The solar cycle as a possible modulator of ecosystem functioning on the decadal time scale: new evidence from North American porcupine (*Erethizon dorsatum*) feeding scars and climatic data

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November 2002

A thesis submitted to the faculty of Graduate Studies and Research in partial fulfilment of the requirements of the degree of Master of Science

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PREFACE

This M.Sc. thesis is presented in the form of a single manuscript to be submitted to *The American Naturalist*.

Contributions of authors

Although Dr. Dominique Berteaux is a co-author of the manuscript, the manuscript should be considered as a normal thesis written by the student. Dr. Berteaux's input was limited to the usual functions of a supervisor. He provided guidance when planning field work and writing the manuscript. He commented on three previous versions of the manuscript. Ilya Klvana developed the field methods and statistical analyses and wrote the manuscript.

Supplementary material

Supplementary material (abstract in both English and French, introduction, literature review and conclusion) was added to the manuscript to orient the reader and as requirements for thesis submission. However, the reader should concentrate on the manuscript.

ABSTRACT

North American porcupine (*Erethizon dorsatum*) feeding scars on trees were used as an index of past porcupine abundance in the Bas St. Laurent region of eastern Quebec, Canada. The frequency distribution of scars revealed that porcupine populations have fluctuated regularly over the past 130 years in the Bas St. Laurent region, with superimposed periodicities of 11 and 22 years. This porcupine population cycle has closely followed the 11 and 22-year solar activity cycles. An analysis of local temperature and precipitation data revealed a close relationship between fluctuations in annual precipitation and both the solar cycle and the porcupine cycle. These results suggest that the solar cycle has sufficiently important effects on the climate along the southern shore of the St. Lawrence estuary to influence terrestrial ecosystem functioning to the point of setting the rhythm of porcupine population fluctuations. This is the strongest available evidence of a top-down cascading effect of solar variability on ecological systems at the decadal time scale and local spatial scale. These results confirm and extend those obtained by others at greater temporal and spatial scales and provide exciting opportunities for future research on the extensively debated topic of solar variability and its impact on our planet.

RÉSUMÉ

Les cicatrices que les porcs-épics d’Amérique (*Erethizon dorsatum*) laissent sur les troncs des arbres lorsqu’ils s’alimentent sont un bon indice de l’abondance passée de ces animaux. Elles ont révélé que les populations de porcs-épics ont fluctué de façon régulière pendant les 130 dernières années dans le Bas St. Laurent (Est du Québec), avec des périodicités superposées de 11 et 22 ans, suivant de près les cycles d’activité solaire de 11 et 22 ans. Une analyse des relevés locaux de température et de précipitation démontre l’existence d’un lien probable entre le cycle solaire, les fluctuations annuelles de précipitation et le cycle d’abondance des porcs-épics. Ces résultats suggèrent que le cycle solaire a des effets suffisamment importants sur le climat de la rive sud de l’estuaire du St. Laurent pour influencer la dynamique des écosystèmes terrestres au point de donner le rythme aux fluctuations des populations de porcs-épics. Ceci constitue l’évidence la plus solide d’un effet de la variation de l’activité solaire sur les écosystèmes à l’échelle du cycle solaire de 11 ans et a une échelle géographique locale, confirmant d’autres travaux à des échelles temporelles et spatiales plus grandes. Ce travail offre des nouvelles avenues pour la recherche sur le lien entre l’activité solaire, le climat, et les écosystèmes, un sujet hautement débattu.

ACKNOWLEDGEMENTS

My greatest thanks are reserved to my supervisor, Dr. Dominique Berteaux. He is truly a great teacher, both in ecology and in life. He guides students in a very personalized way, respecting their individual personalities, and always giving great importance to their personal growth. His passion for ecology and his philosophy of life are very inspiring and will always remain precious to me. I greatly encourage him to continue his still young career in the same grand way with which he began. As his first graduate student to submit my thesis, I dedicate this work to Dominique.

I also wish to thank Patrick Morin for having thought of me in June 2000 when he and Dominique needed an extra hand with putting together the “Porcupine Project” in Parc National du Bic. I had a great experience during the summer of 2000, eventually leading to the elaboration of this work. Patrick also helped me with field work and provided many constructive comments at all stages of this project.

My gratitude also goes to Cedric Daguerre for his help with the field work, to Elodie Bouchon for showing me the principles of dendrochronology, to Dr. Benoit Côté for his help with the tree growth measurements, to everyone who has participated in the Porcupine Project for making our field camp such a pleasant place, to all Parc National du Bic employees for they warm hospitality, and finally to Amélie Robillard for her continued support during the project.

A scholarship from the Natural Sciences and Engineering Research Council of Canada (NSERC) provided financial support.

INTRODUCTION TO THE THESIS

Ever since the emergence of ecology as a science, many efforts have been invested in trying to describe and ultimately understand animal cycles. This interest in cycles probably stems from the fact that periodic recurrence of a phenomenon allows prediction, facilitating experimentation and hypothesis testing. Ecologists of all times have been particularly fascinated by the regular and widespread 10-year cycle of several North American mammal species (see for example Elton 1924; McLulich 1937; Elton and Nicholson 1942; Moran 1949; Keith 1963; Bulmer 1974; Finerty 1980; Krebs et al. 1995; Krebs et al. 2001). Many hypotheses have been put forth to explain this cycle, including a possible link to the 11-year solar cycle, first put forth by Elton (1924), and recently re-examined by Sinclair et al. (1993).

Unfortunately, research on “wildlife’s 10-year cycle” (aptly named as such by Keith (1963)) has always suffered from a major drawback: the scarcity of long term data on abundance of species over vast geographical areas. Direct estimates of abundance over long periods of time and vast expanses of land are very expensive and require continuity in field work.

As a solution, many population ecologists have relied on already existing, yet indirect, estimates of population densities over long periods of time. The Hudson’s Bay Company fur trading records have provided a gold-mine of data that ecologists have been making use of since Elton’s (1924) classic paper first brought them to light. Yet, rigorously recorded fur data exist for only a few species with commercial value. Another indirect method of obtaining long-term abundance data for some species is to use the feeding or trampling scars that they leave on trees or parts of them (Spencer 1964; Payette 1987; Sinclair et al. 1993; Morneau and Payette 1998, 2000; Erlinge et al. 1999; Predavec et al., 2001). These scars can be dated using dendrochronological methods, allowing the reconstruction of past patterns of animal activity and abundance. This method is particularly attractive since decades or even centuries of data can be obtained within just a few days, weeks or months of field work, thereby eliminating the logistical and financial difficulties inherent to long-term experiments or data collection.

One species which creates a particularly large number of scars on trees is the North American porcupine (*Erethizon dorsatum*). These scars are produced during the winter season when porcupines feed to a large extent on the inner bark of trees (Roze 1989). Since porcupines only consume the phloem and cambium, but do not gnaw on xylem tissue when feeding on the bark, the year of scar formation can be determined with precision by counting tree rings (Spencer 1964; Payette 1987).

My purpose was to use porcupine feeding scars as an index of porcupine abundance over the longest possible time period in order to describe and potentially explain porcupine population fluctuations in the Bas St. Laurent region of eastern Quebec, an area where porcupines are an important component of the forest ecosystem. More specifically, I had several objectives to achieve; first, to find the tree species and sites best suited for reconstructing long time series of porcupine abundance using feeding scars; second, to obtain the longest possible chronologies of the number of scars per year at several sites; third, to develop statistical methods of analysis allowing the interpretation of the scar data; fourth, to statistically describe the temporal variations in the scar data (i.e. are there fluctuations in scar frequency and are these fluctuations periodic?); fifth, to investigate whether the temporal variations in porcupine scar data are associated with fluctuations in other variables in the system for which data can be obtained, namely climatic data, tree growth data, and solar activity; sixth, to find, or at least try to find, a biological explanation for the results obtained; seventh, to put my study in perspective relative to similar work in population ecology, as well as other areas of science.

LITERATURE REVIEW

As the format of the manuscript presented in this thesis does not allow a detailed discussion of all cited works, I have added this section in which I give the reader helpful background information.

Porcupine biology

The North American porcupine is a large rodent found throughout North America. It is particularly abundant in Parc National du Bic (my study area), with an estimated density of approximately 40 animals / km^2 in 2000 (Berteaux, unpublished), compared to the usual density of about 10 animals / km^2 found in other areas (Roze 1989; Demeritt 1944; Kelker 1943). The average mass of adult porcupines in Parc National du Bic fluctuates seasonally between a minimum of 6.78 kg (s=1.13; n=114) in early May and a maximum of 9.42 kg (s=1.04; n=48) in mid October (Klvana and Berteaux, in preparation).

Porcupines are long-lived animals, possibly living over 12 years of age (Earle and Kramm 1980). They usually become sexually mature at two and a half years of age and females produce 1 young per year almost every year (Roze 1989). Young are usually born between early May and mid June and maternal investment is long, with gestation lasting 210 days and lactation about 125 days (Roze 1989).

The relatively low birth rate of the porcupine is most probably offset by a low mortality rate, owing to its armour of quills. Nevertheless, fishers (*Martes pennanti*) are known to prey regularly on porcupines (Powell 1982); there is good evidence that such is the case in our study area (Klvana, personal observations). Other predators which may occasionally prey on porcupines in our study area are coyotes (*Canis latrans*), lynx (*Lynx canadensis*) and great horned owls (*Bubo virginianus*) (Roze 1989). Winter is most probably a critical period for porcupine survival. Mortality from starvation in winter may be relatively important, as porcupines subside on a nutritionally poor diet from November to April inclusive and loose mass during that period (Sweitzer and Berger 1993). In addition, they face increased locomotion costs, their short legs being ill-adapted to moving through the snow (Roze 1989), as well as increased thermo-regulation costs. Although they remain active throughout the winter, their home range is greatly reduced and they spend much of their time in rock dens (Klvana, personal observations; Roze 1989).

The porcupine's diet is composed of leaves, buds, and fruits of deciduous trees and forbs during summer and inner bark of trees and conifer foliage during winter (Roze

1989). Winter feeding on inner bark of trees produces characteristic and easily identifiable feeding scars (Spencer 1964; Payette 1987), a key factor in making this research project possible. Since porcupines do not remove xylem tissue when feeding on bark, the year of scar formation can be determined with precision by counting growth rings added around the scar since its formation. By dating hundreds of scars, it is therefore possible to obtain information on past year-to-year fluctuations in porcupine feeding activity and therefore obtain an index of their abundance through time (Spencer 1964; Payette 1987).

“Wildlife’s 10-year cycle” and the solar cycle

Much research effort has been invested to understand “wildlife’s 10-year cycle”, and particularly the 10-year cycle of the snowshoe hare (*Lepus americanus*), as it is a key prey species of the boreal forest. Although it now seems that the hare cycle is a result of the interactions between the hare, its predators and its food supply (Krebs et al. 1995), the synchrony, or near-synchrony, of the cycle across the boreal forest ecosystem remains to be explained (Krebs et al. 2001). One explanation for this synchrony, first put forth by Elton (1924), is that the hare cycle is driven by wide-spread periodic variations in climate related to the 11-year sunspot cycle.

However, Elton himself later rejected the sunspot hypothesis. After compiling 200 years of lynx (*Lynx canadensis*) fur returns in Canada, Elton and Nicholson (1942) showed that the lynx and its prey, the snowshoe hare, undergo a very regular and widespread 9.6-year population cycle that is not related to the 11-year solar cycle. Moran (1949, 1953*a*, 1953*b*) analysed the same lynx data statistically and concluded that “examination of the sunspot and Canadian lynx cycles rules out the possibility of a causal connection between them” (Moran 1949). Bulmer (1974) pursued Moran’s statistical analysis of fur trade data using data for all fur-bearers in North America, finding that the abundance of other species, namely the coyote (*Canis latrans*), red fox (*Vulpes vulpes*), wolf (*Canis lupus*), striped skunk (*Mephitis mephitis*), fisher (*Martes pennanti*), marten (*Martes americana*), mink (*Mustela vison*), muskrat (*Ondatra zibethicus*) and wolverine (*Gulo gulo*), followed the 10-year cycle of the lynx and hare (with various time lags and with lesser amplitude and regularity) and could therefore not be related to the sunspot cycle.

Nevertheless, the possibility of a link between the solar cycle and animal population dynamics has not lost its appeal in recent times. Using browsing stress marks produced in the tree rings of white spruce (*Picea glauca*) by snowshoe hare (the main prey species of the lynx), Sinclair et al. (1993) reconstructed past fluctuations in hare abundance at Kluane, southwest Yukon, back to 1751. Using this tree-ring data, as well as fur trading records, they found that during periods when the amplitude of the 11-year sunspot cycle was particularly high (1751-1787, 1838-1870 and 1948-1986), hare abundance did cycle in phase with the sunspot cycle, although it came out of phase at other times. Based on this new evidence, as well as climatic data somewhat linked with the sunspot cycle, they suggested that the snowshoe hare cycle, although intrinsic to the population dynamics of the hare, "is modulated indirectly by solar activity through an amplified climate cycle that affects the whole boreal forest ecosystem" (Sinclair et al. 1993).

Ranta et al. (1997) criticised the validity of the hypothesis presented by Sinclair et al. (1993) They argued that hare cycles in Finland are not synchronised with those in North America and that the level of synchrony between local hare populations decreases with increasing distance both in Finland and in Canada (Smith 1983), which is contrary to what one would expect if an external factor was "setting the beat" of the hare cycle. Lindstrom et al. (1996) also rejected the possibility of a solar cycle-climate-hare-lynx causal relationship based on a time series analysis of the famous 1821-1934 Mackenzie River lynx fur return time series and sunspot data for the same period.

Sinclair and Gosline (1997) reanalysed the data used by Ranta et al. (1997) and found that, although local hare populations are not always in phase across Canada, they do come into phase during the peak years, suggesting the influence of an external synchroniser such as weather acting on a continental scale. They maintained their hypothesis that solar activity, when it is particularly strong, acts indirectly as the synchroniser of the hare cycle through its effect on climate. They specified that since weather systems have different phase relations with solar activity in different areas of the globe, it is to be expected that solar-hare phase relations also differ. As shown above, the possibility of a link between the solar cycle and animal cycles is still generating a vigorous debate, almost 80 years after it was first put forth by Elton (1924).

