University of Alberta

The post-fire successional ecology of mosses in boreal white spruce (*Picea glauca*) forests in north-central Alberta, Canada

By

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Abstract

The research described in this thesis examined aspects of the post-fire successional ecology of early and late successional mosses in the context of the 2001 Chisholm Fire in north-central Alberta, Canada. One year after fire the bryophyte community consisted mostly of ruderal species. In unburned stands outside the fire boundary the dominant bryophytes were *Pleurozium schreberi*, *Hylocomium splendens*, *Ptilium crista-castrensis* and *Plagiomnium* spp.. Total bryophyte cover and species in burned sites two years after the fire were positively correlated with GSM. Bryophyte cover was negatively correlated with litter cover. Data collected in two study sites over the first three years since fire suggested that acrocarpous mosses can be suppressed by *Marchantia polymorpha*.

Ash was apparently toxic to fragments of *Pleurozium schreberi* and *Ptilium crista-castrensis*. Fragment size also affected the survival and growth of fragments. Large, branched fragments were significantly more successful than small fragments (unbranched side-shoots) or miniature fragments (shredded pieces of leaf and stem). Small and miniature fragments of *Ptilium* were particularly poor propagules.

This thesis also describes a study into the potential for burned feather moss carpets to influence the establishment of white spruce, tamarack (*Larix laricina*), blue flax (*Linum lewisii*) and palmate-leaved coltsfoot (*Petasites palmatus*). Survival of tamarack seedlings was significantly reduced on burned feather moss.

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Of all the sections that I have had to write in this thesis, this one is perhaps the most worrisome. All of the other chapters involve science, and I am confident that any omissions will be amended by those who review this work. I cannot rely on them, however, to bring to my attention the name of anyone whose contribution to this project has not been recognized here. Hence, the first people that I must thank are those whose names I have forgotten to mention below. To those people I say, please be assured that while my memory may be lacking, my appreciation of your efforts definitely was not.

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TABLE OF CONTENTS

List of Tables

List of Figures

Chapter 1: General Introduction

Forest fires are the most frequent form of large scale natural disturbance in boreal spruce forests in Alberta, Canada. Natural succession following fire contributes to the floral diversity of the region because certain species are associated with particular successional stages. This is particularly true of the bryophyte community, which changes distinctly over the course of succession. The species assemblage in recently burned stands is almost completely different from that in old stands (*c.* 100 years). After a stand-replacing fire the community that establishes is typically dominated by acrocarpous ruderal mosses (*sensu* During 1979), including *Ceratodon purpureus* (Hedw.) Brid., *Polytrichum juniperinum* Hedw., *Funaria hygrometrica* Hedw., *Bryum argenteum* Hedw., *Leptobryum pyriforme* (Hedw.) Wils. and the hepatic *Marchantia polymorpha* L. (Rowe and Scotter 1973; Viro 1974; Foster 1985; Bradbury 2006). Species of late successional spruce stands are different in their morphology and ecology. The community is often dominated by the pleurocarpous feather mosses *Pleurozium schreberi* (Brid.) Mitt., *Hylocomium splendens* (Hedw.) BSG and *Ptilium crista-castrensis* (Hedw.) De Not, *Polytrichum commune* Hedw., *Plagiomnium* spp., *Dicranum* spp. and *Rhytidiadelphus triquetrus* (Hedw.) Warnst. may also be present (see, for example, Rowe and Scotter 1973; Foster 1985; Harmon 1989; Jonsson and Esseen 1990; Kershaw et al. 1994; Frego 1996; Johnston and Elliott 1996; Nygaard and Odegaard 1999, Nguyen-Xuan et al. 2000; Boudreault et al. 2002b; Bradbury 2006).

Little research has been conducted on bryophyte succession in spruce forests in Alberta, and the successional ecology of many boreal bryophyte species in is not well known. Bryophytes are important subjects for study, however, because they contribute to biodiversity and they can cover a high proportion of the forest floor in early and late successional stages. They also influence a variety of biotic and abiotic processes, including nutrient cycling (Skre at al. 1983; Weber and van Cleve 1984; Bayley et al. 1987 (all cited in Vitt 1990); Li and Vitt 1997; Syndonia Bret-Harte 2004; Sedia and Ehrenfeld 2005), decomposition and soil faunal activity (Garcia-Pausas et al. 2004), soil formation (Carter and Arocena 2000; Vitt 2000), and vascular plant establishment and growth (Steijlen et al. 1995; Nilsson et al. 1996; Hörnberg at al. 1997; Zackrisson et al. 1997; Kuuluvainen and Juntunen 1998; Kotorová and Lepš 1999; Hanssen 2003; Parent et al. 2003; Sedia and Ehrenfeld 2003; Van der Wal and Brooker 2004). Further studies on the successional ecology of bryophytes could lead to the development of a model of succession for boreal spruce forests in Alberta. This model could help efforts to emulate the effects of fire in human activities that remove forest cover, such as timber harvesting and oil and gas operations.

Previous studies of post-fire succession involving bryophytes

Several studies have described the bryophytes present in the earliest stages of post-fire succession, including Kimmerer and Allen (1982); Brasell and Mattay (1984); Hobbs and Gimingham (1984); Gloaguen (1990); Maltby et al. (1990); Esposito et al. (1999) and Bradbury (2006). In a study of constraints on moss establishment from spores on a severely burned North York moor, Maltby et al. (1990) found that *Ceratodon purpureus* was one of the first colonists of ash whereas burned peat was more frequently colonised by *Dicranella heteromalla*, *Pohlia nutans* and *Polytrichum* spp.. The authors concluded that these preferences were probably linked to pH tolerances and the concentration of water-soluble toxic substances. O'Toole and Synnott (1971) showed levels of calcium carbonate and phosphorous could influence species composition on peat.

Previous studies have also described bryophyte successions in fens, bogs and mires. Glime et al (1982) proposed a succession from an alkaline marsh in which *Drepanocladus revolvens* was the dominant moss to a *Sphagnum* bog. The ability of *Sphagnum* to invade, and the capacity for non-*Sphagnum* species to acidify the water, were thought to drive these changes. Fire frequency was identified as a determinant of the rate of accumulation of *Sphagnum* in peatlands in western boreal Canada by Kuhry (1994). Koojiman and Bekker (1995) found that nutrient enrichment and the mineral content of groundwater could influence changes in dominant species in interactions involving *Scorpidium scorpiodies*, *Sphagnum subnitens*, *Calliergonella cuspidata* and *Sphagnum squarrosum.* In other studies, Magyari et al. (2001) reconstructed succession in a bryophyte-dominated Holocene peat-bog and successional change in Swedish mires has been mapped by Gunnarsson et al. (2000 and 2002).

Research into bryophyte succession in forest systems is rare. Crites and Dale (1998) found that stand age and downed wood were important determinants of the composition of bryophyte assemblages in aspen mixedwood forests. Fenton and

Bergeron (2006) concluded that increasing light availability and the movement of the water table into the forest floor probably leads to the replacement of feather mosses by shade and desiccation tolerant hummock *Sphagnum* species in *Picea mariana* forests. In a study of the post-fire bryophyte community during the first and second growing season after the House River Fire in northeastern Alberta, Bradbury (2006) found differences in community composition and species richness in salvage logged sites compared with burned sites.

A model of succession in the boreal white spruce forest moss community

Fig. 1.1 provides a theoretical schematic of possible successional pathways for early and late successional mosses in a boreal white spruce forest. This schematic forms the basis for most of the research described in Chapters 2, 3 and 4 of this thesis. Each pathway should be viewed as representing a hypothesis concerning the importance of a given factor for driving successional change.

The model presented in Fig. 1.1 assumes that pioneer species will be rare in late successional stages and decline in abundance during succession. Based on the results of previous studies, it is expected that this decline will be preceded by changes in community composition and structure (O'Toole and Synnott 1971; Maltby et al. 1990; Esposito et al. 1999). These changes may be the result of interspecific competition among pioneer species (pathway 3), although competition has not been convincingly demonstrated in ruderal mosses and they are generally thought to be competition avoiders and (During 1979; Watson 1980; Grime et al. 1990; Rydin 1997; Slack 1997). On the basis of current evidence it seems more likely that changes in community structure are driven by abiotic factors (pathway 4). These include increases in shade (pathway 4a), humidity (4b); litter depth (4c) and soil organic matter (OM) content (4d), a decline in pH (4e) and changes in the concentration of nutrients in the soil (4f). These developments are associated with the rapid growth of vascular plants and the decomposition of litter, as well as leaching, chemical reactions in soil water and the presence of the mosses themselves (Armentano and Caponetti 1972; Rowe and Scotter 1973; Viro 1974; Rincon 1988; Carleton 1990; Thomas et al. 1994; Frisvoll and Prestø 1997; Bergamini et al. 2001; Garcia-Pausas et al. 2004; Wiklund and Rydin 2004; Aude and Ejrnæs 2005; Sedia and Ehrenfeld 2005; Légaré et al 2005).

An alternative hypothesis is that the decline of ruderal mosses results from interspecific competition with mosses that arrive in later successional stages (pathway 5). Competition among perennial bryophytes has been investigated in some communities (Rydin 1997; Bergamini et al. 2001; Mulligan and Gignac 2002) but has not been demonstrated in white spruce forests. Evidence for the ability of perennial pleurocarpous mosses to exclude small acrocarpous species can be inferred from studies that have shown that feather mosses can overgrow lichens (Sulyma and Coxson 2001) and dung mosses (Lloret 1991).

The failure of past studies to find late successional species in the early successional community suggests that their establishment is inhibited by unfavourable environmental conditions (pathway 1) or dispersal limitation (pathway 2). The former could include forest floor substrates that contain low amounts of organic matter, high levels of charcoal and potentially toxic compounds (pathway

1a; Scandrett and Gimingham 1989; Vitt 1990; Paré et al 1993; Thomas et al. 1994; Johnston and Elliot 1996; Kellner and Weibull 1998; Wardell et al. 1998; Kischuk 2003), a high level of exposure due to the absence of a tree canopy and the presence of other biota, such as ruderal mosses (pathway 1c). Dispersal limitation may be a result of the low incidence of sexual reproduction in some late successional mosses, particularly feather mosses (Longton and Greene 1979; Rydgren and Økland 2002). These species appear to prioritise vegetative reproduction, which is well suited to short-distance dispersal into gaps on the forest floor (Kimmerer 1994; Frego 1996). Long distance dispersal of vegetative diaspores may depend upon temporally and spatially constrained vectors such as snowmelt and large mammals (McDaniel and Miller 2000; Heinken et al. 2001).

Fig. 1.1 undoubtedly represents an oversimplified picture of succession in white spruce forests, not least because it focuses only on the communities that are widely known. Not all possible pathways it shows could be tested in the research described in this thesis, but it is hoped that the schematic will be useful to researchers who wish to expand upon the results of this project. Pathways 1 to 4 in Fig. 1.1 are considered in Chapters 1 and 2, pathways 4a to 4d will be considered in Chapter 2 and pathways 3 and 5 will be discussed in the context of the results obtained from the studies described in Chapters 3 and 4. Pathways 4e and 4f were not examined as part of this research.

Effects of bryophytes on succession in the vascular plant community

Studies on direct effects of bryophytes on succession in the vascular plant community are lacking in the literature. However, previous research has shown that bryophyte mats can affect the establishment potential of seed-dispersing plants. Bryophytes may thereby influence the dispersion of particular species and the species composition of a habitat patch. During and Van Tooren (1990) reviewed studies that have shown that seed dispersal into bryophyte carpets may result in increased or reduced germination rates, depending on the vascular plant and bryophyte species of interest. Due to the high cover of mosses on the forest floor in mature forests, and the economic value of these forests for timber, several studies have focused on the effects of mosses on the regeneration of tree species. Nilsson et al. (1996) reported that *Pleurozium schreberi* provided a favourable microclimate for regeneration of *Pinus sylvestris* after clearcutting and similar results were found for *Abies balsamea* in *Pleurozium* seedbeds (Parent et al. 2003) and for *Picea abies* (Hanssen 2002), *Picea glauca*, *Picea mariana* and *Pinus banksiana* (Charron and Greene 2002) in *Polytrichum* seedbeds. However, other studies have produced findings that contrast with these. Hörnberg et al (1997) found that emergence of *Picea abies* seeds was reduced in *Pleurozium* microhabitats and similar results were reported for *Pinus sylvestris* by Steijlen et al. (1995) and Zackrisson et al. (1997). Chapter 5 of this thesis describes a study of the hypothesis that the burned remains of feather mosses left by forest fires will also reduce the establishment potential of certain vascular plant species, with concomitant effects upon successional development.

Research objectives

This thesis contains a collection of studies into recolonisation by bryophytes after fire in white spruce (*Picea glauca* (Moench) Voss) forests in north-central Alberta, Canada. These studies were conducted in and around the boundaries of the 2001 Chisholm Fire. The objectives of this research were to (i) compare the species composition of burned and unburned forests in the study area, (ii) identify trends in moss cover and environmental variables in the first three years of succession; (iii) test hypotheses about factors controlling the timing of establishment of *Pleurozium schreberi* and *Ptilium crista-castrensis;* and (iv) test the hypothesis that the viability of vegetative fragments of *Pleurozium* and *Ptilium* varies among fragment sizes. To illustrate a link between bryophytes and succession in the vascular plant community, this thesis also includes a study of the effects of burned feather moss remains on seed germination and seedling survival and growth early in succession.

Nomenclature

In this thesis, nomenclature for vascular plants follows Moss (1996). Scientific names of bryophytes are consistent with ANHIC (2006) and authorities are taken from USDA (2007).

Literature Cited

Alberta Natural Heritage Information Centre (ANHIC). 2006. List of all bryophyte elements. Parks and Protected Areas Division, Alberta Community Development.

Armentano, T.V. and J.D. Caponetti. 1972. The effect of pH on the growth of protonemata of *Tetraplodon mnioides* and *Funaria hygrometrica*. The Bryologist **75**: 147-153.

Aude, E. and R. Ejrnæs. 2005. Bryophyte colonisation in experimental microcosms: the role of nutrients, defoliation and vascular vegetation. Oikos **109**: 323-330.

Bayley, S.E., D.H. Vitt, R.W. Newbury, K.G. Beatty, R. Behr and C. Miller. 1987. Experimental acidification of a *Sphagnum*-dominated peatland: first year results. Canadian Journal of Fisheries and Aquatic Sciences **44** (Supplement 1): 194-205.

Bergamini, A., D. Pauli, M. Peintinger and B. Schmid. 2001. Relationships between productivity, number of shoots and number of species in bryophytes and vascular plants. Journal of Ecology **89**: 920-929.

Boudreault, C., S. Gauthier and Y. Bergeron. 2002a. Epiphytic lichens and bryophytes on *Populus tremuloides* along a chronosequence in the southwestern boreal forest of Québec, Canada. The Bryologist **103**: 725-738.

Boudreault, C., Y. Bergeron, S. Gauthier and P. Drapeau. 2002b. Bryophyte and lichen communities in mature old-growth stands in eastern boreal forests of Canada. Canadian Journal of Forest Research **32**: 1080-1093.

Bradbury, S.M. 2006. Response of the post-fire bryophyte community to salvage logging in boreal mixedwood forests of northeastern Alberta, Canada. Forest Ecology and Management **234**: 313-322.

Carleton, T. 1990. Variation in terricolous bryophyte and macrolichen vegetation along primary gradients in Canadian boreal forests. Journal of Vegetation Science **1**: 585-594.

Carter, D.W. and J.M. Arocena. 2000. Soil formation under two moss species in sandy materials of central British Columbia (Canada). Geoderma **98**: 157-176.

Charron, I. and D.F. Greene. 2002. Post-wildfire seedbeds and tree establishment in the southern mixedwood boreal forest. Canadian Journal of Forest Research **32**: 1607-1615.

Crites, S. and M.R.T. Dale. (1998). Diversity and abundance of bryophytes, lichens and fungi in relation to woody substrate and successional stage in aspen mixedwood boreal forests. Canadian Journal of Botany **76**: 641-651.

Crum, H.A. and L.E. Anderson. 1981. Mosses of Eastern North America. Volumes 1 and 2. Columbia University Press, New York, USA.

During, H.J. 1979. Life strategies of bryophytes: a preliminary review. Lindbergia **5**: 2-18.

