

E.G. Beaubien · H.J. Freeland

Spring phenology trends in Alberta, Canada: links to ocean temperature

Received: 21 October 1999 / Revised: 14 January 2000 / Accepted: 14 January 2000

Abstract Warmer winter and spring temperatures have been noted over the last century in Western Canada. Earlier spring plant development in recent decades has been reported for Europe, but not for North America. The first-bloom dates for Edmonton, Alberta, were extracted from four historical data sets, and a spring flowering index showed progressively earlier development. For *Populus tremuloides*, a linear trend shows a 26-day shift to earlier blooming over the last century. The spring flowering index correlates with the incidence of El Niño events and with Pacific sea-surface temperatures.

Introduction

Inter-annual changes in spring plant phenology may be the most sensitive and observable indicators of the plant response to climate change. In temperate zones of the earth, timing of spring growth phases (phenophases), for example, budding, leafing, and flowering of plants, is primarily a response to accumulated temperature above a threshold value. In particular, timing of spring flowering of perennials correlates well with growing degree-days (Rathcke and Lacey 1985), and a trend to warmer winters and springs should be reflected in a trend to earlier flowering.

In Canada, spring temperatures are increasing nationally; a linear trend of 1.4°C is evident from 1948 to 1999 (Environment Canada 1999). There has been significant warming of from 0.9°C to 1.7°C in the western Canadian

interior over the last century (Gullet and Skinner 1992). Over this period, the trend has been to warmer winters and springs (Environment Canada 1995). Studies that link air temperatures and flowering times are numerous (Lindsey and Newman 1956; White 1995).

Earlier spring development is occurring in parts of Europe. Analysis of Europe's International Phenological Garden data gathered 1959–1993 reveals a lengthening of the growing season of 10.8 days since the 1960s, and specifically a trend to earlier onset of spring phenophases of 6 days (Menzel and Fabian 1999).

Using satellite data, Myneni et al. (1997) note an 8-day increase in the growing season (1981–1991) in the northern latitudes (45–70°N), and an increase in spring temperatures with earlier melting of snow. Sparks and Carey (1995), in an examination of the 200-year Marsham phenological record (up to 1947), noted a positive trend in winter temperature with earlier flowering of some plant species. In Estonia springtime has advanced 8 days over the last 80 years, with faster changes in the last 40 (Ahas 1999).

Trends in timing of phenological events have been described for England by Fitter et al. (1995) and Sparks and Carey (1995). These papers predict that, in general, for a 3.5°C increase in global temperature, spring flowering will occur about 2 weeks earlier. Using a sequential model, Kramer (1996) predicted that leaf unfolding in *Fagus sylvatica* will be advanced by 3.6 days/°C temperature change. Fitter et al. (1995) reported that warmer spring temperatures advanced flowering dates by about 4 days/°C increase in the mean monthly temperature.

The response to climatic warming will vary according to species, to the season of warming (Fitter et al. 1995), and to location variables such as elevation (Murray et al. 1989). Climate warming results in a change in thermal regime, with no corresponding change in photoperiod. Thus the normal development of plants that are locally adapted to a certain combination of light and temperature cues, will be disrupted (Lechowicz 1995). Considerable data are still needed on the response of individual species to temperature and photoperiod so that responses to

Prepared in conjunction with a symposium "The phenological response to climate change" held during the XVI International Botanical Congress, St Louis, Missouri, 4 August 1999

E.G. Beaubien (✉)
Devonian Botanic Garden, University of Alberta,
Edmonton, Alberta T6G 2E1, Canada
e-mail: e.beaubien@ualberta.ca
Tel.: +1-780-987-5455/3054, Fax: +1-780-987-4141

H.J. Freeland
Institute of Ocean Sciences, P.O. Box 6000, Sidney,
British Columbia V8L 4B2, Canada

climate warming can be predicted (Harrington et al. 1999). With increasing interest in global change and interannual variability in climate, phenological data are being recognized as essential inputs into accurate models of biosphere response (Reed et al. 1994; Schwartz 1998; White et al. 1997).

In Canada historical phenological data are beginning to be examined for trends. Canadian studies have generally been of short duration (less than 10 years) and from one location (Beaubien 1991; Beaubien and Johnson 1994).

In western Canada, historical databases dating back to the late 1800s exist with flowering data for many native plant species. Trees and shrubs may be particularly vulnerable to climate shifts (Lechowicz and Koike 1995). The first bloom dates for three woody species in the area of Edmonton, Alberta were combined in an annual spring flowering index. The index and individual species data were used both to examine the role of temperature in determining the time of blooming, and to determine trends in flowering time.

The three woody species flower in this order (earliest to latest): *Populus tremuloides* (aspen poplar), *Amelanchier alnifolia* (saskatoon), and *Prunus virginiana* (chokecherry). They have a “sharp” first flowering [Leopold and Jones (1947) definition: two independent observers would give the same date on observing an event].

P. tremuloides is the major hardwood tree species in western Canada’s boreal forest and parkland, and has become important commercially within the last two decades (Petersen and Petersen 1992). It produces flowers on average 1 month before the last killing frost (Lechowicz 1995). After chilling requirements have been met, spring temperatures above 12°C for a duration of 6 days initiate flower emergence in *P. tremuloides* (Perala 1990).

