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University of Alberta

Fire Ecology of
Betula glandulosa Michx.

by

William J. de Groot ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy

Department of Forest Science

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Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Fire ecology of *Betula glandulosa* Michx.** submitted by William J. de Groot in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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Abstract

The fire ecology of *Betula glandulosa* Michx. is presented through an autecological review, experimental testing of fire effects on *B. glandulosa* and long-term simulations of fire regime influence on shrub populations and community succession dynamics. The effects of clipping, fire severity, and season of treatment on sprout growth and overwinter carbohydrate storage were examined. Lethal heat was applied to various soil depths at different seasonal times. Low fire severity stimulated increased sprout production, height growth and aboveground biomass production. Spring burning caused the greatest increase in sprout production and height growth during the first year and it appeared to cause the greatest increase in height growth and aboveground biomass production after two years. Mortality increased with fire severity. Seasonal timing of burning and cutting significantly influenced overwinter total non-structural carbohydrate storage in rhizomes.

Plants collected from eight fire-prone sites in western and northern Canada were tested in a greenhouse experiment for response to low fire severity and growing temperatures of 14-24°C. Fire-stimulated growth was found in four widely distributed populations. Fire response was enhanced by warmer temperatures, a typical postfire microsite condition. *Betula glandulosa* populations are expected to thrive and expand under future climate change conditions because of warmer growth temperatures and increased fire activity.

A fire effects-shrub population model was developed to test the long-term (>200 years) influence of fire interval and fire severity on shrub population density, cover and biomass. Population characteristics were highly dependant on fire interval. Shorter fire intervals decreased total shrub cover and biomass, and increased population density. Fire severity was most influential during short fire intervals. Fire exclusion simulations eventually caused local extinction. A postfire community succession model was developed to study shrub-grassland community dynamics under different fire regimes. Short fire intervals favoured deep-rooted species and long fire intervals favoured competitive species. Deep burning fires promoted seedling establishment and shallow burning fires promoted clonal expansion. Species cover was primarily determined by the interaction of species survival strategy, community composition (through interspecific competition) and fire regime. This study concludes that *Betula glandulosa* is well-adapted to a wide range of fire regimes.

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And finally. the greatest thanks is given to my wife. Wendy and my father. Bill Sr. who always enthusiastically volunteered to help with field and lab work.

Dedication

To my wife. Wendy who understood.
and my mother. Joyce (†) and father. Bill who taught me first.

TABLE OF CONTENTS

TABLE OF CONTENTS (cont'd)

TABLE OF CONTENTS (cont'd)

Page

CHAPTER

V. A fire effects-population model for *Betula glandulosa* Michx. 107

TABLE OF CONTENTS (cont'd)

Page

CHAPTER

LIST OF TABLES

LIST OF TABLES (cont'd)

Page

TABLE

Chapter VI

LIST OF FIGURES

LIST OF FIGURES (cont'd)

I. General introduction

Background

The genus *Betula* represents some 50 species and subspecies (Schilling 1984) of which *Betula glandulosa* Michx. is one of five birch shrubs in Canada (Scoggan 1978). Interspecific hybridization is quite common between the arborescent and shrub birches, and particularly so within these two growth forms. *B. glandulosa* has a widespread polar distribution, from Greenland to Alaska and southwards to northern California and Maine (Moss 1983, Dugle 1966, Scoggan 1978). It is quite common in northern and western Canada from the subalpine forest region of the Rocky Mountains to the boreal region and beyond the treeline into the subarctic tundra of the Northwest Territories (Weis and Hermanutz 1988).

In southwestern Alberta, it dominates open valley bottoms in the Rocky Mountains, greatly reducing forage production for wildlife species such as wapiti. In the Northwest Territories, a similar problem exists where grass meadows are important bison habitat (Carbyn et al. 1993). Burning to enhance wildlife habitat is a common practice in Canada (Weber and Taylor 1992) and provincial wildlife managers in Alberta have been burning in the East Slopes Region for at least ten years to improve habitat for many ungulate species. The rate of prescribed burning for habitat in the Northwest Territories (e.g., Gates et al. 1994) has also greatly increased in recent years. In shrub-dominated grasslands, the removal of *Betula glandulosa* cover increases the production of forage species and reduces winter snow depths to allow greater access to forage by grazing animals. It is generally believed that many areas became dominated by expanding *B. glandulosa* populations due to a fire exclusion policy during the last six decades (Bork et al. 1996).

A variety of operational treatments have been tried to control *Betula glandulosa*. Prescribed burning is the most popular method used by wildlife managers, primarily due to cost-effectiveness (D. Eslinger - pers. comm.). There is a need for prescribed fire guidelines in this fuel type as questions on the effects and role of fire in these ecosystems remain.

General plant ecology

The taxonomy of *Betula glandulosa* is still uncertain because of extensive hybridization within this genus. Hultén (1968) described complete introgression of *B. glandulosa* with *B. nana* L. ssp. *exilis* (Sukatsch.) Hult. where their ranges overlap. Dugle (1966) reported extensive hybridization between *B. glandulosa* and *B. glandulifera* (Reg.) Butler (*B. pumila* var. *glandulifera* Regel) in the Alberta foothills region, indicating these populations were in fact *B.* x *sargentii* Dugle.

Betula glandulosa is found over a wide range of habitats. In the northern boreal, subarctic and alpine regions it is common on sites ranging from wet to dry, with organic to mineral soils and subarctic to temperate climate (Dugle 1966, Porsild and Cody 1980; S. Payette, pers. comm.). It colonizes sites with minimal soil and organic matter in alpine and subarctic areas (Andrews et al. 1980) as well as peat bogs in subalpine and boreal regions (Ritchie 1960). It is most often found on moist, acidic and nutrient-poor sites (Vitt et al. 1975, Ducruc and Zarnovican 1976, Moore 1984) but also in drier locations (Viereck 1973). The plant morphology changes significantly from a low (<0.5 m) prostate shrub in arctic environments (Jacobs et al. 1985) to shrubs 2.5 m high (Hultén 1968) in more southern areas. The wide geographic and altitudinal range of *B. glandulosa* is a reflection of its edaphic and climatic tolerances.

Betula glandulosa reproduces primarily by sexual means, although populations at its northern limit reproduce by vegetative layering (Hermanutz et al. 1989). This species is monoecious and produces an annual seed crop which disperses during the autumn and winter. It is not a major browse source for most ungulates (Uchytil 1989) although it is a major food supply for caribou in the north (S. Payette, pers. comm.) and is often eaten by hares (Pease et al. 1979). Numerous birds feed on seeds, catkins and buds (Uchytil 1989) but there appears to be no other known parasites or herbivores causing serious damage.

Management problem

Manipulation of *Betula glandulosa* populations is of interest to land managers for several reasons. This species is found on a wide range of sites and has the potential to virtually dominate plant communities once established. Not only are expanding *B. glandulosa* populations a problem in critical wildlife habitat areas (as previously described), but it is also a fire management concern because it has exhibited extreme fire behavior even under moderate burning conditions (pers. observation). High flammability in *B. glandulosa* (Sylvester and Wein 1981) appears at least partly due to the densely resinous twigs.

The primary management problem with *Betula glandulosa* is that it is difficult to eradicate. It responds to fire with prolific sprouting following topkill (Rowe 1983) and prescribed fire trials in the Alberta foothills have given upredictable results (MacCallum and Yakimchuk 1991a, 1991b). Comparison of recently burned (<10 years old) and unburned sites indicate a substantial decrease in *B. glandulosa* cover, although subsequent surveys indicate that this may only be a temporary effect. Postfire plant mortality is relatively low, but aboveground biomass is greatly reduced. Unfortunately, the burning conditions for these prescribed fires were not documented. Operational trials using various types of heavy equipment to remove the species have been costly and the resulting slash piles and windrows are often not visually acceptable to the public. Herbicide trials have proven temporarily successful (until it re-seeds onto the site) but in many situations the use of herbicides is not acceptable to the general public or environmentalists.

Despite various problems with prescribed burning, it is increasingly popular because of low cost, increasing knowledge and experience in fire application, and a general growing awareness of the natural ecological role of fire in plant communities. However, there is still a considerable lack of knowledge on the postfire response of *Betula glandulosa* and the long-term implications of repeated burning.

General fire ecology

The Raunkiaer (1934) life form of *Betula glandulosa* is nanophanerophyte or chamaephyte in the undisturbed state (reflecting morphological differences in subarctic-alpine and boreal regions) and hemicryptophyte in the burned or clipped state. This plant reproduces by seed until disturbed, after which it resprouts from underground buds on the woody rhizome. Weis and Hermanutz (1988) found significant germination potential in buried *B. glandulosa* seeds, but this was greatly reduced at higher latitudes. *B. glandulosa* is capable of surviving most fires because the rhizome is usually sufficiently deep in the soil. The only exception would be when the rhizome is completely rooted in organic matter and droughty conditions resulted in a deep burning fire.

Based on the vital attribute approach of Noble and Slatyer (1977), Rowe (1983) classifies *Betula glandulosa* as an endurer. Such 'V (vegetative-based) species' are said to be able to resprout in the juvenile stage. Under the second vital process of Noble and Slatyer (1977), *B. glandulosa* would be classed as an 'I (intolerant) species' that can only establish immediately after fire as a rapid growth pioneer. Other shrub species have shown varied response to fire, depending on fire severity (depth of burn) and seasonal timing of the burn (e.g., Johnston and Woodard 1985, Kauffman and Martin 1990). It is suspected that *B. glandulosa* may have a similar response to fire severity and season of burn.

General approach

Study purpose

Two primary knowledge gaps regarding the fire ecology of *Betula glandulosa* were investigated: the immediate effects of fire on *B. glandulosa* survival and growth, and the long-term ecological role of fire on *B. glandulosa* populations and associated plants in the community. Addressing the first issue will provide information on the operational aspects of vegetation management to achieve various resource objectives, while the second issue provides the basis for understanding the influence of fire regime (which can be altered by prescribed burning) on *B. glandulosa*-dominated communities. The purpose of this research was to evaluate the effects of fire on *B. glandulosa*, and to describe the larger role that fire plays in its ecology. The specific studies were 1) to determine the effects of fire severity and season of burn on *B. glandulosa*, 2) to examine the extent of fire response over a large portion of its geographical range, and 3) to model long-term fire effects on *B. glandulosa* and associated plant community members using various fire regime scenarios.

Study method

An autecological review of *Betula glandulosa* provides the background for a basic understanding of the species. Because of the close relationship to *Betula nana* L., a more thoroughly-studied species, both of these birch shrubs were reviewed together. Fire effects on plant individuals were studied through field and greenhouse experimentation. The effects of fire severity and season of burn were tested by applying a controlled belowground heat pulse of different lethal depths, at different times during the growing season. The experiment was conducted using field plants from a study site in west-central Alberta, and fire effects were measured in terms of sprouting response from the rhizome. The importance of rhizome carbohydrate storage on sprouting response was evaluated by similar seasonal burning treatments. A second experiment was conducted to extrapolate results from the first experiment across a much wider geographical area. Plants were collected from various sites in western and northern Canada and tested for response to belowground heating in a greenhouse study. The final part of this study included the development of a basic fire effects-population model to determine the long-term effects of fire severity and fire interval on population characteristics, and the development of a post-fire community succession model to determine the impacts of fire interval on community dynamics.

Study area description

The study area covers the western region of Alberta and the Northwest Territories (Figure 1-1). Sites were located in boreal and subalpine regions from 52° - 68° N latitude and 115°-133° W longitude, and from 1350-1940 m elevation in the east slopes region of the Rocky Mountains. This area corresponds to forest sections SA.1 (East Slope Rockies), B.19a (Lower Foothills), B.19c (Upper Foothills), B.23a (Upper Mackenzie), B.23b (Lower Mackenzie), B.27 (Norhtwestern Transition) and B.32 (Forest-Tundra) of Rowe (1972). The sites are found in the Upper and Lower Foothills ecoregions and the Subalpine ecoregion of Alberta (Archibald et al. 1996, Beckingham et al. 1996).

Mean daily temperatures for July range from 9.6°C at high elevation sites in the Rocky Mountains to 16.7°C at Norman Wells (Atmospheric Environment Service 1993a, 1993b). Growing degree days above 5°C are roughly 750 at Inuvik and in valley bottoms of the Rocky Mountain foothills, with the highest values nearing 1500 at southern boreal sites (Atmospheric Environment Service 1984). Mean monthly precipitation for July ranges from 34.1 mm at Inuvik, increasing to 100-120 mm in the Rockies. Historical fire weather data shows a similar wide range in average burning conditions with seasonal Fire Weather Index (Van Wagner 1987) values of 4 in the far north to 14 in southern and mid-study latitudes (Figure 1-2). In terms of seasonal drying, average autumn Drought Code (Van Wagner 1987) values range from a high of over 500 at Yellowknife, NWT to 250 at Rocky Mountain House, Alberta (McAlpine 1990).

Fire history maps of the study area (Delisle and Hall 1987, Territorial Forest Fire Centre 1995) show considerably more large fires and area burned in the central boreal portion of the study area, with decreasing fire frequency and area burned beyond the northern treeline and towards the Rocky Mountains. This general pattern was also evident during the last decade (Figure 1-3). Although the east slopes region of the Rocky Mountains have had no large (>100 ha) fires since records began in 1930, small fires may have been common as fire scar data collected at the Seven Mile Flats site (a major study site) along the Forestry Trunk Road showed fire to be frequent. At that site, trees sampled along the perimeter of the shrub-grassland meadow showed only one fire occurred during the last 40 years, which coincided with construction of the Forestry Trunk Road in the mid-1950's (Murphy 1985). Since the mid 1920's, fire scars provide evidence of only 3 fires, although fires were very common during the 50-year period prior to 1920. It was apparent that some of the sites used in the study area supported fire quite frequently and all are believed to have burned at some time in the recent past.

Concluding remarks

Fire ecology has traditionally been studied in terms of general descriptive ecology or quantitative fire behavior, but very seldom as quantitative fire ecology (Johnson 1992). The purpose of this thesis was to provide a groundwork linking plant ecology to fire behavior in a manner that quantitatively described fire effects. This approach was further pursued to explore the ecological role of fire by quantitatively modelling fire effects under different fire regimes. It is believed that these kinds of fire effects models will be critical to driving future ecosystem and landscape management models that try to emulate natural processes. Fire effects models will provide the critical link between fire response at the plant level and the resulting impacts at the stand level.

Figures

Figure 1-1. General range of the study area. Markers indicate primary sites used in the study; field survey data collection was also done at numerous locations between the two most southerly sites.

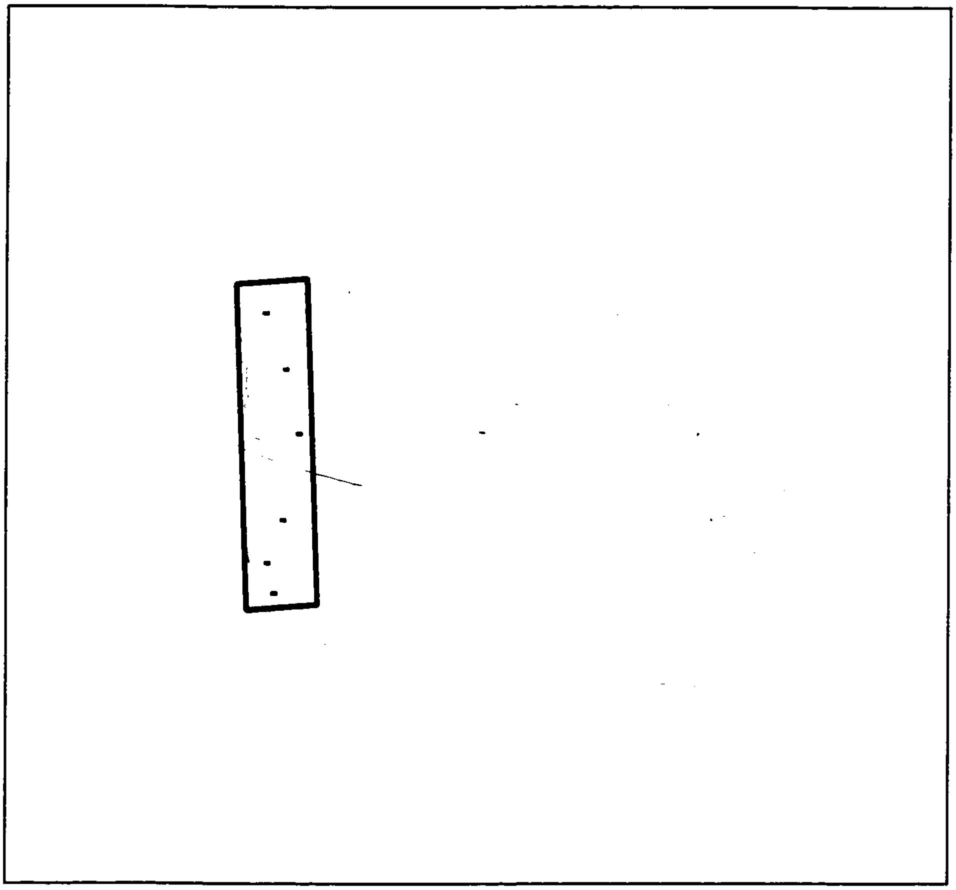


Figure 1-2. Generalized fire weather zones in Canada for the period 1957-66 (adapted from Simard 1973).

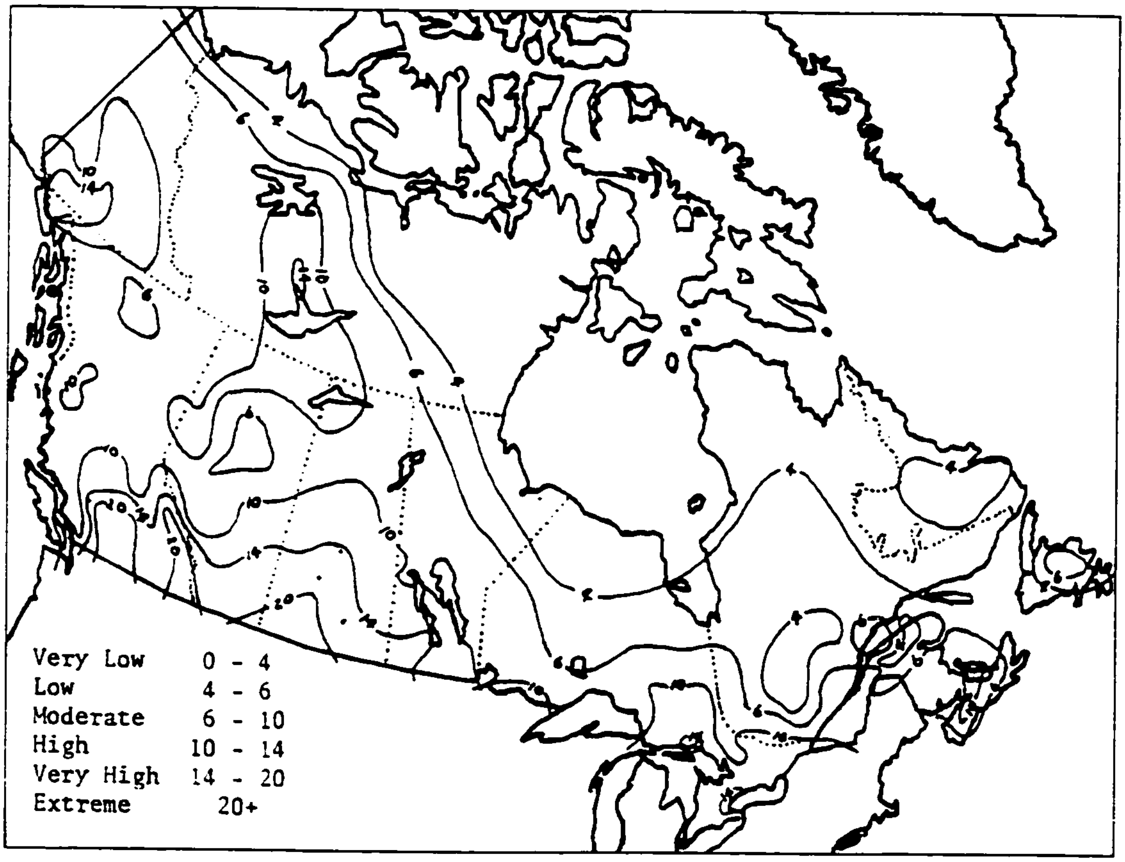
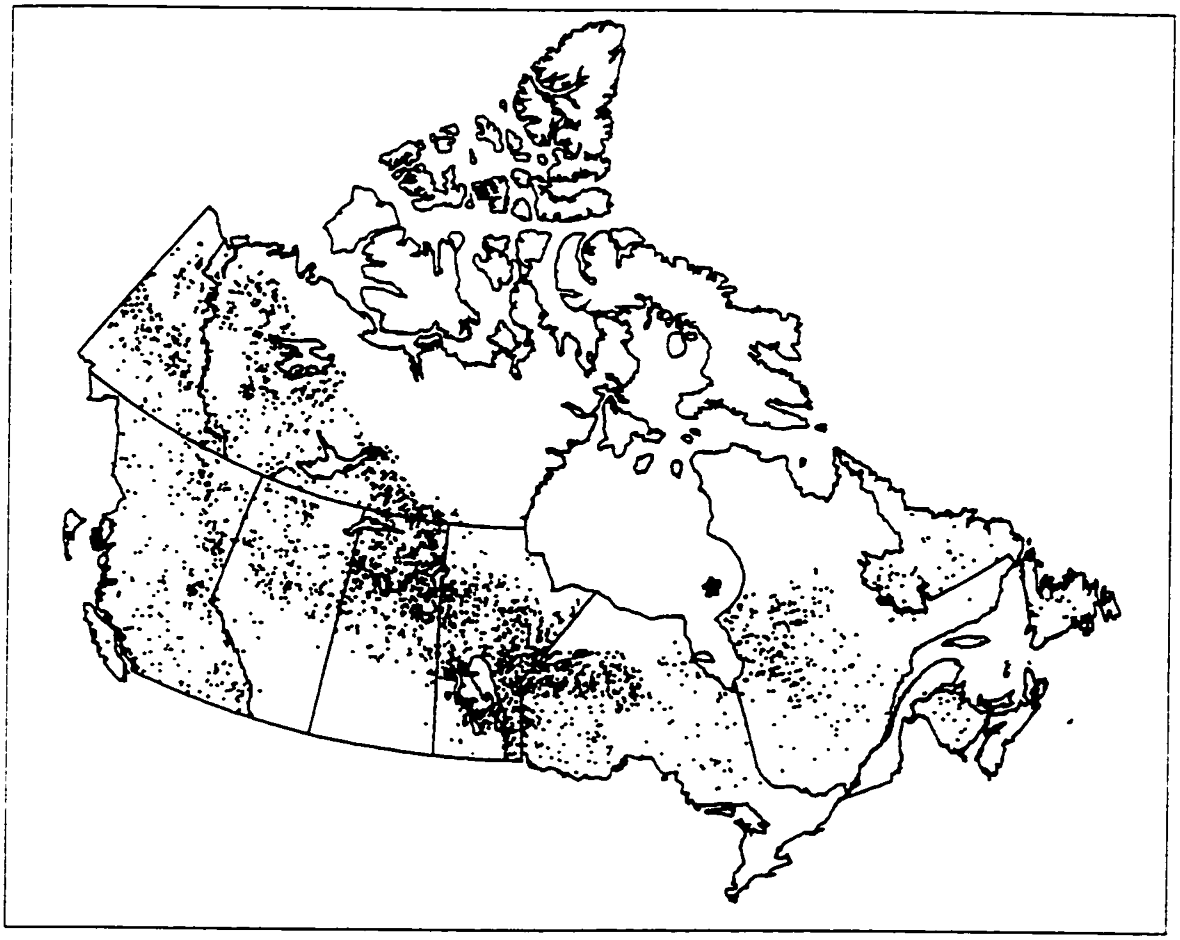


Figure 1-3. Distribution of large (>200 ha) fires recorded in Canada during 1980-89 (Stocks et al. 1995). Large fire records for some northern areas are not complete.



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II. An autecological review of *Betula glandulosa* Michx. (including *Betula nana* L.)[1]

Introduction

There are approximately 50 species (including subspecies) within the genus *Betula* (Schilling 1984) of which three are found in Britain. *Betula pendula* Roth and *Betula pubescens* Ehrh. (Atkinson 1992) are the tree birches while *Betula nana* L. (Clapham et al. 1962) is the only dwarf shrub birch species. Hybridization appears to occur among all three species and intermediates are common. The tree *B. pubescens* Ehrh. ssp. *tortuosa* (Ledeb.) Nyman (Gardiner 1984) (ssp. *carpatica* (Willd.) Asch. & Graebner, ssp. *odorata* sensu E. Warb., ssp. *tortuosa* (Ledeb.)) also grows as a shrub in the northern and mountainous areas of *B. nana* range in the British Isles, while the hybrid *B. nana x pubescens* (*B. x intermedia* Thomas ex Gaudin) can also be found in *B. nana* range, but only rarely (Stace 1991). There is one *B. nana* cultivar (Glencarry) from Scotland (Santamour and McArdle 1989). *B. nana* L. is represented by the subspecies *nana* in Europe and western Asia, and subspecies *exilis* (Suk.) Hult. in North America plus central and eastern Asia (Hultén and Fries 1986).

Betula glandulosa Michx. is a closely-related shrub found across North America and Greenland. Both dwarf birch species are grown in cultivation in Britain (Schilling 1984). Although the genetics of *Betula* has received considerable attention (e.g., Eriksson and Jonsson 1986), the taxonomy of *B. nana* and *B. glandulosa* is very difficult where they occur in the same range. Hultén (1968) recognized that *B. nana* L. ssp. *exilis* (Sukatsch.) Hult. [*Betula exilis* Sukatsch.; *B. nana* var. *sibirica* Ledeb. in part; *B. glandulosa* var. *sibirica* (Ledeb.) Blake; including *B. tundrarum* Perfiljev] is completely introgressed with *B. glandulosa* within the wide overlap of their ranges. In North America, Scoggan (1978) separated *B. nana* L. and *B. glandulosa* Michx. [*B. nana* vars *intermedia* Regal and *sibirica* Ledeb.; *B. ermanii sensu* John Macoun 1886, not Cham.; incl. f. *eucycla* Lepage] although problems of introgression were noted. Viereck and Little (1972) distinguish *B. glandulosa* Michx. from *B. nana* L. [*B. nana* ssp. *exilis* (Sukatch.) Hult., *B. glandulosa* var. *sibirica* (Ledeb.) Blake] but noted hybridization. Brayshaw (1976) equated *B. glandulosa* Michx. with *B. nana* L. ssp. *exilis* (Sukatchev) Hultén [*B. nana* L. var. *sibirica* Ledebour in part]. Moss (1983) included *B. nana* with *B. glandulosa*, while Boivin (1967) described the transition from mid-North American *B. glandulosa* [*B. nana* var. *sibirica* Led.] to northern *B. nana* as part of a morphological continuum.

In Greenland, specimens of *Betula glandulosa* show considerable morphological difference from typical North American specimens (Fredskild 1991), supporting Hultén's view of complete introgression with *B. nana* ssp. *exilis*. Böcher (1954) also noted that *B. glandulosa* var. *rotundifolia* Regel in Greenland "approaches *B. nana* in so many respects". Although both subspecies of *B. nana* are reported in Greenland (Hultén 1971), subspecies *nana* is not described as introgressing with *B. glandulosa*. In southeastern Baffin Island, Canada, dwarf birch shrubs are characteristic of *B. nana* ssp. *exilis* and may be considered *B. glandulosa* (Andrews et al. 1980, Jacobs et al. 1985, Weis and Hermanutz 1988). Moving northward, specimens become more like *B. nana* ssp. *nana* (Andrews et al. 1980).

Being a rare species in the British Isles, there is a dearth of local information on the ecology of *Betula nana*. In this review, considerable use was made of other international *B. nana* studies to supplement this information. *B. glandulosa* was included as part of the circumpolar review of *B. nana* ecology because of the obvious taxonomic difficulty between these two dwarf birch species in North America. Numerous references were also made to *B. pubescens* ssp. *tortuosa*, a *B. nana* hybrid (Vaarama and Valanne 1973, Sulkinoja 1990),

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because it often exhibits similar growth form and habit. The numerous northern European studies on ssp. *tortuosa* provide valuable additional insight into the ecology of *B. nana* where information is scant.

Geographical and altitudinal distribution

Betula nana (Figure 2-1) is a rare species in the British Isles and is found locally in S. Northumberland and mainland Scotland from Perths and Argyll northwards at 245-855m in elevation (Clapham et al. 1962, Stace 1991). It is also recorded in N. Yorks and is probably extinct in Lanark (Clapham et al. 1962). *B. nana* L. is circumpolar in distribution with subspecies *nana* (Suk.) Hult. found from the western coastal regions of Greenland, across Iceland, the British Isles, northern Europe and southward to the N. Alps (Figure 2-2), and into western Siberia. Hultén's (1986) circumpolar range of *B. nana* also appears to include the range from introgression with *B. glandulosa* (Figure 2-3). The subspecies *exilis* (Suk.) Hult. ranges across Siberia, Alaska, and northern Canada to Baffin Island and Labrador. Both subspecies have been reported in Greenland, and their ranges widely overlap in western Siberia. It has been found at 20-1075m elevation in Scandinavia (Kallio and Mäkinen 1978), 380-1000m in northern USSR (Chepurko 1972), and from 20m in the Canadian arctic (Andrews et al. 1980) to at least 1300m in Alaska (McGraw et al. 1983).

Betula glandulosa Michx. occurs across North America from Alaska to Greenland and southward to the northern U.S. (Dugle 1966, Hultén 1968, Scoggan 1978). The range shown by Weis and Hermanutz (1988) (Figure 2-4) is incomplete and should also include the entire Quebec-Labrador peninsula (S. Payette, pers. comm.). It has been found growing at 1219-3475 m elevation in continental North America (others cited in Uchytil 1989) and 10-170 m in coastal arctic areas (Andrews et al. 1980, Fredskild 1991).

Habitat

Climatic and topographical limitations

Betula nana occurs primarily in the wet and cold climates of the northern British Isles where annual rainfall is 1200-2000 mm (160-200 wet days per year) and less than 830 day °C per year (Page 1982, Rodwell 1991). Minimum February temperatures are below freezing and summers are cool. Long, cold winters and short cool summers are typical climatic conditions in other circumpolar countries where mean winter and summer temperatures can be -25°C and 3°C respectively (Andrews et al. 1980). Annual precipitation amounts in these colder climates are also much lower, with 300-400 mm common.

Betula nana is a typical occupant of exposed subarctic and alpine tundra locations, and of swampy montane habitats (Hanson 1951, Poore and McVean 1957, Hutchinson 1966, Elkington 1968, Kallio and Mäkinen 1978, Aleksandrova 1980, Jonasson 1981, Aston 1984, Fredskild 1991). However, it does not exhibit this wide range in ecological amplitude in British populations as it is restricted to blanket peat (Dickson 1984). In Britain, *B. nana* is found generally above 300 m elevation, but at an average of 550 m (Rodwell 1991). It grows higher in west Scotland where conditions are wetter, and to near sea level in the continental east.

Betula nana does not form extensive stands on steeper slopes (Kallio and Mäkinen 1978); Johnson (1987) noted *B. glandulosa* growing on slopes with average angles of 24° and 26°. Neither species is limited by aspect, although slope direction is important in that it influences local edaphic and climatic factors. Andrews et al. (1980) state that elevation, aspect, slope (influencing the angle of incidence to solar radiation) and proximity to water are very significant mesoscale climatic factors in arctic areas. Wind, radiation and snow depth were determined to be important to the distribution of *B. nana*-dominated communities in Iceland (Anderson et al. 1966). In colder climates, dwarf birch is found on lee-slope locations with southern aspects. Topographic protection from wind may be of greater importance than southern exposures (Andrews et al. 1980). Knaben (1950 - cited in Poore and McVean 1957) attributes the scarcity of *B. nana* in oceanic regions to a high heat requirement which can only be found in sheltered locations.

It appears that a primary factor affecting the range difference in these two dwarf birch species is their ability to tolerate temperature extremes. The more northerly range of *Betula nana* (Porsild 1964) indicates an ability to survive colder winter temperatures, although *B. glandulosa* can tolerate average minimum January temperatures of -27°C if sufficient snowfall occurs (Anderson. 1975). As a result, *B. nana* is considered a continental species (Poore and McVean 1957, Fredskild 1991) while Böcher (1954) stated that *B. glandulosa* var. *rotundifolia* "may behave like an oceanic and southern race of *Betula nana* in the widest sense" with a northern limit in Greenland determined not by summer temperature, but by increasing degree of continentality. Böcher (1954) also described *B. glandulosa* s. str. as a continental shrub, which may be an indication of different strains (e.g., Kallio and Mäkinen 1978) and/or hybridization.

Fredskild (1991) also described a difference in climatic tolerance in Greenland, where *Betula nana* is considered a middle-arctic continental species of harsher climate than *B. glandulosa* which occupies low-arctic oceanic (Fredskild and Ødum 1990) locations. In North America, the mean daily July 7°C isotherm that separates the phytogeographic regions of continental Northwest Territories and the arctic archipelago (Terasmäe et al. 1966) appears to provide a reasonable estimate of the northern limit for *B. glandulosa*. The previous existance of dwarf birch several hundred kilometers north of present populations on Baffin Island when July temperatures were 7-10°C (1-4°C higher than present) (Terasmäe et al. 1966) tends to support this limit. North of this isotherm, *B. glandulosa* is restricted to oceanic regions.

Betula nana occurs in the northern belt of the subarctic tundra region which extends north to about the 6°C isotherm for July (Aleksandrova 1980). Conolly and Dahl (1970) also point to the similarity between *B. nana* range and the 22°C maximum summer isotherm in Highland Scotland suggesting that it may not tolerate higher temperatures, although Dickson (1984) suggests this may be the result of greater competition. The mean annual maximum temperature for British *B. nana* communities is less than 21°C (Rodwell 1991). Aleksandrova (1980) described the transition from the East European-West Siberian Province to East Siberian Province as a shift from *B. nana* L. to *B. exilis* Sukacz. This difference in vegetation was attributed to low (cyclonal) pressure circulation in the west and the anticyclonal activity in the east. As a result of the low amount of winter precipition, eastern Siberia was unglaciated. However, it is not clear whether the present ranges of *B. nana* and *B. exilis* are a result of glacial history, greater continentality in the east, or both.

Substratum

Betula nana and *B. glandulosa* are typically found on moist, acidic and nutrient-poor organic sites over their entire circumpolar range (e.g., Hanson 1951, Ritchie 1960, Corns 1974, Vitt et al. 1975, Dierssen 1977, Kallio and Mäkinen 1978, Aleksandrova 1980, Moore 1980, Fredskild 1991). These sites cover a wide range of soil temperature and organic matter depth, and are usually well-drained. The British mires occupied by *B. nana* consist of well-humified peat that is usually more than 2 m thick (Rodwell 1991). These Sphagnetalia bogs are oligotrophic, the surface is highly acidic (pH 4 or less) and they are at least moderately drained. *B. nana* exhibits low growth rates on waterlogged sites (Wein and Bliss 1974). In a seedling growth experiment, Vaartaja (1960) found a faster growth rate in *B. glandulosa* than arborescent birches that was likely due to greater soil acidity. Adaptation to acid soils was also shown by Ducruc and Zarnovican (1976) as the pH of surface soil and surface material layers were found to be the strongest influences on *B. glandulosa* distribution in Labrador, Canada.

Betula nana is also found on more xeric and rocky sites characteristic of subarctic and alpine areas (Viereck and Little 1972, Alexandrova 1980, Jonasson 1981, Fredskild 1991). In Greenland, the soil on these sites is often thin, acidic (pH 4-5) and may not have a humus layer. In northern Finland, it has been noted growing on glacially-derived sands and gravels, along roadside verges, and on bogs, as well as on shallow and deep peats and gravels in Scotland (I. Brodie, pers. comm.). Whittaker (1993), however, showed that *B. nana* was very slow to colonize a glacial foreland in Norway as it appeared to require a greater degree of soil development than other heath shrubs for seedling establishment. *B. glandulosa* has broad habitat requirements similar to *B. nana* (e.g., Ritchie 1960, Moore 1980, Weis and Hermanutz 1988, Eurola et al. 1990). Both birch species grow extensively over permafrost, but Ruuhijärvi (1960 - cited in Kallio and Mäkinen) stated that *B.*

nana does not grow on palsas because of the lack of protective snow cover. Ducruc and Zarnovican (1976) found that *B. glandulosa* was relatively indifferent to the type of surface material, but preferred organic deposits. Slope, depth of organic matter and depth to permafrost had a weak secondary influence on *B. glandulosa* distribution.

Decomposition of *Betula glandulosa* leaves contribute to soil structure and nutrient cycling with mass losses of 30-45% in one year and 45-55% over two years on burned and unburned Canadian boreal woodland sites, a rate that is considerably faster than for other subarctic species (Moore 1983, 1984). *B. nana* leaves showed a slower decomposition rate of about 25% mass loss per year on a Swedish mire site (Heal and French 1974), while *B. pubescens* ssp. *tortuosa* had a summer decomposition rate of 8-13% for a range of elevational sites in Swedish Lapland (Davis et al. 1991). Results from these studies suggest that decreased decomposition rates may be the result of low soil nitrogen, different litter quality, or possibly allelopathic effects. Moore (1983) found a decrease of 80% potassium, 40% phosphorus, 40% magnesium, 20% calcium and 20% nitrogen content in decomposing *B. glandulosa* leaves after one year. Similar results were found in another study by Moore (1984), with additional reductions of 75% calcium and 80% magnesium in decomposing leaves over 2 years. Leaf phenolics and carbohydrates in *B. glandulosa* decreased about 90% within two months during the autumn (Moore 1983).

Communities

Betula nana is usually found as a component of mountain moor and tundra vegetation. Scottish records describe its occurrence in heather moorland (Aston 1984). It is recorded by Rodwell (1991) as a rare species occurring exclusively in *Calluna vulgaris - Eriophorum vaginatum* blanket mires found in higher altitude montane environments.

The *Vaccinium vitis-idaea - Hylocomium splendens* sub-community of upper montane blanket mires includes the *Betula nana* variant (Rodwell 1991), also described as *Betula nana* bogs by Poore and McVean (1957) and as the *Calluneto-Eriophoretum* shrub-rich facies of McVean and Ratcliffe (1962). These communities are characterized by *Eriophorum vaginatum* and *Calluna* co-dominants with lesser components of *Vaccinium myrtillus*, *V. vitis-idaea*, *E. nigrum* ssp. *nigrum* and/or ssp. *hermaphroditum* and possibly *Erica tetralix* (Rodwell 1991). Vegetation is about 20-30 cm high with low growing *B. nana* found among other woody species. *Arctostaphylos alpinus*, *V. microcarpum*, and *Rubus chamaemorus* are present, while *Juncus squarrosus* may be locally abundant. *Sphagnum capillifolium* usually forms an extensive carpet with some *S. fuscum*. Other mosses are common with *Pleurozium schreberi*, *Hylocomium splendens*, *Plagiothecium undulatum* and *Hypnum cuppressiforme/jutlandicum* present. *Ptilidium ciliare* is common with *Mylia anomala* and *Lophozia ventricosa* occasional. Lichens are not prevalent, but *Cladonia arbuscula* and *C. impexa* may be locally abundant with *C. rangiferina* being infrequent.

Betula nana is also found much less frequently in the typical variant of this sub-community which has *Carex bigelowii*, *Sphagnum subnitens*, *S. quinquefarium* and *Cladonia uncialis* occurring as additional species. *B. nana* may also be rare in the *Empetrum nigrum* ssp. *nigrum* sub-community of slightly lower elevations and milder temperatures. This sub-community has a floristic composition similar to the *Vaccinium-Hylocomium* sub-community (in different proportions) with additional associated species represented by *Eriophorum angustifolium*, *Deschampsia flexuosa*, *Sphagnum papillosum*, *S. recurvum*, *Dicranum scoparium*, *Campylopus paradoxus*, *Pohlia nutans*, *Mylia taylori*, *Kurzia pauciflora*, *Cephalozia* spp., *Calypogeia* spp., *Cladonia squamosa*, *C. bellidiflora*, *C. floerkeana*, *Cornicularia aculeata*, and *Hypogymnia physodes*. None of the epiphytes known to grow on birch in the British Isles (Coppins 1984) have been documented on *B. nana*.

Wein and Bliss (1973) record *B. nana* ssp. *exilis* in cottongrass (*Eriophorum vaginatum* ssp. *spissum*) tussock communities in Alaska and Northwest Territories, with a shift to *B. glandulosa* when these communities included scattered black spruce (*Picea mariana*).

Response to biotic factors

Betula nana has shown a tolerance of moderate grazing pressure by sheep and other animals in Britain (Aston 1984). Fredskild (1991) presents evidence that *B. glandulosa* could survive high grazing pressure at one site in South Greenland, and from continuous grazing pressure since 1924 at another location. Kallio and Mäkinen (1978) report that park-like areas could be maintained by repeated mowing and grazing of *B. pubescens*, although vigorous height increment would occur within a few years of treatment removal. This is also the case for *B. nana* in the central Highlands of Scotland under grazing pressure from sheep, where plants grow 20-30 cm per annum after release (I. Brodie, pers. comm.). Brodie (1994) also described the re-emergence of *B. nana* on Rannoch moor from remnant root systems after being fenced to prevent browsing. Susceptibility to herbicides is not known for *B. nana* and *B. glandulosa*, but it is likely similar to other birch species. In this regard, they may be controlled by ammonium sulphamate, Krenite (fosamine ammonium), 2,4,5-T and to a lesser extent 2,4-D; and may be tolerant of simazine and dichlobenil (Fryer and Makepeace 1978, Marrs 1985).

The long-standing practice of burning Calluneto-Eriophoretum bogs in Britain has shown that *Betula nana* is able to regenerate quickly, as long as the fire is not too severe (Aston 1984). Similar results were obtained with *B. glandulosa* in NW Canada (Wein and Bliss 1973; see chapters 2 and 3). It was found that a low severity burn in early spring or late autumn promoted the most vigorous sprouting response. Mid-summer burns appeared to decrease sprout growth, while greater severity increased the mortality rate. Repeated burning (every few years) reduces aboveground biomass, but appears to have only a minimal mortality effect. Viereck (1973) noted in Alaska that repeated fire near tree line and in some wetter sites may result in *B. glandulosa* thickets while Moore (1980) documented revegetation of recently burned sites (1 and 5 years) by *B. glandulosa*.

Drainage of upland bogs was described as the main cause for the disappearance of *Betula nana* in Lithuania (Purvinas 1971, cited in Aston 1984) and may be contributing to the restricted range in Britain (Aston 1984). Burning, grazing by sheep and deer, and peat erosion are other possible causes (Poore and McVean 1957, Rodwell 1991, Brodie 1994). Survival in wetter areas of the British Isles is a reflection of low fire occurrence, and not of a natural distribution (I. Brodie - pers. comm.). Although subarctic and alpine populations of *B. nana* colonize more xeric sites, it is possible that bog populations are less tolerant of moisture stress (see next section). Drainage (20-50 cm drop in water level) of an intermediate fen in western Canada resulted in warmer soil temperatures and earlier flowering and bud flush in *B. pumila* L., another dwarf birch shrub (Lieffers and Rothwell 1987).

Betula glandulosa (possibly including *B. nana* ssp. *exilis*) has proven to be a highly successful colonizer of abandoned borrow pits resulting from highway construction in northwestern Canada (Kershaw and Kershaw 1987). Pits generally provided drier and warmer soil conditions than the surrounding tundra. *B. glandulosa* invaded pits that were only 5-6 years old and showed prominence in older pits and southern regions typified by tall shrub tundra.

Response to environment

Gregariousness

Both dwarf birch species are highly gregarious. Although *Betula nana* populations tend to be small and patchy in distribution in the British Isles (Aston 1984), both species usually form thickets and extensive stands elsewhere in the circumpolar north.

Performance in various habitats

Although the growth rate of individual *Betula nana* stems is slow, total biomass production can be high because of the large number of stems per area (Bhat and Kärkkäinen 1982). Chapin et al. (1980) studied biomass of *B. nana* in Alaska and found 80% (10 000 mg) to be underground, about 60% (6200 mg) of which were roots. Leaves (350 mg) accounted for about 15% of total aboveground biomass (2430 mg). Shaver and Cutler (1979) measured lower belowground components for live *B. nana* phytomass with belowground:aboveground ratios at 1.11-1.24 in healthy Alaskan tussock tundra, and only 0.16 in a decadent tussock. About 80-90% of the current aboveground biomass (measured during peak season) was found to accumulate in the leaf compartment, while 10-15% accumulated in current stems of Alaskan *B. nana* (Johnson and Tieszen 1976, Archer and Tieszen 1980). Chapin (1980) found a leaf relative growth rate of 77 $mg{\cdot}g^{-1}{\cdot}d^{-1}$ using the same data. A wide range in *B. nana* biomass has been documented from 86 $kg{\cdot}ha^{-1}$ in an upland Swedish mire (Backéus 1985), to 279 $kg{\cdot}ha^{-1}$ on the ridge of a polygonal bog in northern USSR (Schamurin et al. 1972), to 4310 $kg{\cdot}ha^{-1}$ on north Swedish alpine tundra (Jonasson 1982). Growth rings for Greenland *B. nana* measured by Miller (1975) ranged 20-414 µm, with an average of 130 µm.

Annual aboveground production in Alaska and the Yukon for *Betula nana* ssp. *exilis* (7% cover) was found to be 1 - 5 $g{\cdot}m^{-2}$, considerably less than other shrub species (Wein and Bliss 1974). Haag (1974) determined aboveground net production in a similar community (measured in early August) to be 23.3 $g{\cdot}m^{-2}$, although *B. nana* was more dominant with 14% cover. Backéus (1985) measured production at 2.5 $g{\cdot}m^{-2}$ in central Sweden. Wein and Bliss (1973) found higher annual production rates for *B. nana* and *B. glandulosa* (combined) on unburned sites (2.9-16.1 $g{\cdot}m^{-2}$) than 1-2 year old burn sites (0.5-11.7 $g{\cdot}m^{-2}$) in northern Canada and Alaska. At a relatively dry and cold area in central British Columbia, three wetland sites with 13-20 *B. glandulosa* $stems{\cdot}m^{-2}$ had a current annual growth of 6.4-7.4 $g{\cdot}m^{-2}$ while a fourth wetland site with 42 $stems{\cdot}m^{-2}$ produced 51.4 $g{\cdot}m^{-2}$ (Marshall et al. 1990).

In Alaska, Kummerow (1983) found that *Betula nana* individuals severed from the parent plant below the moss layer resulted in significantly reduced root/shoot weight ratios (0.15 vs. 0.28 for uncut controls), and significantly increased fine root surface to leaf area ratios (2.44 vs. 1.08 for uncut controls) during the first year of growth. The leaf (0.81 g, 6.2%), stem (9.30 g, 71.6%) and root (2.88 g, 22.1%) components of control shoots were not significantly different from severed shoots. It was determined that shoots were not completely independant of the parent plant, but adjusted during further growth after severing. Long distance transplantation (either south or north) would be expected to result in growth reduction similar to that summarized for *B. pubescens* and *B. pendula* by Eriksson and Jonsson (1986).

For *Betula glandulosa* in northern Quebec, Rencz and Auclair (1978) measured a biomass of 5564 $kg{\cdot}ha^{-1}$ (12% of total site biomass) composed of 6% leaves, 53% stems and 41% roots in an open spruce-lichen woodland. Fine root biomass for Alaskan *B. glandulosa* was measured at 43.5 mg per stem (Kummerow et al. 1983). Using a shrub population of *B. pubescens* ssp. *tortuosa* individuals (2.5 cm to 5 m height), Sveinbjörnsson (1987) found a similar biomass distribution of 6% leaves, 41% roots and 53% branches. In that study, plants under 1 m in height showed linear relationships in surface area and dry weight with plant height, and weight per surface area for leaves, branches, shoots and roots.

Other environmental conditions

Snow cover is important for the protection of birch shrubs from winter deer browse in Scotland (I. Brodie - pers. comm.) as well as from low temperatures in colder locations and wind desiccation. Snow cover affects *Betula nana* by influencing growth form and plant height (Kallio and Mäkinen 1978, Jonasson 1982, Fredskild 1991) although Kallio and Mäkinen (1978) distinguish between mountain and swampy *B. nana* "strains" of which swampy populations are more sensitive to low snow cover. For *B. glandulosa*, snow cover is an important factor controlling its natural range (Jacobs et al. 1985). As snow cover is reduced with increasing continental climate, *B. glandulosa* becomes increasingly excluded from the coldest continental regions. Arseneault and Payette (1992) found a highly significant decrease in *B. glandulosa* height with decreasing average snow depth in northern Quebec. In a study of *B. cordifolia* Regel (another polycormic shrub), Maillette (1987) found that most branch extension occurred on the leeward side in alpine tundra sites.

Birch shrubs growing on slopes have a competitive advantage over trees when avalanche frequency was <15-20 years because they rarely break (Johnson 1987). *Betula glandulosa* was found to grow above treeline on slopes where average avalanche frequency was 2-3 years. *B. glandulosa* has a high frost tolerance (Krajina et al. 1982) and this is also likely true for *B. nana* as Biebl (1967) showed that frost resistance in *B. nana* is increased by short daylength. Corns (1974), Jonasson (1981) and Shaver and Cutler (1979) recorded *B. nana* growing well on soils with frost boils and severe frost heaving.

Neither species appears to be very tolerant of continuous flooding as they are not normally found on waterlogged areas, but grow on elevated hummocks on saturated sites (Wein and Bliss 1974, Vitt et al. 1975, Corns 1974, Backéus 1985, Ebert and Ebert 1989, Hermanutz et al. 1989, Rodwell 1991). Subarctic and alpine populations of both species grow on dry sites (Viereck 1979, Jonasson 1981, Fredskild 1991, I. Brodie - pers. comm.) and in areas of low annual precipitation (Andrews et al. 1980) which may indicate a tolerance for periodic drought.

Structure and physiology

Morphology

Betula nana grows to 1m in height with procumbent, wide spreading stems and strong branching (Clapham et al. 1962, Hultén 1968, Viereck and Little 1972, Bean 1976, Stace 1991). In British populations, it grows as an undershrub with shoots barely reaching the canopy surface of associated *Calluna* (Poore and McVean 1957). Twigs are dull dark brown, not warty, and pubescent. Young twigs are covered with resin spots. Leaves are dark green above and paler beneath with a petiole up to 3 mm. Subspecies *exilis* (Suk.) Hult. has shorter leaf blades (0.5-1 cm long) than the subspecies *nana* (0.5-2.0 cm). Leaves are orbicular or obovate-orbicular, crenate all around, rounded at both ends and glaborous (or with a few glands) at maturity (Figure 2-4). Stomata counts on the lower leaf surface ranged from 69 mm^{-2} on Ben Loyal, N. Sutherland, Scotland to 86 mm^{-2} at Carrour (N. of Rannoch Moor) Inverness-shire, Scotland (P.A. Thomas, unpubl. data). No stomata were found on the upper surface. Bracts lack a resiniferous hump on the back, and possess a cuneate base and three parallel (almost equal) narrow lobes at the apex. Nutlet wings are half as broad as the body. Male inflorescence is about 0.8 cm, while the female inflorescence is 0.5-1.0 cm in fruit. Average pollen size is 18-22 μ, with a grain diameter:pore depth ratio of 11.3-11.5 (Terasmäe 1951, Takeoka and Stix 1963, Birks 1968, Prentice 1981, Edwards et al. 1991).

Wood anatomy by Bhat and Kärkkäinen (1982) define characteristics that separate *Betula nana* from other birches (see also Miller 1975): the average number of bars per perforation plate (up to 17), narrow growth rings (0.25 mm), large vessel numbers (260 mm^{-2}), small vessel size (37 mm tangential diameter, 0.30 mm length), short fibres (0.431 mm), and high ray numbers (14.5 mm^{-1}) and percentage (14.6%). Roots are not well studied, but the rooting zone for *B. nana* in an Alaskan tundra community was determined to be less than 150 cm in diameter (Chapin et al. 1980). *B. nana* and *B. glandulosa* are both considered relatively deep-rooted species (Kummerow et al. 1983, Shaver and Cutler 1979).

Betula glandulosa (Dugle 1966, Hultén 1968) is a prostrate or erect shrub growing 0.3-2.5 m in height. Branchlets are coarse, glabrous, reddish brown to gray and are covered with white to yellowish resinous glands and scattered long white to black hairs. Branches (Figure 2-5) are dark brown to brownish black, dull and bark does not exfoliate. Leaves are 0.5-2 cm long, 0.5-1.5 cm wide, broadly ovate to orbicular, rounded at the apex and base (or cuneate) with less than 10 crenations along each margin. Leaves are usually dark green above and yellowish green to dark green below, turning orange to dark purplish red in autumn. They are coriaceous, glutinous, slightly reticulate with glandular spots beneath. Stomata average 19-39 μ (Dugle 1966) to 39 μ (Inki and Valanne 1979); stomatal counts for plants sampled across western and northern Canada averaged 139 mm^{-2} (de Groot, unpubl. data). Petioles are smooth to puberulent, reddish, 1-5 mm long and are often resinous coated. Stipules are ovate acute, ciliate and scarious. Solitary staminate catkins are 4-7 mm long in winter with ovate, dark green glandular bracts and ciliate margins. Winter buds are chestnut brown, 1-2 mm long, ovoid, acute and very resinous. Catkins become 10-20 mm long at anthesis. Pollen averages 15-25 μ diameter. Pistillate catkins are short-stalked, up to 10 mm long in flower, 10-15 mm long in fruit and 4-6 mm wide, erect ovoid to narrow cylindrical and obtuse. Bracts are finely ciliate, puberulent and possess a resiniferous hump on the back at maturity. Lobes are divergent, rounded at the apices with the median lobe slightly longer than the two lateral lobes. The nutlet has narrow wings that are broader toward the apex. The body of the samara is ovate to orbicular, 1-1.5 mm long, 1-1.5 mm wide and is about twice as wide as the wing.

Betula nana and *B. glandulosa* possess short and long shoots, similar to arborescent birches (Macdonald and Mothersill 1983, Macdonald et al. 1984, Maillette 1987). Proximal axillary buds on the long shoots usually produce short shoots, while the distal buds may elongate into new long shoots. Short shoots show insignificant internodal growth (Macdonald et al. 1984) so crown expansion is a function of the sympodial growth pattern of long shoots.

There is little morphological variation within *Betula nana* populations (Anamthawat-Jónsson and Tomasson 1990) but there is great variation between mire and tundra populations (Kallio and Mäkinen 1978, Aleksandrova 1980, Jonasson 1981). Both *B. nana* and *B. glandulosa* become low and procumbent with small leaves as environmental conditions become more severe (Kallio and Mäkinen 1978, Weis and Hermanutz 1988). *B. glandulosa* grows as a low plant in large contiguous, clonal patches at its northern limit, and as tall, narrow upright shrubs in the core area of its range (Weis and Hermanutz 1993). Seedling growth is very slow for both species. *B. nana* in Scotland develops 4-6 true leaves and never exceeds 3 cm in height during the first year of growth, while *B. glandulosa* may reach 5 cm (I. Brodie - pers. comm.) (Figure 2-6).

Mycorrhiza

There is very little data on fungi associated with *Betula nana* in Britain because of its limited distribution (Watling 1984) although mycorrhizal fungi are often associated with dwarf birch in arctic and alpine areas. On drier peat sites in Scotland, *Lactarius helvus* (Fr.) Fr., *L. rufus* (Scop.: Fr.) Fr. and an unidentified *Russula* sp. of Section *Emeticinae* have been associated with *B. nana* (Watling 1987). In wetter depressions, *Leccinum holopus* (Rostk.) Watling has also been recorded with *B. nana* (Watling 1987).

In Finland and Greenland, *Leccinum rotunifoliae* is most prevalent with *Betula nana* while *L. scabrum*, *L. variicolor* Watl., *Boletus edulis* and many *Cortinarius*, *Lactarius* and *Russula* species (including *L. rufus*, *R. decolorans* and *R. claroflava*) are common associates (Kallio and Mäkinen 1978, Watling 1984, Metsänheimo 1987). *Amanita fulva* (Schaeff.) Pers., *A. arctica* Bas, Knudsen & Borgen sp. nov., *A. battarrae* Boud., *A. mortenii* Knudsen & Borgen sp. nov., *A. nivalis* Grev., *Boletus subtomentosus* Fr. , *Leccinium aatrostipitatum* Smith & Theirs, *L. holopus* (Rostk.) Watling var. *americanum* Smith & Theirs, *L. variicolor* Watling and *Paxillus involutus* (Batsch) Fr. have been recorded in association with *Betula glandulosa* in Greenland, while *Amanita groenlandica* Bas ex Knudsen & Borgen sp. nov. and *Leccinium rotundifoliae* (Sing.) Smith, Theirs & Watling have been found with both *B. nana* and *B. glandulosa* (Knudsen and Borgen 1987). *Russula nana* Killerm. has been associated with *B. nana* in Alaska and Canada by Miller (1982) and Miller et al (1973) as *R. emetica* Schaeff.: Fr. var *alpestris* Boud. (Moser and McKnight 1987). A summary of other mycorrhiza on both dwarf birches in Greenland is given in Table 2-1.

Perennation: reproduction

Both dwarf birch species are generally nanophanerophytes in the undisturbed state, although they may be chamaephytic on some sites. When burned or clipped, they become hemicryptophytes. Both species reproduce primarily by sexual means, but also by vegetative layering as adventitiously-rooting aboveground stems become over grown by moss (Shaver and Cutler 1979) or at nodes underneath the surface moss layer. *Betula nana* also proliferates by fragmentation of the woody rhizome (Whittaker 1993). Sexual reproduction in both species is very poor or almost non-existant in northern latitudes where development by layering is important (Vaarama and Valanne 1973, Weis and Hermanutz 1988, Hermanutz et al. 1989). Hermanutz et al. (1989) postulate that the loss of sexual reproduction in *B. glandulosa* on Baffin Island may be the result of climatic cooling during the last few thousand years. These populations are at the northern extent of their range and they appear to be remnants of sexually producing populations during earlier warmer periods.