During, H.J. and B.F. van Tooren. 1990. Bryophyte interactions with other plants. Botanical Journal of the Linnean Society **104**: 79-98.

Esposito A, S. Mazzoleni and S. Strumia. 1999. Post-fire bryophyte dynamics in Mediterranean vegetation. Journal of Vegetation Science **10**: 261-268.

Fenton, N.J. and Y. Bergeron. 2006. Facilitative succession in a boreal bryophyte community driven by changes in available moisture and light. Journal of Vegetation Science **17**: 65-76.

Foster, D.R. 1985. Vegetation development following fire in *Picea mariana* (black spruce)-*Pleurozium* forests of south-eastern Labrador, Canada. Journal of Ecology **73**: 517-534.

Frego, K.A. 1996. Regeneration of four boreal bryophytes: colonization of experimental gaps by naturally occurring propagules. Canadian Journal of Botany **74**: 1937-1942.

Frisvoll, A.A. and T. Prestø. 1997. Spruce forest bryophytes in central Norway and their relationship to environmental factors including modern forestry. Ecography **20**: 3-18.

Garcia-Pausas, J., P. Casals and J. Romanya. 2004. Litter decomposition and faunal activity in Mediterranean forest soils: effects of N content and the moss layer. Soil Biology and Biochemistry **36**: 989-997.

Glime, J.M., R.G. Wetzel, and B.J. Kennedy. 1982. The effects of bryophytes on succession from alkaline marsh to *Sphagnum* bog. American Midland Naturalist **108**: 209-223.

Gloaguen, J.C. 1990. Post-burn succession on Brittany heathlands. Journal of Vegetation Science **1**: 147-152.

Grime, J.P., E.R. Rincon and B.E. Wickerson. 1990. Bryophytes and plant strategy theory. Botanical Journal of the Linnean Society **104**: 175-186.

Gunnarsson, U., H. Rydin, and H. Sjörs. 2000. Diversity and pH changes after 50 years on the boreal mire Skattlösbergs Stormosse, Central Sweden. Journal of Vegetation Science **11**: 277-286.

Gunnarsson, U., N. Malmer and H. Rydin. 2002. Dynamics or constancy in *Sphagnum* dominated mire ecosystems: a 40 year study. Ecography **25**: 685-704.

Hanssen, K.H. 2003. Natural regeneration of *Picea abies* on small clear-cuts in SE Norway. Forest Ecology and Management **180**: 199-213.

Harmon, M.E. 1989. Effects of bark fragmentation on plant succession on conifer logs in the Picea-Tsuga forests of Olympic National Park, Washington. American Midland Naturalist **121**: 112-124.

Heinken, T., R. Lees, D. Raudnitschka and S. Runge. 2001. Epizoochorous dispersal of bryophyte stem fragments by roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*). Journal of Bryology **23**: 293-300.

Hobbs, R.J. and C.H. Gimingham. 1984. Studies on fire in Scottish Highland communities II: post-fire vegetation development. Journal of Ecology **72**: 585-610.

Hörnberg, G., M. Ohlson and O. Zackrisson. 1997. Influence of bryophytes and microrelief conditions on *Picea abies* seed regeneration patterns in boreal old-growth swamp forests. Canadian Journal of Forest Research **27**: 1015-1023.

Johnston, M.H. and J.A. Elliott. 1996. Impacts of logging and wildfire on an upland black spruce community in northwestern Ontario. Environmental Monitoring and Assessment **39**: 283-297.

Jonsson, B.G. and P-.A. Esseen. 1990. Treefall disturbance maintains high bryophyte diversity in a boreal spruce forest. Journal of Ecology **78**: 924-936.

Kellner, O., and H. Weibull. 1998. Effects of wood ash on bryophytes and lichens in a Swedish pine forest. Scandinavian Journal of Forest Research Supplement **2**: 76-85.

Kershaw, M., R. Wiltshire and C. Hollstedt. 1994. Critical silvics of feathermoss as related to vegetation management. VMAP Technical Report No. 94-03. Vegetation Management Alternatives Program, Ministry of Natural Resources, Ontario.

Kimmerer, R.W. 1994. Ecological consequences of sexual versus asexual reproduction in *Dicranum flagellare* and *Tetraphis pelucida*. The Bryologist **97**: 20-25.

Kimmerer, R.W. and T.F.H. Allen. 1982. The role of disturbance in the pattern of a riparian bryophyte community. The American Midland Naturalist **107**: 370-383.

Kischuk, B. 2003. Soil nutrient and organic matter responses to fire, harvesting and salvage logging: Chisholm Fire. Progress Report prepared for the Foothills Model Forest. Northern Forestry Centre, Canadian Forestry Service.

Kooijman, A.M. and C. Bakker. 1995. Species replacement in the bryophyte layer in mires: the role of water type, nutrient supply and interspecific interactions. Journal of Ecology **83**: 1-8.

Kotorová, I. and J. Lepš. 1999. Comparative ecology of seedling recruitment in an oligotrophic wet meadow. Journal of Vegetation Science **10**: 175-186.

Kuhry, P. 1994. The role of fire in the development of *Sphagnum*-dominated peatlands in western boreal Canada. Journal of Ecology **82**: 899-910.

Kuuluvainen, T. and P. Juntunen. 1998. Seedling establishment in relation to microhabitat variation in a windthrow gap in a boreal *Pinus sylvestris* forest. Journal of Vegetation Science **9**: 551-562.

Légaré, S., D. Paré and Y. Bergeron. 2005. Influence of aspen on forest floor properties in black spruce-dominated stands. Plant and Soil **275**: 207–220.

Li, Y. and D.H. Vitt. 1997. Patterns of retention and utilization of aerially deposited nitrogen in boreal peatlands. Ecoscience **4**: 106-116.

Lloret, F. 1991. Population dynamics of the coprophilous moss *Tayloria tenuis* in a Pyrenean forest. Holarctic Ecology **14**: 1-8.

Longton, R.E. and S.W. Greene. 1979. Experimental studies of growth and reproduction in the moss *Pleurozium schreberi* (Brid.) Mitt. Journal of Bryology **10**: 321-338.

Magyari, E., P. Sumegi, M. Braun, G. Jakab and M. Molnar. 2001. Retarded wetland succession: anthropogenic and climatic signals in a Holocene peat bog profile from north-east Hungary. Journal of Ecology **89**: 1019-1032.

Maltby, E., C.J. Legg and M.C.F. Proctor. 1990. The ecology of severe moorland fire on the North York Moors: effects of the 1976 fires, and subsequent surface and vegetation development. Journal of Ecology **78**: 490-518.

McDaniel, S.F. and N.G. Miller. 2000. Winter dispersal of bryophyte fragments in the Adirondack Mountains, New York. The Bryologist **103**: 592-600.

Moss, E.H. 1996. Flora of Alberta. 2nd Edition. Revised by J.G. Packer. University of Toronto Press, Toronto, Canada.

Mulligan, R.C. and L.D. Gignac. 2002. Bryophyte community structure in a boreal poor fen II: interspecific competition among five mosses. Canadian Journal of Botany **80**: 330-339.

Nguyen-Xuan, T., Y. Bergeron, D. Simard, J.W. Fyles and D. Paré. 2000. The importance of forest floor disturbance in the early regeneration patterns of the boreal forest of western and central Quebec: a wildfire versus logging comparison. Canadian Journal of Forest Research **30**: 1353-1364.

Nilsson, M.-C.., I. Steijlen and O. Zackrisson. 1996. Time restricted seed regeneration of Scots pine in sites dominated by feather moss after clear-cutting. Canadian Journal of Forest Research **26**: 945-953.

Nygaard, P.H. and T. Odegaard. 1999. Sixty years of vegetation dynamics in a south boreal coniferous forest in southern Norway. Journal of Vegetation Science **10**: 5-16.

O'Toole, M.A. and D.M. Synnott. 1971 The bryophyte succession on blanket peat following calcium carbonate, nitrogen, phosphorous and potassium fertilizers. Journal of Ecology **59**: 121-126.

Paré, D., Y. Bergeron and C. Camiré. 1993. Changes in the forest floor of Canadian southern boreal forest after disturbance. Journal of Vegetation Science **4**: 811-818.

Parent, S., M-.J. Simard, H. Morin and C. Messier. 2003. Establishment and dynamics of the balsam fir seedling bank in old forests of northeastern Quebec. Canadian Journal of Forest Research **33**: 597-603.

Rincon, E. 1988. The effect of herbaceous litter on bryophyte growth. Journal of Bryology **15**: 209-217.

Rowe, J.S. and G.W. Scotter. 1973. Fire in the boreal forest. Quaternary Research **3**: 444-464.

Rydgren, K. and R.H. Økland. 2002. Ultimate costs of sporophyte production in the clonal moss *Hylocomium splendens*. Ecology **83**: 1573-1579.

Rydin, H. 1997. Competition among bryophytes. Advances in Bryology **6**: 135-168.

Scandrett, E. and C.H. Gimingham. 1989. Experimental investigation of bryophyte interactions on a dry heathland. Journal of Ecology **77**: 838-852.

Sedia, E.G. and J.G. Ehrenfeld. 2003. Lichens and mosses promote alternate stable plant communities in the New Jersey Pinelands. Oikos **100**: 447-458.

Sedia, E.G. and J.G. Ehrenfeld. 2005. Differential effects of lichens, mosses and grasses on respiration and nitrogen mineralization in soils of the New Jersey Pinelands. Oecologia **144**: 137-147.

Skre, O., W.C. Oechel and P.M. Miller. 1983. Patterns of translocation of carbon in four common moss species in a black spruce (*Picea mariana*) dominated forest in interior Alaska. Canadian Journal of Forest Research **13**: 869-878.

Slack, N.G. 1997. Niche theory and practice: bryophyte studies. Advances in Bryology **6**: 169-204.

Steijlen, I., M-.C. Nilsson and O. Zackrisson. 1995. Seed regeneration of Scots pine in boreal forest stands dominated by lichens and feather moss. Canadian Journal of Forest Research **25**: 713-723.

Sulyma, R. and D.S. Coxson. 2001. Microsite displacement of terrestrial lichens by feather moss mats in late seral pine-lichen woodlands of north-central British Columbia. The Bryologist. **104**: 505-516.

Syndonia Bret-Harte, M., E.A. García, V.M. Sacré, J.R. Whorley, J.L. Wagner, S.C. Lippert and F.S. Chapin III. 2004. Plant and soil response to neighbour removal and fertilization in Alaskan tussock tundra. Journal of Ecology **92**: 635-647.

Thomas, P.A., M.C.F. Proctor and E. Maltby. 1994. The ecology of severe moorland fire on the North York Moors: chemical and physical constraints on moss establishment from spores. Journal of Ecology **82**: 457-474.

Tilman, D. 1986. Nitrogen-limited growth in plants from different successional stages. Ecology **67**: 555-563.

Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. Ecological Monographs **57**: 189-214.

USDA NRCS 2007. *The PLANTS database*. Version: 030211. <http://plants.usda.gov>. National Plant Data Center, Baton Rouge, Louisiana, USA.

Van der Wal, R. and R.W. Brooker. 2004. Mosses mediate grazer impacts on grass abundance in Arctic ecosystems. Functional Ecology **18**: 77-86.

Viro, P.J. Effects of forest fire on soil. Pages 7-46 *in* T.T. Kozlowski and C.E. Ahlgren, editors. Fire and Ecosystems. Academic Press, New York, USA.

Vitt, D.H. 1990. Growth and production dynamics of boreal mosses over climatic, chemical and topographic gradients. Botanical Journal of the Linnean Society **104**: 35-59.

Vitt, D.H. 2000. Peatlands: ecosystems dominated by bryophytes. Pages 312-342 *in* A.J. Shaw and B. Goffinet, editors. Bryophyte Biology. Cambridge University Press, Cambridge, UK.

Wardell, D.A., O. Zackrisson and M.-C. Nilsson. 1998. The charcoal effect in boreal forests: mechanisms and ecological consequences. Oecologia **115**: 419-426.

Watson, M.A. 1980. Shifts in the pattern of microhabitat occupation by six closely related species of moss along a complex altidudinal gradient. Oecologia **47**: 46-55.

Weber, M.G. and K. van Cleve. 1984. Nitrogen transformation in feather moss and forest floor layers of interior Alaska black spruce ecosystems. Canadian Journal of Forest Research **14**: 278-290.

Wiklund, K. and H. Rydin. 2004. Ecophysiological constraints on spore establishment in bryophytes. Functional Ecology **18**: 907-913.

Zackrisson, O., M-.C. Nilsson, A. Dahlberg and A. Jäderlund. 1997. Interference mechanisms in conifer-Ericaceae-feathermoss communities. Oikos **78**: 209-220.

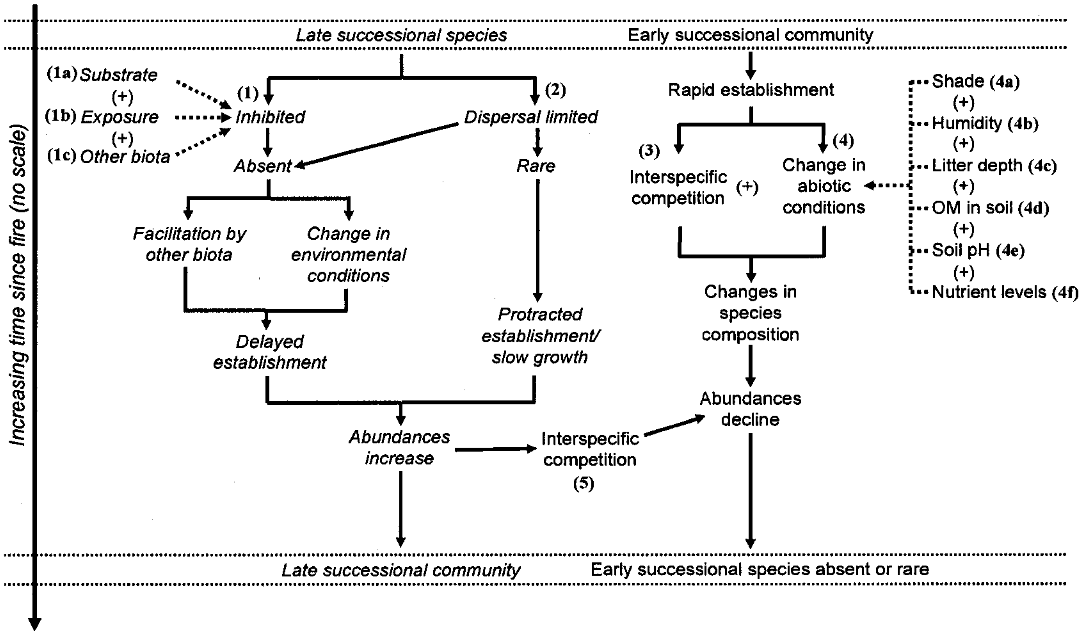


Figure 1.1 Generalized schematic of successional pathways for bryophytes species in boreal white spruce forests following a forest fire. Numbers refer to alternative pathways that are discussed in the text. The symbol (+) indicates the possibility of interactive effects among factors.

Chapter 2: Species composition of burned and unburned *Picea glauca* (Moench) Voss forest stands in and around the Chisholm Fire, north-central Alberta, and trends over the first three years of succession

A feature of the moss community in white spruce dominated boreal forests is that the species assemblage in recently burned stands is almost completely different from that in old stands. The consistency with which this contrast has been recorded suggests that there is a high degree of uniformity in successional trajectories among stands. The pleurocarpous boreal feather mosses *Pleurozium schreberi*, *Ptilium crista-castrensis* (hereafter referred to as *Pleurozium* and *Ptilium*) and *Hylocomium splendens* (Hedw.) B.S.G., are typically the dominant bryophyte species on the forest floor of mature to old-growth white spruce forests (see, for example, Rowe and Scotter 1973; Foster 1985; Harmon 1989; Jonsson and Esseen 1990; Kershaw et al. 1994; Frego 1996; Johnston and Elliott 1996; Nygaard and Odegaard 1999, Nguyen-Xuan et al. 2000; Boudreault et al. 2002b; Bradbury 2006). In contrast, these species are not usually found in early successional stages after a stand-replacing fire. In recently burned forest stands, the dominant species typically include the ruderal bryophytes *Ceratodon purpureus* (Hedw.) Brid., *Polytrichum juniperinum* Hedw., *Funaria hygrometrica* Hedw., *Bryum argenteum* Hedw. *Leptobryum pyriforme* (Hedw.) Wils. and *Marchantia polymorpha* (Rowe and Scotter 1973; Viro 1974; Foster 1985; Bradbury 2006).