Bud development in all the above species is in response to air temperature at the height of their buds (Lechowicz 1984). The earliest-flowering species in the growing season show more variability in bloom time over the years than do later-flowering species (Criddle 1927; Moss 1960; Fitter et al. 1995). Thus, of these three woody species, *P. tremuloides* phenology can be expected to show the most change with climate warming.

A. alnifolia is a self-compatible and mass-flowering species (St. Pierre and Steeves 1990) with short-lived flowers having a mean longevity of 3.5 days (Primack 1985). Flower bud development in the spring is dependent on heat accumulation and bud dehardening is closely correlated with increased bud moisture content (Junttila et al. 1983).

Prunus phenology shows a high dependence on temperature, as shown by Fitter et al. (1995) in an examination of correlations between flowering and temperature accumulation for 243 species of angiosperms and gymnosperms. In this study, woody species and geophytes showed the best correlations between flowering and temperature accumulation.

Correlations of timing of spring flowering in Edmonton, with El Niño events and Pacific ocean sea-surface tempera-

tures, allow investigation of potential links to the climatic forces driving the phenological response on the Canadian Prairies. This work was done with Howard Freeland of the Institute of Ocean Sciences in British Columbia. A warming trend in sea-surface temperature has occurred in the northeast Pacific ocean over the last 60 years (Freeland 1990; Freeland et al. 1997). Much of our analysis is based on ocean temperature data from Langara Island, just north of the Queen Charlotte Islands off the British Columbia coast, where the increase has been 0.95°C/century. El Niño events are triggered by reversals of the trade winds, which allow a surge or bulge of higher sea-level to move along the equator eastwards from the Asian coast towards South America (Philander 1990). This surge sends Pacific oceanic signals north and south along the American continents, from the equator. Both the northward-propagating ocean wave and an anomalous northward airflow are mechanisms that can lead to an unusual warming off the west coast of Canada (Wyrski 1985; Horel and Wallace 1981). The “southern oscillation index”, evaluated from equatorial air pressure distribution, is a standard diagnostic parameter for the intensity of El Niño-like events.

Few studies have linked biological events in the Canadian prairies with El Niño. Most work has been done on the effects of El Niño on temperatures and precipitation (Bonsal 1991; Jones and Peterson 1993), and results indicate that it is only the stronger events that produce significant anomalies in western Canada.

It seems unlikely that events occurring in the equatorial Pacific have a direct impact on the time of flowering in Alberta. Sea surface temperature in the NE Pacific Ocean is modified by the occurrence of El Niño events, and is more likely to be directly related to climatic conditions in Alberta. An examination of 40 years of records of sea surface temperature showed significant correlations with El Niño years and prairie droughts (Bonsal 1991). We correlated February sea surface temperatures with air temperatures in western Canada, and with the timing of subsequent spring flowering in the area of Edmonton.

Method

Spring flowering data for Edmonton, Alberta, were extracted from the following four historical phenological data sets.

1. The Royal Society of Canada initiated a phenology survey in the 1890s, requesting that affiliated natural history and scientific societies gather data on flowering and leafing of selected plants, arrival times of birds, the break-up of ice on rivers, etc. These data were published annually in the *Proceedings and Transactions of the Royal Society* until 1922. “First-seen” flowering dates for *P. tremuloides* were extracted.
2. Russell (1962) summarized first-bloom data for native species for three prairie cities, published annually by the Canadian Plant Disease Survey for 1936–1961. The Edmonton observations were made on marked plants by three staff of the Canada Agriculture Laboratories of Plant Pathology: M. W. Cormack (1936–1948), S. G. Fushtey (1949–1953) and W. P. Campbell (1954–1961). The first bloom was defined as the first flower seen.

- Bird (1983) annually published first-bloom data for 12 plants native to Alberta (1973–1982), from observations made by volunteers. Plant species were selected on the basis of wide distribution, ease of recognition by amateurs, lack of subspecies, and brief flowering period. First blooming was defined as “up to 25% in flower; i.e.: up to 25% of flowers had sepals and/or petals open and stamens and/or pistils visible”.
- The first author, Beaubien, revived Bird’s survey in 1987 and added three species. This ongoing Alberta Wildflower Survey requests volunteers to report annually the dates for three phenophases: 10% of flower buds open or first flowering, 50% or mid-flowering, and 90% or full flowering; approximately 200 observers report per year. A preliminary analysis of growing degree-days required for first flowering has been done (Beaubien and Johnson 1994). A subset of available data (5–15 observers annually) in a 10,000-km² area around Edmonton was used for the following analysis.

Data sets 2–4 above were used to calculate a spring flowering index. This is the annual mean of the first-bloom dates for three species, which were selected on the basis of the following characteristics: short flowering duration, easily recognized first blooms, and low variability in dates reported by observers for an area. Combining phenological variables to derive an index value (Castonguay and Dubé 1985) has the advantage here of summarizing the responses of these plant species to weather conditions over a 6-week development period in April–May.