Solar variability and climate

The hypothesis of a link between the solar cycle, climate and animal cycles put forth by Elton (1924) and again by Sinclair et al. (1993) seems more realistic when considered in the light of research conducted specifically on the link between the solar cycle and climate. In addition to the well known 11-year solar cycle, the sun also displays cycles of activity of about 100 years, 200 years and 1500 years, all of which seem to have an effect on the earth's climate (Rind 2002). Deposits of ^{14}C and ^{10}Be, whose production rates follow solar activity, have been used to show that there is a particularly close association between solar variability and climatic fluctuations at the time scale of centuries and millennia (see for example Bond et al. (2001)). It has already been established for some time that the two coldest historically documented periods, known as the "little ice age", corresponded with periods of very low solar activity, the Sporer Minimum (1460-1550) and the Maunder Minimum (1645-1715) (Eddy 1976). Similarly, a prolonged maximum in solar activity from about 1100 to 1250 is thought to have coincided with the "medieval climatic optimum" (Eddy 1976). More recently, lake sediments cores from the Yucatan Peninsula, Mexico, have revealed that solar variability has played a major role in determining the occurrence of prolonged drought periods at about 200-year intervals during the past 2,600 years, and that some of these solar-induced droughts correspond with discontinuities in Maya cultural evolution (Hodell et al. 2001). Similarly, Lake Naivasha (Kenya) level and salinity fluctuations during the past 1,100 years, as well as development of local human societies, were found to be closely related to fluctuations in solar activity (Verschuren et al. 2000). Over a much longer period, Bond et al. (2001) found strong evidence of solar forcing of the North Atlantic climate during the past 12,000 years.

There is also much evidence which supports a link between variations in solar activity and the earth's climate at the scale of the 11-year and 22-year solar cycles. Evidence of the 11-year solar cycle signal were found in USA precipitation and temperature records, St. Lawrence and Nile river flows, and European fish catches, wine harvests and sea-levels (Currie and O'Brien 1988, 1990; Currie 1993*a*, 1993*b*, 1994). As already mentioned, Perry (1994) found that precipitation fluctuations in certain regions of the USA are closely correlated with solar activity in previous years. This same periodicity in precipitation was detected in net snow accumulation data from a glacier in the Yukon (Sinclair et al. 1993). Variations in cloud cover over the USA were also found to be related to the solar cycle (Udelhofen and Cess 2001). The 22-year Hale solar cycle was shown to play a role in the timing and extent of drought in the USA (Mitchell et al. 1979; Stockton et al. 1983; Cook et al. 1997).

In addition to climatic responses to the solar cycle at the regional and continental scale, global planet-wide responses have also been observed. As already mentioned, White et al. (1997) have shown that changes in solar irradiance, at the scale of both the 11-year and 22-year solar cycles, are reflected in the surface sea temperatures across the Pacific, Atlantic and Indian oceans, and that excess heat in certain years is stored in the upper 100 m or so of the ocean and eventually released to the atmosphere, and not the deep ocean. Reid (2000), using other global sea surface temperature data, corroborated the findings by White et al. (1997) and underscored the importance of oceans when trying to understand climatic fluctuations, since they cover 70 % of our planet and are largely responsible for the transport of heat from low to middle and high latitudes, particularly during the winter season. But it is perhaps the correlation found by van Loon and Labitzke (1988) between the solar cycle and the temperatures and heights of the stratosphere at 30hPa and below in the Northern Hemisphere that is the most well-known and striking evidence of a solar cycle – climate link (Kerr 1987, 1988, 1990; Haigh 2000). Their results have withstood the test of time, as new data were recently added to their original time series (van Loon and Labitzke 1998, 2000). Their correlation was also found to be valid in the Southern Hemisphere, in addition to the Northern Hemisphere (van Loon and Labitzke 1998, 2000).

The advent of satellite technology has allowed a major step in research on the solar cycle – climate link, as it has allowed precise measurements of the total solar irradiance above the earth's atmosphere. It is now known to vary by approximately 0.1 % from a minimum to a maximum of the 11-year solar cycle (Haigh 2000). Reconstructions of past total solar irradiance based on proxy data suggest that this change in irradiance may be of about 0.25% over longer time periods, such as during the Maunder minimum (Lean et al. 1995), although this is not clear due uncertainties in the reconstructions of past total solar irradiance (Lean and Rind 1998).

Although there is much evidence supporting a link between variations in solar activity and climate, there are two key pieces missing in the puzzle. First, our understanding of region-specific responses of climate to variations in solar activity remains unclear, as the response seems to vary in both space (from one region to another) and time (apparently depending on the variable amplitude of solar activity peaks) (Hoyt and Schatten 1997; Rind 2002). Second, there is no well understood underlying physical mechanism for this relationship (Reid 2000). The most obvious mechanism is that changing total solar irradiance directly affects climate (Lean and Rind 1998). However, our actual knowledge suggests that variations in total solar irradiance are too small to generate the observed magnitude of the climate response (Friis-Christensen 2000). Two other mechanisms, allowing amplification of the effect of the solar cycle, have been proposed: 1) changes in UV-radiation, which are far greater than changes over the whole electromagnetic spectrum, and could affect stratospheric ozone and thereby the atmosphere (Haigh 1996, 1999; Shindell et al. 1999); 2) changes in the flux of cosmic rays, which follow changes in solar activity, could affect cloud formation (Marsh and Svensmark 2000*a*, 2000*b*), and thus the climate of the entire globe. It is also very likely that all three mechanisms are acting together, at different spatial and temporal scales (Friis-Christensen 2000).

It is clear that there are good reasons to believe in a link between the solar cycle and climate, despite the fact that this link still remains unclear. It is also tempting to believe that solar-induced climatic fluctuations play a role in the decadal cycle of the snowshoe hare and other species of the boreal forest, and possibly the functioning of entire ecosystems, although the empirical evidence remains scarce and controversial. My research will hopefully contribute to the resolution of this still enigmatic subject.

MANUSCRIPT TO BE SUBMITTED TO *THE AMERICAN NATURALIST*

Title: The Solar Cycle As a Possible Modulator of Ecosystem Functioning on the Decadal Time Scale: New Evidence from North American Porcupine (*Erethizon dorsatum*) Feeding Scars and Climatic Data

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Running heading: Klvana and Berteaux - Solar Cycle and Porcupine Population Fluctuations.

Keywords: animal cycles, solar cycle, climatic oscillations, North American porcupine, *Erethizon dorsatum*, feeding scars, dendrochronology.

Abstract

Using North American porcupine (*Erethizon dorsatum*) feeding scars on trees as an index of past porcupine abundance, we have found that porcupine populations have fluctuated regularly over the past 130 years in the Bas St. Laurent region of eastern Quebec, with superimposed periodicities of 11 and 22 years. Cross correlations and phase shift analyses showed that this porcupine population cycle has closely followed the 11 and 22-year solar activity cycles. Fluctuations in local precipitation were also cyclic and closely related to both the solar cycle and the porcupine cycle. Our results suggest that the solar cycle has sufficiently important effects on the climate along the southern shore of

the St. Lawrence estuary to influence terrestrial ecosystem functioning, to the point of setting the rhythm of population fluctuations of the most abundant mammalian herbivore in the ecosystem we studied. This constitutes the strongest available evidence of a top-down cascading effect of solar variability on ecological systems at the decadal time scale and local spatial scale, which confirms results obtained at greater temporal and spatial scales. Our work provides exciting opportunities for future research on the extensively debated topic of solar variability and its impact on our planet.

Introduction

With the increasing impact of human activities on climate and ecosystems, it is of utmost importance to disentangle naturally occurring changes from human-induced changes. The clarification of the relative importance of variations in solar activity, volcanic activity and anthropogenic sources in climate forcing is of particular concern (Mann et al. 1998; Crowley 2000). Although greenhouses gases have become the dominant force explaining climate change during the twentieth century, solar activity has probably played a major role in climate forcing during pre-industrial times (Mann et al. 1998; Crowley 2000). Several studies have revealed that changes in solar activity on a time scale of centuries to millennia have had significant impacts on the climate of different regions (Verschuren et al. 2000; Bond et al. 2001; Hodell et al. 2001), with probably a cascading effect on human cultural development (Verschuren et al. 2000; Hodell et al. 2001). On the time scale of the 11-year and 22-year solar cycles, there is also growing evidence of a possible link between solar variability and climate, although this link remains somewhat unclear (Hoyt and Schatten 1997; Haigh 2000; Rind 2002).

As one can expect solar-induced climatic oscillations to have an effect on ecosystem functioning, ecologists have considered the possibility that the 11-year solar cycle could play a role in driving, or at least synchronizing, the well known decadal population cycle of many North American mammal species (Elton 1924; Sinclair et al. 1993; Krebs et al. 2001). However, the “sunspot hypothesis” was rejected on several occasions (MacLulich 1937, Elton and Nicholson 1942, Moran 1949, 1953*a*, 1953*b*, Royama 1992, Lindstrom et al. 1996).

Nevertheless, the possibility of a link between the solar cycle and animal population dynamics has not lost its appeal in recent times. Using browsing stress marks produced in the tree rings of white spruce (*Picea glauca*) by snowshoe hare (*Lepus americanus*), Sinclair et al. (1993) reconstructed past fluctuations in hare abundance at Kluane, southwest Yukon, back to 1751. Analysis of this tree-ring data, as well as fur trading records, revealed that during periods when the amplitude of the 11-year sunspot cycle was particularly high (1751-1787, 1838-1870 and 1948-1986), hare abundance did cycle in phase with the sunspot cycle, although it came out of phase at other times. Based on this new evidence, as well as climatic data somewhat linked with the sunspot cycle, they suggested that the snowshoe hare cycle (which is intimately linked to that of the lynx) "is modulated indirectly by solar activity through an amplified climate cycle that affects the whole boreal forest ecosystem" (Sinclair et al. 1993).

Ranta et al. (1997*b*) criticised the validity of the hypothesis presented by Sinclair et al. (1993). They argued that hare cycles in Finland are not synchronised with those in North America and that the level of synchrony between local hare populations decreases with increasing distance both in Finland and in Canada (Smith 1983). This, according to them, is contrary to what one would expect if an external factor was "setting the beat" of the hare cycle. Lindstrom et al. (1996) also rejected the possibility of a solar cycle-climate-hare-lynx causal relationship based on a time series analysis of the famous 1821-1934 Mackenzie River lynx fur return time series and sunspot data for the same period.

Sinclair and Gosline (1997) reanalysed the data used by Ranta et al. (1997*b*) and found that, although local hare populations are not always in phase across Canada, they do come into phase during the peak years, suggesting the influence of an external synchroniser such as weather acting on a continental scale. They maintained their hypothesis that solar activity, when it is particularly strong, acts indirectly as the synchroniser of the hare cycle through its effect on climate. They specified that since weather systems have different phase relations with solar activity in different areas of the globe, we can that solar-hare phase relations will also differ (Sinclair and Gosline 1997).

As shown above, the possibility of a link between the solar cycle, climate and animal cycles is still generating a vigorous debate, almost 80 years after it was first put forth by Elton (1924). This underscores how difficult it is to either accept or reject the hypothesis of a solar cycle – population dynamics link. This difficulty stems from at least three reasons. First, very few long time series of animal population fluctuations are available for analysis. Second, even if empirical correlations are found, testing them experimentally is virtually impossible. Third, the influence of the solar cycle seems discontinuous in time (it can disappear or even reverse phases during periods of low-amplitude solar cycles) and space (it can have different effects in different geographical areas) (Hoyt and Schatten 1997). This last obstacle is probably the most difficult to overcome, as it complicates the testing of the sunspot hypothesis.

Here we present independent evidence from a completely new system supporting the hypothesis of a link between the solar cycle, climate and the cyclical nature of some animal populations in northern ecosystems. Using feeding scars left on trees by a locally dominant mammalian herbivore, the North American porcupine, we show that porcupine abundance has fluctuated periodically since 1868 in the Bas St. Laurent region of eastern Quebec. We demonstrate a strong relationship between this porcupine cycle, fluctuations in local precipitation records, and the solar cycle. Our results suggest that the solar cycle can have sufficiently important impacts on the climate of certain areas to indirectly set the rhythm of animal population fluctuations. This study is the strongest available evidence for the possibility of a top-down cascading effect of the solar cycle on ecological systems.

Methods

Porcupine feeding scars

The North American porcupine is an arboreal rodent found over most of North America. It remains active throughout the winter season. Its diet is composed of leaves, buds, and fruits of deciduous trees and forbs during summer and inner bark of trees and conifer foliage during winter (Roze 1989). Winter feeding on inner bark of trees produces characteristic and easily identifiable feeding scars (Spencer 1964; Payette 1987). Scars are oval or circular in shape, often bear teeth marks and can be found at various heights along the tree trunk, although they are often close to the ground (fig. 1). No other animal in our study sites (described below) produces comparable scars on tree trunks. Fire scars are easily distinguished from porcupine feeding scars by their elongate triangular shape with the base directly at ground level. Mechanically produced scars, such as those made by an axe or by a fallen snag rubbing against a tree trunk, are distinguishable because some wood has been worn off.

Since porcupines do not remove xylem tissue when feeding on bark, the year of scar formation can be determined with precision by counting growth rings added around the scar since its formation. We used coring to obtain samples for dating of scars. Reliability of coring as opposed to taking cross sections (Payette 1987) was verified by comparing dates obtained from cores and cross-sections of 30 scars. Cores were started in sound wood on the surface of a scar or at the edge of a scar and were taken across the entire diameter of the trunk. Since only live trees were sampled, the last growth ring located on the opposite side from the scar, together with diagnostic growth ring sequences, served as reference years for dating back to the scar. Two cores were taken per scar to ensure accurate dating. Cores were glued onto grooved plywood boards directly in the field, air-dried, and finely sanded in the laboratory. Year of scar formation was determined under a binocular lens by counting tree rings (fig. 2). Since most scars in our study sites are produced in November and December (IK, unpublished), all scars were dated as if they were produced at the end of a calendar year (November or December), in the same year as the preceding growing season.