Mature to old growth white spruce-dominated forests in the province of Alberta, Canada, are under pressure from development by natural resource industries. Therefore it is important to understand the characteristics of natural succession and the factors driving it in these forests. Recent large fires in Alberta, such as the Chisholm Fire of 2001 and the House River Fire of 2002, have provided an opportunity to obtain data on bryophyte succession and to test hypotheses about drivers of succession. This information could benefit attempts to emulate the effects of forest fire in human activities that result in deforestation. The study described in this chapter was conducted as part of a research program looking at the post-fire successional ecology of bryophytes in white spruce forests in and around the boundaries of the Chisholm Fire. The primary focus of this research program was the successional ecology of *Pleurozium schreberi* and *Ptilium crista-castrensis*. The timing of the fire also provided the opportunity to compare bryophyte species composition in forest stands burned in the Chisholm Fire with that found in other studies of the earliest stages of post-fire succession. Species surveys were conducted over the first three years of succession. These data were used to (i) describe the species composition of burned and unburned sites in the study area; (ii) determine if *Pleurozium schreberi* and *Ptilium crista-castrensis* were present in the extant community or the diaspore rain; (iii) identify changes in species composition and environmental conditions over the first three years of succession; and (iv) identify factors that may influence bryophyte cover in early successional stages. To evaluate these hypotheses, species and environmental data were collected in surveys of four burned and three unburned forest stands in 2003. Two of the burned stands were also surveyed over a three-year period from 2002 to 2004.

Materials and Methods

Study sites

We surveyed four burned (early successional) and three unburned (late successional, *c.* 80 - 100 years old) *P. glauca*-dominated forest stands in and around the boundaries of the 2001 Chisholm Fire in north-central Alberta. This fire burned an area of approximately 116,000 ha (CFRC 2001) in the summer of 2001. We selected the study sites (hereafter identified numerically using the prefix BRN for burned sites and GRN for unburned sites) on the basis that they had the following current or pre-fire characteristics: canopy composition of 80% *Picea glauca*, 51-70% crown closure and average tree height of 20-25 m (data from Canadian Forestry Service). The fire had killed all above-ground vegetation in the burned sites and exposed mineral soil on most of the forest floor. The exception was BRN1, where areas were covered by charred fibrous roots and duff. In the unburned stands the dominant forest floor substrates were organic humus and decaying wood.

Survey protocol

We surveyed BRN1 and BRN3 in all three years of the study. These sites were intensively surveyed in 2002 to maximize the area over which species and environmental data were collected. We modified the protocol in 2003 to reduce sampling intensity so that we could survey four burned sites. To allow time for surveying the unburned sites in 2004, we used the 2003 surveying protocol.

2002 protocol

Within each study site we marked out a 50 × 50 m plot that encompassed representative vegetation, substrates and structural components such as snags, stumps and fallen logs. We then recorded species cover and environmental variables in 100 quadrats. Quadrats were 0.5 m × 0.5 m in size and were placed at locations determined using a restricted randomized sampling procedure: we subdivided the 50 × 50 m plot into 25 sections, each 10.0 m × 10.0 m in area, and located quadrats at four randomly determined locations in each of these sections.

We estimated the percentage cover of forest floor bryophytes and the dominant litter type in each quadrat using the following cover categories: 0 (no moss present), 0-5%, 6-25%, 26-50%, 51-75% and 76-100%. To maximize precision, we divided quadrats into 25 sections, each 10 cm × 10 cm in area, and recorded cover estimates for each section. To obtain bryophyte and litter cover values for each quadrat, we calculated the mean of the estimates for each 10 cm × 10 cm section using the formula for grouped data given in Fowler et al (1998):

$$\text{Mean cover} = \sum fx \,/\, n$$

where x is the category, and

f is the frequency of occurrence of that category in the quadrat.

We estimated the percent cover of litter using the same method. Litter types were identified *a priori* as the most common types on the forest floor and we recorded a type as present if it comprised at least 50% of the litter present. We recorded litter depth as falling in one of these categories: 0 – 10 mm, 11 – 20 mm or greater than 20 mm. To get a gross estimate of vascular plant cover for each quadrat, we recorded the number of 10 cm × 10 cm sections in which each species occurred and converted this to a percentage of 25 (i.e. the number of 10 cm × 10 cm sections in a quadrat).

2003/2004 protocol

As in the 2002 surveys, we set up a 50 × 50 m plot in each study site (the 2002 plots were re-used in BRN1 and BRN3). In each site we recorded bryophyte, forb, shrub and litter cover in 0.5 m × 0.5 m square quadrats (shrub cover is defined here as all woody plants less than 5.0 m in height). We used restricted randomized sampling to determine the locations of quadrats: the 50 × 50 m plot was subdivided into 15 sections, each 10.0 m × 16.7 m in area. At one randomly determined location in each 10.0 m × 16.7 m section we completed one quadrat survey.

To estimate the percentage cover of bryophytes, we overlayed a grid of 1800 squares onto each quadrat and counted the number of squares that were greater than 50% filled by each bryophyte species. We converted this value to a percentage of 1800. The same procedure was used to estimate litter cover. To estimate the percentage cover of all vascular plant species, we visually subdivided each quadrat into a grid of 100 squares and calculated the percentage of squares greater than 50% filled by each species. In 2003 we also took a gravimetric soil moisture (GSM) reading from each quadrat in the burned stands by collecting a sample of topsoil and drying it in an oven using the method described in Kalra and Maynard (1991). For each sample, we transferred about 5.0 g of soil to an aluminium dish and weighed the sample and dish. These were then dried in an oven at a temperature of 105oC over 24 hours. After we had allowed the samples to cool, they were weighed again. Water content was determined using the following formula:

$$\text{Water content (\% by weight)} = W_2 - W_3\ (g) / W_3 - W_1\ (g) \times 100$$

where W_1 is the weight of the aluminium dish,

W_2 is the combined weight of the soil and the dish before drying, and

W_3 is the combined weight of the soil and the dish after drying.

To obtain a detailed floristic summary of the study sites, we supplemented quadrat surveys with random meanders that involved criss-crossing the plot and recording all bryophyte and vascular plant species that we observed.

Diaspore rain sampling

To obtain a census of the species present in the diaspore rain, we did a spore capture exercise. The protocol was based on the method described in Ross-Davis and Frego (2004). In July and August 2002 we set up three transects at 12.5, 25.0 and 37.5 m along the side of the sampling plot in BRN1 and BRN3. Each transect was the length of the plot (50 m). Starting at 0 m, we placed one 10 cm diameter Petri Plates filled with an agar mix containing 0.05 g/l NH_4NO_3, 0.02 g/l $CaCl_2$, 2.00 g/l KH_2PO_4 and 15 g/l of agar (after Kimmerer 1991) every five metres along the transect and opened it to the air. We placed a second Petri Plate at locations every 10 m and left it closed as a control to test for contamination. We also had seven additional controls that were transported to the site but not placed along the transects. After approximately seven hours, we collected all the plates, sealing each one in an airtight freezer bag. The bagged plates were placed in a growth chamber in the Biotron facility at the University of Alberta's Department of Biological Sciences (exposure time was reduced to *ca.* five hours in BRN1in August because of rain), with conditions set as follows: daytime temperature 24° C, night temperature 10° C, RH 75%, 15 hour day length and light intensity of 250 mE $^{s-1\ m-2}$. Plates remained in the growth chamber until the contents had grown to a stage where species were identifiable. We then inspected all plates and recorded all identifiable species.

Data analysis

To see whether the total cover of mosses, forbs, shrubs and herbaceous and leaf litter showed significant changes over the study period in BRN1 and BRN3, we compared quadrat values between years using Multiple Response Permutation Procedure (MRPP) with Euclidean distances in PC-ORD for Windows version 4.41 (MjM Software Design 2005). MRPP is a non-parametric method that compares groups on the basis of mathematical distances between sampling units. It has the advantage over methods such as the Kruskal-Wallis test and the Mann-Whitney *U* test because it tests for differences between groups using original values from sampling units rather than ranks or median values. The average within-group distance is calculated for each group and weighted by the number of sampling units in the group. All weighted averages are then summed to derive an observed delta (δ_O). This is compared with the mean value, or expected delta (δ_E), of a reference distribution generated by calculating δ for every possible rearrangement of sampling units among groups. The probability (P) of getting a delta that is less extreme than δ_O is determined by calculating a test statistic ($T = (\delta_O-\delta_E)/\sigma(\delta_E)$) and numerical integration of a Pearson type III distribution (McCune & Mefford 1999). MRPP also provides a measure of effect size (A), calculated as $1-\delta_O/\delta_E$ (McCune & Mefford 1999). A problem with MRPP is that divide-by-zero errors can occur in the calculation of distance matrices when there are several zero values in a data set. Therefore, we replaced values of zero in our data set with 0.0001. For comparisons with 2002 data, we converted 2003 and 2004 bryophyte, litter and vascular plant cover data to the categories used for 2002 data.

To see if total bryophyte cover in the burned stands was correlated with forb cover, shrub cover, total litter cover, litter depth and gravimetric soil moisture (GSM), we calculated Spearman's rank correlation coefficients in SPSS based on data collected in 2003 (SPSS version 11.5, SPSS Inc. 2002).

Results

Species composition

We found 13 bryophyte species or genera in quadrat surveys of the burned stands across the three years of the study (Table 2.1). Another 7 species were identified in meanders. *Ceratodon purpureus*, *Bryum argenteum*, *Bryum* *caespiticium,* and *Funaria hygrometrica* were present in all sites in all years. *Ceratodon* always had the highest cover but cover varied considerably between sites. Only 4.8% of the ground was occupied by Ceratodon in BRN4, compared with 31.3% in BRN3. We found *Aulacomnium palustre* in BRN1 in surveys in 2002 and 2004 and in meanders in BRN2 in 2003, but did not find this species in BRN3 or BRN4. *Barbula convoluta*, *Plagiothecium* sp. *Eurhynchium pulchellum* and *Isopterygium pulchellum* were found only in BRN1.

We also found 13 species in quadrat surveys in the unburned stands. Another 36 were found only in meanders. *Pleurozium schreberi*, *Hylocomium splendens* and *Ptilium crista-castrensis had the highest cover in GRN2 and GRN3,* whereas *Plagiomnium* spp. and *Brachythecium* spp. had the highest cover in GRN1. We recorded these mosses to the level of genera in the field because we could not reliably differentiate species. When we examined samples returned to the laboratory for identification, we found examples of *Plagiomnium cuspidatum*, *P. drummondii*, *Brachythecium velutinum*, *B. campestre*, *B. curtum* and *B. salebrosum*. Voucher specimens were retained at the University of Alberta cryptogammic herbarium.

There was little overlap in species composition of the burned and the unburned sites (Table 2.1). In species surveys we found *Ceratodon purpureus, Bryum caespiticium*, *Leptobryum pyriforme* and *Marchantia polymorpha* only in (GRN1). These were growing on mineral soil exposed by a tip-up mound around a fallen tree. In the burned sites we did not find *Pleurozium schreberi*, *Ptilium crista-castrensis* or any other species that was common in the unburned sites.

Tables A.3 to A.6 in the Appendix provide means of environmental variables recorded in the study sites and floristic summaries of vascular plant cover and species composition.

Spore captures

We were able to identify four bryophyte species in Petri Plates. *Ceratodon purpureus* was the most frequently occurring species Fig. 2.1). We found no gametophytes of species that were common in the unburned stands. Table 2.2 gives mean protonema counts for exposed and control plates. Protonemata were found in several of the control plates that were placed along transects but total counts in these trays were much lower than those in the exposed plates. One protonema was also recorded in the control trays that were not placed along the transects.

Changes in bryophyte cover and environmental variables over three years

Figs. 2.2 and 2.3 show trends from 2002 to 2004 in the mean cover and relative abundance of the most common mosses. Only *Leptobryum pyriforme* increased in cover significantly in both stands over the study period. In BRN1 the cover of *Bryum caespiticium* did not change between 2002 and 2003 but decreased significantly between 2003 and 2004. The trend for this species was different in BRN3; there a significant increase in cover between 2002 and 2003. The cover of this species also increased between 2003 and 2004 in BRN3, but the change was not significant. We also found differences between the sites in the trend for *Ceratodon purpureus*. In BRN1, cover of *Ceratodon* increased significantly between 2002 and

2003 and decreased significantly between 2003 and 2004. In BRN3 *Ceratodon* cover increased significantly between 2002 and 2003 but did not change between 2003 and 2004. The mean cover of *Polytrichum juniperinum* varied considerably among quadrats in 2003 in BRN1 and in 2004 in BRN3. We found no change in the cover of this species in BRN1 and although mean cover increased between 2003 and 2003 in BRN3, the difference between years was not significant. Trends in relative abundance were similar to those for mean cover except in the case of *Bryum caespiticium* and *Funaria hygrometrica* in BRN3. Both species declined in relative abundance even though cover increased.

Figure 2.4 shows trends from 2002 to 2004 in the means of total moss cover, forb cover, shrub cover and herbaceous and leaf litter cover. We found no significant change in total moss cover in BRN1 over the study period but cover increased significantly between 2002 and 2003 in BRN3. In both stands the between-year trend in forb cover matched that for total moss cover. Mean shrub cover was higher in BRN1 than BRN3 in all years, although shrub cover increased significantly in both sites. Herbaceous and leaf litter cover increased significantly between 2002 and 2003 in both sites. Modal litter depth increased from the range 0 – 10 mm in 2002 and 2003 to 11 – 20 mm in 2004 in both sites.

Correlations with total bryophyte cover two years after fire (2003)

Total bryophyte cover was significantly positively correlated with GSM (Spearman's rho = 0.397; $P = 0.002$; $N = 60$) and forb cover (Spearman's rho = 0.294; $P = 0.023$; $N = 60$) and significantly negatively correlated with litter cover, (Spearman's rho = -0.258; $P = 0.046$; $N = 60$). Bryophyte richness was also significantly positively correlated with GSM (Spearman's rho = 0.488; $P < 0.001$; $N = 60$).

Discussion

Bryophyte species composition

Most of the species we found in the burned sites are frequent colonizers of mineral soils in the earliest stages of post-fire succession. Bradbury (2006) found *Aulacomnium palustre*, *Ceratodon purpureus*, *Funaria hygrometrica*, *Leptobryum pyriforme*, and *Polytrichum juniperinum* in the first two growing seasons after the House River Fire in northeastern Alberta. *Ceratodon purpureus* has also been reported in other burned boreal spruce forests (Foster 1985; Schimmel and Granstrom 1996; Nguyen-Xuan et al. 2000; Bradbury 2006), heathlands and moorlands (Hobbs and Gimingham 1984; Gloaguen 1990; Maltby et al. 1990; Thomas et al. 1994), and eucalyptus forest (Brasell and Mattay 1984). *Polytrichum juniperinum* was found in the early stages of succession by Brasell and Mattay (1984); Hobbs and Gimingham (1984); Foster (1985); Gloaguen (1990); Schimmel and Granstrom (1996); Nguyen-Xuan et al. (2000) and Bradbury (2006). *Funaria hygrometrica* and *Barbula convoluta* were identified as characteristic of intense fires in Mediterranean macchia vegetation by Esposito et al. (1999) and Nguyen-Xuan et al. (2000) often found *Marchantia polymorpha* in burned *Picea mariana* forests in Quebec.

In general, the structure and composition of the forest floor bryophyte community in the unburned stands was also consistent with what has been reported for boreal spruce forests elsewhere (Rowe and Scotter 1973). The feather mosses *Pleurozium schreberi*, *Hylocomium splendens* and *Ptilium crista-castrensis* were the dominant species in two of the unburned sites (GRN2 and GRN3). In the other unburned site (GRN1) *Plagiomnium* spp. were abundant (Table 2.1). *Plagiomnium cuspidatum* and *P. drummondii* favour humid locations or places that provide frequent hydration (e.g. tree bases, periodically flooded ground and pool edges; Crum and Anderson (1981)). Although GRN1 appeared to be wetter than the other unburned sites, mean GSM was only slightly higher in GRN1 than in the other unburned sites. Therefore, it is not clear from the data why *Plagiomnium* was more common than *Pleurozium*, *Ptilium* and *Hylocomium* in BRN1.