While the full bloom of *P. tremuloides* may be a sharper phenophase than the first bloom (Moss 1960), comparisons of Alberta Wildflower Survey data for the two phases showed no significant difference in variability.

To investigate the role of temperature in initiating flowering, the temperature for much of the analysis was calculated as the mean of the monthly temperatures for 2 or 3 months preceding blooming.

Correlations were calculated between flowering data and heat residual for 17 years of Edmonton flowering data (1973–1982, 1987–1993). Using residuals removes the mean value for accumulated heat and is a good way to examine the relations between the linked variables of flowering date and accumulated temperature. “Accumulated heat” was defined as the sum of the maximum daily temperatures in degrees Celsius, from 1 January up to the first flowering date. Negative average temperatures were not included

in the sum. We then averaged the accumulated heat for a particular date (say 12 May), over the 17 years of data, to get the mean accumulated heat. We then subtracted the accumulated heat (say for 12 May 1989) from this mean to get the heat residual for 12 May 1989. For each plant species we calculated the correlation coefficients between heat residual at the median flowering date and the median flowering date.

To investigate the role of climatic influences, correlations between the timing of blooming in central Alberta, and the occurrence of El Niño events (including strength of the southern oscillation index), and sea surface temperatures of the Pacific Ocean, were determined. We used daily sea surface temperature data from nine lighthouse stations in British Columbia, selected to be representative of various oceanographically distinct regions. In addition, correlations between the sea surface temperature and air temperatures over western Canada were mapped.

Results

The mean first-flowering dates for Edmonton for the two most recent phenology data sets (a 20-year period: 1973–1996; note 4 years missing: 1983–1986) are: *P. tremuloides*, 13 April; *A. alnifolia* 14 May; and *P. virginiana*: 22 May.

The timing of flowering of these three species is largely a response to temperature, with earlier blooms seen in years of higher spring temperatures (Fig. 1). Here, most of the natural variation (69%–75%) can be explained by a linear relationship between the two variables.

The heat residual (defined in methods) is positive in warm years and negative in cool years. Correlations for 17 years of Edmonton flowering data (1973–1982, 1987–1993) between day and heat residual were negative: *P. tremuloides*: $r = -0.936$, *A. alnifolia*: $r = -0.835$, *P. virginiana*: $r = -0.823$. (P. Hooper, personal communica-

Fig. 1 Relationship between temperature and flowering for *Populus tremuloides*, *Amelanchier alnifolia*, and *Prunus virginiana* in the area of Edmonton, Alberta. The graph is based on available phenological data for 1936–1998: each point is for 1 year. The x axis is the average spring temperature for that year, calculated as the mean of the monthly mean temperatures for 2 months before the usual bloom time. For *P. tremuloides* the average temperature is based on March–April means; for the other two species it is based on April–May means. The y axis is the Julian date of first bloom. The resulting values for the linear relationships are: *Populus tremuloides*, ($r^2 = 0.75$); *Amelanchier alnifolia*, ($r^2 = 0.69$); and *Prunus virginiana* ($r^2 = 0.74$)