Porcupines are the dominant herbivore in our study area (DB, unpublished). During the winter, they feed extensively on the bark of several tree species: white birch (*Betula papyrifera*), larch (*Larix laricina*), balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), jack pine (*Pinus banksiana*), red pine (*Pinus resinosa*) and white pine (*Pinus strobus*). Scars on jack pine are best suited to obtain a long-term index of porcupine activity for four reasons: 1) dating of scars is accurate due to clearly visible growth rings and presence of diagnostic ring sequences; 2) jack pine resin efficiently preserves scars from rot and weathering 3) rate of scar closure is very slow, with scars usually remaining visible for over a century; 4) two even-aged and almost pure jack pine stands were over a century old in our study area and a third one was only slightly younger, which allowed us to reconstruct long time series of past porcupine activity.

Scars were sampled in the three oldest jack pine stands in the Bas St. Laurent region of eastern Quebec (fig. 3). All stands were located on dry, rocky hills within 1 km of the St. Lawrence estuary. The area surrounding the stands was composed primarily of mixed forest dominated by balsam fir and trembling aspen (*Populus tremuloides*).

Stands 1 and 2 were 3 km apart and stand 3 was 17 km from stand 1 and 15 km from stand 2 (fig. 3). Our ongoing study of a tagged population of over 100 porcupines 3 km east of stand 1 suggests that individual dispersal movements are short and that there is probably little exchange of individuals between our sites (DB, unpublished). The main predator of porcupines in the study area, the fisher (*Martes pennanti*), may however travel over long distances in short periods of time (Powell 1982), so we treat our study sites as pseudo-replicates rather than true replicates.

Stand 1 (48°21’30”N; 68°48’30”W) had an area of 14 ha and was even-aged, composed mostly of 117-year old jack pine (unimodal age distribution centered around 117 years of age), although some trees were up to 150-year old and had porcupine feeding scars up to 133 years old. Scars were sampled within 29 circular 400 m^2 plots located at 25 m intervals along a transect running through the entire jack pine stand. Within the plots, all jack pines were inspected for presence of scars and all scars found on the trunks between 0 and 1.8 m off the ground were cored (n = 575). Of these, 501 scars located on 357 trees were dated with accuracy and used for analysis. Stand 2 (48°20’30”N; 68°49’30”W) had an area of 5 ha and was even-aged, composed mostly of 105-year old jack pine (unimodal age distribution centered around 105 years of age). Because of the relative scarcity of scars, all jack pines in stand 2 were inspected and all scars found on the trunks between 0 and 1.8 m off the ground were cored (n = 519). Of these, 487 scars located on 369 trees were dated with accuracy and used for analysis. Stand 3 (48°15’30”N; 68°59’30”W) had an area of 2 ha and was also even-aged, composed mostly of 77-year old jack pine (unimodal age distribution centered around 77 years of age). All jack pines in the stand were inspected and all scars found on the trunk between 0 and 1.8 m off the ground were cored (n = 373). Of these, 302 scars located on 206 trees were dated with accuracy and used for analysis. All raw data are available for consultation at http://www.------------ (address available after acceptation of manuscript).

The frequency distribution of the number of feeding scars per year was computed for each site. This frequency distribution has been shown to be a good indicator of relative porcupine abundance (Spencer 1964). This is similar to the relationship between feeding scars on willow (*Salix spp.*) stems and vole (*Microtus agrestis* and *Clethrionomys glareolus*) abundance (Danell et al. 1981), between feeding scars on willow stems and lemming (*Lemmus sibiricus* and *Dicrostonyx groenlandicus*) abundance both in Eurasia and Arctic North America (Danell et al. 1999; Erlinge et al. 1999; Predavec et al. 2001), between dark stress marks in the rings of browsed white spruce and snowshoe hare abundance (Sinclair et al. 1993) and between trampling scars on roots and caribou (*Rangifer tarandus*) activity (Morneau and Payette 1998, 2000). Non-systematic interviews with past and present residents and users of the study area also confirmed the close link between fluctuations in porcupine abundance and our scar data.

When two or more scars of the same age were found on the same tree (5.3% of cases), only one of them was considered in a preliminary analysis. However, this decision did not affect the results, so we included all scars in our final analyses. Some authors considered temporal changes in the availability of trees (based on age distribution of trees) when reconstructing past animal activity from tree-ring data (Sinclair et al. 1993; Morneau and Payette 1998, 2000). We did not do so because the trees sampled were mostly even-aged jack pine.

Since our study sites should be considered as pseudo-replicates rather than true replicates, the average number of scars per year for all sites was also calculated, after weighing data from each site according to sampling effort (weight used for a given site = mean number of scars per year at this site / average number of scars per year for all sites). Given the varying length of the time series, the average number of scars per year for all sites is based on data from the three sites for the period 1944-2000, and from sites 1 and 2 for 1906-1943. Only data from site 1 were available for 1868-1905.

Solar activity data

We used the sunspot number, which is a count of the number of dark spots observed on the surface of the sun, as a proxy of solar activity for the period 1868-2000. Data were obtained from the World Data Center for the Sunspot Index (2001). The sunspot number is the most often used proxy of solar activity at the decade to century time scale since it has been recorded since about 1600, with an accurate record existing since 1848 (Hoyt and Schatten 1997). It must not be forgotten, however, that the sunspot cycle is but one manifestation of a complex 22-year magnetic cycle (the Hale cycle) consisting of two 11-year phases with reversed polarities, during which the sun's output of visible and ultraviolet light, X-rays and cosmic rays varies (Foukal 1990; Hoyt and Schatten 1997; Storini and Sykora 1997; Mursula et al. 2001).

Climatic data

We obtained monthly temperature and precipitation records from the Meteorological Service of Canada (2000) for the two weather stations closest to our study sites. The Trois-Pistoles station (48°09'N, 69°07'W, mean distance from study sites = 25 km), provided data for 1951-2000. The Pointe-au-Père station (48°30'N, 68°29'W, mean distance from study sites = 35 km) provided data for 1877-1951. Since there was no station in the vicinity of our study sites with a complete record for the entire period, the data from the two stations were spliced together (Pointe-au-Père, 1877-1951; Trois-Pistoles, 1952-2000) to form a continuous 1877-2000 time series. Mean temperature and total precipitation were calculated from the monthly data, for the following four periods of each year:

- November to April inclusive (hereafter referred to as winter), which corresponds to the period during which vegetation is dormant in our study area and porcupines feed only on tree bark and conifer foliage. During this period, porcupines loose mass and mortality from starvation and predation is highest (DB, unpublished). In addition to mean winter temperature and total precipitation, we also calculated total snowfall.

Although snow penetrability may be more relevant to porcupine winter ecology, only snowfall data was available. We assigned to each winter the year of the corresponding month of January. This way, the number of scars in a given year is an indicator of porcupine abundance after the winter (and summer).

- May to October inclusive (hereafter referred to as summer), which corresponds to the period during which porcupines gain mass while feeding on leaves, buds and fruits of deciduous trees and forbs (DB, unpublished).
- May and June (hereafter referred to as spring), which is the period when climate can be expected to have the greatest influence on survival of newborn porcupines, most of them being born in mid-May in our study area (DB, unpublished).
- Over the entire year, winter and summer periods combined (from November to October). To ensure that results were not dependant on the choice of the annual period, mean temperature and total precipitation was also calculated for the January to December period, but this did not affect our results.

In addition to these climatic variables, we used the North Atlantic Oscillation (NAO) index as a measure of global climatic variations, both for annual and winter periods as defined by Hurrell (1995). NAO index data were obtained from the Climatic Research Unit (2001).

Tree growth data

We measured yearly increments of radial tree growth for jack pines at site 1 for the period 1868-2000 to detect a possible effect of the solar cycle on tree growth. This served to establish whether effect of the solar cycle could be felt in vegetation productivity. Eleven-year periodicities related to the solar cycle have been found in tree-ring chronologies from all continents (Currie 1991*a*, 1991*b*; Mori 1981; Dutilleul and Till 1992). Cross-sections were cut at about 1 m aboveground from 32 live jack pine at site 1 that had no sign of porcupine feeding scars. For each cross-section, ring widths were measured along 2 opposing radii using a MacDendro system version 5.1 (Regent Instruments Inc., Quebec). All ring-width chronologies were then averaged. Cross-dating was not necessary as several easily recognizable tree-ring sequences were present in all cross-sections, ensuring accuracy of dating.

Statistics

All time series had to be treated to control for both short-term (1-2 years) and long-term (> 30 years) variability in order to isolate the medium-term variability, which was of interest here. Furthermore, the statistical methods used for periodicity analysis required data to be second-order stationary, meaning that the local mean and variance had to be relatively stable over the entire length of each series (Chatfield 1989; Legendre and Legendre 2000). As a result, preliminary data treatment involved three steps which were applied identically to all time series (porcupine scar data, sunspot data, climatic data and tree growth data). First, to remove short-term variability, all time series were smoothed using a 3-year moving average. Second, to stabilize the variance, all time series were log-transformed after the addition of 1 to all values (in the case of NAO and mean winter temperature data, an addition of 3 and 10, respectively, were needed to avoid null or negative values). Third, to stabilize the mean, each value in a series was divided by the mean within a 31-yr mobile window centered around the value of interest. The 15 values at both ends of a series were divided by the mean of the first or last 31 values in the series (the window was locked in place). This method proved to be much better at rendering our data stationary than commonly used analytical methods of detrending, such as using the residuals of a linear or polynomial regression. Also, it produced a series of relative values in reference to surrounding values, which is more pertinent for the analysis of recurrent fluctuations than absolute values. A 30-yr window is commonly used as a reference for calculating climatic anomalies (Hoyt and Schatten 1997). We used a 31-yr, rather than a 30-yr window so it could be centered around individual values. To ensure that data treatment itself was not responsible for generating a periodic signal, we tried windows of various lengths, ranging from 15 to 55 years, and obtained identical periodicities regardless of window length. However, a 31-yr window proved best suited to our data since shorter windows somewhat dampened a 22-yr cycle present in our data, while longer windows were unsuccessful at stabilizing series towards their ends, which was particularly problematic for shorter series (e.g. scar data at site 3).

Treated time series were analyzed using autocorrelation to detect the main periodic components in each series. To assess the significance of periodic signals with a period *T*, we used the P = 0.05 Bartlett band (Chatfield 1989; Wei 1990), as well as the periodic recurrence of this signal at interval *T* in the autocorrelograms. Cross correlations were then used to assess possible relationships between series with similar periodicities, with the significance level calculated in the same way as for the autocorrelations.

A significant cross correlation should not be used to draw final conclusions as to possible links between two time series because spuriously significant results can occur between two unrelated periodic functions if they have a sufficiently similar period (Sinclair et al. 1993; Sinclair and Gosline 1997). In addition to the cross correlations, we therefore used the method of phase shift analysis described by Sinclair et al. (1993) to assess possible relationships between series. With this method, instead of calculating cross correlations using the entire data set, cross correlations are calculated for short blocks of data along the entire data set in order to establish how the phase difference (or lag) between the two periodic phenomena evolves. If both periodic phenomena follow each other with the same lag throughout the series, which would be expected in the case of a causal relationship, the phase difference will remain constant (phase shift curve relatively flat). On the other hand, if the two phenomena are unrelated, the phase difference will drift or jump. This analysis is the definitive test to confirm that animal populations or climate data are linked to the solar cycle (Sinclair and Gosline 1997). To perform our phase shift analysis, we used a 30-year window which we gradually moved along the entire data series with 1-year increments. For each 30-year block of data, we performed cross correlations using lags between –15 and 15 years (although they do not make biological sense, negative lags were also used here, as the objective was only to assess phase relations between two periodic series). We recorded the lag for which the cross correlation coefficient was equal to zero (r = 0) and plotted this value in reference to the last year in the block of data. This was better than recording the maximal cross correlation coefficient because for r = 0 the curve is steep and the lag can be determined with decimal precision using interpolation.

Results

Porcupine feeding scars

The frequency of scars fluctuated synchronously among the three sites with a recurrent periodic signal composed of a major peak followed by a minor peak about every two decades (fig. 4a-c), with the exception of the 1995 peak at site 1 which was of similar amplitude as the preceding peak in 1987 (fig. 4a). The autocorrelogram for the site 1 scar data (fig. 5a) displays highly significant ($P < 0.001$) peaks at 22 and 44 years and minor non-significant, yet obvious, peaks at 10 and 33 years, implying a dominant periodic signal of about 22 years superimposed with a periodic signal of about 10-11 years of lesser amplitude and regularity. The autocorrelogram for the site 2 data (fig. 5b) shows only peaks at 21-22 years and 42 years, implying a periodic signal of about 21 years. However, as in site 1, minor peaks do occur between the major 21-year peaks at site 2 (fig. 4b), but are relatively unimportant and too irregularly spaced to appear in the autocorrelogram (fig. 5b). At site 3, despite the short length of the time series, there is also a significant ($P < 0.05$) periodicity of 22 years (fig. 5c), as well as an indication of a superimposed periodicity of 10-11 years of lesser amplitude and regularity. When data from all sites are pooled, the treated data (fig. 4d) and the autocorrelogram (fig. 5d) reveal the same patterns found at individual sites, with a highly significant 22-year periodicity ($P < 0.001$) (fig. 5d). This confirms synchrony of the porcupine abundance cycle among sites.

Relationship between porcupine feeding scars and the solar cycle

The sunspot number displays a highly significant ($P < 0.001$) periodic signal of about 10.8 years for 1868-2000 (fig. 6), commonly referred to as the 11-year sunspot cycle. Mursula et al. (2001) have shown that the underlying 22-year solar magnetic cycle, which consists of two 11-year phases with reversed polarities and is visible in many solar phenomena, is also present in the entire 400-year long sunspot record, but represents only about 10% of the amplitude of the 11-year cycle and is therefore not obvious. This 22-

year cycle is empirically visible in the sunspot data in the form of the Gnevyshev and Ohl rule (Storini and Sykora 1997; Mursula et al. 2001) stating that every second peak is of slightly greater amplitude and is preceded by a peak of slightly lesser amplitude (fig. 6a, b). The alternation of major and minor peaks in the sunspot data is not perfect because of the superimposed long-term changes in the amplitude of 11-year peaks (Mursula et al. 2001). The third step of our data treatment (division by the mean in a 31-yr surrounding window) somewhat removes this long-term change, but is offset by the log-transformation which reduces the variation in amplitude of peaks (fig. 6a, b). It must not be forgotten that although in our analyses we used sunspot data as a measure of solar variability, it is nevertheless possible that the 22-year periodicity is more pronounced relative to the 11-year periodicity in some other manifestation of the Hale solar magnetic cycle which could have an effect on earth, but for which there is no long-term record.