None of the species that were common in the unburned sites were found in the burned sites and occurrences of ruderal bryophytes in the unburned stands were rare. Opportunities for the establishment of ruderal bryophytes in mature forest stands are likely to be limited by (i) intolerance of habitat conditions; or (ii) competitive exclusion. In a study of constraints on establishment of ruderal mosses from spores, Thomas et al. (1994) found that *Ceratodon purpureus* and *Polytrichum piliferum* were unlikely to colonise substrates with a high organic matter content. If this is true for other ruderal species, colonization of gaps on the forest floor of mature stands by early successional bryophytes may be a rare event. Furthermore, acrocarpous mosses can be overgrown by pleurocarpous feather mosses and may be rapidly excluded from gaps on the forest floor. We found ruderal mosses, growing on mineral soil exposed by the roots of a fallen tree. This finding supports the conclusions of Jonsson and Esseen (1990) that such treefall disturbances are important for maintaining bryophyte diversity in mature forest habitats because they expose new substrates and delay competitive exclusion.

Two hypotheses that may explain the absence of *Pleurozium, Ptilium* and other late successional species from early successional stages are: (i) habitat intolerance; and (ii) dispersal limitation (Fig. 1.1). Habitat intolerance is suggested by the contrast in environmental conditions between early successional stages and those in which *Pleurozium* and *Ptilium* are abundant. There is no tree canopy in the earliest stages of post-fire succession to create shade; studies have found reduced growth in late successional mosses as a result of high light intensity and evaporation stress (Busby et al. 1978; Longton and Greene 1979). Substrates also differ between early and late successional stages. Fires consume humus on the soil surface, exposing mineral soil, and they can leave a layer of ash, charred fine woody debris and duff (Ahlgren 1960; Viro 1974; Flinn and Wein 1977; Van Wagner 1983; Schimmel and Granstrom 1996; Ne'eman et al. 2004; Certini 2005). Charred and mineral substrates can have an alkaline pH and contain potentially toxic ions (Lloyd 1971; Brown 1982; Thomas et al. 1994; Kellner and Weibull 1998; Ne'eman et al. 2004; Mandre et al. 2006). Feather mosses are indicators of acidic, organic substrates (Ringius and Sims 1997) and may be intolerant of substrates with an alkaline pH. The dispersal limitation hypothesis is based on the rarity of sexual reproduction in *Pleurozium* and *Ptilium*. Research has shown that gametophyte fragments of these species have the potential to act as propagules following short-distance dispersal in mature forests (Longton and Greene 1979; Myrmael 1993; Kershaw et al. 1994; Kimmerer 1994; Frego 1996; Rydgren et al. 1998; Rydgren and Økland 2001; Huttunen 2003). Little is known about the long distance dispersal of vegetative fragments, although previous studies have identified several potential vectors, including slugs (Kimmerer and Young 1995), snowmelt (McDaniel and Miller 2000), deer and wild boar (Heinken et al. 2001).

This study found no evidence of colonization by *Pleurozium* and *Ptilium* in the earliest stages of succession. This is consistent with the findings of Foster (1985), who estimated that *Pleurozium* entered a *Picea mariana* forest in Labrador after around 10 – 12 and. *Ptilium* established at around 80 years. Such estimates are lacking in the literature and further research is needed to clarify when these species first establish in the successional sequence and identify factors that can affect this. Further studies should also consider the relative importance of the different process by which recolonisation might occur. Chapters 3 and 4 will focus on questions related to these issues.

Trends over the first three years since fire

Bryophyte cover

A feature of some post-fire successions has been a transition in the dominant species from *Ceratodon* to *Polytrichum* spp. (Morneau and Payette 1989; Maltby et al. 1990; Thomas et al. 1994; Schimmel and Granstrom 1996). In a Brittany heathland, Gloaguen (1990) found that the cover of *Ceratodon* increased rapidly up to second year after fire and then declined. Their results indicate that it was rare or absent after four years. *Polytrichum juniperinum* also entered soon after the fire but it increased more slowly than *Ceratodon*, peaking at 4 years. Brasell and Mattay (1984) reported similar findings after a slash burn in a eucalyptus forest in Tasmania. They found that although *Ceratodon* and *Polytrichum junipernum* became well established in the second year after the fire, *Polytrichum* was overgrowing *Ceratodon* by end of second year. This interaction between *Polytrichum* and *Ceratodon* was also seen in a burned Swedish *Picea abies/Pinus sylvestris* forest by Schimmel and Granstrom (1996). They reported that the cover of *Ceratodon* started to decrease after 2-3 years, while that of *Polytrichum* continued to increase. We found that the absolute cover and relative abundance of *Ceratodon* in BRN1 declined between 2003 and 2004 (Fig. 2.2). In BRN3 absolute cover of *Ceratodon* changed little between 2003 and 2004, while relative abundance declined slightly over the same period. These results may indicate that *Ceratodon* has reached its peak abundance in the study sites. The pattern for absolute cover of *Polytrichum juniperinum* in BRN3 was also consistent with that seen in other studies (Fig. 2.3); absolute cover was relatively low in 2002 and 2003 and increased substantially between 2003 and 2004. Relative abundance varied little between years, though, implying that the increase in *Polytrichum* cover was not matched by a substantial decline in the cover of any other species. The trend in the relative abundance of *Polytrichum* in BRN1 was similar to that seen in BRN3, while the trend in absolute cover matched that of *Ceratodon* in the same site, peaking in 2003. Therefore, the decline in cover and relative abundance of *Ceratodon* cannot be explained by increases in *Polytrichum* cover. Trends in the cover of both species in

BRN1 may, instead, be linked to an increase in the cover of *Marchantia polymorpha* between 2003 and 2004 (Fig. 2.4). *A posteriori* examination of survey data showed that the abundance of *Marchantia* colonies did not change substantially over the study period in BRN1. Therefore the increase in the cover of this species must be largely due to the growth of existing colonies. Expanding *Marchantia* colonies may have overgrown mosses in those quadrats in which they co-occurred. The semi-rigid thalli of *Marchantia* are likely to physical obstruct the upward growth of mosses and prevent light and precipitation from reaching gametophytes that have been overgrown. During surveys of BRN1 we often found the brown remains of gametophytes under *Marchantia* thalli. *Marchantia* cover in BRN1 was always lower than that in BRN3 and the data indicate a different pattern of expansion in BRN3. The frequency of individual colonies increased over the study period but there was no significant increase in cover. This implies that new colonies were becoming established but growth of existing colonies was limited. While competitive effects on mosses could occur where new colonies established in existing moss mats, new colonies that established in open spaces would not impact mosses in the short-term.

Environmental variables

In most cases, trends in the cover of forbs, shrubs and HLL matched expectations. With the exception of forb cover in BRN1, mean values of these variables increased in both stands over the study period. Forb cover in BRN1 peaked in 2003, matching the trend for total moss cover. One possible explanation for this is that *Marchantia* thalli acted as a barrier between seeds and the soil, preventing the establishment of seed-dispersing forbs.

The similar trends in mean total moss cover and forb abundance between 2002 and 2004 in both sites suggests a close relationship between these variables (Fig. 2.4). The positive direction of this correlation could indicate that mosses benefited from forb cover or vice versa. Forbs provide shade that will reduce the frequency and intensity of wetting-drying cycles. Mosses may also be able to assimilate nutrients leached from decomposing herbaceous litter. Both of these effects could lead to increased growth rates (Busby et al. 1978; Furness and Grime 1982; Csotonyi and Addicott 2004; Monique et al. 2004). Forbs may have benefited from high moss cover if moss carpets enhanced the rate of seed germination. Such effects have previously been found in grasslands and other habitats (Watson 1981; Mishler and Newton 1988; During and van Tooren 1990; Equihua and Usher 1993; Nilsson et al. 1996; Hörnberg et al. 1997; Zackrisson 1997; Delach and Kimmerer 2002; Hanssen 2003; Parent et al. 2003). Higher germination rates could occur in moss carpets if they (i) hide seeds from granivores; or (ii) provide a moist microclimate (Parker et al. 1997). The impact of moss patches on seed germination in early successional stages warrants further study because it may reveal ways in which ruderal mosses influence succession.

Correlations between bryophyte cover and environmental variables

Both total bryophyte cover and bryophyte richness were found to be positively correlated with GSM. This result is consistent with the poikilohydric nature of bryophytes. The implication is that moist soils (i) encourage colony expansion through increased protonema production, higher rates of spore germination or increased gametophyte growth; and (ii) provide conditions that are within the regeneration niche of a greater ranger of species than dry soils.

The negative association between total bryophyte cover and litter cover could indicate that (i) bryophytes are unable to establish where litter is present; or (ii) that litter suppresses existing bryophyte growth. Thick accumulations of litter may be detrimental to small acrocarpous mosses because they block out light and obstruct the upward growth of sporophytes. Decomposing leaves and herbaceous litter also appear to be an unsuitable substrate for colonization by ruderal mosses because moss cover is typically low under a canopy of *Populus* spp. (personal observation). Interactions between litter and bryophytes warrant further investigation because they may help to explain declines in *Ceratodon purpureus* that other studies have reported after the first few years of succession.

Limitations of this study

Due to time constraints, the number of sites that could be surveyed within each year of this study was limited. Furthermore, only two sites could be surveyed over all years. We acknowledge that the inclusion of so few sites reduces the confidence with which results can be generalized to *Picea glauca*-dominated forests elsewhere. Nevertheless, we hope that this study will provide a basis for further research into early successional dynamics in white spruce forests following fire and the processes that influence the timing of establishment of late successional species.

Subsequent chapters in this thesis will focus on questions related to the latter topic with a focus on *Pleurozium* schreberi and *Ptilium crista-castrensis*.

We also note that the results of the spore capture exercise may not reflect the full range of species present in the diaspore rain. Identification of species growing on agar was not completed until several months after the capture experiment took place. By that time the agar had become desiccated. Furthermore, some species may not germinate on the agar mix that was used. The reliability of this method of sampling the diaspore rain requires further testing.

Conclusions

The species composition of burned and unburned *Picea glauca*-dominated forest stands in and around the boundaries of the 2001 Chisholm Fire in north-central Alberta, Canada, was consistent with previous studies of similar habitats. Most of the mosses that were found in burned sites were ruderal species, whereas *Pleurozium schreberi*, *Ptilium crista-castrensis*, *Hylocomium splendens* and *Plagiomnium* spp. had the highest cover in unburned sites. There was little overlap in the species composition of the burned and unburned study sites. Some early successional bryophytes were found in unburned sites on mineral soil exposed by a fallen tree. Limited evidence was found of a peak in the cover of *Ceratodon purpureus* in the burned sites. The cover of *Marchantia polymorpha* also increased substantially in one burned study site and may have been outcompeting mosses and preventing the establishment of forbs from seed. Trends in total moss cover over the first three years since fire matched those for forb cover. Bryophyte cover was positively associated with gravimetric soil moisture and forb cover, and negatively correlated with litter cover. Bryophyte species richness also tended to be higher on wetter soils.

Literature Cited

Ahlgren, C.E. 1960. Some effects of fire on reproduction and growth of vegetation in northeastern Minnesota. Ecology **41**: 431-445.

Boudreault, C., Y. Bergeron, S. Gauthier and P. Drapeau. 2002. Bryophyte and lichen communities in mature old-growth stands in eastern boreal forests of Canada. Canadian Journal of Forest Research **32**: 1080-1093.

Bradbury, S.M. 2006. Response of the post-fire bryophyte community to salvage logging in boreal mixedwood forests of northeastern Alberta, Canada. Forest Ecology and Management **234**: 313-322.

Brasell, H.M. and J.P. Mattay. 1984. Colonization by bryophytes of burned *Eucalyptus* forest in Tasmania, Australia: changes in biomass and element content: The Bryologist **87**: 302-307.

Brown, D.H. 1982. Mineral nutrition. Pages 383-344 *in* A.J.E Smith, editor. Bryophyte Ecology. Chapman and Hall, New York, USA.

Busby, J.R., L.C. Bliss and C.D. Hamilton. 1978. Microclimate control of growth rates and habitats of the boreal forest mosses, *Tomenthypnum nitens* and *Hylocomium splendens.* Ecological Monographs **48**: 95-110.

Certini, G. 2005. Effects of fire on properties of forest soils: a review. Oecologia **143**: 1-10.

Chisholm Fire Review Committee (CFRC). 2001. Final Report submitted to the Minister of Alberta Sustainable Resource Development. Downloaded November 2006 from: http://www.srd.gov.ab.ca/forests/chisholm/pdfs/Chisholm.pdf

Crum, H.A. and L.E. Anderson. 1981. Mosses of Eastern North America. Volumes 1 and 2. Columbia University Press, New York, USA.

Csotonyi, J. and J.F. Addicott. 2004. Influence of trampling-induced microtopography on growth of the soil crust bryophyte Ceratodon purpureus in Jasper National Park. Canadian Journal of Botany **82**: 1382-1392.

Delach, A and R.W. Kimmerer. 2002. The effect of *Polytrichum piliferum* on seed germination and establishment on iron mine tailings in New York. The Bryologist **105**: 249-255.

During, H.J. and B.F. van Tooren. 1990. Bryophyte interactions with other plants. Botanical Journal of the Linnean Society **104**: 79-98.

Esposito A, S. Mazzoleni and S. Strumia. 1999. Post-fire bryophyte dynamics in Mediterranean vegetation. Journal of Vegetation Science **10**: 261-268.

Equihua, M. and M.B. Usher. 1993. Impacts of carpets of the invasive moss *Campylopus introflexus* on *Calluna vulgaris* regeneration. Journal of Ecology **81**: 359-365.

Flinn, M.A. and R.W. Wein. 1977. Depth of underground plant organs and theoretical survival during fire. Canadian Journal of Botany **55**: 2550-2554.

Foster, D.R. 1985. Vegetation development following fire in *Picea mariana* (black spruce)-*Pleurozium* forests of south-eastern Labrador, Canada. Journal of Ecology **73**: 517-534.

Frego, K.A. 1996. Regeneration of four boreal bryophytes: colonization of experimental gaps by naturally occurring propagules. Canadian Journal of Botany **74**: 1937-1942.

Furness, S.B. and J.P. Grime 1982. Growth rate and temperature response in bryophytes I: an investigation of *Brachythecium rutabulum*. Journal of Ecology **70**: 513-523.

Gloaguen, J.C. 1990. Post-burn succession on Brittany heathlands. Journal of Vegetation Science **1**: 147-152.

Hanssen, K.H. 2003. Natural regeneration of *Picea abies* on small clear-cuts in SE Norway. Forest Ecology and Management **180**: 199-213.

Heinken, T., R. Lees, D. Raudnitschka and S. Runge. 2001. Epizoochorous dispersal of bryophyte stem fragments by roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*). Journal of Bryology **23**: 293-300.

Hobbs, R.J. and C.H. Gimingham. 1984. Studies on fire in Scottish Highland communities II: post-fire vegetation development. Journal of Ecology **72**: 585-610.

Hörnberg, G., M. Ohlson and O. Zackrisson. 1997. Influence of bryophytes and microrelief conditions on *Picea abies* seed regeneration patterns in boreal old-growth swamp forests. Canadian Journal of Forest Research **27**: 1015-1023.

Huttunen, S. 2003. Reproduction of the mosses *Pleurozium schreberi* and *Pohlia nutans* in the surroundings of copper smelters at Harjavalta, S.W. Finland. Journal of Bryology **25**: 41-47.

Johnston, M.H. and J.A. Elliott. 1996. Impacts of logging and wildfire on an upland black spruce community in northwestern Ontario. Environmental Monitoring and Assessment **39**: 283-297.

Jonsson, B.G. and P-.A. Esseen. 1990. Treefall disturbance maintains high bryophyte diversity in a boreal spruce forest. Journal of Ecology **78**: 924-936.

Kalra, Y.P. and D.G. Maynard. 1991. Methods manual for forest soil and plant analysis. Information Report NOR-X319, Canadian Forest Service, Northwest Region. Edmonton, Alberta.

Kellner, O and H. Weibull. 1998. Effects of wood ash on bryophytes and lichens in a Swedish pine forest. Scandinavian Journal of Forest Research Supplement **2**: 76-85.

Kershaw, M., R. Wiltshire and C. Hollstedt. 1994. Critical silvics of feathermoss as related to vegetation management. VMAP Technical Report No. 94-03. Vegetation Management Alternatives Program, Ministry of Natural Resources, Ontario.

