Climatic determinants of berry crops in the boreal forest of the southwestern Yukon

C.J. Krebs, R. Boonstra, K. Cowcill, and A.J. Kenney

Abstract: Berry crops in the southwestern Yukon were quantified from 1997 to 2008 at 10 locations along 210 km of the Alaska and Haines highways. We tested the hypothesis that the size of berry crops could be predicted from spring and summer temperature and rainfall of years *t*, *t*–1 (1 year prior), and *t*–2 (2 years prior). Six common species were studied in the boreal forest of the Kluane region: *Arctostaphylos rubra* (Rehd. & Wils.) Fern., *Arctostaphylos uva-ursi* (L.) Spreng. s.l., *Empetrum nigrum* L., *Vaccinium vitis-idaea* L., *Geocaulon lividum* (Richards) Fern, and *Shepherdia canadensis* (L.) Nutt.. For the first five species we counted berries on fixed 40 cm × 40 cm quadrats to obtain an index of berry production for the Kluane region for each of the 12 years, and for *S. canadensis* we counted berries on two tagged branches of 10 bushes at each location. Stepwise multiple regressions were utilized to predict the size of berry crops for each species. For all species, predictive equations could explain statistically 80%–96% of the variation in berry crops. Different weather variables characterized each plant species, and there was no common weather regression that could explain the variation in berry crops in all species. Rainfall and temperature from years *t*–1 and *t*–2 were typically the significant predictors. There was no indication of a periodicity in berry production, and 43%–60% of the quadrats counted had large berry crops at one year intervals, while other quadrats never had a high crop during the study interval.

Key words: berry production, Yukon, climate, Kluane, dwarf shrubs.

Résumé : Les auteurs ont quantifié les récoltes de baies dans le sud-ouest du Yukon de 1997 à 2008, à 10 endroits sur 210 km le long des autoroutes d'Alaska et de Haines. Ils ont vérifié l'hypothèse qu'on pourrait prédire l'importance des récoltes de petits fruits à partir des températures estivales des années *t*, *t*–1 et *t*–2. Ils ont étudié six espèces communes de la forêt boréale dans la région de Kluane: *Arctostaphylos rubra* (Rehd. & Wils.) Fern., *Arctostaphylos uva-ursi* (L.) Spreng. s.l., *Empetrum nigrum* L., *Vaccinium vitis-idaea* L., *Geocaulon lividum* (Richards) Fern et *Shepherdia canadensis* (L.) Nutt. Chez les 5 premières espèces, on a compté les baies sur des quadrats fixes de 40 cm × 40 cm afin d'obtenir un index de la production des baies dans la région de Kluane pour chacune des 12 années, et pour le *S. canadensis* on a compté les baies sur deux branches marquées chez 10 bosquets sur chaque site. Les auteurs ont utilisé la régression multiple progressive pour prédire la dimension des récoltes de petits fruits pour chaque espèce. Chez toutes les espèces, les équations prédictives peuvent expliquer statistiquement 80–96 % de la variation des récoltes de petits fruits. Différentes variables climatiques caractérisent chaque espèce de plante, et on n'observe pas de régression commune qui peut expliquer la variation des récoltes de baies chez toutes les espèces. La précipitation et la température des années *t*–1 et *t*–2 constituent des pronostiques significatifs. Il n'y a pas d'indication qu'il existerait une périodicité dans la production des baies, et 43–60 % des quadrats énumérés montrent de fortes productions de baies à un an d'intervalles, alors que les autres quadrats n'ont jamais montré de fortes récoltes tout au long de l'étude.

Mots-clés : production de baies, Yukon, climat, Kluane, arbustes nains.

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Introduction

Berry crops in the boreal forest region vary dramatically from year to year. A combination of soil factors and climatic events are usually put forward to explain these variations in plant production (Kuchko 1988; Yudina and Maksimova 2005). There are limited data from the Canadian boreal forest on the amount of variation in berry production from year to year, and no quantitative analysis of the factors that might control this variation.

Traditional knowledge from northern residents recognizes abundant berry years and years of no production. These mast years and the factors that produce them are well studied in perennial plants and particularly in deciduous tree species (Kelly and Sork 2002; Koenig and Knops 2005), but relatively little work has been done looking at mast years in dwarf shrubs (Dyke 1971; West 1982). It is only recently that regular berry cycles in ericaceous shrubs (*Vaccinium* spp.) have been documented (Vander Kloet and Cabilio 1996). Ericaceous shrubs seem to have their own internal cycle that is dependent upon the previous year's production. For example, Selås (2000) using 50 years of berry production data in *Vaccinium myrtillus* concluded that the

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best predictor of berry production was the berry production of the previous 3 years, providing climatic factors were also taken into account.