Individual clones (genets) up to 5 m in diameter have been formed by vegetative layering in *Betula glandulosa* (Campbell 1983, Weis and Hermanutz 1988) while Kallio and Mäkinen (1978) report a *B. nana x B. pubescens* clone near the Finnish-Norwegian border that covers hundreds of square meters. Kummerow (1983) showed that *B. nana* clones are not independant of the parent plant. He severed individuals from the original plant in early summer and severed clones had smaller, slightly chlorotic leaves while most flowers and fruits aborted. These characteristics were not present the following year.

Both dwarf birches are polycormic shrubs with strong suckering capacity, an important characteristic of subsection *Nanae* (Vaarama and Valanne 1973, Sulkinoja 1990, Weis and Hermanutz 1993). Suspected *Betula nana* and *B. pubescens* hybrids (*B. pubescens* Ehrh. ssp. *tortuosa* [Ledeb.]) in south Greenland have shown the ability to sprout from stem basal buds and rooted branches. Although most buds on *B. pubescens* Ehrh. were found belowground in large clusters, the majority of sprouting occurred from aboveground buds which were located singly or in small clusters (Kauppi et al. 1988). It was determined that sprouting was inhibited by clustering, a trait found in *B. glandulosa*. Kauppi et al. (1988) also found that clustering increased with plant age and that clusters formed more often on stumps in peat soil (vs. mineral soil) and on seed origin stumps (vs. sprout origin). Prolific sprouting has been induced in the dwarf birches by cutting. Decreasing light intensity decreased starch content in roots of *B. pendula* Roth which reduced sucker production and mean sprout height (Johansson 1986). Sprout height growth in *B. nana* and *B. glandulosa* was greater under warmer temperatures (Backéus 1985, chapter 3) and in *B. pendula* (Johansson 1986). Underground stems and roots are usually much older than suckers or sprouts, as sprouting may occur from centuries-old root remnants (Brodie 1994). One *B. nana* stem sampled in southeast Greenland had 147 growth rings, while others having 50-80 rings were common (Miller 1975).

Chromosomes

Both dwarf birch species have chromosome counts of $2n=28$ (Löve and Löve 1961, 1982; Moore 1982). Triploids and tetraploids are reported only in hybrids, often between *Betula nana* and *B. pubescens* ($2n=56$). The F_1 hybrid between these two *Betula* species have chromosome numbers that range from 28 to 56 (both euploid and aneuploid) (Kallio and Mäkinen 1978, Anamthawat-Jónsson and Tomasson 1990). The basic chromosome number of the genus is generally accepted as $X=14$, although it has been suggested that it could be $X=7$ (Brown and Al-Dawoody 1979, Brown and Williams 1984, Eriksson and Jonsson 1986). Discrepency in chromosome counts may exist because of the large number and small size of chromosomes.

Physiological data

Light

As northern circumpolar species, both birches are adapted to long growing season photoperiods. *Betula nana* has shown a positive net assimilation rate even at midnight during the continuous daylight of mid-summer (cited in Kallio and Mäkinen 1978). *B. nana* leaves possess a high number of accessory pigments which may be an adaptation to short growing seasons with longer daylight (Kenworthy et al. 1972). *B. glandulosa* seedlings showed extremely suppressed growth in treatments of short (9 hour) photoperiod (Vaartaja 1960), a typical response of northern species. *B. glandulosa* leaves were abnormally small when grown under short daylength, but were abnormally large with artificial long day treatments (night having four 3-hour dark periods broken by one hour of light). Seedling tips also appeared rosetted in short daylength treatments because of short internodes. Biebl (1967) demonstrated that a reduced photoperiod of 8 hours (during the normal 24-hour long day in mid-summer) for 10 days was sufficient to increase heat resistance and significantly increase frost resistance of *B. nana*. It also appears to have a low tolerance to shade as *B. nana* can be found in the understory of open tree stands but not under closed canopies (Malmer 1965, Hutchinson 1966), similar to *B. glandulosa* (e.g., Rencz and Auclair 1978, Viereck 1979, Moore 1980, Ducruc and Zarnovican 1976).

Photosynthetic capacity of *Betula nana* was found to be about 37 mg $CO_2 \cdot h^{-1} \cdot g^{-1}$ by Johnson and Tieszen (1976), a high value in comparison to other arctic tundra plants. A lower rate of 11 mg $CO_2 \cdot h^{-1} \cdot g^{-1}$ was measured for excised leaves of northern USSR *B. nana* by Zalenskij (1972). Maximum potential photosynthetic activity (saturated CO_2 conditions) occurred near 20°C, and increased with light intensity as it approached 50×10^3 lux. Prudhomme (1982) found previously defoliated *B. pubescens* ssp. *tortuosa* to fix CO_2 at a rate 63% higher than undamaged individuals. Prudhomme (1982) indicated that carbon was partitioned to initially support photosynthesis which then provided an increased carbon source for chemical defenses and storage reserves.

Stoner et al. (1978) found total photosynthetic leaf area for *Betula nana* in Alaskan alpine tundra to be 1.4 - 3.9 $m^2 \cdot m^{-2}$, and the projection (shadow-casting) area for stems to be 0.3 - 0.8 $m^2 \cdot m^{-2}$. In Alaskan shrub tundra communities where *B. nana* was a dominant member, average daily carbon dioxide output (including aerial plant parts) was about 2.6 $g \cdot m^{-2}$, with a peak rate of 3.0-3.4 $g \cdot m^{-2}$ in mid season (Poole and Miller 1982). Plant nutrient level is important to photosynthesis in the dwarf birches as 51% of photosynthetic variation in *B. pubescens* ssp. *tortuosa* was explained by leaf nitrogen concentration (Karlsson and Nordell 1988). Photosynthetic rate may be maintained following defoliation (as found in *B. pubescens* ssp. *tortuosa*) through reallocation of stored carbohydrates (Hoogesteger and Karlsson 1992).

Water relations

Using a null balance porometer, Oberbauer and Miller (1981) report an absolute maximum leaf conductance of 1.09 $cm \cdot s^{-1}$ (mean maximum leaf conductance of 0.61 $cm \cdot s^{-1}$) for *Betula nana* samples from interior Alaska. Using the drying curve method (which includes boundary layer resistance), they recorded a lower maximum leaf conductance of 0.47 $cm \cdot s^{-1}$, and a relative water content of 66.8% at minimum leaf conductance. Out of twelve shrub and herbaceous species measured, *B. nana* showed the lowest field transpiration rate (0.5-2.5 $g \cdot m^{-2} \cdot min^{-1}$). *B. nana* also showed the smallest change in xylem pressure potential with relative water content (-15 bars at 78%) and consistently had low maximum pressure potentials over a range of moisture regimes (Oberbauer and Miller 1981). It also had the lowest seasonal pressure potentials (-10.6 bars).

In a study by Bliss (1960), transpiration rates of 0.674 and 0.906 $cm^3 \cdot dm^{-2} \cdot$30-hour period (0.037 and 0.050 $g \cdot m^{-2} \cdot min^{-1}$) were measured for *Betula nana* ssp. *exilis* using the potometer method with detached branches. These rates were about 2-3 times greater than rates found in alder and willow at the same site, but 10-50% less than *B. minor* (Tucherm.) Fern. at an eastern North American alpine site. These rates, which were based on water drawn by detached stems over a long time period, were much lower than those measured by Oberbauer and Miller (1981) which used the weight loss of detached leaves over a short time period. Transpiration rates for *B. nana* (Bliss 1960) increased with temperature and vapour pressure deficit, and decreased with cloud cover and wind speeds greater than 10-13 $km \cdot h^{-1}$ (a direct relationship for speeds less than this). Greater rates per leaf area in *Betula* were attributed to higher transpiration rates per unit leaf size because of thicker and smaller leaves, while the small shrub size reduced the total loss per plant. Using *B. pubescens* ssp. *tortuosa*, Kauhanen (1990) found dry and moist habitat birches showed no difference in stomatal behavior under natural conditions, but artificial stress caused the dry habitat specimens to close stomata more abruptly with decreasing xylem-water potential.

Temperature

Ungerson and Scherdin (1962, cited in Backéus 1985) describe the optimum temperature for net photosynthesis of *Betula nana* to be around 13°C, while Johnson and Tieszen (1976) found a value near 10°C. In an experiment by Backéus (1985) in central Sweden, physiological growth started to decrease when the cumulative daily temperature sum approached 400°C and the cumulative shoot length growth began to plateau at a cumulative daily temperature sum of about 600°C.

Nutrition

In Alaska, early spring growth of leaves and inflorescences in *Betula nana* placed a high demand for nitrogen, as well as phosphorus and (to a lesser degree) potassium (Chapin et al. 1980). Belowground storage of nitrogen appears critical since growth often starts when the ground is frozen and soil nutrients are unavailable. The fact that *B. nana* is able to utilize organic N (which can be derived from fresh litter) explains its ability to grow in tundra locations that have very low inorganic N concentrations (Michelsen et al. 1996). It may also take up NO_3^- if it is available. Nitrogen decrease in belowground stems and roots in spring were coupled with a substantial increase in leaf nitrogen. Maximum leaf nitrogen content was reached 3-4 weeks after snow-melt, eventually accumulating 6.7% of total plant nitrogen (32% of aboveground nitrogen) even though leaves only accounted for 2.8% of total plant biomass. Nitrogen demand continued as root growth followed leaf and inflorescence growth. Nitrogen content in leaves decreased sharply later in the growing season. Potassium and phosphorus followed similar patterns to nitrogen level and distribution within the plant. Between the end of June and the end of August, leaf nitrogen, phosphorus and potassium decreased from 3.7% to 1.2% (leaf dry weight), 0.4% to 0.1%, and 1.0% to 0.4%, respectively.

A similar Alaskan study by Shaver and Chapin (1980) using *Betula nana* stems and buds in mid-June and stems and leaves in mid-August showed similar decreasing trends with about 0.5% to 0.35% phosphorus, and 0.7% to 0.5% potassium; however, nitrogen increased slightly from 2.8 to 3.0%. Chapin et al. (1980) found calcium accumulated in leaves during the same period from 0.2% to 0.35%, while magnesium remained at a relatively constant level throughout the season. Mid-August values by Shaver and Chapin (1980) were about 0.55% calcium and 0.28% magnesium (very high in comparison to other tundra plants). *B. glandulosa* showed similar peak leaf nitrogen concentration in spring with a steady decline through the growing season (Prudhomme 1983).

Betula nana soil nitrogen uptake did not balance with demand until later in the growing season (Chapin et al. 1980). Prior to leaf drop, substantial translocation of leaf nitrogen, phosphorus and potassium occurs, although the movement and storage of potassium appears to be less effective. Calcium concentration continually increased in leaves over the growing season, while stem concentrations decreased (magnesium distribution was similar). This shows a lack of calcium movement from senescing leaves, and the use of stems for calcium storage.

Chepurko (1972) found the following elemental content (kg/ha) for leaves and other perennial aboveground parts (in brackets) for *Betula nana* (1030 kg/ha aboveground biomass) in northern USSR alpine tundra (time of year not stated): 1.92 (6.19) N, 0.12 (0.50) Si, 0.79 (3.64) Ca, 0.18 (0.64) Mg, 0.11 (0.46) P, 0.04 (0.13) Al, 0.08 (0.16) Fe, 0.02 (0.06) Mn, 0.01 (N/A) Ti, 0.14 (0.56) S, and 0.03 (0.12) Na. Paribok et al. (1967) examined the content of eleven micronutrients in *B. nana* and found that it accumulated manganese and had a high cobalt content. January nutrient concentrations in *B. glandulosa* twigs was found by Pease et al. (1979) to be 0.15-0.35% potassium, 0.09-0.14% phosphorus, 0.07-0.12% magnesium and 0.5-0.7% calcium. Sveinbjörnsson et al. (1992) found that leaf nitrogen (1.86-2.23%), phosphorus (0.20-0.25%) and potassium (0.98-1.14%) concentrations increased in *B. pubescens* ssp. *tortuosa* with elevation in Swedish Lapland.

Total nonstructural carbohydrate (TNC) concentrations are high in *Betula nana* and *B. glandulosa* root and belowground stem tissues (about 9% and 7.5%, respectively) in the early spring, and decline up to 45% as shoot and root growth proceed (Chapin 1980, Chapin et al. 1986, Kummerow et al. 1983). Lipids do not appear to be a major energy reserve for spring growth, although concentrations are high in *B. nana* stems (about 12-22%) which may be the result of a high allocation to anti-herbivore metabolites (Chapin et al. 1986). Following spring flush, leaf expansion and secondary cell wall development is supported by current photosynthesis (Chapin et al. 1986). They also found TNC levels were lowest for all Alaskan *B. nana* tissues in early July (about 3.5-6%; a level similar to Shaver and Chapin 1980) with all tissues increasing to 8-12% (except for inflorescence at about 13-14%) by early August. Substantial allocation of carbohydrates to overwinter storage was shown by a total plant TNC increase of 78% between mid July and late August. There also was a TNC decrease in leaves in autumn, with a large accumulation in roots and stems (primarily in underground stems).

In *Betula glandulosa*, total January twig carbohydrate content was found to be 54-58% (Pease et al. 1979). Leaf TNC values of *B. pubescens* ssp. *tortuosa* were measured at 21.1-23.1% (Sveinbjörnsson et al.

1992). Prudhomme (1983) found that sugar content in *B. glandulosa* leaves declined from mid-July to late August, suggesting that translocation of photosynthate to growing and storage areas was important throughout the growing season.

In studying *Betula nana* and several other tundra species in Alaska, Chapin et al. (1986) found that TNC concentrations correlated positively with fibre and negatively with nitrogen, phosphorus, potassium and tannin cell contents. This suggests that deficiency in these minerals leads to carbohydrate accumulation, or that increased carbohydrate levels induces increased fibre content. The authors suggest this may indicate that nutrient fertilization will cause higher tissue concentration of mineral nutrients and reduced TNC and fibre. However, Sveinbjörnsson et al. (1992) found no correlation between TNC and foliar nutrient concentration levels in *B. pubescens* ssp. *tortuosa*. They also found that application of nitrogen-containing fertilizer (ammonium nitrate [28% N]; NPK 11-5-18) resulted in increased numbers of long shoots, increased height growth, and a 30% increase in individual leaf area and weight.

Fertilization of Alaskan *Betula nana* with nitrogen, phosphorus and potassium was found to increase leaf area per shoot, leaf and stem nitrogen (Kummerow et al. 1987) and branch growth but may cause shrub decline in the longterm (Ebert and Ebert 1989). Fertilization of Alaskan *B. nana* with N, P and K (separately and in combination) resulted in highly significant increases in new plant tissue concentrations (Shaver and Chapin 1980). *B. nana* was much more responsive to phosphorus fertilization later in the growing season, while Ca and Mg concentrations decreased with N fertilization (due to stimulated growth and dilution of non-limiting nutrients). New shoot mass increased most with N fertilization, particularly in combination with P, while TNC was not significantly affected by treatments. Fertilization with sugar reduced nitrogen and phosphorus levels, and N was also reduced by additions of lime ($CaCO_3$).

Application of low rates of nitrogen fertilizer to *Betula nana* in arctic Canada showed increased primary production, while applications of only phosphorus fertilizer generally reduced production (Haag 1974). It appeared that production was limited more by available soil nitrogen (a similar result found in *B. pubescens* ssp. *tortuosa* by Sveinbjörnsson et al. 1992) than phosphorus, although nitrogen could be taken up and metabolized at low soil temperatures. McKendrick et al. (1980) showed that soil fertilization by decomposing caribou carrion increased leaf nitrogen and phosphorus content in *B. nana*.

Other aspects

Although there is no specific data on *Betula nana* or *B. glandulosa* response to acid rain, laboratory experiments on *Betula pubescens* ssp. *tortuosa* showed that pollen germination and germ tube length was reduced by increased acidity of the incubation solution; field experiments suggest there are mechanisms that may buffer the effects of acidity on pollen germination *in vivo* (Neuvonen et al. 1991). There was no effect by acid rain on the number or size of catkins, or on the germination capability of seeds. It also appears that acid rain may result in decreased decomposition rates of birch litter (Neuvonen and Suomela 1990).

Biochemical data

Both *Betula nana* and *B. glandulosa* have chemical defense mechanisms to deter browsing, although Bryant et al. (1989) have indicated that the strength of these defenses varies by region. The carbon-nutrient balance of plants affects palatability and herbivore response, and plants in nutrient-poor ecosystems tend to use carbon-based defenses (Bryant et al. 1983, Prudhomme 1983). A negative correlation between leaf nitrogen and foliage phenols was found in *B. pubescens* ssp. *tortuosa* (Haukioja et al. 1985).

The allocation of carbon to defense compounds in *Betula glandulosa* was found to be greatest in the spring and declined with leaf age. A high carbon use priority was shown for total phenolics and the organic acid fraction in the spring when sugar and nitrogen concentrations were highest in new tissues (Prudhomme 1983). The production of alkaloids and volatile oils began in mid season and continued during the remainder of the growth period. It appears that *B. glandulosa* establishes a high level of dosage dependant (quantitative) and some toxic (qualitative) defenses in spring, switching to a lower total level of mostly toxic compounds (alkaloids and volatile oils) later. A high priority was also placed on relatively recoverable alkaloids and organic acids, as opposed to phenolics and volatile oils (Prudhomme 1983). There was also a higher proportion of potentially recoverable hemicellulose suggesting a carbon conservation strategy.

Chapin et al. (1986) found higher lipid concentrations in *Betula nana* in younger tissues, of which anti-herbivore metabolites such as phenolic resins and terpenes were a component. Preferences of eight generalist herbivores were found to correlate positively with nitrogen, phosphorus and potassium, and negatively with lipid and cellulose contents (Chapin et al. 1986). Low nutritional quality and repellency by allelochemicals were found to be potential active defenses against insect herbivores in *B. pubescens* ssp. *tortuosa* (Haukioja 1978, Haukioja et al. 1991). Browsing of *B. glandulosa* was also found to stimulate the production of chemical defenses (Pease et al. 1979, Bryant et al. 1983). In nutrient-poor soils, defoliation may result in nutrient stress which results in greater production of carbon-based allelochemicals as hypothesized in *B. pubescens* ssp. *tortuosa* (Tuomi et al. 1984).

Reichardt et al. (1987) examined the chemical composition of *Betula nana* ssp. *exilis* shoot tips which typically have resinous deposits on the bark surface. An isolated compound was found to be very similar to the triterpenoid papyriferic acid (a substance which deters hare browsing), although there is no evidence to verify if this particular substance has the same effect on vertebrate herbivores. The identified compound was found in high concentration in the Alaskan samples, and was also present in *B. nana* subsp. *nana* in Finland. Chemical investigation of *B. glandulosa* extracts which deter snowshoe hare browsing indicate a minor component of papyriferic acid and a primary component of deacetoxypapyriferic acid, another triterpenoid (Williams et al. 1992). Although the latter compound was the major component, deterrent properties appear to be the result of a mixture with other minor triterpenes. Further analysis of *B. nana* triterpenoids is provided by Pokhilo et al. (1985, 1990) and Atopkina et al. (1987).

A strong positive correlation was found between nitrogen, phosphorus and potassium content and preference by generalist tundra herbivores (Chapin et al. 1986). There was also a strong avoidance of fibre, terpenes and resins. Nutrient concentration was most important for vertebrate herbivores, while cellulose avoidance was most important to invertebrates. Resistance to insect herbivores was shown to be quite variable in *Betula pubescens* ssp. *tortuosa* (Hanhimäki 1989, Hanhimäki and Senn 1992).

Other internal protection mechanisms from insect herbivores were not located for the dwarf birches, although delayed inducible resistance and poor performance of late season herbivores following early season foliage damage was found in *Betula pubescens* ssp. *tortuosa* (Neuvonen et al. 1987, 1988). Birch leaves were also found to be less usable by herbivores in the year following defoliation, and shrub birches were able to recover after defoliation better than trees, particularly after a warm summer (Haukioja 1979). The type of herbivorous damage may also influence plant nutrition and chemistry, as removal of apical buds (animal browse) may induce improved foliar quality while foliage removal may induce resistance through chemical defense (Prudhomme 1982, Haukioja et al. 1990). If the plant reverts to juvenile growth (e.g., suckering), then resistance may also be induced (Bryant et al. 1983, Haukioja et al. 1990).

Betula nana leaves sampled in a Finnish study showed a relatively low content of essential oils in comparison to other *Betula* species, although these differences were greatest in the spring and least in the autumn (Inki and Väisänen 1980). Oil components in *B. nana* are primarily monoterpenes. There was a large amount of oil found in the leaves of the hybrid between *B. nana* and *B. pubescens* and biosynthesis has proceeded to the sesquiterpene level.

Phenology

Leaf growth commences soon after snowmelt and, as in other birches, early leaves form on both short and long shoots (Maillette 1982, Macdonald and Mothersill 1983, Macdonald et al. 1984, Tuomi et al. 1989b). Fine root growth begins about 1 week after bud break (Kummerow et al. 1983). As early leaves expand, a single female inflorescence appears at the apex of short shoots. Long shoots are heterophyllous with additional late leaves developing throughout the growing season as the shoot elongates. Naked male inflorescences are formed on long shoot terminals as elongation ceases, unless shoot tip abortion occurs (usually mid-season). Heat-sums are strongly correlated with the onset of anthesis in birch (Pelham et al. 1984).

Autumn leaf senescence is genetically influenced, with colours ranging from yellow to red and reddish brown (Kallio and Mäkinen 1978). *Betula nana* in Scotland generally develops red autumn colours, but colour intensity appears to be a reflection of level of air temperature (I. Brodie - pers. comm.). *B. glandulosa* plants in western Canada that were transplanted to a milder temperature regime turned red in autumn, while the original population turned yellow (chapter 2). There is some disagreement on the mechanisms triggering the onset of autumn colours. Kallio and Mäkinen (1978) describe the induction of autumn colours in *B. nana* by an artificial long night of 12 hours for 10 successive nights starting in the last week of July. Biebl's (1967) experiment also induced leaf colouring in early July with reduced photoperiod; however, McGraw et al. (1983) document early senescence of *B. nana* which appears to be the result of low overall temperatures during July. Eriksson and Jonsson (1986) indicated that photoperiod is likely the dominating factor, with temperature acting as a modifier. Fertilization caused earlier anthesis and later leaf color change in *B. nana* (Kummerow et al. 1987).

Betula nana female catkins flower in early June in Scotland, with seeds ripening in August (I. Brodie - pers. comm.). Backéus (1985) records flowering and initiation of shoot growth in *B. nana* occurring in central Sweden near mid-May. Most leaves were formed quickly on short shoots, while early leaves appeared on long shoots before the end of May. Late leaves developed singly until shoot growth ceased during the second half of July, and autumn colours appeared in early September. At a mid-latitude site in eastern Canada, bud break in *B. glandulosa* started in mid June, with leaf expansion complete in one week (Prudhomme 1983). New shoot growth began immediately and continued until early August. Male catkins and resin coated overwinter buds were formed in August, while new stem tissue became darker and tougher. Some leaf senescence started in August, but most occurred in September. Leaf abscission was complete by the end of September. In west-central Canada, leaf flush typically occurred in early May, with leaves turning colour in mid-September (chapter 2). *B. nana* in northern Alaska initiated bud break in early June and leaf color change occurred in early August (Kummerow et al. 1987). Tuomi et al. (1989a) found that manual defoliation could induce a delay in bud break during the next growing season in *B. pubescens* ssp. *tortuosa*.

Floral and seed characteristics

Floral biology

Both dwarf birch species are amphimictic and show a high capacity for sexual reproduction in the core and southern extent of their ranges. *Betula glandulosa* relies on vegetative layering at its northern limit of distribution where viable seed is rarely produced (Weis and Hermanutz 1988, 1993; Hermanutz et al. 1989). *B. glandulosa* is monoecious, producing numerous pistillate catkins that contain 30-50 winged fruits. Each samara contains a single small seed with seed weight averaging 6.5-11.3 million per kilogram (Brinkman 1974).

Male inflorescence induction in birch generally occurs in May prior to bud burst (Macdonald et al. 1984). In summer, male flowers in narrow catkins develop from buds at long shoot apices. These remain naked until the following spring when they elongate and bloom prior to leaf expansion. Pollen is released shortly after snowmelt (Pelham et al. 1984, Maillete 1987, Weis and Hermanutz 1993). Late flowering does not produce viable pollen in *Betula nana* (pers. comm. cited in Kallio and Mäkinen 1978). Induction of female inflorescences occurs in mid-summer (Macdonald and Mothersill 1983) in short shoot buds and appear with the leaves in spring (Weis and Hermanutz 1993). They are wind pollinated and become conelike as they mature in late summer or early autumn. Localized defoliation was shown to reduce biomass of female inflorescences in *B. pubescens* ssp. *tortuosa* (Tuomi et al. 1989b). Samaras are primarily dispersed by wind in the autumn, while the remaining seed is released as catkins disintegrate during winter (aided by foraging activity of small birds) and blown over the snowcover.

In general, cross-fertilization is promoted in *Betula* through dichogamy (Fryxell 1957) and a strong self-incompatibility system (Hagman 1971, cited in Eriksson and Jonsson 1986) although it is not completely self-incompatible (Stern 1963a, Eriksson and Jonsson 1986). Incompatibility appears to increase at high temperature because of reduced pollen tube growth (Eriksson and Jonsson 1986). Male and female functions of northern *B. glandulosa* and *B. nana* are almost simultaneous (Weis and Hermanutz 1993, Anamthawat-Jónsson and Tomasson 1990). Staminate catkins were found to mature slightly before pistillate catkins, but pollen shedding and stigmatic receptivity showed some overlap within the same branch and considerable overlap within the entire genet (Weis and Hermanutz 1993). Stern (1963b) determined that male flowering was strongly controlled by genetics while environment had a greater control on female flowering. The decumbent growth form of subarctic populations may also be a restricting factor in the dispersal of pollen (Hermanutz et al. 1989).

Hybrids

Hybridization within *Betula* is extensive, particularly in subarctic areas where the short growing season reduces differences in timing of flowering. The range of many northern *Betula* species overlap, and incompatibility may be reduced by environmental conditions (Hagman 1971). Macrofossils from Late Glacial and Early Glacial deposits show the earliest record of the hybrid *B. nana* x *B. pubescens* Ehrh. in the United Kingdom (Godwin 1975). Several hybrid studies have been conducted on the slopes of Ben Loyal in Sutherland. Morphological, cytological and biochemical examination of this population shows evidence of hybrid origin (Kenworthy et al. 1972). It appears that backcrossing between the *B. nana* x *B. pubescens* hybrid and *B. nana* may also occur but there is no evidence of backcrossing to *B. pubescens* (pers. comm. cited in Aston 1984). Introgressive hybridization from *B. nana* to *B. pubescens* ssp. *tortuosa* has been reported in Finland and Greenland (Kallio 1978, Kallio and Mäkinen 1978, Sulkinoja and Valanne 1987, Sulkinoja 1990). Using a reference population of *B. nana* from Scotland, Elkington (1968) concluded that introgressive hybridization was also taking place between these two species in northwest Iceland. Using petiole length and relative fruit wing width, examination of the Icelandic populations indicate they are composed of F_1 hybrids and backcrosses mainly to *B. pubescens* ssp. *tortuosa*. Further study using Icelandic plants produced F_1 hybirds that were primarily triploid (2n=42), and some diploid (2n=28) (Anamthawat-Jónsson and Tomasson 1990). The diploid hybrids were morphologically similar to *B. nana* (2n=28) and easily distinguished from the triploids. Backcrossing with *B. pubescens* ssp. *tortuosa* (2n=56) produced plants with 42 and 56 chromosomes, indicating that triploid hybrids are not completely sterile. Gene flow appears to be primarily from *B. nana* to *B. pubescens* ssp. *tortuosa* via intermediate triploids (not by aneuploid complexes), although gene transfer can occur in the opposite direction much less extensively (Anamthawat-Jónsson and Tomasson 1990). Clausen (1962) suggested that birch of higher ploidy is introgressed by birch of lower ploidy, and this appears to hold true when other factors are equal (Dugle 1966). Physical mapping of rDNA by *in situ* hybridization of Icelandic *B. nana* and *B. pubescens* suggested that the genomes were of different evolutionary origins and that rDNA polymorphism may reflect gene flow between and within populations of the two birch species (Anamthawat-Jónsson and Heslop-Harrison 1995).

Hybridization of *Betula nana* with *B. pendula* Roth in Europe (Kallio and Mäkinen 1978, Inki and Väisänen 1980) and *B. papyrifera* Marsh. in North America (Viereck and Little 1972) have also been reported. Hybridization of *B. nana* and *B. glandulosa* is extensive (Clausen 1970, Fredskild 1991) and Hultén (1968, 1971) considered North American *B. glandulosa* populations to be a complete introgression of *B. glandulosa* with *B. nana* ssp. *exilis*.

Introgressive hybridization between *Betula glandulosa* and *B. pubescens* Ehrh. in Greenland is suggested by Elkington and Jones (1974), while Sulkinoja (1990) noted that intermediates were frequent and that the hybrid may also backcross to parent species. Introgression of *B. glandulosa* with *B. pumila* L. var. *glandulifera* Regel (*B.* x *sargentii* Dugle) with gene flow towards *B. pumila* (Dugle 1966, Brunsfeld and

Johnson 1986), and with *B. fontinalis* Sarg. (*B.* x *eastwoodae* Sarg.) with backcrossing to both parents (Dugle 1966) are also noted, although Dancik and Barnes (1972) suggest that the intermediate population of *B.* x *eastwoodae* may only be a group of F_1 hybrids. *B. glandulosa* hybridizes with *B. pendula* and produces viable seed (Inki and Valanne 1979). Hultén (1968) suggested that Alaskan *B. occidentalis* Hook. is a hybrid population of *B. glandulosa* and *B. papyrifera* Marsh. subsp. *humilis* (Regel) Hult., and that its similarity to eastern North American *B. minor* Fern. may indicate that population to be a hybrid of *B. glandulosa* with eastern birches. *B.* x *sargentii* also hybridizes with *B. papyrifera* Marsh. (*B.* x *arbuscula*) (Dugle 1966).

There is strong evidence to suggest that hybridization and introgression from *Betula nana* to *B. pubescens* has resulted in the evolution of *B. pubescens* Ehrh. ssp. *tortuosa* (Ledeb.) (*B. tortuosa* Ledeb.) (Vaarama and Valanne 1973, Hämet-Ahti 1987, Sulkinoja 1990). Backcrossing was found to be evident with the *B. nana* parent (Vaarama and Valanne 1973) and introgression from *B. nana* to *B. pubescens* ssp. *tortuosa* has also been suggested (Stace 1991). Generally, there is tendancy for *Betula* hybridization to occur between diploid (*B. nana*, *B. glandulosa*) and tetraploid species (*B. pubescens*). There is better crossing success with *B. pubescens* when *B. nana* or *B. glandulosa* is the female parent as the reciprocal cross is highly incompatible (Clausen 1970, Sulkinoja 1990). *B. nana* and *B. pubescens* hybrid progenies have shown chromosome numbers from the triploid to pentaploid (2n=70) levels, including introgressants with aneuploid and tetraploid individuals (Sulkinoja 1990). A few F_3 seedlings have been grown from a tetraploid F_2 individual.

Experiments with various *Betula* tree species showed reduced fertility in virtually all crosses (Johnsson 1945). Infertility usually occurred to a high degree, and appeared to be greatest within the same section. The receptive timing varies between pistillate catkins on the same plant, as well as between stigmas within the same catkin. Incompatibility within *Betula* is reduced at low temperature (Eriksson and Jonsson 1986), as pollen tube growth may be reduced by high temperature. Hybridization occurs at a greater rate when the female parent is of low ploidy. Clausen (1970 - cited in Eriksson and Jonsson 1986) found *B. nana* and *B. glandulosa* to have at least moderate success at hybridizing with *B. nigra*, *B. pendula*, and *B. pubescens*.

Seed production and dispersal

In *Betula*, fruits develop regardless of seed development and pollination. Seed production was shown to occur in vegetatively propagated two-year old *B. glandulosa* clones (Sulkinoja 1990) and in three-year old (including one year in greenhouse) *B. glandulosa* grown from seed, although only female flowers were produced in that year (Inki and Valanne 1979). Sulkinoja (1990) found an abundant production of fruiting catkins in south Greenland *B. glandulosa*, but episodic and low seed production in subarctic areas may be the result of a reduced number of growing degree days (Hermanutz et al. 1989). *B. nana* seeds examined in Iceland suggest less development at higher altitudes and harsher climates (Elkington 1968). A reduction in fertility is expected from hybridization. Kullman (1984) concluded that the amount of seed produced in *B. pubescens* ssp. *tortuosa* is determined by the thermal conditions of the previous year because the initiation of flower buds occurs in the preceding year. Reduced seed production also occurred when individuals became too widely spaced for effective wind pollination. *Betula* has a relatively long seed ripening time in comparison to other boreal and subarctic catkin bearing genera such as *Salix* and *Populus* (Johnsson 1945).

Samaras mature late in the season and are wind dispersed primarily during late fall and early spring, although some dispersal occurs during winter as well. Annual seed production can be quite high as Weis and Hermanutz (1988) determined that high density *Betula glandulosa* stands released over 13,000 samaras m^{-2} within the stand. Low density stands averaged over 350 samaras m^{-2}, and populations near the northern extent of its range produced 136 and 670 samaras m^{-2} in low and high density areas, respectively.

Viability of seeds: germination

Germination begins mid-May in Scotland, although Aston (1984) and I. Brodie (pers. comm.) have found low germination rates in Sutherland *Betula nana* seed. Aston (1984) also quotes other sources with 21-40% germination rates. In Finland, Kallio and Mäkinen (1978) report good germination (30-60%) in the birch belt and lower subalpine belt. Several months of storage is required to break dormancy (Polosova 1962, cited in Kallio and Mäkinen 1978). High germination rates (>90%) were obtained by Junttila (1970) using *B. nana* seed from Norway treated by stratification or gibberellic acid. Weis and Hermanutz (1988) determined that there was an asymptotic exponential weight dependance on germination of *B. glandulosa*. Near the core range of *B. glandulosa*, they found no germination for samaras <0.09 mg, while all samaras greater than 0.34 mg germinated; total germination rate was about 70%. Northern populations had germination rates <1%.

Sulkinoja (1990) found a high percentage of germinants in south Greenland *Betula glandulosa*. The germination rate of hybrids was generally lower than the parent species, although Inki and Valanne (1979) documented 60% germination for *B. nana* x *B. pendula* hybrids. Weis and Hermanutz (1988) found a high germination rate in buried *B. glandulosa* seeds in northern Quebec, with 229 and 2164 emergants m^{-2} in low and high density stands, respectively. Half of the emergants resulted from seed located in the uppermost layer of living material (about 0-2 cm deep) while the deeper mineral soil layer (5-15 cm) produced 15% of the germinants.

Dormancy of *Betula nana* seed is a function of germination temperature. Dormancy at low germination temperature (12°C) was effectively broken by moist stratification in darkness at 2-3°C for 5-15 days, or by application of gibberellic acid (Junttila 1970). Low germination temperature required longer startification or higher gibberellic concentration (up to 1000 mg l^{-1}) to break dormancy, and interaction between these two treatments was often significant (significant variation occurred between seed provenances). Germination occurred at high temperature (24°C) without special treatment. Germination (after cold stratification) of *B. glandulosa* seed from northern Quebec, Canada was over 60% within 15 days (germination started on day 6) at day:night temperatures of 10:5°C and a light:dark time of 20:4hrs (Weis and Hermanutz 1988). Kullman (1984) found decreasing germination with increasing altitude in *B. pubescens* ssp. *tortuosa* due to the temperature gradient. Germinability was correlated to the mean temperature in the late summer and early autumn of the current year. Germination rate also increased during the fall to a maximum in early winter.

As in all birches, germination of *Betula glandulosa* and *B. nana* seed is also light dependant. Vaartaja (1959) found no germination of *B. glandulosa* in total darkness and increasing germination with decreasing dark periods. As temperature increased from 17°C to 25°C, germination increased from 1% to 3%. In the same experiment, *B. papyrifera* seed collected from sites located across North America had no correlation between origin and germination rate. The best seed lots were less inhibited by reduced light. In an experiment with *B. pendula* and *B. pubescens*, Vaartaja (1956) found that seed germinated well at 25-35°C under all photoperiod conditions. At temperatures of 10-20°C, germination became more dependant on increased photoperiods. Germination was slightly dependant on light intensity with maximum germination occuring at 200 ft-c, although stratified seed had no light requirement for germination.

Herbivory and disease

Animal feeders or parasites

Betula nana has considerably fewer host-specific insects in Britain than the arborescent birches, although it has a far more extensive fauna in other geographical areas (Bachmaier 1965, Shaw 1984). It appears that *Swammerdamia passerella* (Zetterstedt) and *Stigmella nanivora* (Petersen) (Agassiz 1981) are the only specifically phytophagous insects in Britain, but it is also fed upon by a variety of moderately polyphagous moorland moths such as *Argyrotaenia pulchellana* (Haworth) (Shaw 1984) and by *Operophtera fagata* Scharfenberg in Scotland (I. Brodie - pers. comm.).

In other circumpolar areas, insect herbivores on the dwarf birches can be separated primarily into leafchewers and sapsuckers. In an Alaskan study on *Betula nana* and *B. glandulosa* by Koponen (1984), sapsuckers were found to dominate most sites. *Euceraphis betulae*-complex aphids were most common, but psyllids such as *Psylla betulaenanae* Oss. (found extensively in Alaska and in northeast USSR (Hodkinson and MacLean 1980, MacLean and Hodkinson 1980)) and *P. striata* Patch were also found. Other species in this group included *Oncopsis albicollis* Hamilton, *Colladonus youngi* Nielson, *Thamnotettix confinis*

(Zetterstedt) and *Coulinus usnus* Beirne. Leafchewers included *Rheumaptera hastata* (Linnaeus) and *Epinotia solandriana* (Linnaeus). *Eriocrania semipurpurella* (Stephens) was the most common miner. Herbivore fauna generally declined in both numbers and species richness with distance from forest and increase in altitude and latitude. For instance, *B. nana* range was found to extend farther north in Alaska than did *P. betulaenanae* (MacLean 1983).

Serious damage to *Betula glandulosa* by insect herbivory in Greenland is usually caused by defoliating lepidopteran larvae represented by *Operophtera bruceata* (Hults.), *Eucosma indecorana* (Zett.) which also feeds on *B. nana*, and *Acleris caryosphena* (Meyr.) (Koponen 1978). Sapsucking insects include the Homoptera members *Psylla betulaenanae* Oss., the aphid *Euceraphis punctipennis* (Zett.) and the cicadid *Deltocephalus lividellus* (Zett.). In the Canadian west-central prairie provinces, insects on *B. glandulosa* foliage (Ives and Wong 1988) include the caterpillars *Nymphalis antiopa* (Linnaeus) and *Phyllodesma americana* (Harris), the tent caterpillar *Malacosoma californicum pluviale* (Dyar), and the loopers *Aethalura intertexta* (Walker), *Anagoga occiduaria* (Walker), *Campaea perlata* (Guenée), *Cyclophora pendulinaria* (Guenée), *Eufidonia discospilata* (Walker), *Hydriomena furcata* (Thunberg), *Pero morrisonaria* (Hy. Edwards), *Plemyria georgii* Hulst., *Rheumaptera hastata* (Linnaeus) (also a leaftier) and *Semiothisa ulsterata* (Pearsall).

Other lepidopteran larvae documented as feeding on *Betula nana* leaves include *Gynaephora rossii* Curtis (showing strong preference), *Polia* spp., *Paramesia parthenost* Harris, and *Apentisis* spp. apparently feeding with low preference (MacLean and Jensen 1985, Chapin et al. 1986). Sawfly species significantly selected against *B. nana* (MacLean and Jensen 1985). Weis and Hermanutz (1988) reported seed predation by an unidentified wasp larvae in *B. glandulosa*.

Senn et al. (1992) noted that in a *Betula pubescens* ssp. *tortuosa* population in northern Finland, where introgression with *B. nana* occurs, insect herbivores (lepidopteran and sawfly species) selected taller, early flushing, large-leaved trees over the low, late flushing, small-leaved (and poorer quality) *nana*-like trees. In Finland, Kallio and Mäkinen (1978) noted that *Oporinia* caterpillars have caused serious damage to *B. nana* stands, but it does not appear as susceptible as *B. pubescens* ssp. *tortuosa*. Distribution of the geometrid moth *Epirrita (Oporinia) autumnata* (Bkh), and hence defoliation of birch, appears to be limited by winter temperatures as eggs were found to freeze (and subsequently die) between -28°C and -36.5°C (Tenow and Nilssen 1990). Although there is limited information regarding insect herbivores specifically found on *B. nana* or *B. glandulosa*, other possible species may be found on the tree birches (Atkinson 1992) or the morphologically-variable *B. pubescens* ssp. *tortuosa* (Koponen 1973a, 1973b). In colder locations, defoliation in birches may begin and/or concentrate on the lowest foliage because of warmer surface temperatures, or on mid-slope plants where flushing occurs first in the thermal belt as shown with *B. pubescens* ssp. *tortuosa* (Tenow 1990).

Browsing of *Betula nana* by sheep and deer in the British Isles (Brodie 1994) and feeding by reindeer (*Rangifer tarandus tarandus* L.), tundra vole (*Microtus oeconomus* [=*M. oeconomus gilmorei* Setzer] - Bee and Hall 1956), collared lemming (*Dicrostonyx torquatus* [=*D. groenlandicus rubricatus* (Richardson) - Bee and Hall 1956]) and arctic ground squirrel (*Spermophilus parryii* Richardson) in Alaska has been recorded (Batzli and Jung 1980, Batzli and Sobaski 1980, White and Trudell 1980, Trudell and White 1981, Chapin et al. 1986). Birch seed is also an important autumn and winter food source for siskin (*Cardaelis spinus* L.) and redpolls (*Acanthis flammea* L.) as well as finches and crossbills to a lesser extent (Pelham et al. 1984). Browsing of shoot tips by hares is the most widely recognized type of mammalian herbivory on *B. glandulosa* (Pease et al. 1979, Bryant et al. 1983). However, browsing by reindeer (Trudell and White 1981), of leaves by caribou (*Rangifer tarandus caribou*) (Crête et al. 1990), leaders by cattle (Roath and Krueger 1982) and buds, stems and fruits by willow ptarmigan (*Lagopus lagopus* L.) (Williams et al. 1980) has also been recorded. Uchytil (1989) summarized the forage preference of *B. glandulosa* by domestic sheep, horses, goats and cattle as poor to fair. Browse preference by elk (*Cervus canadensis*) was poor to good, while moose (*Alces alces*) was rated as good. Antelope, white tailed deer, mule deer, small mammals and waterfowl also showed fair to poor preference. Numerous bird species including ptarmigan, sharp-tailed grouse, spruce grouse, ruffed grouse, redpolls, pine siskin, chickadees and kinglets feed on catkins, buds and seeds (Uchytil 1989).

Plant parasites, saprophytes and diseases

The only parasitic fungi documented on *Betula nana* in Britain is the rust *Melampsoridium betulinum* (Fr.) Kleb., *Mycena epipterygia* (Scop.: Fr.) S.F. Gray and other Tricholomataceae that are also found in adjacent communities (Bennell and Millar 1984, Watling 1987). Elborne and Knudsen (1990) document *Taphrina carnea* Johans. on *Betula nana* and *B. glandulosa* in arctic, subarctic and temperate areas of Greenland. Other trunk and branch fungi include *Exidia repanda*, *Mycena rubromarginata* and *Pluteus atricapillus* which are occasional or rare saprophytes. *Agaricus semotus* Fr., *Collybia obscura* Favre and *Entoloma olidum* Noord. are common or occasional saprophytes of *B. nana/B. glandulosa* litter. As well, dwarf birch may be infected by *Euryachora betulina* (Fr.) Schröter at higher altitudes (Kallio and Mäkinen 1978). *Galerina vittaeformis* (Fr.) Sing. was reported by Petersen (1977) in *B. nana* heath and fens near the high arctic zone of Greenland (Gulden 1987). In Alaska, *Hygrocybe coccineocrenata* (Orton) Moser was found with *B. glandulosa*, and *Hygrophorus* aff. *chrysodon* (Batsch: Fr.) Fr. and *H. melizeus* (Batsch: Fr.) Fr. were associated with *B. nana* (Miller 1982, Laursen et al. 1987). Elborne and Knudsen (1990) found numerous parasites and saprophytes on *B. pubescens* but very few on the dwarf birches, indicating a significant difference in parasitism between tree and shrub birches. Other parasites documented on *B. nana* and *B. glandulosa* in North America and Greenland are found in Table 2-2. Of the seven viruses known to infect *Betula* (Cooper and Massalski 1984) none have been documented on *B. nana* or *B. glandulosa*.

History

The *Betula nana* record in Britain dates to the Beestonian stage of the middle Pleistocene (Godwin 1975). Macroscopic and pollen evidence show its presence in the Cromerian and Wolstonian stages, although no evidence has yet been found during the early Anglian or sub-stages of the Hoxnian and Ipswichian interglacial periods (ca. 150,000 and 90,000 years B.P.). The persistence of *B. nana* is presumed during this time because of the strong Weichselian record that shows a wide distribution including southern England and Ireland. Dwarf birch remains from glacial times were also found in the East Walton Pingos (Rackham 1986). Jóhansen (1975) records *B. nana* in the Shetland Isles about 10,000 B.P. and the Faroe Islands near 9,300 B.P. Both populations expanded soon afterwards, although *B. nana* is no longer present in either location, due no doubt to grazing pressure. A great decline in frequency and restriction to northern Scottish mountains has only recently occurred since the early postglacial period.

In contrast to Godwin's persistence view, Fredskild (1991) described the most recent occurrence of *Betula nana* as a westward extension from the European continent after the last glacial period, reaching Scotland and SW Norway by 13,000-12,000 B.P. Whether or not *B. nana* survived in Britain *in situ* may be debated, although Hutchinson (1966) provided strong evidence this did occur along with pine and other birches in known western refugia. In other areas, it was recorded in the southwest area of the Baltic Sea 10,500 B.P. (Bennike and Jensen 1995), SW Iceland c. 8,200 B.P. (Vasari and Vasari 1990 - cited in Fredskild 1991) and E Greenland c. 8,000 B.P. (Funder 1978). *B. nana* was present in northern Norway at least 11,800 B.P. after which it declined during the start of the early Holocene until a major expansion 9,000-9,500 B.P. (Prentice 1981). It was also a dominant species in northern Finland prior to 8,000-8,500 B.P. (Reynaud 1974). Dwarf birch pollen (possibly *B. nana*) was recorded in north-central Baffin Island samples that indicate a strong continuous presence since >40,000 years B.P.

The first historical record of *Betula glandulosa* is about 24,000 B.P. in western Illinois (Baker et al. 1989). It became a dominant member of a wetland community during this time when climatic cooling occurred as glaciers were advancing into the midwest United States of America. *Betula* series *Humiles* fruits and *Betula* pollen suggest that *B. glandulosa* probably occurred in central Minnesota 14,700 - 13,600 B.P. when vegetation was shifting from a phase of tundra-like barrens to spruce-dominated woodlands (Birks 1976). *B. glandulosa* macrofossils were also found in northeastern Minnesota dating up until about 10,500 B.P. (Watts 1967), while

Spear (1989) found *B. glandulosa* to occur about 11,000 to 10,300 B.P. at higher elevations in New Hampshire. This was a period following deglaciation as mean annual temperatures were increasing. Dwarf birch dominated the landscape of NE Labrador, Canada from about 6,800-6,500 B.P. to 4,000 B.P., and *B. glandulosa* is still present in the tundra of that region (Short and Nichols 1977). *B. glandulosa* arrived in SW Greenland from North America about 5,700 B.P. (Kelly and Funder 1974) and somewhat later than 4,000 B.P. in southern Greenland (Fredskild 1973). The late immigration in southern Greenland may be attributed to difficulty in spreading in tundra regions (Fredskild and Ødum 1990).

Dwarf birch appears to have migrated east from N Yukon and Alaska to the Mackenzie Delta region about 11,300-10,300 B.P. (Ritchie 1977). Tree pollen was dominant until 8,900-6,500 B.P. when dwarf birch appeared mixed with other tree species. *Betula glandulosa* (or the *B. nana* introgressed hybrid, cf. Hultén 1968) has a strong presence in the region today. It also appears to have been present in east-central Alaska since at least 4,600 B.P. (Anderson 1975). Jacobs et al. (1985) hypothesize that the present distribution of *B. glandulosa* on southern Baffin Island, Canada was established during an early Holocene climatic optimum.

The historical distribution of both species appears to have been strongly influenced by climatic variation. In particular, they became more dominant and widespread when climate was similar to conditions typical of the present circumpolar north. This is reflected in their southern occurrence during the advance or retreat of glaciers, or greater representation during cold stages (Dickson 1984).

Tables

Table 2-1. Occurrence and distribution of mycorrhizal symbionts associated with *Betula nana* and *Betula glandulosa* in Greenland (after Elborne and Knudsen 1990).

	Occurrence[1]	Distribution[2]
Amanita arctica Bas. Knud. & Borg.	O	SA, A
A. battarrae Boud.	O	T, SA
*A. groenlandica*Bas ex Knu. & B.	C	SA, A
A. mortenii Knud. & Borgen	O	SA
A. nivalis Grev.	C	SA, A
Boletus subtomentosus Fr.	O	T, SA
Cortinarius cinnamomeus (L.: Fr.) Fr.	O	T, SA
C. croceus (Schff.) Bi. & Gu.	O	T, SA, A
Lactarius glyciosmus Fr.	C	T, SA, A
L. pubescens Fr.	C	T, SA, A
L. repraesentaneus Britz.	O	T, SA, A
L. rufus (Scop.) Fr.	O	T, SA, A
L. theiogalus (Bull.) Fr.	O	T, SA
Leccinum atrostipitatum Smi. & Thie.	O	T, SA
Paxillus involutus (Batsch) Fr.	C	T, SA
Rozites caperatus (Pers. ex Fr.) Karst.	O	T, SA
Russula claroflava Grove	C	T, SA

[1] Occasional (O), common (C).

[2] Arctic (A), subarctic (SA), temperate (T)

Table 2-2. Plant parasites and saprotrophs on *Betula nana* and *Betula glandulosa* documented in North America and Greenland (compiled from Conners 1967 and Ginns 1986).

	B. nana	*B. glandulosa*	Authority[a]
Antennatula arctica Rostr.		x	25
Apiospora rosenvingei Rostr.		x	25
Atopospora betulina (Fr.) Petr.	x	x	4,5,8,10,12,14,15,16,19,22,24
Cladosporium herbarum Lk.	x		26
Coniothecium betulinum Cda.	x	x	25,26
Corticium lacteum Fr., nom. dub.	x		26,27
Coryneum kunzei Cda.	x		25
Cytospora salicella Sacc.	x		26
C. salicis (Cda.) Rabh.	x		26
Dasyscyphus bicolor Bull. ex Fckl.		x	25
Diatrypella sp.		x	22
D. decorata Nits.		x	19
Didymosphaeria nana Rostr.	x		24
Diplodia betulae West.	x		26
Exidia sp.		x	15
E. candida Lloyd		x	18
Gloeosporium betularum Ell. & Martin		x	25
Gnomonia campylostyla Auersw.	x	x	24,25,26,29
G. intermedia Rehm.		x	10
Melampsoridium betulinum (Fr.) Kleb.	x	x	2,5,7,12,15,18,19,21,23,28,29
Mollisia cinerea (Batsch) Karst.		x	26
M. ramealis Karst.	x		26
Mycosphaerella maculiformis (Pers. ex Fr.) Schroet.		x	9
Naemospora microspora Desm.	x		26
Plagiostoma alneum (Fr.) Arx var. *betulinum* Barr		x	11
P. campylostylum (Auersw.) Barr var. *campylostylum*		x	18
Polyporus varius (Pers.) Fr.: Fr.		x	8
Sphaerella harthensis Auersw.		x	12
Taphrina alpina Johans.	x		26
T. bacteriosperma Johans.	x	x	4,18,24
T. carnea Johans.	x	x	1,3,13,17,20,24,25,26
T. nana Johans.		x	6,13,15,18,20
Venturia ditricha (Fr.) Karst.		x	9,10,25

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[a] (1) Anon. 1959; (2) Anon. 1962; (3) Anon. 1963; (4) Anon. 1964; (5) Anon. 1965; (6) Anon. 1970; (7) Arthur 1934; (8) Baranyay 1968; (9) Barr 1959; (10) Barr 1961; (11) Barr 1978; (12) Cash 1954; (13) Conners and Savile 1953; (14) Corlett and Carter 1976; (15) Evans et al. 1978; (16) Lind 1910 (cited in Connors 1967); (17) Linder 1947; (18) Lowe 1977; (19) McArthur 1966; (20) Mix 1954; (21) Parmelee 1960; (22) Pilley and Trieselmann 1968; (23) Pilley and Trieselmann 1969; (24) Rostrup 1888; (25) Rostrup 1891; (26) Rostrup 1894; (27) Rostrup 1904; (28) Ziller 1957; (29) Ziller 1962.

Figures

Figure 2-1. Present distribution of *Betula nana* in the British Isles (after Perring and Walters 1962).

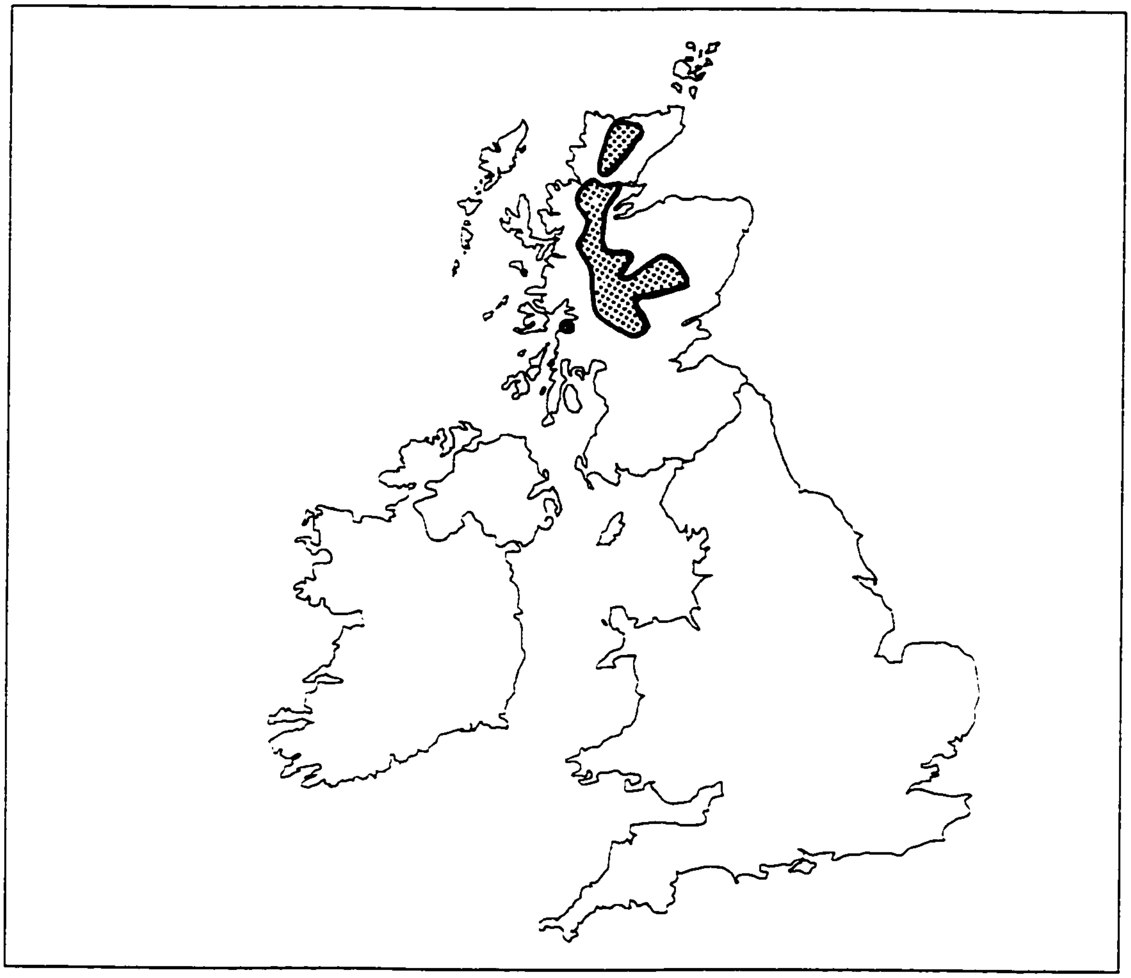


Figure 2-2. Distribution of *Betula nana* in Europe (after Jalas and Suominen 1976).