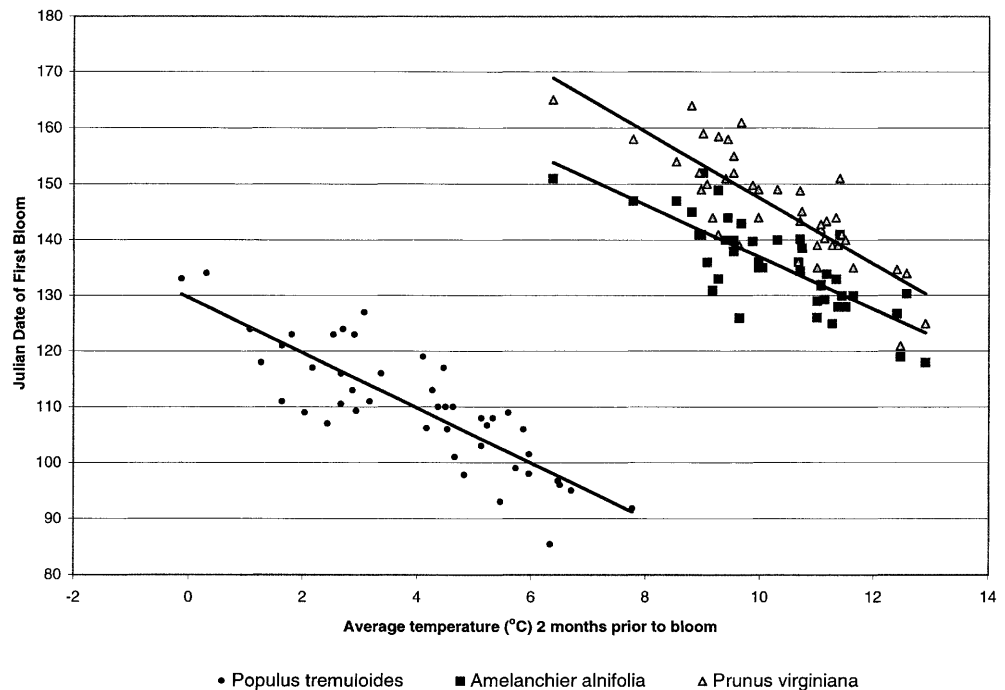


Fig. 2 Spring flowering index and temperatures with deviations from the means (1973–1996), for Edmonton, Alberta. Vertical bars represent the annual spring flowering indices expressed as deviations from the mean 20-year value. The spring flowering index is the mean of the first-flowering dates for *P. tremuloides*, *A. alnifolia*, and *P. virginiana*. The line represents the annual deviation in °C from the 20-year spring mean temperatures. Note that years with El Niño events are marked as follows: * medium El Niño event; ** strong El Niño event

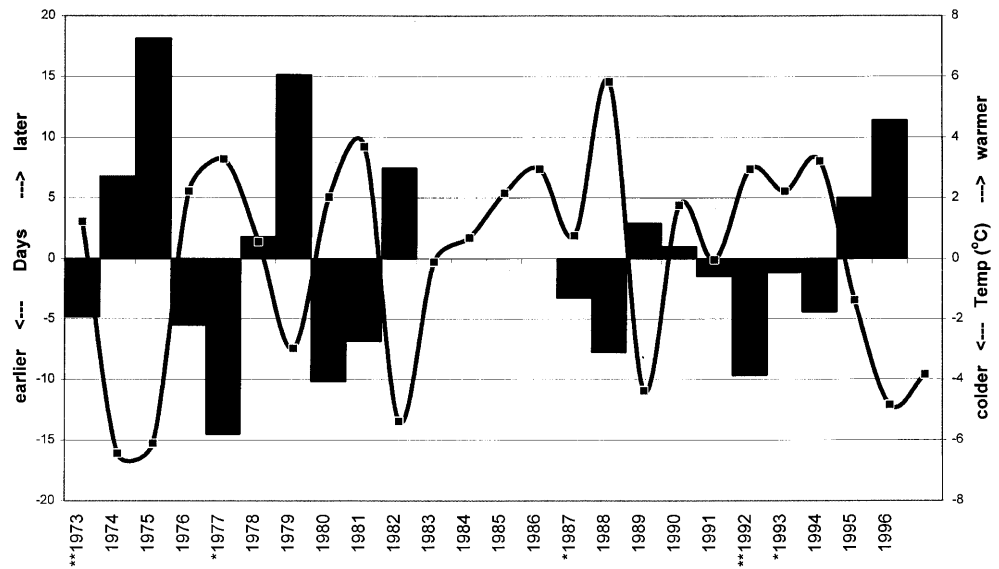
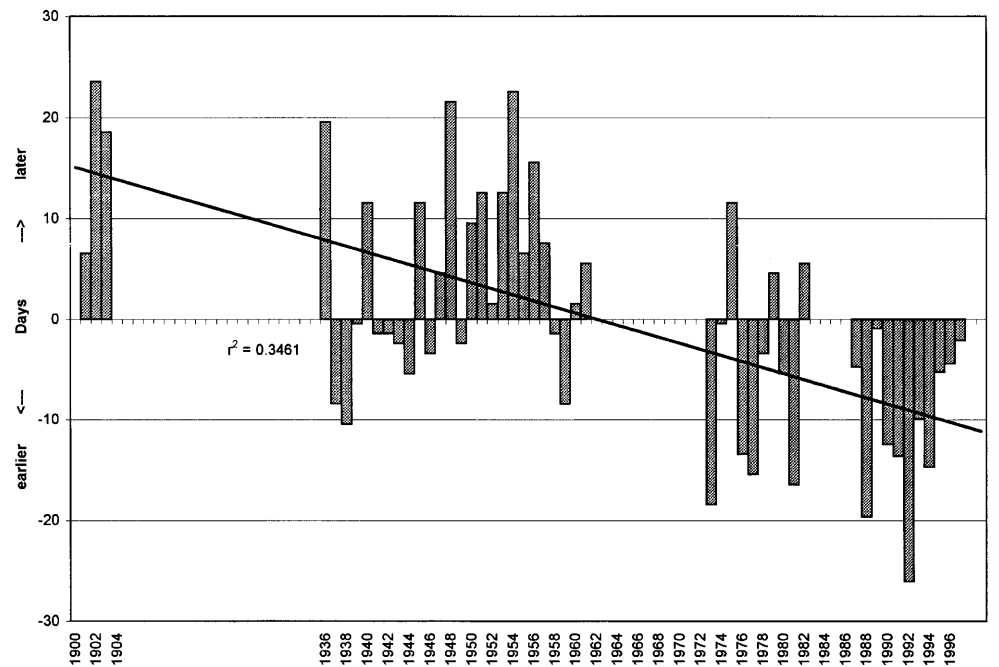


Fig. 3 Long-term trend (1901–1997) in first-flowering dates of *P. tremuloides*, at Edmonton, Alberta. The Julian dates of flowering are shown as deviations from the mean bloom date for all data. Phenology data for 1901–1903, 1936–1961, 1973–1982, and 1987–1997 are plotted (no deviation values = zero)



tion). Later dates are associated with lower than average temperatures. Differences among the correlations are not statistically significant (two-sided p value = 0.15); however, the analysis suggests that, of the three species, *P. tremuloides*' spring phenology may be more strongly linked to temperature accumulation.