The relationship between the 11-year and 22-year cycles in our porcupine scar data and the 11-year and 22-year cycles in solar activity is striking. Major peaks in scar data (treated data, all sites pooled together) occur in 1876, 1899, 1922, 1943, 1963, and 1987 (fig. 4d) following major peaks in sunspot number (treated data) in 1871, 1893, 1917, 1938, 1958, and 1980 (fig. 6b) by 5, 6, 5, 5, 5, and 7 years respectively (compare fig. 4d and fig. 6b). Minor peaks in scar data occur in 1886, 1909, 1931, 1954, 1972, and 1995 (fig. 4d) following minor peaks in sunspot number in 1883, 1906, 1927, 1948, 1969, and 1990 (fig. 6b) by 3, 3, 4, 6, 3, and 5 years respectively (compare fig. 4d and fig. 6b). All 12 porcupine peaks, whether minor or major, occur 3-7 years after a solar peak, even though there are 11 possible yearly lags. If porcupine peaks were randomly distributed, we would expect only 5 out of 12 peaks to occur 3-7 years after a solar peak. The observed distribution of porcupine peaks is significantly different from this random distribution ($\chi^2 = 14.42$, $df = 1$; $P < 0.001$). The probability of all 12 peaks falling 3-7 years after a solar peak solely by chance is $(5/11)^{12}$. If we consider that there are 11 possible lag ranges (0-4 yrs, 1-5 yrs, 2-6 yrs, etc…) with which we could obtain such a close association, the probability of having such a regular lag between solar peaks and porcupine peaks is $11 \times (5/11)^{12}$ or 0.00086. In addition, the probability of having an alternation of major and minor peaks matching that of the solar cycle is $(1/2)^{12}$ or 0.00024. The combined probability of having both an alternation of major and minor peaks and a regular lag between solar peaks and porcupine peaks is $(1/2)^{12}$ x 11 x $(5/11)^{12}$ or 2 x 10^{-7}.

In addition to the 11-year and 22-year cycles, the sunspot record displays another form of variability. The actual period of the solar cycles varies, with cycles of greater amplitude having shorter periods than cycles of lesser amplitude (Friis-Christensen and Lassen 1991). The autocorrelogram of the sunspot number for 1868-1934 (first half of the 1868-2000 series) reveals a cycle period of approx. 23 years (fig. 7a), whereas for 1934-2000 the cycle period is approximately 21 years (fig. 7b). The autocorrelogram of our scar data (site 1 only, as data for sites 2 and 3 do not span the entire 1868-2000 period) also shows periods close to 23 and 21 years for 1868-1934 (fig. 7c) and 1934-2000 (fig. 7d), respectively. This demonstrates that as the solar cycle “speeds up”, the porcupine abundance cycle also speeds up.

The occurrence of very similar periodic signals in both the sunspot record and porcupine scar data is confirmed when scar data are cross correlated with the sunspot number in previous years. There is a highly significant ($P < 0.001$) positive correlation between scar data (all sites pooled together) and sunspots 4-5 years previously and a highly significant ($P < 0.001$) negative correlation between scar data and sunspots 9-10 years previously (fig. 8). Phase shift analysis shows that this relationship between scar data (at all sites separately, as well as when pooled together) and sunspots displayed a very constant phase difference (lag) throughout the entire 1868-2000 period (fig. 9). This test confirms that there is a remarkably close statistical link between the porcupine cycle and the sunspot cycle.

In order to confirm that slight changes in the period of the sunspot cycle between 1868 and 2000 are reflected in a slight change in the period of the scar data cycle, we compared the relationship we obtained between scar data and sunspots with the relationship between scar data and a sinusoidal curve with a period of 10.8 years (the mean period of the “11-year” sunspot cycle for 1868-2000). When scar data (all sites pooled together) were cross-correlated with the sinusoidal curve in previous years, the maximal correlation coefficient obtained was inferior than when scar data were cross-correlated with sunspots ($r_{\text{max sine}} = 0.38$; $r_{\text{max sunspots}} = 0.54$). Phase analysis of the scar data and the 10.8-year sinusoidal curve showed no obvious phase drift, but the range of phase differences obtained was greater than for the phase analysis of scar data and sunspots ($\text{range}_{\text{sine}}$ = 3.7 years; $\text{range}_{\text{sunspots}}$ = 2.2 years). This implies that fluctuations in scar data follow the sunspot cycle more closely than they follow a perfectly regular sinusoidal curve having a period equal to the average period of the solar cycle (10.8 years) and confirms that there is a close association between fluctuations in porcupine scar data and the solar cycle.

Climatic and tree growth data

Autocorrelation of all nine climatic variables, the two NAO indices, as well as the tree growth data, revealed that only five series, namely annual precipitation, winter precipitation, snowfall, summer temperature and spring temperature, had significant periodic components similar to those found in the scar data (in the range of 20-22 years) (fig. 10). It is noteworthy that annual precipitation had an autocorrelation structure particularly similar to that of the scar data, especially at site 1 (compare fig. 5a and fig. 10d). These five variables were therefore kept for a further analysis using cross correlations and phase shift analysis to closely examine the relationships between climatic variables and scar data and between climatic variables and sunspots. We also performed the same analyses using the annual NAO index and both scar data and sunspots to show results obtained using series with a different dominant periodic signal.

Relationship between climatic data and porcupine feeding scars

Cross correlation of scar data with the five climatic variables containing a periodic signal of 20-22 years produced significant ($P < 0.05$) positive and negative peaks spaced about 20-22 years apart for all five variables (fig. 11a-e). Scar data were negatively correlated with annual precipitation, winter precipitation and snowfall 5-6 years previously ($P < 0.001$) and with summer ($P < 0.001$) and spring ($P < 0.05$) temperature in the same year (fig. 11a-e). Scar data were also positively correlated with annual precipitation, winter precipitation and snowfall 12-13 years previously ($P < 0.001$) and with summer and spring temperature 10-11 years previously ($P < 0.01$) (fig. 11a-e), but because of the longer time lag involved (10-13 years), these relationships appear of lesser importance, especially when considered biologically. Phase shift analysis showed that scar data has been cycling in phase with annual precipitation (fig. 12a), with the exception of a short uncoupling of the relationship around 1920, displayed by a 2-year gap in the phase shift curve which occurred because there was no intercept at $r = 0$ in the cross-correlogram for the 30-yr blocks of data ending in 1919 and 1920. Interestingly, the phase relation is about the same before and after the short gap. The phase relation between scar data and winter precipitation, as well as between scar data and snowfall, also remained relatively constant, with the exception of a jump in the curve around 1984, but with the phase relation between the variables drifting back to its original value (fig. 12b, c). In contrast, the phase relation between scar data and both summer and spring temperatures did not remain constant throughout the 1877-2000 period for which we obtained data, meaning that these variables did not cycle together.

Relationship between climatic data and the solar cycle

Cross correlations of the five climatic variables of interest with sunspots in previous years produced peaks and lows spaced about 10-11 years apart for all variables (fig. 13a-e). However, strong relationships were obtained using only annual and winter precipitation, with all or almost all peaks and lows being significant ($P < 0.05$) or even highly significant ($P < 0.001$ for 8 out of 10 positive or negative peaks with annual precipitation and 3 out of 10 with winter precipitation). Annual precipitation and winter precipitation were highly correlated ($P < 0.001$) with sunspots 3-4 years previously (fig. 13a-e). Phase analysis confirmed that the strongest relationships were between sunspots and annual and winter precipitation (fig. 14a, b). The phase relation between sunspots and both annual and winter precipitation was constant throughout the period for which we obtained data (fig. 14a, b), meaning that sunspots and precipitation cycled together. This is not the case for snowfall and for summer and spring temperatures, which drift out of phase with sunspots (fig. 14c-e), implying a weak relationship between the sunspot cycle and fluctuations in summer and spring temperatures.

Discussion

A link between the solar cycle, precipitation and porcupine abundance

Our results provide five pieces of evidence for a strong relationship between the solar cycle and fluctuations in porcupine abundance, at least from the statistical point of view. First, a periodic component of about 11 years was found in both sunspots and porcupine scar data. Second, a superimposed 22-year period was also present in both sunspots and porcupine scar data. Third, slight changes in the length of the porcupine cycle mirrored slight changes in the length of the solar cycle. Fourth, porcupine scar data were highly positively correlated with sunspots 4-5 years previously and highly negatively correlated with sunspots 9-10 years previously. Fifth, when considering short 30-year windows of data, there was a constant phase relation between porcupine scar data and sunspots throughout the entire 1868-2000 time series obtained. One could add as a sixth piece of evidence the synchrony of porcupine cycles at the three study sites, supporting the hypothesis of an external factor (i.e. the solar cycle) affecting population dynamics. This point is however debatable because the three sites are not true replicates due to probable dispersal movements of predators (fishers), as well as possible porcupine dispersal.

Our results also suggest that precipitation plays a key role in linking the solar cycle and the porcupine cycle. Annual precipitation fluctuated periodically and this precipitation cycle was closely linked with both the porcupine cycle and the sunspot cycle. Annual precipitation was highly positively correlated with sunspots 3-4 years previously, while porcupine abundance was highly negatively correlated with annual precipitation 5-6 years previously. Based on these two relationships, porcupine abundance should be negatively correlated with sunspots 8-10 years previously. This is in concordance with the highly significant negative correlation we obtained between scar data and sunspots 9-10 years previously.

Summer precipitation did not fluctuate periodically, but winter precipitation followed similar fluctuations as annual precipitation. This suggests that although the link between the solar cycle, precipitation and porcupine abundance seems to depend on fluctuations in precipitation on an annual basis, winter precipitation is the primary contributor to this relationship. Although snowfall represents 70.6 % of winter precipitation in our climatic data, snowfall did not seem to follow the solar cycle as closely as winter precipitation. This may be due to records of snowfall being too imprecise as they are usually estimated based on the melted volume of water obtained (Gilles Allaire, Environment Canada, personal communication). In addition, it may be more appropriate to consider winter precipitation instead of only snowfall when attempting to understand the solar cycle – precipitation – porcupine link, as snowfall on its own may not be an adequate descriptor of winter severity for porcupines.

The strong statistical relationships between the sunspot cycle and the annual and winter precipitation cycle, between the annual and winter precipitation cycle and the porcupine cycle, and between the sunspot cycle and the porcupine cycle, as well as the overall concordance of these three relationships, represents strong evidence of a causal relationship between the solar cycle, winter precipitation and porcupine abundance.

Proposed mechanisms for the solar cycle – precipitation – porcupine link

Our results bring up questions about the mechanisms underlying both the solar cycle – precipitation link and the precipitation – porcupine population dynamics link. We can only speculate about the mechanism behind the solar cycle – precipitation link in our study system. Although there is growing evidence that variations in solar activity have effects on the earth's climate at several time scales, much about these effects remains to be understood (Rind 2002). Evidence of a solar activity – climate link appears strongest at the time scale of centuries and millennia, as suggested by both region-specific (Verschuren et al. 2000; Bond et al. 2001; Hodell et al. 2001) and planet-wide studies (Mann et al. 1998; Crowley 2000). These long-term solar-related climatic oscillations have even been shown to affect human cultural development, both in Africa (Verschuren et al. 2000) and America (Hodell et al. 2001), suggesting a cascading effect of variations in solar activity on entire ecosystems.

There is also much evidence of a solar activity – climate link at the time scale of the 11-year and 22-year solar cycles. The 11-year solar cycle signal was detected in various climatic and climate-related data - USA precipitation and temperature records, St.

Lawrence and Nile river flows, European fish catches, wine harvests and sea-levels (Currie and O'Brien 1988, 1990; Currie 1993*a*, 1993*b*, 1994). Perry (1994) found that precipitation fluctuations in certain regions of the USA were highly correlated with solar activity in previous years, while in other regions the correlation was weak or absent. This same periodicity in precipitation was detected in net snow accumulation data from a glacier in the Yukon (Sinclair et al. 1993). Variations in cloud cover over the USA were also found to be related to the solar cycle (Udelhofen and Cess 2001). The 22-year Hale solar cycle was shown to play a role in the timing and extent of drought in the USA (Mitchell et al. 1979; Stockton et al. 1983; Cook et al. 1997).

In addition to climatic responses to the solar cycle at the regional and continental scale, global planet-wide responses have also been observed. White et al. (1997) and Reid (2000), have shown that changes in solar irradiance at the scale of both the 11-year and 22-year solar cycles are reflected in the surface sea temperatures across the Pacific, Atlantic and Indian oceans. But it is perhaps the correlation found by van Loon and Labitzke (1988, 1998, 2000) between the solar cycle and the temperatures and heights of the stratosphere at 30hPa and below that is the most well-known and striking evidence of a solar cycle – climate link (Kerr 1987, 1988, 1990; Haigh 2000). Modeling studies of the earth's climate (Haigh 1996, 1999; Shindell et al. 1999) corroborate some of the empirical evidence of a solar cycle – climate link. However, in many cases, the observed climatic response is much greater than what can be expected based on the fact that solar irradiance varies by only 0.1 % from the minimum to the maximum of an 11-year cycle. This raises serious questions about the underlying physical mechanisms and suggests the existence of amplifying mechanisms (Friis-Christensen 2000; Haigh 2000; Rind 2002). Also, the effect of the solar cycle is not felt in the same way and with the same intensity in different regions of our planet and our limited knowledge of our planet's climate does not allow us to understand these regional discrepancies (Hoyt and Schatten 1997; Rind 2002).