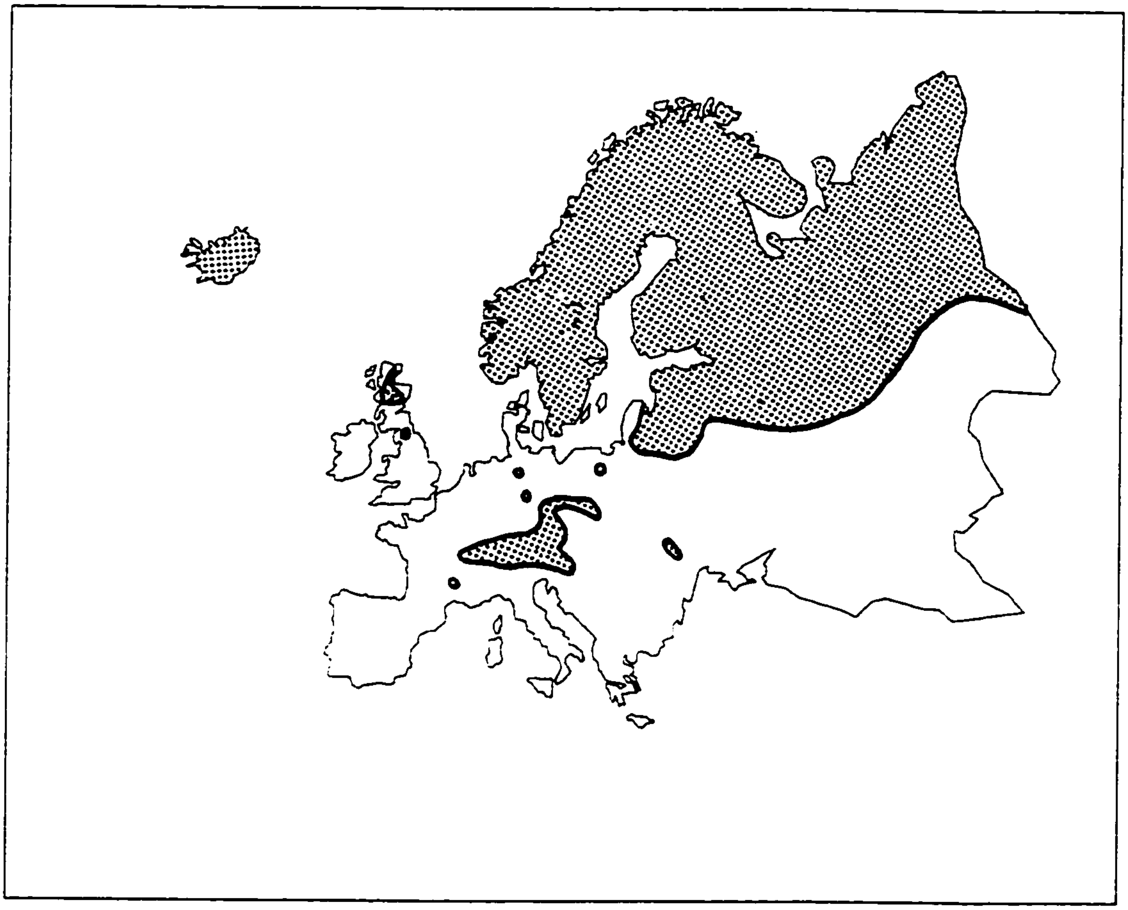


Figure 2-3. Circumpolar range of *Betula nana* (after Hultén 1986).

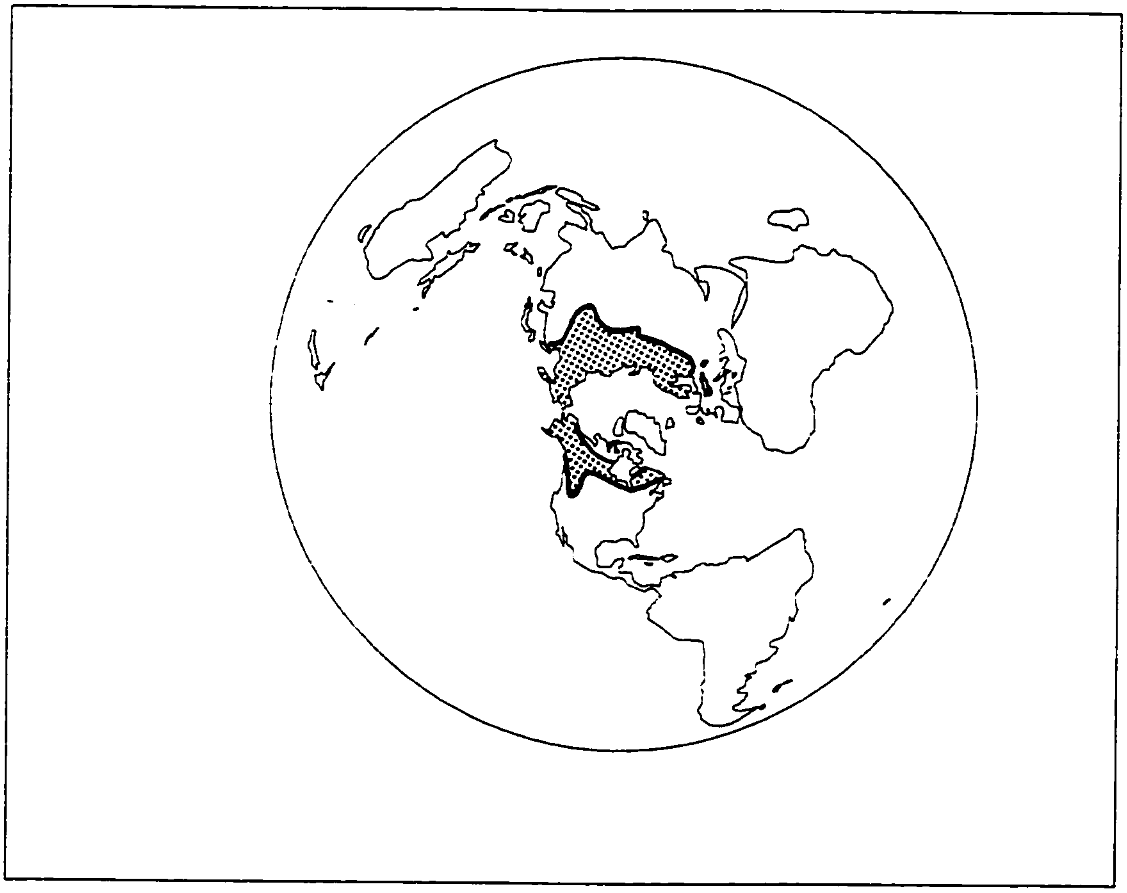


Figure 2-4. Distribution of *Betula glandulosa* in North America and Greenland (adapted from Weis and Hermanutz 1988).

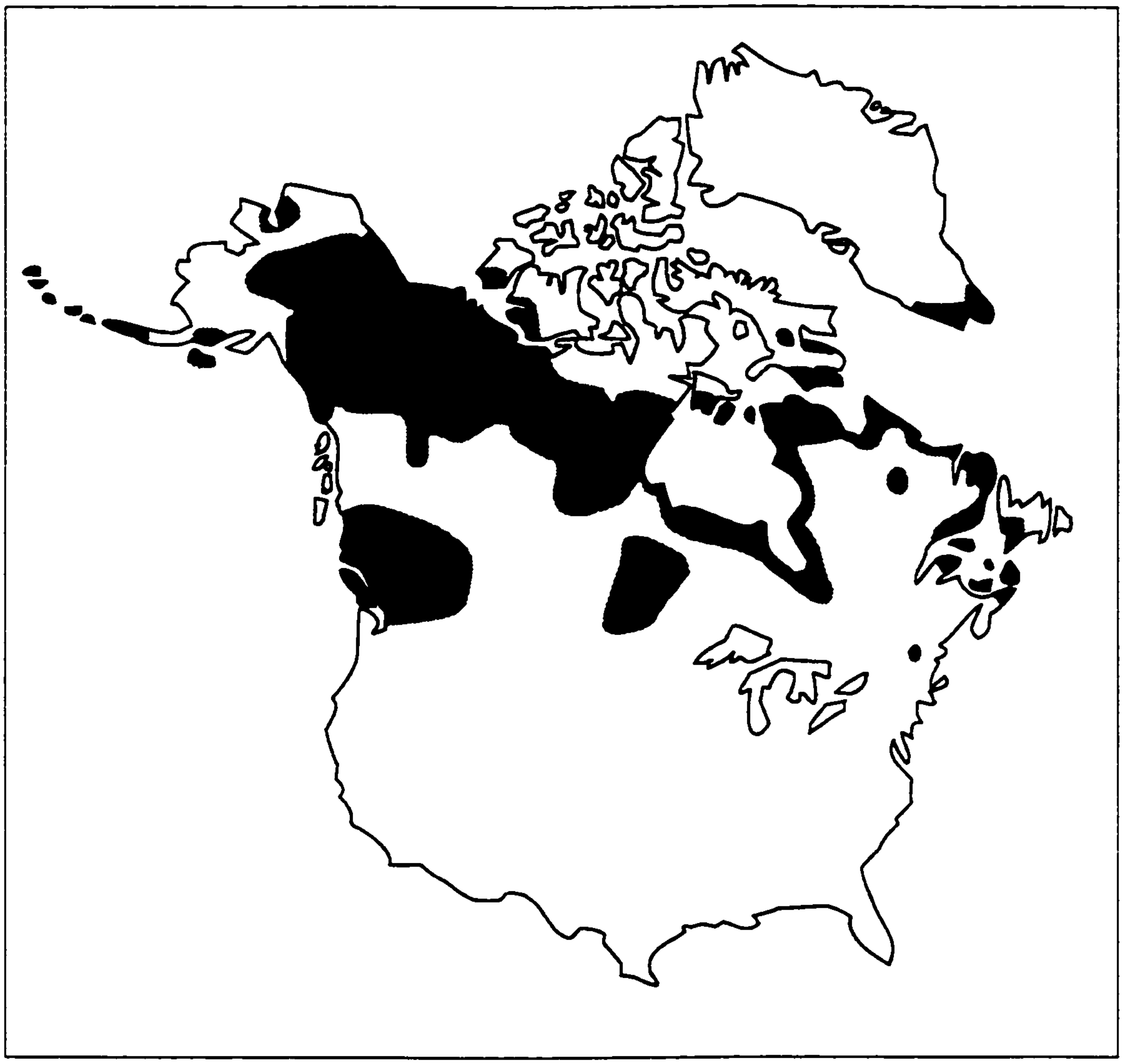


Figure 2-5. *Betula glandulosa* branch showing leaves and female catkins (after Corns and Annas 1986).

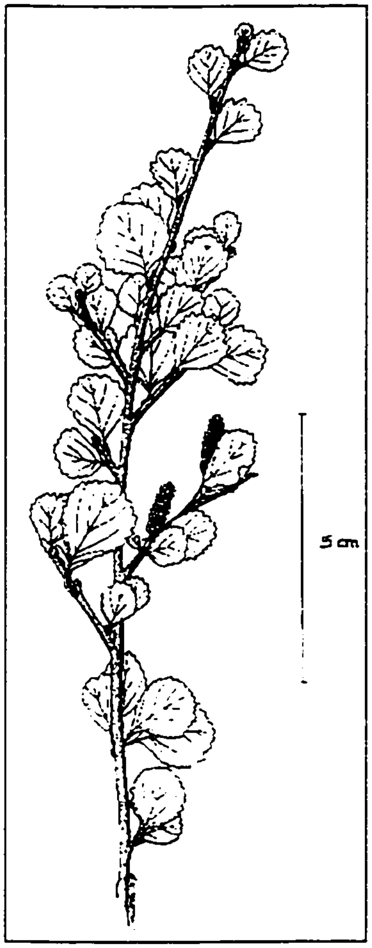
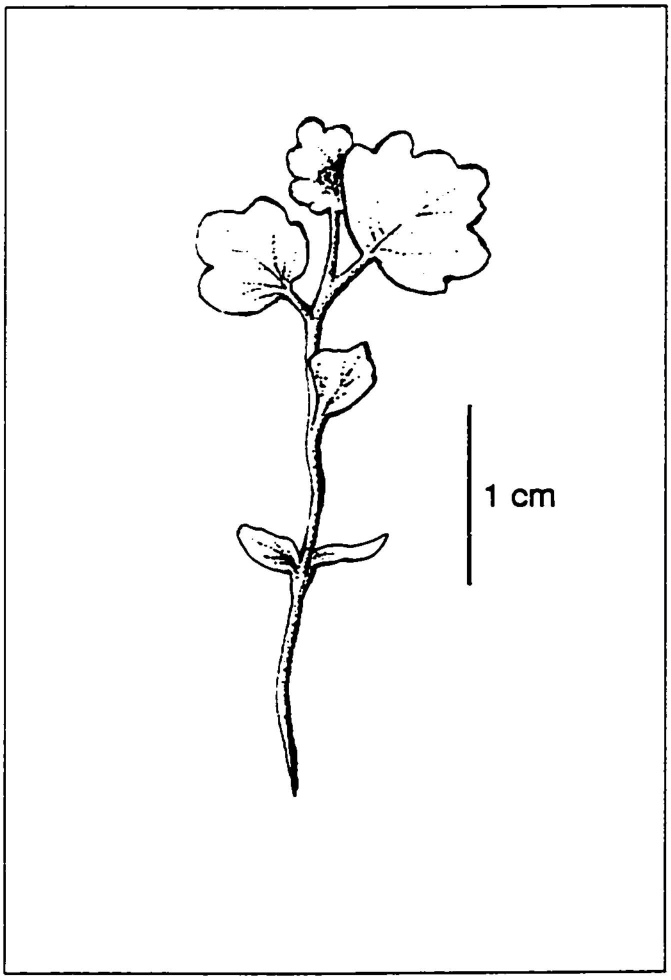


Figure 2-6. Three-week old *Betula glandulosa* seedling (after Inki and Valanne 1979).



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III. Effects of fire severity and season of burn on *Betula glandulosa* growth dynamics[1]

Introduction

Betula glandulosa Michx. is a small to moderate sized (0.5-2.5 m) shrub of widespread polar distribution (de Groot *et al.* 1997). This plant occupies a diverse range of sites in North America including rocky subarctic and alpine tundra (Dugle 1966, Wein & Bliss 1973, Weis & Hermanutz 1988) and deep organic soils in the boreal region (Ritchie 1960, Moore 1980). Fire is a prevailing force over much of its natural range and appears to have substantial influence on population and growth dynamics of *B. glandulosa*. For example, the formation of extensive, closed-canopy stands and encroachment on rangelands has been attributed to past fire suppression (Bork *et al.* 1996) while postfire growth is often quite vigorous.

Low growth form, small stem diameter, thin bark, and densely resinous twigs (Dugle 1966) make *Betula glandulosa* plants susceptible to fire. Even though leaves have a high moisture content during summer, high caloric contents in the leaves and stems (Sylvester & Wein 1981) and formation of dense stands can result in high intensity surface fires in spring and autumn when shrub foliage and understory vegetation is cured. *B. glandulosa* grows over a wide range of fire regimes, and is often found in communities that may burn as frequently as every 10 years (see Heinselman 1981). Although some *B. glandulosa* seedlings may become established after fire, populations are primarily maintained by surviving plants that resprout from dormant buds on the woody rhizome.

The effect of fire severity and season of burn on sprouting has been examined in several other northern shrub species (e.g., Flinn & Pringle 1983, Johnston & Woodard 1985, Flinn & Wein 1988, Noste *et al.* 1989, Kauffman & Martin 1990). Significant variation in sprouting response has been observed in those studies due to heat pulse characteristics, phytohormone levels and stored carbohydrates at the time of burning. The annual carbohydrate storage cycle of *Betula nana*, a closely-related shrub birch studied by Chapin (1980) and Chapin *et al.* (1986), indicated high levels of non-structural carbohydrates in underground tissues prior to leaf expansion and lowest levels immediately after leaf expansion. Carbohydrate levels increased towards autumn as plants sequestered all available carbohydrates and moved them to storage tissues, as similarly found in *B. glandulosa* by Prudhomme (1983). However, there are few data for any birch shrub species on the seasonal effect of disturbance on overwinter carbohydrate reserves which are used for sprouting in the following spring. In general, spring fires following snowmelt are of low severity due to high soil moisture content and autumn fires are of much greater severity due to soil drying (McAlpine 1990) during the summer.

The purpose of this study was to determine the effects of fire severity and season of burn on the sprouting ability of *Betula glandulosa*, and to compare the levels of overwinter total non-structural carbohydrates (TNC) stored in the rhizome relative to seasonal burning. It was hypothesized that the lowest sprout production, sprout growth and overwinter TNC storage would result from burning after spring leaf expansion due to low TNC reserves, and that greater fire severity would result in greater mortality.

Methods

Study site description

The field site was located on 6 ha of open shrub-grassland meadow in west-central Alberta, Canada (52° 00' N 115° 21' W) that had previously been burned by prescribed spring fires in 1984 and 1987. The site was characterised by a valley bottom floodplain (elev. 1350 m) with Orthic Humic Regosol soils of silty loam texture (approximately 15 cm deep) over glacio-fluvial gravels. Birch shrubs were generally 40-70 cm high

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[1] This chapter was submitted to *Journal of Ecology*.

and 30-50 cm in diameter. Rhizomes were 2-6 cm thick and possessed numerous buds, some of which showed swelling and initial growth, and a few short shoots which had not grown above the surface litter layer. To permit daily observation of plant growth, a second site (referred to as the nursery site) was established at Edmonton (53° 30' N 113° 35' W, elev. 670 m) using plants from the field site. In early May 1992, 130 field plants were randomly selected and removed with a soil ball approximately 30 cm x 30 cm in area and 15 cm deep. The nursery site was a 3 m x 20 m x 0.3 m deep trench that was lined with plastic, filled with commercial peatmoss and watered regularly. The growing season at the field site was shorter and considerably cooler than the nursery site in 1992 (Table 3-1). In 1993, growing degree days at the field site for May 1 - September 15 totalled 1437, while the nursery site recorded 2038 during the same period (Table 3-2).

Sprouting dynamics

Experiments in the field and nursery used a completely randomized design with three replications of each season and severity treatment combination. A temperature of 60°C was used for severity treatments because this temperature was found to be lethal to rhizomes of many plant species (Flinn & Pringle 1983). The four severity treatments were defined as a temperature of 60°C reached at 2 cm below the top of the plant rhizome (low severity), at 4 cm below the top of the rhizome (moderate severity), at 6 cm below the top of the rhizome (high severity) and a no-burn treatment control (Figure 3-1). These severity levels represent the depth range that most buds were found during field observation. There were five and six season of treatment dates (Table 3-1) used at the field (N=60) and nursery (N=72) sites, respectively.

Immediately prior to burning, stems were clipped to ensure that all subsequent top growth was directed to new sprouts. Stems were also clipped on the no-burn control. Heat was applied using a propane radiation heater (20,000 Btu) while buried thermocouples indicated when soil at the appropriate depth reached 60°C. Prior to burning, the organic soil around each plant rhizome was removed to the appropriate depth of heat penetration and replaced with dry peatmoss. This was done to ensure that the required heat pulse could be achieved even under moist soil conditions. The heater was removed when a temperature of 60°C was reached at the required depth and then water was applied to extinguish the fire and cool the soil. The average duration of heat application was about 2, 8 and 30 min for low, moderate and high severity treatments, respectively.

Early in the second year of postfire growth (1993), the field site was burned over by a low intensity surface fire prior to leaf expansion. The tops of most sprouted plants (representing the first two season of treatment dates) were scorched so all other plants were top-clipped immediately after the fire to ensure an equal treatment across the experiment. In effect, this simulated two disturbances in two years for the first two season of treatment dates; the last three season of treatment dates were unaffected because those plants had not yet sprouted.

Numbers of sprouts and maximum sprout height (measured using the tallest sprout) were recorded at the field and nursery sites in the late autumn of 1992 and approximately monthly through the 1993 growing season. Aboveground and belowground biomass were measured at the end of the 1993 growing season. Treatment-induced plant mortality was calculated as a percentage of initial sample size. Dead plants were removed from the data set prior to analysis of the various growth responses. Analysis of the response variables (maximum sprout height, number of sprouts and aboveground biomass) was done by ANOVA, using rhizome weight as a covariate when it was a significant ($\alpha = .05$) factor.

Carbohydrate dynamics

Forty shrubs at the nursery site were used to examine the effect of seasonal burning and clipping on overwinter total non-structural carbohydrate (TNC) storage. The two treatments used were clipping with low severity heating and clipping with no heat applied. These treatments were applied at four times during the 1993 growing season that were defined as prior to leaf flush, immediately after leaf flush, mid-summer, and late summer (Table 3-2). There were four replicates of each burning and season treatment combination, and eight untreated control plants.

All plants were removed from the ground in late November, 1993 and frozen within 48 hours. Two weeks later, plants were thawed and rhizomes were removed from the soil ball, freeze-dried and stored at -30°C until analysis. A small portion (about 0.7 g) of each rhizome was ground to 20 mesh (1 mm) size. Samples of 0.3 g were extracted using 50 ml of boiling 85% ethanol for 30 min. The sample was homogenized at 20,000 rpm for 2 min and extracts were filtered through Whatman No. 1 filter paper. Residues were extracted again with 50 ml of boiling 85% ethanol for another 10 min. After homogenization at 20,000 rpm for another 2 min, the filtered extracts were combined and reduced to water phase using a rotary flash evaporator and adjusted to a volume of 50 ml with distilled water. Residues were freeze-dried and stored at -30°C for later starch analysis. A small amount (1 ml) of the extracted sample was centrifuged at 14,000 rpm for 10 min and soluble sugars were quantified as β-D-glucose equivalents using the anthrone method of Ashwell (1957).

Starch extraction was based on the method described by Carpita & Kanabus (1987). A 75 mg sample of the tissue residues was suspended in 8 ml of dimethyl sulfoxide (DMSO) and stirred vigorously for 24 h at room temperature. The extracted samples were centrifuged at 2,400 *g* for 15 min and 0.2 ml of the supernatant was evaporated under a stream of air using a small flask in a 60°C water bath. The dried starch residue was hydrolysed with glucoamylase using 3 ml of a mixture of 20 ml 20% DMSO solution, 55 ml distilled water, 23 ml of 220 mM sodium acetate at pH 5.0, and 1 mg of enzyme. The sealed flask was placed in a 40°C water bath for 12 h. The anthrone method was used to measure the glucose released from starch by the glucoamylase. TNC values were estimated by combining starch and soluble sugar amounts. Significance of treatments on overwinter TNC levels was determined by ANOVA.

Results

Sprouting dynamics

1992

Plants in both the field and nursery studies produced exceptionally large leaves during the first year of growth regardless of treatment or season. Recently burned plants commonly produced leaves greater than 4 cm long and 3 cm wide, more than twice the length and width of leaves of unburned plants near the field site. These larger leaves also senesced considerably later than leaves on unburned plants. Field plants turned yellow in autumn 1992, while nursery plants turned red.

Data collected in the autumn of 1992 at both study sites showed that shrubs treated in earlier seasons produced the most sprouts, especially in low severity treatments (Figure 3-2). No sprouting occurred on plants treated after late June at the field site or after late July at the nursery site. There was also an exceptionally large number of sprouts for one set of low severity treatments at each site although this occurred early at the field site and mid-summer at the nursery site. Maximum sprout height was greatest for the earliest low severity treatments at both study sites (Figure 3-3). Statistical analysis at the end of the first growing season indicated that severity and season of treatment were highly significant ($\alpha = .01$) for maximum sprout height at both study sites, with significant to highly significant interaction (Table 3-3). Season had a highly significant effect on sprout production at both sites while severity was significant at the nursery site and interaction of severity and season were close to being significant at the field site. Rhizome weight was not a significant covariate.

1993

At the end of September 1993, 90% of the leaves on newly sprouted field plants had changed color but were still attached, while untreated plants in the surrounding area were 80% abscissed. Plants at the nursery site exhibited similar behavior between treated and untreated plants. Within treated plants, the earliest treatments also senesced earlier (70% colored vs. 20% colored for late season treatments at the end of September). Mortality data collected in October showed that increasing fire severity caused higher mortality rates (Figure 3-4), although high fire severity still resulted in about a 30% survival rate. The nursery site had a trend of decreasing mortality with later season treatments (Figure 3-5).

The autumn nursery data indicated that low fire severity increased sprout numbers (Figure 3-6), maximum sprout height (Figure 3-7) and aboveground biomass (Figure 3-8) while a further increase in fire severity caused a reduction in all three characteristics. The greatest maximum height growth resulted from spring (and to a lesser degree autumn) treatment, while the greatest aboveground biomass occurred with spring treatment. Fire severity was significant to highly significant for all three growth characteristics in the nursery study (Table 3-4) . Season of treatment and interaction of fire severity with season of treatment were also significant (or very close to significance) for maximum height growth and aboveground biomass. Sprout numbers were not influenced by season of treatment, but sprout numbers and aboveground biomass significantly increased with rhizome weight.

Autumn field data showed that low severity burning treatments generally increased sprout numbers (Figure 3-6) and that burning had little effect on maximum height growth (Figure 3-7) and aboveground biomass (Figure 3-8). Sprout numbers and aboveground biomass significantly increased with rhizome weight (Table 3-4). Overall, sprout production was highest at the field site, while maximum sprout height and aboveground biomass were greatest at the nursery site.

Carbohydrate dynamics

Plants resprouted after all seasonal treatments except for the late summer treatment. Mean rhizome TNC for burned plants (10.92%, SE=0.65) was lower than the control plants (11.59%, SE=0.49) while clipped plants had the highest TNC concentration (11.99%, SE=0.41). TNC values were highest for spring treated plants and lowest when burned at mid-summer (Figure 3-9). Data analysis indicated that season of treatment significantly (α=0.05) influenced the storage of TNC while differences between burning and clipping treatments were not significant. Although the pre and post leaf expansion treatment data appeared to show an interactive influence between treatment and season, statistical analysis showed there was no significant difference between treatment combinations. Rhizome weight had no statistical influence on TNC storage concentrations.

Discussion

It is well-known that the onset of sprouting after cutting or burning is the result of release from apical dominance (Sachs & Thimann 1967, Bergström & Danell 1987, Maillette 1987, Haukioja *et al.* 1990). Dominance is lost when the inhibitory effect of auxin is stopped by the removal of apical buds, and release from inhibition is achieved by cytokinin produced in roots. Domanski & Kozlowski (1968) found cytokinins, together with other growth promoters, to be important in the release of buds from dormancy in *Betula*. Gibberellic acid (synthesized in root and stem tips) has also been demonstrated to break bud dormancy and promote stem extension in birch (Eagles & Wareing 1964). Post treatment sprouting response showed significant seasonal differences and it is suggested that this may have been caused by seasonal variation in the level or balance of growth promoters with other phytohormones.

Previous studies indicate that birches sprout almost exclusively from dormant buds (Rinne *et al.* 1987). Treated plants were found to sprout from buds found singly and in clusters around the rhizome. The increased sprout production that followed low fire severity treatments did not appear to be caused by heat stimulation of shoot buds as many sprouts originated from the bottom of the rhizome which was protected from direct heat. Sprouting is known to increase in birches with greater light intensity (Johansson 1986, 1987) such as when the ground level is lowered (Kauppi *et al.* 1991). In this study, all rhizomes were covered with soil after treatment so light-induced sprouting was not a factor. Other fire response cues include smoke which has been found to stimulate enhanced seed germination in some species (Brown 1993) and ethylene (occurring in smoke and resulting from tissue injury) which has been shown to induce inflorescence production (Gill and Ingwersen 1976); these are possible factors in postfire birch sprouting response but they have not been tested. Fire response is probably triggered by the interaction of several cues and factors (Brown 1993). In this experiment, it appeared that increased postfire sprouting in *Betula glandulosa* may be at least partly due to a longer period of reduced apical dominance following fire. Numerous small sprouts and newly-initiated bud growth were found on the rhizomes of many plants in the study, as well as on untreated field plants. It appeared that new sprouts were initiated in the early spring but further growth was soon prevented by the re-establishment of apical dominance when top growth began. It is believed that those initiated buds and shoots grew quickly after the clipping treatments, thereby re-establishing apical dominance over dormant buds. However, new sprouts would primarily originate from dormant buds after burning treatments because the heat pulse would have damaged initiated buds and shoots. The longer time period for new sprouts to grow after burning (a typical result found in the experiment) from dormant buds would create a longer period of reduced apical dominance, eventually resulting in a greater number of sprouts being produced.

The experimental results showed some differences in sprout production between field and nursery sites. During the first year of growth, the greatest sprout production occurred after low severity spring fire at the field site, while the nursery site had increased sprouting after low severity fire that was not seasonally influenced. This difference may have been caused by transplanting shock at the nursery site. After spring treatment, when sprout production was highest in the field study, nursery plants were probably still experiencing a priority for root growth over shoot growth as they re-established following transplanting. This may have influenced the seasonal interaction with increased postfire sprout production at the nursery site. After the second growing season, the shrubs on the field site did not have the same strong response of increased sprout production after low severity fire as found at the nursery site. It is believed that this difference was caused by the additional disturbance at the field site in the spring of the second year which damaged the two earliest season treatments, including the plants which had the greatest postfire sprout production after one year (this had a similar effect on second year height growth and biomass field results). Field plants also sprouted more than nursery plants, a result which may be attributed to a cooler climate in the field; Rinne *et al.* (1987) found similar results with *Betula pendula* Roth and *B. pubescens* Ehrh. which produced a greater number of adventitious buds and sprouts under cooler growing conditions. Differences in autumn foliage colour intensity between field (yellow) and nursery (red) plants may also be due to the different temperature regimes (I. Brodie pers. comm.). In general, decreased sprout production and longer time periods to sprout after high severity treatments were probably caused by increased root mortality which established a priority for root growth over new shoot production. Increased bud mortality with increasing fire severity may also have contributed to reduced sprout production.

Increased maximum sprout height growth following a low severity spring, and to a lesser degree autumn, fire was a prominent result of this experiment. This suggests an increased response period from autumn to early spring, a concept supported by other reports of vigorous sprouting after cutting during the dormant season (others cited in Cays & Canham 1991). The exact mechanism stimulating this response was not obvious although it could include any of the previously discussed fire response cues. The seasonal variation in response suggests that phytohormones have an important role in fire-stimulated height growth. The fact that similar height growth trends were found at the field and nursery site after the first year indicates that transplanting had little or no effect on post-treatment response. Height growth was also not related to rhizome biomass, further indicating that height growth was not influenced by condition of belowground plant parts. The nursery site had greater overall height growth than the field site and this was attributed to warmer growing conditons at the nursery, an effect also described for *Betula nana* (Backéus 1985). The strong similarity in postfire response between aboveground biomass production and maximum sprout height indicates the close relationship between these two characteristics, although aboveground biomass was also found to be highly dependant on rhizome biomass.

The carbohydrate study suggests that *Betula glandulosa* has an adaptive strategy to maintain elevated overwinter root TNC levels. Plants treated during the last half of the growing season did not resprout in the same year, an apparent strategy to conserve root reserves as carbohydrates used for new growth would not likely be compensated by new photosynthate due to the shortness of the remaining growing season. Mid-summer treated plants resprouted but the burned plants had much lower overwinter TNC levels than clipped plants, probably because burned plants sprouted later causing a reduction in total time available for photosynthate production. Differences in seasonal TNC may influence subsequent growth rates and this appears to be reflected in the sprouting experiment as mid-summer treatments generally had the least height growth. Kays & Canham (1991) describe similar results in *B. populifolia* following seasonal cutting, with the lowest autumn starch concentrations occurring after mid-summer treatment. In that study, sprout height two years after treatment showed a trend that followed the autumn starch concentration, with mid-summer treated plants growing only half the height of early and late season-treated plants.

Plant mortality appeared to be determined by fire severity and rhizome size, although recent transplanting was also identified as the probable cause for higher mortality rates found in early season nursery treatments. At both study sites, only the smallest rhizomes were killed by low severity treatments. These represented the most juvenile plants which probably seeded onto the field site sometime after the 1984 burn. The majority of rhizomes were large, and were at least as old as fires that occurred in 1966 and 1952. There was also a number of large rhizomes that appeared very old and easily killed. From this evidence, fire appears to have the role of removing young and old plants from the population, thus opening the canopy for new seedlings to establish. *Betula glandulosa* is a prolific annual seeder and viability is usually high (Weis & Hermanutz 1988) but the low numbers of young plants in the experiment attests to low germination and/or high seedling mortality. Field observation also indicates that postfire regeneration is predominantly from surviving rhizomes.

The response to fire found in this study is an important aspect of *Betula glandulosa* ecology. The ability to stimulate increased sprout height growth after fire provides a strong competitive advantage during the critical period of postfire site re-establishment. This is an important trait for a shade intolerant plant such as *B. glandulosa* (de Groot *et al.* 1997) which must compete with many other shade intolerant, invading pioneer species. Fire induced increases in sprout and biomass production may also provide advantage in spatial dominance or increased photosynthetic area. The increased response to fire in spring, and to a lesser extent in autumn, reflects the natural fire regime of communities where *B. glandulosa* is often found. Dead herbaceous material provides a continuous surface fuel layer in shrub-grasslands during the spring and autumn; fire can seldom spread through this vegetation type during the summer growing season because of high moisture content in the live biomass. Response to low severity fire also reflects the general nature of shrub-grassland fires in spring which tend to be fast-spreading due to fine fuel characteristics and shallow burning because of high soil moisture levels after snowmelt.

It was hypothesized that burning plants in the spring when TNC reserves were lowest would reduce subsequent sprout production, growth and overwinter TNC storage but this was not supported by the study. It was also hypothesized that increased fire severity would increase mortality, which was shown to be true. Autumn burning was found to have more negative effects on *Betula glandulosa* than spring burning due to greater mortality and reduced sprouting response.

Conclusion

Betula glandulosa responds to topkill (by burning or clipping) with the production of extremely large leaves that senesce later in the autumn than undisturbed plants. Plants topkilled later in the growing season also retain their leaves later in the autumn than earlier topkilled plants. These appear to be adaptations to maximize photosynthate production which is used for current annual growth and restocking of belowground TNC reserves. This plant has a conservative TNC strategy in that it places a high priority on maintaining overwinter TNC storage levels regardless of season of topkill. Differences in overwinter TNC also appear to influence subsequent growth rates. *B. glandulosa* had increases in sprout production, sprout height growth and aboveground biomass production after low severity fire. Fire response was found to be greatest in the spring and, to a lesser degree, in the autumn. These characteristics provide *B. glandulosa* with a strong ecological advantage in the natural fire regime of this species.

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Tables

Table 3-1. Phenological stage and climatic conditions at the field and nursery sites when treatments were applied in 1992.

Treatment Number	Date	Degree Days[1]	Phenological stage
Field Study[2]			
	May 5	0	Most plants initiating leafbud break
1	June 10	253	Male catkins dropped; female catkins small and turning darker green
2	June 29	504	
3	July 29	850	
4	August 11	1014	
5	September 1	1243	Half of leaves on most plants were yellow
Nursery Study			
	May 5	0	Most plants initiating leafbud break
1	May 26	160	Male catkins dark, beginning to drop; female catkins small and green
2	June 16	479	Male catkins dropped; female catkins at mature size; leaves were dark green and leathery
3	July 9	868	Female catkins dark green; terminal buds beginning to form on some plants
4	July 31	1240	Female catkins starting to turn brown
5	August 18	1584	Large terminal buds on all plants; female catkins turning brown
6	September 12	1839	Some leaves beginning to turn red
	September 22	1911	All leaves on all plants were red

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[1] The cumulative daily sum of averaged maximum and minimum temperatures relative to the May 5 leaf break.

[2] Field weather taken from Clearwater Station (51° 59' 02" N 115° 14' 31" W, elev. 1280 m).

Table 3-2. Phenological stage, climatic conditions and dates of burn treatments at the nursery site during the 1993 carbohydrate study.

Treatment Number	Date	Degree Days[1]	Phenological stage
1	April 23	-30	Most plants with swelling buds
	April 27	0	Leaf break initiated in all plants
2	May 5	94	All plants fully flushed
	May 11	184	Male catkins brown
	May 2	329	Leaves turning dark green and leathery; all male catkins dropped
	June 7	555	Female catkins at mature size
3	July 2	920	
4	August 5	1480	Most female catkins turning brown
	August 26	1818	Some leaves becoming colored
	Sept. 3	1928	Most plants showing colored leaves
	Sept. 28	2201	Leaf abscission starting in most plants

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[1] The cumulative daily sum of averaged maximum and minimum temperatures relative to the April 27 leaf break.

Table 3-3. Summary of F and R-square values for sprout height growth and sprout production responses by surviving field (N=41) and nursery (N=51) study plants after the 1992 growing season. Significant (*) and highly significant (**) variables are indicated.

Source of Variation	Maximum Height		Number of Sprouts	
	Field	Nursery	Field	Nursery
Fire Severity	0.0005**	0.0025**	0.1227	0.0166*
Season of Treatment	0.0001**	0.0001**	0.0001**	0.0004**
Interaction Severity*Season	0.0001**	0.0156*	0.0699	0.1450
Rhizome Weight (covariate)	NS	NS	NS	NS
R-square	0.945	0.878	0.775	0.723

Table 3-4. Summary of F and R-square values for various growth response characteristics of surviving field (N=41) and nursery (N=51) study plants after the 1993 growing season. Significant (*) and highly significant (**) variables are indicated.

Source of Variation	Maximum Height		Number of Sprouts		Aboveground Biomass	
	Field	Nursery	Field	Nursery	Field	Nursery
Fire Severity	0.3858	0.0397 *	0.1069	0.0005 **	0.4258	0.0053 **
Season of Treatment	0.1784	0.0501 *	0.3906	0.5197	0.1329	0.0255 *
Interaction Severity * Season	0.8168	0.0711	0.4336	0.3942	0.3346	0.0511 *
Rhizome Weight (covariate)	N/S	N/S	0.0182 *	0.0001 **	0.0252*	0.0203 *
R - square	0.410	0.605	0.650	0.792	0.675	0.710

Figures

Figure 3-1. Depths of lethal heat penetration used in this study. Low, moderate and high fire severities correspond to a lethal heat penetration depth of 2, 4 and 6 cm below the top of the rhizome.

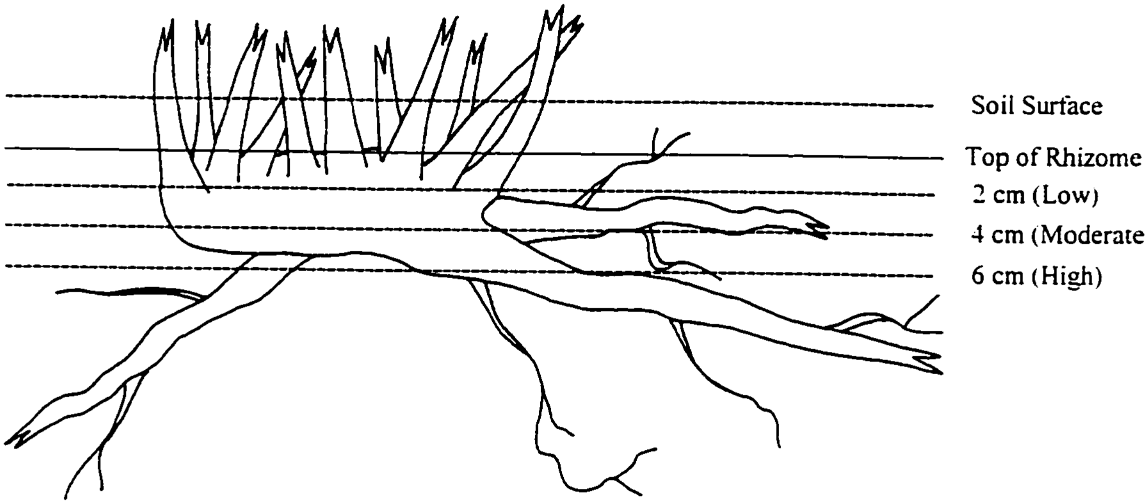


Figure 3-2. Number of sprouts (and SE) for field and nursery plants in October 1992 by fire severity level and 1992 treatment date.

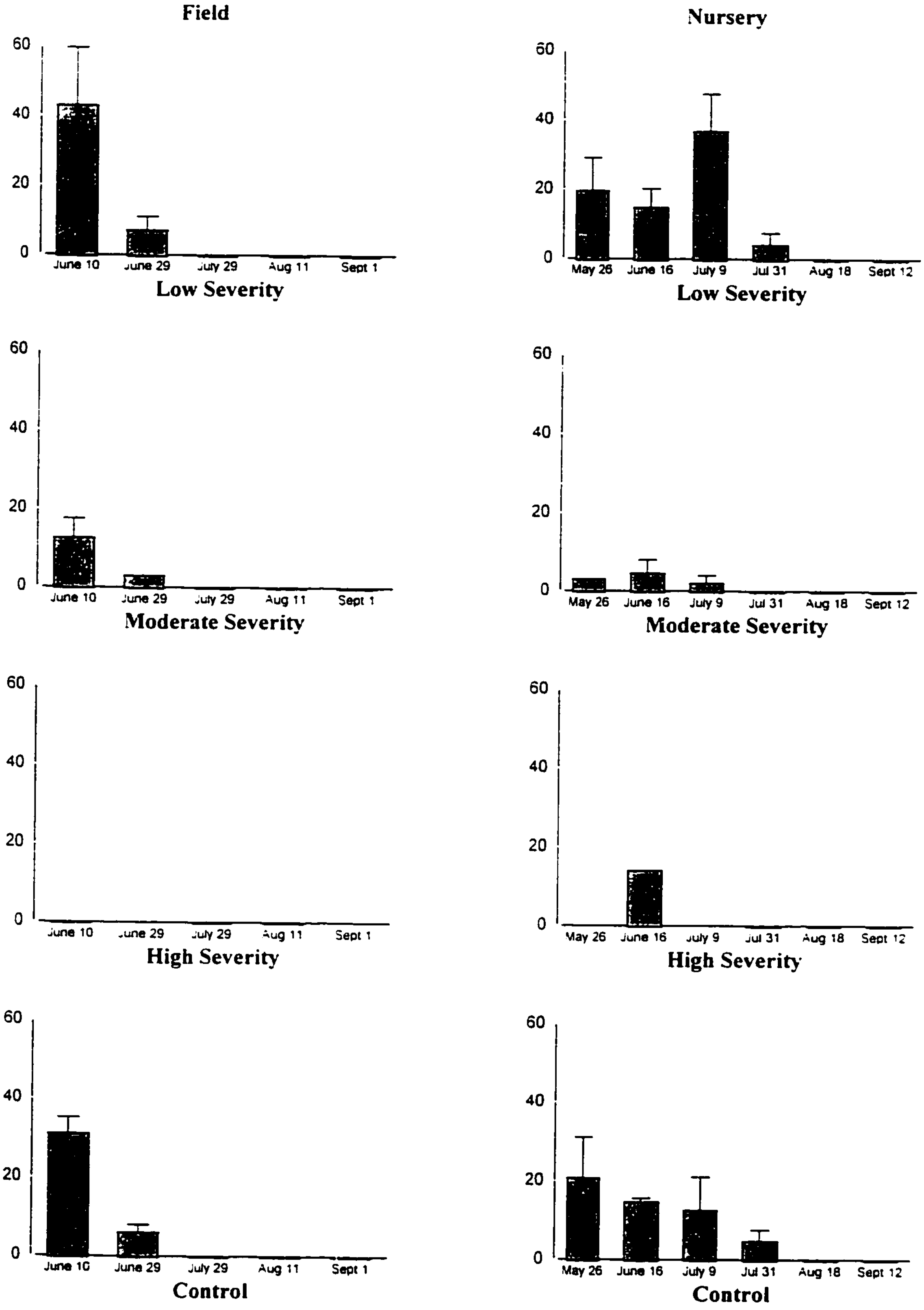


Figure 3-3. Maximum sprout height (and SE) for field and nursery plants in October 1992 by fire severity level and 1992 treatment date.

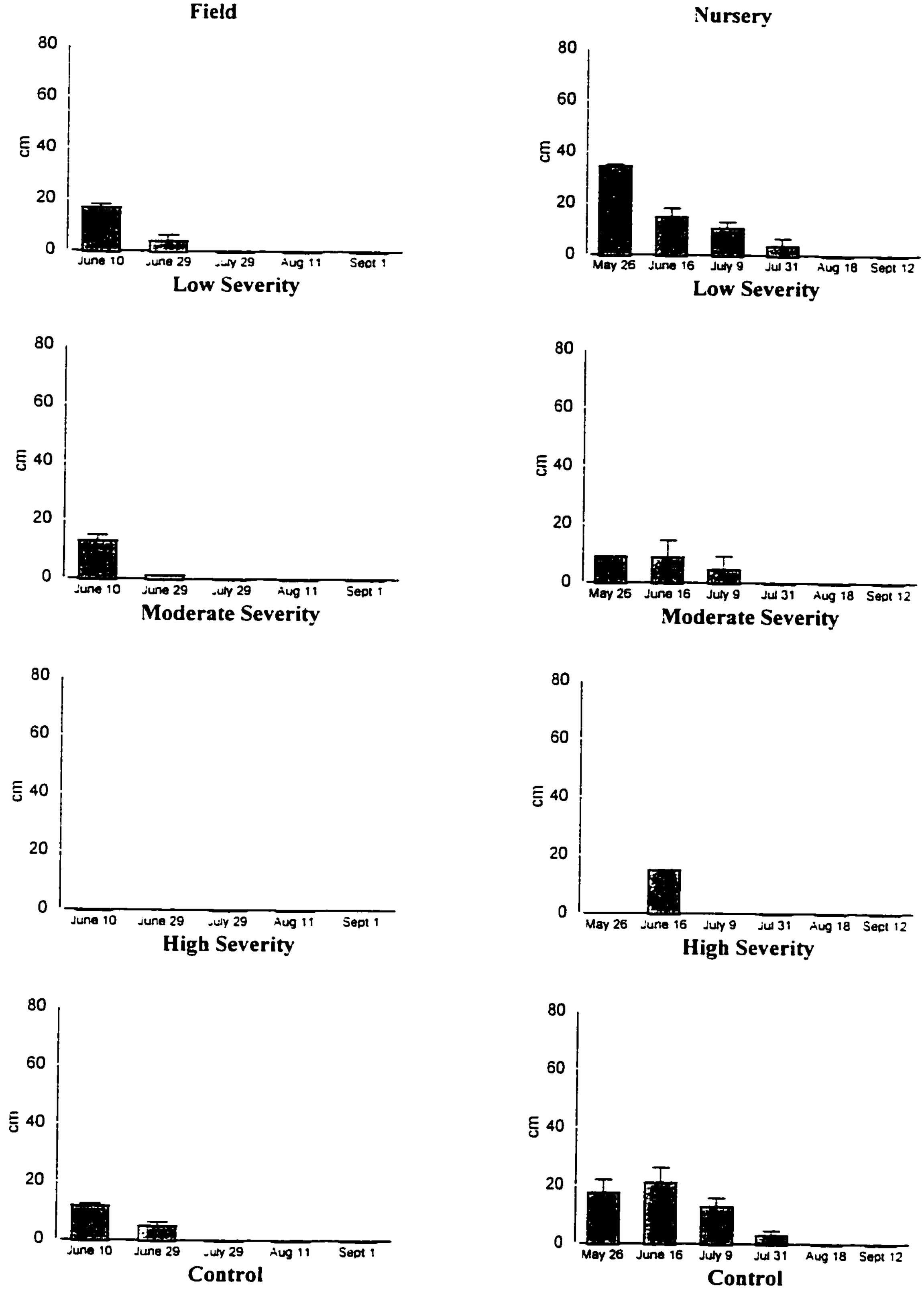
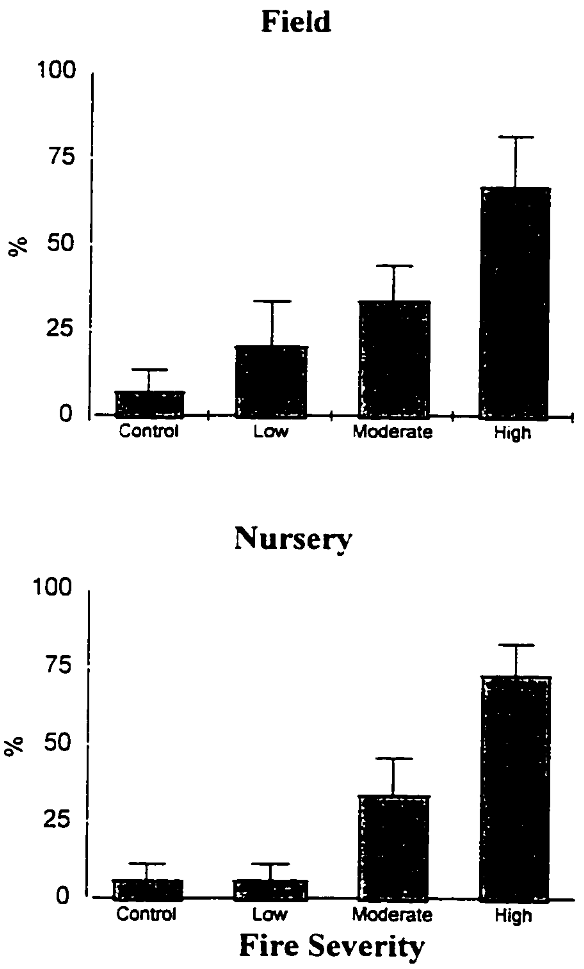


Figure 3-4. Plant mortality at the field and nursery sites in autumn 1993 by fire severity level.



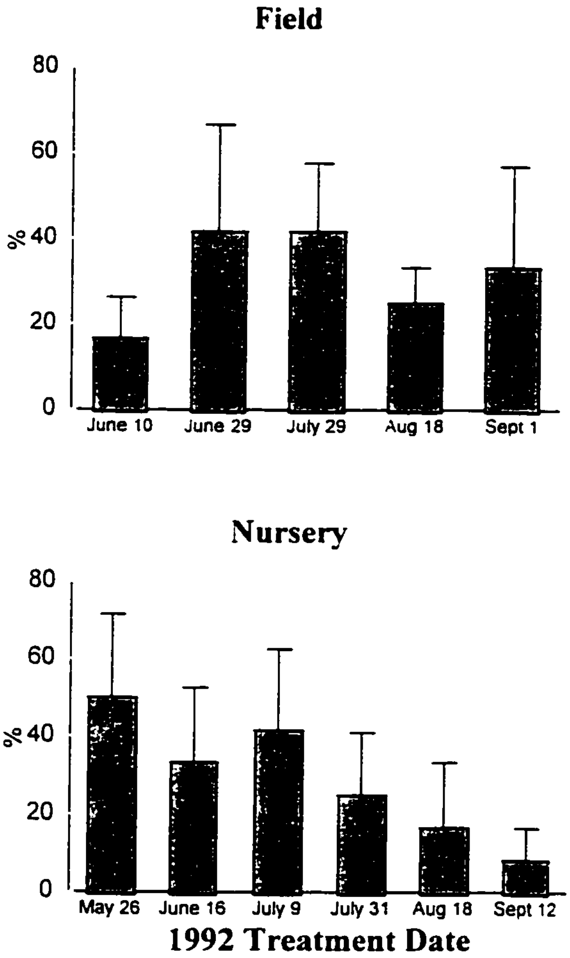


Figure 3-5. Plant mortality for all fire severity treatments at the field and nursery sites in the autumn of 1993 by season of treatment.

Figure 3-6. Number of sprouts (and SE) for field and nursery plants in October 1993 by fire severity level and 1992 treatment date. Means adjusted for rhizome weight covariate.

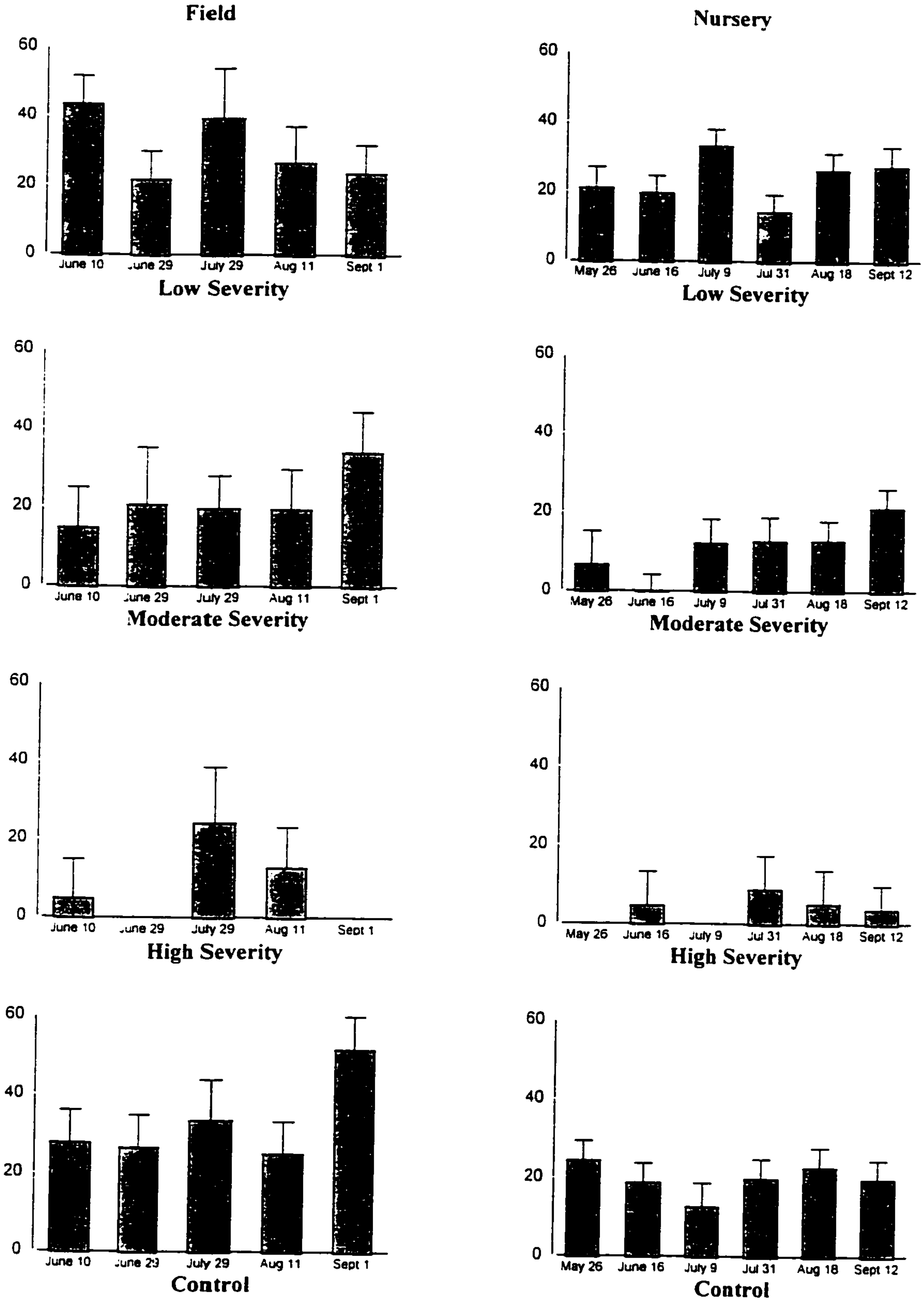


Figure 3-7. Maximum sprout height (and SE) for field and nursery plants in October 1993 by fire severity level and 1992 treatment date.

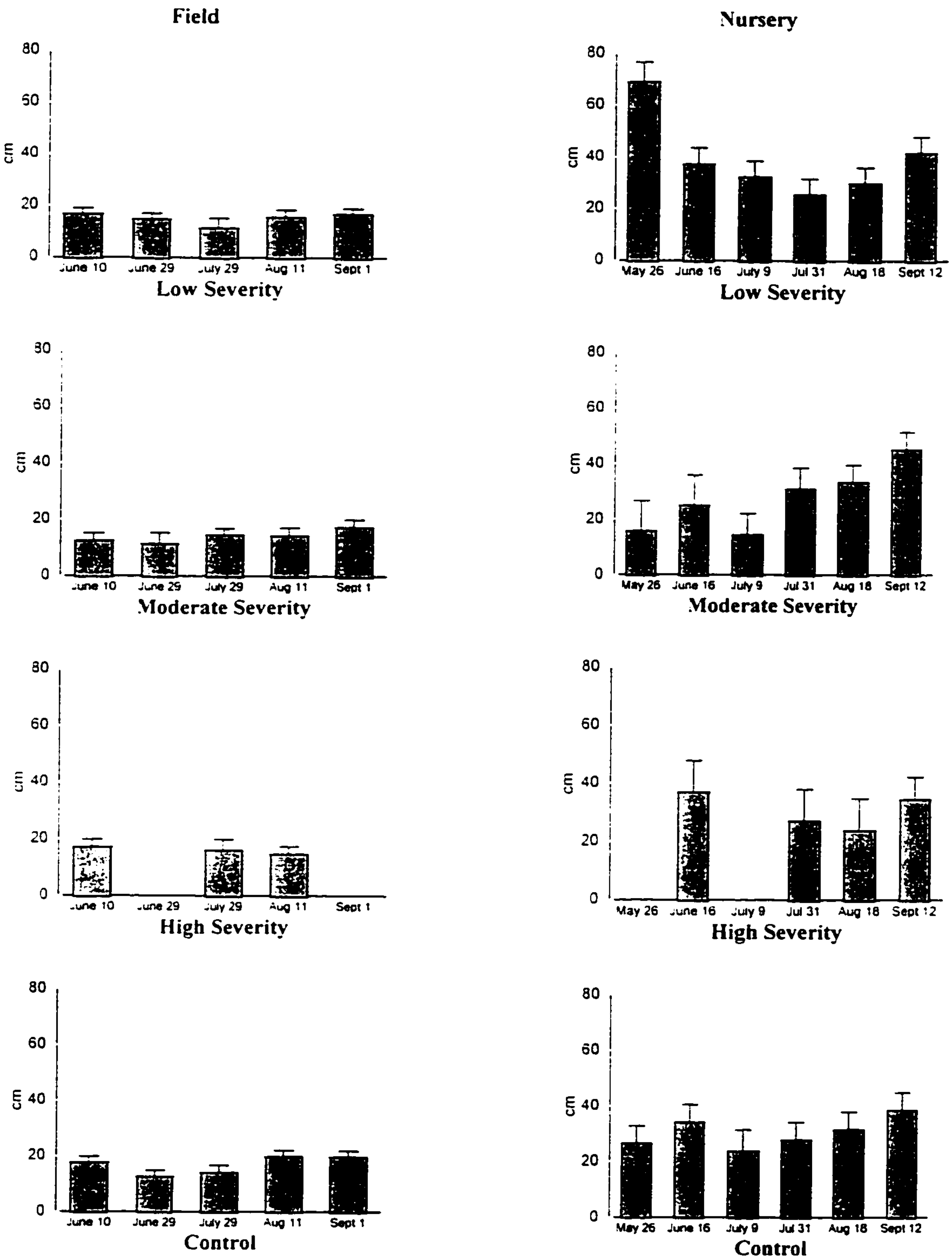
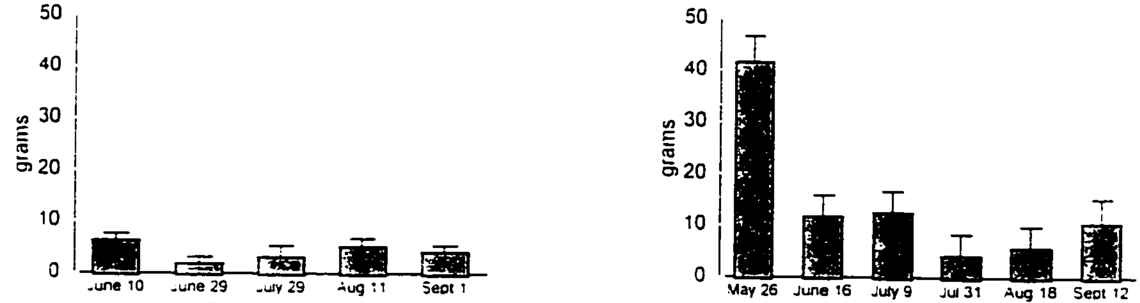


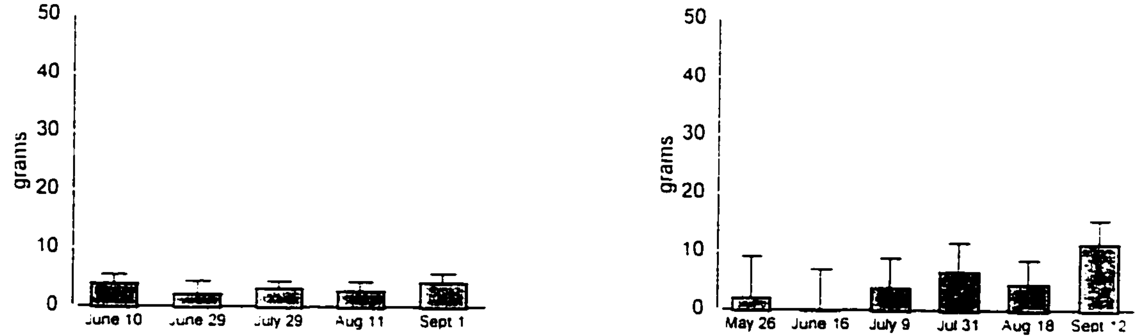
Figure 3-8. Aboveground biomass (and SE) for field and nursery plants in October 1993 by fire severity level and 1992 treatment date. Means adjusted for rhizome weight covariance.