Berry crops in northern Canada are of great importance to Aboriginal people and to everyone living in the north (Murray et al. 2005). For example, Murray et al. (2005) estimated a total of 16 000 L of berries were collected by 450 households in the Gwich'in Settlement Area of the Northwest Territories. In addition to human use of these resources, animals from grizzly bears (*Ursus arctos* L.) to red-backed voles (*Myodes rutilus* Pallas) depend on berries for a substantial part of their food supply (Dyke 1971; Rode et al. 2001). The dominant berry-producing plants differ substantially in different parts of the boreal forest zone, as well as within local areas between forested and alpine tundra plant communities. In spite of many natural history observations of large changes from year to year in berry production, no one seems to have pinpointed the reasons for these annual changes. They are universally believed to be due to weather events, and if this is correct it is important to determine exactly which weather events are critical, given the changing climate of northern Canada.

We began measuring berry production by dwarf shrubs in the Kluane region in 1997 and this paper reports on the statistical associations between climatic measurements and berry production for the interval 1997–2008. We test the hypothesis that changes in the size of berry crops can be predicted by measurements of mean temperature and rainfall during the months of the summer growing season. All of the literature on commercial and wild berry crops propose that weather events in the year prior to the berry crop or two years prior can affect berry numbers (Dyke 1971; Kuchko 1988). Flower primordial for the berries of year t are set in year t–1 (1 year prior), and may be influenced by weather in that year or by general good growth in the year previous (t–2, 2 years prior) and they could be damaged by frost in the spring of year t. Alternative hypotheses to explain variation in berry production could involve winter weather or herbivory on flower primordia. We are not able to test all these alternative models here.

Methods

The study area

The study site was located in the 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 rainshadow of the St. Elias Mountains. Mean annual precipitation is ca. 280 mm and includes an average annual snowfall of approximately 100 cm. The tree community is dominated by white spruce (*Picea glauca* (Moench) Voss) interspersed with trembling aspen (*Populus tremuloides* Michx.) and balsam poplar (*Populus balsamifera* L.). The upper shrub layer is composed of willow (*Salix* spp.), soapberry (*Shepherdia canadensis* (L.) Nutt.), and dwarf birch (*Betula glandulosa* Michx.), while the ground layers are composed of dwarf shrubs and herbaceous plants such as bearberries (*Arctostaphylos rubra* (Rehd. & Wils.) Fern. and *Arctostaphylos uva-ursi* (L.) Spreng. s.l.), crowberry (*Empetrum nigrum* L.), cranberry (*Vaccinium vitis-idaea* L. subsp. *minus* (Lodd.) Hultén.), toadflax (*Geocaulon lividum* (Richards) Fern.), arctic lupine (*Lupinus arcticus* S. Wats), and other forbs (Turkington et al. 2002).

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 and we found that either could be used in the analysis. We chose the Haines Junction weather data because it had slightly fewer missing data.

Berry production indices

We measured berry production at 10 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). For *A. rubra*, *A. uva-ursi*, *E. nigrum*, *V. vitis-idaea*, and *G. lividum* berry plots were 0.8 m × 0.4 m in size and consisted of two 0.4 m × 0.4 m quadrats laid side by side for a total of 100 quadrats (50 points × 2 quadrats each) at each location. Each quadrat typically held only one or two of the five species. Fewer than 100 quadrats were counted on each of the sites in 1997 (total n = 229 quadrats over all sites), 1998 (n = 344), and 1999 (n = 350) because we were working out the sampling design. Quadrats were placed systematically at 100 m intervals on snowshoe hare trapping grids at grid points that had adequate plant coverage, and the same quadrats were counted every year. Some quadrats (<1%) were moved each year because of tree falls or animal digging. The experimental design was of subplots (40 cm × 40 cm) nested within plots (40 cm × 80 cm) nested within locations (10) nested within years. We are not interested here in the variance structure of the nested design, and the mean berry index for each year averaged over all locations was the variable used in the statistical analysis.

The quadrats within a location were not laid out at random and we deliberately selected sites with good berry cover (minimum 20% cover of one or more berry species). Quadrats could have a high berry cover but no berries in some years. We were not trying to estimate the total production of berries per hectare but rather wanted to obtain an index of berry production. Not all species were present on each quadrat and we selected quadrats to provide data on as many species as possible at each location. The design was set up to provide an index of berry production to measure year to year changes in berry counts in the Kluane boreal forest.

Plant cover was estimated for all species within each subplot, and all ground berries within the plots were counted while still green, typically early- to mid-July. Because berry counts within each subplot are higher when cover is higher, we adjusted each berry counts for all species to a standard 50% cover for each species. We tested each species to determine whether the regression of berry counts on cover values had a slope of 1.0, and thus validated the adjustment of counts to a standard of 50% cover. Species with less than 5% cover in a quadrat were not included in the data analysis.