In the case of our study system, it appears that the observed link between the solar cycle and precipitation is relatively localized, as precipitation data from more distant weather stations (Quebec City, 250 km southwest of our study area; Cap Madeleine, 300 km east of our study area; Magdalen Islands, 600 km east of our study area) did not display the same regular 11-year and 22-year cycles. This is similar to the localized correlations that Perry (1994) found between precipitation fluctuations and the solar cycle in certain regions of the USA. Perry (1994) proposed that this pattern is a result of solar energy being stored in ocean water and transported by currents to certain regions where it is released, affecting regional climate. Such a mechanism may very well apply to our study system, as waters of the adjacent St. Lawrence estuary are known to warm up substantially during the summer from solar radiation (White and Johns 1997). Although solar irradiance varies by only about 0.1 % from a solar minimum to a maximum (Haigh 2000), storage of this energy over one or several summers of high solar activity and over the whole St. Lawrence estuary, combined with its localized release in winter, could serve as an amplification mechanism allowing local climate to strongly respond to variations in solar activity. This would be in agreement with White et al. (1997), who found that excess heat in years of high solar activity is stored in the upper 100 m of the ocean and is eventually released to the atmosphere, and not to the deep ocean. At present, we do not have sufficiently long time series of water temperature for the St. Lawrence estuary to verify this. However, this mechanism could be tested with similar bodies of water for which data exists and should be considered seriously when trying to understand solar cycle – climate links, as oceans cover 70 % of our planet and are largely responsible for the transport of heat from low to middle and high latitudes, particularly during the winter season Reid (2000).

The mechanism underlying the link between precipitation and porcupine population dynamics also remains to be understood, although it appears more straightforward and easier to test. Our results strongly suggest that precipitation, particularly during the winter, plays a key role in the population dynamics of porcupines. This hypothesis is in agreement with our present knowledge of porcupine biology. First, winter precipitation greatly reduces the mobility of porcupines, and therefore their access to food (Roze 1989). Second, porcupine mortality in our study area is greatest during winter, with individuals frequently dying from starvation (DB, unpublished). Third, it is likely that stressful winter conditions negatively impact porcupine reproductive success, as is the case with other mammalian herbivores (Post et al. 1997; Forchhammer et al. 2001). Fourth, based on trapping records, there is no indication that populations of the fisher, the main predator of the porcupine, would be cyclic in eastern Quebec (Pelletier and Lafond 1989). Winter precipitation is therefore likely to affect both birth and death rates of porcupines in our study system.

However, it would be naive to conclude that the solar-induced precipitation cycle itself causes the porcupine population cycle. Rather, we suggest that density-dependent factors alone are enough to generate porcupine population fluctuations, but that a density-independent climatic factor may act as a perturbation, “setting the beat” of these fluctuations. We therefore propose that, in our study system, solar-induced periodic fluctuations in winter precipitation set the beat of porcupine population fluctuations through their recurrent perturbing influence on survival and reproductive success.

Previous data on porcupine population fluctuations in other locations, although very scarce, support the idea that this species undergoes fluctuations in abundance, but that these are not necessarily periodic. Keith and Cary (1991) reported a 5-fold difference between extremes in porcupine abundance based on 11 years of capture data in Alberta, but their data do not suggest that this population fluctuated periodically. Spencer (1964) obtained 80 years of porcupine scar data in Colorado, and although he identified 3 peaks in porcupine abundance, these did not seem regularly spaced and were not related to our data nor to the solar cycle. Payette (1987) used porcupine feeding scars as an indicator of past porcupine presence along the Hudson Bay coast of Quebec, but found no periodicity in his results. It therefore appears that the periodicity of porcupine fluctuations found in our study system is not widespread, but may only exist in certain locations in which there is a strong influence of the solar cycle on climate, which is consistent with the spatially discontinuous nature of the relationship between the solar cycle and regional climate (Perry 1994; Hoyt and Schatten 1997).

It has been shown that climatic perturbations can set the beat and synchronize the dynamics of distinct populations in a variety of taxa, such as mammals (Ranta et al. 1997*a*), birds (Cattadori et al. 2000), reptiles (Chaloupka 2001) and insects (Liebhold and Kamata 2000). At present, there are only two examples of a solar-induced climatic oscillations setting the beat of animal population dynamics. Sinclair et al. (1993) proposed a similar explanation to ours for the snowshoe hare cycle, but it remains controversial (Ranta et al. 1997*b*) and the association between the two cycles is discontinuous in time (see results presented by Sinclair et al. (1993)). A similar hypothesis was also put forth to explain synchrony and periodicity of insect outbreaks, but the empirical evidence was not strong enough to conclude to a strong relationship (Myers 1998; Ruohomaki et al. 2000). Our results appear unique in that they are the first example of a population cycle that follows both the solar cycle and precipitation fluctuations with such regularity and consistency over an extended period of time (130 years). Elton (1924) may therefore not have been completely wrong when he suggested that animal cycles are an effect of a periodically recurring climatic factor possibly linked to the solar cycle.

Solar-cycle driven climatic and ecological oscillations

It is now well established that global climatic oscillations, such as the North Atlantic Oscillation (NAO) and El Nino Southern Oscillation (ENSO), can affect not only the population dynamics of mammalian herbivores (Post et al. 1997; Lima et al. 1999; Forchhammer et al. 2001), but also entire ecosystems (Jaksic 2001; Ottersen et al. 2001; Blenckner and Hillebrand 2002). Similarly, we hypothesize that the climate of certain regions (such as the area surrounding the St. Lawrence estuary) responds particularly well to decadal variations in solar activity and that this solar-induced climatic oscillation has cascading effects on entire ecosystems. Our new finding of a link between the solar cycle and fluctuations in the abundance of the dominant mammalian herbivore in a forest ecosystem would therefore be just an example of a more global phenomenon.

Such a hypothesis raises questions about the approach which should be used to test it. Holling and Allen (2002) recently summarized what we think is the best avenue to progress in such complex, multi-system and multi-scale science. They proposed that to distinguish credible from incredible patterns in nature, a cycle of inquiry (called "adaptive inference") is the most likely to lead to progress. In this cycle, no unambiguous test can distinguish among alternative hypotheses. Only a suite of tests of different kinds can do so, producing a body of evidence in support of one line of argument and not others. This contrasts with strong inference (Platt 1964), which is based on hypothesis falsification and where the main objective is to avoid type I error. Research on both the multi-year population cycles of northern mammals and the effects of solar variability on climate and ecosystems is likely to benefit from the use of adaptive inference in addition to strong inference.

Acknowledgements

We thank P. Morin and C. Daguerre for assistance with field work and B. Côté for his help with the tree growth measurements. P. Morin was also very helpful for his comments on the manuscript. Parc National du Bic provided facilities. Research was supported by a scholarship from the Natural Sciences and Engineering Research Council of Canada (NSERC) to I. Klvana and by grants from the Natural Sciences and Engineering Research Council of Canada (NSERC) and the Fonds de Recherche sur la Nature et les Technologies du Québec (NATEQ) to D. Berteaux.

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Figure 1: Photograph of a jack pine trunk showing a porcupine scar being cored.

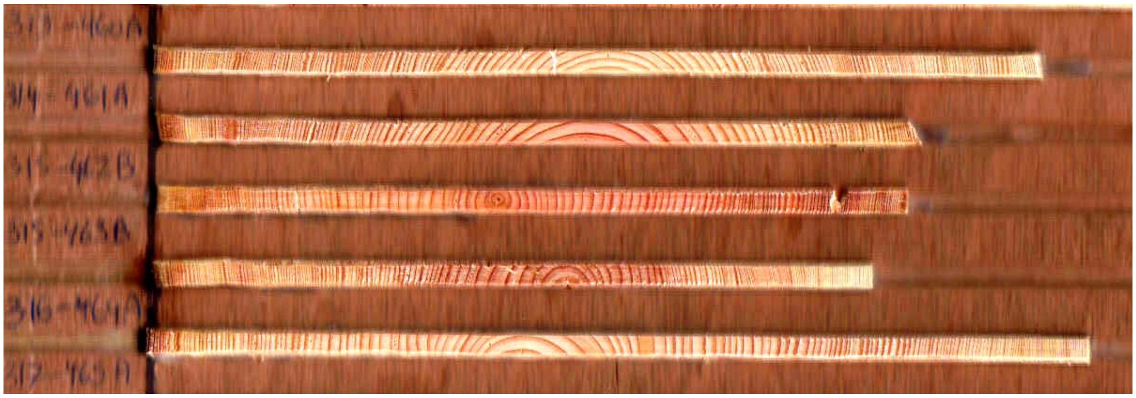

Figure 2: Photograph of mounted cores used for dating of porcupine feeding scars. The scar ends are on the left side and the live ends are on the right side; (a) number of rings added between the center (or approximate center) of the tree and the scar; (b) number of rings added between the center of the tree and year of sampling (in the case of live trees). The age of the scar is obtained by subtracting (a) from (b).

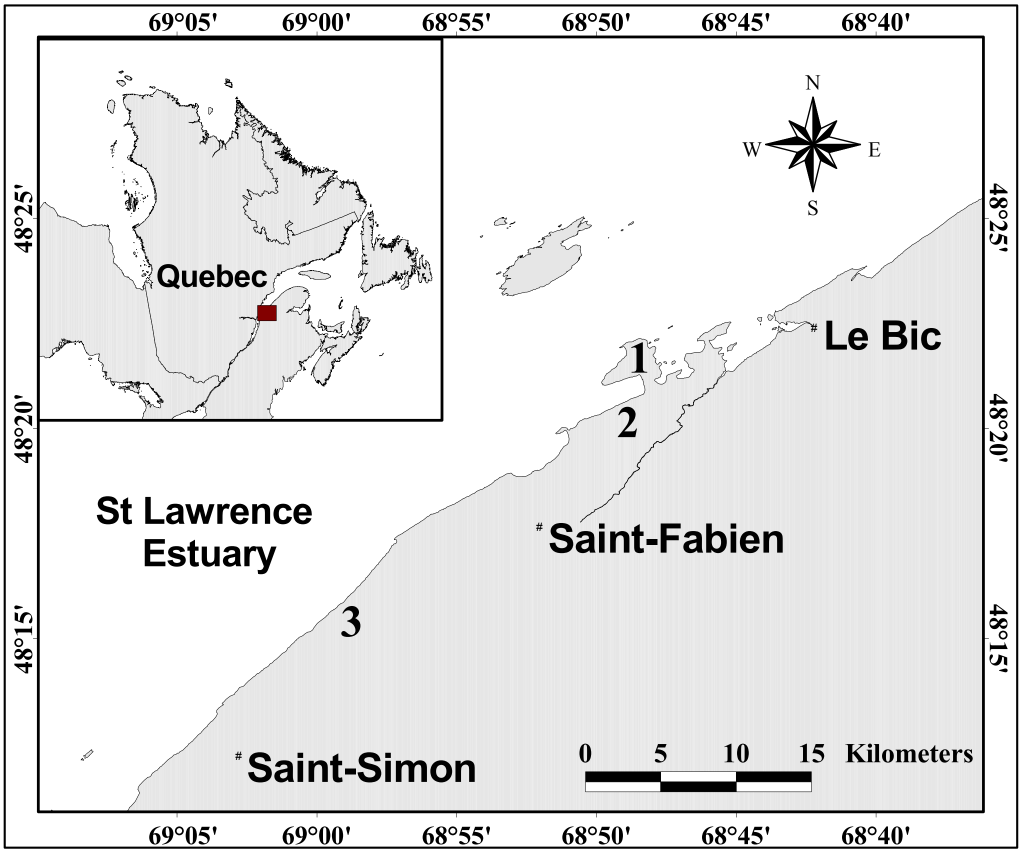

Figure 3: Map showing the location of the three jack pine stands (labeled 1, 2 and 3) in which porcupine feeding scars were sampled.

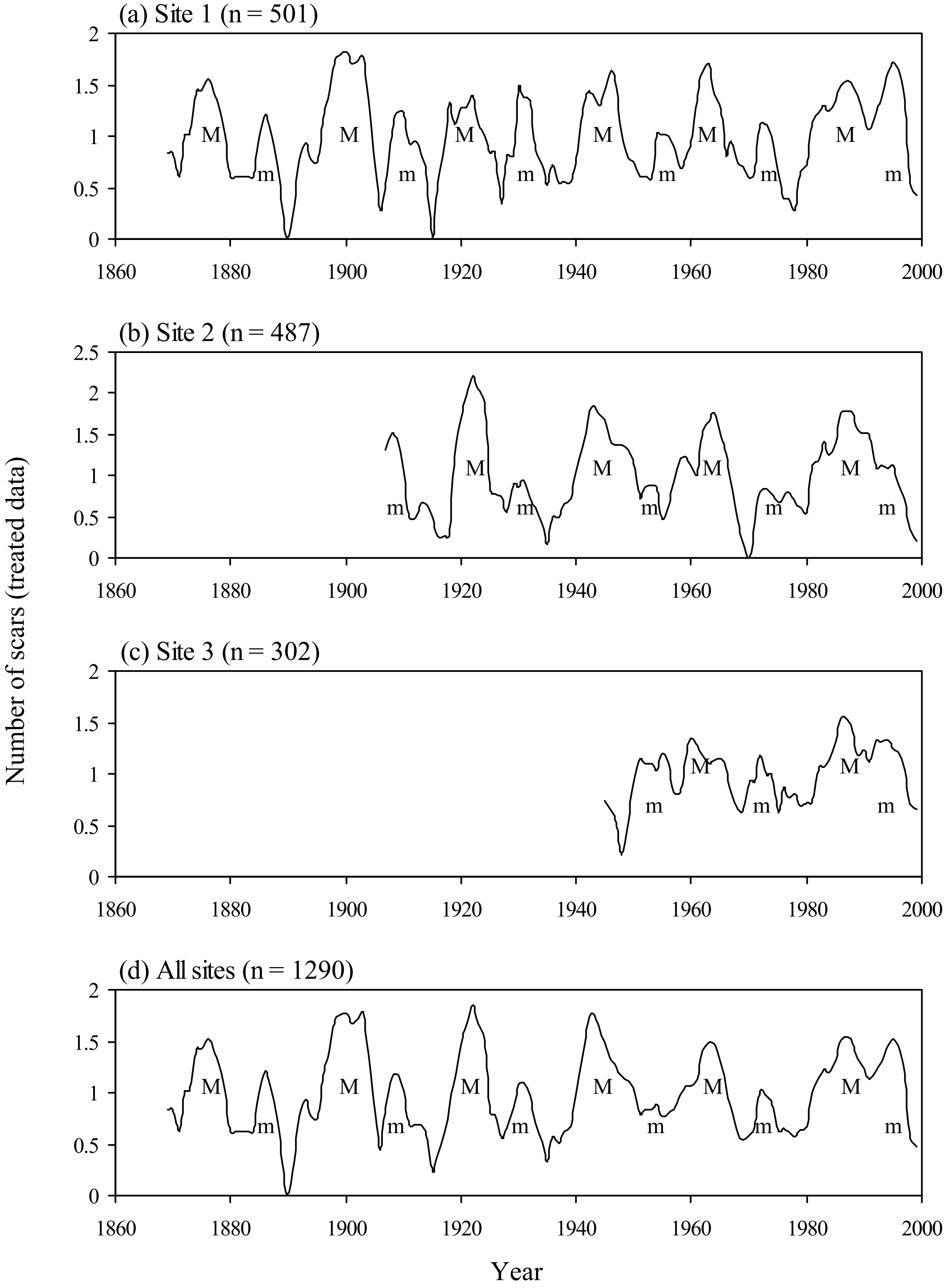

Figure 4: Yearly frequency distribution of porcupine feeding scars (treated data – see methods) from 3 study sites in eastern Quebec, Canada. Results shown separately for each site (a-c) and for all sites pooled together (d). M: major peak; m: minor peak.