Field **Nursery**



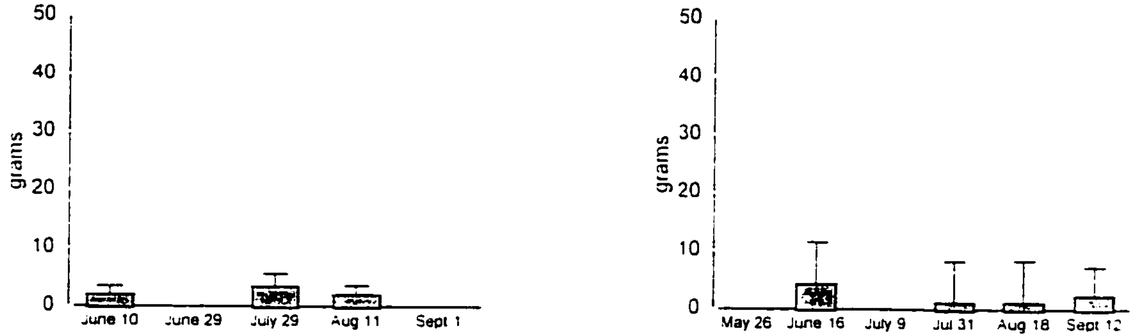
Low Severity

Low Severity



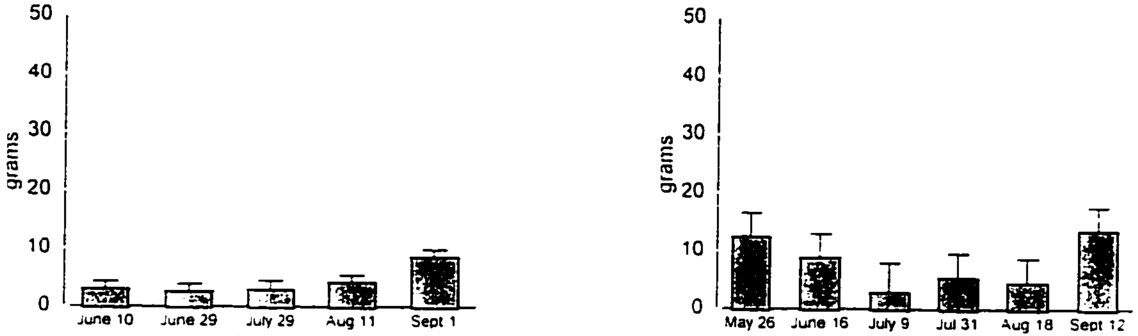
Moderate Severity

Moderate Severity



High Severity

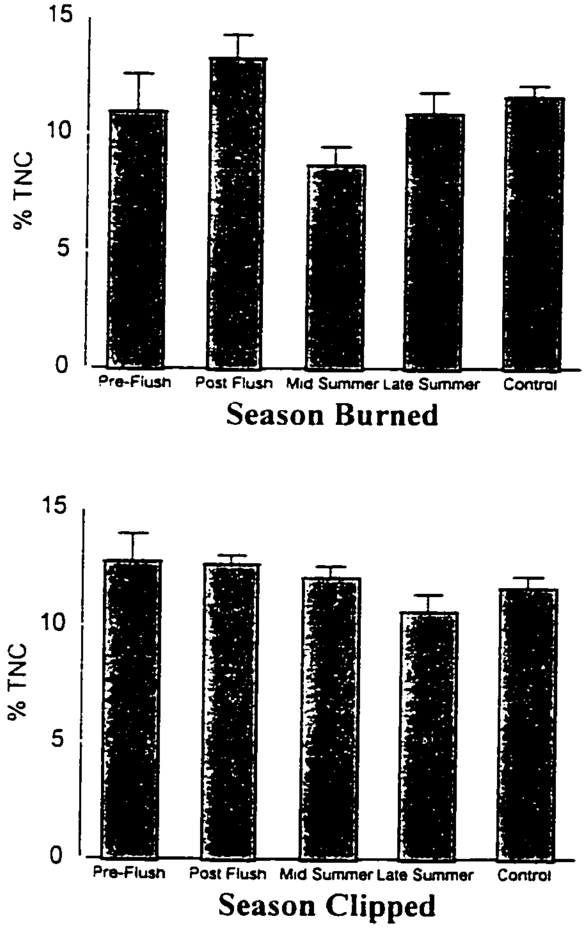
High Severity



Control

Control

Figure 3-9. Level of total non-structural carbohydrates (TNC) expressed as a percentage of weight of underground plant parts in late autumn, by season and type of treatment.



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IV. Postfire response of *Betula glandulosa* Michx. from western and northern Canada[1]

Introduction

Fire adaptation has been documented in many plant species which use strategies of plant survival, fire-enhanced flowering, fire-promoted germination and fire-stimulated seed dispersal (Gill 1981, Rowe 1983, Trabaud 1987). True fire adaptations are those that go beyond providing the ability to survive a fire disturbance as they also provide a fire-stimulated advantage through enhanced survival rates, reproduction or growth. Most northern shrub species respond to fire by resprouting from protected underground plant organs (Payette 1992) and some have shown varied postfire growth response due to different fire characteristics and physiological plant condition (e.g., Flinn and Pringle 1983, Johnston and Woodard 1985, Flinn and Wein 1988, Noste et al. 1989, Kauffman and Martin 1990).

Betula glandulosa Michx. is a low to moderate sized (0.5-2.5 m) shrub with a wide geographic distribution from Alaska to Labrador and Baffin Island, with southward extensions along both coasts to northern California and Maine (Dugle 1966, Hultén 1968). It is commonly found in many northern and mountainous plant communities and occurs on many different sites ranging from swampy boreal peatbogs to rocky sites with shallow soils typical of subarctic and alpine regions (de Groot et al. 1997). Most sites are acidic, moist (but not wet), nutrient-poor and generally treeless or open because of shade intolerance. Fire is a pervasive force over much of its range. Regeneration is primarily from resprouting dormant buds on the rhizome, although seedlings may also become established after site disturbance.

Betula glandulosa is stimulated by the belowground heat pulse of a fire to increase sprout production, sprout height growth and aboveground biomass production during the first 1-2 years of postfire growth (chapter III). Greater plant mortality was found to occur with increasing fire severity, while seasonal timing of fire also influenced subsequent growth response. Spring burning resulted in the greatest sprout production and height growth after the first growing year and it appeared to cause the greatest increase in height growth and aboveground biomass production after two years. The data from that study also indicated that fire-stimulated height growth response was much greater for plants transplanted from the Rocky Mountain foothills to the aspen parkland region of south-central Alberta. It was hypothesized that warmer growth temperatures at the transplant site enhanced this fire response trait. If other *B. glandulosa* populations in northern and mountainous regions also show a fire-stimulated increase in growth rate that is further increased by warmer temperature, then the future range and abundance of this plant may be significantly influenced by the interaction of this characteristic with the warmer conditions and altered fire regimes expected with climate change.

The purpose of this study was to determine if postfire ambient air temperature affects fire response in *Betula glandulosa*, and to determine if the fire response found in the southwest Alberta study was characteristic of other western and northern populations. It was hypothesized that fire response would be detected across the range of *B. glandulosa* in western and northern Canada and that warmer ambient air temperatures during postfire growth would result in greater fire-stimulated height growth response. It was also hypothesized that populations at the most northern and highest elevations would show the greatest increase in postfire growth response because those populations normally experience the lowest field temperatures and therefore, will receive the greatest benefit from increased growth temperature. *B. glandulosa* fire ecology and climate change predictions for this region are reviewed to determine the expected impact of altered growth and fire regimes on future populations.

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[1] This chapter has been submitted to *The International Journal of Wildland Fire*.

Methods

Study site description and field sampling

Eight field locations within the forested zone were selected to cover a large portion of the western geographic and topographic range of *Betula glandulosa* (Figure 4-1, Table 4-1). Sample sites were restricted to well-drained areas with topographic and fuel continuity features that would allow a naturally spreading fire to pass over the site. This was to ensure that all samples were collected from fire-prone (see Whelan 1995) populations. All sites used in this study represent fire regimes 1 or 2 of Heinselman (1981) with frequent (<25-year return interval) or infrequent (>25-year return interval) light surface fires, with possible infrequent occurrence of severe surface fires (fire regime 3). Most sites had direct evidence of recent fire occurrence.

Sample locations were selected to represent large, contiguous populations on mesic sites within the core area of western *Betula glandulosa* range as much as possible. Ground vegetation typically consisted of *Arctostaphylos uva-ursi*, *Fragaria virginiana* with occasional *Achillea millefolium*, *Potentilla fruticosa*, *Vicia americana*, *Salix* spp. and *Rosa* spp., ground lichens including *Cladina mitis* and feathermosses including *Pleurozium schreberi* and *Hylocomium splendens*. The Norman Wells site differed from the others in that it was an open *Picea mariana* bog with *Ledum groenlandicum* and *Equisetum* spp. Although this area was wetter than the others, previous fires had been noted on this sloped upland site. The Fairview site represented a small population on a mesic site near the eastern limit of *B. glandulosa* in west-central Alberta.

Climate data for the weather stations nearest to the field sites showed a general decrease in average summer temperatures with increasing latitude and increasing elevation (Table 4-2). The subarctic region had much higher summer temperatures than the alpine region, while alpine locations received 3-5 times the monthly precipitation of subarctic areas during the summer growing season.

A minimum of 25 vigorous plants of about 1 m in height and 0.25 m^2 in area were collected with a rootball of approximately 0.6 m in diameter and 0.25 m in depth from each site in the autumn of 1994. Additional spare plants were collected to replace plants that did not survive transplanting. All plants were collected after leaf coloration to ensure maximum root carbohydrate storage (Chapin et al. 1986). Plants were immediately transported to Edmonton where stems were counted, measured for height, clipped at ground level and ovendried for biomass determination. Root balls were packed into plastic bags with moist peatmoss and stored at 5°C for one week, at 2°C for 2-4 weeks, at -3°C for about three months, and then gradually brought to room temperature over a two week period.

Experimental design

This experiment included three growth temperature treatments and two burning treatments (burn and no-burn). Three room temperatures (14°C, 19°C, and 24°C) representing typical summer ambient air temperatures for the study area were randomly assigned within each of two greenhouses that had 8 m × 0.8 m × 0.15 m bench troughs filled with commercial peatmoss. Four plants from each field site were randomly assigned to each greenhouse room and planted in the troughs. Additional spare plants were assigned to rooms where it appeared that some rhizomes were small and may not survive transplanting. During the experiment, sodium vapor lights were used in the morning to supplement natural light. This provided 12 hours of daylight at the beginning of the experiment to 16 hours near the end, or conditions that approximated summer photoperiod in southern Alberta.

All greenhouse rooms were initially held at 17°C until rhizomes started sprouting (3-4 weeks). Then two samples from each site per room were randomly selected for burning. Burning treatments consisted of clipping sprouts and heating rhizomes with a propane heat radiator to 60°C at a depth of 2 cm below the top of the rhizome (the low severity treatment of chapter III). All sprouts were clipped for the no-burn control treatment (also referred to as clipping). Sprout numbers and heights were measured 42 and 84 days after treatment: aboveground and belowground biomass were measured after 84 days.

All response data were combined for analysis by ANOVA to determine the effect of burning on postfire sprout production, height growth and aboveground biomass production and to determine the effect of ambient air temperature on postfire growth response across the range of study. This analysis was used to determine if fire response was common and widespread, and if it varied significantly between fire-prone sites. Where site significantly influenced sprout height growth, sprout production or aboveground biomass production, a comparison of means was made using the LSD method to illustrate differences. All sites were also analysed separately by ANOVA to determine if fire response and the influence of postfire ambient air temperature on fire response were significant within the sampled population. A rhizome (or belowground) weight covariate was used in the analyses where its influence was significant. Levels of significance for all analyses were defined as highly significant (**) at $\alpha = 0.01$ and significant (*) at $\alpha = 0.05$.

Results

Within one week of planting, sprouts appeared on many of the northern plants while southern plants followed about one week later. Burned plants sprouted more slowly than clipped plants and all plants produced extremely large leaves. Of the 242 original plants, 24 had considerable stem necrosis from *Phoma* spp. and another seven died from infection after 84 days. These were removed from the final data set, reducing the sample size to 211 plants.

Maximum sprout height

After 42 days, mean maximum sprout height by site and treatment combination ranged from 1.5 to 33.5 cm with the highest temperature producing the greatest sprout heights (Figure 4-2). Overall, burning increased sprout height growth at the highest growth temperature while decreasing it at the two lower temperatures. This interactive effect between the burning treatment and growth temperature was found to be significant in the analysis of combined data (Table 4-3). Analysis by site (Table 4-4) indicated the significance of the interaction between burning and temperature at the Inuvik and Ram Mountain sites which resulted in a large increase in postfire sprout height growth at the highest temperature treatment, while the Fairview site showed a significant overall decrease in height growth after burning. Increasing temperature caused highly significant increases in sprout height for all sites. The greenhouse treatment had a significant effect on height growth after 42 days, and this experimental artifact was attributed to slightly higher room temperatures (+0.4 to +0.6 C°) for the two lowest temperature treatments in one of the greenhouses causing greater sprout height growth. Increasing rhizome weight significantly increased sprout height for plants from the Norman Wells site but had no significant effect for individuals from other sites.

After 84 days, mean maximum sprout height by site and treatment combination increased to 5.8-50.6 cm (Figure 4-3). Sprout height generally increased with burning treatment and increasing temperature while the interactive effect of these two treatments was still evident. Analysis of combined data (Table 4-3) indicated that burning alone significantly increased sprout height, and that the interaction of burning with temperature was no longer statistically significant. The influence of site was highly significant and the following comparison of means illustrates the differences in sprout height growth after 84 days (lines denote sites with no significant difference) between Inuvik (IN), Norman Wells (NW), Fort Providence (FP), Fairview (FV), Grande Cache (GC), Ram Mountain (RM), Ram Falls (RF) and 7 Mile Flats (7M):

Site	FP	7M	GC	FV	RM	RF	NW	IN
Mean height (cm)	32.0	28.8	24.9	22.6	22.2	21.5	17.7	12.5
	———	———		———	———	———	———	
			———	———	———	———	———	———
		———	———	———	———			

Analysis by site of the 84-day data (Table 4-4) showed that a highly significant increase in sprout height due to burning occurred at Inuvik, with a similar significant increase at Grande Cache. Material from the Ram Mountain site showed an increase in height after burning at all growth temperatures, but it was not significant at $\alpha=0.05$. Inuvik plants significantly increased in sprout height due to the interactive effect between burning and higher postfire growth temperature while 7 Mile Flats material had a very similar response. The Fort Providence data indicated that postfire height only exceeded post-clipping height at the highest temperature treatment. Increasing rhizome weight had a significant increasing effect on sprout height at two sites after 84 days.

Sprout numbers

Mean sprout numbers by site and treatment combination ranged from 6.6 to 66.4 after 42 days (Figure 4-4). Growth temperature did not appear to affect sprout numbers while burning tended to decrease sprout numbers in most cases. Analysis of combined data (Table 4-3) showed that burning significantly decreased sprout production and analysis by site (Table 4-5) confirmed this effect on plants from Inuvik, Ram Mountain and Ram Falls. Increasing temperature caused increasing sprout production at Inuvik while Ram Falls specimens had a significant increase in sprout production under the middle temperature treatment (a similar trend found in the Ram Mountain data). Increasing rhizome weight significantly increased sprout production at five of the eight sites.

After 84 days, the range of mean sprout numbers by site and treatment combination was relatively unchanged at 6.8 to 66.8 (Figure 4-5). The combined analysis (Table 4-3) indicated that burning was no longer a significant factor affecting sprout production while growth temperature also had no effect. Differences in sprout production were quite variable between sites with the following comparison of means for Inuvik (IN), Norman Wells (NW), Fort Providence (FP), Fairview (FV), Grande Cache (GC), Ram Mountain (RM), Ram Falls (RF) and 7 Mile Flats (7M):

Site	FP	NW	IN	RF	GC	FV	7M	RM
Mean sprouts	50.0	42.9	34.4	30.5	29.1	25.5	24.1	11.6

Analysis of the 84-day data by site (Table 4-5) showed that burning significantly decreased sprouts at Ram Mountain and also had a strong decreasing influence at Ram Falls and possibly Inuvik. Sprout production appeared to increase after burning at the two lower temperature treatments at the Norman Wells site and at all temperatures at the Fairview site, but neither was statistically significant. Increasing rhizome weight greatly increased sprout numbers at six of the eight sites.

Aboveground biomass

Mean aboveground biomass by site and treatment combination after 84 days ranged from 6.5 to 20.9 g (Figure 4-6). Biomass production generally increased with temperature while the effect of burning had no strong trend. The combined data analysis (Table 4-3) indicated that a highly significant amount of biomass increase was attributable to increased rhizome weight and increased temperature. Aboveground biomass production was also shown to be significantly different between Inuvik (IN), Norman Wells (NW), Fort Providence (FP), Fairview (FV), Grande Cache (GC), Ram Mountain (RM), Ram Falls (RF) and 7 Mile Flats (7M) with the following comparison of means:

Site	FP	7M	RF	GC	NW	FV	RM	IN
Mean biomass (g)	16.4	11.8	11.2	10.9	10.4	9.1	8.7	8.4

Analysis of individual sites (Table 4-6) showed that there was a significant interactive effect between burning and increased growth temperature that increased aboveground biomass at Inuvik. Burning also increased aboveground biomass at 7 Mile Flats and Grande Cache, although it was not significant after 84 days. Increasing rhizome weight significantly increased aboveground biomass production at seven of the eight sites.

Discussion

The results indicate that fire response is characteristic of many *Betula glandulosa* populations growing in fire-prone areas as burning significantly increased sprout height growth at four of the eight sites used in this study. There appears to be no geographic or topographic pattern to the distribution of populations exhibiting fire response characteristics as they were located across the study area. Fire-induced height growth also did not appear to be influenced by height growth vigour since fire response was found in populations with a wide range of mean sprout heights.

The data also indicated that temperature is an important factor affecting fire response as warmer postfire ambient air temperatures caused significant increases in fire-stimulated height growth response. In some cases, fire response could only be detected through the interactive effect between burning and the warmest growth temperature, indicating that a lower temperature threshold for increased postfire growth response may have been reached. It is possible that the highest temperature treatment used in this study may not have reached the lower temperature threshold for increased postfire growth response at all sites. The temperatures used in this study were representative of summer ambient air conditions for the study area but were lower than typical postfire field surface temperatures. Viro (1974) documented an average postfire soil surface temperature of 31°C (seasonal maximum of 52°C) in a Finnish study while Sims (1976) recorded average daily postfire soil surface temperatures of 46-63°C during the warmest days (air temperatures of 26-36°C) in a southeastern Manitoba study. If *Betula glandulosa* is adapted to increase fire-stimulated growth rates at typical postfire surface temperatures rather than ambient air temperatures, then greater fire response may be detected at higher temperatures than those used in this study.

The increased postfire aboveground biomass production rates found in our previous *Betula glandulosa* study (chapter III) was also detected in this study. Burning significantly increased aboveground biomass at the site with the greatest postfire height growth response while the three other sites exhibiting fire-stimulated height growth response showed similar trends. The two studies suggest that increased postfire aboveground biomass production becomes increasingly significant as growth progresses over several years.

A fire-induced decrease in sprout production was found in several of the study populations, a result also found in the early season treatments of a transplant experiment in our previous study (chapter III). It appears that the effect of recent transplanting was to reduce postfire sprout production because of a priority for root growth over shoot growth at the time of burning. Therefore, fire-stimulated sprout production could not be tested in this transplant study.

Many plants had a minimal height growth response to burning during the first 42-day period, but later responded with an increased growth rate after 84 days. This was attributed to an initial growth advantage by unburned plants due to the presence of numerous initiated buds and partially grown shoots that quickly continued to grow when apical dominance was removed (chapter III). Many of these would have been killed by the burning treatment, necessitating the initiation of new shoots with a consequent delay in sprouting response (a typical response for burned plants). Overall, the most northerly plants sprouted first, indicating their adaptation to shorter growing seasons (Savile 1972).

Rhizome weight was important to sprout and aboveground biomass production but had little influence on maximum sprout height growth. Belowground biomass is an indicator of carbohydrate storage capacity but because carbohydrate concentration was not determined for rhizomes in this study, belowground biomass does not indicate total nonstructural carbohydrates (TNC). It is possible that site differences in carbohydrate concentrations may have influenced sprouting and aboveground biomass production. A late autumn TNC value of 11.6% was found for *B. glandulosa* in south-central Alberta (chapter III): only when plants were clipped or burned at different times in the previous growing season did autumn TNC values show significant difference. TNC values in belowground biomass of Alaskan *Betula nana* were found to be 10-12% in pre-flush spring and 8-10% in late summer (Chapin et al. 1986). Differences in winter carbohydrate content of *B. glandulosa* terminal shoots were found to be not significant between years and between local areas in central Alberta (Pease et al. 1979). This evidence suggests that overwinter TNC concentrations in *B. glandulosa* tend to be fairly consistent, unless the plant has experienced exceptional stress in the previous growing season. Therefore, rhizome weight was considered a surrogate for overwinter available TNC in this study.

Northern plants experienced the greatest departure from normal summer daylength during the experiment (20-24 hours during May to August at Inuvik, versus 14-17 hours in southern Alberta). Therefore, the 12-16 hour photoperiod used in this study potentially provided a greater advantage to plants from southern populations. However, arctic plants possess a great ability to adapt to reduced photoperiod (Savile 1972) and daylength did not appear to influence the ability to detect fire response.

Much of the post-treatment variation in maximum sprout height and aboveground biomass was found to be caused by ambient air temperature. The significant effect of greenhouse treatment on maximum sprout height during the first 42 days due to a slightly higher temperature in one greenhouse indicates that even a minor air temperature difference of 0.5 C° can be very influential during the early stages of growth. This is an important factor for a plant that resprouts on burned areas because the earliest growth occurs during a period of increased postfire surface temperatures due to reduced albedo and shading (Macadam 1989, Whelan 1995). However, increased postfire growth and production rates are not believed to be longterm responses in *Betula glandulosa*. Because of its shade intolerant nature, increased growth rates are most important during the first few critical years after fire when competition from other invading pioneers is very high (Rowe 1983). Once *B. glandulosa* is re-established, it is usually very dominant in the plant community and the need for a fire-induced competitive advantage is no longer necessary. As well, the advantage of warmer surface temperatures decreases with time as the plant grows higher and surface temperatures decline to pre-fire levels due to increased shading and surface albedo.

The fire ecology of *Betula glandulosa* is expected to be an important factor affecting its future abundance and distribution under predicted climate change conditions. The current northern limit of *Betula glandulosa* is roughly the 7°C mean daily July isotherm (de Groot et al. 1997). Lack of sexual reproduction at higher latitudes (Weis and Hermanutz 1993) which may be caused by adverse climate conditions and low summer heat sums (Hermanutz et al. 1989, Weis and Hermanutz 1993) is probably responsible for this limit. A predicted increase in summer temperatures of 3-4 C° under 2×CO_2 conditions (Bergeron and Flannigan 1995) will probably extend the *B. glandulosa* range further north. The southern range appears to be limited by high summer temperatures (as similarly suggested for *B. nana* in the British Isles; Conolly and Dahl 1970) or low precipitation in the grassland region, or both. Present populations extend to the subhumid grassland and aspen parkland regions where evapotranspiration is slightly greater than precipitation (Campbell et al. 1994). A general northern migration of the boreal and aspen parkland forests is expected under climate change (Hogg and Hurdle 1995) which will affect *B. glandulosa* populations east of the Rocky Mountain foothills but will have a minimal affect on more westerly populations. Fire will be an important ecological force over the vast majority of the future *B. glandulosa* range as climate change progresses. It is also expected to be very influential on populations at the southern range limit in the aspen parkland where fire can control the expansion of aspen onto rangelands (Anderson and Bailey 1980). It probably will not affect populations at the future northern *B. glandulosa* limit because of low fire frequencies in far north biomes (Payette et al. 1989).

Because *Betula glandulosa* seedlings are very shade intolerant, disturbance is required for it to colonize new communities where competition is high. Any increase in fire activity will assist this plant to invade new areas, thereby increasing its abundance and expanding its range. This will be facilitated by climate change which is predicted to cause greater fire weather severity in western and northern Canada (Flannigan and Van Wagner 1991, Bergeron and Flannigan 1995). The increased summer temperatures associated with climate change will also provide an additional advantage to *B. glandulosa* by inducing greater fire-stimulated growth rates, making it a more competitive species. The deep rooting nature of *B. glandulosa* allows it to resprout after low and moderate severity fires. Survival decreases when fires are severe, but the opportunity for new seedling establishment increases due to a greater reduction in competition and surface organic layers, and is assisted by the wide dispersal of seeds (allowing off-site seed sources) and high annual seed production rates. Therefore, *B. glandulosa* is well-adapted to a wide range of fire regimes including the increased frequency of severe burning conditions as predicted to occur under climate change (Flannigan and Van Wagner 1991). In general, *B. glandulosa* populations will expand and thrive under climate change due to its fire ecology.

Conclusion

The first hypothesis that fire response is a widespread characteristic of *Betula glandulosa* was supported as increased postfire sprout height growth was found in fire-prone populations that were widely distributed over the geographic range of study. Not all fire-prone populations showed a significant response to fire, although it is possible that fire-stimulated height growth may occur in those populations at higher temperatures than tested in this study. The second hypothesis that an increase in postfire sprout height growth would result from warmer ambient air temperatures was also supported. The last hypothesis that the most northerly and highest populations would show the greatest increase in postfire response at higher temperatures was supported by the most northerly site but not by the highest elevation site. Fire response characteristics will benefit *B. glandulosa* populations in the future as increasing fire activity and summer temperatures occur during climate change.

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Tables

Table 4-1. Field locations and pre-treatment shrub characteristics (SE in brackets).

Site	Latitude (N)	Longitude (W)	Elev. (m)	Number of Stems	Stem Height (m)	Aboveground Biomass (g)	Cover Area (m^2)
Inuvik	68° 18'	133° 29'	59	17.4 (2.1)	1.07 (0.05)	293.3 (39.3)	0.44 (0.05)
Norman Wells	65° 17'	126° 48'	67	19.5 (2.0)	0.87 (0.05)	228.4 (29.0)	0.29 (0.03)
Fort Providence	61° 23'	117° 26'	171	22.8 (2.0)	1.08 (0.03)	259.2 (23.2)	0.32 (0.03)
Fairview	56° 36'	118° 45'	840	12.5 (1.3)	1.29 (0.04)	165.3 (13.4)	0.19 (0.02)
Grande Cache	53° 46'	118° 19'	1450	19.7 (1.9)	1.01 (0.02)	229.0 (20.8)	0.17 (0.01)
Ram Mountain	52° 00'	116° 06'	1940	14.3 (1.0)	0.58 (0.02)	126.7 (8.3)	0.19 (0.01)
Ram Falls	52° 05'	115° 51'	1635	20.9 (1.5)	0.89 (0.02)	294.1 (27.0)	0.23 (0.02)
7 Mile Flats	52° 00'	115° 21'	1350	18.0 (1.4)	0.86 (0.02)	213.5 (16.1)	0.22 (0.02)

Table 4-2. Climate normals for selected AES stations, provincial Ranger Stations (RS), and forestry Lookouts (LO) near study sites. Additional sites in southwestern Alberta are shown to illustrate elevational differences.

Site	Latitude (N)	Longitude (W)	Elev. (m)	Mean Daily Temperature (°C)					Mean Monthly Precipitation (mm)				
				May	June	July	August	September	May	June	July	August	September
Inuvik [a]	68° 18'	133° 29'	59	-0.7	10.6	13.8	10.5	3.3	19.1	22.2	34.1	43.9	24.2
Norman Wells [a]	65° 17'	126° 48'	67	5.8	14.6	16.7	13.5	6.3	19.7	43.2	50.4	49.0	30.6
Fort Providence [b]	61° 19'	117° 37'	162	7.1	13.1	16.3	14.5	7.8	19.4	25.9	37.5	30.4	28.6
Fairview [a]	56° 04'	118° 23'	670	10.2	14.3	16.2	15.0	9.9	43.5	71.7	75.5	54.5	36.2
Grande Cache RS [b]	53° 54'	119° 06'	1250	7.3	11.0	13.8	13.0	8.7	60.5	96.7	67.1	57.5	46.5
Baldy LO [a]	52° 33'	116° 07'	2083	N/A	7.0	9.6	9.3	N/A	63.7	92.4	108.0	75.5	42.9
Kiska LO [b]	52° 18'	116° 11'	2073	N/A	7.4	10.5	9.8	5.6	N/A	102.9	98.7	73.1	N/A
Baseline LO [a]	52° 08'	115° 25'	1897	4.4	8.6	11.2	10.9	N/A	89.3	109.1	120.5	86.8	57.3
Blackstone LO [a]	52° 47'	116° 21'	1570	N/A	10.9	13.2	12.6	N/A	N/A	95.4	110.2	86.9	N/A
Aurora LO [a]	52° 39'	115° 43'	1341	N/A	12.4	14.7	13.7	N/A	N/A	115.7	118.7	86.4	N/A
Clearwater RS [a]	51° 59'	115° 15'	1280	7.1	11.0	13.2	12.9	7.9	82.6	112.7	114.3	76.0	71.2
Brazeau LO [a]	53° 01'	115° 25'	1088	9.2	12.7	14.8	14.1	9.5	66.8	107.1	122.8	86.0	59.0

[a] Atmospheric Environment Service (1993a, 1993b)

[b] Atmospheric Environment Service (1981, 1982a, 1982b)

Table 4-3. Summary of F significance values by burning treatment, growing temperature and site after 42 and 84 days (N=220 and 211, respectively) using combined data.

	Maximum Sprout Height (cm)		Number of Sprouts		Aboveground Biomass (g)
	42 days	84 days	42 days	84 days	84 days
Greenhouse	0.0012**	0.8761	0.6066	0.7047	0.4281
Site	0.0001**	0.0001**	0.0248*	0.0751	0.0001**
Temperature	0.0001**	0.0001**	0.1481	0.6833	0.0001**
Burning	0.2511	0.0413*	0.0305*	0.2570	0.6438
Site · Temperature	0.0856	0.4936	0.4828	0.2483	0.3429
Site · Burning	0.3506	0.0937	0.2594	0.5304	0.5647
Burning × Temperature	0.0234*	0.1048	0.6746	0.7011	0.6007
Site · Temperature × Burning	0.5924	0.6753	0.9448	0.9094	0.7823
Rhizome Weight (covariate)	0.0293*	NS	0.0001**	0.0001**	0.0001**

Table 4-4. Summary of sample size (n) and F significance values for maximum sprout height after 42 and 84 days by burning treatment, growing temperature and site.

Maximum Sprout Height after 42 days								
	Inuvik	Norman Wells	Fort Providence	Fairview	Grande Cache	Ram Mountain	Ram Falls	7 Mile Flats
n	26	28	28	30	27	30	25	26
Greenhouse	0.9367	0.9059	0.1023	0.1183	0.0390*	0.3496	0.4008	0.0744
Temperature	0.0001**	0.0001**	0.0002**	0.0020**	0.0004**	0.0001**	0.0006**	0.0002**
Burning	0.6848	0.8793	0.2483	0.0437*	0.5727	0.3677	0.9677	0.2424
Burning × Temperature	0.0632	0.9758	0.3587	0.7783	0.5400	0.0605	0.1802	0.7253
Rhizome Wt (covariate)	NS	0.0448*	NS	NS	NS	NS	NS	NS

Maximum Sprout Height after 84 days								
	Inuvik	Norman Wells	Fort Providence	Fairview	Grande Cache	Ram Mountain	Ram Falls	7 Mile Flats
n	23	29	28	28	21	35	21	26
Greenhouse	0.4933	0.6423	0.4374	0.9214	0.8121	0.1299	0.1466	0.7496
Temperature	0.0001**	0.0001**	0.0226*	0.0942	0.0383*	0.0045**	0.1272	0.0014**
Burning	0.0065**	0.5385	0.7370	0.7062	0.0283*	0.0973	0.4117	0.1281
Burning × Temperature	0.0275*	0.4472	0.3334	0.9129	0.3126	0.5335	0.9052	0.0667
Rhizome Wt (covariate)	NS	0.0309*	NS	NS	NS	0.0192*	NS	NS

Table 4-5. Summary of sample size (n) and F significance values for number of sprouts after 42 and 84 days by burning treatment, growing temperature and site.

Number of Sprouts after 42 days								
	Inuvik	Norman Wells	Fort Providence	Fairview	Grande Cache	Ram Mountain	Ram Falls	7 Mile Flats
n	26	28	28	30	27	30	25	26
Greenhouse	0.6360	0.8004	0.9577	0.3141	0.3237	0.2923	0.2531	0.4131
Temperature	0.0628	0.3920	0.7129	0.7282	0.7036	0.0957	0.0387*	0.5278
Burning	0.0763	0.2958	0.4630	0.2452	0.8163	0.0798	0.0095**	0.9471
Burning × Temperature	0.2439	0.5001	0.9577	0.7798	0.8907	0.3677	0.0899	0.8257
Rhizome Wt (covariate)	0.0013**	0.0003**	0.0070**	NS	0.0342*	NS	NS	0.0629

Number of Sprouts after 84 days								
	Inuvik	Norman Wells	Fort Providence	Fairview	Grande Cache	Ram Mountain	Ram Falls	7 Mile Flats
n	23	29	28	28	21	35	21	26
Greenhouse	0.4976	0.5606	0.9437	0.4294	0.5151	0.8219	0.9219	0.2474
Temperature	0.2963	0.0783	0.5185	0.3840	0.6175	0.0098**	0.7867	0.8880
Burning	0.0899	0.5885	0.8936	0.2223	0.2344	0.0312*	0.0606	0.8181
Burning × Temperature	0.8863	0.4772	0.5125	0.8679	0.7691	0.0820	0.6007	0.7040
Rhizome Wt (covariate)	0.0007**	0.0001**	0.0028**	NS	NS	0.0001**	0.0161*	0.0460*

Table 4-6. Summary of sample size (n) and F significance values for aboveground biomass after 84 days by burning treatment, growing temperature and site.

	Inuvik	Norman Wells	Fort Providence	Fairview	Grande Cache	Ram Mountain	Ram Falls	7 Mile Flats
n	23	29	28	28	21	35	21	26
Greenhouse	0.3253	0.3438	0.8393	0.6319	0.4294	0.1254	0.2202	0.7153
Temperature	0.0002**	0.0001**	0.2456	0.8072	0.0304*	0.0018**	0.0865	0.0188*
Burning	0.3371	0.6911	0.5449	0.5028	0.2254	0.5976	0.2142	0.4076
Burning × Temperature	0.0538	0.5585	0.8077	0.4868	0.7648	0.3672	0.2981	0.3112
Rhizome Wt (covariate)	0.0279*	0.0001**	0.0357*	0.0190*	NS	0.0001**	0.0255*	0.0043**

Figures

Figure 4-1. Location of sample sites used in this study. Weather stations (+) located at Ranger Stations (RS) and provincial fire lookout towers (LO) referred to in the text are also shown.

Figure 4-2. Maximum sprout height (and SE) after 42 days by burning treatment, growing temperature and site (means adjusted for rhizome weight covariate where significant).

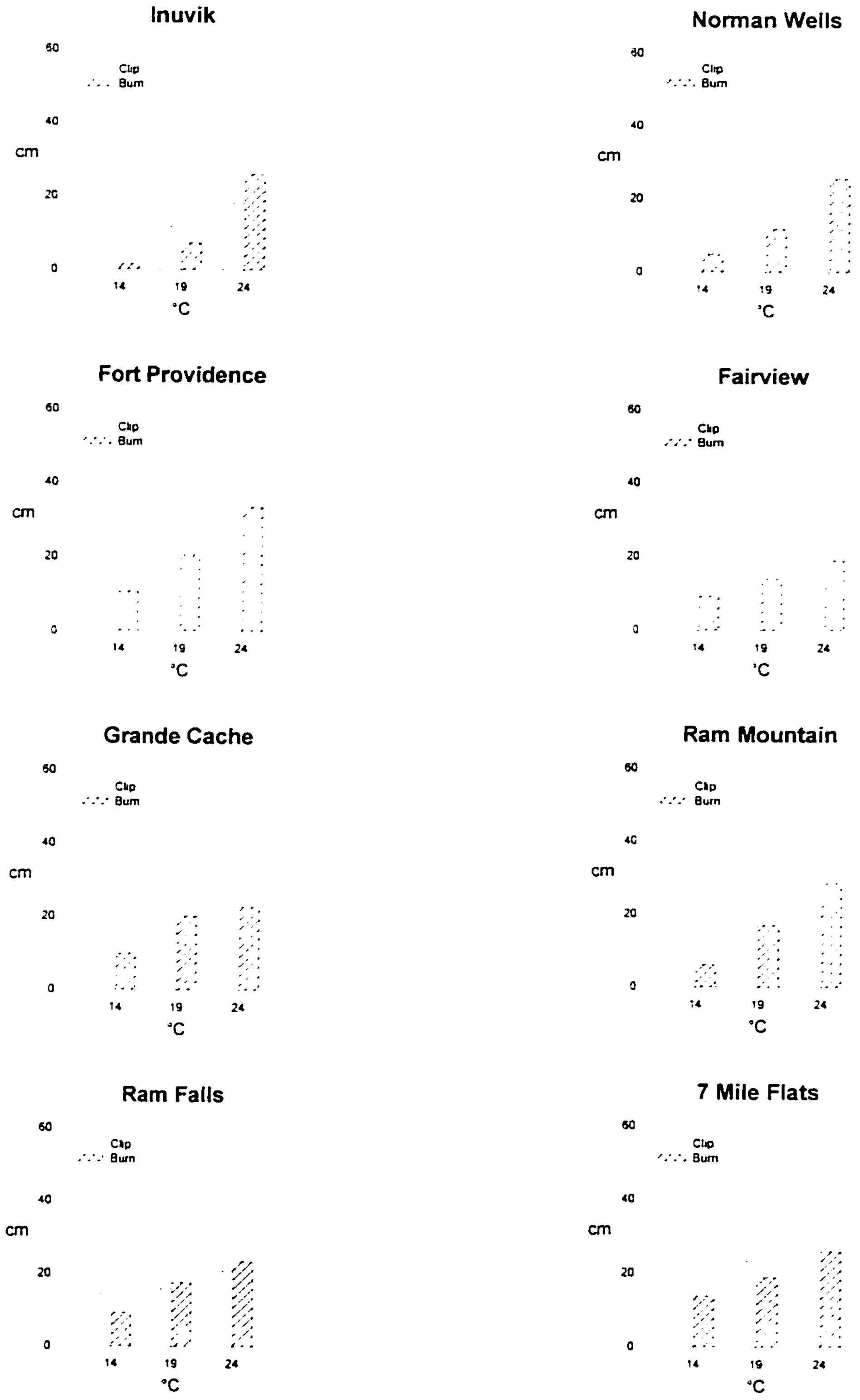
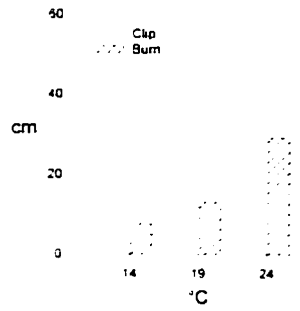
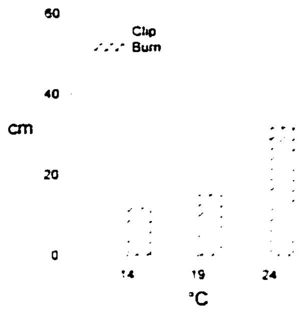


Figure 4-3. Maximum sprout height (and SE) after 84 days by burning treatment, growing temperature and site (means adjusted for rhizome weight covariate where significant).

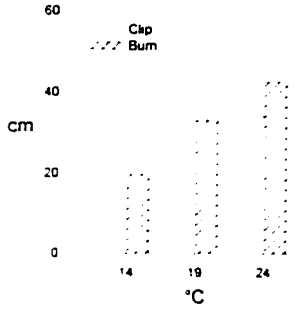
Inuvik



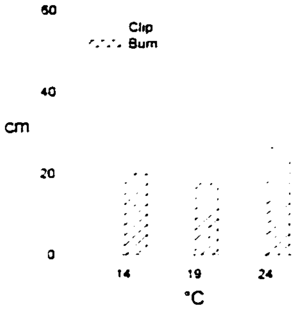
Norman Wells



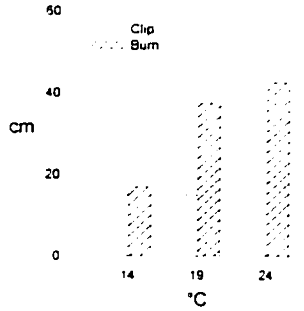
Fort Providence



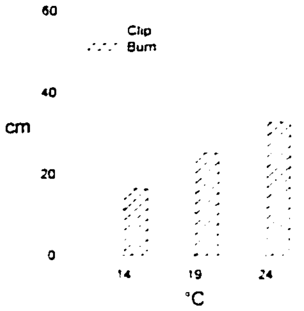
Fairview



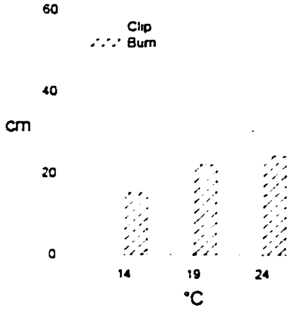
Grande Cache



Ram Mountain



Ram Falls



7 Mile Flats

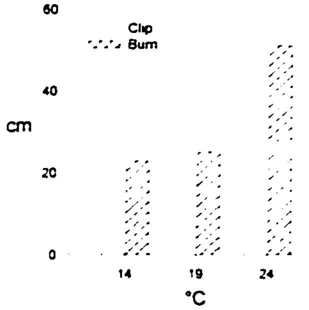


Figure 4-4. Number of sprouts (and SE) after 42 days by burning treatment, growing temperature and site (means adjusted for rhizome weight covariate where significant).

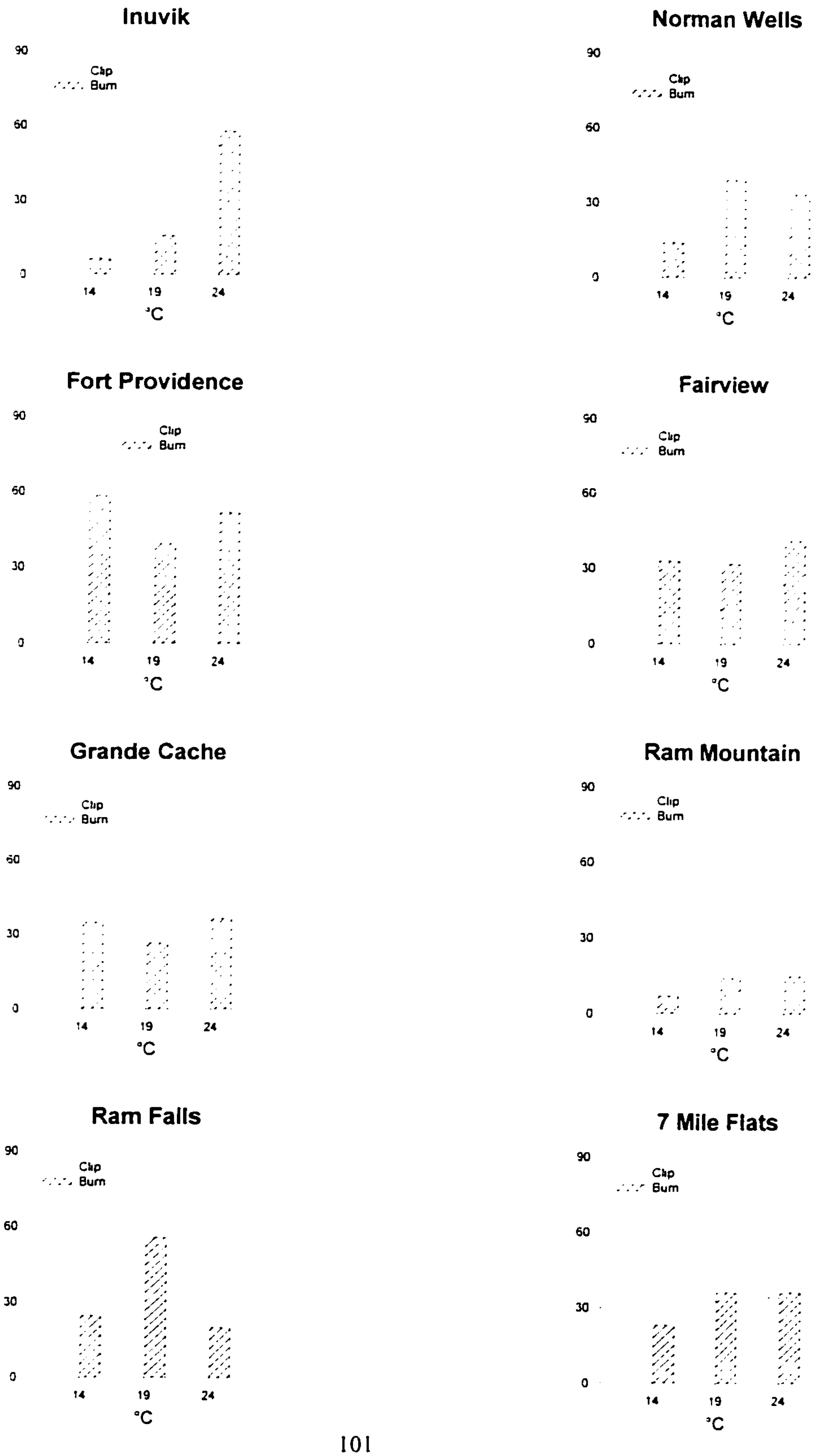


Figure 4-5. Number of sprouts (and SE) after 84 days by burning treatment, growing temperature and site (means adjusted for rhizome weight covariate where significant).

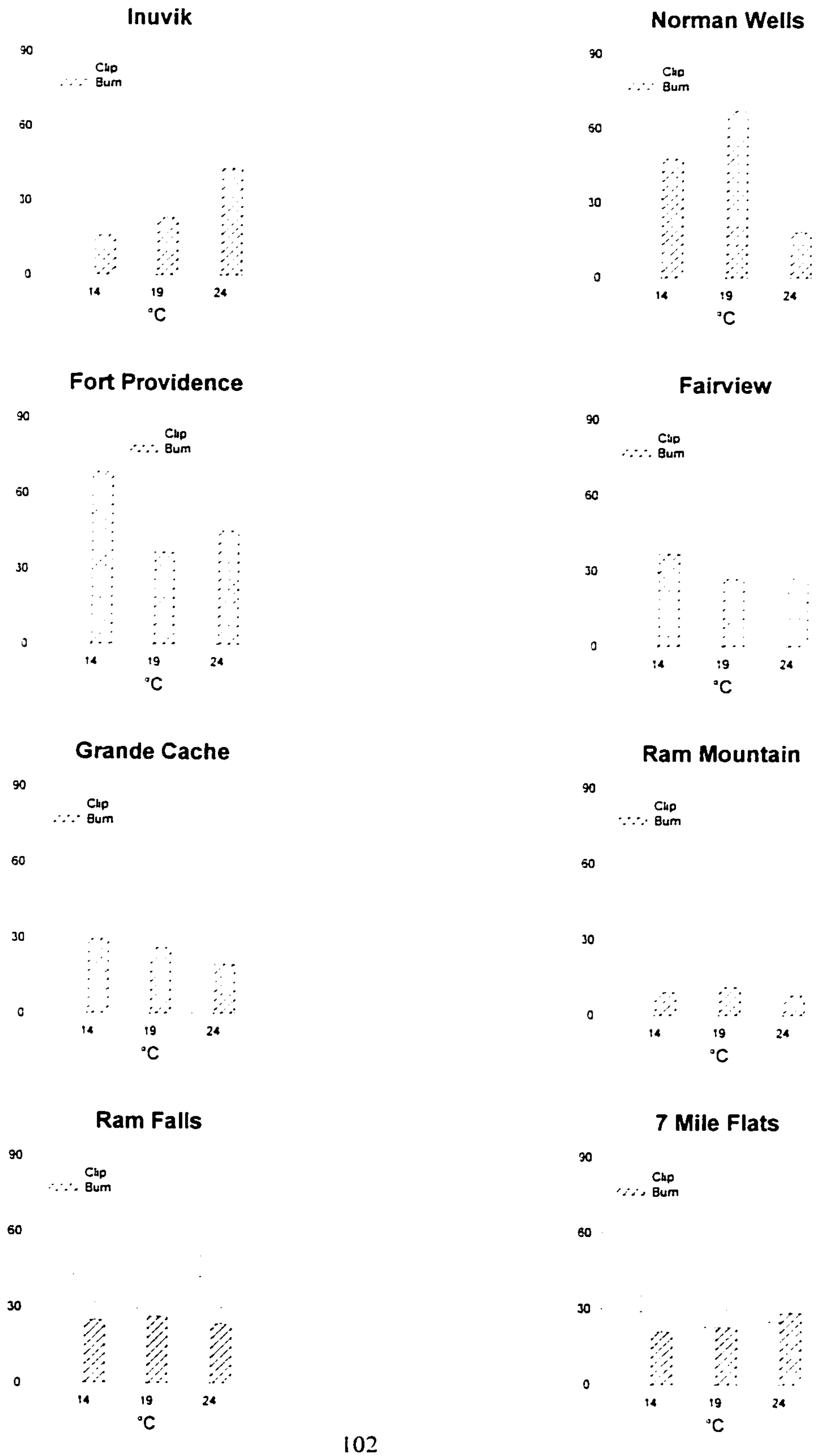
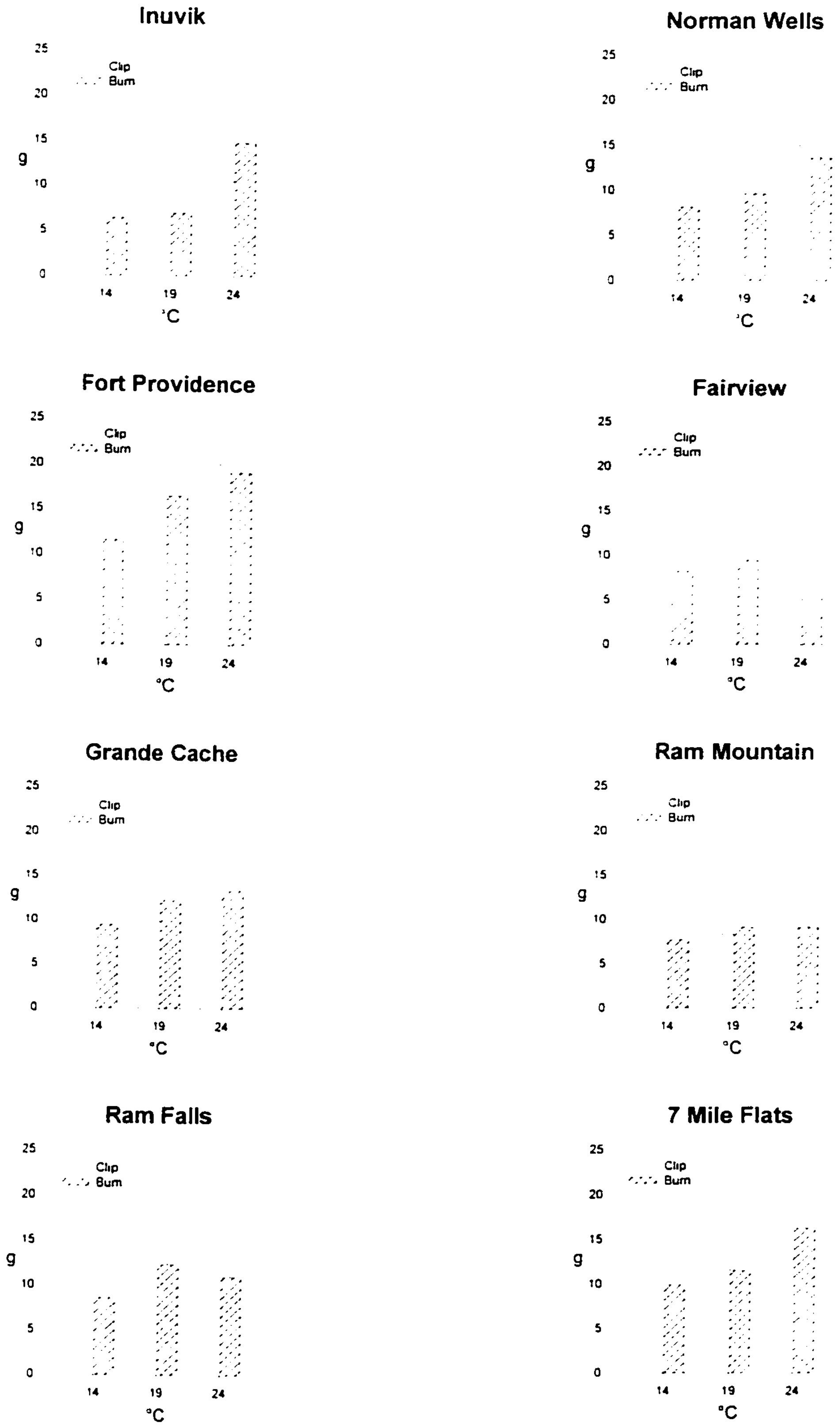


Figure 4-6. Aboveground biomass (and SE) after 84 days by burning treatment, growing temperature and site (means adjusted for rhizome weight covariate where significant).



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V. A fire effects-population model for *Betula glandulosa* Michx.

Introduction

Betula glandulosa Michx. is one of several circumpolar birch shrub species occurring in North America (Hultén and Fries 1986). It has a wide range from Greenland to Alaska and southward along both coasts to the northern US (Dugle 1966, Viereck and Little 1972, Weis and Hermanutz 1993). *B. glandulosa* grows on a wide range of sites including xeric and rocky locations in the subarctic tundra, cold and moist alpine tundra with shallow soils, and deep peaty bogs in the boreal region (chapter 2). Its widespread nature is an indication of adaptability to many different environmental stresses including climate, insect defoliation (Koponen 1984, Ives and Wong 1988), animal browse (Pease et al. 1979, Trudell and White 1981) and fire. Chapters 3 and 4 have shown that *B. glandulosa* responds to fire with increased sprout numbers, greater sprout height growth, and increased aboveground biomass during the immediate postfire years.

Expanding populations of *Betula glandulosa* are a wildlife habitat problem in areas where animals forage on grasses and forbs. In western Canada, open valley bottoms in the Rocky Mountains are critical elk winter habitat (Bork et al. 1996) while grass meadows in north-western Canada are important forage production areas for bison (Carbyn et al. 1993). Many of these open sites can become dominated by *B. glandulosa*, virtually eliminating graminoid and herbaceous forage species. Fire immediately reduces cover, although longterm results can be quite variable depending on burning conditions, seasonal timing of the burn, and subsequent growing conditions.

The purpose of this study was to construct a fire effects-population model for *Betula glandulosa* to simulate population response to fire beyond current field data sets. In particular, the objective was to examine *B. glandulosa* population dynamics in response to different fire intervals and fire severities, and to do so using a wider range of conditions than studied in previous experiments. The model was designed to be representative of typical *B. glandulosa*-dominated stands that are wildlife habitat management problems in western and northern Canada. In this way, testing the effects of fire interval and fire severity (two primary factors that can be manipulated within a prescribed burn program) with the model will provide an assessment of the ability to manage these areas with prescribed fire. The predictions to be tested with this model are that population density, cover and biomass are highly dependant on fire interval and fire severity. More specifically, all three population characteristics will decrease with increasing fire severity and decreasing fire interval.

Methods

Field data

Boundary conditions of the model were based on field data collected along the East Slopes Region of Alberta (Figure 5-1). To represent areas of habitat management concern, field sampling was restricted to mineral soil sites below treeline. Of 23 sites that were sampled in 1996 to collect biomass, cover and population density data for a range of stand ages, seven sites (Table 5-1) were used to calibrate the model and 16 (Table 5-2) were used for model corroboration. The 7 Mile Flats sites were used for calibration because of the detailed fire history available for them. Other calibration sites were randomly selected to represent a range of moisture regimes.