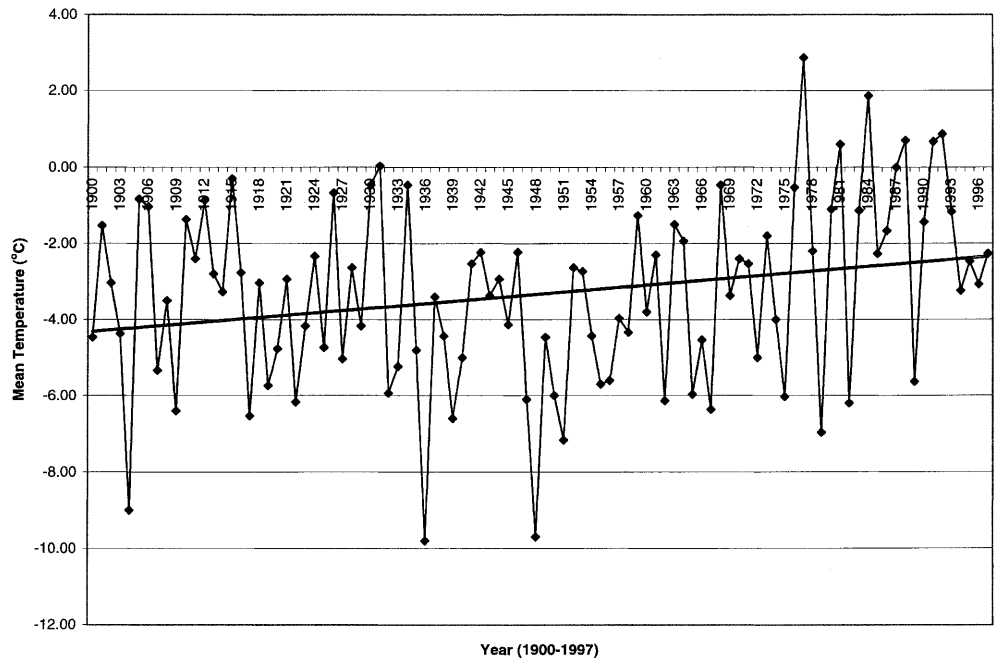
A comparison of the spring flowering index and temperature shows the same inverse relationship (Fig. 2). Annual monthly temperatures for Edmonton City Centre airport for March, April and May were averaged for each year, and these temperatures and the spring flowering index correlate at $r = -0.851$.

Mean values of the annual spring flowering indices (SFI) within each historical data set are as follows: Russell (1936–1961), 14 May; Bird (1973–1982), 7 May

and Beaubien (1987–1996), 6 May. This represents a movement forwards of 8 days in the timing of spring development in the Edmonton area over the last six decades. The trend to earlier flowering is actually more pronounced, since Russell's definition of first blooming "first flower seen" would, in most cases, be a few days earlier than "10% blooming" used in the most recent data set. Early flowering in Edmonton correlates with early flowering over much of the province of Alberta (Beaubien, unpublished data).

The long-term trend (1900–1997) in timing of the first blooming of *P. tremuloides* shows an advance of 26 days over this period (Fig. 3). Of the four historical data sets used, the earliest Royal Society data are the most limited, representing only one observation per year for

Fig. 4 Late winter temperatures for Edmonton Municipal Airport, Alberta, 1900–1997. Mean temperatures for the months of February, March and April were averaged for each year



1901–1903. However the same trend, a movement forward of 0.26 days/year, is shown for the well-reported years 1973–1997. Late winter temperatures over the century show a linear trend towards a 2°C increase (Fig. 4).

For 20 years between 1973 and 1996, all medium and strong El Niño events (Quinn et al. 1987; Cowan 1992) are associated with early spring flowering in Edmonton (Fig. 2).

To evaluate the influence of El Niño, February values of the southern oscillation index (SOI) were correlated with the mean phenology index ($r=0.66$), using the phenology data from 1973–1982 and 1987–1996 inclusive, 20 separate values. The February values correlate more highly than values for other months. Assuming that the phenology data and the estimates of the southern oscillation index are independent, then 95% and 99% confidence intervals can be computed as ± 0.46 and ± 0.58 respectively.

Correlation coefficients were determined between February sea surface temperatures at each lighthouse location and the subsequent spring flowering index for Edmonton, Alberta. These were significant at the 99% confidence level at all locations except those in protected locations in the Strait of Georgia east of Vancouver Island. All sites show a strong response, of higher temperatures, to the occurrence of El Niño.