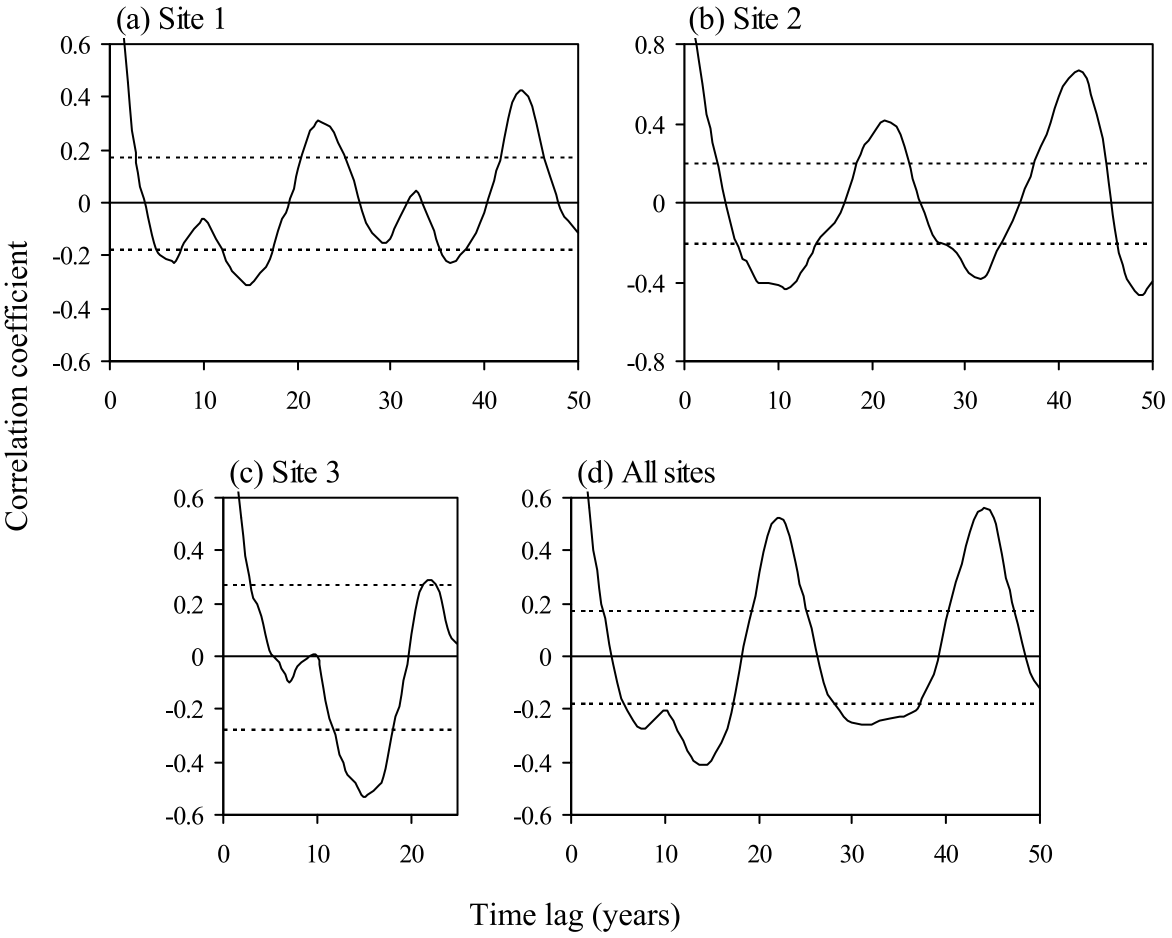

Figure 5: Autocorrelation of porcupine feeding scar data from 3 study sites in eastern Quebec, Canada. Results shown separately for each site (a-c) and for all sites pooled together (d). Broken lines show the 5 % probability Bartlett band.

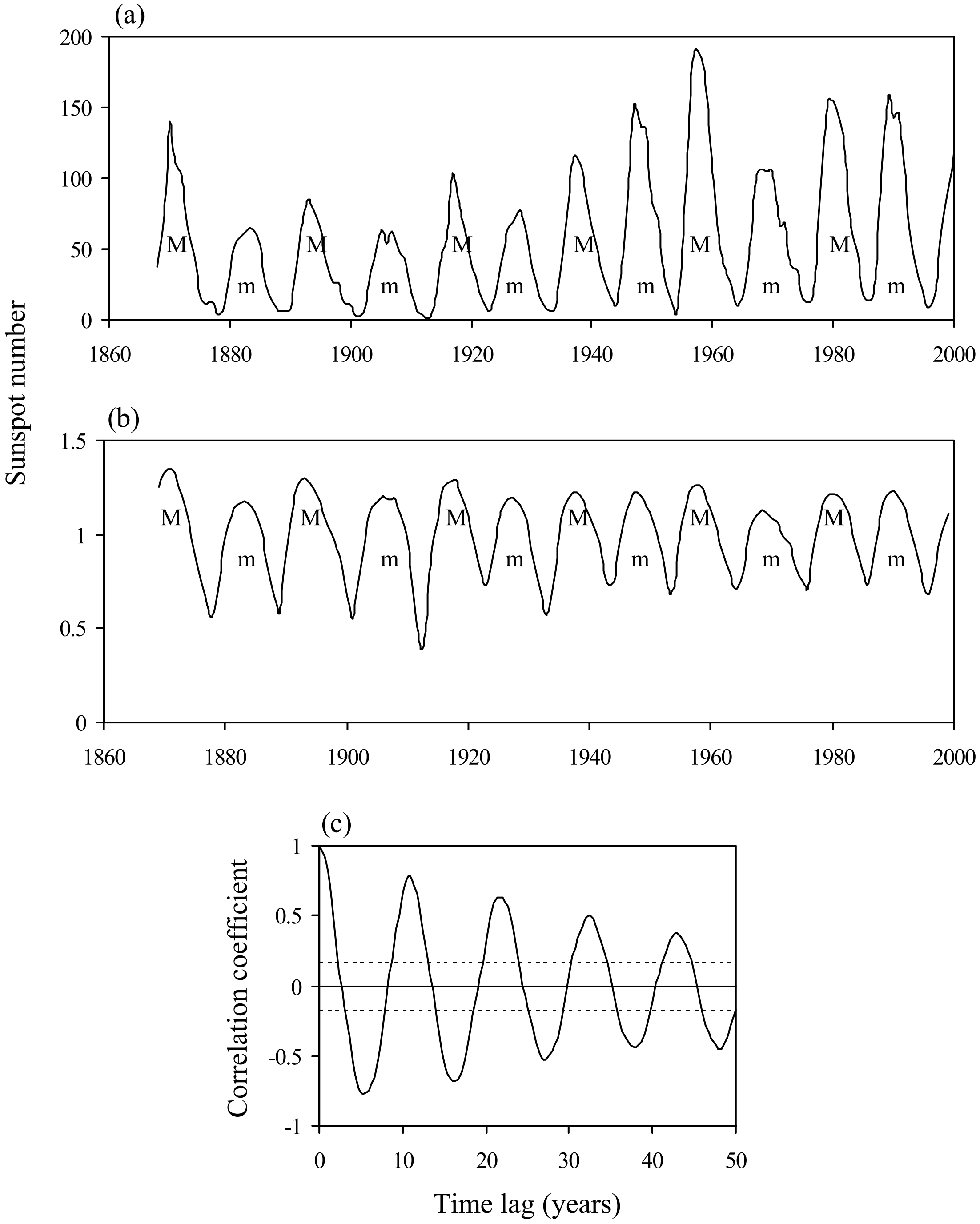

Figure 6: Sunspot number; (a) raw data; (b) treated data (see methods); M: major peak; m: minor peak. (c) autocorrelation of (b); broken lines show the 5 % probability Bartlett band.

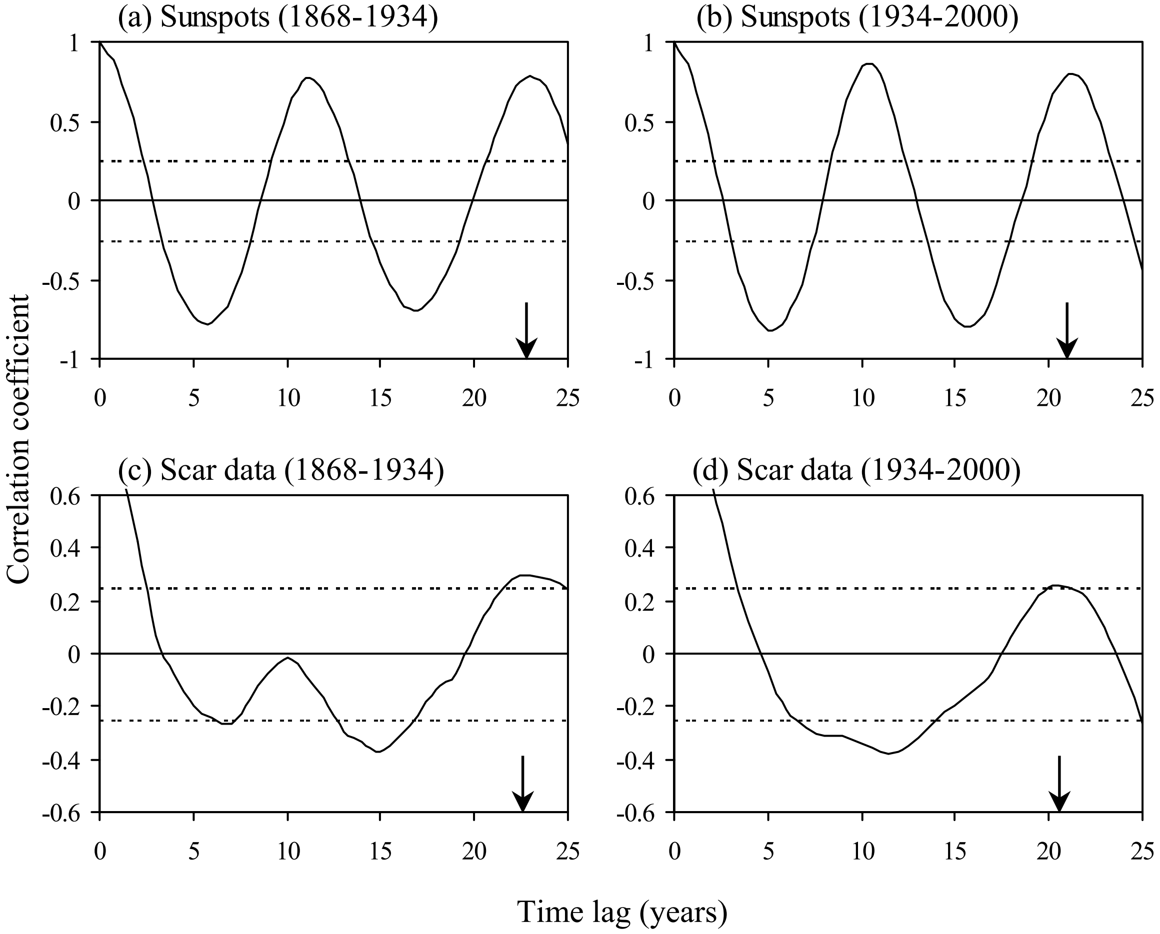

Figure 7: Autocorrelation of (a) sunspots for 1868-1934; (b) sunspots for 1934-2000; (c) site 1 scar data for 1868-1934; (d) site 1 scar data for 1934-2000. Broken lines show the 5 % probability Bartlett band. Arrows indicate time lags corresponding to significant positive peaks of autocorrelation in the 20-25 years lag range to show the close correspondence between sunspots and scar data.