Each site was sampled along three randomly located 50 m transects (two transects were used in high density, homogeneous stands). Twenty-five 1m^2 plots were located every two metres on alternating sides along the transect. This plot size was found to be appropriate for sampling canopy volume of low and moderate sized shrubs by Bentley et al. (1970). Shrubs were measured for height and diameter if the center of the plant (as determined by the sprouting rhizome) fell within the plot. Individual canopy volume was calculated using canopy area and plant height, while total cover for the site was measured using the line intersect method along the three 50 m transect lines.

Moisture regime (MR) was determined for each site following the classes used by Corns and Annas (1986) for west-central Alberta. Study area sites had the following typical characteristics: MR-2 (subxeric), sparse grass and forb component, no mosses present and minimal (<2 cm) surface organic layer; MR-3 (submesic), shallow (4-10 cm) surface organic layer over mineral soil, dense grass and forb component, and feather moss in shaded and/or low microsite locations; MR-4 (mesic), moderate (10-20 cm) organic layer over mineral soil, lower vegetation included significant feather moss component; MR-5 (subhygric), dense feather moss understory, sparse grass and forb component; MR-6 (hygric), sphagnum-dominated understory. Average daily summer temperature for June, July and August was determined for each site by interpolating from local weather stations.

The ages of all young stands, or about one-third of all sampled stands, were determined from prescribed burn records. Older stands were aged using nearby trees (primarily lodgepole pine). Young pine were assumed to have arrived immediately following the last fire event in the birch stand, and these dates were cross-referenced with increased growth rates in older pines where possible. Sampling sites were selected to provide situations where pine trees were located within the birch stand, or either slightly uphill or downwind of the prevailing wind direction.

Aboveground biomass was estimated for each plant measured using a canopy volume:biomass regression developed from previous field data (clipping and ovendrying of entire canopy - see chapters 3 and 4) that was supplemented with additional field data. This approach has been found to provide strong relationships for other shrub species (Bentley et al. 1970). Because previous field data (n=375 from eight stands) utilized plants that were generally small (0.007-0.829 kg/plant), larger plants (0.102-6.778 kg/plant, n=82) were sampled from two additional stands and added to the database (N=457). Of the 82 larger plants, biomass values for 31 samples were determined by clipping and ovendrying (100°C for 24 hrs) the complete canopy, and 51 were estimated using a stem count with a basal stem diameter:biomass regression. Telfer (1969) and Brown (1976) used this technique for numerous other shrub species.

Approximately thirty stems were randomly sampled from each of three stands (4, 44 and 52 years old) to provide a range of basal stem diameters (1.5-24.2 mm) for ovendry weight determination of total aboveground biomass (N=89) (Figure 5-2). The final regression ($r^2 = 0.93$) was:

$$\mathit{ln}\ W = -0.7402 + 1.93974\ \mathit{ln}\ D \qquad [1]$$

where W = weight of stem (g) and D = basal stem diameter (mm). Final biomass estimation for the 51 larger plants was determined by counting stems in 0-0.5, 0.5-1.0, 1.0-1.5, 1.5-2.0 and 2.0-3.0 cm size classes (Brown 1976, 1982). Stem biomass was calculated by using 0.4, 0.75, 1.25, 1.75 and 2.5 cm size class means as suggested by Brown (1976). Crown volume and biomass for the 457 sampled plants (Figure 5-3) provided the following regression ($r^2 = 0.89$):

$$\mathit{ln}\ W = -0.204 + 0.915\ \mathit{ln}\ V \qquad [2]$$

where W = weight of plant canopy (kg) and V = volume of plant canopy (m^3).

Model description

Boundary conditions

A dynamic modelling program (High Performance Systems Inc. 1994) was used to model changes in state variables of population density, cover and aboveground live biomass as they respond to forcing variables of fire severity (or depth of burn), fire interval, moisture regime and growing season temperature. For the purposes of this model, every fire burns the entire area being modelled. Therefore, fire interval is synonymous with fire cycle (Romme 1980, Merrill and Alexander 1987) in this instance.

Interactive submodels (Appendix I) were constructed for population, cover and biomass (Figure 5-4). Cover affected the rate of mortality in seedlings, while the number of surviving mature plants ultimately affected the amount of cover. There was no limit to the number of plants per hectare or the size that an individual plant could grow, and cover was allowed to reach 10,000 m^2 ha^{-1}. A summary of model criteria is provided in Table 5-3.

Population submodel

Population size (P, plants ha^{-1}) was a result of recruitment and mortality to the initial condition:

$$P_{t+1} = P_t\,(1-n) + g \qquad [3]$$

where n = natural (non-fire) mortality, and g = new germinants. The total population was divided into juvenile or seedling (S, plants ha^{-1}) and mature (M, plants ha^{-1}) subpopulations to separate plants that were young and susceptible to environmental stress, from those that were established and relatively hardy:

$$P_t = S_t + M_t \qquad [4]$$

Using two subpopulations allowed the simulation of two different mortality rates. The age of maturity that separated seedlings from mature plants was defined as the point when seed production begins. A value of 4 years (Inki and Valanne 1979) was used to model the maturation rate (m, plants ha^{-1} yr^{-1}):

$$m = g\,(1-n)^4 \qquad [5]$$

although this time period may be slightly longer in less favorable environments. Mature plants are considered to be rhizomes older than 4 years, regardless of the age of top growth.

Generally, *Betula glandulosa* is a prolific annual seeder (Weis and Hermanutz 1988) but field observation showed that rates for seedling recruitment are usually very low. This is probably a result of seedling intolerance to competition and drought (Atkinson 1992). Sites with young (6-10 year old) populations had few seedlings while older populations had none, indicating that the period for recruitment of new plants on a disturbed site is quite short and likely due to rapid colonization of competing grasses and forbs and to expansion of mature shrubs.

In the model, seeds are assumed to be supplied after fire by neighbouring plants surrounding the burn which are then widely distributed over the winter snowcover by wind. Recruitment was estimated to occur only during the first 4 years following a fire due to increasing competition over time. Canopy openings that occur due to natural mortality after this 4-year period were not available for recruitment in the model since mortality is a gradual process over a number of years, allowing an encroaching takeover by competing grasses, forbs and other expanding shrubs.

In the absence of actual recruitment rates, the model used an estimated rate which was reduced by an amount based on the level of competition from mature plants (representing seedling and germinant mortality). The largest population density sampled in the field was 18,000 plants ha^{-1}, so a maximum annual recruitment rate (g) of 4,500 ha^{-1} (Table 5-4) for four years after fire was estimated for the model.

Field observation suggests that mortality is very high during the seedling and overmature stages and slight during the mature stage. In the seedling stage, high mortality appears due to competition from expanding mature plants. This was simulated by reducing the number of new germinants that survived to become seedlings and the number of seedlings that survived to become mature plants as total shrub cover increased.

This cover-influenced mortality was controlled by a death factor (df, dimensionless) such that seedling mortality was set at 80% for 50% cover, and near 100% mortality for 100% cover:

$$df = 1.05\,(1 - e^{-0.032 \cdot CT}) \qquad [6]$$

where CT = total shrub cover. These values were determined using the population data for 7 Mile Flats such that a population density of 11,000-12,500 was maintained under a 30-year fire interval (the estimated conditions occurring at 7 Mile Flats). The model removed seedlings from the population using the death factor function by removing germinants as they enter the seedling population, and removing seedlings as they transfer to the mature population. Seedling and mature populations were then calculated as:

$$S_{t+1} = S_t(1-n) + g\,(1-df) - Sf \qquad [7]$$

$$M_{t+1} = M_t(1-n) + g\,(1-df) - Mf \qquad [8]$$

where Sf = seedling fire mortality, and Mf = mature fire mortality (described in fire section).

Natural, non-fire mortality (n, proportion yr^{-1}) was modelled using a constant rate (Begon and Mortimer 1986) as it appeared that mortality was a very gradual process once plants reach the mature stage. This rate was estimated at 0.5% (Table 5-4) based on general observation of population survey data (Tables 5-1, 5-2). This rate was included in both seedling and mature subpopulation calculations since it represented mortality beyond competition (e.g., herbivores, disease, frost, etc.).

Increased mortality in overmature populations was only observed at one field site (site 23). This was an 84-year old stand on a poor, dry site (MR-2) that showed extensive dieback and an obvious increase in mortality. Similar old populations found from MR-3 to MR-6 appeared quite healthy, suggesting that average lifespan on those sites is much longer. *Betula nana* L. has been documented at 147 years old in Greenland (Miller 1975). For the purposes of this model, overmature mortality was not included since the average lifespan appears to be much longer than normal fire interval.

Biomass submodel

Aboveground live biomass was modelled as a function of accumulation by growth and reduction by fire. Biomass accumulation was calculated in several steps, starting with the biomass accumulation rate for the moisture regime with the greatest growth rate (MR-3). This rate was determined using a linear regression of the average plant biomass for sites 2 and 3 (Table 5-1) representing young and old (4 and 44 years) fire origin stands. This basic accumulation rate was then adjusted by a moisture regime factor (MRf, dimensionless) to account for different growth rates on sites with different moisture regimes. These were estimated using data from randomly selected sites representing MR-2, MR-4, MR-5 and MR-6 (sites 10, 11, 17 and 22 in Table 5-1). Using site 10 (MR-5) as an example of this procedure, the estimated MRf for MR-5 was determined by:

$$\text{Biomass (MR-5)} / \text{Biomass (MR-3)} \qquad [9]$$

The MRf values calculated by this method are summarized in Table 5-4. Biomass accumulation was also adjusted by a temperature factor (tf, dimensionless) and previous burn factor (pbf, dimensionless) which are described later. Aboveground live shrub biomass (B, kg $plant^{-1}$) was calculated by:

$$B = 0.1393 \cdot tf \cdot MRf \cdot pbf \qquad \text{if } tsb = 1 \qquad [10]$$

$$B_{t+1} = B_t + (0.0173 \times tf \times MRf \times pbf) \qquad \text{if } tsb > 1 \qquad [11]$$

where tsb = time since burn (yrs). Total live shrub biomass (BT, kg ha^{-1}) was determined by average plant biomass (B) and the number of plants per hectare (P):

$BT = B \times P$ if tsb > 0 [12]

If a fire event occurred, total aboveground live shrub biomass was adjusted by the amount of area burned (AB, proportion: described in the fire section):

$BT_{t+1} = BT_t (AB)$ if tsb = 0 [13]

Shrub cover submodel

Average individual plant area was modelled as a function of expansion due to growth and cover loss due to fire. Cover expansion was determined in a similar manner to biomass accumulation: a basic expansion rate was calculated using a linear regression of plant area data collected at sites 2 and 3 (Table 5-1) which was then adjusted by MRf (Table 5-4), tf and pbf. Additionally, the expansion rate was also adjusted by a total cover factor (cf, dimensionless) which reduced expansion to zero as total cover (CT, $m^2\ ha^{-1}$) approached 10,000 $m^2\ ha^{-1}$. This factor was estimated so that it gradually decreased expansion rate as total cover increased while having no influence when total cover was below 5,000 $m^2\ ha^{-1}$:

$cf = 1 - ((CT - 5000) \times 0.0002)$ if CT > 5,000 [14]

$cf = 1$ if CT < 5,000 [15]

Individual plant cover (C, $m^2\ plant^{-1}$) was then calculated by:

$C = 0.2676 \times tf \times MRf \cdot pbf \cdot cf$ if tsb = 1 [16]

$C_{t+1} = C_t + (0.0146 \cdot tf \times MRf \times pbf \times cf)$ if tsb > 1 [17]

Total shrub cover (CT) was calculated by the number of plants (P) and average individual canopy size (C):

$CT = C \times P$ if tsb > 0 [18]

If a fire event occurred, total shrub cover was adjusted by the amount of area burned :

$CT_{t+1} = CT_t (AB)$ if t = 0 [19]

Forcing variables

Climate

Temperature was modelled to affect individual plant canopy expansion and biomass accumulation. These rates were adjusted by a temperature factor (tf, dimensionless) which was based on the average summer temperature (AST, °C) during June, July and August. The base rate used for this model was an average summer temperature of 12.13°C which represented 7 Mile Flats (where the shrub growth data was collected). Differences in expansion rate due to site temperature were accounted for by adjusting with the temperature factor. Results in chapter 4 showed that biomass increased an average of 4.4% for every 1°C increase in temperature between 14-19°C. The canopy expansion and biomass accumulation rates were adjusted using the chapter 4 data by:

$tf = 1 + ((AST - 12.13^{\circ}C) \times 0.044\ ^{\circ}C^{-1})$ [20]

Fire

Fire was included as a periodic event that caused an immediate decrease in shrub population density, cover and biomass. Fire mortality was modelled as a function of depth of lethal heat penetration and affected population characteristics in several ways. Except for the most severe burning conditions, most (or all) juvenile plants were killed by fire while most mature plants survived to resprout from rhizomes. The removal of a proportion of the mature population also had a secondary effect on shrub cover by reducing the rate at which total cover returned. Fire also caused an immediate removal of all competition, providing maximum opportunity for recruitment of new seedlings. Fire variables used to determine the level of these responses were quantified using parameters from the Canadian Forest Fire Danger Rating System (Stocks et al. 1989).

Depth of lethal heat penetration was simulated by depth of burn in this model. The Duff Moisture Code (DMC) of the Canadian Forest Fire Weather Index (FWI) System (Van Wagner 1987) was used to estimate depth of burn (DOB, cm) with the duff depth reduction equation of Brown et al. (1985):

$$\mathrm{DOB} = \mathrm{DuffD} \times ((83.7 - 0.426 \times \mathrm{DuffMC})/100) \qquad [21]$$

where DuffD = duff depth (cm) and DuffMC = duff moisture content (%) which is determined using Van Wagner's (1987) relationship:

$$\mathrm{DuffMC} = 20 - e^{(\mathrm{DMC} - 244.72)/-43.43} \qquad [22]$$

It should be noted that there is a dearth of information on depth of lethal heat penetration (Steward et al. 1990) and depth of burn. Soil heating is still a difficult issue (Hartford and Frandsen 1992) with moisture and mineral soil content (Frandsen and Ryan 1986, Frandsen 1987) bulk density and other soil factors causing great variation in heat transfer. Depth of burn was used to replace depth of lethal heat penetration because it is assumed to be closely related. It should also be noted that the definition of lethal heat may also vary by the species being considered (Flinn and Pringle 1983). There are numerous empirical depth of burn models, but almost all are for slash fuel types (e.g., Stocks and Walker 1972, Chrosciewicz 1978a, 1978b, McRae 1980). Site specific models for immature and mature jack pine stands have been constructed (Stocks 1987, 1989). In this case, the model provided by Brown et al. (1985) is used for general application.

When a fire event occurred, mortality of seedlings and mature plants was set at a minimum value of 5%. As depth of burn increased, seedling mortality (Sf, plants ha^{-1}) was modelled to increase exponentially to 100% at 6 cm depth of burn:

$$\mathrm{Sf} = \mathrm{S}\,(0.047\, e^{0.5068\,(\mathrm{DOB})}) \qquad [23]$$

Mortality of mature plants was determined by the same method, except that 100% mortality occurred at 10 cm depth of burn:

$$\mathrm{Mf} = \mathrm{M}\,(0.0487\, e^{0.3020\,(\mathrm{DOB})}) \qquad [24]$$

These values were estimated from the results found in chapter 3 (assuming a 2.0 cm soil layer over the rhizome) and from field observations on burned sites.

Although aboveground mortality is usually modelled by fire intensity (Van Wagner 1973, Alexander 1982, Ryan and Reinhardt 1988), removal of shrub cover was controlled by rate of fire spread in this model. Because *Betula glandulosa* is a relatively low shrub (<2m) with thin stems and bark, any fire was considered intense enough to be lethal to stem cambial tissue. Therefore, topkill is not so much dependant on fire intensity as it is a function of the continuity, or areal coverage of a spreading fire. In general, a slow-spreading fire has a narrow flame depth and the fire front tends to meander amongst the shrubs, often leaving unburned patches. A fast rate of spread creates a wide flame depth across a continuous flame front, resulting in more complete burn coverage as indicated by Muraro (1975).

The Initial Spread Index (ISI) of the FWI System was used to estimate fire rate of spread (ROS, m min^{-1}) through the O-1b grass fuel type of the Canadian Forest Fire Behavior Prediction (FBP) System (Forestry Canada Fire Danger Group 1992):

$$\mathrm{ROS} = 250\,(1 - e^{-0.0350\,(\mathrm{ISI})})^{1.7} \qquad [25]$$

The estimated amount of area burned (AB, proportion) was modelled as a negative exponential of ROS such that 10% of the area burned when ROS = 0.5 m min^{-1}, and 100% burned when ROS ≥ 10 m min^{-1}:

$$\mathrm{AB} = 100\,(1 - 1.048\, e^{-0.3042\,(\mathrm{ROS})}) \qquad [26]$$

Repetitive burning decreased canopy expansion and biomass accumulation rates in early postfire years and was estimated using a previous burn factor (pbf, proportion) based on postfire growth data for sites 1 and 2 (Table 5-1). If a previous fire had occurred within 10 years of the current fire, the model reduced both rates by as much as 50% (for one year between fires and declining to 0% for 10 years between fires) during the first year of growth:

$$\mathrm{pbf} = 1 - (0.5 \times (1 - (\mathrm{PB}/10))) \qquad \text{if PB<10} \qquad [27]$$

$$\mathrm{pbf} = 1 \qquad \text{if PB>9} \qquad [28]$$

where PB = time since previous burn. This function allows expansion and accumulation rates to gradually increase to their original value over the following 10-year period. In effect, a reduced growth rate would only occur if two fires occurred within a 10-year period.

Corroboration

Sixteen field sites (Table 5-2) were used to corroborate the cover and biomass submodels. Actual average plant canopy size and biomass was compared to predicted model estimates using a paired *t*-test. Model estimates included canopy cover influence by adjusting the initial population density (and germination rate when necessary) such that the final population density was equal to the actual population density at the time of sampling. A regression of actual on predicted data was also done.

Application and predictions

After corroboration of the model, simulations were done for fire exclusion and repeated fire (or short fire interval) scenarios. There were very few sites found during field data collection that were over 75 years old. The lack of older stands (or remnants of dead stands) is most likely explained by a relatively frequent fire occurrence. Therefore, a fire exclusion limit of 200 years and a maximum fire interval limit of 150 years could be considered inclusive of most fire intervals found in the boreal forest and much of the subalpine forest (Heinselman 1981). Various population densities were used as initial conditions and the model used an iteration period of one year. Simulations were used to show sensitivity of population characteristics to changes in temperature and moisture regime and initial population density. A site 'standard' with MR-3 and average summer temperature of 12°C was used to test combinations of short and long fire intervals with low and high fire severities on population density, cover and biomass. The effect of average summer temperature and moisture regime on population parameters was similarly examined.

The use of short fire intervals (<30 yrs) to reduce shrub cover as a habitat management strategy was also examined by simulation. This included comparison of shrub cover levels under different fire intervals for one land unit; comparison of average cover levels for a management area comprised of numerous land units using different burn distribution strategies (e.g., burn the entire management area once or half the management area twice within one burn rotation); and comparison of average cover levels for a management area under different rates of annual area burned.

Results

Model corroboration

The actual and predicted plant canopy area (Figure 5-5) ranged from 0.24-1.36 m^2, while actual and predicted plant biomass (Figure 5-6) ranged from 0.16-1.43 kg. There was no significant difference ($t_{(0.05, 15)} = 2.131$) between the model predictions and actual field data for plant canopy area ($t = 0.724$) or plant biomass ($t = 1.529$). The regressed data are:

$$A = 0.032 + 0.9936\,(A_p),\quad r^2 = 0.80 \qquad [29]$$

and

$$B = 0.012 + 0.9107\,(B_p),\quad r^2 = 0.91 \qquad [30]$$

where A = actual plant canopy area (m^2), A_p = predicted plant area (m^2), B = actual plant biomass (kg)and B_p = predicted plant biomass (kg).

Model simulations

Fire exclusion

The first simulations examined the effect of fire exclusion on population parameters under various conditions and indicate model sensitivity to moisture and temperature regime. To start all test populations at the same growth stage, the simulations were initiated as if populations were recovering from a fire at time zero. All initial populations had no cover and no survivors in the seedling population.

The simulations showed a steady decline in population density over time when fire was excluded as a result of the constant natural mortality factor and the lack of recruitment of new germinants after the initial 4-year postfire period. Total shrub cover generally increased to a maximum value within 50 years and decreased only slightly thereafter. Total biomass increased at a gradual rate, eventually reaching a peak value at the end of the 200-year period. Simulations using average summer temperatures of 10°C and 14°C show only a minimal increase in population density, and a minimal decrease in total cover and total biomass with decreasing temperature (Figure 5-7).

Moisture regime had a strong influence on population density, cover and biomass under fire exclusion (Figure 5-8). Moisture regime 3 (submesic) provided the maximum growth in terms of cover expansion and biomass accumulation, while plant growth reduced gradually as site moisture increased, and reduced quite sharply as site moisture reduced to moisture regime 2 (subxeric). Population density change was inverse to the change in cover and biomass as moisture regime changed. An initial population density of 2000 plants ha^{-1} resulted in a population density and total biomass level about half that of the initial population, showing the promotion of higher population density in this model (Figure 5-9). Total plant cover for the smaller population was only about 10% less than the larger population.

Repeated fires

Simulations were also run for different population densities using various fire intervals. The same burning conditions were used for all trials, with BUI = 19.2 (a depth of burn of 4 cm) and ISI = 10 (a rate of spread of 30 m/min and complete burn coverage). The model continued with fire returning at a regular interval until population density, total cover and total biomass showed stable, cyclic patterns. The period to reach complete equilibrium was about 100 years for a 10-year fire interval to 500 years for a 100-year fire interval. It is noteworthy that initial population condition had no influence on the equilibrium population density, cover or biomass (Figure 5-10) indicating the strong dependancy of population parameters on fire interval.

Moisture regime had the same effect on the equilibrium population density, total cover and total biomass under various fire intervals as it had under fire exclusion (Figure 5-11). That is, cover and biomass growth was greatest and population density was lowest under moisture regime 3. However, shorter fire intervals greatly increased the effect of moisture regime on population density (showing much greater separation of population density between moisture regimes), and sharply decreased cover and biomass for all moisture regimes. Average summer temperature showed a minimal impact on population characteristics (Figure 5-12). Increasing depth of burn to 8 cm (BUI = 49.5) reduced population density (while increasing population density range) and had a minimal effect on total cover and total biomass (Figure 5-13).

Population density, total cover and total biomass under the influence of regularly spaced fires was highly correlated with fire interval (Table 5-5). Maximum and minimum population density decreased with longer fire interval. Maximum total cover and biomass increased with longer fire interval when fire intervals were shorter than the time to reach maximum total cover and biomass. This represents the point in time where cover expansion and/or biomass accumulation becomes lower than cover loss and/or biomass reduction values due to declining population density. For the conditions used in the Table 5-5 simulation, this occurred at 104 years for total cover and near 200 years for total biomass. For fire intervals longer than these time periods, maximum total cover and biomass decreased with longer fire interval. This decreasing relationship is also highly correlated to fire interval (Table 5-5). Minimum total cover and biomass decreased with longer fire interval, but was always a very low value.

Short fire intervals

Total cover values for populations at equilibrium with fire interval (Figure 5-14) show that short fire intervals of 5, 10 and 30 years were very similar until the second fire event, after which the shortest fire interval resulted in the greatest reduction in total shrub cover. Using a scenario of 30 equal land units comprising a management area, 30-year projections of average cover for the management area were simulated using an initial stand population of 10,000 plants ha^{-1} and 80% cover. For a 30-year burn rotation (i.e., burning an area equal in size to the entire management area in a 30-year period), the lowest average cover level for the management area (54%) was achieved by burning each land unit once (Figure 5-15). Burning half of the management area twice (i.e., a 15-year fire interval) and leaving half of the area unburned resulted in an average of 64% cover for the management area. Overall, decreasing the number of land units burned resulted in increasing average cover while no burning resulted in 83% cover after 30 years.

Increasing the amount of annual area burned reduced the average cover for the management area (Figure 5-16), although the greatest decrease occurred at the lowest rates of annual area burned. For instance, there is a 15% decrease in average cover when the burning rate is increased from ½ land unit yr^{-1} to 1 land unit yr^{-1}, whereas there is only a 5% decrease when the burning rate is increased from 2 land units yr^{-1} to 3 land units yr^{-1}.

Discussion

The simulations in this model illustrate the strong relationship between fire interval and population density, total cover and total biomass. The fact that initial population density had no effect on the equilibrium population density under all fire intervals underscores the extent of population density control by fire interval. In effect, initial population density only influences the time it takes to achieve population equilibrium (which also causes cover and biomass equilibrium). Shorter fire intervals require more fire events to reach this point (up to 10 fires for a 10-year fire interval), but much less time overall than longer fire intervals (about 300 years for a 100-year fire interval). However, the greatest adjustment towards equilibrium occurred during the period between the earliest fire events, so even short fire intervals are within 5% of equilibrium within 4 fire events. Most simulations achieved this within 3 fire events (or 2 equal fire intervals in succession). This suggests that the present population is primarily a reflection of the latest fire interval with declining remnant influence by previous fire intervals. In terms of fire influence on *Betula glandulosa* populations, the model suggests that fire regime may have a temporal definition of the most recent 3-4 fire events.

Increasing fire severity caused a sharp decrease in minimum population density, but only a small decrease in maximum population density as the high germination rate ensured high population levels. This contributed to a minimal effect on total shrub cover and total shrub biomass. Fire severity would have a stronger influence on population characteristics for species with a low rate of recruitment.

The fire exclusion simulations show that moisture regime had a very strong influence on population parameters, while temperature was of minor importance for the range of sites studied. Sites that promoted faster growth rates (by temperature or moisture regime) resulted in lower population densities because the faster rate of cover expansion caused a higher seedling mortality rate. Population density is proportionately related to total biomass, but has a weaker influence on total cover. This is because total cover becomes self-regulated above 50% cover through a reduced cover expansion rate. The germination rate used in this model promotes higher population densities (>10,000 plants ha^{-1}) by increasing low initial values following disturbance.

The cover and biomass submodels appeared to mimic a wide range of field conditions for fire exlusion and single and repeated fires, and the results corroborated closely with short-term field data. The natural mortality, fire mortality, maturation rate and cover-influenced seedling mortality functions of the population submodel appeared to perform well under all tested conditions as the simulated findings were consistent with field observations. Because the germination rate represented a high level, modelling of populations with low recruitment rates could be achieved through further refinement of the germination function.

There are very few other fire effects-shrub population models to compare processes and results. The population density response to fire in this model follows the same pattern as Whelan's (1995) population model (Type E) for plant species which show a burst of germination for a short period after fire, followed by a period of high mortality in seedlings while the population maintains a component of mature plants which endures fire. A fire-based population model for *Adenostoma fasciculatum*, a resprouting shrub typical of chapparal, modelled mortality by fire and thinning using a mean value of 28.7% which was applied to each fire event (Stohlgren and Rundel 1986). Fire was required for a plant to move from one size class to another, with fire occurring at intervals of about 30-80 years. This resulted in an average annual mortality rate (for fire and thinning) of 0.34-0.96%; fire and competition mortality for 30 and 80-year fire intervals in this model (MR3, 12°C average summer temperature and 4 cm depth of burn) resulted in an average annual mortality of 0.99-1.49%. The *A. fasciculatum* model also had a maximum germination rate of 10,000 seedlings per hectare versus 18,000 in this model. Because the lifespan of *Betula glandulosa* is much shorter than *A. fasciculatum*, higher mortality and germination rates are expected.

Applications and recommendations

In terms of management implications, this model provides a basis for selecting appropriate fire severity and interval levels to meet resource objectives over a range of field conditions. The primary concern for wildlife habitat management of *Betula glandulosa*-dominated areas has always been the reduction of shrub cover levels. The model supports a strategy of frequent burning to reduce average total cover, even though short fire intervals result in a higher population level which causes a slightly faster annual rate of cover increase. However, this is more than compensated for by a greater amount of time at low cover levels due to more frequent burning. Maximum cover levels are also lower when there is a shorter fire interval.

The benefits of shorter fire interval versus greater fire severity have often been discussed while determining management strategy. Although deeper burns result in reduced population density, reduced annual rate of cover increase in early years and slightly lower maximum cover levels, shorter fire intervals result in the greatest amount of time at low cover levels. The best option to reduce shrub cover is to burn frequently during the driest soil conditions (usually in autumn) to maximize the benefits of both strategies, but short fire intervals are more important to reduce cover than increased fire severity. Therefore, in order to maximize cover reduction, it is better to burn regularly under low severity conditions than delay burns (extending fire interval) in an attempt to only burn under high severity conditions.

Prescribed fire strategies should include burning of all land units within the management area, as opposed to repeated burning of a few land units and leaving others untreated. If prescribed fire is being applied to several management areas and only a certain amount of area can be burned each year, it is better to burn a small amount in each management area than a lot in one area while leaving other areas untreated. This will reduce the average cover of all the management areas combined since the greatest rate of shrub cover decrease occurs when low annual burning rates are increased slightly.

The model could also be used to test other research predictions. For example, the effect of different climate regimes on *Betula glandulosa* growth could be tested by incorporating other site factors such as elevation, aspect, latitude and longitude (as indicators of growing season length and temperature sums). The effect of different climate change scenarios on plant growth could be tested by using estimated changes in temperature and moisture regimes. The resulting changes in growth vigor would provide an indication of the plant's ability to maintain itself in that community. This approach could also be used to estimate changes in the natural range of this plant. A fire effects-population model is ideal for testing climate change effects on vegetation because fire is expected to be the environmental force that initiates most vegetation change and these types of models deal specifically with postfire vegetation recovery. Obviously, adjustments to the model, such as the refinement or addition of variables, may be necessary to adapt it for other research studies.

Conclusions

In summary, the prediction that population density, cover and biomass were dependant on fire interval was supported by the model simulations, as indicated by the strong relationship between fire interval and those population parameters. The prediction that all population characteristics would decrease with increasing fire interval was partially supported since population cover and biomass decreased while density increased. The prediction that population characteristics would depend on fire severity was also partly supported as increasing fire severity reduced population density at short fire intervals but only had a minimal decreasing effect on cover and biomass.

The results of this study suggest that *Betula glandulosa*-dominated stands can be successfully managed through the use of prescribed fire. Because fire severity is a relatively minor factor affecting *B. glandulosa* population condition, there is not much long-term difference between spring and autumn burning (which generally has higher severity burning conditions). On the other hand, fire interval is highly influential on population characteristics and short fire intervals will cause significant decreases in shrub cover and biomass and an increase in population density.

Tables

Table 5-1. Summary of field site descriptions, sample size (n) and mean (and SE) aboveground plant characteristics used for model calibration.

Location	Site	Age (yrs)	Elevation (m)	Average Summer Temperature (°C)	Moisture Regime[a]	Previous Burns[b]	Population (plants/ha)	Plant Characteristics				
								n	Height (m)	Area (m^2)	Volume (m^3)	Biomass (kg)
7 Mile Flats	1	3.5	1350	12.13	3	3	9083	33	0.59 (0.02)	0.183 (0.017)	0.115 (0.012)	0.114 (0.011)
7 Mile Flats	2	3.5	1350	12.13	3	1	12292	30	0.64 (0.02)	0.311 (0.026)	0.205 (0.020)	0.191 (0.017)
7 Mile Flats	3	44	1350	12.13	3	0	11062	30	1.24 (0.04)	0.894 (0.077)	1.129 (0.115)	0.881 (0.080)
South Ram	10	36	1660	11.05	5	0	6933	52	0.74 (0.02)	0.422 (0.061)	0.341 (0.053)	0.290 (0.042)
Elk Creek	11	23	1510	11.57	2	0	16000	120	0.51 (0.01)	0.241 (0.017)	0.131 (0.010)	0.126 (0.009)
Berland N	17	80	1450	11.78	6	0	17297	64	1.06 (0.03)	0.274 (0.032)	0.305 (0.040)	0.266 (0.030)
Jarvis Creek	22	30	1143	12.84	4	0	10533	79	1.16 (0.04)	0.45 (0.047)	0.573 (0.069)	0.466 (0.050)

[a] 2=subxeric, 3=submesic, 4=mesic, 5=subhygric, 6=hygric
[b] Number of previous fires within the last 10 years

Table 5-2. Summary of field site descriptions, sample size (n) and mean (and SE) aboveground plant characteristics used for model corroboration.

Location	Site	Age (yrs)	Elevation (m)	Ave Summer Temp (°C)	Moisture Regime[a]	Previous Burns[b]	Population (plants/ha)	Plant characteristics				
								n	Height (m)	Area (m²)	Volume (m³)	Biomass (kg)
Clearwater - burn	4	10.5	1219	12.58	3	1	8800	66	0.97 (0.04)	0.477 (0.071)	0.551 (0.092)	0.439 (0.066)
Brazeau - 3 burn	5	5.5	1135	12.87	3	3	17213	105	0.73 (0.01)	0.295 (0.028)	0.240 (0.027)	0.212 (0.021)
Brazeau - 2 burn	6	5.5	1135	12.87	3	2	6533	49	0.86 (0.03)	0.361 (0.045)	0.348 (0.052)	0.299 (0.040)
Brazeau - old	7	42	1135	12.87	4	0	11562	74	1.02 (0.03)	0.543 (0.066)	0.634 (0.092)	0.504 (0.066)
N. Ram River 1	8	53	1508	11.58	3	0	6000	45	1.33 (0.04)	0.957 (0.094)	1.346 (0.150)	1.017 (0.103)
N. Ram River 2	9	33	1500	11.61	5	0	11333	85	0.79 (0.09)	0.289 (0.035)	0.284 (0.073)	0.238 (0.049)
Bighorn River -burn	12	8.5	1554	11.42	3	1	8667	65	0.55 (0.02)	0.308 (0.046)	0.205 (0.039)	0.181 (0.030)
Bighorn River - old	13	50	1540	11.47	4	0	4933	37	0.99 (0.05)	0.793 (0.126)	0.931 (0.177)	0.710 (0.124)
Clearwater (herb)	14	10.5	1219	12.58	3	0	17733	133	0.83 (0.02)	0.241 (0.018)	0.226 (0.019)	0.203 (0.016)
Clearwater - old	15	58	1219	12.58	4	0	6533	49	1.34 (0.04)	0.753 (0.075)	1.085 (0.126)	0.835 (0.089)
Berland 1	16	35	1450	11.78	3	0	3733	28	0.97 (0.06)	1.003 (0.133)	1.002 (0.148)	0.781 (0.104)
Berland 2	18	77	1450	11.78	3	0	3067	23	1.46 (0.05)	1.257 (0.153)	1.888 (0.260)	1.386 (0.173)
Mountain Park	19	46	1750	10.74	3	0	4533	34	0.78 (0.03)	1.294 (0.129)	1.094 (0.146)	0.847 (0.101)
Cardinal River 1	20	21	1750	10.74	4	0	9467	71	0.54 (0.01)	0.426 (0.035)	0.241 (0.023)	0.219 (0.018)
Cardinal River 2	21	61	1650	11.09	3	0	5867	44	1.03 (0.02)	0.928 (0.079)	0.984 (0.095)	0.775 (0.067)
Berland S	23	84	1450	11.78	2	0	2933	22	0.82 (0.04)	0.797 (0.165)	0.712 (0.162)	0.568 (0.114)

[a] 2=subxeric, 3=submesic, 4=mesic, 5=subhygric, 6=hygric
[b] Number of previous fires within the last 10 years

Table 5-3. Summary of the equations used in the model.

Population (plants ha^{-1})	$P_{t+1} = P_t (1-n^a) + g^b$		[3]
	$P_t = S_t + M_t$		[4]
Maturation rate (plants ha^{-1})	$m = g (1-n)^4$		[5]
Death Factor (proportion)	$df = 1.05 (1 - e^{-0.00032 \cdot CT})$		[6]
Seedling subpopulation (plants ha^{-1})	$S_{t+1} = S_t (1-n) + g (1-df) - Sf$		[7]
Mature subpopulation (plants ha^{-1})	$M_{t+1} = M_t (1-n) + g (1-df) - Mf$		[8]
Biomass (kg plant^{-1})	$B = 0.1393 \cdot tf \cdot MRf^c \cdot pbf$	if $tsb^d = 1$	[10]
	$B_{t+1} = B_t + (0.0173 \cdot tf \cdot MRf \cdot pbf)$	if $tsb > 1$	[11]
Total Biomass (kg ha^{-1})	$BT = B \cdot P$	if $tsb > 0$	[12]
	$BT_{t+1} = BT_t (AB)$	if $tsb = 0$	[13]
Cover Factor (proportion)	$cf = 1 - ((CT-5000) \cdot 0.00002)$	if $CT > 5{,}000$	[14]
	$cf = 1$	if $CT < 5{,}000$	[15]
Cover (m^2 plant^{-1})	$C = 0.2676 \cdot tf \cdot MRf \cdot pbf \cdot cf$	if $tsb = 1$	[16]
	$C_{t+1} = C_t + (0.0146 \cdot tf \cdot MRf \cdot pbf \cdot cf)$	if $tsb > 1$	[17]
Total Shrub Cover (m^2 ha^{-1})	$CT = C \cdot P$	if $tsb > 0$	[18]
	$Ct_{t+1} = CT_t (AB)$	if $tsb = 0$	[19]
Temperature Factor (proportion)	$tf = 1 + ((AST^e - 12.13\,^{\circ}C) \cdot 0.044\,^{\circ}C^{-1})$		[20]
Depth of Burn (cm)	$DOB = DuffD^f \cdot ((83.7 - 0.426 \cdot DuffMC)/100)$		[21]
Duff Moisture Content (%)	$DuffMC = 20 + e^{(DMC^g - 244.72)/-43.43}$		[22]
Seedling Fire Mortality (plants ha^{-1})	$Sf = S (0.047\, e^{1.5068 (DOB)})$		[23]
Mature Fire Mortality (plants ha^{-1})	$Mf = M (0.0487\, e^{1.3020 (DOB)})$		[24]
Rate of Fire Spread (m min^{-1})	$ROS = 250 (1 - e^{-0.0350 (ISI^h)})^{1.7}$		[25]
Area Burned (%)	$AB = 100 (1 - 1.048\, e^{-0.042 (ROS)})$		[26]
Previous Burn Factor (proportion)	$pbf = 1 - (0.5 \times (1 - (PB^i/10)))$	if $PB<10$	[27]
	$pbf = 1$	if $PB>9$	[28]

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[a] n = natural non-fire mortality rate, see Table 5-4; [b] g = germination rate, see Table 5-4; [c] MRf = moisture regime factor, see Table 5-4; [d] tsb = time since burn (yrs); [e] AST = average (daily) summer temperature for June, July and August (°C); [f] DuffD = duff depth (cm); [g] DMC = Duff Moisture Code; [h] ISI = Initial Spread Index; [i] PB = years since the last previous burn.

Table 5-4. Parameter values used in the model.

Parameter	Criteria
Germination rate (plants ha^{-1} yr^{-1})	g = 4500
Natural non-fire mortality rate (proportion yr^{-1})	n = 0.005
Moisture Regime factor (MRf, proportion)	MR-2: 0.4 MR-3: 1.0 MR-4: 0.75 MR-5: 0.5 MR-6: 0.2

Table 5-5. Equilibrium levels and correlation to fire interval for simulated population density, total shrub cover and total aboveground live shrub biomass.

Population Parameter	Fire Interval (FI)							min (or max) = a + b (ln FI)		
	10	25	50	75	100	125	150	a	b	r^2
Population density (plants/ha)										
maximum	13503	12793	12023	11551	11252	10988	10827	-5968.36	4052.994	0.99
minimum	10968	9638	7991	6772	5820	5040	4381	298.52	-42.704	0.97
Total Shrub Cover (%)										
maximum										
0-100 yr FI	52.64	66.88	76.65	79.65	80.07			25.72	12.381	0.97
100-150 yr FI[a]					80.07	79.69	79.37	88.02	-1.726	0.99
minimum	1.53	0.95	0.55	0.41	0.35	0.31	0.29	2.49	-0.462	0.96
Total Shrub Biomass (kg/ha)										
maximum	3895	6431	9488	11564	12965	13847	14316	15942	-1016.6	0.99
minimum	191.2	168.2	139.7	118.6	102.1	88.6	77.2	17167.7	-2467.2	0.97

[a] Cover declining

Figures

Figure 5-1. Location of field sites (•) providing biomass, canopy cover and population size data. Several stands were sampled at some locations.

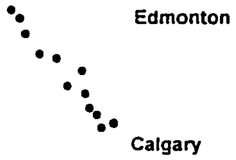


Figure 5-2. Stem biomass and diameter data for bog birch in southwestern Alberta (N=89). The regression equation is: *ln*(stem weight) = -0.7402 + 1.93974 *ln*(stem diameter), r^2=0.93.

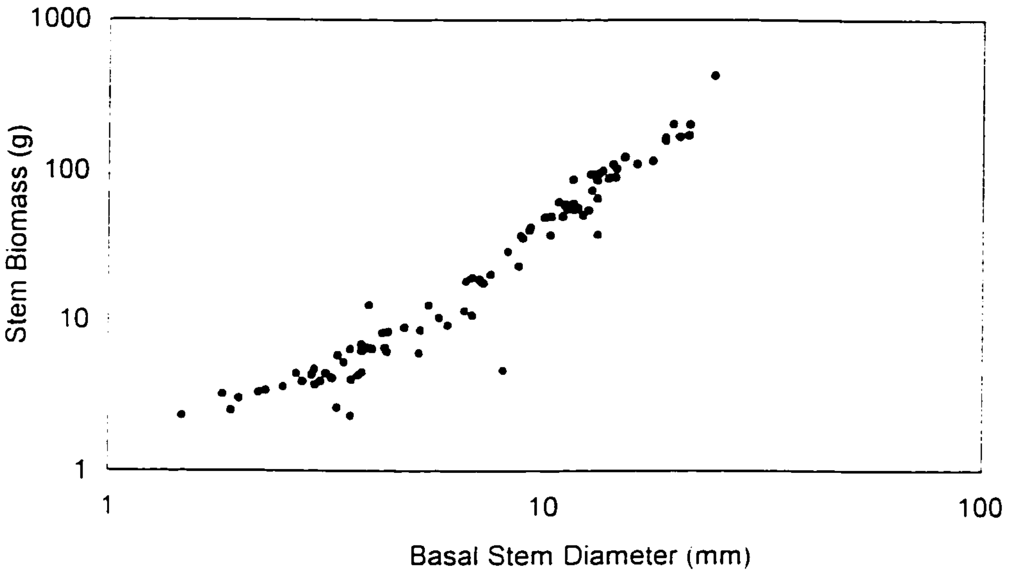


Figure 5-3. Aboveground bog birch biomass and volume data collected from sites in Alberta and the Northwest Territories (N=457). The regression equation is: *ln*(aboveground biomass) = -0.204 + 0.915 *ln*(canopy volume). r^2=0.89.

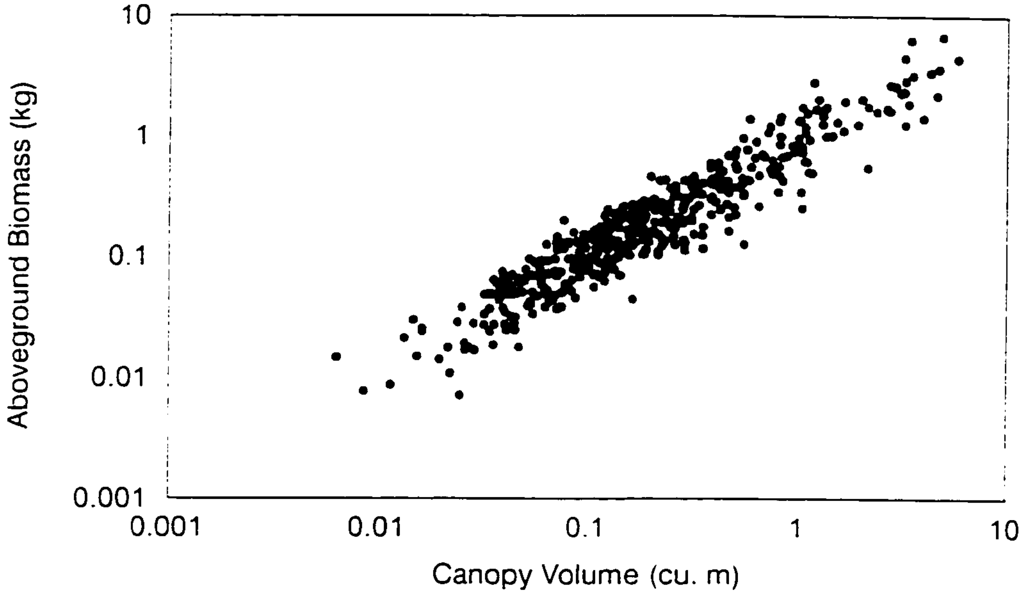


Figure 5-4. Simplified structure of the fire effects-population model for bog birch showing modelled variables (square), processes (ellipse) and driving variables (parallelogram).

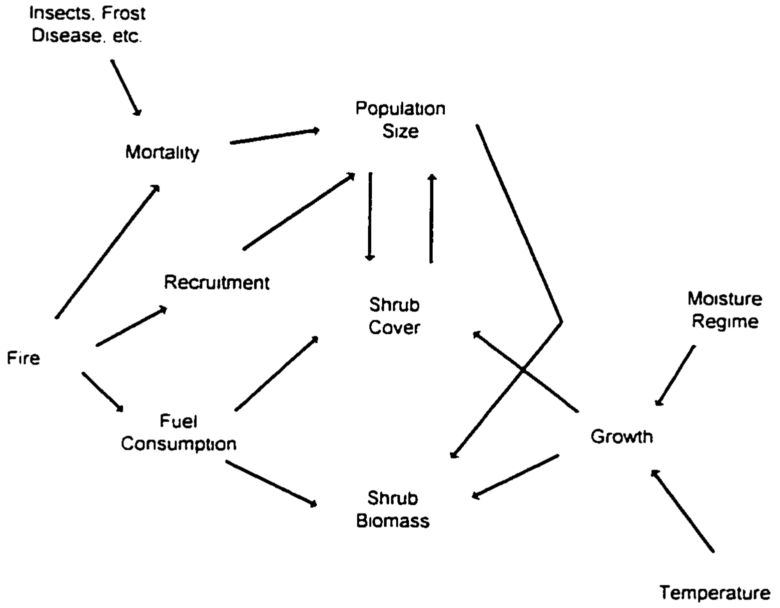


Figure 5-5. Comparison of actual and predicted individual plant canopy area and line of best fit (r^2=0.80)

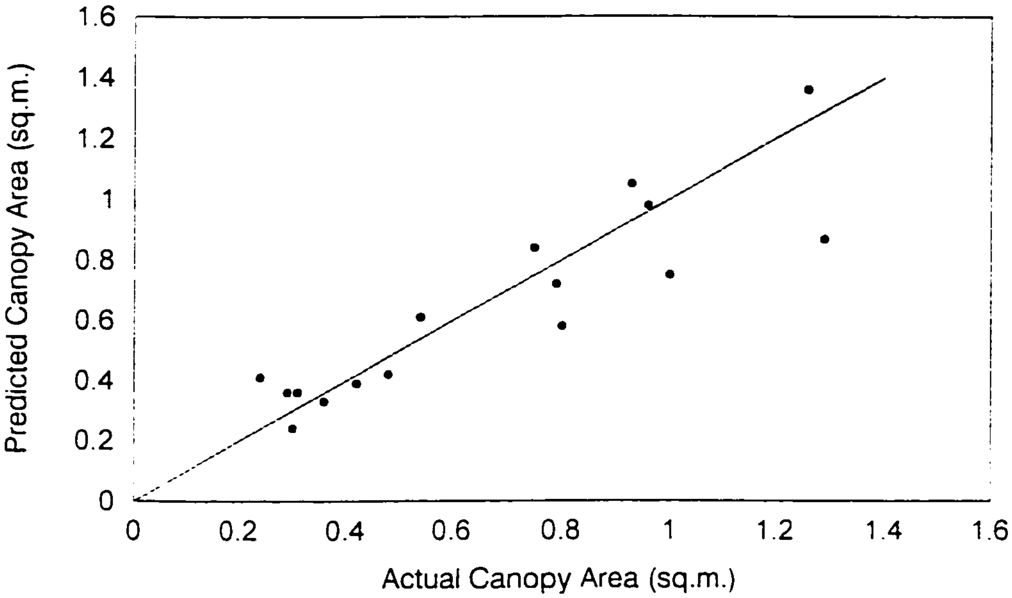


Figure 5-6. Comparison of actual and predicted aboveground live plant biomass for individual shrubs and line of best fit ($r^2=0.91$).

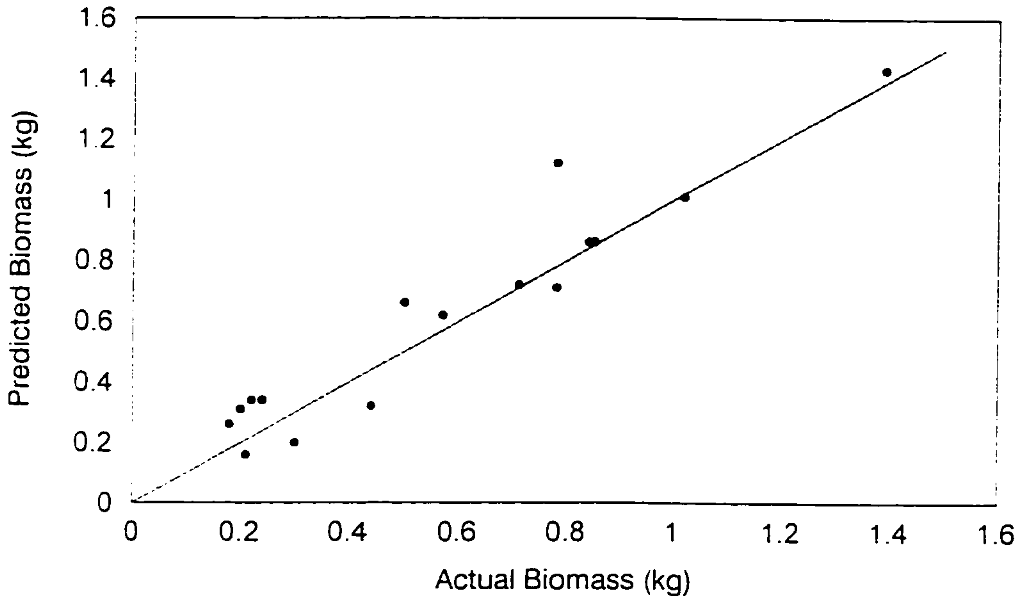


Figure 5-7. Effect of average summer temperature (June, July and August) on population density, total shrub cover and biomass under fire exclusion. Values for 10°C (···) and 14°C (—) are based on an initial population size of 10,000 plants per hectare and moisture regime 3.

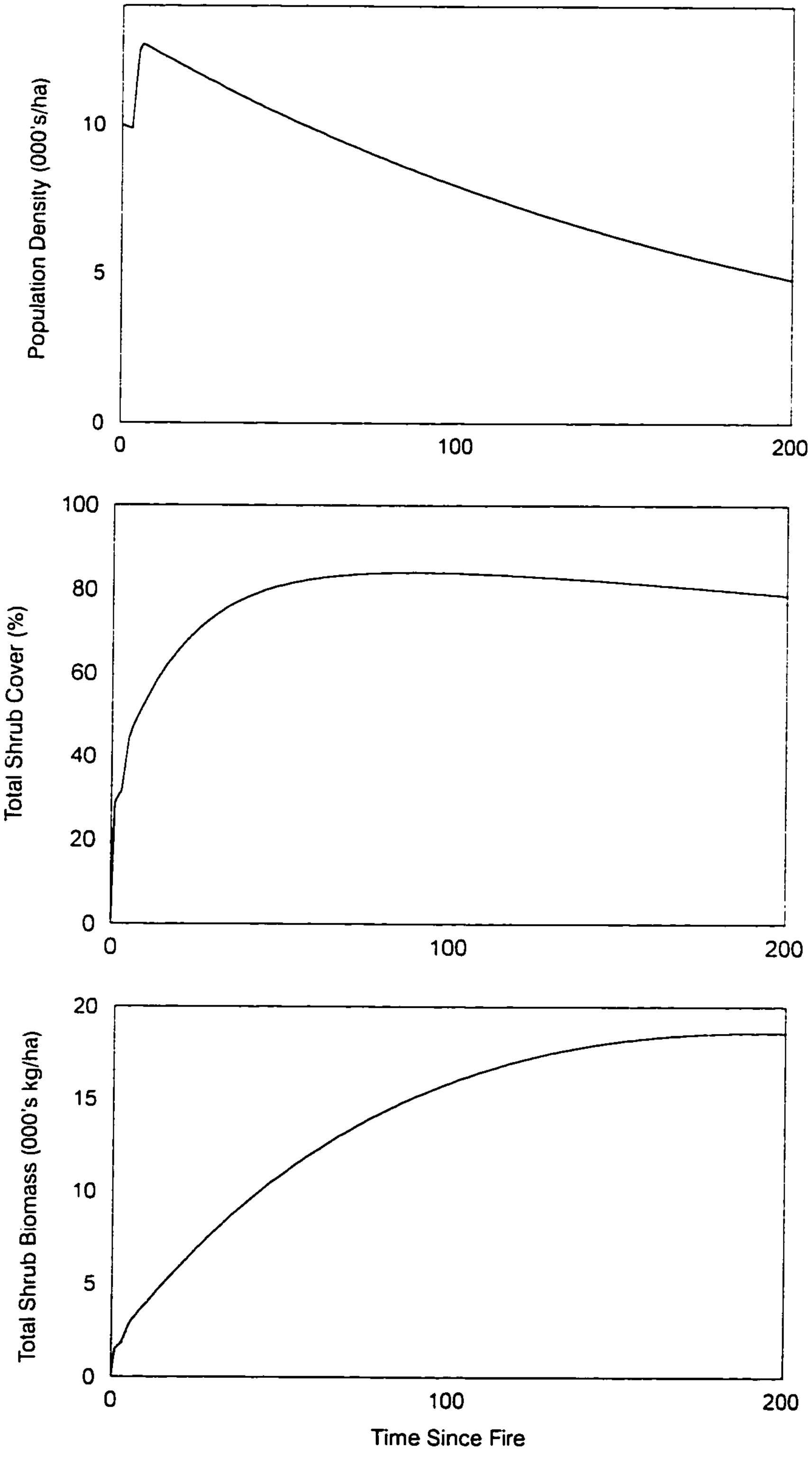


Figure 5-8. Effect of moisture regime (2=driest, 6=wettest) on population density, total shrub cover and biomass under fire exclusion. Values are based on an initial population density of 10.000 plants per hectare and an average summer temperature (June, July and August) of 12°C.

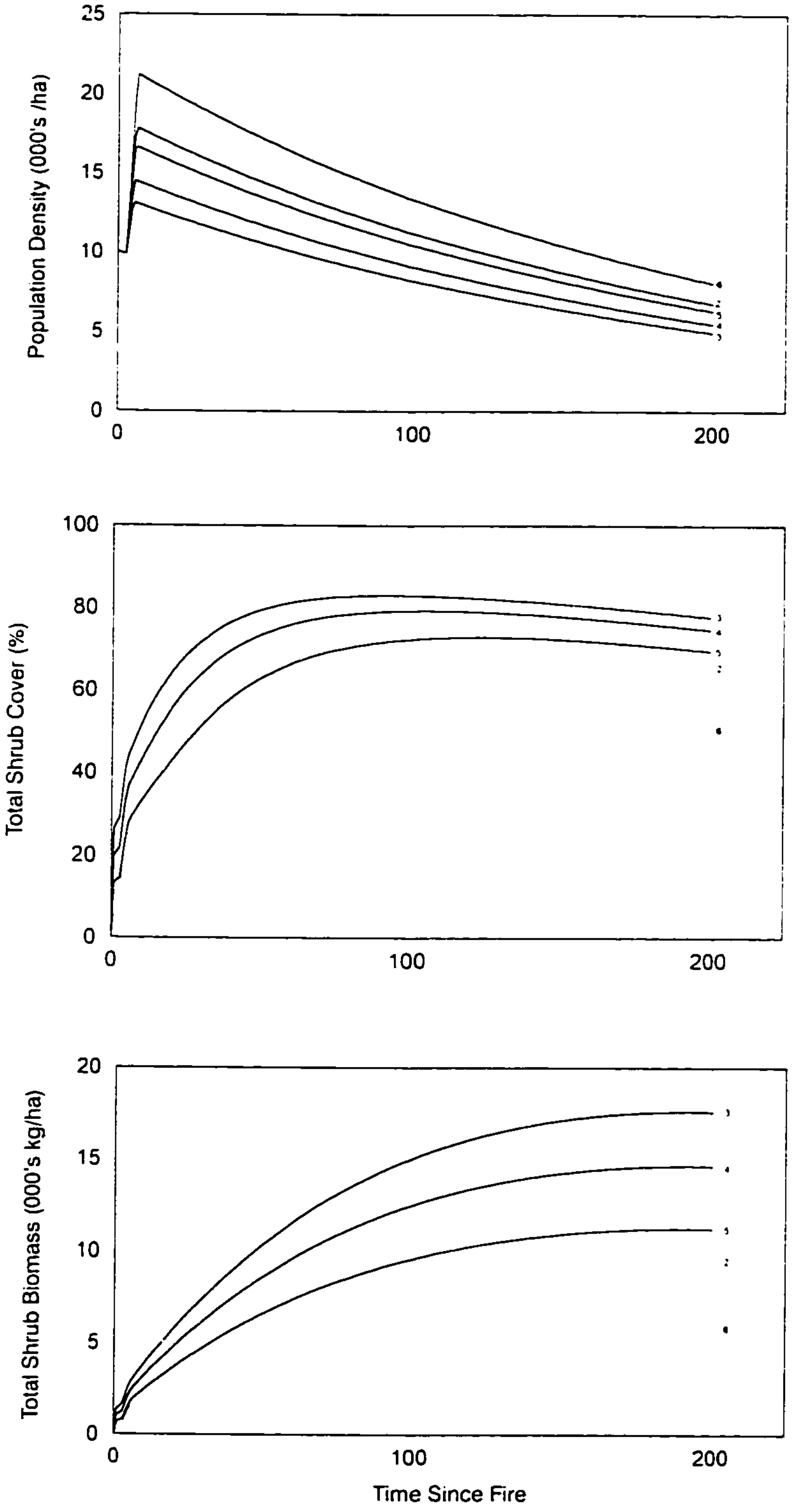


Figure 5-9. Effect of initial population density on population density, total shrub cover and biomass under fire exclusion. Values for 2,000 plants per hectare (···) and 20,000 plants per hectare (—) are based on an average summer temperature (June, July and August) of 12°C and moisture regime 3.