Kimmerer, R.W. 1994. Ecological consequences of sexual versus asexual reproduction in *Dicranum flagellare* and *Tetraphis pelucida*. The Bryologist **97**: 20-25.

Kimmerer, R.W. and C.C. Young. 1995. The role of slugs in dispersal of the asexual propagules of *Dicranum flagellare*. The Bryologist **98**: 149-153.

Lloyd, P.S. 1971. Effects of fire on the chemical status of herbaceous communities of the Derbyshire Dales. Journal of Ecology **59**: 261-273.

Longton, R.E. and S.W. Greene. 1979. Experimental studies of growth and reproduction in the moss *Pleurozium schreberi* (Brid.) Mitt. Journal of Bryology **10**: 321-338.

Maltby, E., C.J. Legg and M.C.F. Proctor. 1990. The ecology of severe moorland fire on the North York Moors: effects of the 1976 fires, and subsequent surface and vegetation development. Journal of Ecology **78**: 490-518.

Mandre M., H. Parn and K. Ots. 2006. Short-term effects of wood-ash on the soil and the lignin concentration and growth of *Pinus sylvestris* L. Forest Ecology and Management **223**: 349-357.

McCune, B. & M. J. Mefford. 1999. PC-ORD. Multivariate analysis of ecological data, ver. 4.0. MJM Software Glenenden Beach, Oregon.

McDaniel, S.F. and N.G. Miller. 2000. Winter dispersal of bryophyte fragments in the Adirondack Mountains, New York. The Bryologist **103**: 592-600.

Mishler, B.D. and A.E. Newton. 1988. Influences of mature plants and desiccation on germination of spores of gametophytic fragments of *Tortula*. **15**: 327-342.

Monique, M., P.D. Heijmans, W.J. Arp and F.S. Chapin III. 2004. Controls on moss evaporation in a black spruce forest. Global Biogeochemical Cycles **18**: GB2004, doi:10.1029/2003GB002128

Morneau C. and S. Payette 1989. Postfire lichen-spruce woodland recovery at the limit of the boreal forest in northern Quebec. Canadian Journal of Botany **67**: 2770-2782.

Myrmael, A. 1993. Regeneration studies of five spruce, *Picea abies*, forest bryophytes. Lindbergia **18**: 7-18.

Ne'eman, G., S. Goubitz, and R. Nathan. 2004. Reproductive traits of *Pinus halepensis* in the light of fire - a critical review. Plant Ecology **171**: 69-79.

Nilsson, M.-C., I. Steijlen and O. Zackrisson. 1996. Time restricted seed regeneration of Scots pine in sites dominated by feather moss after clear-cutting. Canadian Journal of Forest Research **26**: 945-953.

Nguyen-Xuan, T., Y. Bergeron, D. Simard, J.W. Fyles and D. Paré. 2000. The importance of forest floor disturbance in the early regeneration patterns of the boreal forest of western and central Quebec: a wildfire versus logging comparison. Canadian Journal of Forest Research **30**: 1353-1364.

Nygaard, P.H. and T. Odegaard. 1999. Sixty years of vegetation dynamics in a south boreal coniferous forest in southern Norway. Journal of Vegetation Science **10**: 5-16.

Parent, S., M.-J. Simard, H. Morin and C. Messier. 2003. Establishment and dynamics of the balsam fir seedling bank in old forest of northeastern Quebec. Canadian Journal of Forest Research **33**: 597-603.

Parker, W.C., S.R. Watson, and D.W. Cairns. 1997 The role of hair-cap mosses (*Polytrichum* spp.) in natural regeneration of white spruce (*Picea glauca* (Moench) Voss). Forest Ecology and Management **92**: 19-28.

Ringius, G.S. and R.A. Sims. 1997. Indicator Plant Species in Canadian Forests. Canadian Forest Service, Ottawa, Canada.

Ross-Davis, A.L. and K.A. Frego. 2004. Propagule sources of forest floor bryophytes: spatiotemporal composition patterns. The Bryologist **107**: 88-97.

Rowe, J.S. and G.W. Scotter. 1973. Fire in the boreal forest. Quaternary Research **3**: 444-464.

Rydgren, K., R.H. Økland and T. Økland. 1998. Population biology of the clonal moss *Hylocomium splendens* in Norwegian boreal spruce forests. 4. Effects of experimental disturbance. Oikos **82**: 5-19.

Rydgren, K. and R.H. Økland. 2001. Sporophyte production in the clonal moss *Hylocomium splendens*: the importance of shoot density. Journal of Bryology **23**: 91-96.

Schimmel, J. and A. Granstrom. 1996. Fire severity and vegetation response in the boreal Swedish forest. Ecology **77**: 1436-1450.

SPSS Inc. 2002. SPSS Base 11.0 for Windows User's Guide. SPSS Inc., Chicago, Illinois.

Thomas, P.A., M.C.F. Proctor and E. Maltby. 1994. The ecology of severe moorland fire on the North York Moors: chemical and physical constraints on moss establishment from spores. Journal of Ecology **82**: 457-474.

Van Wagner, C.E. 1983. Fire behaviour in northern coniferous forests and shrublands. Pages 65-80 *in* R.W. Wein, and D.A. MacLean, editors. The Role of Fire in Northern Circumpolar Ecosystem. John Wiley and Sons, New York, USA.

Viro, P.J. Effects of forest fire on soil. Pages 7-46 *in* T.T. Kozlowski and C.E. Ahlgren, editors. Fire and Ecosystems. Academic Press, New York, USA.

Watson, M.A. 1981. Chemically mediated interactions among juvenile mosses as possible determinants of their community structure. Journal of Chemical Ecology **7**: 367-376.

Zackrisson, O., M.-C. Nilsson, A. Dahlberg and A. Jäderlund. 1997. Interference mechanisms in conifer-Ericaceae-feathermoss communities. Oikos **78**: 209-220.

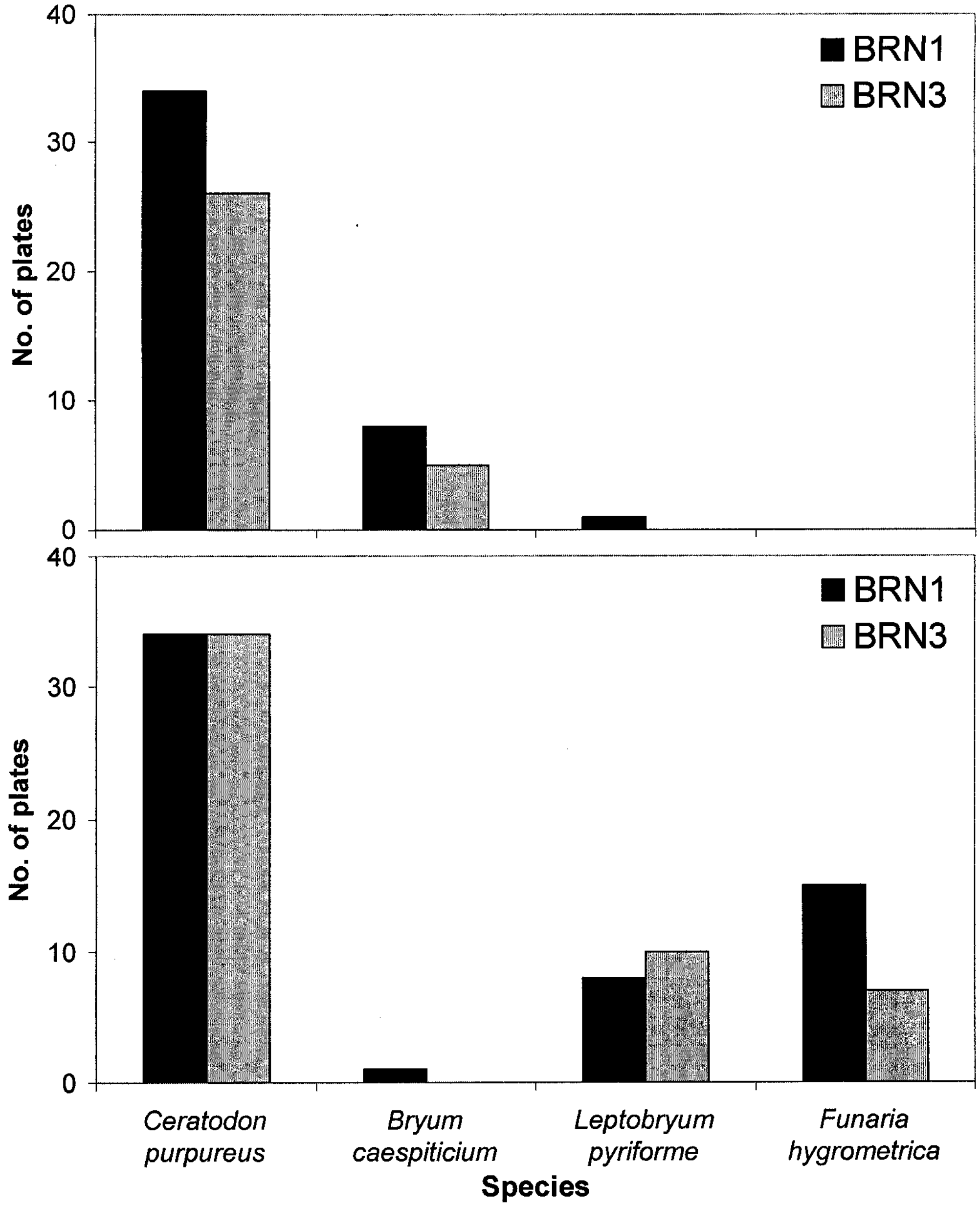


Figure 2.1 Histograms showing the number of Petri Plates exposed to the diaspore rain in which the four most common moss species were found. Plates were exposed in two sites, BRN1 and BRN3, in July 2002 (top) and August 2002 (bottom).

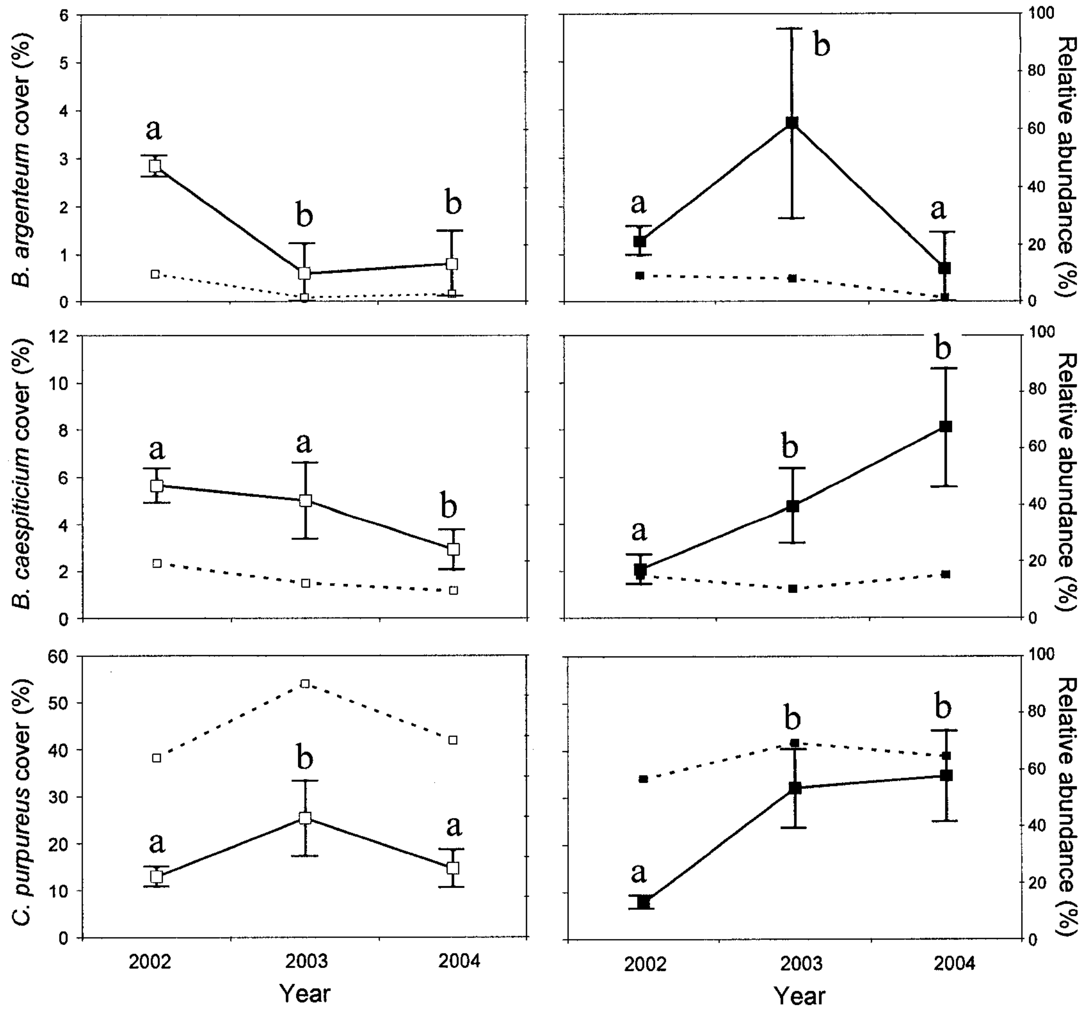


Figure 2.2 Trends in the relative abundance (dashed lines) and mean percent cover, with 95% confidence intervals (solid lines), of mosses in BRN1 (left) and BRN3 (right) over the first three years after the Chisholm Fire. Lower case letters show significant differences between years found using Multiple Response Permutation Procedure. Effects sizes and *P*-values are given in Tables A.1 and A.2 in the Appendix.

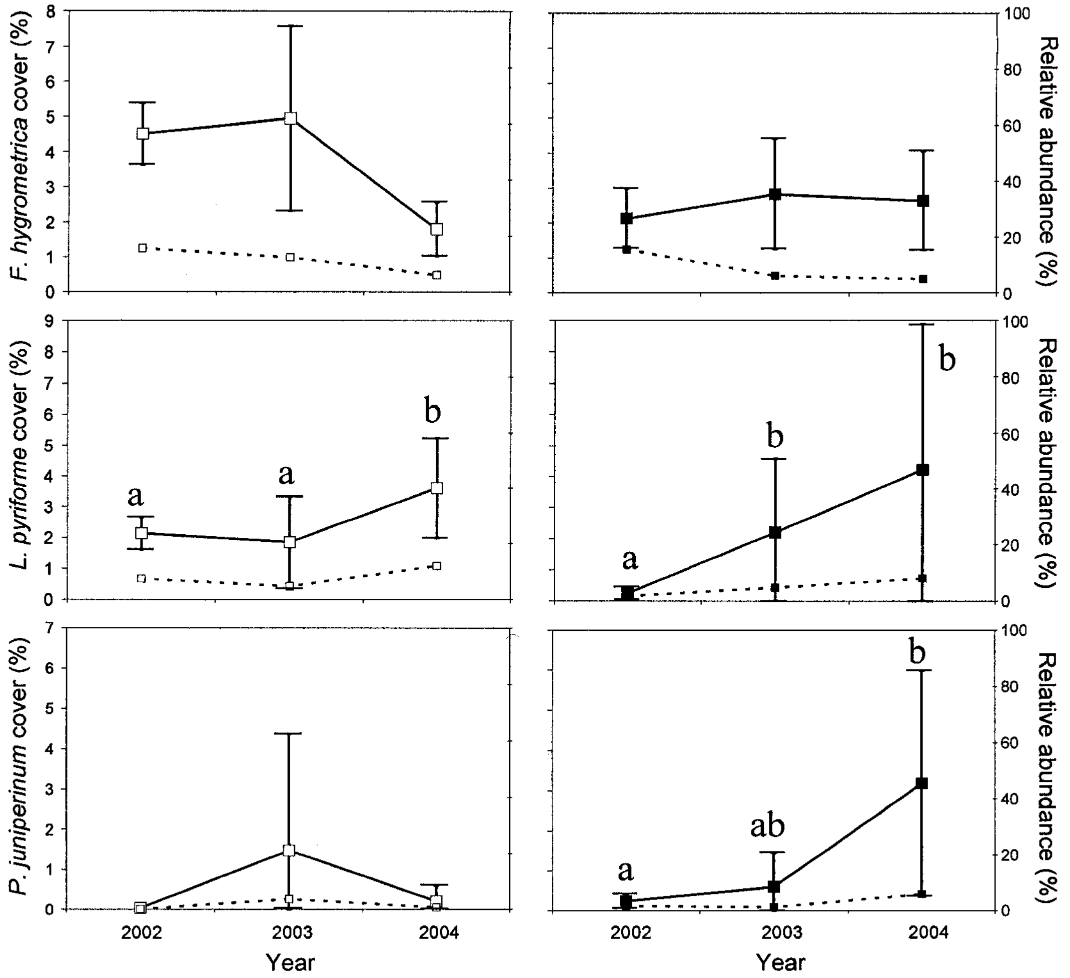


Figure 2.3 Trends in the relative abundance (dashed lines) and mean percent cover, with 95% confidence intervals (solid lines), of mosses in BRN1 (left) and BRN3 (right) over the first three years after the Chisholm Fire. Lower case letters show significant differences between years found using Multiple Response Permutation Procedure. Effects sizes and *P*-values are given in Tables A.1 and A.2 in the Appendix.

