance in fieldwork. We thank Andrea Byrom for a critical review of the manuscript. Research funding was provided by the Natural Sciences and Engineering Research Council of Canada (RB, CK) and Environment Yukon. 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.

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