At each of 14 sites along this same stretch of highway soapberry (*S. canadensis*) berries were counted on two stems on each of 10 plants. The same two marked stems per bush were counted every year in July while the berries were still green. Stem diameter was measured at the base in millimetres. Soapberry counts were adjusted to a standard 10 mm diameter stem by the use of an average slope (0.7105) for the regression of soapberry numbers on stem diameter for all sites ($n = 1325$):

$$\text{Adjusted no. of soapberries} = \{\sqrt{(\text{observed no. of soapberries})} + [(10 - \text{observed diameter}) \times 0.7105]\}^2$$

The resultant standardized numbers of soapberries are meant as an index of soapberry production and not as an absolute estimate per unit area.

Birds and small rodents harvest berries, and we could not measure these impacts on our berry counts. By counting berries early in the summer while they were still green we tried to minimize the harvesting losses to herbivores. At the same time, counting green berries can overestimate final berry numbers because of lack of resources or abortion due to insects or pathogen attack on the developing fruit.

Berry records are available from 1997 onwards and Table 1 gives the sample sizes for each species for each year of study. Statistical analysis is limited to a 12-year period from 1997 to 2008. All statistical analyses were done in NCSS (Number Crunching Statistical System, Kay, Utah, www.ncss.com) Stepwise multiple regression was used to select the best climatic variables, 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. We have decided to use summer monthly means for temperature and totals for rainfall as our climatic variables. Table 2 shows that monthly temperatures and rainfall amounts for the Haines Junction weather station from 1997–2008 are completely uncorrelated with each other, so that they can be considered in the short term to be independent variables. We explored the utility of combining climatic variables into summer means and totals, but we found that for berry production, mean temperature or total rainfall over an entire summer did not distinguish among years in a biologically useful manner. Two years with equal average summer temperature are not equal biologically if one year has a warm May and a cold August and the other year has a cold May with a warm August. We included in our analysis the minimum temperature for 15–31 May to test for possible frost damage to flower primordia.

Berry production

The conventional wisdom is that plants that seed irregularly store energy for one or more years and then use that energy to flower and fruit (e.g Vander Kloet and Cabilio 1996). We checked to see whether there was any evidence of inherent rhythms in the Yukon berry crops. We do not have data on individual ramets but we used the yield of fixed quadrats to test for the frequency of large berry crops. Large crops were defined as those exceeding the median number of berries per quadrat for each species. We tallied the intervals between large berry crops, with the results given in Table 3. While the mean interval between large crops is around 2 years, there are many quadrats (43% to 60% of the total counted) that produced large berry crops at one year intervals, while others never produced any large crops. We infer from this that there are no inherent rhythms in the physiology of these plants that prevent them from producing a large crop of berries every year.

Berry production fluctuated dramatically over the time period from 1997 to 2008 (Fig. 1). There was little correlation between the yearly indices of the five main species. Only 3 of the 15 possible correlations was statistically significant (*A. uva-ursi* vs. *Vaccinium vitis-idaea*, $r = 0.59$, $n = 12$; *A. rubra* vs. *Empetrum*, $r = 0.68$; *Empetrum* vs. *Geocaulon*, $r = -0.59$), and this could be because these species respond similarly to climate, or it could be a chance event. The most productive plant for the number of berries per unit area was *E. nigrum*, which produced 1.5–4.6 times more berries than the other species sampled in quadrats in this part of the Yukon[2].

Relationship between berry production and climate

We now address the key question of whether changes in berry production are associated with the summer temperature and rainfall of years t, t–1, and t–2. Berry production has an inherent 2 year time frame. Two favourable years (e.g., optimum temperature, rainfall, no late frosts) are necessary to produce a bumper crop of berries. Flowering primordia are set in year t–1, and in year t a climatically favourable spring and summer should allow the flowers to develop (Dyke 1971; Kuchko 1988). We used weather data from year t–2 in our analyses because we wished to consider the possibility for these northern ecosystems that good plant growth in year t–2 might lead to better flower primordia production in year t–1. We used multiple regressions to test whether the climatic measures listed in Table 2 were related to berry production. Sample size was limited to 12 years for all time-lag models, and since there are eight climatic variables, we needed to search for those that correlated best to include in the multiple regressions. We used the variable selection regression routine in NCSS and the stepwise regression routine to select the best subset of climatic variables to include in each multiple regression. We tested alternative

[2] K. Cowcill, C.J. Krebs, and R. Boonstra. Do changes in berry crops drive population fluctuations in small rodents in the southwest Yukon? Submitted for publication.

Table 1. Sample sizes for each year for each species.

Year	*Arctostaphylos uva-ursi*	*Arctostaphylos rubra*	*Empetrum nigrum*	*Vaccinium vitis-idaea*	*Geocaulon lividum*	*Shepherdia canadensis*
1997	101	87	17	8	16	64
1998	178	179	29	7	28	124
1999	187	175	27	15	32	144
2000	339	328	94	76	138	183
2001	385	401	159	180	158	264
2002	358	380	146	189	160	264
2003	357	406	141	208	174	264
2004	367	420	152	202	175	264
2005	325	405	154	171	178	264
2006	329	417	164	186	178	268
2007	332	367	160	165	126	272
2008	237	352	188	222	108	276
Mean	291	279	119	135	123	221

Note: For all ground berries, samples are number of 40 cm quadrats containing the species with a cover of >5%. For soapberry sample size is the number of bushes sampled (two stems subsampled per bush). Not all species are equally abundant, and most quadrats had only one or two species.