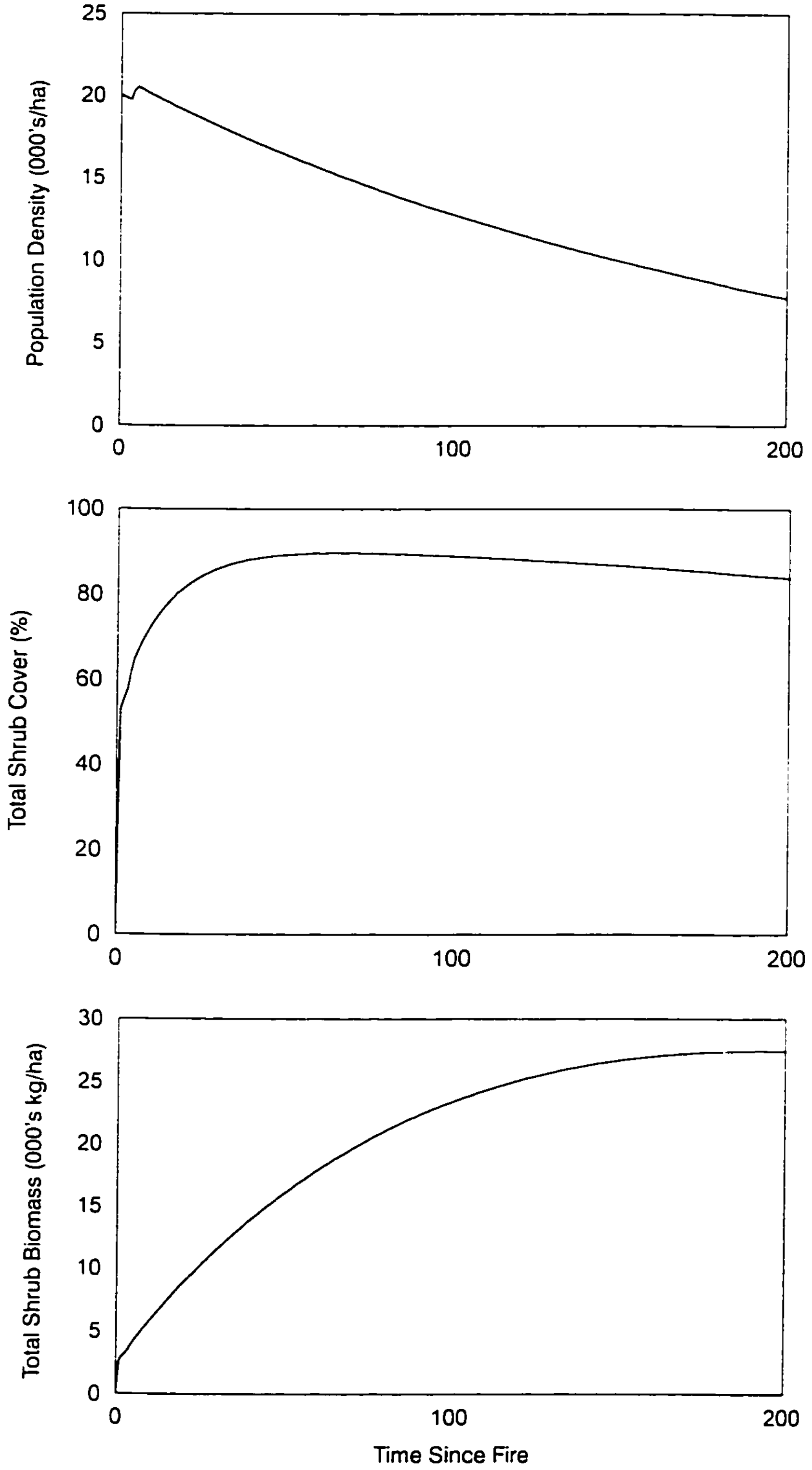


Figure 5-10. Effect of initial population density on the population density, total shrub cover and biomass for a 100-year fire interval. Values for 25,000 plants per hectare (—) and 250 plants per hectare (···) are based on an average summer temperature (June, July and August) of 12°C and moisture regime 3.

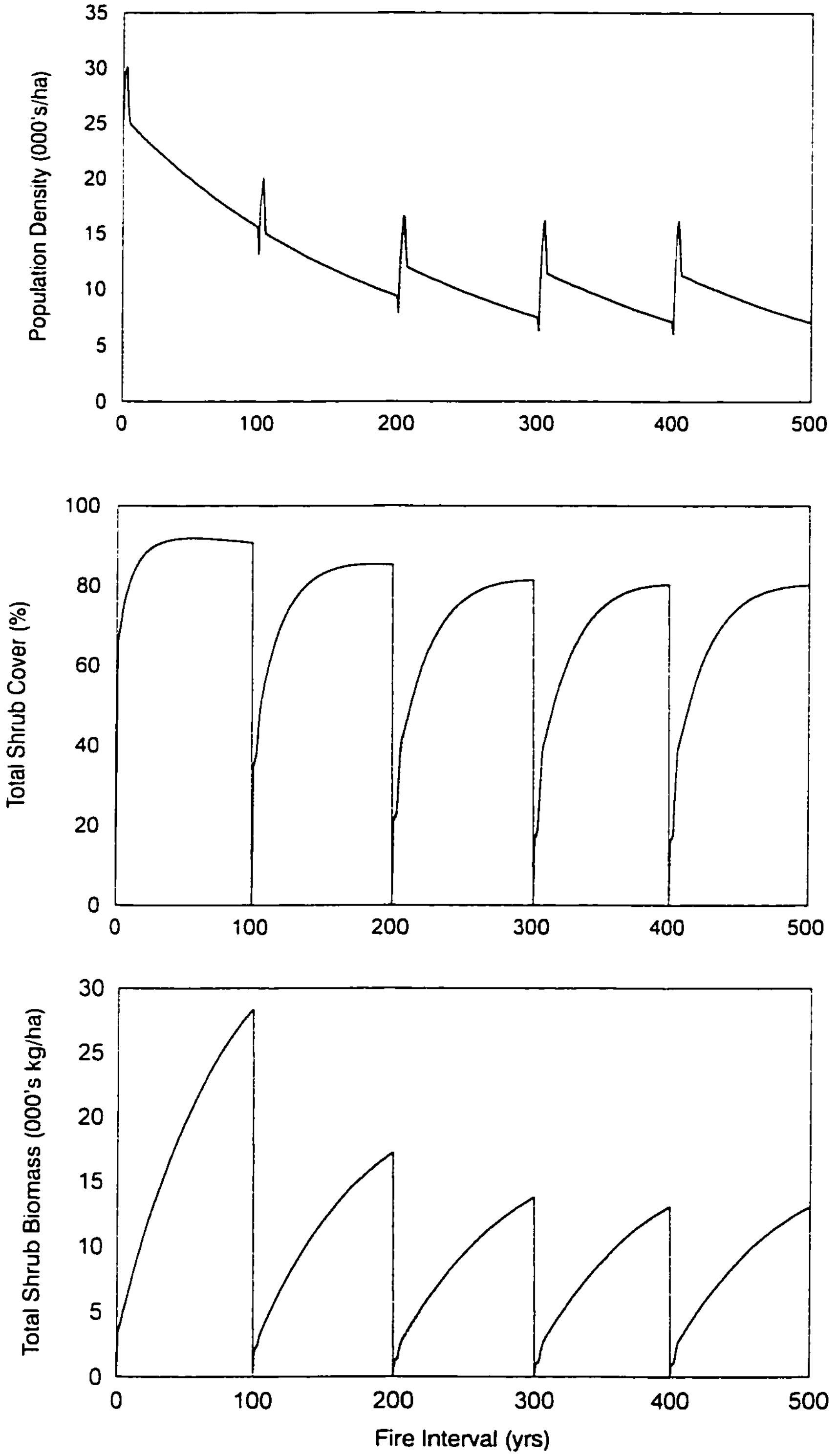


Figure 5-11. Effect of moisture regime on range of population density, maximum total cover and biomass by fire interval. Values for MR2 (···), MR3 (·· – ··) and MR6 (—) based on an average summer temperature (June, July and August) of 12°C.

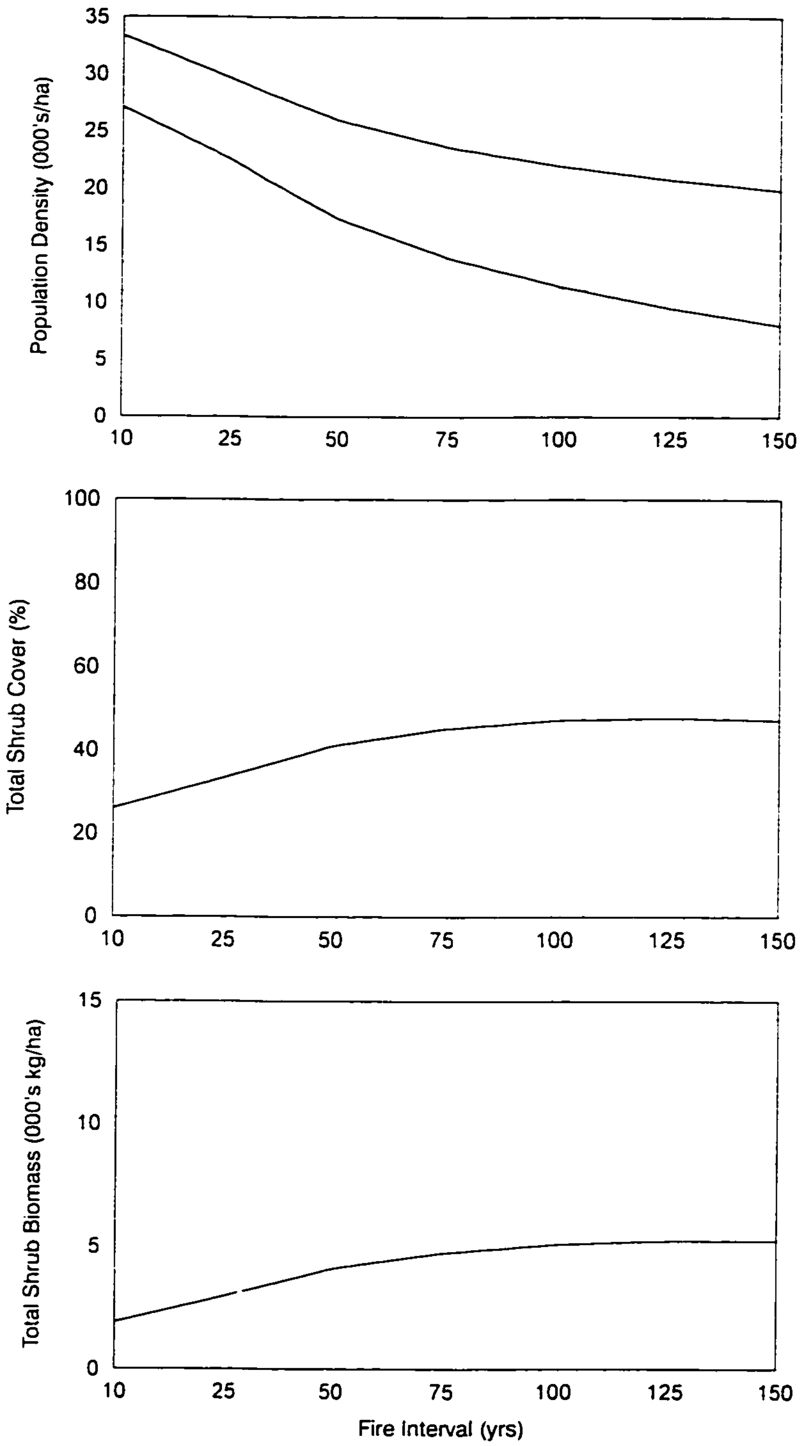


Figure 5-12. Effect of average summer temperature (June, July and August) on range of population density, maximum total cover and biomass by fire interval. Values for 10°C (—) and 14°C (···) are based on moisture regime 3.

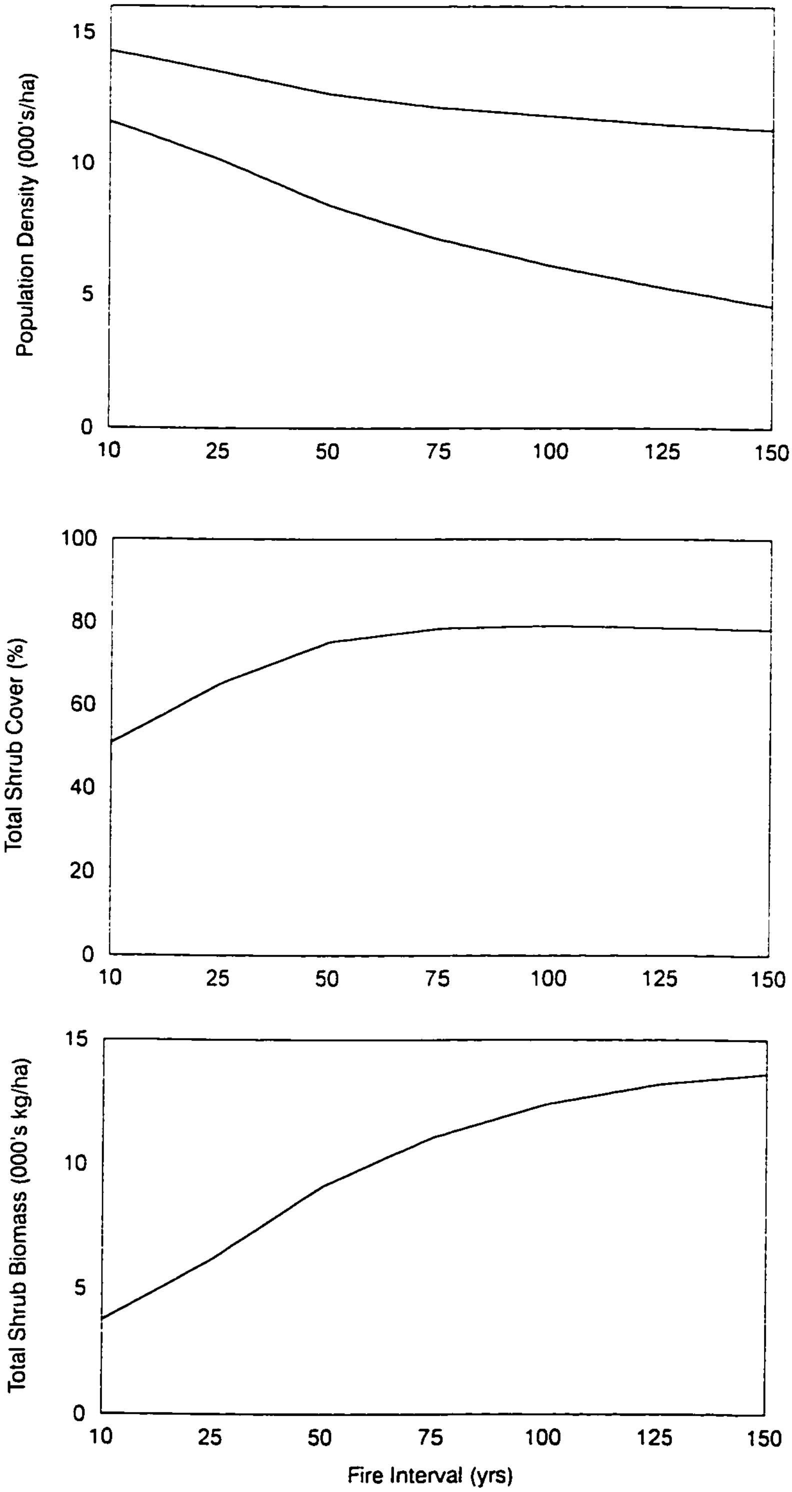


Figure 5-13. Effect of fire severity on range of population density, maximum total cover and biomass by fire interval. Values for 4 cm depth of burn (—) and 8 cm depth of burn (···) are based on an average summer temperature (June, July and August) of 12°C and moisture regime 3.

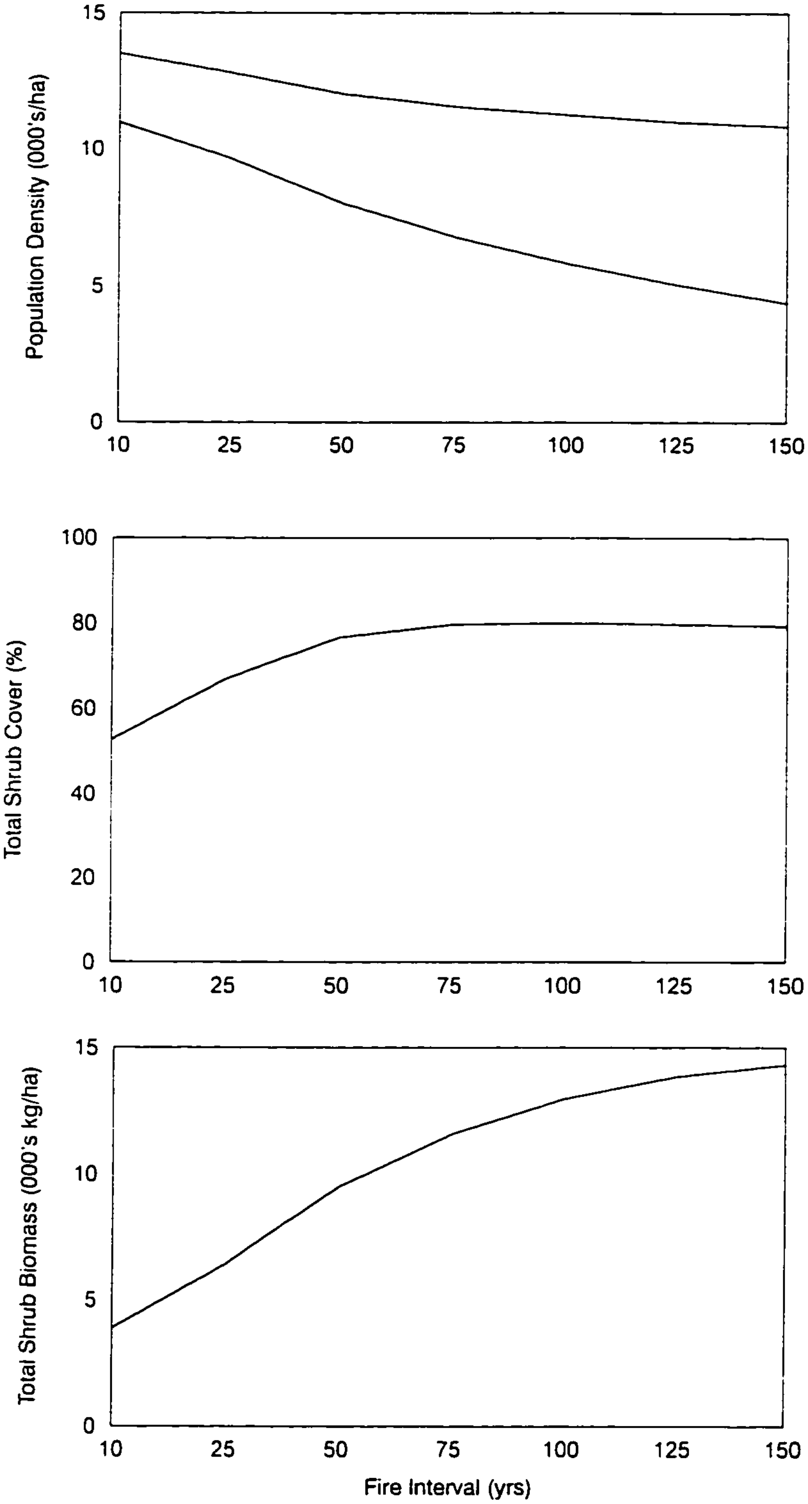


Figure 5-14. Comparison of total shrub cover over a 30-yr period for 5-yr fire interval (···), 10-yr fire interval (—) and 30-yr fire interval (·· – ··). Simulations based on moisture regime 3 and an average summer temperature (June, July and August) of 12°C.

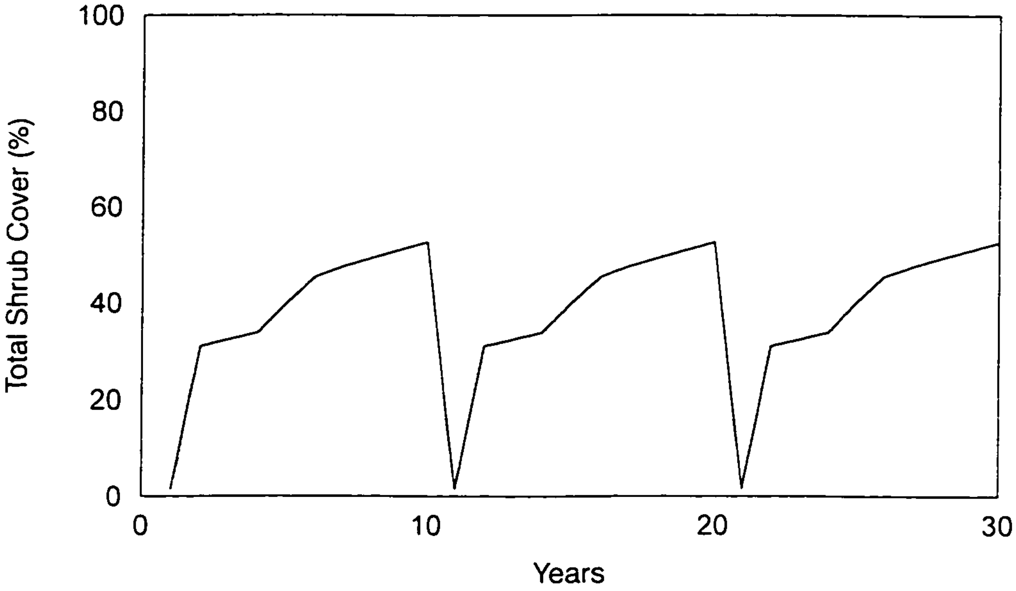


Figure 5-15. Comparison of average shrub cover for entire management area after 30 years by proportion of area being managed by fire. Initial population size was 10.000 plants/ha. cover was 80% and annual burn rate was held constant at 3.3%.

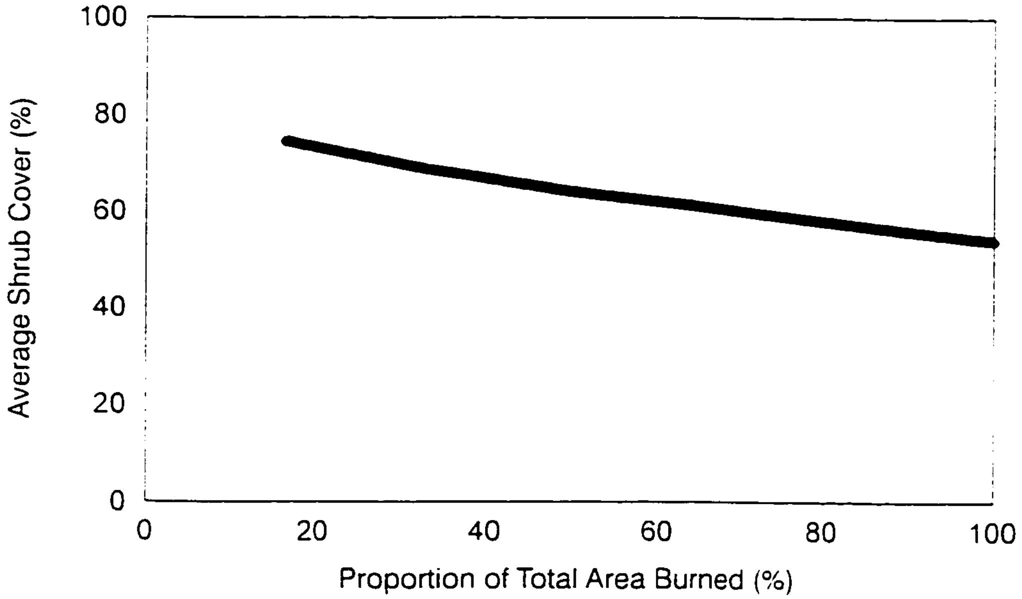
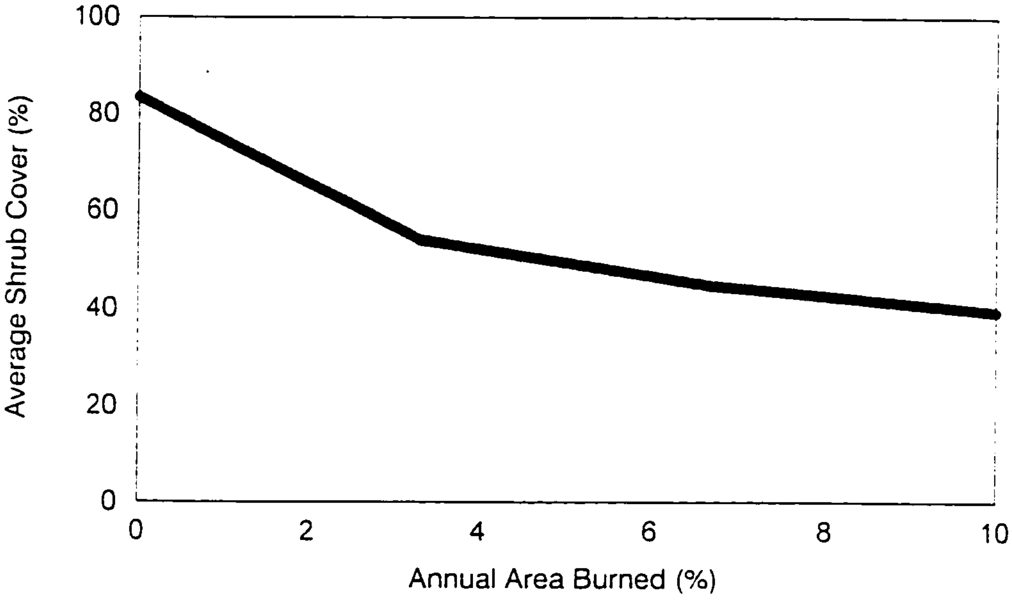


Figure 5-16. Comparison of average shrub cover for entire management area after 30 years by annual rate of burning. Initial population density was 10.000 plants/ha and shrub cover was 80%.



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VI. BORSHRUB: a postfire community succession model for northern shrub-grasslands

Introduction

Betula glandulosa Michx. is a dominant member of many open plant communities in forest and tundra regions and has a habitat range that extends over 30% of the Canadian landscape. It is a very competitive plant that is well-adapted to recurrent fire (chapters III, IV and V). Numerous other grasses and forbs are also found in association with *B. glandulosa* in the open meadows of boreal, montane and subalpine regions. In areas where fire is a prevailing force on the landscape, community composition is strongly influenced by the local fire regime. In the regions that *B. glandulosa* occupies, fire frequency can range from a low of 10 years in southern shrub-grasslands (e.g. Heinselman 1981) to thousands of years in far north areas (Payette et al. 1989). Other fire regime characteristics include fire intensity which is dependant on the amount of dead biomass (Byram 1959), a factor that is influenced by fire frequency and biomass accumulation rates, and fire severity which is affected by moisture content of the organic soil and the depth to mineral soil. Fires can occur in either the spring or autumn but rarely in the summer due to a high live fuel moisture content in the herbaceous understory. Over this wide range of fire regime characteristics, community structure reflects species survival strategy in relation to fire occurrence and interspecific competition.

Current postfire community succession (or 'fire succession') models are among a group of forest growth models that have evolved from the JABOWA model (Botkin et al. 1972). These have become known as gap replacement models which simulate the dynamics of individual trees on a small spatial unit such as a forest canopy gap or sample quadrat (Shugart and West 1980). This approach has been used extensively in subsequent models (see Botkin 1993) to study ecological succession and ecosystem-level processes. The original JABOWA model simulated forest succession in the New England mountains and was later modified in SILVA to simulate the effects of fire on forest dynamics in the California Sierra Nevada (Kercher and Axelrod 1984). SILVA underwent further modification to simulate fire succession in conifer forests of the Inland Northwest and northern US Rocky Mountians in FIRESUM (Keane et al. 1989). That fire succession model deterministically simulated tree growth, woody fuel and litterfall accumulations while tree establishment, mortality and fire events were incorporated using stochastic algorithms. Most recently, it was merged with the FOREST-BGC (BioGeoChemical) model (Running and Coughlan 1988, Running and Gower 1991) to form FIRE-BGC (Keane, Morgan and Running 1996; Keane, Ryan and Running 1996). This integrated the fire component of FIRESUM with the mechanistic tree growth approach of FOREST-BGC which based increment on the daily flow of carbon, nitrogen and water across ecosystem components. FIRE-BGC is a landscape model that also uses spatial data layers to simulate some ecological processes such as fire and seed dispersal.

Another line of models includes the Forest Vegetation Simulator (FVS) (Teck et al. 1996) for which a fire extension submodel is currently being developed (Beukema et al. 1996). The FVS is a family of forest simulation models that were designed after the Prognosis Model for stand development (Stage 1973) for use in forests of the US Inland Northwest region. The FVS-Fire model will have a fuel model and a burn model, including fire effects and smoke production routines and a portion of the FIRESUM model for fire intensity calculations. An additional COVER model extends the Prognosis model to include canopy and biomass for tree and understory stand components (Moeur 1985).

These fire succession models focussed almost entirely on tree species while shrubs and herbaceous plants were minor components incorporated through a general fuel load contribution. A few fire models have been developed specifically for shrubs and rangelands (e.g., Stohlgren and Rundel 1986, Engle et al. 1996, Pivello and Norton 1996) although these kinds of models were designed to either simulate population and cover dynamics of a single species or assist with operational planning for prescribed burns. Fire succession models that deal with shrub-grassland community dynamics at the species level have not been found in the literature.

The purpose of this study was to develop a fire succession model (BORSHRUB) for northern shrub-grassland meadow communities. Although this region is primarily boreal, the model should also represent similar areas of the subalpine and montane forest regions. The specific objective of this study was to examine the long-term dynamics of shrub and understory species in the main thesis study area under different fire regimes. It was predicted that the model would indicate the promotion of fire-resistant species by high fire frequencies and the increase of fire susceptible species at low fire frequencies.

Model development

BORSHRUB was developed using a dynamic modelling software package (High Performance Systems 1997). The general structure and processes used in the model were similar to those of FIRESUM and SILVA although there were extensive differences due to vegetation type, use of the Canadian system for measuring fire behaviour, and different methods of simulation used in some aspects of the model (Figure 6-1, 6-2). The BORSHRUB fire succession model is the result of combining a fire effects-shrub population model (chapter V) with new understory and fuels (or biomass) submodels. BORSHRUB utilized a mixed spatial resolution to integrate the dynamics between relatively few, large overstory shrubs and numerous small, subdominant understory plants. The shrub submodel simulated growth on an average plant basis (canopy size per plant in m^2 and biomass per plant in kg) while spatial parameters for shrub cover (m^2 ha^{-1}), density (plants ha^{-1}) and biomass (kg ha^{-1}) were based on population dynamics at a large scale (1 ha). Non-fire mortality was assumed to be random across the population and was modelled to occur at a constant rate. Shrub population recruitment was a short-term event triggered by fire disturbance while recruitment occurred at a constant spatial rate for that period, subject to available growing space. The understory component used a gap replacement approach such that understory plants competed for growing space that became available when shrub or understory canopy was removed by fire or shrub mortality, or as shade intolerant understory species declined in the community when competition was high. Understory plants were simulated as a proportion of total vegetation cover by species using a small sample plot area (1 m^2). All simulated plant growth occurred deterministically and random fire events were incorporated using a Monte Carlo method. All model calculations used an annual timestep.

The BORSHRUB model contains four primary submodels. Because shrubs and understory vegetation were modelled in different ways, those components were dealt with using separate submodels. A fuels submodel recorded biomass accumulation that resulted from annual vegetation growth, dieback and litterfall and losses from decomposition, respiration and fire. The physical fire aspects of the model were incorporated in the fire submodel. The fuels submodel data was used to determine fire behaviour characteristics such as rate of spread and fire intensity, as well as first order fire effects (Reinhardt et al. 1997) including depth of burn and fuel consumption. In turn, these factors were used to update the fuels inventory and to establish mortality and postfire recruitment rates for each species based on their fire ecology. The fire submodel also maintained a record of the time since burn which was used by the shrub and understory submodels to determine changes in species composition as succession proceeded between fire events. The BORSHRUB model can be run in two modes: an actual mode which allows entry of historical fire and weather data, and a forecasting mode which bases simulations on future estimated weather conditions and a stochastic approach to fire events.

Shrub submodel

The shrub population model described in chapter V was used as the shrub component for this community succession model with several modifications to integrate it with the other BORSHRUB components (Appendix II). The major change from the original population model was to incorporate the effect of understory cover on shrub seedling establishment. In the population model, shrub cover was used to estimate a death factor which then reduced the number of surviving germinants and seedlings. The BORSHRUB model used total plant cover (shrub and understory) to reduce seed germination (g, plants ha^{-1} yr^{-1}: which occurred during the first four postfire years) at a rate equivalent to the amount of total cover (TC):

$$g = 2500\,(1-TC) \qquad \text{for } tsb<5 \qquad [1]$$

where tsb=time since burn. This was based on the assumption that seeds were randomly distributed and that shade intolerant germinants could only survive if they were not overtopped by other vegetation during their first year of growth. Equation 1 was estimated using population data from chapter 5. Seeds that successfully germinated entered the regeneration pool and these seedlings were considered mature plants (capable of seed production) four years later and were transferred to the mature plant pool. Because plant cover and biomass were driven by the same variables in chapter 5, shrub cover (C, m^2 $plant^{-1}$) calculations were simplified in the BORSHRUB model by dividing the cover expansion rate of equation 16 in chapter 5 by the biomass (B) accumulation rate of equation 10 in chapter 5:

$$C_t = 1.9210 \cdot B_t \cdot cf \qquad \text{if } tsb = 1 \qquad [2]$$

and similarly using equations 17 and 11 in chapter 5:

$$C_{t+1} = C_t - (0.8439 \cdot B_t) \cdot cf \qquad \text{if } tsb > 1 \qquad [3]$$

where cf = cover factor (dimensionless). Calculation of shrub cover expansion rate (SCe, m^2 m^{-2} yr^{-1}) was included in the shrub submodel and was used as an input to the understory submodel (discussed later):

$$SCe_t = (CT_t - CT_{t-1}) / 10{,}000 \qquad [4]$$

where CT = total shrub cover (m^2 ha^{-1}). All other equations and factors for the shrub submodel were obtained from chapter 5.

Although the shrub submodel was originally designed using *Betula glandulosa*, it can also be adapted to other dominant shrub species by adjusting growth and fire response data. To adapt this submodel to other shrub species, the following factors need to be provided:

Maximum germination rate (seeds ha^{-1} yr^{-1})
Germination Period (yrs)
Age of seed production 9yrs)
Average natural mortality rate (yr^{-1})
Fire mortality rate (dimensionless)
Maximum biomass accumulation rate (kg $plant^{-1}$ yr^{-1})
Maximum canopy expansion rate (m^2 $plant^{-1}$ yr^{-1})
Relative growth rate by moisture regime (dimensionless)
Growth rate change by average seasonal temperature ($°C^{-1}$)

Understory submodel

Major lower vegetation species often associated with dwarf birch stands in the East Slopes region of the Rocky Mountains and the western boreal region were incorporated into the model based on their fire ecology and growth characteristics. Twenty-seven species were selected on the basis of previous surveys (Alberta Forest Service 1990, MacCallum and Yakimchuk 1991, MacCallum 1992, MacCallum and

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[1] Determined for seedlings and mature plants by depth of resprouting structure. Mortality increased exponentially with depth of burn from a minimum of 5% to a maximum of 100% at maximum depth of resprouting structure (estimated from Chapter 3).

Yakimchuk 1992, Bork et al. 1996) and personal field observation. The model can be run with any number of understory species. Community composition is determined at model initiation and unselected species are excluded from the simulation.

Understory vegetation dynamics (Appendix II) were calculated using species cover as the main criteria since understory field data typically consists of this data type (i.e., individuals are often not easily identifiable in many species). Simulated changes in species cover were driven by two distinct mechanisms: fire, and the succession that occurred between fire events. Fire affected the species composition of lower vegetation through fire-induced mortality and the reduction of competition and surface organic layers which influenced postfire plant recovery (resprouting, seedling establishment and clonal expansion). Understory changes due to succession were the result of interspecific differences in growth rate on various sites, expansion rate and shade tolerance.

Fire effects

The immediate postfire site is a very competitive environment as surviving plants resprout and try to quickly regain dominance of their previous growing space while many new invading plants attempt to become established during this brief period of community disturbance. The general fire response of understory species summarized in Table 6-2 indicates that some species appear promoted by fire while the occurrence of others is reduced. In this model, postfire species composition is determined by fire ecology characteristics, or vital attributes, that influence the number of surviving individuals, the ability for seed to germinate on the site, and the rate of cover expansion. General classification of fire adaptive characteristics have been made in previous studies (Lyon and Stickney 1976, Noble and Slatyer 1980, Rowe 1983) and were used as a basis for this model. Understory cover by species (UC_i, $m^2\ m^{-2}$) was calculated as a function of cover expansion (CE_i, $m^2\ m^{-2}$) and cover decrease (CD_i, $m^2\ m^{-2}$):

$$UC_{i(t)} = UC_{i(t-1)} + CE_i - CD_i \qquad [5]$$

Fire mortality

The ability for an individual understory plant to survive a fire event is primarily dependant on the depth of lethal heat penetration and the type and depth of the resprouting organ (McLean 1969, Flinn and Pringle 1983). The fire mortality rates for understory species in this model were estimated by classifying the type and depth of resprouting structure (Table 6-3). Four categories of rooting depth were defined as shallow (<2cm), moderate (2-5 cm), deep (5-8 cm) and very deep (8-15 cm). Plants with resprouting structures deeper than 15 cm or those rooting in mineral soil were considered fire resistant. The four classes of fire mortality were based on the type and depth of resprouting structure, similar to the approach taken by McLean (1969). Fire mortality by species was estimated by assuming a minimum 5% mortality rate for any fire event, which exponentially increased to 100% (estimated from chapter 3 data) at the lowest depth of rooting in that class. Using this criteria, fire survival (FS, dimensionless) was represented by:

$$FS = 1 - (0.05\ e^{a(DOB)}) \qquad [6]$$

where DOB = depth of burn (cm) and a = 1.5 for shallow roots, 0.6 for moderately-deep roots, 0.3 for deep roots and 0.15 for very deep roots.

All understory vegetation cover is assumed to be consumed at the time of a fire event (tsb=0). Understory cover expansion by species (CE_i, $m^2\ m^{-2}$) after the first postfire year was simulated as a function of fire survival and pre-fire understory cover (UC_i $m^2\ m^{-2}$) by:

$$CE_{i(t)} = a \times FS_i \times UC_{i(t-1)} \qquad \text{for tsb}=1 \qquad [7]$$

Although data on postfire plant recovery rates under various fire and growth conditions are scarce, vegetation regrowth occurs very quickly and forbs are known to exhibit a higher growth rate and general increase after fire (Bailey and Anderson 1978, Anderson and Bailey 1980, Romme et al. 1995). This was simulated in the model by using estimated values of a=1 in equation 7 for surviving forb and low shrub plants and a=0.8 for surviving graminoids. In effect, surviving forbs and low shrubs grew to their pre-fire cover in one year (under optimal conditions) while surviving graminoids only grew to 80% of their original cover in that time. Spring fire is more detrimental to cool-season grasses than autumn fire (Bailey and Anderson 1978, Anderson and Bailey 1980) and this was simulated in the model using an estimated value of a=0.67 when that situation occurred. *Danthonia intermedia* and *Agropyron trachycaulum* were the only species in this model that were treated as warm-season grasses. After the first postfire growth year, the remaining growing space that became available as a result of shrub cover reduction and plant mortality was then able to be colonized in the second year by the expansion of surviving plants and new seedlings.

Clonal expansion

Expansion of surviving plants occurred in the model during the second postfire growing season. Because clonal expansion occurs from an established root network, this form of colonization took precedence over new seedling establishment. Although clonal expansion rate is not documented for most understory species, it is known to occur very rapidly in strongly rhizomatous species such as *Epilobium angustifolium* (Myerscough 1980, Broderick 1990) or *Calamagrostis canadensis* which can completely colonize an open site in 1-3 years (Lieffers et al. 1993). *E. angustifolium* rhizomes may spread up to 1 m per year (van Andel 1975) while *C. canadensis* rhizomes have been found to grow 50 cm per year (Macdonald and Lieffers 1993). Due to the lack of data on clonal expansion rates under various growth and competitive conditions, the model used a simple three-level subjective classification of expansion ability to establish relative rates between species. Plants that expanded by rhizomes were placed into one of two categories: short or creeping rhizomes, and extensive or strong rhizomes. The latter were modelled to annually expand up to 100% of their original cover (under optimum conditions) and the former to annually expand up to 50% of their original cover. Plants that expanded by resprouting from a basal point (such as bunchgrasses) had the lowest annual expansion rate of one-eighth their original cover. The three expansion rates were represented by relative expansion factors (Ef_i, dimensionless) in model calculations (8 for strong rhizomes, 4 for short rhizomes and 1 for basal sprouters). A summary of the method of expansion and expansion factor that was estimated for each understory species is summarized in Table 6-4. *Epilobium angustifolium* was treated as a special case by proportionately reducing its expansion factor to zero when total plant cover (TC) reached 1 $m^2\ m^{-2}$:

$$Ef_{EpiAng} = 8\,(1\text{-}TC) \qquad [8]$$

This estimate was used to simulate its early successional nature and inability to maintain high cover levels in late seral, highly competitive environments (Myerscough 1980, Broderick 1990). The potential expansion for each understory species (PE_i, $m^2\ m^{-2}$) was calculated by:

$$PE_i = (Ef_i/8) \cdot UC_{i(t-1)} \cdot Gf_i \cdot tf_i \qquad [9]$$

where tf_i = temperature factor (seeTable 6-6) and Gf_i = growth factor. The influence of site on growth rate was incorporated in the model using moisture regime, similar to the use of basal area to account for site influence in FIRESUM, SILVA and JABOWA. A relative growth rate (low, moderate or high) was assigned to each species (Table 6-1) for moisture regimes 1 (xeric) through 5 (subhygric) (Corns and Annas 1986) and an estimated Gf_i (dimensionless; see Table 6-6) for each relative growth rate was used to adjust cover expansion.

If the potential expansion sum of all understory species was less than the available growing space including total plant cover and shrub cover expansion [i.e., $\sum PE_{1\text{-}n} < (1\text{-}(TC+SCe))$], then the expansion of each understory species (E_i, $m^2\ m^{-2}$) was equal to their potential expansion. If there was less available growing space than the potential expansion sum of all understory species, the available growing space was proportionately allocated to each species by their relative potential expansion amount:

$$E_i = (PE_i/\sum PE_{1\text{-}n}) \times (1\text{-}(TC+SCe)) \qquad [10]$$

Seedlings

Seedling establishment is related to a number of seeding characteristics and microsite condition. Plant species with an 'Invader' strategy (Rowe 1983) typically produce large amounts of small seed that is wind dispersed over large areas to aggressively colonize recently burned areas. 'Evaders' (Rowe 1983) are known to store seed in the soil for long periods of time until a fire event establishes conditions suitable for germination, although a deep burning fire may also destroy buried seed. Seed storage has been shown to be an important factor in boreal mixedwood (Archibold 1979) and eastern hardwood forests (Moore and Wein 1977) but appears to be of lesser importance in coniferous forests and bogs (Moore and Wein 1977) and northern forests (Johnson 1975). Seed storage appears to only occur in herbaceous weed species with a relatively long period of induced dormancy (Chepil 1946a, 1946b). In general, weed species have higher germination rates on mineral soil microsites (Chepil 1946b).

Seed production, dissemination and storage characteristics are generally known for most of the major understory plant species, although quantification of seedling establishment rates under various postfire conditions are not well-documented. In this model, seedling establishment was dealt with as a relative rate in comparison to other competing plant species. In effect, the number of individual seedlings that successfully invaded newly-available growing space was simulated by the proportion of area that each invading species successfully colonized by seed. These relative rates were based on a classification of seeding and postfire site characteristics (Table 6-4). Seed production was classified as low (100's plant^{-1}), moderate (1000's plant^{-1}) or high (10,000+ plant^{-1}); seed dispersal distance was classified as low (heavy seeds dispersed by gravity or animals), moderate (wind dispersed, 100's of metres) or high (wind dispersed, 1km+); and seed storage was classified as low, moderate, or high according to the available literature. A relative seeding factor was then estimated from these three seeding characteristics. The lowest seeding rate was assigned to species which produce low amounts of seed; species which produce moderate amounts of seed that are either stored or dispersed moderate distances were assigned a seeding rate twice that of low seed producers; and species which produce large amounts of seed that are dispersed over large areas were assigned a seeding rate four times the rate of low seed producers. Corresponding seeding factors (Sef, dimensionless) of 1, 2 and 4 were used for model calculations. *Epilobium angustifolium* was a special case in the seeding component because of high seeding ability on exposed mineral soil and decreased seeding ability with increasing organic soil depths (Broderick 1990). This was estimated in the model with a seeding factor of 4 on mineral soil which exponentially decreased to a seeding factor of 1 when the surface organic matter was 2 cm deep:

$$\mathrm{Sef}_{\mathrm{EpiAng}} = 4\,e^{-0.693(\mathrm{OM\ Depth})} \qquad [11]$$

Seedling establishment occurred at the end of the second postfire year in the model to simulate the need for new seedlings to grow two years before being able to compete with established plants. Similar to the shrub submodel, seedling recruitment was restricted to the first four postfire years and the total area invaded through seed ingress by species (S_i, m^2 m^{-2}) was equal to the product of the proportionate seeding ability for each species and the area not occupied by resprouted plants or their expansion:

$$S_i = (\mathrm{Sef}_i / \textstyle\sum \mathrm{Sef}_{1-n}) \times (1-(TC+SCe+\textstyle\sum E_{1-n}) \qquad \text{for tsb}<5 \qquad [12]$$

and the cover expansion by species for subsequent postfire years was:

$$CE_i = E_i + S_i \qquad \text{for tsb}>1 \qquad [13]$$

Postfire succession

Changes in postfire understory vegetation was simulated through interspecific competition. This was based on changes in shrub cover and the shade tolerance, plant height and relative expansion rate for understory species. Loss of understory cover due to expanding shrub canopy was assumed to be random, so the model assigned these changes proportionately to understory species by the area they occupied. Other non-fire mortality was also assumed to be random and proportional by species. However, because this type of mortality is usually very low (<1% annually) it was assumed that all species were equally capable of encroaching on this minor amount of growing space by the expansion of existing individuals. Therefore, the net change in species cover due to random shrub expansion and non-fire mortality should be negligible and was not included in the model *per se*.

The total amount of area available for understory plants was calculated as the growing space not being occupied by shrubs. Changes in the proportion of understory plant area occupied by any species was the balance between competition-induced cover loss and the proportion of this new growing space that was encroached upon by expanding plants. Therefore, species with the lowest shade tolerance declined in cover while species with the greatest expansion rates increased in cover.

Competition between understory species was estimated using a height class and shade tolerance class for each species and the relative expansion rates previously described. Species were assigned a height class of low (<35 cm), moderate (35-75 cm) or high (75+ cm) and a similar shade tolerance class (Table 6-5). Plant species that were highly tolerant of shade lost minimal cover due to competition in the model while shade intolerant species of the lowest height class lost the most cover due to competition. This was done using an estimated competition factor (Cof, dimensionless) from the height and shade tolerance classes (see Table 6-6). The low shrub *Potentilla fruticosa* was a special case in this model as it was allowed to overtop other understory vegetation (so it was included as a shade tolerant species) but it could also be overtopped by the dominant birch shrub layer in the same manner as the other understory species. Cover decrease due to competition was adjusted proportionately by total plant cover so that cover decrease was reduced at lower levels of competition. Total cover decrease by species (CD_i, $m^2\ m^{-2}$) was estimated by the sum of the proportionate loss due to shrub expansion (based on amount of understory species cover) and cover loss due to competition:

$$CD_i = ((UC_i / \sum UC_{i..n}) \times SCe) + (Cof_i \times UC_i \cdot TC) \qquad [14]$$

Fuels submodel

The fuels submodel maintained an inventory of the various biomass pools in the plant community (Appendix II). Aboveground biomass pools included live shrub, dead shrub stems and understory biomass while surface litter and duff comprised the two belowground biomass pools. Increase in live shrub biomass, or shrub growth (SG, $kg\ m^{-2}\ yr^{-1}$), was transferred directly from the shrub submodel using individual plant biomass increase and population size, while *Potentilla fruticosa* biomass increase was included using an estimate based on field data from MacCallum and Yakimchuk (1991a):

$$SG = (BT_t - BT_{t-1}) + (CE_{PotFru} \cdot 0.98) \qquad [15]$$

Every year, leaf-fall material ($0.4 \times BT_t$ $kg\ m^{-2}\ yr^{-1}$; estimated from Bessie and Johnson 1995 biomass data) was transferred to the surface litter pool (SL) and stem dieback biomass ($0.05 \times SG$, $kg\ m^{-2}\ yr^{-1}$; estimated from Bessie and Johnson 1995 biomass data) was transferred to the dead stem (DS, $kg\ m^{-2}$) pool. A portion of the dead stem material was lost annually to decay using a rate ($0.025 \times DS$, $kg\ m^{-2}\ yr^{-1}$) estimated from the medium and fast soil carbon pool inputs of Kurz et al. (1992). Increases in understory biomass growth (UG, $kg\ m^{-2}\ yr^{-1}$) were calculated as the product of understory cover and the site productivity estimate. Productivity has been shown to increase after fire (e.g., Gates et al. 1994) and this maximum productivity rate was scaled back to 70% by year 35 (determined from field data in Alberta Forest Service 1990):

$$UG = \sum UC_{i..n} \cdot Max\ UP \times e^{-0.0102 \cdot tsb} \qquad [16]$$

where Max UP = maximum understory productivity (kg m^{-2} yr^{-1}). All live understory biomass (except for the low shrub *Potentilla fruticosa*) was transferred to the surface litter pool at the end of each year as annual understory dieback.

Decomposed surface litter was transferred to the duff pool using the rate (0.65 × SL, kg m^{-2} yr^{-1}) by Keane et al. (1989). Surface litter also decreased due to respiration using the decay rate (0.07 × SL, kg m^{-2} yr^{-1}) from Kurz et al. (1992) and due to overwinter decomposition using the rate (0.04 × SL, kg m^{-2} yr^{-1}) by Keane et al. (1989). The duff pool recorded respiration (Rd, kg m^{-2} yr^{-1}) losses that were determined by the effect of shading and insulation of shrubs and litter on the fast soil carbon pool. Respiration under shrub cover (SC, m^{2} m^{-2}) occurred at the minimum rate (0.127 kg m^{-2} yr^{-1} for western boreal hardwood; from Kurz et al. 1992), while other areas varied between the minimum rate at a surface litter depth (SLD) >2cm to the maximum rate (0.253 kg m^{-2} yr^{-1}; from Kurz et al. 1992) when no surface litter was present. The following equations used in BORSHRUB were a direct application (using a 2 cm surface litter depth limit) of those by Kurz et al. 1992:

$$Rd=SL\cdot((SC\cdot 0.127)+((1-SC)\times(0.127+((0.253-0.127)\times e^{-0.21(SLD/2)})))) \quad \text{for SLD<2cm} \qquad [17]$$

$$Rd=SL\cdot((SC\cdot 0.127)+((1-SC)\cdot(0.127+((0.253-0.127)\times e^{-0.21})))) \quad \text{for SLD>2cm} \qquad [18]$$

When a fire occurred, it was assumed that 20% of the live shrub biomass was consumed and that the remaining 80% was moved to the dead stem pool. Dead stem consumption was determined from the Buildup Index (BUI, Van Wagner 1987) of the Canadian Forest Fire Danger Rating System (Forestry Canada Fire Danger Group 1992) using data from Stocks and Walker (1972). In that study, all fine, dead woody fuels (<2cm) were consumed near a BUI = 25 and dead stem consumption (0.04 × BUI, dimensionless) was estimated from this value using BUI. Fire was assumed to burn 95% of the live understory biomass and the remaining 5% was transferred to the surface litter pool. Loss of surface litter and duff layers were determined by the depth of those layers using bulk density values of 36 kg m^{-3} for litter and 97 kg m^{-3} for duff (estimated from eastern hardwood stands in Stocks et al. 1990) and the depth of burn.

Fire submodel

The effects of fire on shrub and understory vegetation was driven by the fire submodel (Appendix II). The fire frequency component used a Monte Carlo method to determine the timing of fire events based on an average fire return interval. Season of burn (spring or autumn) was randomly assigned to each fire event. The Buildup Index (BUI), an indicator of total amount of fuel available for combustion, Initial Spread Index (ISI), an indicator of fire rate of spread and Duff Moisture Code (DMC), an indicator of duff moisture content (Van Wagner 1987) were calculated for each fire using historical occurrence of those parameters by season. The model randomly selected BUI, ISI and DMC values from normal distributions for spring (May) and autumn (August and September) based on historical 28-year mean and extreme values (standard deviation was assumed to be one half of the difference between mean and extreme values) from Harrington et al. (1983). The ISI was used to determine rate of fire spread (ROS, m min^{-1}) with the O-1 (grass) fuel type of the Canadian Forest Fire Behavior Prediction System (Forestry Canada Fire Danger Group 1992):

$$ROS = 250 \times (1-e^{-0.0350(ISI)})^{1.7} \qquad [19]$$

Duff burn depth was calculated using DMC to determine duff moisture content (Duff MC,%) from Van Wagner's equation (1987):

$$\text{Duff MC} = 20+e^{(DMC-244.72)/-43.43} \qquad [20]$$

which was then applied to the duff depth of burn (DBD) model from Brown et al. (1985):

$$DBD = \text{Duff Depth}\times((83.7-0.426\times \text{Duff MC})/100) \qquad [21]$$

Total depth of burn was the sum of duff depth of burn and litter depth (all surface litter was consumed during a fire in the model) and was used to model fire survival of understory plants. Duff burn depth was used for fire survival determination of the shrub species. Dead stem consumption in the fuels submodel was determined with BUI using slash consumption data from Stocks and Walker (1972) as previously described. Rate of fire spread (ROS, m sec^{-1}) and total fuel consumption (TFC, kg m^{-2}; from the fuels submodel) were used to determine overall fire intensity (I, kW m^{-1}) using Byram's (1959) equation:

$$I = h \cdot TFC \cdot ROS \qquad [22]$$

where h=low heat of combustion (a constant value of 18,000 kJ kg^{-1}).

Model simulations and testing

The BORSHRUB model was corroborated using two previous studies for which pre- and postburn data was available (Alberta Forest Service 1990, MacCallum and Yakimchuk 1991b). Both data sets used for testing were independent of the model development data. Simulations were initiated using a litter depth of 0.3 cm, a duff depth of 4 cm and the pre-burn cover for shrub and understory species. Pre-burn data for the 7 Mile Flats study (Alberta Forest Service 1990) indicated that unlisted graminoid species accounted for 18.9% cover and unlisted forbs occupied 12.9% cover. The test data was adjusted by proportionately assigning these cover differences to the other species within the same vegetation group during model initiation. The Brazeau study (MacCallum and Yakimchuk 1991b) included numerous minor understory species which were not represented in the model, and that cover (11.2%) was proportionately assigned to the other species within the same vegetation group to adjust the data set. The simulations were run using the DMC, BUI and ISI values for the burns. Comparison of actual and simulated postburn cover for shrub and understory species was made graphically by vegetation type and statistically by species using a paired t-test.

Long-term (200 year) simulations were run to observe successional trends under different fire frequencies. The simulations were initiated to reflect a community of 10 common understory species recovering from a recent fire. Each species had an equal level of fire survival (equivalent to 3% cover) while the shrub population was set at 10,000 ha^{-1} with no initial canopy. Determination of DMC, ISI and BUI values was based on historical data for Rocky Mountain House, Alberta (Harrington et al. 1983) and was similarly done for average seasonal temperature from historical weather data (Atmospheric Environment Service, 1982). Initial surface litter and duff depths were set at 1cm and 8 cm, respectively. Fires occurred randomly at 10-, 25-, and 50-year average fire frequencies and each scenario was simulated 30 times. Average cover values for shrub and each understory species were summarized for the 200-year simulation period.

All parameters in the BORSHRUB model were tested in a sensitivity analysis using the technique devised for SILVA (Kercher and Axelrod 1984) and utilized in FIRESUM (Keane et al. 1989). All model parameters were held constant while one parameter was increased by 10% (except for the Moisture Regime factor which was increased by one factor value) and the sensitivity factor (SF) was measured by the change in cover relative to the change in the parameter value:

$$SF = \left(\frac{cover_{new} - cover_{old}}{cover_{old}} \right) / \left(\frac{\mu_{new} - \mu_{old}}{\mu_{old}} \right)$$

where μ is the input parameter, 'new' refers to the changed parameter value and 'old' refers to the original parameter value. The 10 understory species used in the long-term simulations were also used in this analysis with the same initial conditions. Fire frequency was held constant at 25-years, fire events occurred in the spring, and the DMC, ISI and BUI values were held constant at the average spring values for Rocky Mountain House. Cover values for shrub, *Vicia americana* and *Calamagrostis canadensis* (the most prominent forb and grass species in the long-term simulations) at 30, 60 and 99 years were used to evaluate sensitivity. The subjective division of the SF scale (Kercher and Axelrod 1984) was: $SF < 0.1$, very insensitive; $0.1 < SF < 0.5$, insensitive; $0.5 < SF < 1.1$, sensitive; and $SF > 1.1$, very sensitive.

