FORUM

FORUM is a lighter channel of communication between readers and contributors; it aims to stimulate discussion and debate, particularly by presenting new ideas and by suggesting alternative interpretations to the more formal research papers published in ECOGRAPHY and elsewhere. A lighter prose is encouraged and no summary is required. Contributions should be concise and to the point, with a relatively short bibliography. Formal research papers, however short, will not be considered.

Bison extirpation may have caused aspen expansion in western Canada

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The aspen *Populus tremuloides* parkland that forms the northern margin of the North American grassland or prairie has been variously attributed either individually or in different combinations to the ecological effects of prairie fire, fire suppression, frequent drought, and grazing. Plains bison *Bison bison bison*, formerly abundant on the western North American plains, inhibited growth of aspen by browsing, wallowing, trampling and toppling. Historical references show that aspen populations have expanded over the past century, and fossil pollen evidence suggests that the expansion occurred mainly after the near extinction of bison but before European homesteading and subsequent fire suppression in the late 1800s. We suggest that a prehistoric cycle of grassland, fire, aspen suckering, bison activity, and return to grassland was interrupted by the removal of bison, allowing aspen expansion.

Introduction

Aspen *Populus tremuloides* Mixch. is an early successional tree species occurring in a wide range of climates throughout most of Canada and the northern United States (Perala 1990). It often occupies recently disturbed sites, and in the boreal forest may succeed to conifers and other boreal species (Perala 1990). In southwestern Canada, it is the dominant tree species in the aspen parkland, which is bounded by prairie grassland to the south and boreal forest to the north (Bird 1961). Aspen reproduces well by sprouting after surface fires or droughts that kill trees and conifer seedlings, and both these mechanisms have been implicated in the development and maintenance of the aspen parkland (e.g. Bird 1961, Strong 1977, Looman 1979, Hildebrand and Scott 1987). If these, or other non–anthropogenic processes are responsible, the expansion of aspen parkland (e.g. Strong 1977, Archibold and Wilson 1980) should not be an exclusively historic phenomenon.

Although most researchers agree that aspen populations have expanded during the last 100 yr (e.g. Strong 1977, Looman 1979, Archibold and Wilson 1980, Hildebrand and Scott 1987), the mechanism most often proposed is historic fire suppression by cultivation and related activities (e.g. Bird 1961, Strong 1977, Looman 1979, Archibold and Wilson 1980). Some ecologists have maintained, however, that the exclusion of conifers by drought is the primary controlling factor, and that fire is secondary (e.g. Lynch 1955).

Fossil pollen from ten sites (Fig. 1) shows that while small numbers of aspen were present prehistorically, the region was predominantly grass–covered. Well-dated pollen diagrams covering the last 200 yr are available in Alberta (Pine Lake) and Saskatchewan (Pasqua Lake; McAndrews 1988). The Pine Lake diagram is dated by ^{210}Pb, *Salsola* (a weed of cultivation) pollen, and volcanic ash from the 1980 eruption of Mt. St. Helens; the Pasqua Lake diagram is dated by *Salsola* pollen. Pollen preservation in both sites is excellent, with no indications of aspen pollen degradation.

Aspen pollen started its historic expansion in the 1880's in Pasqua Lake and 1890's in Pine Lake (Fig. 2), suggesting that some mechanism not operative prehistorically (i.e., neither drought nor prairie fire) was responsible for its development. Because aspen does not pollinate until 10–20 yr of age (Perala 1990), the increase in aspen populations must have started in the late 1870's in Saskatchewan and early 1880's in Alberta. Widespread homesteading did not start until after the construction of the railway in the 1880's in Saskatchewan (Richards and Fung 1969) and 1890's in Alberta (Government of Al-

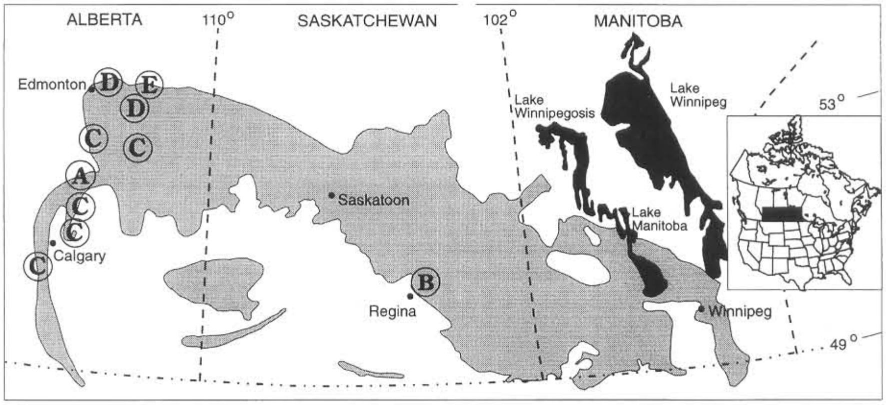

Fig. 1. Southwestern Canada showing the extent of the aspen parkland (Bird 1961) and locations of fossil pollen sites. A: Pine Lake, B: Pasqua Lake (McAndrews 1988), C (Strong 1977), D and E (Vance et al. 1983): other sites showing an historic increase in aspen pollen abundance (E also marks Elk Island National Park).

berta and Univ. of Alberta 1969) so fire suppression due to cultivation and other settlement–related activities cannot be invoked to explain the initial expansion.