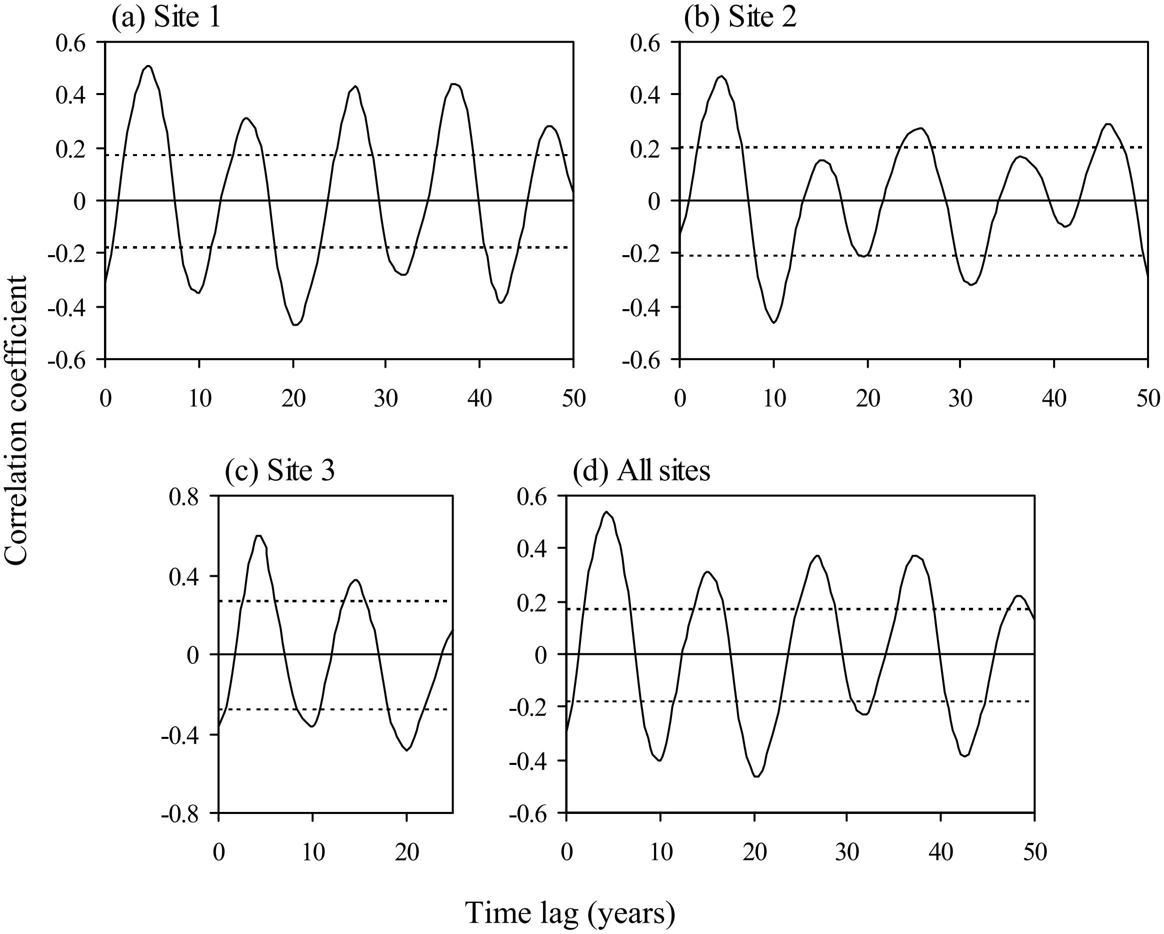

Figure 8: Cross correlation of scar data with sunspots in previous years. Results shown separately for each site (a-c) and for all sites pooled together (d). Broken lines show the 5 % probability Bartlett band.

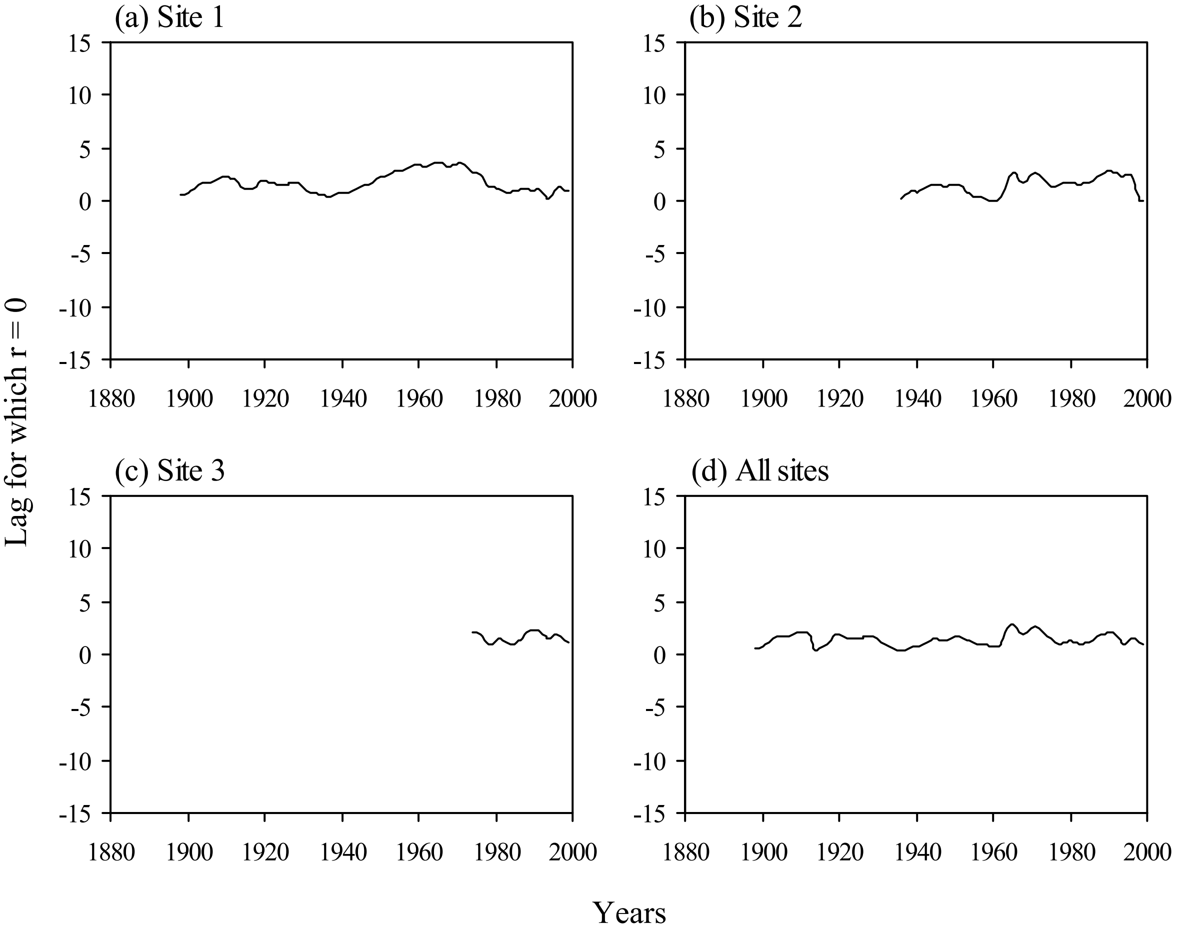

Figure 9: Phase shift analysis of the relationship between scar data and sunspots. Results shown separately for each site (a-c) and for all sites pooled together (d). For each 30-year block of data, the lag for which the cross correlation coefficient is equal to zero (r = 0) is plotted in reference to the last year in the data block – see methods for details.

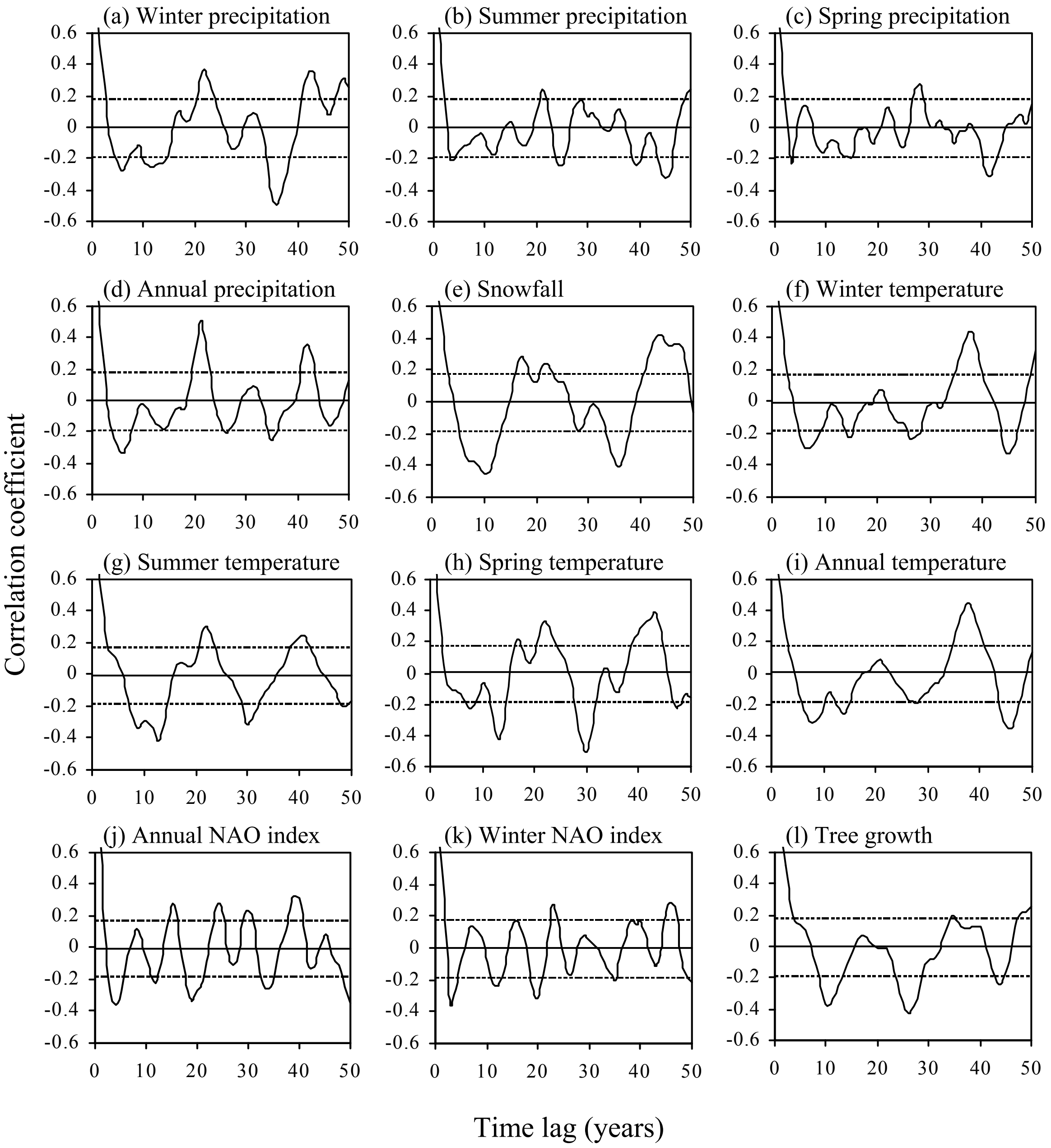

Figure 10: Autocorrelation of climatic data recorded at Pointe-au-Père (1877-1951) and Trois-Pistoles (1952-2000) (both data sets spliced together), eastern Quebec, Canada (a-k) and tree growth data (l). Broken lines show the 5 % probability Bartlett band.

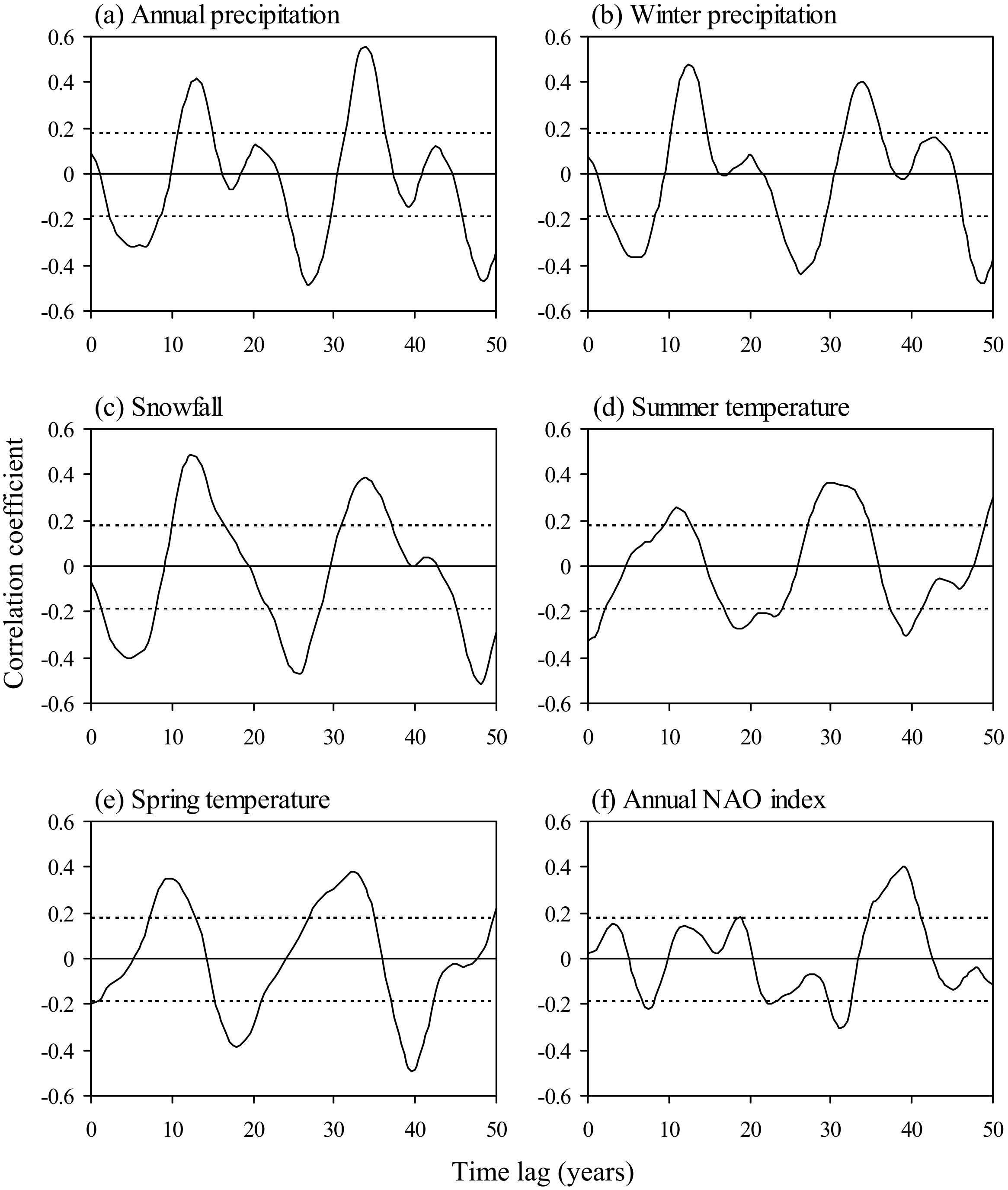

Figure 11: Cross correlation of scar data with climatic data in previous years (a-e). Cross correlation of scar data with annual NAO index in previous years (f) shown as an example of two variables with fluctuations of different periodicities. Broken lines show the 5 % probability Bartlett band.