Table 2. Pearson correlations (r) among the climatic variables considered as possible drivers of berry production, 1996–2008.

	Temperature				Rainfall			
	May	June	July	August	May	June	July	August
May temp.	—	0.50	0.16	0.24	–0.33	–0.24	–0.01	–0.06
June temp.		—	**0.76**	0.46	–0.04	–0.31	–0.18	0.15
July temp.			—	0.31	0.28	–0.48	–0.09	–0.11
August temp.				—	–0.01	0.34	–0.00	–0.24
May precip.					—	–0.03	–0.17	0.17
June precip.						—	0.17	–0.11
July precip.							—	0.27

Note: Significant correlations are in bold face ($p < 0.05$).

Table 3. Mean interval between large berry crops for five species of dwarf shrubs and herbs of the Kluane region.

	No. of years between large berry crops									
	1	2	3	4	5	6	≥7	Total n	Mean	Median
Arctostaphylos uva-ursi	118	43	19	33	21	16	24	274	2.78 (2.53–3.02)	1.94
Arctostaphylos rubra	187	86	52	48	30	10	14	427	2.38 (2.22–2.53)	1.81
Empetrum nigrum	110	50	37	23	14	8	8	250	2.35 (2.14–2.55)	1.8
Vaccinium vitis-idaea	218	51	26	18	20	15	18	366	2.15 (1.96–2.33)	1.00
Geocaulon lividum	81	25	28	11	10	2	5	162	2.19 (1.96–2.44)	1.00

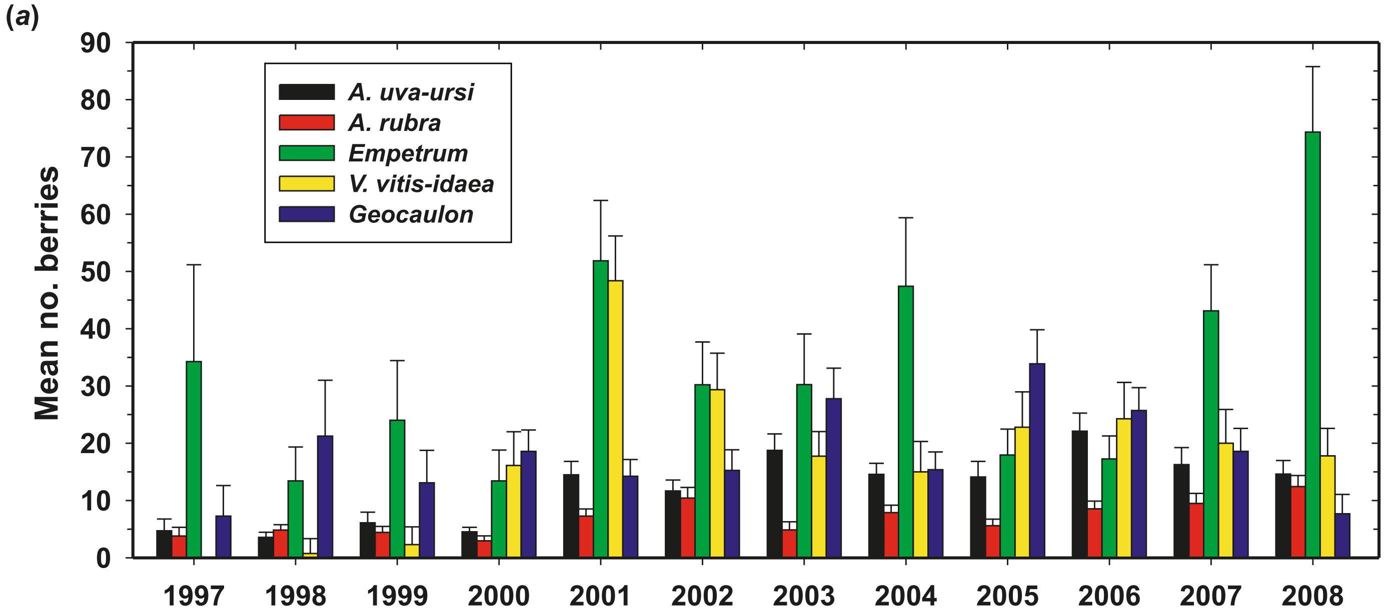
Note: Intervals were measured between large crops in fixed 40 cm × 40 cm quadrats for the sequence of years available from 1997–2008. Total sample size is the number of quadrats for which we had sequential data over the 12 years. Parentheses enclose 95% confidence limits.