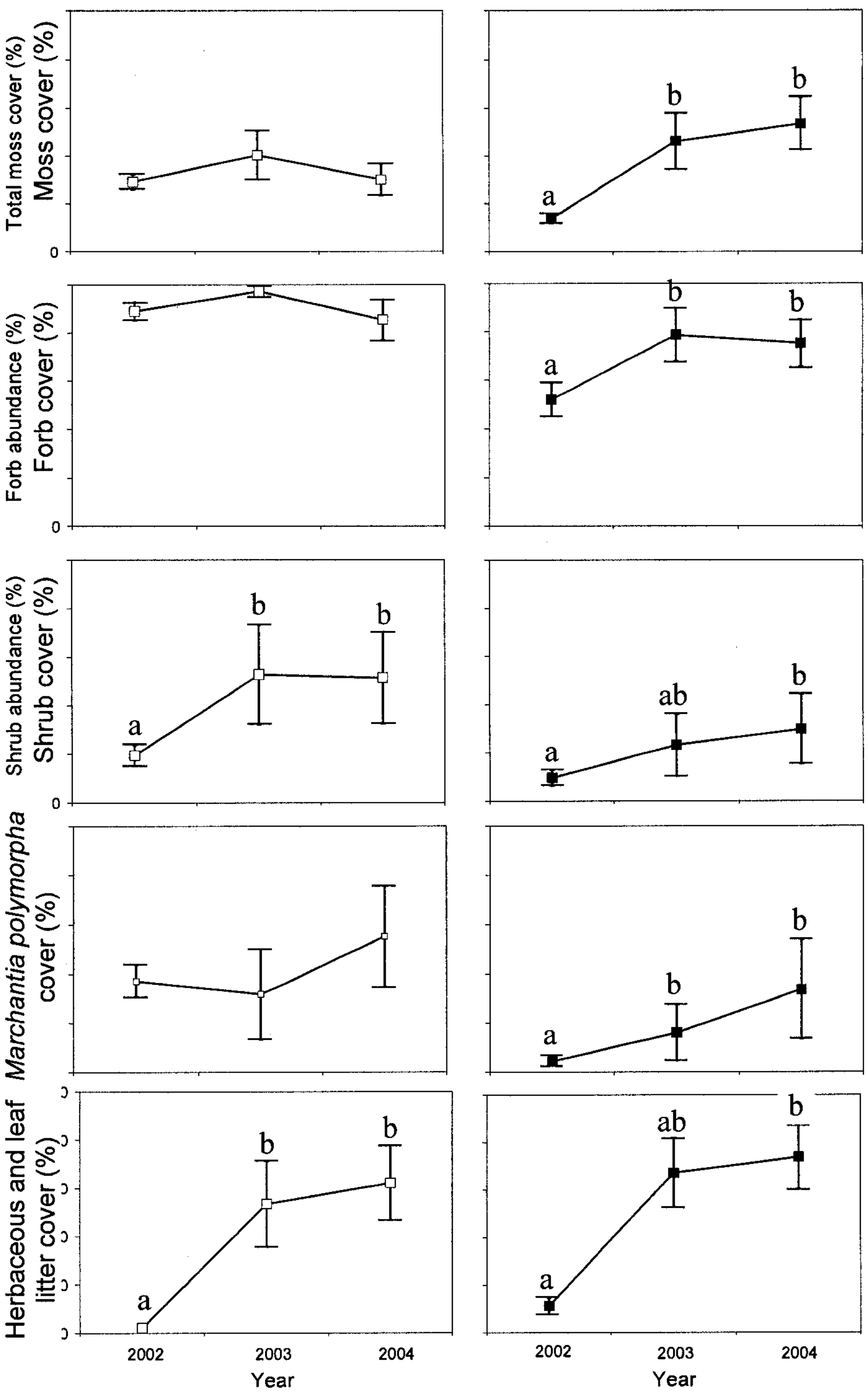


Figure 2.4 Trends in mean values (with 95% CI) of environmental variables and *Marchantia polymorpha* in BRN1 (left) and BRN3 (right). Lower case letters show significant differences between years found using MRPP. Effects sizes and *P*-values are given in Tables A.1 and A.2 in the Appendix.

Table 2.1 Bryophytes recorded in burned and unburned white spruce stands in and around the 2001 Chisholm Fire in Alberta, Canada, during the first, second and third growing seasons (2002 – 2004) after the fire.

	Burned sites								Unburned sites		
	2002		2003				2004		2004		
Species	BRN1	BRN3	BRN1	BRN2	BRN3	BRN4	BRN1	BRN3	GRN1	GRN2	GRN3
Amblystegium sp.	-	-	-	-	-	-	-	-	-	M	M
Aulacomnium palustre	0.40	-	-	M	-	-	M	-	M	-	M
Barbula convoluta	0.23	-	-	-	-	-	0.04	-	-	-	-
Brachythecium salebrosum	-	-	-	M	-	-	M	-	M	M	M
Brachythecium spp.	0.18	-	0.09	<0.01	-	-	0.22	-	3.84	3.71	1.53
Bryum argenteum	2.85	1.27	0.04	0.07	1.49	0.16	0.04	0.09	-	-	-
Bryum caespiticium	5.65	2.06	2.54	0.57	2.40	0.22	0.79	4.47	<0.01	M	-
Bryum sp.	-	-	-	M	-	M	M	M	M	-	M
Campylium hispidulum	-	-	-	-	-	-	M	-	-	M	-
Ceratodon purpureus	13.01	7.81	22.45	21.63	31.32	4.78	12.25	34.83	<0.01	-	-
Dicranum flagellare	-	-	-	-	-	-	-	-	-	M	-
Dicranum fragilifolium	-	-	-	-	-	-	-	-	M	-	-
Dicranum fuscescens	-	-	-	-	-	-	-	-	-	-	M
Dicranum polysetum	-	-	-	-	-	-	-	-	-	-	0.02
Dicranum scoparium	-	-	-	-	-	-	-	-	M	M	M
Dicranum sp.	-	-	-	-	-	-	-	-	M	-	M
Dicranum undulatum	-	-	-	-	-	-	-	-	-	-	M
Ditrichum sp.	-	-	-	-	-	-	-	-	-	-	M
Eurhynchium pulchellum	-	-	-	-	-	-	0.03	-	0.55	0.23	1.01
Funaria hygrometrica	4.51	2.13	2.60	2.24	0.71	0.05	0.10	0.56	-	-	-
Herzogiella turfacea	-	-	-	-	-	-	-	-	-	M	-
Hylocomium splendens	-	-	-	-	-	-	-	-	1.04	6.56	10.92
Hypnum pratense	-	-	-	-	-	-	-	-	-	-	M
Hypnum revolutum	-	-	-	-	-	-	-	-	-	-	M
Hypnum sp.	-	-	-	-	-	-	M	-	M	M	M
Isopterygiopsis pulchella	-	-	-	-	-	-	0.29	-	-	-	0.04
Jamesoniella autumnalis	-	-	-	-	-	-	M	-	-	0.02	M
Lepidozia reptans	-	-	-	-	-	-	-	-	-	-	M
Leptobryum pyriforme	2.13	0.24	0.32	0.01	1.17		0.92	2.79	0.01	-	-
Lophozia sp.	-	-	-	-	-	-	M	-	M	M	-
Marchantia polymorpha	37.25	4.28	1.11	1.04	0.27	-	23.73	4.73	0.29	-	-
Mnium sp.	-	-	-	-	-	-	-	-	M	M	M
Oncophorus wahlenbergii	-	-	-	-	-	-	-	-	M	<0.01	M
Orthotrichum speciosum	-	-	-	M	-	-	M	-	0.01	0.01	0.01
Plagiochila asplenioides	-	-	-	-	-	-	-	-	-	-	M
Plagiomnium cuspidatum	-	-	-	-	-	-	-	-	M	M	M
Plagiomnium medium	-	-	-	-	-	-	-	-	M	-	M
Plagiomnium spp.	-	-	-	-	-	-	-	-	19.32	1.88	0.43
Plagiothecium sp.	0.09	-	-	-	-	-	-	-	0.01	-	-
Platydictya jungermannioides	-	-	-	M	-	-	-	-	M	-	-
Platygyrium repens	-	-	-	-	-	-	-	-	-	-	M
Pleurozium schreberi	-	-	-	-	-	-	-	-	1.36	3.37	7.77
Pohlia nutans	-	-	-	-	-	-	-	-	0.05	0.01	M
Polytrichum commune	-	-	-	-	-	-	-	-	M	M	M
Polytrichum juniperinum	0.03	0.24	0.79	-	0.07	M	0.02	0.75	M	M	M

Values are percent cover estimates from quadrat surveys and M indicates species recorded only during meanders; dashes indicate that species were not found.

The survey protocol was changed between 2002 and 2003; details are given in the text.

Table 2.1 (cont.) Bryophytes recorded in burned and unburned white spruce stands in and around the 2001 Chisholm Fire in Alberta, Canada, during the first, second and third growing seasons (2002 – 2004) after the fire.

	Burned sites								Unburned sites		
	2002		2003				2004		2004		
Species	BRN1	BRN3	BRN1	BRN2	BRN3	BRN4	BRN1	BRN3	GRN1	GRN2	GRN3
Polytrichum strictum	-	-	-	-	-	-	-	-	M	-	-
Ptilidium pulcherrimum	-	-	-	-	-	-	-	-	0.02	M	M
Ptilium crista-castrensis	-	-	-	-	-	-	-	-	1.49	3.06	7.95
Pylaisiella polyantha	-	-	-	-	-	-	-	-	M	0.08	M
Rhizomnium sp.	-	-	-	-	-	-	-	-	-	M	-
Rhytidiadelphus triquestris	-	-	-	-	-	-	-	-	-	-	3.28
Sanionia uncinata	-	-	-	-	-	-	-	-	0.30	0.31	<0.01
Sphagnum angustifolium	-	-	-	-	-	-	-	-	-	-	M
Sphagnum girgensohnii	-	-	-	-	-	-	-	-	M	-	-
Sphagnum squarossum	-	-	-	-	-	-	-	-	M	-	M
Sphagnum teres	-	-	-	-	-	-	-	-	-	-	M
Tetraphis pellucida	-	-	-	-	-	-	-	-	M	-	-
Thuidium recongitum	-	-	-	-	-	-	-	-	-	-	M
Unidentified liverwort	-	-	-	M	-	-	M	M	-	-	M
Warnstorfia fluitans	-	-	-	-	-	-	-	-	-	-	M

Values are percent cover estimates from quadrat surveys and M indicates species recorded only during meanders; dashes indicate that species were not found.

The survey protocol was changed between 2002 and 2003; details are given in the text.

Table 2.2 Mean protonema counts (± 1 standard deviation) in opened (exposed) and unopened (control) Petri Plates placed along transects across the survey plots in two unburned sites (BRN1 and BRN3) in July and August 2002.

	Exposed		Control	
Date	Percent of plates with protonemata	Mean no.of protonemata/plate	Percent of plates with protonemata	Mean no.of protonemata/plate
BRN1				
July 2002	100	329.64 ± 186.69	28	1.22 ± 3.44
August 2002	100	263.21 ± 279.47	56	9.22 ± 27.42
BRN3				
July 2002	94	59.61 ± 35.32	0	0
August 2002	100	114.06 ± 37.39	22	0.44 ± 1.01

Chapter 3: Short-term survival of gametophyte fragments of *Pleurozium schreberi* (Brid.) Mitt. and *Ptilium crista-castrensis* (Hedw.) De Not. on early successional substrates

Ecological succession can be defined as a process of change in the composition and structure of a species assemblage over time (Gurevitch et al. 2002). This process generally involves a combination of changes in the relative abundance and a series of local colonization and extinction events. For example, in post-fire succession in boreal white spruce (*Picea glauca* (Moench) Voss) forests, many vascular plant species (e.g. *Cornus canadensis* L., *Mertensia paniculata* (Ait.) G. Don., *Rubus ideaus* L., *Populus tremuloides* Michx., *Populus balsamifera* L. and *Picea glauca*) appear early in succession and can still be found in mid to late successional stages. In contrast, many boreal bryophytes that are common in mature white spruce forests are absent in early successional stages, and vice versa.

The pleurocarpous boreal feather mosses *Pleurozium schreberi* and *Ptilium crista-castrensis* (hereafter referred to as *Pleurozium* and *Ptilium*) show a distinct temporal trend in abundance in white spruce-dominated boreal forests in Alberta, Canada. In a 2004 survey of bryophytes in three unburned white spruce stands near the boundary of the 2001 Chisholm Fire, *Pleurozium* and *Ptilium* were found to be among the most widespread species on the forest floor, whereas they were not found in burned stands in the first three years of succession (Chapter 2). These findings are consistent with literature reports that indicate that although *Pleurozium* and *Ptilium* are frequent on the forest floor of mature to old growth white spruce forests, they are not usually found in studies of the earliest stages of post-fire succession (see, for example, O'Toole and Synnott 1971; Rowe and Scotter 1973; Viro 1974; Hobbs and Gimingham 1984; Foster 1985; Gloaguen 1990; Maltby et al. 1990; Thomas et al. 1994; Esposito et al. 1999).

Two hypotheses that may explain the absence of *Pleurozium* and *Ptilium* from early successional stages are: (i) habitat intolerance; and (ii) dispersal limitation (Fig. 1.1). Habitat intolerance is suggested by the contrast in environmental conditions between early successional stages and those in which *Pleurozium* and *Ptilium* are abundant. There is no tree canopy in the earliest stages of post-fire succession to create shade; studies have found reduced growth in late successional mosses as a result of high light intensity and evaporation stress (Busby et al. 1978; Longton and Greene 1979). Substrates also differ between early and late successional stages. Fires consume humus on the soil surface, exposing mineral soil. They can also leave a layer of ash, charred fine woody debris and duff (Ahlgren 1960; Viro 1974; Flinn and Wein 1977; Van Wagner 1983; Schimmel and Granstrom 1996; Ne'eman et al. 2004; Certini 2005). Charred and mineral substrates can have an alkaline pH and contain potentially toxic ions (Lloyd 1971; Brown 1982; Thomas et al. 1994; Kellner and Weibull 1998; Ne'eman et al. 2004; Mandre et al. 2006). Feather mosses are indicative of acidic, organic substrates (Ringius and Sims 1997). The dispersal limitation hypothesis is based on the rarity of sexual reproduction in *Pleurozium* and *Ptilium*. Research has shown that gametophyte fragments of these species have the potential to act as propagules following short-distance dispersal in mature forests (Longton and Greene 1979;

Myrmael 1993; Kershaw et al. 1994; Kimmerer 1994; Frego 1996; Rydgren et al. 1998; Rydgren and Økland 2001; Huttunen 2003). Little is known about the long distance dispersal of vegetative fragments, although previous studies have identified several potential vectors, including slugs (Kimmerer and Young 1995), snowmelt (McDaniel and Miller 2000), deer and wild boar (Heinken et al. 2001).

The habitat intolerance hypothesis can be tested by sowing propagules under conditions they would encounter early in succession. If they survive, it would disprove the habitat intolerance hypothesis and support dispersal limitation. This chapter describes the first of two limited tests of this hypothesis. The objective of this study is to address the question of whether *Pleurozium* and *Ptilium* can survive and grow on common post-fire substrates. Chapter 4 describes studies that test survival and growth under high levels of exposure and different hydration regimes in recently burned forests. Survival and growth are tested because both are essential if a fragment is to establish a new colony.