One factor in the prehistoric ecology of the region that did change prior to widespread settlement was the fauna. Formerly, the prairie harboured vast herds of plains bison *Bison bison bison* L., estimated at up to 75 million (Seton 1929), though one calculation suggests that the available range could not have supported >30 million (McHugh 1972). Bison browsed aspen shoots (Blyth and Hudson 1987), wallowed and trampled the grassland, and toppled mature aspen by rubbing against them and hence may have contributed significantly to the suppression of aspen growth on the prairies (Knapp and Seastedt 1986). The plains bison was over–hunted in the 1800s, and was nearly exterminated in the 1870's (Soper 1941). Extirpation progressed from east to west as railway construction allowed greater access for hunters (Branch 1929). Prehistorically, a fire that killed aspen would have promoted aspen sprouting, potentially increasing the number of aspen stems present. Bison activity, however, would have continuously suppressed the new sprouts, preventing an increase in aspen cover. After the extirpation of bison, aspen populations expanded rapidly as there was no longer a check on aspen growth to maturity.

Drought, fire, and bison likely all had a role in limiting aspen populations, and the removal of any one of these limiting factors could have allowed aspen populations to expand. There is no evidence, however, for a reduction in drought on the prairies during the historic period as compared to the preceding moister Little Ice Age (Vance et al. 1992), and the aspen expansion that followed bison extirpation predated significant land clearance and consequent fire suppression. Thus the near extinction of bison is the most likely cause for aspen expansion in the late 1800's.

There are two modern analogues for this hypothesis. First, elk populations have been implicated in the demise of a 200-ha aspen stand in Wyoming which had been burned to promote new aspen shoots. Although 10–20 000 stems ha^{-1} were produced within 3 yr following the controlled burn (similar to the number of mature stems in the aspen stand before the controlled burn), elk reduced that to 1 500–2 400 short and unhealthy aspen stems after 12 yr (Bartos et al. 1994). Second, the region of Elk Island National Park, Alberta (Fig. 1), was described by early explorers as aspen groves in a grassland. By 1895, the extirpation of bison and severe reduction in other ungulates had allowed the development of an aspen forest which burned in 1895 (Blyth and Hudson 1987). Following park establishment, bison were reintroduced; ungulate populations increased rapidly and there were major culls of the bison and elk populations in the 1930's and 1950's. Park records show that grassland expanded with the ungulate populations, while aspen expanded following each cull (Blyth and Hudson 1987).

It is possible that prehistoric aspen populations may have cycled; at times, the intervals between killing fires may have been long enough or the bison population low enough to allow a cohort of aspen to reach pollinating age before being strongly suppressed. Such an event may

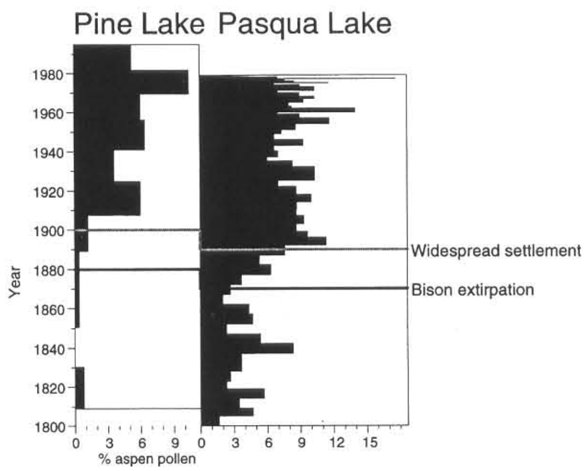

Fig. 2. Relative abundances of aspen pollen in sediments from Pine Lake and Pasqua Lake (McAndrews 1988), show similar increases in the late 1800s, after the extirpation of bison but before land clearance and fire suppression.

explain the brief high aspen pollen count in the prehistoric portion of the Pasqua Lake diagram. Longer pollen diagrams however (e.g. Kroker 1979, Vance et al. 1983) support the notion that prehistoric aspen populations were generally much lower than historic aspen populations during the last several thousand years.

If this hypothesis is correct, then the recent expansion of the aspen parkland may continue until it reaches a new balance with land use and climate. Furthermore, a southward advance of conifers and other boreal species may follow as aspen canopies shade the soil and allow moister, cooler microsites to increase in number. There may in turn be impacts on the regional hydrology (e.g. Campbell et al. 1994), as well as ramifications for the management of rangelands, woodlots, and nature preserves.

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