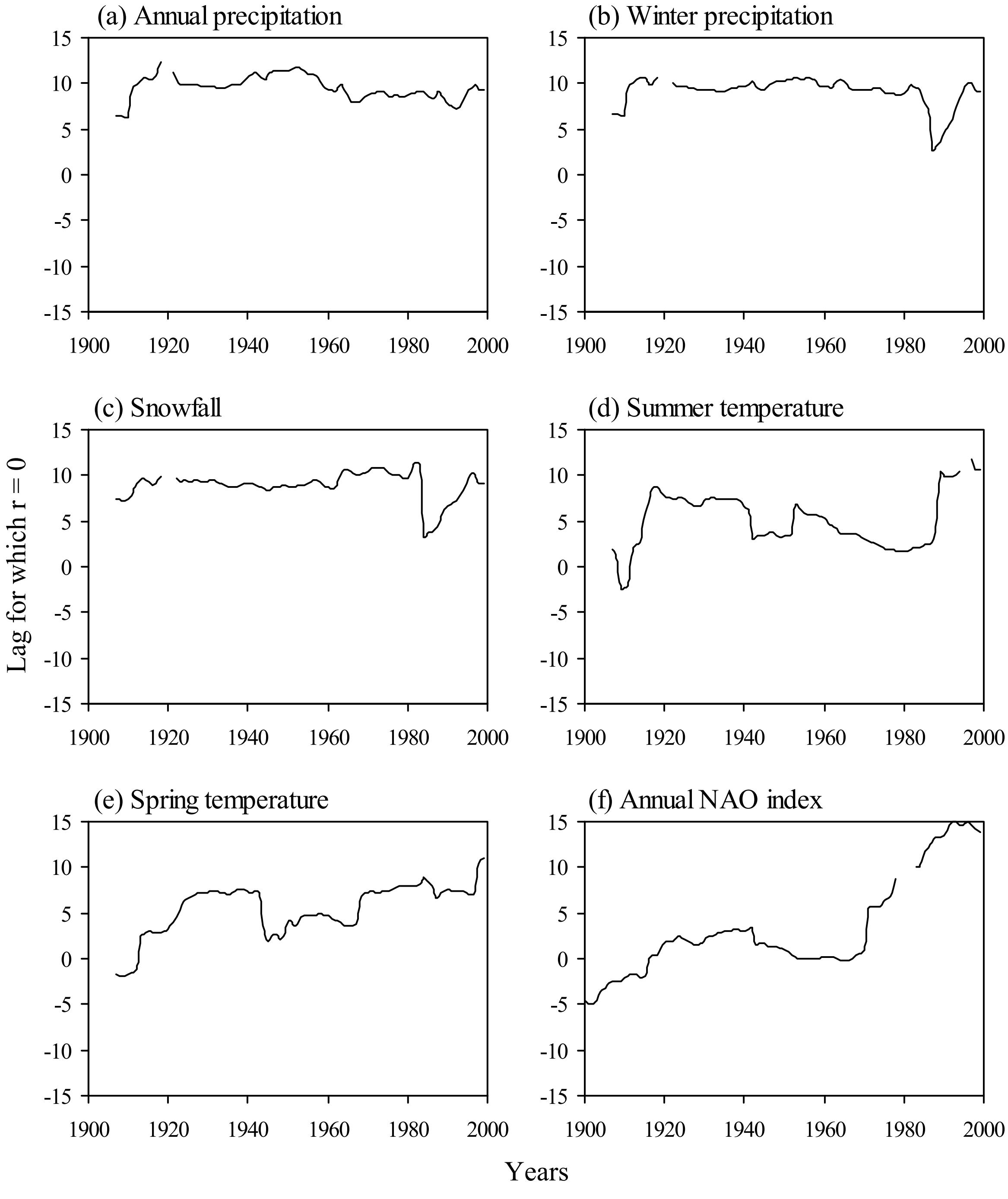

Figure 12: Phase shift analysis of the relationship between scar data and climatic data (a-e). Phase shift analysis of the relationship between scar data and annual NAO index (f) shown as an example of two variables with fluctuations of different periodicities. For each 30-year block of data, the lag for which the cross correlation coefficient is equal to zero (r = 0) is plotted in reference to the last year in the data block – see methods for details.

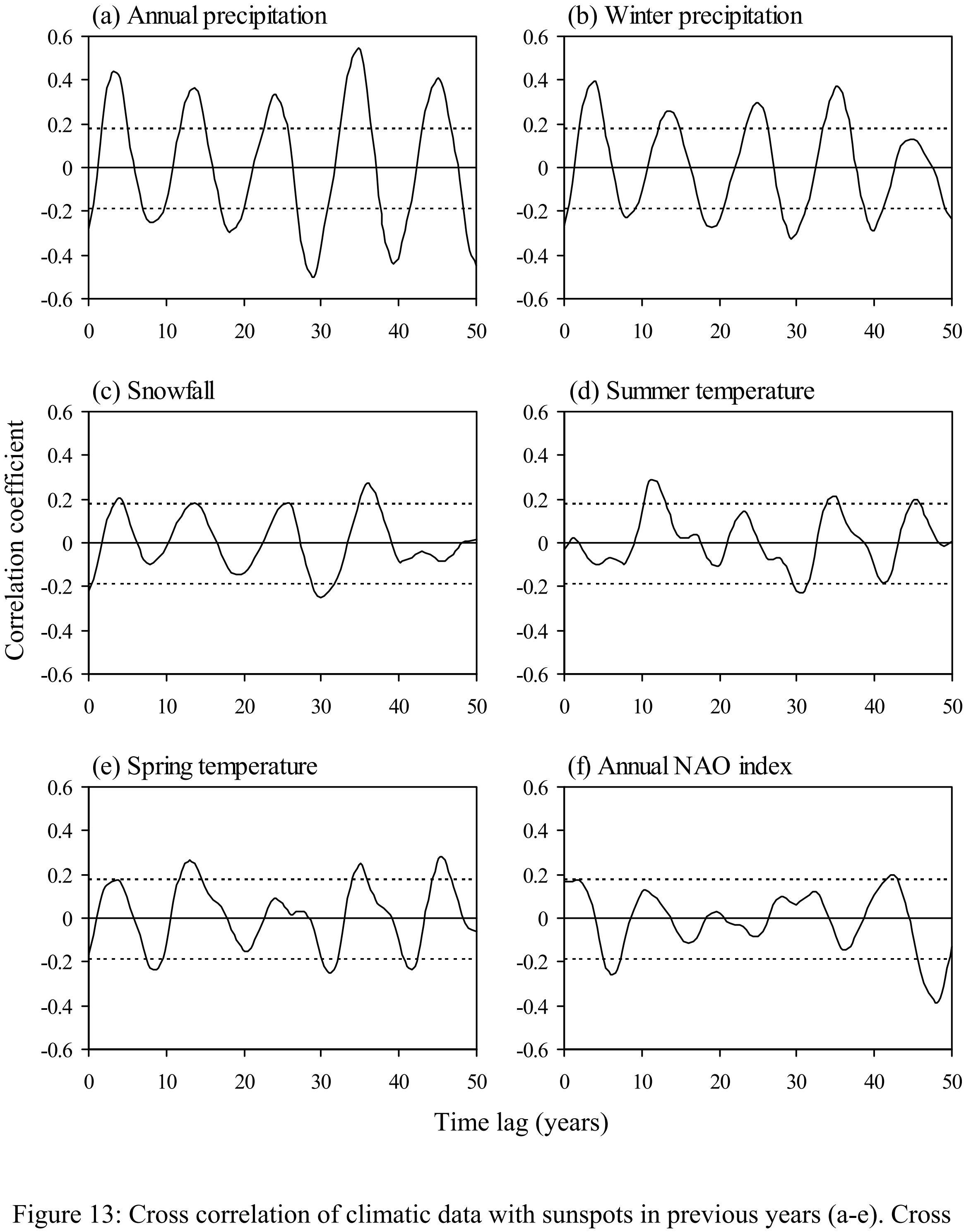

Figure 13: Cross correlation of climatic data with sunspots in previous years (a-e). Cross correlation of annual NAO index with sunspots in previous years (f) shown as an example of two variables with fluctuations of different periodicities. Broken lines show the 5 % probability Bartlett band.

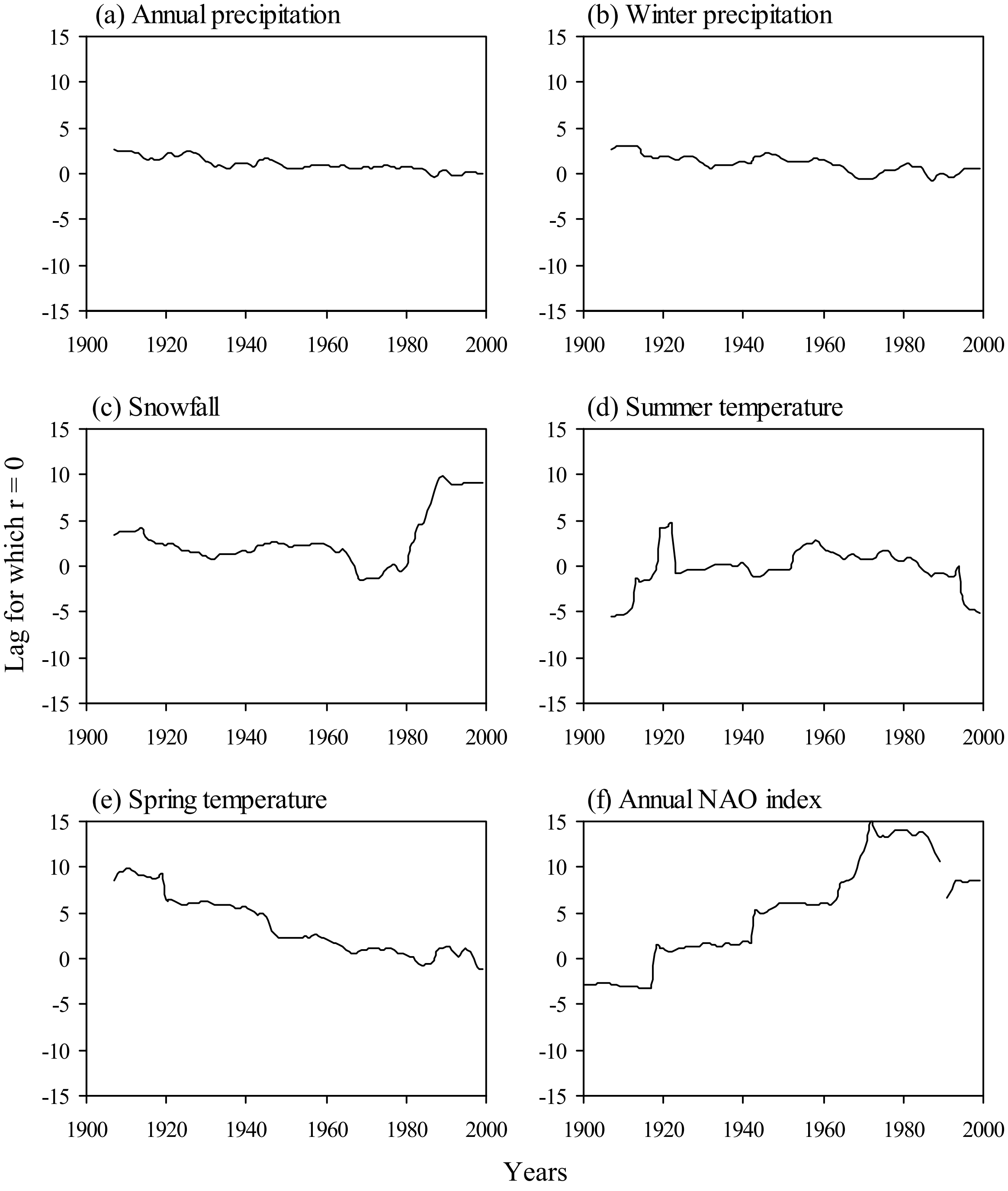

Figure 14: Phase shift analysis of the relationship between climatic data and sunspots (a-e). Phase shift analysis of the relationship between annual NAO index and sunspots (f) shown as an example of two variables with fluctuations of different periodicities. For each 30-year block of data, the lag for which the cross correlation coefficient is equal to zero (r = 0) is plotted in reference to the last year in the data block – see methods for details.

CONCLUSION AND SUMMARY OF THESIS

Porcupine feeding scars on jack pine have allowed the reconstruction of temporal changes in past porcupine abundance at three sites in the Bas St. Laurent region of eastern Quebec over periods of up to 133 years. The results showed that at each site, the number of porcupine scars has fluctuated periodically with superimposed cycles of 10-11 years and 21-22 years. Fluctuations in scar data were synchronised among the three sites and closely followed both the 11-year and 22-year solar activity cycles for the entire 1868-2000 time series obtained. Furthermore, an analysis of local climatic data revealed that annual and winter precipitation also fluctuated with the same periodicities and that there was a close association between both the solar cycle and fluctuations in precipitation and fluctuations in precipitation and porcupine scar data. This suggests a causal link between the solar cycle, local climate and porcupine population dynamics.

Previous attempts to link animal cycles to the solar cycle have failed for the most part. Work by Sinclair et al. (1993) is one exception. Based on evidence from browsing stress marks in the tree rings of white spruce dating back to 1751 in the Yukon, they suggested a relationship between the sunspot cycle, climate and the hare cycle, at least during periods of unusually high solar activity (1751-1787, 1838-1870 and 1948-1986) (Sinclair et al. 1993). However, this evidence remains controversial (Ranta et al. 1997). The results presented here appear unique in that they represent the first example of a population cycle that follows both the solar cycle and climatic fluctuations with such regularity and consistency over an extended period of time (130 years).

Although the mechanisms underlying this empirical relationship remain to be understood, both growing evidence of a causal relationship between variations in solar activity and climate (Haigh 2001; Rind 2002) and examples of the sometimes localised manifestation of this relationship (Perry 1994; Hoyt and Schatten 1997) suggest that the climate along the St. Lawrence estuary strongly responds to the solar cycle. Also, the results presented here, as well as our knowledge of porcupine biology, suggest that this solar-induced climatic oscillation sets the beat of porcupine population fluctuations through the effect of winter precipitation on survival and reproductive success. This work thus points to the possible existence of solar-induced climatic oscillations in certain regions, with cascading effects on entire ecosystems, similarly to already known oscillations such as the ENSO and NAO.

LITERATURE CITED IN SUPPLEMENTARY MATERIAL

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