Results

Comparison of model predictions for shrub, forb and graminoid cover to actual cover data in the 7 Mile Flats and Brazeau studies was summarized in Figure 6-3. Model estimates of shrub cover were close to actual values in both studies. The model predicted lower forb coverage at the 7 Mile Flats site (mostly occurring immediately after the fire) and slightly higher values at the Brazeau site. Graminoid cover predictions were higher for 7 Mile Flats and lower for the Brazeau study. The paired t-test of actual and predicted values for individual understory species in the two studies (Table 6-7, Figure 6-4) showed no significant difference between field data and model predictions ($t = 1.22$; $t_{(0.05,\,95)} = 2.00$).

Examples of long-term model predictions are shown in Figure 6-5. The first simulation shows that the absence of fire results in litter and duff depths that reach an equilibrium between fuel accumulation from vegetation and losses from decomposition and respiration. At the same time, shrub cover increases to a high level which causes a decrease in forb and graminoid cover. The second simulation shows the effect of fire occurring at a regular interval, such as would happen in a prescribed burn program. This results in the formation of a regular pattern in the fuel and vegetation components. The third simulation shows that a stochastic fire interval and depth of burn can result in constantly changing conditions of soil depth and vegetation composition.

The simulations that were run for 10, 25 and 50-year fire cycles showed changing responses in the understory species (Figures 6-6, 6-7 and 6-8). All understory species responded immediately with a sharp increase in cover due to the lack of shrub cover in the early years. All forb species steadily declined to a low level except for *Vicia americana* which increased to a higher level, particularly at shorter fire intervals. *Potentilla fruticosa* had declining cover at the highest fire frequency and a stable to increasing cover level at the lowest fire frequency. *Epilobium angustifolium* had the slowest rate of decrease with time and this was most notable at the highest fire frequency. *Agropyron trachycaulum* declined to no cover in a very short period of time (most quickly at the highest fire frequency) with only sporadic low occurrence afterwards. *Calamagrostis canadensis* maintained the highest graminoid cover in all simulations although it appeared to be declining in the 10-year fire cycle, slightly declining in the 25-year fire cycle and stable or slightly increasing in the 50-year fire cycle. *Poa pratensis* had declining coverage at all fire cycles but to a lesser degree at the longest fire cycle. Shrub cover increased to the highest level at the lowest fire frequency while the highest fire frequency indicated the greatest amount of shrub cover variability between years.

The sensitivity analysis (Table 6-8) indicated that shrub cover is sensitive to the shrub canopy expansion rate, shrub density factor, shrub biomass productivity rate, moisture regime and average seasonal temperature. It is less sensitive to the germination rate and somewhat sensitive to the natural mortality rate. It is very insensitive to all other factors. *Vicia americana* and *Calamagrostis canadensis* cover had high sensitivity to shrub canopy expansion rate, shrub density factor, shrub biomass productivity and their own expansion rate. They were also sensitive to average seasonal temperature, moisture regime, shrub germination rate and their own competition factor. They were insensitive to all other factors.

Discussion

Model corroboration with the 7 Mile Flats and Brazeau field data suggests that the model is capable of making statistically acceptable cover predictions for shrub and understory species. Validation data is scarce but further testing with future additional independent data sets would provide added confirmation.

The long-term simulations indicate the cumulative effect of a 10, 25 or 50-year fire cycle (over a 200-year period) on the simulated plant community and suggest hypotheses regarding the influence of different fire regimes on general succesional trends. After the 200-year simulations, most species appeared to have reached (or were close to approaching) an equilibrium level of cover as they attained a balance with the given fire cycle and community composition. The fact that a species declined or increased to reach that level was only an indication of the difference between the initial starting cover and the equilibrium cover level induced by the fire regime and community composition. In the model simulations, *Agropyron trachycaulum* was quickly lost from the community because it had a very low fire survival rate. The historical DMC values for Rocky Mountain House were fairly low, resulting in generally shallow burn depths. This resulted in high fire survival rates for most species (except *A. trachycaulum*) and a highly competitive postfire community with little opportunity for re-seeding. *A. trachycaulum* was found to occur sporadically after it declined and this was caused by infrequent deeper burns that allowed a minor amount of seed to become established. However, new *A. trachycaulum* plants expanded very little and were usually removed during the next few fires.

At the other end of the fire survival spectrum was *Vicia americana*. It was the deepest-rooted plant in the simulated community which provided it with the highest fire survival rate. Higher fire frequency promoted this plant over all others and increased its cover. It also maintained high cover levels at low fire frequency because of its high level of shade tolerance, making it a very competitive plant species. *Calamagrostis canadensis* and *Poa pratensis* survived well at all fire frequencies because they were relatively deep rooted and could quickly expand in the postfire environment through extensive clonal growth, although a slight cover decrease was evident under the highest fire frequency. Both species increased in cover at low fire frequency because of their high competitive ability which resulted from moderate shade tolerance and tall plant stature.

Potentilla fruticosa was the most competitive of all the understory plants because it was dominant in height over all others. This gave it a higher coverage at low fire frequency. It survived well at higher fire frequency due to its deep rooted nature, but its minimal ability to expand restricted cover increase after fire. *Astragalus alpinus*, *Fragaria virginiana* and *Galium boreale* maintained low cover levels at all fire frequencies. *F virginiana* was the most susceptible to fire of these three species, but maintained a minimal cover level by expansion through stolon runners. *A. alpinus* and *G. boreale* remained in the community through moderate fire survivability although postfire expansion was moderate to minimal. All three of these herbaceous species were minor components because of their lower level of competitive ability due to shade tolerance and plant stature. *Achillea millefolium* was slightly more prominent than most other forbs because of its deep rooting habit and moderate ability to expand. *Epilobium angustifolium* had at least twice the cover of *A. millefolium* due to its deep rhizomes and extensive clonal expansion after fire and these characteristics made it a very competitive plant at high fire frequencies.

In general, graminoid cover was suppressed by frequent fire which allowed an increase in forb cover. Seeding characteristics were not very important in these simulations because of the generally low depths of burn which favoured clonal plants over obligate seeders. In the case of *Epilobium angustifolium*, seedling establishment was further reduced by the significant duff layer depth. Deep burns and more frequent burns are expected to produce a greater diversity of understory species (a response found in frequently burned rangeland by Anderson and Bailey 1980) because of greater opportunity for seedling establishment. Although forbs were generally much lower in cover than the graminoids, forbs were very prominent in the immediate postfire community. However, increased forb coverage was a temporary postfire response and the long-term simulations reflected this with low average values.

Besides fire frequency and depth of burn, the species makeup of a plant community had a strong influence on the amount of cover that each species attained. For instance, the removal of *Vicia americana* from the long-term simulations would have taken away a very competitive component of the community and provided much additional growing space for other species that would otherwise remain at low cover levels. In turn, because the dominance of *V. americana* was highest at the highest fire frequency, other species which had very low cover at high fire frequency could have had exceptionally higher levels if *V. americana* was removed. In effect, the presence or absence of a dominating species may be the difference between a species which appears to be flourishing or receding under a certain fire regime. Therefore, species cover was determined in great part by the fire ecology and competitive characteristics of each species in relation to those of the other community members.

The sensitivity analysis provided a relative measure of parameter influence and the importance of that parameter in model processes. Sensitive factors need to be accurately estimated for accurate model results. The shrub density factor, shrub canopy expansion rate and shrub biomass productivity rate affected shrub cover at a level that was generally proportional to the change in value, although cover for the two understory species showed much greater changes because they represented the largest components of the understory community. The rates for these three factors were found to be quite reliable in the shrub model (see chapter V validation). Shrub and understory cover were also sensitive to average seasonal temperature and the moisture regime factor because they affected shrub growth rates (which then affected understory cover). Average seasonal temperature can be estimated with confidence using long-term weather data; estimation of moisture regime requires careful examination of the field site. To improve the accuracy of the moisture regime estimate, the moisture regime factor may be replaced by:

(average shrub biomass for the site/average shrub biomass for MR3)

as similarly done in SILVA and FIRESUM to adjust for site using tree basal area. This effectively replaces the five-class scale of moisture regime with a much finer scale of possible values. This procedure also requires knowledge of the time since last fire.

The influence of shrub germination rate on cover was shown to range from sensitive to insensitive, while cover was generally insensitive to the natural mortality rate. Long-term population data is not available to test the accuracy of these rates, although model simulations produced population sizes that were comparable to field survey data. Understory cover was very sensitive to the understory expansion and competition rates because they represent the ability to colonize a disturbed site and the longevity of a species within the community. Comparison of model predictions with field cover data suggests that the estimates for these relative rates are sufficiently accurate, although further testing with future independent data sets is recommended.

Future model development

Additional model testing is necessary to provide further validation over a wider range of field conditions. FIRE-BGC, FIRESUM and SILVA have used basal area as the primary criteria for validating the model with field data, although fuel loading and duff/litter depth were also used in FIRE-BGC. Future testing of BORSHRUB should take a similar approach using cover, biomass and litter/duff depth. Data sets should cover a wide range of possible environmental conditions including temperature, moisture regime (site), fire frequency and depth of burn as well as a wide range of community composition.

The present BORSHRUB model was developed to simulate annual postfire community succession over relatively large areas (100 ha+) so that it could be used as an operational planning tool for vegetation management. Further development of the BORSHRUB model may follow several different directions, depending on the purpose of the model. For instance, site-specific habitat management applications may require refinement of the model to a weekly timestep if forage production or availability was critical at certain times during the year. A weekly timestep would also determine the seasonal influence of fire (in relation to physiological plant condition) in greater detail so that the model performed with greater site-specific accuracy. This would require weekly biomass production data for the entire growing season and a more detailed exploration of fire effects at various physiological stages.

BORSHRUB could also be developed for management planning at the landscape level (i.e., determining changes in vegetation and age-class distribution under different fire regimes) by being incorporated as a range or forest understory component of other landscape fire succession models. The amount of adjustment necessary to the BORSHRUB model would depend on the architecture of the landscape model. For instance, integration with the Forest Vegetation Simulator (Stage 1973, Wykoff et al. 1982, Wykoff 1986, Crookston and Stage 1991) would be simpler than integration with FIRE-BGC because plant growth in the former is based on empirical data (the same approach used in BORSHRUB) and the latter is based on carbon flow. Adapting the BORSHRUB model to serve as a forest understory component could be accomplished by incorporating light availability as another factor affecting understory growth rate (the present model assumes no overhead canopy in rangelands) and calibration with forest understory data.

Lastly, BORSHRUB could be further developed as a research tool to examine the effects of environment on succession processes and plant growth. This type of application requires a high level of model resolution which would necessitate significant modification of BORSHRUB to simulate growth using a physiological approach. This could be accomplished by using available light to drive the carbon and nutrient dynamics which account for plant growth, as done in FIRE-BGC. This would allow the BORSHRUB model to be utilized by a wider range of applications.

Conclusion

The BORSHRUB model provided estimates of cover for shrub, forb and graminoid species with a level of reliability that appears appropriate for vegetation management purposes. The model is at a stage where it is ready for further testing with management and field applications.

The model suggests hypotheses regarding the relationship between fire regime and shrub-grassland plant communities. For instance, the simulations indicated that higher fire frequency decreased average shrub cover and promoted understory species with a high fire survival rate. Forbs were promoted by frequent fire at the expense of graminoids, although this was a temporary postfire response and average forb cover was usually very low. Postfire recolonization was greatest for species with an extensive clonal habit, provided that the species was capable of surviving the fire depth of burn. Species of low expansion ability could only be maintained in the plant community through a high fire survival rate or seed ingress. Seeding characteristics became increasingly important to postfire colonization after deeper burning fires, and it is through this mechanism that species diversity is expected to increase. Low fire frequency tended to promote species with highly competitive traits through the combined influence of shade tolerance and plant height. Therefore, species of low competitive ability were generally found in early seral stages and in frequently burned communities.

The prediction that fire-resistant species would be promoted by high fire frequencies was supported by the model simulations. However, the model suggests that this is not a simple response mechanism and that there is a more complex interaction of fire survival and competitive traits that determines which species will benefit the most from fire disturbance. Postfire dynamics could also be very different in other situations, such as high depths of burn or shallow organic sites when seed ingress becomes more important. The prediction of an increase in fire-susceptible species at low fire frequencies was not supported by the model simulations. Fire susceptible plants had more opportunity to survive at low fire frequencies but they did not increase if they were not also highly competitive.

Tables

Table 6-1. Summary of estimated relative growth rates for understory plants by miosture regime. Summarized from Looman and Best (1979), Porsild and Cody (1980), Moss (1983), Johnson et al. (1995) and other references cited.

Species	Moisture Regime 1 xeric	 2	 3 moist	 4	 5 subhygric	References^{1,2}
			Relative Growth Rate^{3}			
Low Shrubs						
Arctostaphylos uva-ursi (L.) Spreng.	M	H	H	M	L	16
Potentilla fruticosa L.	L	M	H	M	L	16
Forbs						
Achillea millefolium L.	M	H	M	L		15
Aster conspicuus Lindl.	L	M	H	M	L	9
Astragalus alpinus L.		L	H	H	H	
Epilobium angustifolium L.	L	M	H	M	L	5, 8, 16
Fragaria virginiana Duchesne	L	M	H	M	L	
Galium boreale L.		L	M	H	M	
Geum triflorum Pursh			M	H	H	
Lathyrus ochroleucus Hook.		L	M	H	M	16
Oxytropis deflexa (Pall.) DC.	M	H	M	L		16
Smilacina stellata (L.) Desf.		L	M	H	M	
Solidago canadensis L.	M	H	H	M		2
Thalictrum venulosum Trel.		L	H	H	H	
Vicia americana Muhl.	M	H	H	H	M	16

Table 6-1 (cont'd). Summary of estimated relative growth rates of understory plants by moisture regime. Summarized from Looman and Best (1979), Porsild and Cody (1980), Moss (1983), Johnson et al. (1995) and other references cited.

Species	Moisture Regime					References[1,2]
	1 xeric	2	3 moist	4	5 subhygric	
	Relative Growth Rate[3]					
Graminoids						
Agropyron trachycaulum Link (Malte)	L	M	H	M	L	11, 16
Bromus inermis Leyss.	L	M	H	H	M	11, 16
Calamagrostis canadensis (Michx.)Beauv.	L	M	H	H	M	7, 16
Carex siccata Dewey		L	M	H	M	
Danthonia intermedia Vasey	L	M	H	M	L	4
Elymus innovatus Beal	L	M	H	M	L	16
Festuca scabrella Torr.	M	H	H	M	L	6, 11
Festuca idahoensis Elmer.	M	H	H	M		1, 11
Juncus balticus Willd.		L	M	H	M	10
Koeleria macrantha (Ledeb.) Schult.	L	M	H	H	M	7, 12, 14, 16
Poa pratensis L.		L	M	H	M	11, 13, 16
Stipa richardsonii Link	L	M	H	M	L	3

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[1] (1) Bradley 1986; (2) Coladonato 1993a; (3) Esser 1992; (4) Holifield 1987; (5) Landhäusser and Lieffers 1994; (6) McMurray 1987; (7) Meuller-Dombois and Sims 1966; (8) Myerscough 1980; (9) Reed 1993; (10) Snyder 1992; (11) Stubbendieck et al. 1994; (12) Tirmenstein 1987b; (13) Uchytil 1993; (14) Volland and Dell 1981; (15) Warwick and Black 1982; (16) Watson et al. 1980.

[2] See Fischer et al. (1996) for accessing sources cited from the Fire Effects Information System.

[3] H = 100% of maximum growth rate; M = 75% of maximum growth rate; L = 50% of maximum growth rate.

Table 6-2. General fire effects on understory species in the BORSHRUB model.

Species	Fire Effects	References[1,2]
Low Shrubs		
Arctostaphylos uva-ursi (L.) Spreng.	Seed germination may be stimulated by heat. Occurs mostly in mid-seral stages.	8, 16
Potentilla fruticosa L.	Cover decreases sharply after fire but resprouts quickly; seedling establishment is slow. Occurs in all seral stages.	15, 21
Forbs		
Achillea millefolium L.	Rapid increase after fire from rhizomes. Repeated annual spring burning increased cover.	1, 3
Aster conspicuus Lindl.	Rapid increase afer fire by seed and rhizomes.	17
Astragalus alpinus L.	Milkvetches increase with fire but may decrease with repeated fire. Successful colonizer of disturbed sites.	1, 3, 12
Epilobium angustifolium L.	Rapid resprouter; seed requires mineral soil. Successful colonizer; expands quickly. Most prominent on postfire sites.	2, 5, 10, 12, 14, 18
Fragaria virginiana Duchesne	Cover increase after fire; frequency increase with repeated fire.	1, 15
Galium boreale L.	Cover increase with repeated fire, but no change in frequency.	1
Geum triflorum Pursh	Decreased cover after fire but increases quickly.	1, 15
Lathyrus ochroleucus Hook.	Decreases with repeated fire. Seed appears to have lengthy dormancy. Most prominent in mid and late seral stages.	1, 25
Smilacina stellata (L.) Desf.	Frequency increase with repeated fire, but no change in cover.	1
Solidago canadensis L.	Generally increased by fire. Primarily occurs in early and mid seral stages.	6
Vicia americana Muhl.	Increases with occassional and repeated fire. Prominent on postfire sites.	1, 7

Table 6-2 (cont'd). General fire effects on understory species in the BORSHRUB model.

Species	Fire Effects	References[1, 2]
Graminoids		
Agropyron trachycaulum Link (Malte)	May increase or decrease with spring burning.	3, 15
Bromus inermis Leyss.	Decreases with repeated fire.	1
Calamagrostis canadensis (Michx.) Beauv.	Aggressive colonizer of newly disturbed areas. Often dominant once established. Found in all seral stages.	13, 19, 20
Carex siccata Dewey	Decreases sharply with repeated spring fire.	1
Danthonia intermedia Vasey	Indicator of climax stage in many communities.	11
Elymus innovatus Beal	Pioneer colonizer.	25
Festuca scabrella Torr.	Fire susceptible only in dry season. Large bunch development can cause higher fire mortality rates. Decreases with spring burning, especially with repeated spring fires.	1, 3
Festuca idahoensis Elmer.	Very sensitive to fire. Decreases with spring burning.	4, 15
Juncus balticus Willd.	Successful colonizer. No change in cover with repeated spring fire.	1, 12
Koeleria macrantha (Ledeb.) Schult.	Increases slightly with fire. Decreases with late spring burns. Usually found in early seral stages.	22, 25
Poa pratensis L.	Spring burning reduces cover and vigour. Can not withstand frequent spring burning. Often dominant in recent burns.	23, 24
Stipa richardsonii Link	Least fire resistant of the bunchgrasses. Occurs mostly as a a climax codominant.	3, 9

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[1] (1) Anderson and Bailey 1980; (2)Archibold 1980; (3) Bailey and Anderson 1978; (4) Bradley 1986; (5) Broderick 1990; (6) Coladonato 1993a; (7) Coladonato 1993b; (8) Crane 1991; (9) Esser 1992; (10) Haeussler et al. 1990; (11) Holifield 1987; (12) Kershaw and Kershaw 1987; (13) Lieffers et al. 1993; (14) Myerscough 1980; (15) Nimir and Payne 1978; (16) Noste and Bushey 1987; (17) Reed 1993; (18) Romme et al. 1995; (19) Rowe 1983; (20) Tesky 1992; (21) Tirmenstein 1987a; (22) Tirmenstein 1987b; (23) Uchytil 1993; (24) Volland and Dell 1981; (25) Watson et al. 1980.

[2] See Fischer et al. (1996) for accessing sources cited from the Fire Effects Information System.

Table 6-3. Summary of resprouting traits of understory plants. Rooting characteristics summarized from Looman and Best (1979), Porsild and Cody (1980), Moss (1983), Johnson et al. (1995) and other references cited. Estimated parameters (in italics) are shown where information was unavailable.

Species	Resprouting Structure	Depth of Structure[1]	References[2,3]
Low Shrubs			
Arctostaphylos uva-ursi (L.) Spreng.	stolons, root crown	shallow	10, 13, 14, 20, 22
Potentilla fruticosa L.	rhizome, root crown	deep	17, 22
Forbs			
Achillea millefolium L.	rhizome	deep	6, 10, 21
Aster conspicuus Lindl.	stout rhizome	*mod*	10
Astragalus alpinus L.	rhizome	*mod*	
Epilobium angustifolium L.	rhizome	deep	2, 8, 10, 15
Fragaria virginiana Duchesne	rhizome	*shallow*	10, 20
Galium boreale L.	rhizome	*mod*	20
Geum triflorum Pursh	stout rhizome	*mod*	
Lathyrus ochroleucus Hook.	rhizome	deep	10, 22
Oxytropis deflexa (Pall.) DC.	taproot	very deep	
Smilacina stellata (L.) Desf.	rhizome	*mod*	
Solidago canadensis L.	rhizome	*deep*	3
Thalictrum venulosum Trel.	rhizome	*mod*	
Vicia americana Muhl.	rhizome, taproot	very deep	4, 10

Table 6-3 (cont'd). Summary of resprouting traits of understory plants. Rooting characteristics summarized from Looman and Best (1979), Porsild and Cody (1980), Moss (1983), Johnson et al. (1995) and other references cited. Estimated parameters (in italics) are shown where information was unavailable.

Species	Resprouting Structure	Depth of Structure[1]	References [2,3]
Graminoids			
Agropyron trachycaulum Link (Malte)	fibrous rootstock	shallow	20
Bromus inermis Leyss.	rhizome	*mod*	24
Calamagrostis canadensis (Michx.)Beauv.	rhizome	deep	8, 9, 13
Carex siccata Dewey	stout rhizome	*deep*	
Danthonia intermedia Vasey	fibrous rootstock	mod	7, 20
Elymus innovatus Beal	rhizome	mod	
Festuca scabrella Torr.	rhizome, rootstock	deep	11
Festuca idahoensis Elmer	fibrous rootstock	shallow	1, 20
Juncus balticus Willd.	stout rhizome	deep	16
Koeleria macrantha (Ledeb.) Schult.	Fibrous rootstock	shallow	18, 20
Poa pratensis L.	stoloniferous rhizome	deep	19, 20, 22
Stipa richardsonii Link	fibrous rootstock	shallow	5

[1] shallow = 0-2 cm, mod = 2-5 cm, deep = 5-8 cm, very deep = 8-15 cm.

[2] (1) Bradley 1986; (2) Broderick 1990; (3) Coladonato 1993a; (4) Coladonato 1993b; (5) Esser 1992; (6) Hickerson 1986; (7) Holifield 1987; (8) Lieffers and Stadt 1994; (9) Lieffers et al. 1993; (10) McLean 1969; (11) McMurray 1987; (12) Meuller-Dombois and Sims 1966; (13) Noste and Bushey 1987; (14) Remphrey et al. 1983; (15) Romme et al. 1995; (16) Snyder 1992; (17) Tirmenstein 1987a; (18) Tirmenstein 1987b; (19) Uchytil 1993; (20) Volland and Dell 1981; (21) Warwick and Black 1982; (22) Watson et al. 1980; (23) Winkler 1987.

[3] See Fischer et al. (1996) for accessing sources cited from the Fire Effects Information System.

Table 6-4. Summary of seeding ability and expansion method of understory plants. Characteristics summarized from Looman and Best (1979), Porsild and Cody (1980), Moss (1983), Johnson et al. (1995) and other references cited. Estimated parameters are shown in italics.

Species	Seed Production	Seed Dispersal	Seed Storage	Seeding Factor	Method of Expansion	Expansion Factor	References[1,2]
Low Shrubs							
Arctostaphylos uva-ursi (L.) Spreng	low	low	high	1	layering stolons	4	16, 18, 26, 29
Potentilla fruticosa L	high	high	low	4	basal sprouting	1	23, 29
Forbs							
Achillea millefolium L	mod	mod	high	2	rhizome	4	8, 13
Aster conspicuus Lindl		high	low	4	extensive rhizome	*8*	15
Astragalus alpinus L.	low			1	creeping rhizome	4	
Epilobium angustifolium L	high	high	low	4	extensive rhizomes	8	1, 3, 10, 14, 17
Fragaria virginiana Dcne	mod	low		2	creeping stolons	4	27
Galium boreale L.	low	low		1	seed	1	27
Geum triflorum Pursh				2		*1*	
Lathyrus ochroleucus Hook	low	*low*		2	creeping rhizome	4	29
Oxytropsis deflexa (Pall.) DC			*mod*	2	seed	1	29
Smilacina stellata (L.) Desf	low			*1*		*8*	
Solidago canadensis L.	low	low	mod	2	short rhizomes	4	4, 7, 19
Thalictrum venulosum Trel	low			1		*1*	
Vicia americana Muhl	low	low	high	1	creeping rhizome	4	5, 29

Table 6-4. Summary of seeding ability and expansion method of understory plants. Characteristics summarized from Looman and Best (1979), Porsild and Cody (1980), Moss (1983), Johnson et al. (1995) and other references cited. Estimated parameters are shown in italics.

Species	Seed Production	Seed Dispersal	Seed Storage	Seeding Factor	Method of Expansion	Expansion Factor	References[1] [2]
Graminoids							
Agropyron trachycaulum Link (Malte)	high	mod	mod	4	short rhizomes/bunchgrass	1	29
Bromus inermis Leyss	low	mod		1	long rhizomes	8	29, 30
Calamagrostis canadensis (Michx.) Beauv. low	low	mod	mod	1	extensive rhizomes	8	10, 11, 22, 29
Carex siccata Dewey		mod		*1*	long rhizomes	4	
Danthonia intermedia Vasey		mod		*2*	tillers/bunchgrass	1	9, 21
Elymus innovatus Beal	high	mod		4	creeping rhizomes	4	29
Festuca scabrella Torr	erratic	mod	low	2	short rhizomes	1	12, 21
Festuca idahoensis Elmer	mod	mod		*2*	tillers/bunchgrass	1	2, 21
Juncus balticus Willd		mod		*2*	extensive rhizomes	8	20
Koeleria macrantha (Ledeb.) Schult	mod	mod		2	bunchgrass	1	24, 29
Poa pratensis L.	high	mod		4	long rhizomes	8	25, 27, 29
Stipa richardsonii Link		mod		2	bunchgrass	1	6

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[1] (1) Archibold 1980, (2) Bradley 1986, (3) Broderick 1990, (4) Coladonato 1993a, (5) Coladonato 1993b, (6) Esser 1992, (7) Hartnett and Bazzaz 1985, (8) Hickerson 1986, (9) Hohfield 1987, (10) Landhausser and Lieffers 1994, (11) Lieffers et al. 1993, (12) McMurray 1987, (13) Myerscough 1980, (14) Pavek 1992, (15) Reed 1993, (16) Remphrey et al. 1983, (17) Romme et al. 1995, (18) Rowe 1983, (19) Schmid and Bazzaz 1990, (20) Snyder 1992, (21) Stubbendieck et al. 1994, (22) Tesky 1992, (23) Tirmenstein 1987a, (24) Tirmenstein 1987b, (25) Uchytil 1993, (26) United States Department of Agriculture 1948, (27) Volland and Dell 1981, (28) Warwick and Black 1982, (29) Watson et al. 1980, (30) Winkler 1987

[2] See Fischer et al. (1996) for accessing sources cited from the Fire Effects Information System

Table 6-5. Summary of competitive ability of understory plants. Plant characteristics summarized from Looman and Best (1979), Porsild and Cody (1980), Moss (1983), Johnson et al. (1995) and other references cited. Parameters were estimated (shown in italics) where information was unavailable.

Species	Height (cm)	Height Class[1]	Shade Tolerance Class[2]	References[3, 4]
Low Shrubs				
Arctostaphylos uva-ursi (L.) Spreng.	7-10	3	3.	4, 16
Potentilla fruticosa L.	20-100	1	1'	12, 16
Forbs				
Achillea millefolium L.	30-70	2	2	15
Aster conspicuus Lindl.	20-100	1	2	9
Astragalus alpinus L.	5-30	3	2	
Epilobium angustifolium L.	30-200	1	2	6, 8, 10,16
Fragaria virginiana Duchesne	5-10	3	2	
Galium boreale L.	20-60	2	2	
Geum triflorum Pursh	20-40	2	2	
Lathyrus ochroleucus Hook.	30-100	1	2	16
Oxytropis deflexa (Pall.) DC.	10-40	2	2	16
Smilacina stellata (L.) Desf.	15-60	2	2	
Solidago canadensis L.	30-90	1	3	3
Thalictrum venulosum Trel.	20-70	2	2	
Vicia americana Muhl.	30-100	1	1	2, 6

Table 6-5 (cont'd). Summary of competitive ability of understory plants. Plant characteristics summarized from Looman and Best (1979), Porsild and Cody (1980), Moss (1983), Johnson et al. (1995) and other references cited. Parameters were estimated (shown in italics) where information was unavailable.

Species	Height (cm)	Height Class[1]	Shade Tolerance Class[2]	References[3]
Graminoids				
Agropyron trachycaulum Link (Malte)	50-90	1	2	16
Bromus inermis Leyss.	20-100	1	1	16
Calamagrostis canadensis (Michx.) Beauv.	60-120	1	2	6, 16
Carex siccata Dewey	15-80	1	2	
Danthonia intermedia Vasey	5-50	2	2	11
Elymus innovatus Beal	50-100	1	2	16
Festuca scabrella Torr.	50-100	1	*3*	7
Festuca idahoensis Elmer.	30-80	1	3	1
Juncus balticus Willd.	10-60	2	2	
Koeleria macrantha (Ledeb.) Schult.	20-50	2	2	13, 16
Poa pratensis L.	30-100	1	2	14, 16
Stipa richardsonii Link	50-100	1	*1*	5

Height classes: 1 = high, 2 = moderate, 3 = low.

[2] Shade tolerance classes: 1 = high, 2 = moderate, 3 = low.

[3] (1) Bradley 1986; (2) Coladonato 1993b; (3) Coladonato 1993a; (4) Crane 1991; (5) Esser 1992; (6) Lieffers and Stadt 1994; (7) McMurray 1987; (8) Myerscough 1980; (9) Reed 1993; (10) Romme et al. 1995; (11) Stubbendieck et al. 1994; (12) Tirmenstein 1987a; (13) Tirmenstein 1987b; (14) Uchytil 1993; (15) Warwick and Black 1982; (16) Watson et al. 1980.

[4] See Fischer et al. (1996) for accessing sources cited from the Fire Effects Information System.

[5] Indicated as shade tolerant due to competitive ability as a shrub overtopping other understory plants.

Table 6-6. Summary of model criteria.

Parameter	Criteria		Equation
Shrub Submodel			
Population (plants ha^{-1})	$P_{t+1} = P_t (1-n) + g$		Chapter 5
	$P_t = S_t + M_t$		Ch. 5
Natural Mortality rate (yr^{-1})	$n = 0.005$		Ch. 5
Germination rate (plants ha^{-1} yr^{-1})	$g = 2500\,(1-TC^{a})$	for tsb^{b}<5	[1]
Maturation rate (plants ha^{-1} yr^{-1})	$m = g\,(1-n)^4$		Ch. 5
Seedling subpopulation (plants ha^{-1})	$S_{t+1} = S_t(1-n) + g - Sf$		Ch. 5
Mature subpopulation (plants ha^{-1})	$M_{t+1} = M_t(1-n) + g - Mf$		Ch. 5
Biomass (kg plant^{-1})	$B = 0.1393 \cdot tf \cdot MRf^{c} \cdot pbf$	if tsb= 1	Ch. 5
	$B_{t+1} = B_t + (0.0173 \cdot tf \cdot MRf \cdot pbf)$	if tsb > 1	Ch. 5
Total Biomass (kg ha^{-1})	$BT = B \cdot P$	if tsb > 0	Ch. 5
Cover Factor (proportion)	$cf = 1 - ((CT-5000) \cdot 0.0002)$	if CT > 5,000	Ch. 5
	$cf = 1$	if CT < 5,000	Ch. 5
Shrub Cover (m^2 plant^{-1})	$C_t = 1.9210 \cdot B_t \cdot cf$	if tsb= 1	[2]
	$C_{t+1} = C_t + (0.8439 \cdot B_t) \cdot cf$	if tsb > 1	[3]
Shrub Cover expansion rate (m^2 m^{-2} yr^{-1})	$SCe_t = (CT_t - CT_{t-1})/10,000$		[4]
Total Shrub Cover (m^2 ha^{-1})	$CT = C \cdot P$		Ch. 5
Temperature Factor (proportion)	$tf = 1 - ((AST^{c} - 12.13°C) \cdot 0.044\ °C^{-1})$		Ch. 5
Seedling Fire Mortality (plants ha^{-1})	$Sf = S\,(0.047\,e^{(.5068(DOB))})$		Ch. 5
Mature Fire Mortality (plants ha^{-1})	$Mf = M\,(0.0487\,e^{(.3020(DOB))})$		Ch. 5
Previous Burn Factor (proportion)	$pbf = 1 - (0.5 \times (1 - (PB^{d}/10)))$	if PB<10	Ch. 5
	$pbf = 1$	if PB>9	Ch. 5

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^{a} TC = total plant cover (m^2 m^{-2}); ^{b} tsb = time since burn (yrs); ^{c} AST = average (daily) summer temperature for June, July and August (°C). ^{d} PB = time since previous burn (yrs).

Table 6-6 (cont'd). Summary of model criteria.

Parameter	Criteria	Equation
Moisture Regime factor (dimensionless)	MR[c]-2: Mrf = 0.4 MR-3: Mrf = 1.0 MR-4: Mrf = 0.75 MR-5: Mrf = 0.5 MR-6: Mrf = 0.2	Ch. 5
Understory Submodel		
Understory Cover ($m^2\ m^{-2}$)	$UC_{i(t)} = UC_{i(t-1)} + CE_i - CD_i$	[5]
Growth factor (dimensionless)	Gf_i = 0.5 (low), 0.75 (mod) or 1 (high) see Table 1	
Fire Survival factor (dimensionless)	$FS = 1 - (0.05e^{a DOB_i})$ a = 1.5 (shallow), 0.6 (mod), see Table 3 0.3 (deep) or 0.15 (very deep)	[6]
Cover Expansion ($m^2\ m^{-2}$)	$CE_{i(t)} = a \cdot FS_i \cdot UC_{i(t-1)}$ for tsb=1 a = 1 (forbs, low shrubs), 0.67 (cool-season graminoids and spring fire), 0.8 (other graminoids and season of burn) $CE_i = E_i + S_i$ for tsb>1	[7] [13]
Expansion factor (dimensionless)	$Ef_{EpiAng} = 8\,(1-TC)$ Ef_i = 1 (low), 4 (mod) or 8 (high) see Table 4	[8]
Potential Expansion ($m^2\ m^{-2}$)	$PE_i = (Ef_i/8) \cdot UC_{i(t-1)} \cdot Gf_i \cdot tf_i$	[9]
Expansion ($m^2\ m^{-2}$)	$E_i = (PE_i/\sum PE_{i..n}) \cdot (1-(TC+SCe))$	[10]
Seeding factor (dimensionless)	$Sef_{EpiAng} = 4e^{(-0.05\,OM\ Depth)}$[d] Sef_i = 1(low), 2 (mod), or 4 (high) see Table 4	[11]
Seed Ingress ($m^2\ m^{-2}$)	$S_i = (Sef_i/\sum Sef_{i..n}) \cdot (1-(TC+SCe+\sum E_{i..n})$ for tsb<5	[12]
Competition factor (dimensionless)	shade class 1: Cof_i = 0.01 see Table 5 shade class 2, height class 1: Cof_i = 0.025 height class 2: Cof_i = 0.05 height class 3: Cof_i = 0.1 shade class 3, height class 1: Cof_i = 0.05 height class 2: Cof_i = 0.1 height class 3: Cof_i = 0.2	
Cover Decrease ($m^2\ m^{-2}$)	$Cd_i = ((UC_i/\sum UC_{i..n}) \cdot SCe)+(Cof_i \cdot UC_i \cdot TC)$	[14]

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[c] MR = moisture regime; [d] OM Depth = Organic Matter Depth.

Table 6-6 (cont'd). Summary of model criteria.

Parameter	Criteria	Equation
Biomass/Fuel Submodel		
Shrub Growth (kg m^{-2} yr^{-1})	$SG = ((BT_t - BT_{t-1})/10.000) + (CE_{postFire} \cdot 0.98)$	[15]
Understory Growth (kg m^{-2} yr^{-1})	$UG = \sum UC_{1-n} \cdot$ Max UP[a] $\cdot e^{-0.0102(tsb)}$	[16]
Stem Dieback (kg m^{-2} yr^{-1})	if no fire: $0.05 \cdot SG$ if fire: $0.8 \cdot BT/10.000$	
Leaf Fall (kg m^{-2} yr^{-1})	$0.04 \cdot BT/10.000$	
Understory Dieback (kg m^{-2} yr^{-1})	if no fire: UG if fire: $0.05 \cdot UG$	
Overwinter Litter Decomposition (kg m^{-2} yr^{-1})	$0.04 \cdot SL$[b]	
Duff Respiration (kg m^{-2} yr^{-1})		
	$Rd=SL \cdot ((SC \cdot 0.127)+((1-SC) \cdot (0.127+((0.253-0.127) \cdot e^{(-2(SLD^{c}/2))}))))$ for SLD<2cm	[17]
	$Rd=SL \cdot ((SC \cdot 0.127)+((1-SC) \cdot (0.127+((0.253-0.127) \cdot e^{(-1)}))))$ for SLD>2cm	[18]
Litter Respiration (kg m^{-2} yr^{-1})	$0.07 \cdot SL$	
Litter to Duff Decomposition (kg m^{-2} yr^{-1})	$0.65 \cdot SL$	
Dead Stem Decay (kg m^{-2} yr^{-1})	$0.025 \cdot$ Dead Stem Biomass	
Biomass Consumption during Fire (kg m^{-2})		
Litter	SL	
Duff	DBD $\cdot$ Duff Bulk Density	
Dead Stems	DSC $\cdot$ Dead Stem Biomass	
Understory	$0.95 \cdot UG$	
Shrub	$0.2 \cdot BT/10.000$	

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[a] Max UP = Maximum Understory Productivity (kg m^{-2}); [b] SL = Surface Litter Biomass (kg m^{-2}); [c] SLD = surface litter depth (cm).

Table 6-6 (cont'd). Summary of model criteria.

Parameter	Criteria	Equation
Fire Submodel		
Fire Rate of Spread (m min^{-1})	$ROS = 250 \cdot (1 - e^{(-0.0350 ISI^{j})})^{\text{[illegible]}}$	[19]
Duff Moisture Content (%)	$Duff\ MC = 20 + e^{(DMC^{k} - 244.72)/-43.43}$	[20]
Duff Burn Depth (cm)	$DBD = Duff\ D^{l} \cdot ((83.7 - 0.426 \cdot Duff\ MC)/100)$	[21]
Total Depth of Burn (cm)	DOB = Litter Depth + DBD	
Dead Stem Consumption (dimensionless)	$DSC = 0.04 \cdot BUI^{m}$	
Fire Intensity (kW m^{-1})	$I = h^{n} \cdot TFC^{o} \cdot ROS$	[22]

[j] ISI = Initial Spread Index; [k] DMC = Duff Moisture Code; [l] DuffD = duff depth (cm); [m] BUI = Buildup Index; [n] low heat of combustion (kJ kg^{-1}); [o] TFC = Total Fuel Consumption.

Table 6-7. Comparison of adjusted species cover (%) field data with model predictions.

	7 Mile Flats				Brazeau		
		Actual	Predicted			Actual	Predicted
1986	*Achillea millefolium*	3.5	4.2	1989	*Achillea millefolium*	2.1	3.7
	Aster conspicuus	6.3	4.5		*Aster conspicuus*	1.0	7.1
	Astragalus alpinus	2.0	0.4		*Astragalus alpinus*	0.4	1.4
	Fragaria virginiana	1.1	0.6		*Fragaria virginiana*	2.8	3.1
	Geum triflorum	6.4	11.3		*Galium boreale*	2.6	8.5
	Thalictrum venulosum	1.7	0.1		*Geum triflorum*	0.7	1.4
	Carex siccata	14.9	13.3		*Lathyrus ochroleucus*	0.8	1.0
	Festuca scabrella	40.0	38.5		*Oxytropsis deflexa*	2.8	2.0
1988	*Achillea millefolium*	9.3	5.2		*Potentilla fruticosa*	0.2	0.9
	Aster conspicuus	8.5	8.1		*Smilacina stellata*	0.3	0.5
	Astragalus alpinus	4.4	0.5		*Thalictrum venulosum*	5.1	7.9
	Fragaria virginiana	3.7	0.8		*Vicia americana*	0.6	2.1
	Geum triflorum	6.6	11.2		*Agropyron trachycaulum*	9.9	14.9
	Thalictrum venulosum	4.7	0.1		*Bromus inermis*	0.9	5.2
	Carex siccata	16.8	11.3		*Carex siccata*	6.1	6.1
	Festuca scabrella	30.5	26.7		*Poa pratensis*	0.2	0.1
1989	*Achillea millefolium*	8.9	7.2		*Stipa richarsonii*	0.0	2.5
	Aster conspicuus	10.4	16.9	1991	*Achillea millefolium*	7.4	4.5
	Astragalus alpinus	1.1	0.7		*Aster conspicuus*	13.9	12.1
	Fragaria virginiana	5.1	1.2		*Astragalus alpinus*	1.0	1.8
	Geum triflorum	11.2	12.0		*Fragaria virginiana*	6.5	3.7
	Thalictrum venulosum	0.8	0.2		*Galium boreale*	10.5	8.3
	Carex siccata	31.0	15.7		*Geum triflorum*	0.4	1.4
	Festuca scabrella	16.8	29.4		*Lathyrus ochroleucus*	3.4	1.3
1990	*Achillea millefolium*	8.5	7.1		*Oxytropsis deflexa*	0.0	2.0
	Aster conspicuus	9.1	18.0		*Potentilla fruticosa*	0.6	0.9
	Astragalus alpinus	6.8	0.7		*Smilacina stellata*	0.2	0.7
	Fragaria virginiana	1.7	1.1		*Thalictrum venulosum*	9.0	7.9
	Geum triflorum	9.3	11.5		*Vicia americana*	5.8	2.8
	Thalictrum venulosum	1.3	0.2		*Agropyron trachycaulum*	18.8	11.3
	Carex siccata	14.6	15.9		*Bromus inermis*	3.3	6.1
	Festuca scabrella	27.4	28.3		*Carex siccata*	14.3	5.0
					Poa pratensis	1.1	0.1
					Stipa richarsonii	0.8	1.6

Table 6-8. Summary of sensitivity analysis. Sensitivity factor values indicate the change in plant cover relative to change in the tested parameter at 30, 60 and 99 years in the simulation (all other parameters were held constant).

Parameter		Birch Shrubs			*Vicia americana*			*Calamagrostis canadensis*		
	Years	30	60	99	30	60	99	30	60	99
Average Seasonal Temperature		1.00	0.58	0.44	-0.36	-0.56	-0.83	-0.79	-0.78	-0.85
Moisture Regime Factor		1.05	1.15	1.00	-0.30	-0.63	-1.66	-0.51	-0.38	-0.62
Shrub Germination Rate		0.48	0.58	0.44	-0.21	-0.61	-1.09	-0.33	-0.58	-0.86
Shrub Fire Mortality Rate		0	0	0	0.04	0.10	0	0.05	0.10	0.16
Shrub Natural Mortality Rate		0	-0.19	-0.29	0.08	0.32	0	0.16	0.29	0.56
Shrub Density Factor		0.95	0.96	0.74	-0.71	-1.31	-1.97	-1.01	-1.21	-1.48
Shrub Canopy Expansion Rate		0.95	0.96	0.74	-0.71	-1.31	-1.97	-1.01	-1.21	-1.48
Shrub Biomass Productivity Rate		0.95	0.96	0.74	-0.71	-1.31	-1.97	-1.01	-1.21	-1.48
Depth of Burn		0	0	0	0.02	0.01	0.01	0.01	-0.01	-0.03
Duff Moisture		0	0	0.15	-0.07	-0.11	-0.16	-0.06	-0.07	-0.10
Duff Depth		0	0	0	0.01	0.01	0.02	0.01	0.01	0
Litter Depth		0	0	0	0.01	0.01	0.01	0.01	-0.01	-0.01
Leaf fall		0	0	0	0	0	0	0	-0.01	-0.01
Max. Understory Productivity		0	0	0	0.01	0	0.01	0.01	-0.01	-0.01
Total Shrub Biomass Production Rate		0	0	0	0	0	0	0	-0.01	-0.01
Litter to Duff Decomposition Rate		0	0	0	-0.01	0	0.01	0	0.01	0.01
Overwinter Litter Decomposition Rate		0	0	0	0	-0.01	0	0	0	0
Litter Respiration Rate		0	0	0	0	-0.01	0	0	0	0
Duff Respiration Rate		0	0	0	-0.01	-0.01	-0.01	0	-0.01	-0.01
Duff Moisture Code		0	0	0	0.07	0.08	0.12	0.01	0.02	0.04
Buildup Index		0	0	0	0	0	0	0	0	0
Initial Spread Index		0	0	0	0	0	0	0	0	0
Understory Expansion Rate		NA	NA	NA	1.01	1.54	1.94	1.22	1.95	2.77
Understory Seeding Rate		NA	NA	NA	0.16	0.15	0.14	0.10	0.09	0.09
Understory Fire Survival Rate		NA	NA	NA	0.05	0.10	0.14	0.05	0.09	0.14
Understory Competition Factor		NA	NA	NA	-0.22	-0.42	-0.61	-0.38	0.86	-1.47

Figures

Figure 6-1. Basic structure of the BORSHRUB model.

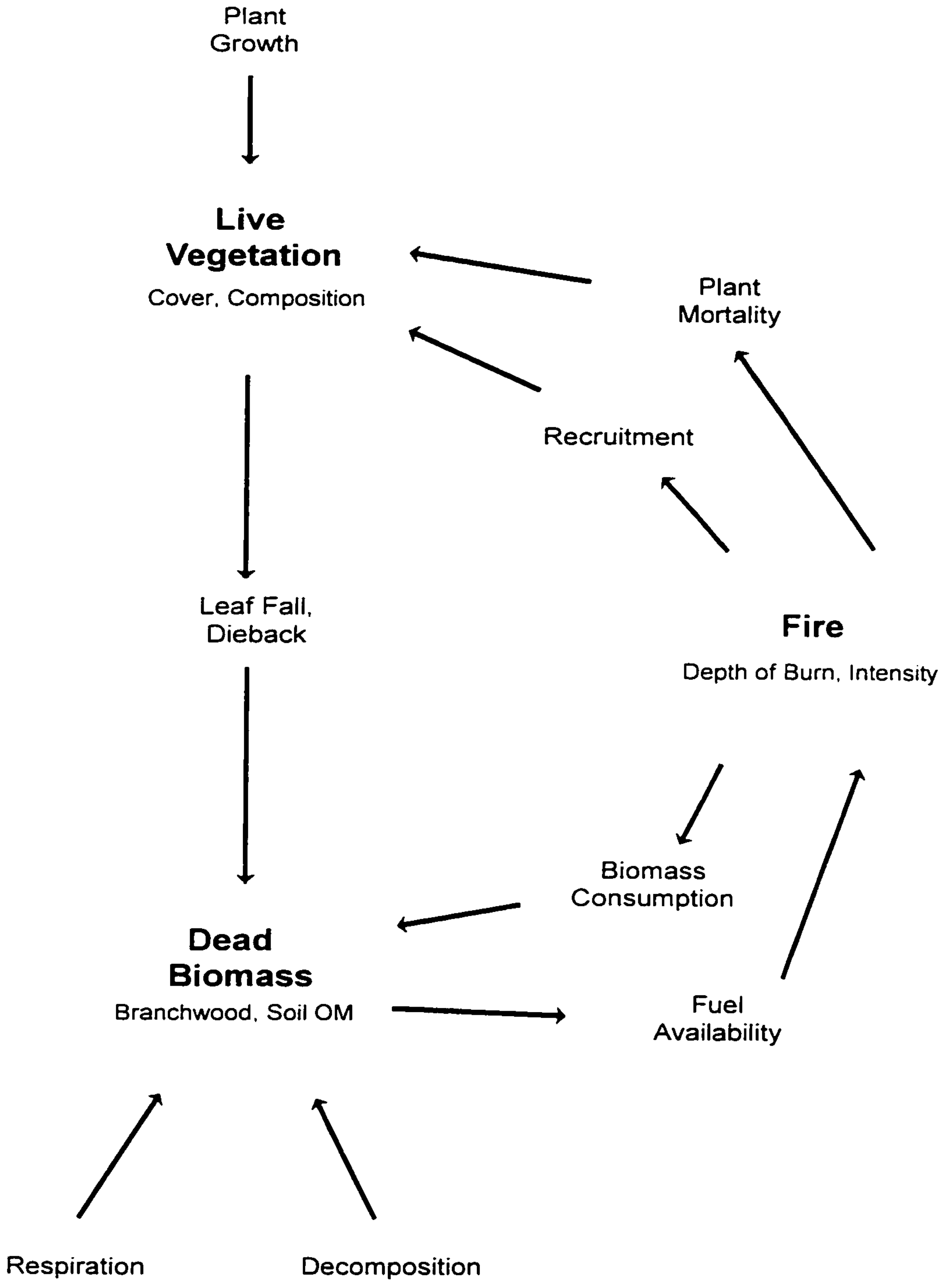


Figure 6-2. Flow chart of the BORSHRUB model.

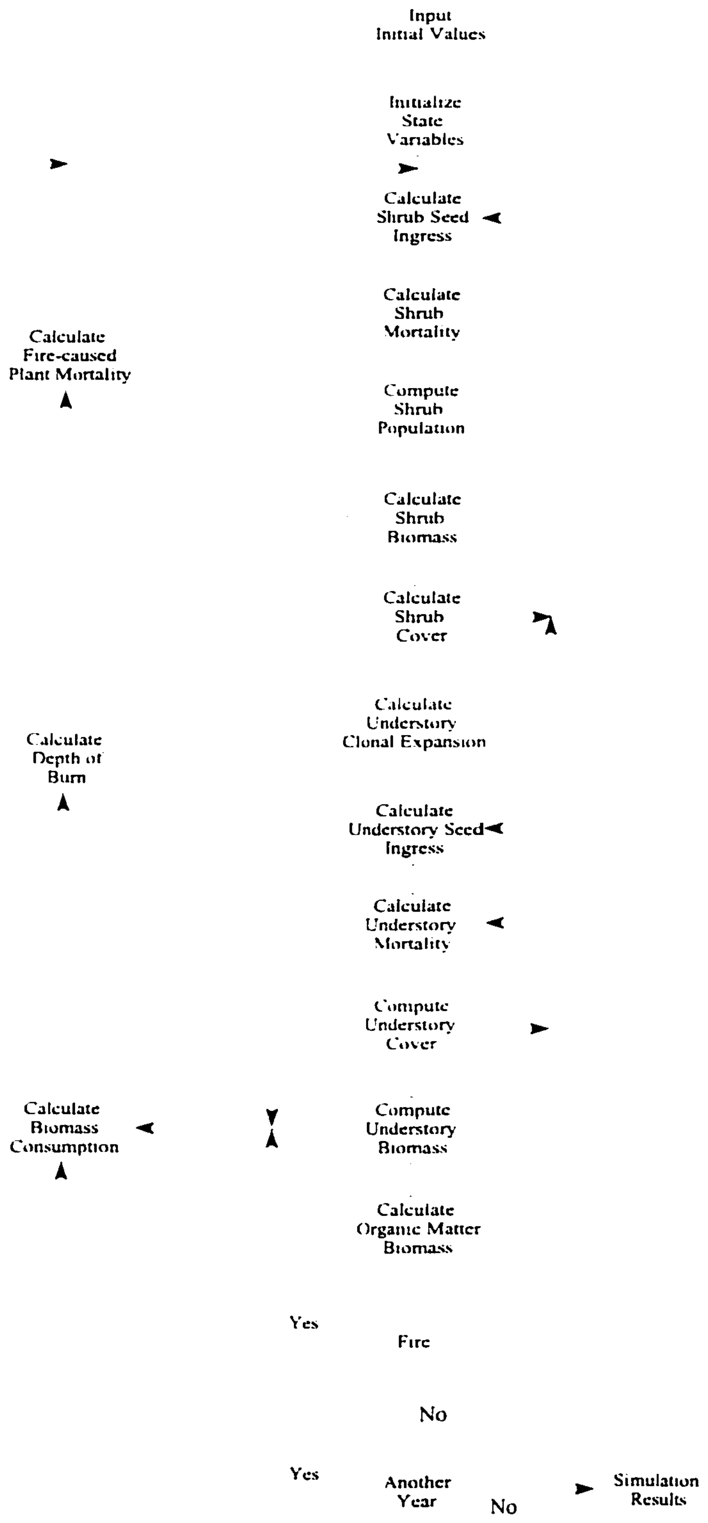


Figure 6-3. Comparison of actual and predicted cover by vegetation type in the 7 Mile Flats and Brazeau studies. Fires occurred in 1987 at 7 Mile Flats and in 1989 and 1991 at the Brazeau site.

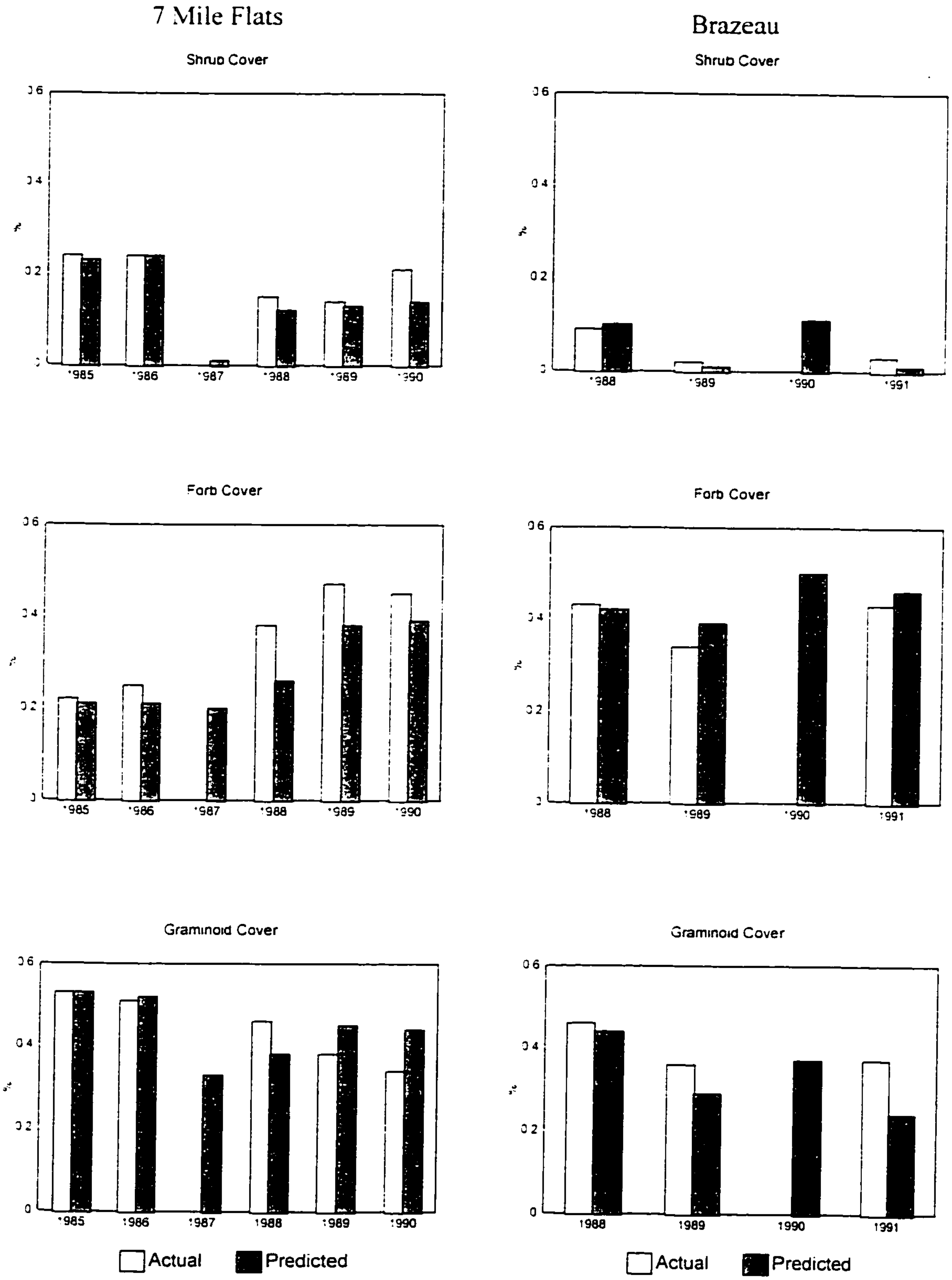


Figure 6-4. Comparison of adjusted actual and predicted cover for understory species in the 7 Mile Flats and Brazeau studies and line of best fit.

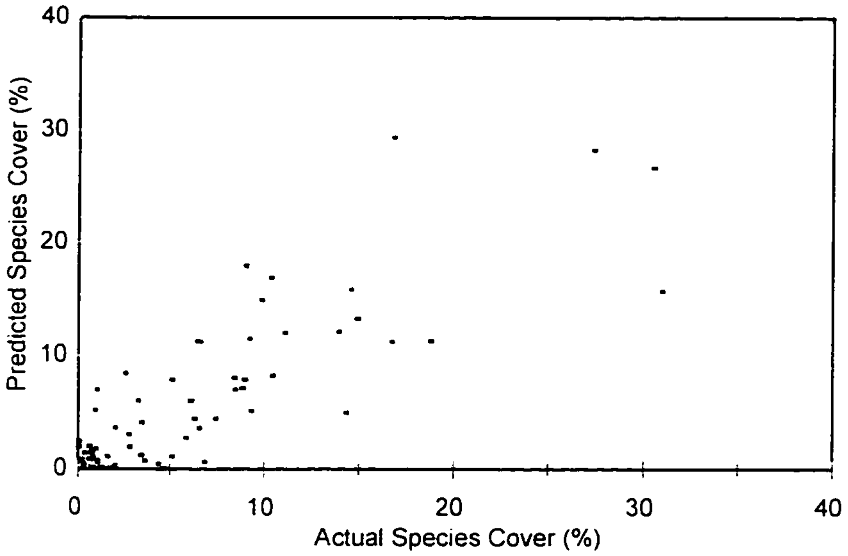


Figure 6-5. Examples of longterm model simulations. Graph 8a shows vegetation cover (left) and litter and duff depths (right) in the absence of fire. Graph 8b indicates cover, surface material depths and depth of burn for a 20-year fixed fire cycle; Graph 8c indicates the same for a stochastic 25-year fire cycle.