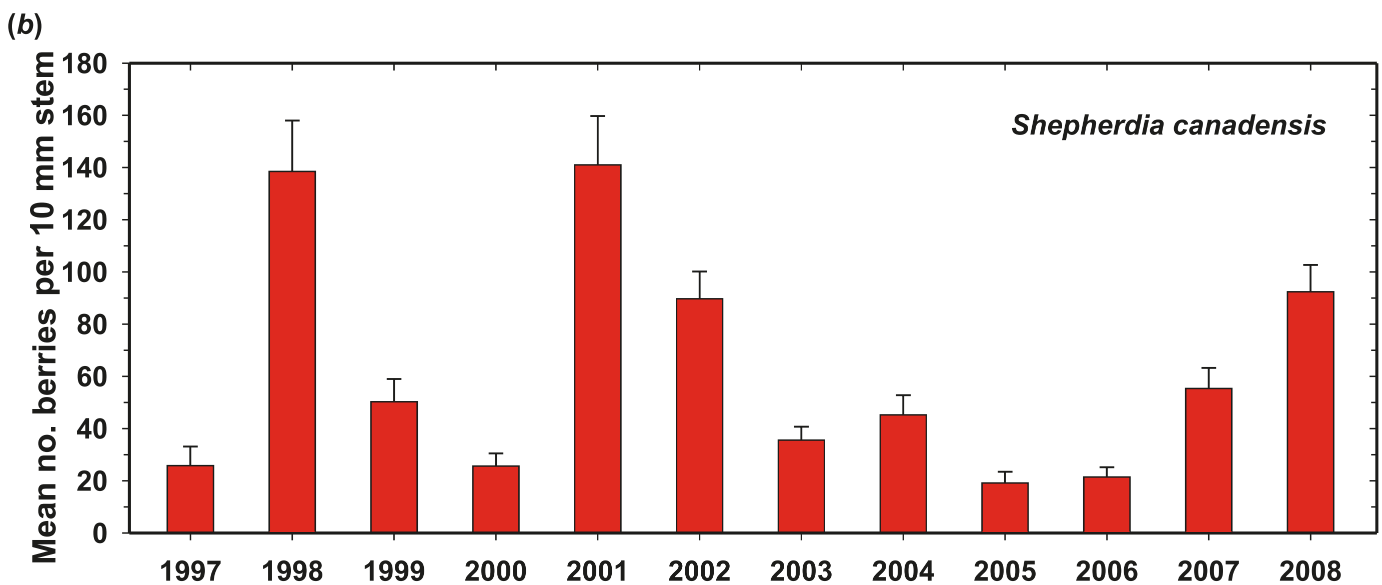
models for each species using AIC_c and chose the model with the best evidence ratio (Anderson 2008).

For berry counts from *A. uva-ursi*, there were two significant variables in the multiple regression: precipitation in May of year t–2 and minimum temperature for May of year t. These two variables produced a highly significant regression with R^2 = 0.87. No improvement in prediction was obtained by adding-in weather data from year t–1 or temperature data from years t or t–2 weather variables in the multiple regression. Table 4 give the correlation coefficients for all the weather variables, and Table 5 gives the detailed statistics for the multiple regressions. The relative importance of the variables in the regression was minimum May temperature (standardized coefficient 0.65) > May precipitation in t–2 (0.32). The suggestion is that for bearberry, relatively low night temperatures in May of the current year and good May rainfall in year t–2 determine the success of flower primordial and subsequent berry production in year t.

For berry counts from *A. rubra*, a multiple regression utilized four weather variables: one from year t–1 and three from t–2 with R^2 = 0.96. None of the weather variables of the current year were significant. The overall importance of spring temperature and rainfall in both year t–1 and t–2 are notable, with both rainfall and temperature from t–2 having greater relative importance in the multiple regression than rainfall in spring of year t–1.

Fig. 1. Indices of berry production of six plant species in the Kluane region of the Yukon, 1997–2008. (*a*) Ground berries. Means are the number of berries in a 40 cm × 40 cm quadrat adjusted to a plant cover of 50%. (*b*) Soapberry. Means are the number of berries per 10 mm diameter stem. Error bars are 95% confidence limits.





For berry counts from *E. nigrum*, a multiple regression utilizing the June temperature and rainfall of year *t*–1 and the rainfall of May of year *t*–2 allowed a significant prediction (p = 0.003) with R^2 = 0.80. No other weather measurements from the current year or any previous years added any power to this estimate. The relevant weather variables for a high *Empetrum* berry crop seem to be cool spring temperatures in year *t*–1 and good rainfall in May of year *t*–2.

For *Shepherdia canadensis* berry counts, a simple regression utilizing a single weather variable, the July rainfall of year *t*–1, allowed the best prediction (p < 0.0001) with R^2 = 0.85. No other weather measurements added any power to this estimate. None of the weather measurements of the current year were useful in prediction of soapberry crops. High summer rainfall in year *t*–1 seems to be the key predictor of large soapberry crops.