We see a clear relationship between Pacific Ocean temperatures and spring flowering in Edmonton. However, Edmonton is a long distance (1000 km) east of the Pacific Ocean. Presumably the atmosphere acts as an intermediary and we should see a clear relationship between air temperature in the Edmonton region and Pacific Ocean temperatures. Figure 5 shows a plot of the correlation between monthly averaged sea-surface temperatures at Langara Island in February, and monthly mean

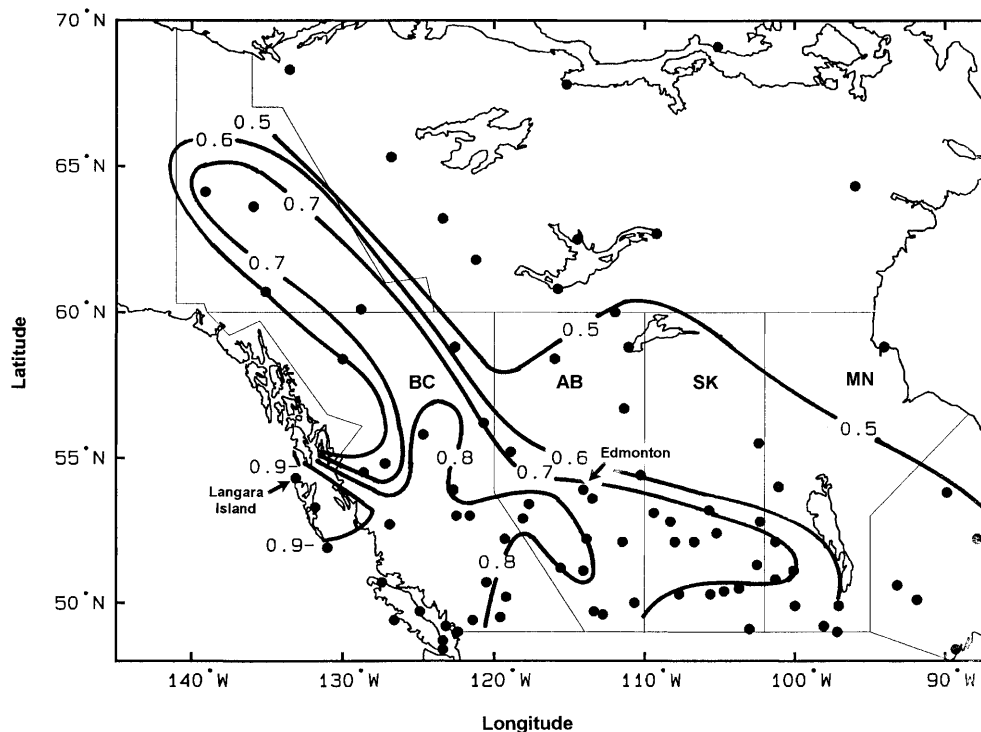
air temperatures across western and arctic Canada. The highest correlations are observed with air temperatures in the Queen Charlotte Islands. Very high correlations are also seen across the rest of British Columbia and extending into Alberta. Clearly air temperature over much of western Canada is largely determined by the surface temperature of the Pacific Ocean.

Discussion

We see from the results that plants in central Alberta, as in parts of Europe, show a trend towards earlier flowering. Unfortunately, data on fall phenology are not available for western Canada, preventing an examination of any possible trend towards lengthening of the growing season. Fall temperatures, which influence chilling responses in woody plants, were not analysed here. We have assumed that, because Alberta winters are so cold, chilling requirements are always met.

The role of urban heat islands in augmenting the trend to earlier poplar flowering over the last century in the Edmonton area, still remains to be thoroughly investigated. However the normal climatic parameters for 1961–1990 (<http://www.cmc.ec.gc.ca/climate/>) for two stations were compared. The first, at Edmonton Municipal Airport, is within the city, north of downtown, at 53°34'N/113°31'W. The second station, at Edmonton International Airport, is 10 km south of the city limits, at 53°18'N/113°35'W. Prevailing winter southerly winds would carry the city heat of Edmonton away from the international airport. If the late winter temperatures for February/March/April are compared, the mean of the monthly averages of daily temperatures is only 1.6°C higher for the Municipal Airport.

Fig. 5 Isolines of correlation between February average sea-surface temperatures at Langara Island, and monthly averaged air temperatures across Western Canada. Dots meteorological stations; lines r values



The historical data sets vary somewhat, the most precise method being that of Russell (1936–1961), where tagged plants were observed over many years by the same individuals. The Royal Society and Bird’s observers did not receive detailed instructions and images of phenophases for each plant species. Alberta Wildflower Survey observers are sent photos and sketches of species, particularly important to illustrate the first blooming of the poplar, defined as “10% pollen shed of male poplar catkins”.

By gathering baseline data on phenological responses, trends in the response to climatic changes can be tracked on a wide geographical basis. “Plantwatch”, a current program launched in 1995 (Beaubien 1996), involves students and the public internationally in reporting bloom times for selected plant species via the Internet (<http://www.devonian.ualberta.ca/pwatch/>). The website instructs observers how to report timing of two flowering phenophases. Selected “key indicator” plants include seven native species found in North America plus a cultivated species, *Syringa vulgaris* (common purple lilac), for which international reports are received. Currently the species are: *S. vulgaris* L., *P. tremuloides* Michx., *Anemone patens* L. var *wolfgangiana* (Bess.) Koch, *Amelanchier* spp; *Trillium ovatum* Pursh., *Trillium grandiflorum* (Michx.) Salisb., *Saxifraga oppositifolia* L., and *Dryas octopetala* L., / *Dryas integrifolia* M. Vahl. As more observations are received in future for British Columbia, our understanding of the plant phenological response to El Niño events, sea surface temperatures, and air temperatures, can be refined further.