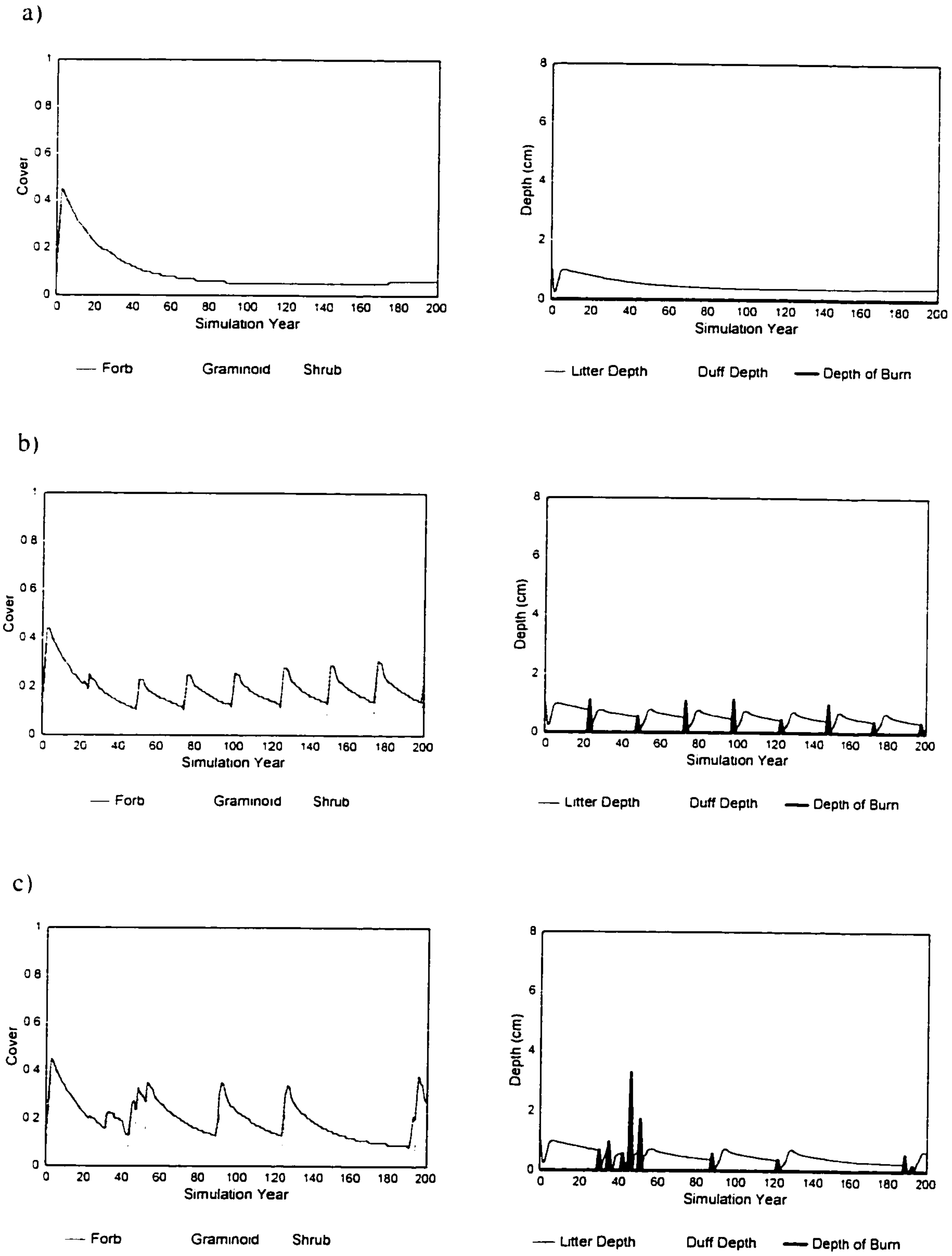


Figure 6-6. Shrub and understory species cover for a stochastic 10-year fire cycle. Data represesents an average of 30 model simulations using historical weather and burning conditions for Rocky Mountain House, Alberta. The indicated species are *Achillea millifolium* (AchMil), *Astragalus alpinus* (AstAlp), *Epilobium angustifolium* (EpiAng), *Fragaria virginiana* (FraVir), *Galium boreale* (GalBor), *Potentilla fruticosa* (PotFru), *Vicia americana* (VicAme), *Agropyron trachycaulum* (AgrTra), *Calamagrostis canadensis* (CalCan) and *Poa pratensis* (PoaPra).

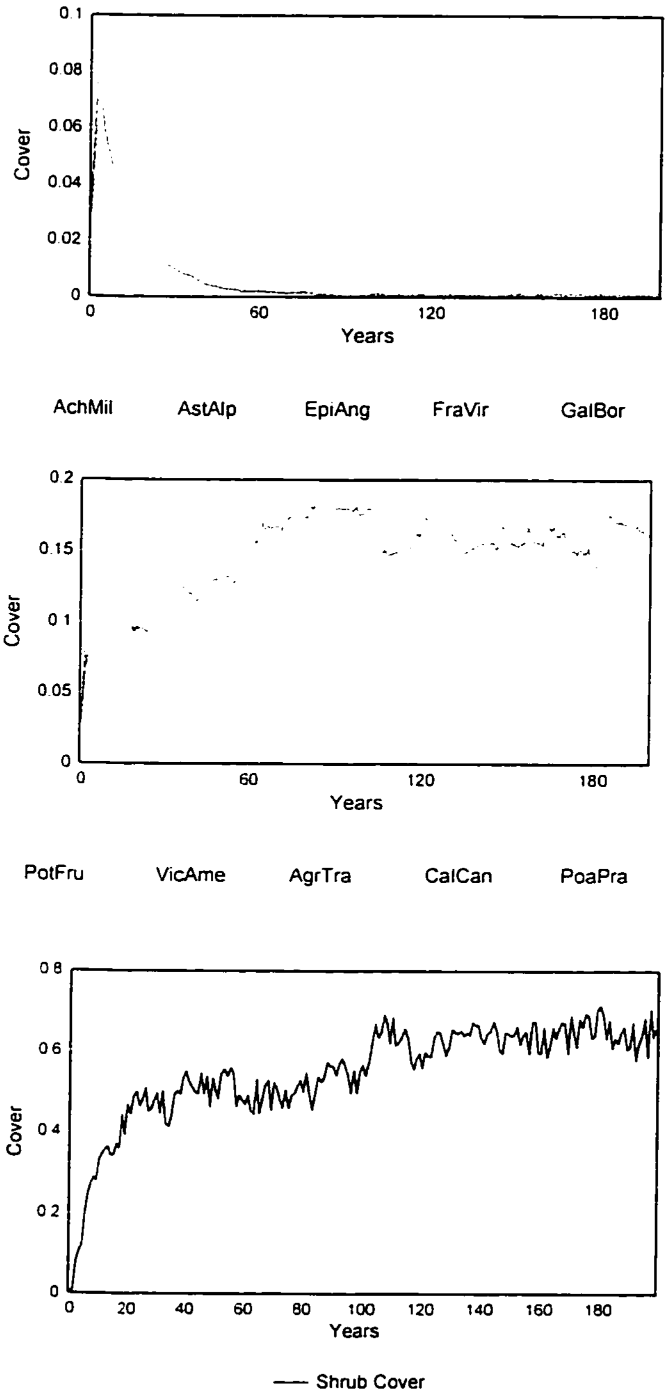


Figure 6-7. Shrub and understory species cover for a stochastic 25-year fire cycle. Data represesents an average of 30 model simulations using historical weather and burning conditions for Rocky Mountain House, Alberta. The indicated species are *Achillea millifolium* (AchMil), *Astragalus alpinus* (AstAlp), *Epilobium angustifolium* (EpiAng), *Fragaria virginiana* (FraVir), *Galium boreale* (GalBor), *Potentilla fruticosa* (PotFru), *Vicia americana* (VicAme), *Agropyron trachycaulum* (AgrTra), *Calamagrostis canadensis* (CalCan) and *Poa pratensis* (PoaPra).

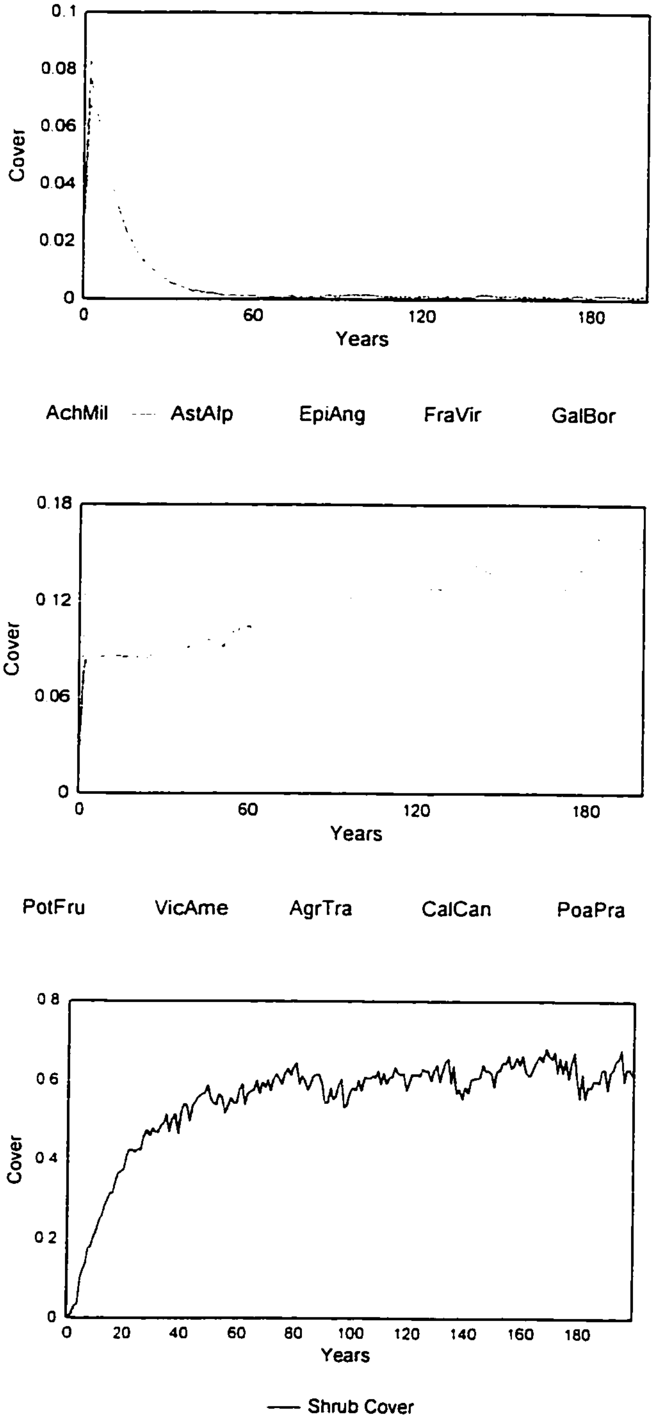
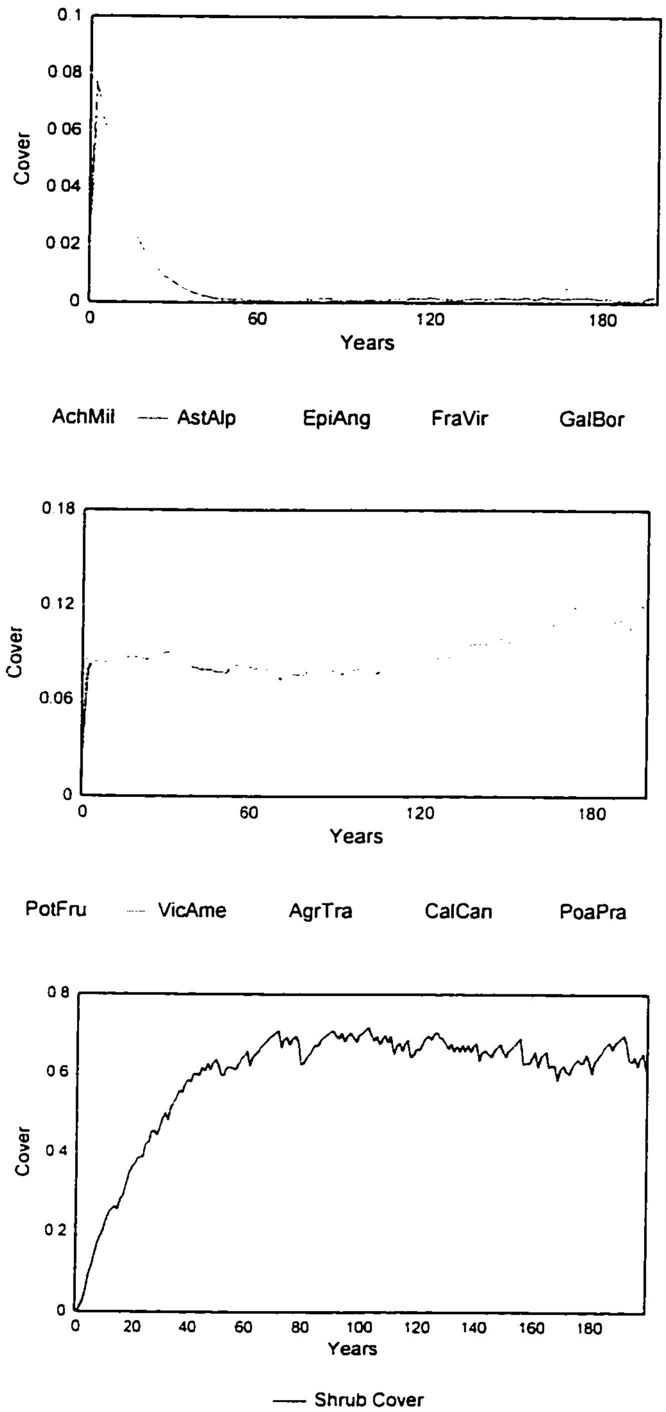


Figure 6-8. Shrub and understory species cover for a stochastic 50-year fire cycle. Data represesents an average of 30 model simulations using historical weather and burning conditions for Rocky Mountain House, Alberta. The indicated species are *Achillea millifolium* (AchMil), *Astragalus alpinus* (AstAlp), *Epilobium angustifolium* (EpiAng), *Fragaria virginiana* (FraVir), *Galium boreale* (GalBor), *Potentilla fruticosa* (PotFru), *Vicia americana* (VicAme), *Agropyron trachycaulum* (AgrTra), *Calamagrostis canadensis* (CalCan) and *Poa pratensis* (PoaPra).



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VII. Synthesis

Background

Betula glandulosa Michx. is an important northern species that dominates many plant communities in non-forested areas and is found scattered throughout the forested boreal, montane and subalpine regions. The habitat range of this plant is represented by 44.8 million ha of nonforest and 67.1 million ha of unproductive forest in the Forest and Barren sections of the Boreal Forest Region (Rowe 1972); 34.5 million ha of nonforest in the Predominantly Forest sections of the Boreal Region; and 10.6 million ha of unproductive forest in the northern tundra (Gray 1995). Altogether, *B. glandulosa* is found extensively across 30% of the Canadian forest landscape.

Management of *Betula glandulosa* with fire for improved forage production is an important wildlife habitat issue (Bork et al. 1996). Prescribed burning in Canada has steadily increased during the last decade with approximately 100-150,000 ha burned annually (Weber and Taylor 1992). Up to half of the total area is burned for wildlife habitat purposes. Although burning of *B. glandulosa* for wapiti habitat has been ongoing in Alberta for about 15 years, as well as more recently and much more extensively for bison habitat in the Northwest Territories (e.g., Gates et al. 1994), very little was known about the fire ecology of this species or the influence of fire regime on *B. glandulosa* populations.

Thesis experimentation

A critical knowledge gap in the fire ecology of *Betula glandulosa* was the immediate effects of fire on sprouting response. Resource managers were unsure if fire was stimulating increased plant growth, or whether spring or autumn burning resulted in the greatest reduction of growth and cover. The latter issue was in regard to the theory that spring burning would reduce new sprout growth because of reduced carbohydrate storage levels at leafbud flush, although autumn burning was expected to result in reduced population density and cover because generally drier soil conditions would cause greater plant mortality.

Few studies on plant response to fire severity and season of burn have been conducted. This study used a new technique to control heat pulse into the soil profile in order to test fire severity treatments. Previous studies have used variable surface fuel loads or surface fuel consumption as fire severity indicators although these factors may have little effect on heat penetration into the soil due to the strong influence of soil moisture content. This study also removed the effect of apical dominance on resprouting by using a clipped control treatment, a procedure not always used in previous studies. This ensured that sprouting in control plants would not be suppressed by hormone production in the stem apices, allowing the comparison of fire-induced sprouting in burned plants to normal sprouting in control plants (i.e., sprouting was unrestricted for both treatments).

The results of this experiment provide further understanding of how fire affects sprouting response. It was clearly identified that this plant possessed fire-stimulated growth response mechanisms including increased height growth, sprout production and aboveground biomass production during the first 1-2 years of growth. Spring burning caused the greatest increase in sprout production and height growth during the first year and it appeared to cause the greatest increase in height growth and aboveground biomass production after two years. These responses were only stimulated under the lowest severity burning treatment as increased severity caused reduced growth and sprouting response and greater mortality. Analysis of total nonstructural carbohydrate (TNC) levels after burning and clipping treatments showed that fire did not stimulate any change in TNC storage levels, although a significant change in TNC concentration can occur due to the season of treatment. This plant demonstrated a strong adaptive strategy for maintaining high overwinter TNC levels regardless of type or season of treatment (burning or clipping). All of these results are new findings about the effects of fire on *B. glandulosa*.

It was also apparent from this study that autumn burning is more successful at reducing *Betula glandulosa* cover than spring burning because soil moisture conditions are usually lowest in the autumn which results in greater plant mortality. There appears to be no advantage to burning at spring leaf flush when underground stored TNC levels are lowest because the plant is stimulated to increase growth rates and the depleted TNC reserves are quickly restocked for the following growing season. However, if the plant were subjected to more than one burning (or clipping) treatment within one growing season, then it may be possible to take advantage of low TNC levels in spring. If one treatment applied at leaf flush was followed by a second treatment shortly afterwards to remove the new sprouts before they restock the depleted TNC reserves, it may be possible to increase the mortality rate. Burning twice in succession is usually not a viable option due to a lack of fine fuels but two successive fires may be possible if the first burn is a very light surface fire (but continuous enough to induce complete topkill) and the second burn is conducted when the upper organic layer is drier. If this strategy is used, increased mortality should result even if fire severity is low, although greater severity of the second burn would further increase mortality.

The second experiment provided further clarification of the nature of fire-stimulated response in *Betula glandulosa* and the probable influence it will have on future populations under expected climate change conditions. It was hypothesized that fire response was a widespread characteristic of *B. glandulosa* and that greater height growth occurred under warmer growth temperatures. This study showed that fire response was widely distributed over the natural range of *B. glandulosa* in western and northern Canada. It also showed that warmer postfire growth temperatures significantly increased fire-stimulated height growth. In some cases, height growth response to fire was only detectable under warmer growth temperatures. Not all fire-prone populations showed a response to fire and this may have been caused by adaptation to typical postfire surface temperatures which are higher than those used in the experiment.

Betula glandulosa is expected to thrive and expand under predicted future climate change conditions because of its fire ecology. Increased fire activity will assist this plant to invade new areas, thereby increasing its abundance and expanding its range. Increased average growing season temperature will make it a more competitive species in the immediate postfire environment as warmer temperatures will induce increased sprouting response. At the southern extent of its present range in the aspen parkland region, fire is expected to be very influential on *B. glandulosa* populations as fire will limit the ability of aspen to expand onto rangelands.

Thesis models

The experimental components of this thesis were an examination of the immediate effects of fire on *Betula glandulosa*. The modelling studies were designed to examine the implications of fire regime on plant populations and community dynamics over longer time periods. The modelling process was used because the long time period required to study these impacts precludes practical field experimentation and control.

Shrub model

It was hypothesized that increasing fire severity and fire interval would decrease population density, cover and biomass because of higher mortality rates. In fact, the predicted dynamics between fire and population structure over time were much more complicated. For example, increasing fire interval caused sharply decreasing density (and increasing range between maximum and minimum density values between fire events), moderately increasing cover and strongly increasing biomass. Increasing fire severity had a minimal decreasing effect on cover and biomass and a significant decreasing effect on plant density, but the latter effect only occurred at short fire intervals. Increasing ambient air temperature was found to have a minimal decreasing effect on population density and a minimal increasing effect on cover and biomass. In contrast, soil moisture regime had a very strong influence on population parameters. Submesic sites had the lowest population densities and the highest cover and biomass levels. As sites became drier or wetter, density sharply increased and cover and biomass sharply decreased.

Although there is a lot of complexity in the model results. there were only a few basic principles driving these responses. First. population density changed inversely to cover and biomass change. For instance. on better growth sites (such as warmer temperatures or improved moisture regime) shrub biomass accumulated at a faster rate following fire while shrub cover also expanded at a faster rate. causing higher mortality of new seedlings due to increased competition. This resulted in lower population density.

Second. decreasing fire interval caused increasing population density because there was more frequent opportunity for seedling recruitment. The range between minimum and maximum density (representing density after fire and density after recruitment) decreased with shorter fire interval because the change in this range was a reflection of population decrease due to natural mortality (a constant annual rate) which is lessened due to the shorter amount of time between fire events. Maximum shrub cover and biomass decreased with decreasing fire interval because plants have a shorter time between fires for canopy expansion and biomass accumulation.

Last. increasing fire severity caused higher mortality rates and decreasing population densities. This effect was minimal at long fire intervals because fire events were less frequent but it was more influential at short fire intervals. However. the density range was greater for all fire intervals because of lower minimum density values that reflected greater fire mortality. Maximum population cover decreased with increasing fire severity at short fire intervals as a reflection of higher mortality rates. This effect became nonexistant at longer fire intervals because there was a longer time period for canopy expansion (canopies continued to expand until they reached a self-regulated equilibrium near 75-85% cover due to decreased expansion rates at higher cover levels). Total population biomass decreased slightly with increasing fire severity for all fire intervals because of decreased population density. Biomass was not a self-regulated parameter in this model (i.e.. shrubs continually accumulated biomass at a constant rate and did not reach an upper asymptote biomass value) so the effect of fire severity was constant over all fire intervals.

The literature provides very few studies on shrub growth dynamics in relation to fire. The model simulations indicate strong interrelationships between fire regime parameters and population characteristics that have not been previously reported. Each population characteristic (P) was found to be highly predictable ($r^2 = 0.96-0.99$) by fire interval (FI) over a wide range of site. temperature and fire severity conditions by $P = a + b$ (*ln* FI). In other words. the model indicates that shrub population structure (e.g., density, cover and biomass) is highly dependant on fire interval. This hypothesis suggests that the role of fire in wildland ecosystems may be a lot more substantial than previously thought. Van Wagner (1978) and Johnson and Gutsell (1994) showed that fire cycle (or frequency) promotes structure in the age-class distribution of forest stands within a landscape. The hypothesis put forth by this model suggests that fire interval also promotes structure in the physical characteristics within a stand.

Community model

The shrub model was further expanded to include other grassland species and a fuels submodel in order to study the dynamics of the entire plant community under different fire regimes. The simulations showed that postfire community succession was dependant on a number of interacting biological and environmental factors. In general. deep-rooted species had the highest fire survival rates which promoted an increase in their cover at high fire frequency while fire susceptible species tended to have greater cover at low fire frequency. However. this was also highly dependant on the expansion ability and competitive tolerance of the species. For instance. a high fire survival rate only resulted in an increased cover rate if the surviving plant was able to take advantage of the new area available for colonization by expanding quickly. Similarly. fire susceptible species only increased in cover at low fire frequency if they were also tolerant of competition because it was necessary to maintain itself in the community over long time periods.

The model also indicated the importance of fuels and depth of burn in community succession. Increased accumulations of duff resulted in reduced seedling establishment. Greater depths of burn promoted a higher rate of seed ingress due to reduced duff depth and reduced competition from resprouting plants because of higher mortality rates. Deeper burns promoted the greatest shift in species composition.

The simulations showed that community composition was also very important in assessing species cover because of interspecific competition. The ability of a species to maintain cover in any particular community was largely dependant on how its individual survival, expansion, seeding and competitive characteristics compared to other species in the community. Because of this, it was possible for one species to have different cover levels under the same fire regime if it occurred in communities of different composition.

The postfire community succession model illustrated the interactive effect of fire regime, species survival characteristics and species composition on community structure and indicated the complexity of shrub-grassland dynamics.

Fire ecology of *Betula glandulosa*

Fire-stimulated height growth, sprout production and aboveground biomass production in *Betula glandulosa* provides a competitive advantage over other plant species for at least the first 1-2 postfire years. This is a critical period of time as resprouting plants compete with invading species that are generally shade-intolerant, highly competitive pioneers. Increased height growth after fire in *B. glandulosa* provides an advantage for this shade-intolerant species so that it is not overgrown by competing species, while fire-stimulated sprout production and aboveground biomass production may also provide an advantage in spatial dominance or perhaps an increased photosynthetic surface area (see Wallace 1966 in Whelan 1995). The warmer soil surface temperatures that are typically associated with postfire microsites provide additional advantage to *B. glandulosa* by further enhancing fire-stimulated growth response. The combination of these traits provide *B. glandulosa* with strong ability to survive in an environment of periodic fire as a resprouting 'fire endurer' species (Rowe 1983). Fire-enhanced growth advantage is not believed to affect long-term growth rates or morphology. *B. glandulosa* is generally very dominant once established and this growth advantage is not necessary once it has reached that point. The advantage of warmer surface growing conditions also begins to decrease within several years after fire as the plant grows higher and as surface soil temperatures decline due to increased albedo, shading and litter accumulation.

Fire also provides an opportunity for the recruitment of new *Betula glandulosa* seedlings. On sites with high plant cover levels, *B. glandulosa* is deemed to be a fire dependant species because seedlings rarely become established without removal of competing vegetation and disturbance of soil to generally improve microsite conditions (such as reducing the litter layer). In this regard, *B. glandulosa* is considered a 'fire invader' species (Rowe 1983) because it produces a large amount of widely-disseminated seed that will colonize recently burned areas. Fire also appears to have the effect of removing the most susceptible plants from the population including old plants, young seedlings (less than 4-5 years old) and those that are under severe environmental stress (e.g., disease, herbivory, drought etc.). In this manner, fire assists to maintain the population in a healthy and vigorous condition.

Betula glandulosa is well-adapted to a very wide range of fire regimes. The strongest fire response appears to occur after spring and (to a lesser degree) autumn burning, the two seasons when these areas are most fire-prone. However, some form of fire-stimulated increase in either sprout growth or production occurs regardless of season. Therefore, *B. glandulosa* is well-adapted to fire regimes with different seasonal trends. The strongest fire response is also found after a low severity heat pulse into the soil. Summaries of long-term burning conditions (Harrington et al. 1983) in western and northern Canada indicate that low fire severity conditions (based on mean monthly Duff Moisture Code values of the Canadian Forest Fire Weather Index System) occur during a large majority of the fire season. This is especially true during the spring when soil moisture conditions are highest and fire response is greatest.

Betula glandulosa is also adapted to a wide range of fire intervals. Its lifespan (estimated at 100-150 years) is longer than most fire frequencies (see Heinselman 1981) on sites within its forested range. The model simulations suggest that short fire intervals promote an increase in population density (because of more opportunity for seedling recruitment) which results in a high level of canopy cover. Although long fire intervals promote a reduced population density, it also provides more time for each individual plant to grow to a larger size. This also allows the development of an extensive canopy cover. Therefore, *B. glandulosa* can be found with high cover levels under all fire intervals.

It appears that a *Betula glandulosa* population could only become locally extinct under a few fire regime scenarios. The first situation is a very short fire interval of 3 years or less because fire would effectively remove all new seedlings from the population while older plants slowly died out, although this would have to occur continuously for a long period of time. The second scenario is a fire interval that was longer than the plant lifespan, thereby providing no opportunity for seedling establishment until all local plants had died. Even in this situation, fire would eventually occur and re-colonization would be promoted by widespread seed dispersal from other areas. Therefore, local extinction would only be temporary. Neither of these two scenarios is very likely to occur.

A last possibility of local extinction exists for *Betula glandulosa* growing on peatbogs where fire is relatively infrequent due to high soil moisture levels. These sites may become dry after a lengthy period of drought (i.e., several years) and allow fires to become deep burning. On these sites, plants are completely rooted in organic material and mortality can be extensive if not complete. The frequency of occurrence for these conditions is low but they have happened in recent times (such as the early 1980's in the western Northwest Territories). Again, local extinction may only be temporary until conditions are suitable for the establishment of new seedlings.

In general, the possibility of local population extinction due to fire is rare. Because this plant annually produces a high number of seeds that are primarily wind-distributed over snow cover, it has the potential to spread across large areas very quickly. As well, fire rarely removes all plants in a local population because individuals often survive within unburned islands or near the fire boundary where burning is discontinuous and erratic. Therefore, new seed is virtually always available on previously occupied sites although conditions must be right for *B. glandulosa* seedlings (which are very shade-intolerant and drought sensitive) to become established. Populations are also expected to continue to thrive and expand in the future under expected climate change conditions due to increased rates of fire activity and warmer postfire growing conditions.

Management implications

The results of this thesis indicate that it is possible to manipulate *Betula glandulosa* with fire in order to meet certain management objectives. However, there is a limit to the range of changes that can be made to a population. It is not realistically possible to completely remove *B. glandulosa* by fire on most sites because it is either rooted in mineral soil or because deep organic soil sites are usually too wet. Very short fire intervals (e.g., every three years) would eventually cause population decline but it would have to be continued for many years and it is doubtful that surface fuel load buildup between fires would be sufficient. If *B. glandulosa* is presently on a site, it will likely remain as a member of that community.

Although *Betula glandulosa* cannot be removed by fire, populations can be managed by fire. Autumn burning will result in the greatest mortality, but frequent burning is the most important factor for cover reduction. Distributing burns over all burn units of a management area (as opposed to burning only a few units many times) will result in the greatest reduction in shrub cover. Increasing the amount of annual area burned will obviously decrease the total cover for the managed area, but the greatest reward in cover reduction is realized by increasing the annual area burned to about 3-4%.

There has been much discussion by land managers in regards to fire exclusion and increases in shrub populations. Many believe that fire exclusion (which has arguably been effective for only about 30 years) results in a vegetative condition that will take many centuries to return to a 'natural' state (if at all possible). In terms of population structure, the shrub model indicates that there is no support for this theory. In fact, the model indicates that population characteristics quickly return to conditions found in a 'natural' fire regime simply by applying a 'natural' fire interval (usually achieved within 3-4 equally spaced fire events).

Shrub populations have also been described as expanding and encroaching in grasslands by comparison of present and historical conditions. This is usually attributed to fire exclusion, and to a certain degree it is true because individual plants grow larger between fire events that are spaced farther apart in time. However, populations do not increase in density or encroach onto new areas without disturbance. Interpretation of historical descriptions must be careful because they are only a snapshot in time and do not indicate changes in population structure or the reasons for change by themselves.

Conclusion

In summary, the results of this study on the fire ecology of *Betula glandulosa* indicate that its two fire-adaptive strategies as a resprouting fire endurer and a seed-dispersing fire invader make it a very stable plant community member. It is promoted by fire to increase growth and production rates in the postfire environment and is capable of surviving in a wide range of fire regimes. These characteristics have been found over a wide portion of its western and northern range on fire-prone sites. This evidence suggests that it will remain a prominent species in many plant communities despite potential changes in vegetation management policy, including prescribed fire and fire suppression. Operational burning programs may change the *B. glandulosa* population structure to achieve specific resource objectives, but this plant will continue to survive in these areas because of its wide adaptability.

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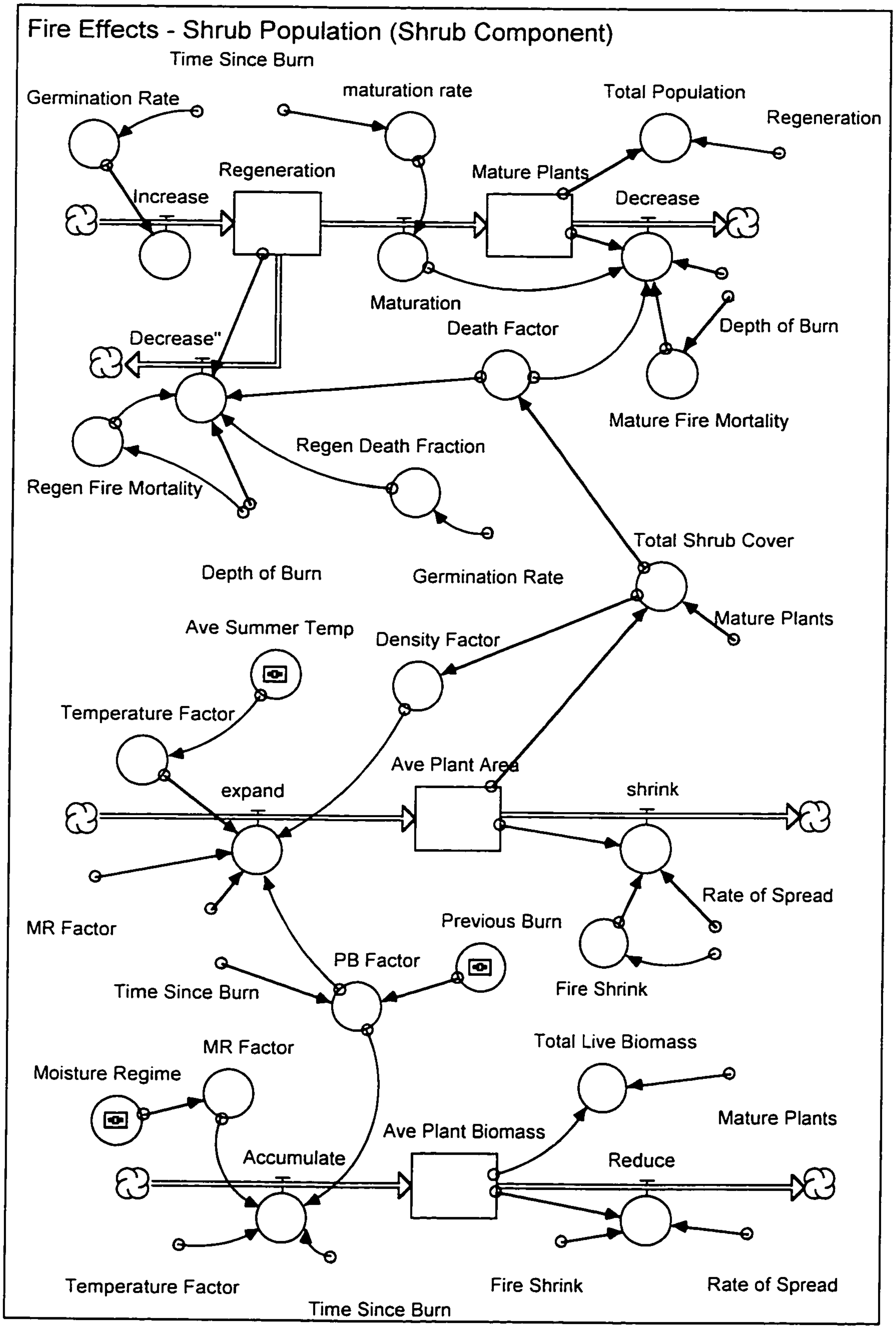
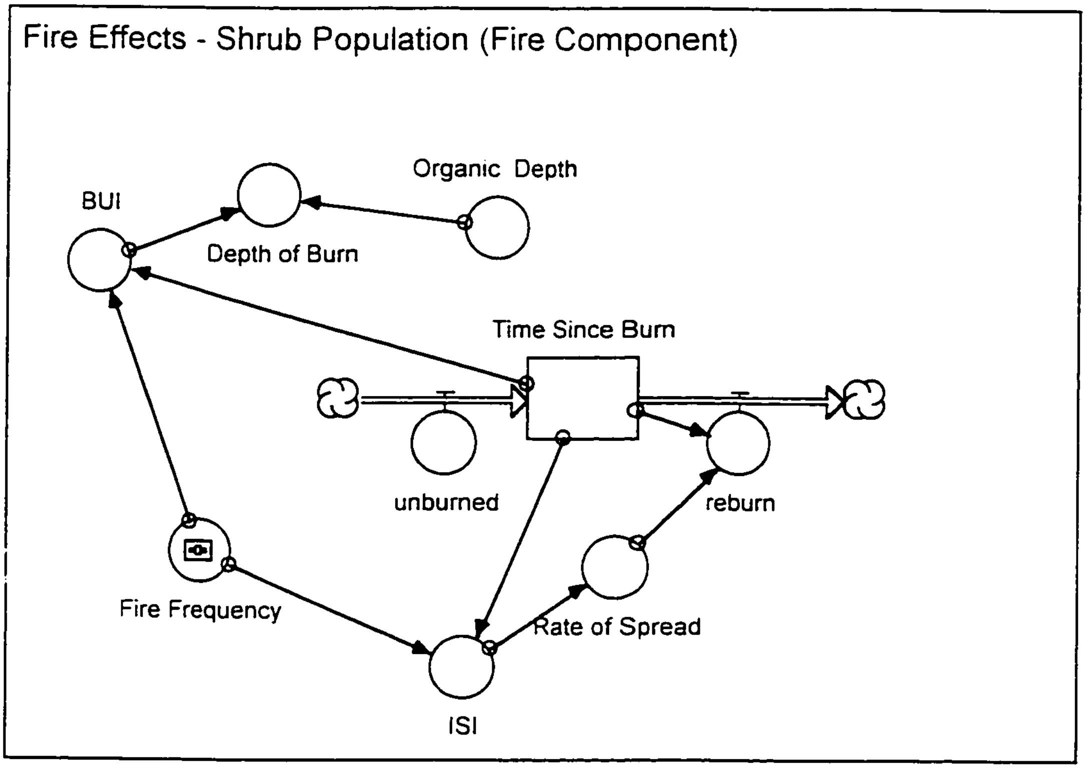
Appendix I

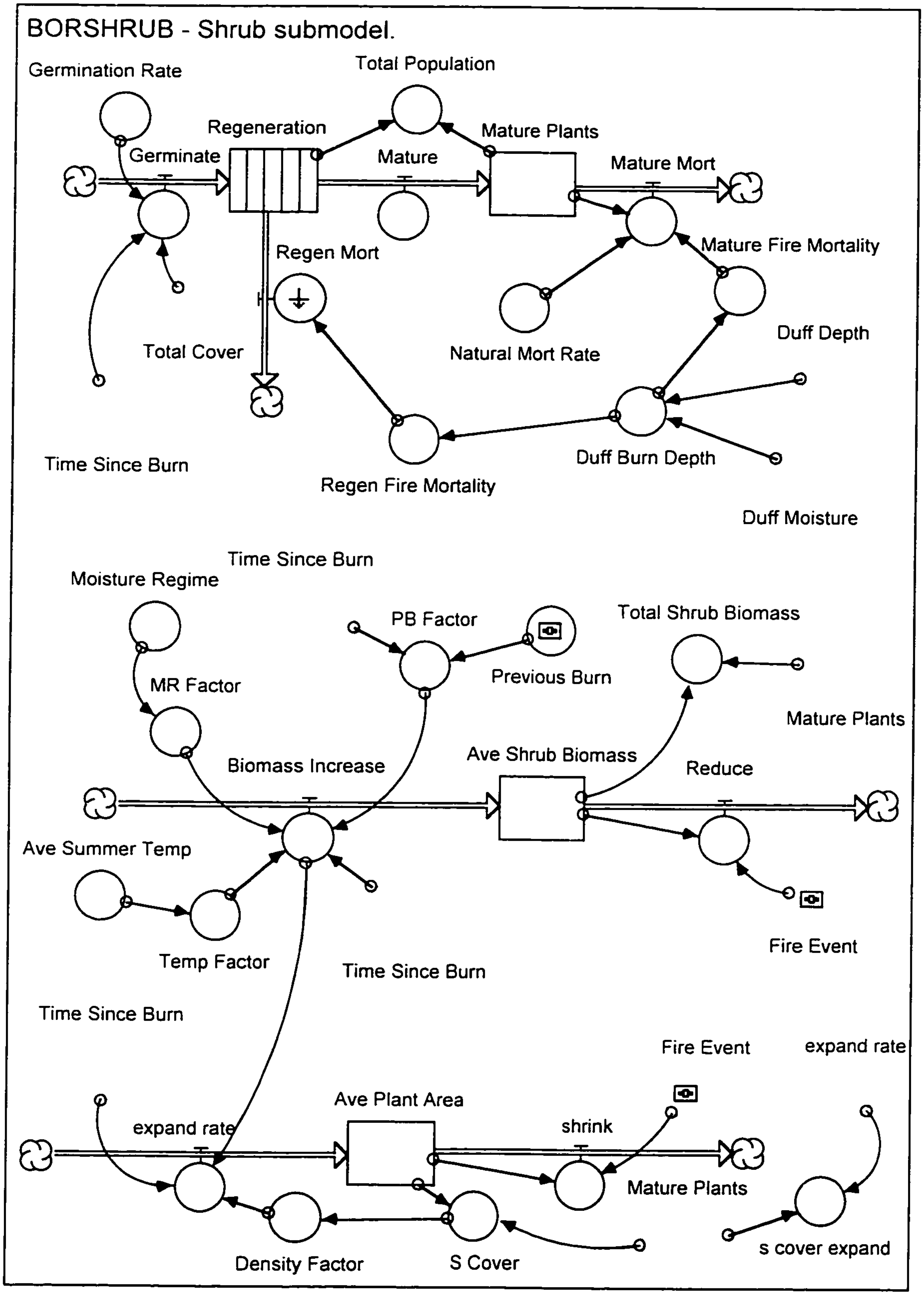
Detailed structure of the fire effects-population model
for *Betula glandulosa*

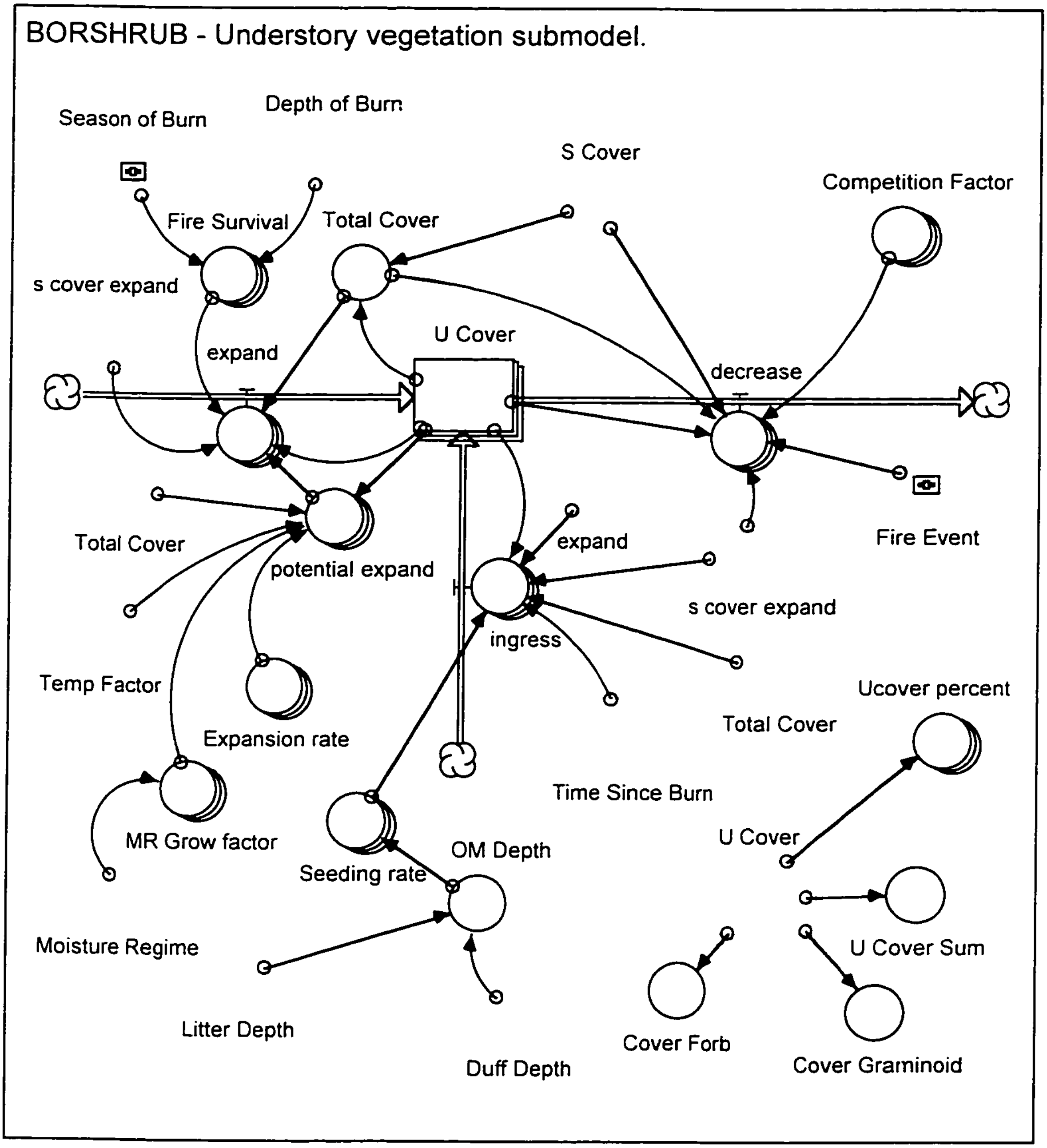

Fire Effects - Shrub Population (Shrub Component)


Fire Effects - Shrub Population (Fire Component)
Organic Depth
BUI
Depth of Burn
Time Since Burn
unburned
reburn
Fire Frequency
Rate of Spread
ISI

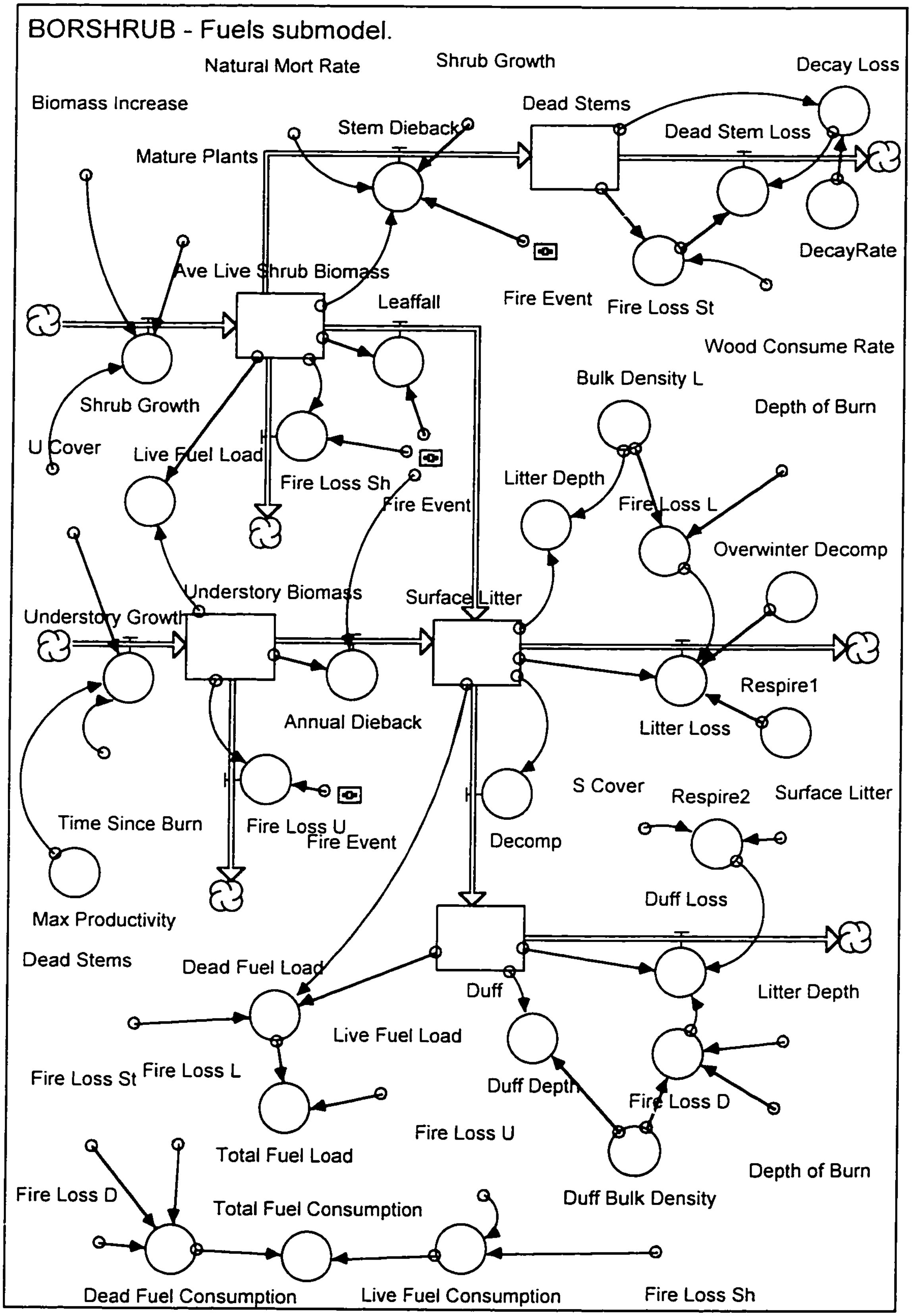
Appendix II

Detailed structure of the BORSHRUB model components

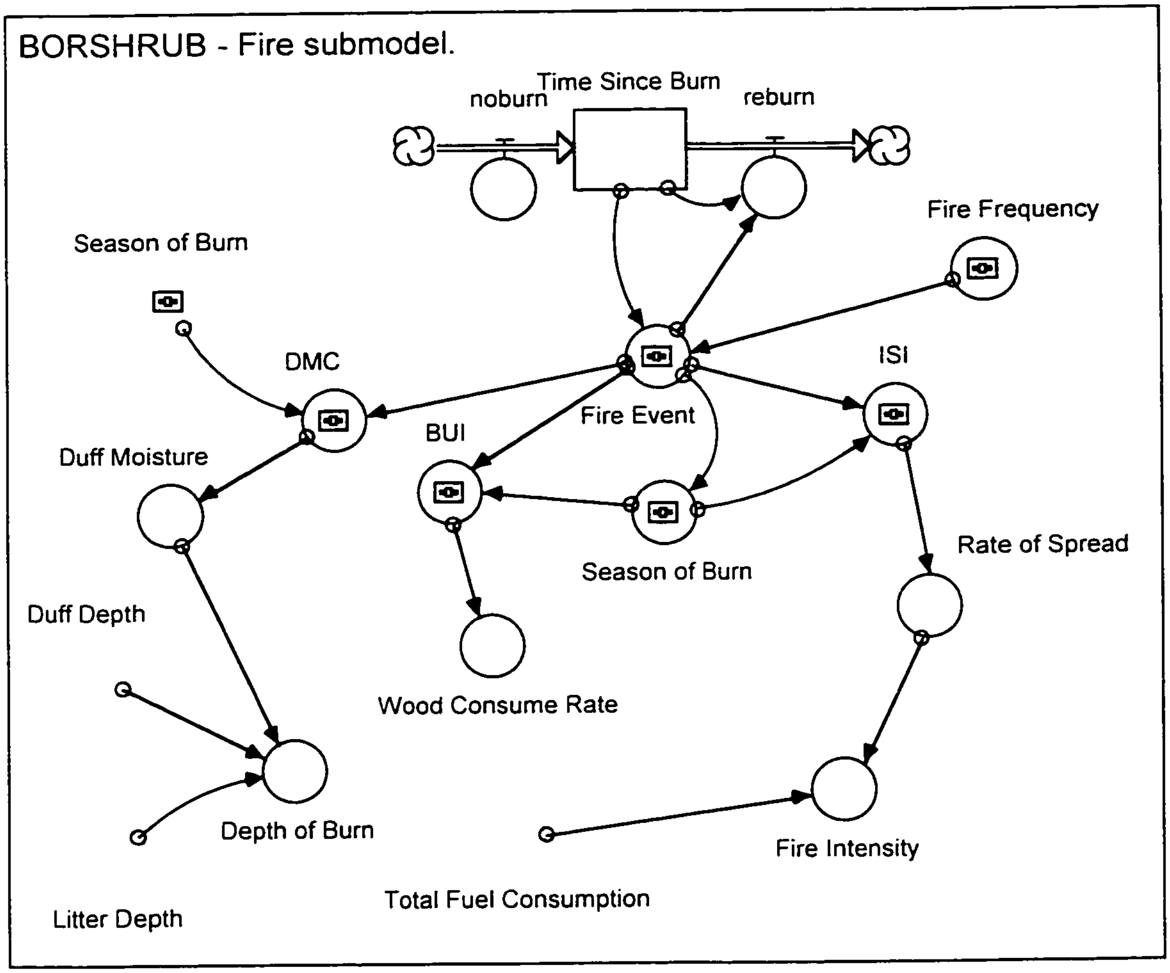

BORSHRUB - Shrub submodel.
Germination Rate
Total Population
Regeneration
Mature Plants
Germinate
Mature
Mature Mort
Regen Mort
Mature Fire Mortality
Duff Depth
Total Cover
Natural Mort Rate
Time Since Burn
Duff Burn Depth
Regen Fire Mortality
Duff Moisture
Time Since Burn
Moisture Regime
PB Factor
Total Shrub Biomass
Previous Burn
MR Factor
Mature Plants
Ave Shrub Biomass
Biomass Increase
Reduce
Ave Summer Temp
Fire Event
Temp Factor
Time Since Burn
Time Since Burn
Fire Event
expand rate
Ave Plant Area
expand rate
shrink
Mature Plants
Density Factor
S Cover
s cover expand



BORSHRUB - Understory vegetation submodel.

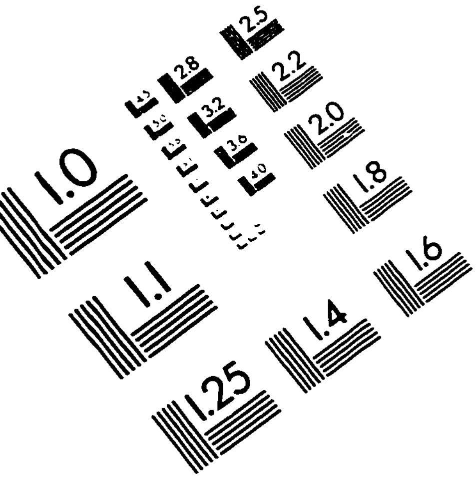


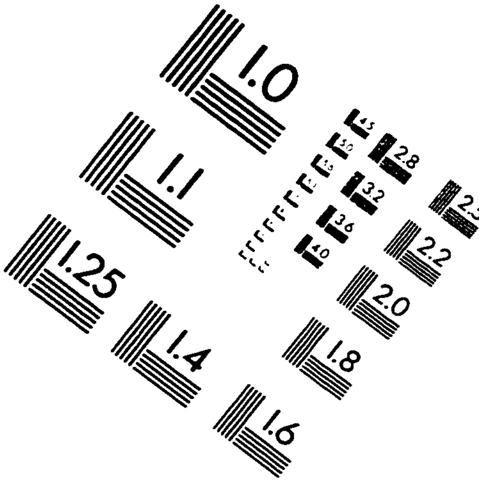
BORSHRUB - Fuels submodel.

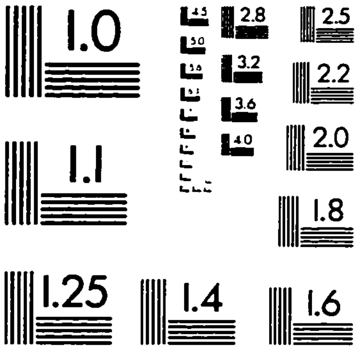


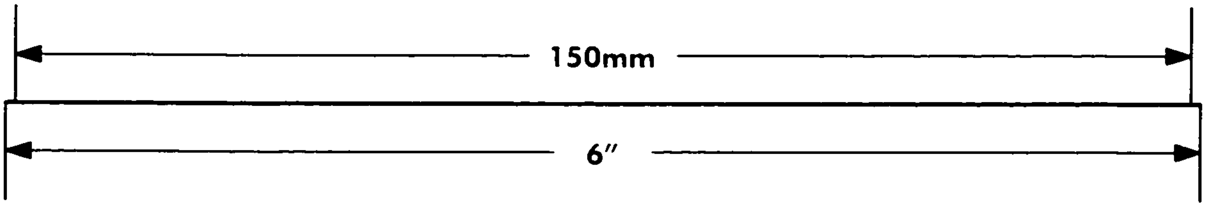
BORSHRUB - Fire submodel.

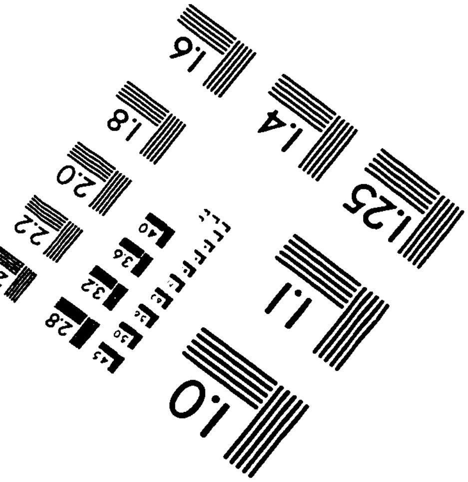
IMAGE EVALUATION TEST TARGET (QA-3)











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