For berry counts from *V. vitis-idaea*, three rainfall variables were significant climatic predictors from May in years *t*, *t*–1, and *t*–2. Rainfall of the current May was of less importance (standardized coefficient 0.36) than rainfall of the previous 2 years (standardized coefficients for *t*–1 and *t*–2 were both 0.92). The overall multiple regression with these three variables produced an R^2 = 0.87 (p = 0.0008). Wet spring weather in years *t*, *t*–1, and *t*–2 favoured large crops in *V. vitis-idaea*.

For berry counts from *G. lividum*, May and August temperatures of year *t*–1, August temperature of year *t*–2, and May rainfall of year *t*–1 were significant climatic predictors with

Table 4. Pearson correlations between climate and annual berry production indices at Kluane, Yukon, 1997–2008.

Time lag	Parameter	*Arctostaphylos uva-ursi*	*Arctostaphylos rubra*	*Empetrum nigrum*	*Shepherdia canadensis*	*Vaccinium vitis-idaea*	*Geocaulon lividum*
Current year	May temperature	–0.08	0.18	0.03	–0.17	–0.23	0.03
	Minimum May temperature	–0.50	–0.37	0.04	–0.01	–0.18	**–0.58***
	June temperature	–0.28	–0.40	–0.17	–0.11	–0.30	0.01
	July temperature	–0.10	–0.43	–0.31	–0.16	–0.28	0.06
	August temperature	0.20	–0.03	0.31	–0.18	0.20	–0.15
	May rainfall	0.06	–0.04	–0.24	–0.10	0.17	–0.12
	June rainfall	–0.01	–0.25	0.14	–0.16	0.08	–0.16
	July rainfall	–0.38	–0.29	–0.10	–0.16	–0.05	–0.32
	August rainfall	–0.48	–0.06	–0.07	–0.14	0.02	–0.34
One year lag	May temperature	–0.05	–0.24	–0.44	–0.21	–0.32	**0.65***
	June temperature	–0.34	–0.22	–0.47	–0.20	–0.07	0.46
	July temperature	–0.39	–0.30	–0.22	–0.23	–0.20	0.34
	August temperature	0.11	0.19	–0.36	0.06	0.13	**0.61***
	May rainfall	0.09	–0.23	–0.18	–0.15	0.32	0.28
	June rainfall	0.04	0.08	–0.40	0.40	0.22	0.10
	July rainfall	–0.15	–0.11	0.16	**0.70***	0.07	–0.13
	August rainfall	–0.21	–0.16	0.20	0.25	0.47	–0.23
Two year lag	May temperature	–0.25	–0.14	–0.11	–0.48	**–0.60***	–0.35
	June temperature	0.03	–0.32	–0.27	–0.32	–0.04	–0.12
	July temperature	–0.05	–0.25	–0.29	–0.29	0.20	0.18
	August temperature	0.22	0.04	–0.09	–0.36	0.06	0.29
	May rainfall	0.50	**0.59***	0.51	0.51	0.49	–0.16
	June rainfall	0.15	0.17	0.19	0.19	0.19	0.03
	July rainfall	–0.35	–0.18	–0.18	–0.06	–0.33	–0.13
	August rainfall	–0.13	0.11	0.04	0.48	0.04	–0.41

Note: Berry crops of year *t* were predicted from temperature and rainfall data of years *t*, *t*–1, and *t*–2. Significant correlations in bold type. *, $p < 0.05$; **, $p < 0.01$.

Table 5. Multiple regressions to predict berry crops in the Kluane region from summer climatic data in year *t*, *t*–1, and year *t*–2.

Species	No of weather variables in regression	Multiple regression terms	*p*-values for each term	R^2
Arctostaphylos uva-ursi	2	I = –2.021 MinMayTemp(*t*) + 0.2433 MayPpt(*t*–2)	$p = 0.005$; $p = 0.12$	0.87
Arctostaphylos rubra	4	I = 1.511 JuneTemp(*t*–2) – 0.278 MayPpt(*t*–1)	$p = 0.017$; $p = 0.009$	0.96
		+ 0.400 MayPpt(*t*–2) + 2.394 MayTemp(*t*–2)	$p = 0.001$; $p = 0.007$	
Empetrum nigrum	3	I = 127.058 –0.427 JunePpt(*t*–1) – 7.880 JuneTemp(*t*–1)	$p = 0.006$; $p = 0.012$	0.80
		+ 1.016 MayPpt(*t*–2)	$p = 0.008$	
Shepherdia canadensis	1	S = 1.685 JulyPpt(*t*–1)	$p < 0.001$	0.85
Vaccinium vitis-idaea	3	I = –24.152 + 1.256 MayPpt(*t*–1) + 1.259 MayPpt(*t*–2)	$p < 0.001$; $p < 0.001$	0.87
		+ 0.455 MayPpt(*t*)	$p = 0.034$	
Geocaulon lividum	4	I = –63.776 + 3.630 AugTemp(*t*–1) + 2.173 AugTemp(*t*–2)	$p = 0.011$; $p = 0.081$	
		+ 0.366 MayPpt(*t*–1) + 1.922 MayTemp(*t*–1)	$p = 0.015$; $p = 0.190$	0.85

Note: I, index count of number of berries in 40 cm square quadrat with 50% plant cover; S, number of soapberries on a standard 10 mm diameter branch; Temp, mean temperatures in °C; Ppt, total monthly precipitation (mm) from the Haines Junction weather station. $N = 12$ for all multiple regressions; *p*-values indicate the significance level within each multiple regression.