Climate warming in western Canada will lead to increased potential evapotranspiration, and it is predicted

that the southern boreal forest will be replaced by aspen parkland (Hogg and Hurdle 1995). *P. tremuloides* is the dominant tree of the parkland, and the illustrated trend to earlier development has implications for population dynamics. Specifically, a negative impact on reproduction can be expected on this and other early flowering woody species such as *Salix* and *Betula*. An increasing frequency of warmer winters and springs may result in very early flowers being killed by subsequent frosts and the year’s seed production being lost (Hänninen 1991; Myking 1997). This reduced reproductive potential may have a negative impact on the ability of these species to move north in response to shifting climatic zones.

Future work is needed to examine flowering trends in a wider selection of plant species, using historical and current phenology data.

In conclusion, we have seen that stronger El Niño events, warmer ocean temperatures, and warmer winter-spring temperatures are correlated with subsequent early flowering in central Alberta. There is an 8-day trend to earlier flowering when the mean spring flowering indices for three Edmonton data sets, which together span the last six decades, are compared. The early blooming *P. tremuloides* shows a 26-day change in bloom time over the century.

Acknowledgements The University of Alberta Devonian Botanic Garden and its director, Dale Vitt, provide space and administrative support for this phenological research. Mryka Hall-Beyer and Geoff Holroyd provided comments on this manuscript, and Tim Goos, Dan Johnson and Dale Vitt commented on an earlier version. Thanks to Peter Hooper, Professor of Mathematical Sciences at University of Alberta, for flowering-date/temperature analysis. Professor Ed Lozowski, Earth and Atmospheric Sciences, University of Alberta, provided heat-island information. Thanks are also due to many funding agencies including Environment Canada

(Action 21, Biodiversity Convention, Ecological Monitoring and Assessment, Atmospheric Environment Service); Natural Resources Canada: Canadian Forestry Service; Shell Canada Limited; Canada Trust: Friends of the Environment; Alberta Agriculture Research Institute; Alberta Sport, Recreation, Parks and Wildlife Foundation; and the University of Alberta's Vice-President, Research.