It was beyond the scope of this study to examine propagule survival at different stand ages so we collected substrates from a two-year old burned forest to represent conditions at a very early stage of succession. This study was also restricted to survival and growth of fragments because we could easily observe changes in their condition and recover them at the end of the study.

Materials and Methods

Study sites

For study sites we used three closed-canopy unburned white spruce stands on the boundaries of the Chisholm Fire, which took place in north-central Alberta in 2001. Stands will be referred to as GRN1, GRN2 and GRN3 and are described in more detail in Chapter 2.

Study species

Pleurozium schreberi

Pleurozium schreberi is a dioecious, pinnately branched perennial pleurocarpous feather moss (Fig. 3.1). It is regarded as a climax species in closed and semi-open coniferous boreal forests and bogs (Kershaw et al. 1994). In bogs it is restricted to drier sites and is most abundant at 30 cm above the water table (Mulligan and Gignac 2002). *Pleurozium* can tolerate a variety of substrates, including organic humus, exposed mineral soil, rotting logs and stumps and *Sphagnum* hummocks (Crum and Anderson 1981; Kershaw et al. 1994). It may be an indicator of acidic conditions and is not usually found on calcareous soils (Kershaw et al. 1994)

In some populations of *Pleurozium* spore production can be rare (Crum and Anderson 1981). The clonal growth form of this species may result in archegonia and antheridia that are too far apart to allow sexual reproduction. In some cases, plants bearing antheridia may be entirely absent from the population (Longton and

Greene 1979). Under experimental conditions viable spores have shown high germination rates. Longton and Greene (1979) found that over 95% of spores that were not aborted in the capsule germinated on agar. Leaves, shoots and multiple-branching gametophyte fragments may also be effective propagules if they originate from close to the stem apex (Bates 1979). Previous studies suggest that short-distance dispersal of gametophyte fragments into gaps on the forest floor is an important mode of colony expansion in mature spruce forests (Kimmerer and Young 1995; Frego 1996).

Ptilium crista-castrensis

Ptilium differs morphologically from *Pleurozium* in that gametophyte branches grow in a single plain and the shoots produced along the main axis are apparently determinate in their growth in length. The structure of a typical *Ptilium* branch is similar to that of a feather, with side shoots being analogous to barbs (Fig. 3.1). Small, bulbous leaf clusters are produced along the main axis, but their function is not known.

Few studies have been conducted on the ecology of *Ptilium. Ptilium* is associated with organic humus and rotting wood in mesic coniferous forests. Where it occurs with *Pleurozium* and *Hylocomium splendens*, it is often the least common of the three species. Carter and Arocena (2000) hypothesized that *Ptilium* has different elemental requirements from *Pleurozium* because they found that tissues from specimens of these species growing on sandy soils in British Columbia showed different levels of Fe, Al and Mg. Their results also indicated that each species has different effects on soil properties; a higher intensity of podzolization was suggested under *Ptilium* and soils under this species had a thicker Ae horizon and more Fep + Alp in the Bf horizon. Clay mineral composition also differed between species.

Preparation of fragments

In June 2003, we collected gametophyte material of *Pleurozium* and *Ptilium* from a mature *Picea mariana*/*Picea glauca* stand in northern Alberta. We produced gametophyte fragments from this material by brushing it against a fine soil sieve to dislodge the tips of branches. Fragments with branches, buds or broken tips were rejected. The mean initial length (± 1 standard deviation) of 10 randomly selected fragments was 8.2 ± 2.3 mm for *Pleurozium* and 5.6 ± 1.4 mm for *Ptilium* (Fig. 3.1).

Preliminary results suggested that these fragments were poor propagules, so we set up a second experiment in May 2004 using larger fragments. We produced these by cutting the main axis of gametophyte branches at approximately 40 mm from the apex with a pair of scissors (Fig. 3.1). Initial mean lengths, calculated from 10 randomly selected fragments, were *Pleurozium* 37.1 ± 2.1 mm, *Ptilium* 37.7 ± 1.3 mm. Fragments created in 2003 are hereafter referred to as small fragments and those made in 2004 will be called large fragments. These terms are used only to reflect the relative difference in size.

Substrate collection and preparation

Four substrates were used in this study: ash (AS), burned moss (BM), mineral soil (MS) and unburned humus (UH). We cut mineral soil from the top 2 cm of exposed soil in a *Picea mariana* stand that burned in the House River Fire in northern Alberta in 2002. This site was chosen because existing moss cover on mineral soil was low. We collected clumps of BM, consisting of charred but identifiable remains of *Pleurozium, Ptilium, Hylocomium splendens* and *Dicranum polysetum*, from the same site. AS was collected from a camp fire on which we burned logs of *Picea glauca*, *Populus tremuloides*, *Populus balsamifera* and *Betula papyrifera*. We obtained UH from under live feather mosses in GRN2 and GRN3.

We collected substrates in June 2003 for the small fragment experiment and in May 2004 for the large fragment study. To determine the initial mean pH of each substrate, we calculated the mean of six samples when trays were placed in the field. We recorded final pH as the mean of five samples of each substrate in each stand (one from each block) when trays were recovered.

Field protocol

In July 2003 we filled 480 62.5 × 62.5 mm plastic pots to a depth of approximately 75 mm with the experimental substrates. We attempted to maintain the vertical profile of MS and BM but disregarded the dominant species in BM. Mosses growing on MS and gametophyte fragments found in UH were removed.

Pots were allocated to one of 20 blocks of 24 pots, each block containing 6 pots of each substrate. We used a restricted randomised design to ensure that substrates were evenly distributed in blocks (Fig. 3.2). This protocol was repeated in May 2004 except that we prepared only 5 blocks, each containing 36 pots (9 pots of each substrate per block) because we had insufficient time to create additional replicates.

In the small fragment experiment, we placed one *Pleurozium* fragment in each of two replicates of each substrate in each block. To secure fragments in pots, we tied them to plastic-coated aluminium paper clips with cotton thread. Each clip was bent and inserted into the substrate. We repeated this protocol with *Ptilium* fragments and left two replicates (blanks) of each substrate in each tray to see if unsown fragments of the study species grew on any of the substrates (Fig. 3.2). We duplicated this protocol for the large fragment experiment except that in each block we placed fragments of each species in three replicates of each substrate and three replicates were left as blanks.

For both the small and the large fragment experiment, we placed five blocks in each study site. For the small fragment experiment, we put blocks in all three study sites. For the large fragment experiment we put all blocks in one site (BRN2). One block was placed in the centre of a 2500 m^2 plot that had been marked out for species surveys (Chapter 2). The other blocks were placed at four locations around this block, at directions N, S, E and W and random distances greater than 5 m from it. The actual distance of each block was haphazardly determined by hurling a tennis ball. We placed blocks in hollows made by removing forest floor humus to a depth equal to the pot height and removed growing mosses from a 15 cm perimeter around each block.

Survival measures

All pots were recovered between August 24 and 27, 2004. We considered fragments to be alive if the gametophyte material was green, if new shoots were present or if filamentous growth (protonemata or rhizoids) were attached. For each treatment combination, we calculated survivorship as a weighted proportion using the formula $(A_{sp.i}/R_{sp.i}) \times (R_{sp.i}/S_{sp.i})$, where

A is the number of recovered fragments of species i (sp$i$) that were alive,

R is the number of fragments of species i that were recovered, and

S is the number of fragments of species i that were sown.

We used this weighting to avoid overestimating survivorship because we found that when recovery rates were high, the proportion of recovered fragments that are found alive was likely to be a reasonable estimate of the proportion in the population, but as recovery rate decreased, the estimate became less reliable. For example, if only one fragment is recovered and alive, an unweighted proportion would show that 100% of fragments survived without accounting for the fact that most were not recovered.

In both experiments, we further assessed survival potential by measuring variables that reflect fragment growth. This was based on the assumption that if, on average, fragments were larger on some substrates than others, this should reflect growth rather than differences in initial size. We assumed that higher rates of growth would indicate an increased probability of survival. For small fragments we measured total fragment length. For large fragments we measured dry weight, length of the main axis (LMA) and the number of first-order side branches (SB).

Large fragments were washed and air dried for 48 hours prior to weighing but we could not remove some grains of AS and MS that were under leaves.

Statistical analyses

We analysed survival data using stepwise binary logistic regression (SPSS version 11.5, SPSS Inc. 2002). The variables we included were species, substrate (each level entered as a dummy variable), stand, mean initial H+ concentration for each substrate, final mean H+ concentration for each substrate in each stand, bryophyte cover in the pot and species × substrate interactions. All except bryophyte cover were entered as categorical indicator variables. We measured bryophyte cover by placing a plastic grid of 68 squares over each pot and determining the proportion of squares that were more than 50% covered by moss.

We used a general linear model (GLM) was used to test the effects of stand and substrate on the final length of small fragments and the final dry weight of large fragments. Post hoc pairwise comparisons were done using a Bonferroni test. A Levene's test showed that variances were not homogeneous so we log transformed data prior to analysis.

LMA and SB could not be normalised so we compared substrates within species using Multiple Response Permutation Procedure (MRPP), with Euclidean distances (PC-ORD for Windows version 4.14; McCune and Mefford 1999). MRPP is a non-parametric method that compares groups on the basis of mathematical distances between sampling units. For details see Chapter 2.

To test whether survivorship on each substrate in each stand was correlated with the mean initial and mean final pH of each substrate, we calculated Spearman's rank correlation coefficients.

Results

Survival

Small fragments

Of the 78 *Ptilium* fragments recovered (65.0% of those sown), we found only one alive at the end of the study (weighted proportion = 0.8%). In contrast, 96 *Pleurozium* fragments were recovered (80.0% of those sown) and 53 were alive (weighted proportion = 44.2%). Three fragments, all *Pleurozium*, survived on AS (weighted proportion = 5.0% of all fragments on AS). Fragments were much less likely to be found alive on AS compared with BM (weighted proportion = 30.0%), MS (weighted proportion = 28.3%) and UH (weighted proportion = 26.7%). *Ptilium* fragments were found alive only on MS (2 fragments) and UH (2 fragments). Summary statistics are given in Table 3.1.

Species (SE: 1.183, $Z = 2.112$, $P<0.035$, odds ratio 12.158) and an AS × species interaction (SE: 0.669, $Z = 3.857$, $P<0.001$, odds ratio 13.194) were significant predictors of survival in the logistic regression model ($\chi^2 = 94.06$, df = 2; $P<0.001$). The model correctly predicted 83.9% of cases. The final model was:

$$\text{Predicted logit (survival)} = -4.344 + (2.498 \times \text{species}) - (2.580 \times [\text{ash} \times \text{species}])$$

Because of the low survivorship of small fragments on AS, it was excluded from the Spearman's rank correlation analyses. For the other four substrates there were no significant correlations between survivorship and initial or final pH.

Large fragments

Thirty-eight replicates containing fragments (21 *Pleurozium*, 17 *Ptilium*) were destroyed by animals while the experiment was running. In our analyses we assumed that these fragments had not been sown. We recovered all 39 of the remaining *Pleurozium* fragments that were sown and 40 of the 43 remaining *Ptilium* fragments (93.0%). Recovery rates for fragments on different substrates were 100.0% for MS ($n = 20$) and 95.0% for AS ($n = 20$), BM ($n = 21$) and UH ($n = 21$). All recovered fragments were green at the end of the experiment and we could not identify new growth with certainty. Therefore, we assumed that survivorship was 100% and no statistical tests were run on survival data.

Fragment condition

Small fragments

Due to the low sample size of *Ptilium* (4 fragments), we only measured final lengths for small *Pleurozium* fragments. We also excluded ash replicates from the substrate treatments because two of the four fragments found alive on this substrate were incomplete. The mean final lengths (± 1 standard deviation) of fragments on all other substrates were BM: 18.53 ± 10.42, $n = 18$; MS: 19.73 ± 15.24, $n = 22$; and UH: 16.63 ± 13.73, $n = 12$. We found no significant differences between substrates.

Large fragments

Figure 3.3 shows the mean dry weight, mean LMA and mean SB for large fragments. The growth of *Pleurozium* fragments was lower on burned substrates than on UH and there were statistically significant differences between the mean dry weights and mean SBs of fragments on UH and AS (dry weight: $F_{3, 34} = 3.43$, $P = 0.028$; Bonferroni test: $P = 0.030$; SB: $T = -2.591$, $\delta_{\text{observed}} = 8.055$, $A = 0.140$, $P = 0.027$). *Ptilium* fragments on AS had significantly lower mean dry weight than those on MS or UH (AS v UH: $F_{3, 33} = 5.20$, $P = 0.005$; Bonferroni tests: AS v UH $P = 0.005$, AS v MS $P = 0.041$). The mean LMA of *Ptilium* was highest on BM and significantly higher on BM than on AS ($T = -4.905$, $\delta_{\text{observed}} = 5.756$, $A = 0.225$, $P = 0.003$). The mean SB of *Ptilium* was highest on MS and there was a significant difference between MS and AS ($T = -5.642$, $\delta_{\text{observed}} = 1.479$, $A = 0.362$, $P = 0.001$), MS and BM ($T = -7.655$, $\delta_{\text{observed}} = 1.229$, $A = 0.407$, $P < 0.001$), and UH and BM ($T = -2.544$, $\delta_{\text{observed}} = 1.382$, $A = 0.099$, $P = 0.028$).

Presence of unsown fragments

Unsown fragments were least likely to be found on AS (*Pleurozium* 0, *Ptilium* 1) and most likely to be found on UH (*Pleurozium* 7, *Ptilium* 10). We also found unsown fragments on 4 BM blanks (1 *Pleurozium,* 3 *Ptilium*) and 4 MS blanks (3 *Pleurozium*, 1 *Ptilium*).

Substrate pH

Mean initial and final pH values for each substrate are given in Table 3.2. AS had the highest initial and final pH in all cases. In the small fragment experiment the organic substrates increased in pH over the study period and the mineral substrates became more acidic or remained unchanged. In the large fragment experiment the pH of AS and UH decreased and that of MS and BM increased.

Discussion

Substrate effects

The results of this study do not support the hypothesis that *Pleurozium schreberi* and *Ptilium crista-castrensis* are excluded from recently burned stands because they are intolerant of burned and mineral substrates. Short-term survival and growth of small *Pleurozium* fragments was similar on all substrates except AS. Less than one percent of small fragments survived on AS (Table 3.1). Furthermore, the mean values of the growth variables of large fragments were almost always lowest on AS. These results are concordant with the classification of *Pleurozium* as a calcifuge moss (Bates and Farmer 1990; Bharali and Bates 2004) and the tendency for *Pleurozium* and *Ptilium* to grow on acidic organic humus. Intolerance of high pH could explain the reduced survival and growth of *Pleurozium* and *Ptilium* on AS. The initial pH of AS in this study was relatively high at 10.4 in the small fragment experiment and 9.5 in the large fragment experiment. This could be due to the presence of soluble oxides and hydroxides (Kellner and Weibull 1998).

High concentrations of phosphorous, potassium, ammonia and calcium have also been reported in ash (Ahlgren 1960; Lloyd 1971). Strengbom et al. (2001) and Hartley and Mitchell (2005) reported adverse reactions from *Hylocomium splendens* to NH_4NO_3 and Jappinen and Hotanen (1990, cited in Bates 2000) found that fertilization with rapidly soluble PK and NPK had a "burning" effect on gametophytes of *Pleurozium schreberi* and *Hylocomium splendens*. Kellner and Weibull (1998) recorded similar effects in *Ptilium crista-castrensis* and *Hylocomium splendens* after applications of loose and crushed ash in a Swedish Pine forest. Streeter (1970) and Vanderpoorten and Klein (1999; both cited in Bates 2000) suggested that negative effects of Ca can occur due to a synergistic relationship with pH.

Although we found that survival and growth were not consistently reduced on BM (Fig. 3.3, Table 3.1), the tolerance that fragments would have for this substrate under natural conditions may be less than was suggested by these results. We included BM because it is commonly left by less severe fires. Structurally, it is similar to living carpets of feather moss, but the charred gametophyte surfaces are hard and appear to have low water absorption potential (personal observation). Furthermore, the blackened surface of a burned moss carpet would be conducive to rapid evaporation. These characteristics could make it a hostile substrate (Chapter 5). In the site from which BM was collected, we noted that this material was always dry, but in many pots that were recovered from the field, it was moist. Limiting drainage by placing material in pots may have reduced moisture loss. Because pots were located in closed canopy forests, shading would also have lowered the evaporation rate (Busby et al. 1978; Monique et al. 2004).