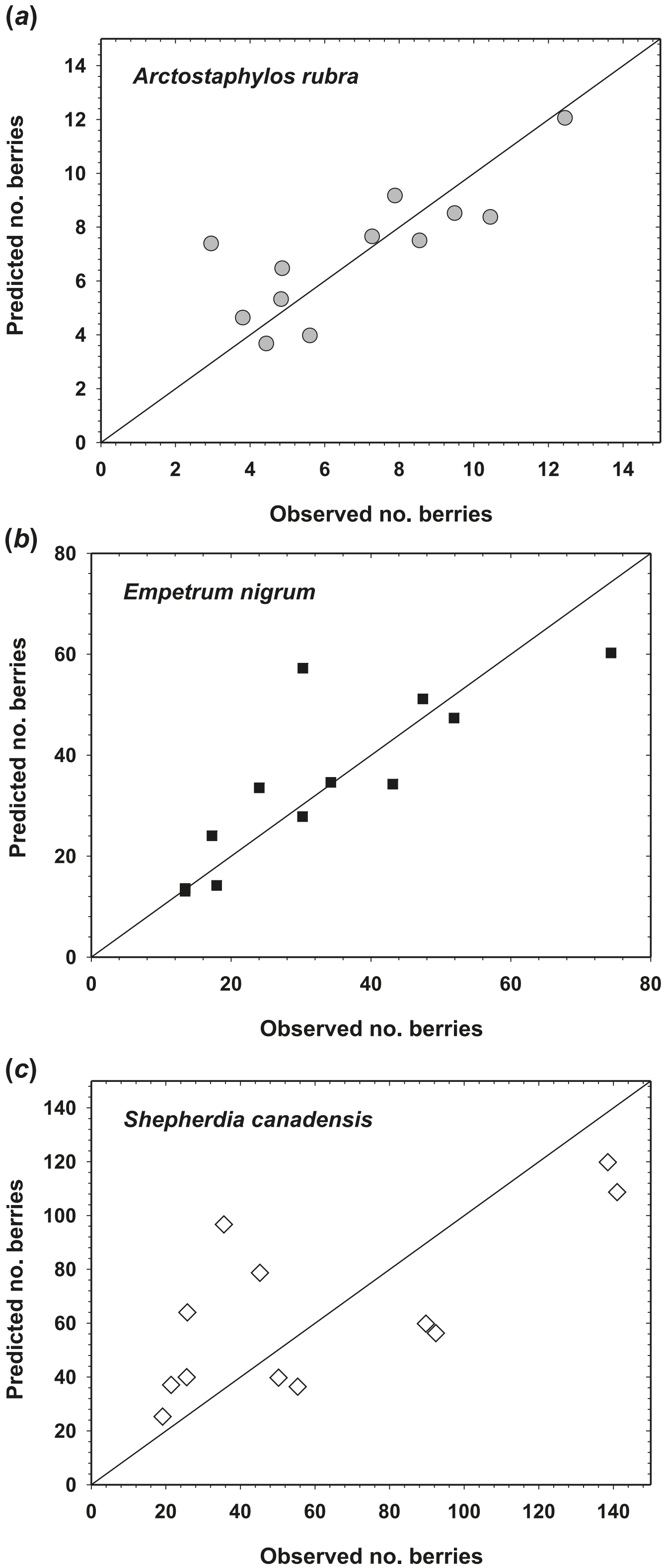
$R^2 = 0.85$ ($p = 0.005$). None of the weather measurements of the current year added any predictability to the regression.

Table 5 summarizes the general patterns with respect to climatic control of berry production. For most species weather in both years *t*–1 and *t*–2 can be utilized as statistical predictors. Weather in the current year was key for only two species. In *A. uva-ursi*, May minimum temperatures are a good predictor, which may indicate frost damage to flower primordia. For *V. vitis-idaea*, May rainfall of the current year was a significant if somewhat weak predictor of berry crops.

Discussion

There were several constraints to this study design. The measurement of berry production was robust, and we pooled all the data from the 10 locations because there was general synchrony among sites: good berry years are good across the boreal forest area of Kluane. But we have only 12 years of data with which to do exploratory data analysis. 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

Fig. 2. Relationship between observed and predicted number of berries for 1997–2008 for (*a*) red bearberry, *Arctostaphylos rubra* (average absolute percent error 27%), (*b*) crowberry *Empetrum nigrum* (percent error 21%), and (*c*) soapberry *Shepherdia canadensis* (percent error 60%). The line in each graph indicates when observed = predicted counts. The predictive equations are given in Table 5.



size at least five times the number of predictor variables (Sokal and Rohlf 1995, p. 655; Hintze 2007). We do not have enough data to subdivide it for prediction, so the test of these simple regression models will have to come from further work to determine their level of predictive precision.