References

- Ahas R (1999) Long-term phyto-, ornitho- and ichthyophenological time-series analyses in Estonia. *Int J Biometeorol* 42: 119–123
- Beaubien EG (1991) Phenology of vascular plant flowering in Edmonton and across Alberta. MSc thesis, Department of Botany, University of Alberta, Edmonton, Alberta, Canada
- Beaubien EG (1996) Plantwatch, a model to initiate phenology in school classes. *Phenol Season* 1:33–35
- Beaubien EG, Johnson DL (1994) Flowering plant phenology and weather in Alberta, Canada. *Int J Biometeorol* 38:23–27
- Bird CD (1983) 1982 Alberta flowering dates. *Alta Nat* 13 [Suppl] 1:1–4
- Bonsal BR (1991) Possible teleconnections between north Pacific sea surface temperatures and extended dry spells and droughts on the Canadian prairies. Masters thesis, Geography Department, University of Saskatchewan
- Castonguay Y, Dubé PA (1985) Climatic analysis of a phenological zonation: a multivariate approach. *Agric For Meteorol* 35:31–45
- Cowan C (1992) El Niño and Alberta's climate. Report for Tim Goos, Chief, Scientific Services. Atmospheric Environment Services, Environment Canada Western Region, Edmonton, Alberta
- Criddle N (1927) A calendar of flowers. *Can Field-Nat* 41:48–55
- Environment Canada (1995) The state of Canada's climate: monitoring variability and change. SOE Report 95-1. Atmospheric Environment Service, Environment Canada, Ottawa, Canada
- Environment Canada (1999) Climate trends and variations bulletin for Canada. Environment Canada Atmospheric Environment Service Climate Research Branch, <http://www1.tor.ec.gc.ca/ccrm/bulletin/tchtrnd.htm>
- Fitter AH, Fitter RSR, Harris ITB, Williamson MH (1995) Relationships between first flowering date and temperature in the flora of a locality in central England. *Funct Ecol* 9:55–60
- Freeland HJ (1990) Sea surface temperatures along the coast of British Columbia: regional evidence for a warming trend. *Can J Fish Aquat Sci* 47:346–350
- Freeland H, Denman K, Wong CS, Whitney F, Jacques R (1997) Evidence of change in the winter mixed layer in the Northeast Pacific Ocean. *Deep-Sea Res I* 44:2117–2129
- Gullet DW, Skinner WR (1992) The state of Canada's climate: temperature change in Canada 1895–1991. Environment Canada SOE Report 92-2. Department of Supply and Services, Ottawa, Canada
- Hänninen H (1991) Does climatic warming increase the risk of frost damage in northern trees? *Plant Cell Environ* 14:449–454
- Harrington R, Woiwod I, Sparks TH (1999) Climate change and trophic interactions. *Trends Ecol Evol* 14:146–150
- Hogg EH, Hurdle PA (1995) The aspen parkland in western Canada: a dry-climate analogue for the future boreal forest? *Water Air Soil Pollut* 82:391–400
- Horel JD, Wallace JM (1981) Planetary scale atmospheric phenomena associated with the southern oscillation. *Mon Weather Rev* 109:813–829
- Jones K, Peterson B (1993) El Niño's effect on the prairies. In: Proceedings of the long-range weather and crop forecasting working group meeting, April 1993, National Hydrology Research Centre, Saskatoon, Saskatchewan
- Junttilla O, Stushnoff C, Gusta LV (1983) Dehardening in flower buds of saskatoon-berry, *Amelanchier alnifolia*, in relation to temperature, moisture content, and spring bud development. *Can J Bot* 61:164–170
- Kramer K (1996) Phenology and growth of European trees in relation to climate change. PhD thesis, Agricultural University, Wageningen, The Netherlands
- Lechowicz MJ (1984) Why do temperate deciduous trees leaf out at different times? Adaptation and ecology of forest communities. *Amer Nat* 124:821–842
- Lechowicz MJ (1995) Seasonality of flowering and fruiting in temperate forest trees. *Can J Bot* 73:175–182
- Lechowicz MJ, Koike T (1995) Phenology and seasonality of woody plants: an unappreciated element in global change research? *Can J Bot* 73:147–148
- Leopold A, Jones SA (1947) A phenological record for Sauk and Dane Counties, Wisconsin, 1935–1945. *Ecol Monogr* 17:81–122
- Lindsey AA, Newman JE (1956) Use of official weather data in spring time – temperature analysis of an Indiana phenological record. *Ecol* 37:812–823
- Menzel A, Fabian P (1999) Growing season extended in Europe. *Nature* 397:659
- Moss EH (1960) Spring phenological records at Edmonton, Alberta. *Can Field-Nat* 74:113–118
- Myking T (1997) Dormancy, budburst and impacts of climatic warming in coastal-inland and altitudinal *Betula pendula* and *B. pubescens* ecotypes. In: Lieth H, Schwartz MD (eds) Phenology in seasonal climates, I. Backhuys Publishers, Leiden, the Netherlands, pp 51–66
- Murray MB, Cannell MGR, Smith RI (1989) Date of budburst of fifteen tree species in Britain following climatic warming. *J Appl Ecol* 26:693–700
- Myneni RB, Keeling CD, Tucker CJ, Asrars G, Nemanii RR (1997) Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* 386:698–701
- Perala DA (1990) *Populus tremuloides* Michx. quaking aspen. *Salicaceae* Willow family. In: Burns RM, Honkala BH (eds) Silvics of North America, vol 2. Hardwoods. US Department of Agriculture Agriculture Handbook 654, pp 555–569
- Petersen EB, Petersen NM (1992) Ecology, management and use of aspen and balsam poplar in the prairie provinces, Canada. NW Region. Special Report 1. Forestry Canada, Edmonton, Alberta
- Philander SG (1990) El Niño, La Niña, and the southern oscillation. Academic Press, San Diego, Calif
- Primack RB (1985) Patterns of flowering phenology in communities, populations, individuals, and single flowers. In: White J, (ed) The population structure of vegetation. Dr. W. Junk, Publishers, Dordrecht, pp 571–594
- Quinn WH, Neal VT, Antunez de Mayolo SE (1987) El Niño occurrences over the past four and a half centuries. *J Geophys Res* 92:14 449–14 461
- Rathcke B, Lacey EP (1985) Phenological patterns of terrestrial plants. *Annu Rev Ecol Syst* 16:179–214
- Reed BC, Brown JF, VanderZee D, Loveland TR, Merchant JW, Ohlen DO (1994) Measuring phenological variability from satellite imagery. *J Veg Sci* 5:703–714
- Russell RC (1962) Phenological records of the prairie flora. *Can Plant Disease Survey* 42:162–166
- Schwartz MDS (1998) Green-wave phenology. *Nature* 394:839–840
- Sparks TH, Carey PD (1995) The responses of species to climate over two centuries: an analysis of the Marham phenological record, 1736–1947. *J Ecol* 83:321–329
- St Pierre RG, Steeves TA (1990) Observations on shoot morphology, anthesis, flower number, and seed production in the saskatoon, *Amelanchier alnifolia* (Rosaceae). *Can Field Nat* 104: 379–386
- White LM (1995) Predicting flowering of 130 plants at 8 locations with temperature and daylength. *J Range Manage* 48:108–114
- White MA, Thornton PE, Running SW (1997) A continental phenology model for monitoring vegetation responses to interannual climatic variability. *Global Geochem Cycles* 11:217–234
- Wyrski K (1985) Water displacements in the Pacific and the genesis of El Niño cycles. *J Geophys Res* 90:7129–7132