Our data show that, on average, one can explain statistically about 80%–96% of the observed variation in the size of the berry crop in any particular species in a given year. Figure 2 shows the strength of this predictive ability for three of the common species of shrubs. Most of these relationships show considerable scatter in both low and high berry crop years.

Few seem to doubt the general hypothesis that climatic conditions 1 or 2 years prior have a strong influence on the size of a berry crop (Kelly and Sork 2002; Yudina and Maksimova 2005). Vander Kloet and Cabilio (1996) claimed that blueberry (*Vaccinium corymbosum*) crops in Nova Scotia were not related to temperature or rainfall, but they tested only climatic variables from the current year rather than from years *t*–1 and *t*–2. We can find no cases in which this general hypothesis of climatic influence has been rigorously quantified. Selås (2000) reported an array of climatic impacts on 50 years of bilberry (*Vaccinium myrtillus*) production in Norway, but the statistical relationships he reported were very weak ($R^2 < 0.19$). Nevertheless, Selås (2000) strongly supported the view that climatic conditions were responsible for variation in berry production in this species.

We would not expect the exact quantitative relationships given here to be general across the boreal forests of northern Canada and Alaska. We would translate the relationships in Table 5 into qualitative hypotheses that require further tests if they are to be applied in other parts of the boreal zone. For example:

- *Arctostaphylos uva-ursi*, *A. rubra*, and *E. nigrum* berry counts are heavily influenced by spring rainfall 2 years prior.
- *Vaccinium vitis-idaea* berry counts can be predicted by early spring rainfall from the current year and 2 years prior.
- *Shepherdia canadensis* berry counts can be predicted from midsummer rainfall one year prior.

We found that there was no simple pattern of impacts of weather conditions on berry production across all species, but rather each plant species responded individualistically to weather variables. No one multiple regression seems to apply across all species. Moreover, aggregated climatic variables like mean summer temperature or total summer rainfall were of little use in predicting future berry crops, and monthly averages were needed, a reflection of the lack of correlation among summer weather measures (Table 2). The individualistic response of plant species to weather is reflected in the lack of correlation between the berry crops of the different species (Fig. 1).

We had expected to find a periodicity in berry production among individual dwarf shrubs as is common in trees (Kelly and Sork 2002). We do not have the ability to monitor individual ramets of our plant species and can rely only on fixed quadrats that may contain several ramets as indicators of synchrony. We found no indication of any periodicity in berry production in individual 40 cm quadrats. From 43%–60% of the quadrats had large berry crops at one year intervals, while many quadrats never produced a large crop over 7 or more years of observation. We do not know what makes a favourable site for these species, but once a plant is established on a site that is favourable because of soil characteristics and local climatic conditions, berry production can occur each year.

Our study was not designed to estimate the total berry crop per unit of forest habitat, but rather to obtain an index of year to year variation in berry crops. The next step would be to expand this study to a landscape level, such as that carried out by Suring et al. (2008) in Alaska, and determine the forest and soil factors that favour one berry species over another so that we could determine a landscape model for berry production in the Yukon boreal zone.

We conclude that we can explain a large part of the changes in berry production for these six species from spring and summer weather variables of the current year, as well as 1 or 2 years prior. We have not explored winter-weather effects on future berry crops, and more data will be required to achieve this.

There may be some utility in being able to predict berry crops in advance. For example, Parks Canada typically has more problems with bears in the Kluane region when the soapberry crop is poor. Some advance warning might be useful in planning park management restrictions. Local human harvest of berries in the Yukon is significant, and an advance prediction of large crops for particular species would be beneficial.

We have not discussed a set of alternative models for berry production that depend on single day events like a late frost in spring or an early frost 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 for only one species. But spring frosts may be a critical weather event. For example, a late frost in 1992 may have killed bearberry flowers and reduced subsequent overwinter survival in deer mice (*Peromyscus maniculatus*) in Alberta but the detailed data are not available to test this speculation (Kalcounis-Rueppell et al. 2002; R. Boonstra, personal communication). We do not know, for example, the critical thermal limits for flower-bud loss and we do not have the ground 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 known for all these berry-producing species, and there is much important work left to be done in the area.

We suggest that future efforts focus on testing the relationships given in Table 5 with further studies in the Kluane region of the Yukon, and that the general hypotheses of climatic control of berry production be tested in other sites of the boreal forest where the plant species 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 berry production would provide advance warning of expected changes. We acknowledge that soil nutrients as well as climate can affect plant production, and in a subsequent paper we will explore whether the experimental addition of nitrogen to boreal forest soils increases berry crops.

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