Mean LMA of *Ptilium* was highest on BM but the mean dry weight and mean SB of *Ptilium* on this substrate were comparatively low (Fig. 3.3). This implies that elongation of the main axis was due to etiolation rather than increased growth. A different response was found for SBs in this species: *Ptilium* fragments produced significantly more SBs on MS and UH than on AS and BM. One hypothesis is that these results represent different growth strategies for feather moss gametophytes in a moss carpet and those not in a carpet: (i) etiolation is induced in gametophytes in the presence of other feather mosses; and (ii) branching growth is prioritised when other mosses are not present. Gametophyte branches of *Ptilium* grow in a single plane and etiolation could be an advantageous strategy as a means of competing for space and light in the moss carpet. In the absence of other mosses, branching could be more advantageous because it would allow gametophytes to pre-empt surrounding open space. The mechanism by which these responses would be induced is not known, but possibilities include sensitivity to chemicals in surrounding mosses and substrates or released by micro-organisms in the moss carpet. Exudates that affect the growth of surrounding mosses have been identified in some species (Schneider and Sharp 1962; Watson 1981), but have not been thoroughly investigated in boreal mosses. The microflora associated with boreal moss carpets also need further study.

Implications of fragment size

Although we did not test it in this study, fragment size may influence the potential of feather moss fragments to survive and grow. Moreover, our results suggest that the establishment potential of different sized fragments may differ among species. In this study a higher proportion of large *Pleurozium* fragments produced growth than did small fragments. Also, while there was little difference between species in the performance of large fragments, the small fragments that were used for *Ptilium* were poor propagules. Only 3.9% of those recovered had new growth, compared with 58.3% of small *Pleurozium* fragments.

When small fragments of *Ptilium* were being prepared, the parts that we most frequently obtained were the side shoots off the main axes. A typical mature *Ptilium* branch has many of these side shoots (Fig. 3.1), which represents a large potential pool of fragments. The low survival and growth potential of small fragments indicates that this morphology is not an adaptation to maximise vegetative reproduction. A characteristic feature of *Ptilium* is the similar length of all side shoots, which may indicate that they have limited potential for growth in length. Moreover, they are typically unbranching (personal observation), so they may be unable to give rise to the main axis of a new gametophyte. Due to their small size, these side shoots might also lack physiological reserves, which would make them vulnerable at times of stress. Together these features could substantially reduce the value of these fragments as propagules.

Frego and Carleton (1995) suggested that the relative abundance of several late successional bryophytes, including *Pleurozium* and *Ptilium*, might be determined by the conditions they require in the regeneration phase. The poor performance of small *Ptilium* fragments in this study could help to explain why this species is often less common than *Pleurozium*. If new colonies establish primarily from vegetative fragments, *Ptilium* may be at a disadvantage because its re-establishment is dependent upon large fragments. If larger fragments are less well suited to long-distance dispersal than small fragments, fewer viable *Ptilium* fragments than *Pleurozium* fragments will reach sites that are distant from fragment sources. The number of potential colonisation events will therefore be lower for *Ptilium* than for *Pleurozium* and this could be manifested as lower cover later in succession. Even in areas close to the edge of a burn, establishment of *Ptilium* should occur less frequently than *Pleurozium* because the latter's pool of potentially viable propagules will be greater.

Limitations of this study

The results of this study should be considered in the context of two major limitations: (i) we tested survival over a maximum of only two growing seasons; and (ii) we did not examine interactions between substrates and other environmental factors. Although it lasted only one growing season, the large fragment experiment produced results for *Pleurozium* fragments that were generally in line with our expectations. Fragments produced the most growth on UH, the substrate on which they usually grow naturally, and the least on AS, which, in terms of pH and physical structure, was least similar to UH. Results for large *Ptilium* fragments were not consistent among growth variables and may reflect morphological or physiological differences between the study species. This hypothesis cannot be evaluated on the basis of current evidence because the literature is lacking in studies on the ecology and biology of *Ptilium*. A longer term study is necessary to confirm these results.

To avoid confounding the effects of substrates and other environmental conditions, we set up this experiment in closed canopy forests on the assumption that these provided ideal climatic conditions for *Pleurozium* and *Ptilium* fragments. A problem with this approach is that the quality of burned substrates is likely to be different under a closed canopy than under the exposed conditions of a burned forest. For example, temperatures at the soil surface tend to be much higher in burned stands (Viro 1974), which will affect the moisture regime on the forest floor. Substrates might remain moist in shade under a closed canopy but dry out rapidly under intense heat. Therefore, our results may underestimate differences between burned and unburned substrates.

Conclusions

We found no evidence that *Pleurozium schreberi* and *Ptilium crista-castrensis* are prevented from establishing in recently burned boreal spruce forests because burned or mineral substrates inhibit their survival or growth. Only ash was consistently suboptimal for the study species, possibly due to high initial pH. Large *Ptilium* fragments appeared to become etiolated on BM. However, our results may underestimate differences between substrates. Survival rates on BM, in particular, may be unrepresentative because this substrate remained moist under a closed canopy. Our results also indicate that the effectiveness of small fragments as propagules, especially those of *Ptilium*, appears to be limited; few small *Ptilium* fragments survived two years in the field. Species-specific differences in the success of small fragments might provide a partial explanation for the lower relative abundance of *Ptilium* in some late-successional boreal moss communities.

Literature Cited

Ahlgren, C.E. 1960. Some effects of fire on reproduction and growth of vegetation in northeastern Minnesota. Ecology **41**: 431-445.

Bates, J.W. 1979. The relationship between physiological vitality and age in shoot segments of *Pleurozium schreberi* (Brid.) Mitt. Journal of Bryology 10: 339-351.

Bates, J.W. 2000. Mineral nutrition, substratum ecology, and pollution. Pages 248-311 *in* A.J. Shaw and B. Goffinet, editors. Bryophyte Biology. Cambridge University Press, Cambridge, UK.

Bates, J.W. and A.M. Farmer. 1990. An experimental study of calcium acquisition and its effects on the calcifuge moss *Pleurozium schreberi.* Annals of Botany **65**: 87-96.

Bharali, B and J.W. Bates. 2004. Influences of extracellular calcium and iron on membrane sensitivity to bisulphate in the mosses *Pleurozium schreberi* and *Rhytidiadelphus triquetrus*. Journal of Bryology **26**: 53-59.

Brown, D.H. 1982. Mineral nutrition. Pages 383-344 *in* A.J.E Smith, editor. Bryophyte Ecology. Chapman and Hall, New York, USA.

Busby, J.R., L.C. Bliss and C.D. Hamilton. 1978. Microclimate control of growth rates and habitats of the boreal forest mosses, *Tomenthypnum nitens* and *Hylocomium splendens*. Ecological Monographs **48**: 95-110.

Certini, G. 2005. Effects of fire on properties of forest soils: a review. Oecologia **143**: 1-10.

Crum, H.A. and L.E. Anderson. 1981. Mosses of Eastern North America. Volumes 1 and 2. Columbia University Press, New York, USA.

Esposito A, S. Mazzoleni and S. Strumia. 1999. Post-fire bryophyte dynamics in Mediterranean vegetation. Journal of Vegetation Science **10**: 261-268.

Flinn, M.A. and R.W. Wein. 1977. Depth of underground plant organs and theoretical survival during fire. Canadian Journal of Botany **55**: 2550-2554.

Foster, D.R. 1985. Vegetation development following fire in *Picea mariana* (black spruce)-*Pleurozium* forests of south-eastern Labrador, Canada. Journal of Ecology **73**: 517-534.

Frego, K.A. 1996. Regeneration of four boreal bryophytes: colonization of experimental gaps by naturally occurring propagules. Canadian Journal of Botany **74**: 1937-1942.

Gloaguen, J.C. 1990. Post-burn succession on Brittany heathlands. Journal of Vegetation Science **1**: 147-152.

Gurevitch, J., S.M. Scheiner and G.A. Fox. 2002. The Ecology of Plants. Sinauer Associates, Sunderland, Massachusetts, USA.

Hartley, S.E. and R.J. Mitchell. 2005. Manipulation of nutrients and grazing levels on heather moorland: changes in *Calluna* dominance and consequences for community composition. Journal of Ecology **93**: 990-1004.

Hobbs, R.J. and C.H. Gimingham. 1984. Studies on fire in Scottish Highland communities II: post-fire vegetation development. Journal of Ecology **72**: 585-610.

Huttunen, S. 2003. Reproduction of the mosses *Pleurozium schreberi* and *Pohlia nutans* in the surroundings of copper smelters at Harjavalta, S.W. Finland. Journal of Bryology **25**: 41-47.

Jappinen, J.-P. and J.-P. Hotanen. 1990. Effect of fertilization on the abundance of bryophytes in two drained peatland forests in Eastern Finland. Annales Botanici Fennici **27**: 93-108.

Kellner, O and H. Weibull. 1998. Effects of wood ash on bryophytes and lichens in a Swedish pine forest. Scandinavian Journal of Forest Research Supplement **2**: 76-85.

Kershaw, M., R. Wiltshire and C. Hollstedt. 1994. Critical silvics of feathermoss as related to vegetation management. VMAP Technical Report No. 94-03. Vegetation Management Alternatives Program, Ministry of Natural Resources, Ontario.

Kimmerer, R.W. 1994. Ecological consequences of sexual versus asexual reproduction in *Dicranum flagellare* and *Tetraphis pelucida*. The Bryologist **97**: 20-25.

Kimmerer, R.W. and C.C. Young. 1995. The role of slugs in dispersal of the asexual propagules of *Dicranum flagellare*. The Bryologist **98**: 149-153.

Lloyd, P.S. 1971. Effects of fire on the chemical status of herbaceous communities of the Derbyshire Dales. Journal of Ecology **59**: 261-273.

Longton, R.E. and S.W. Greene. 1979. Experimental studies of growth and reproduction in the moss *Pleurozium schreberi* (Brid.) Mitt. Journal of Bryology **10**: 321-338.

Mandre M., H. Parn and K. Ots. 2006. Short-term effects of wood-ash on the soil and the lignin concentration and growth of *Pinus sylvestris* L. Forest Ecology and Management **223**: 349-357.

Maltby, E., C.J. Legg and M.C.F. Proctor. 1990. The ecology of severe moorland fire on the North York Moors: effects of the 1976 fires, and subsequent surface and vegetation development. Journal of Ecology **78**: 490-518.

McCune, B. and Mefford, M. J. 1999. PC-ORD. Multivariate analysis of ecological data, ver. 4.0. MJM Software Glenenden Beach, Oregon.

Monique, M., P.D. Heijmans, W.J. Arp and F.S. Chapin III. 2004. Controls on moss evaporation in a black spruce forest. Global Biogeochemical Cycles **18**: GB2004, doi:10.1029/2003GB002128

Mulligan, R.C. and L.D. Gignac. 2002. Bryophyte community structure in a boreal poor fen II: interspecific competition among five mosses. Canadian Journal of Botany **80**: 330-339.

Myrmael, A. 1993. Regeneration studies of five spruce, *Picea abies*, forest bryophytes. Lindbergia **18**: 7-18.

Ne'eman, G., S. Goubitz, and R. Nathan. 2004. Reproductive traits of *Pinus halepensis* in the light of fire - a critical review. Plant Ecology **171**: 69-79.

O'Toole, M.A. and D.M. Synnott. 1971 The bryophyte succession on blanket peat following calcium carbonate, nitrogen, phosphorous and potassium fertilizers. Journal of Ecology **59**: 121-126.

Rowe, J.S. and G.W. Scotter. 1973. Fire in the boreal forest. Quaternary Research **3**: 444-464.

Rydgren, K., R.H. Økland and T. Økland. 1998. Population biology of the clonal moss *Hylocomium splendens* in Norwegian boreal spruce forests. 4. Effects of experimental disturbance. Oikos **82**: 5-19.

Rydgren, K. and R.H. Økland. 2001. Sporophyte production in the clonal moss *Hylocomium splendens*: the importance of shoot density. Journal of Bryology **23**: 91-96.

Schimmel, J. and A. Granström. 1996. Fuel succession and fire behavior in the Swedish boreal forest. Canadian Journal of Forest Research **27**: 1207-1216.

Schneider, M.J. and A.J. Sharp. 1962. Observations on the reproduction and development of the gametophyte of *Tetraphis pellucida* in culture. The Bryologist. **65**: 154-166.

SPSS Inc. 2002. SPSS Base 11.0 for Windows User's Guide. SPSS Inc., Chicago, Illinois.

Streeter, D.T. 1970. Bryophyte ecology. Science Progress **58**: 419-434.

Strengbom, J., A. Nordin, T. Nasholm and L. Ericson. 2001. Slow recovery of boreal forest ecosystem following decreased nitrogen input. Functional Ecology **15**: 451-457.

Thomas, P.A., M.C.F. Proctor and E. Maltby. 1994. The ecology of severe moorland fire on the North York Moors: chemical and physical constraints on moss establishment from spores. Journal of Ecology **82**: 457-474.

Van Wagner, C.E. 1983. Fire behaviour in northern coniferous forests and shrublands. Pages 65-80 *in* R.W. Wein, and D.A. MacLean, editors. The Role of Fire in Northern Circumpolar Ecosystem. John Wiley and Sons, New York, USA.

Vanderpoorten, A. and J.-P. Klein. 1999. Variations of aquatic bryophyte assemblages in the Rhine Rift related to water quality. 2. The waterfalls of the Vosges and the Black Forest. Journal of Bryology **21**: 109-115.

Viro, P.J. Effects of forest fire on soil. Pages 7-46 *in* T.T. Kozlowski and C.E. Ahlgren, editors. Fire and Ecosystems. Academic Press, New York, USA.

Watson, M.A. 1981. Chemically mediated interactions among juvenile mosses as possible determinants of their community structure. Journal of Chemical Ecology **7**: 367-376.

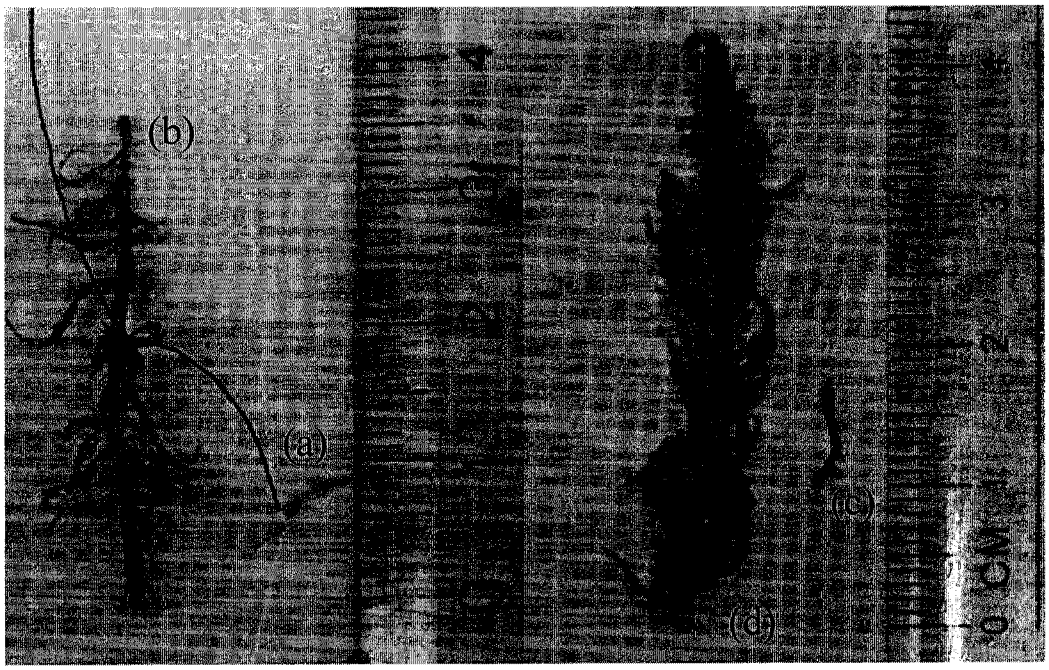
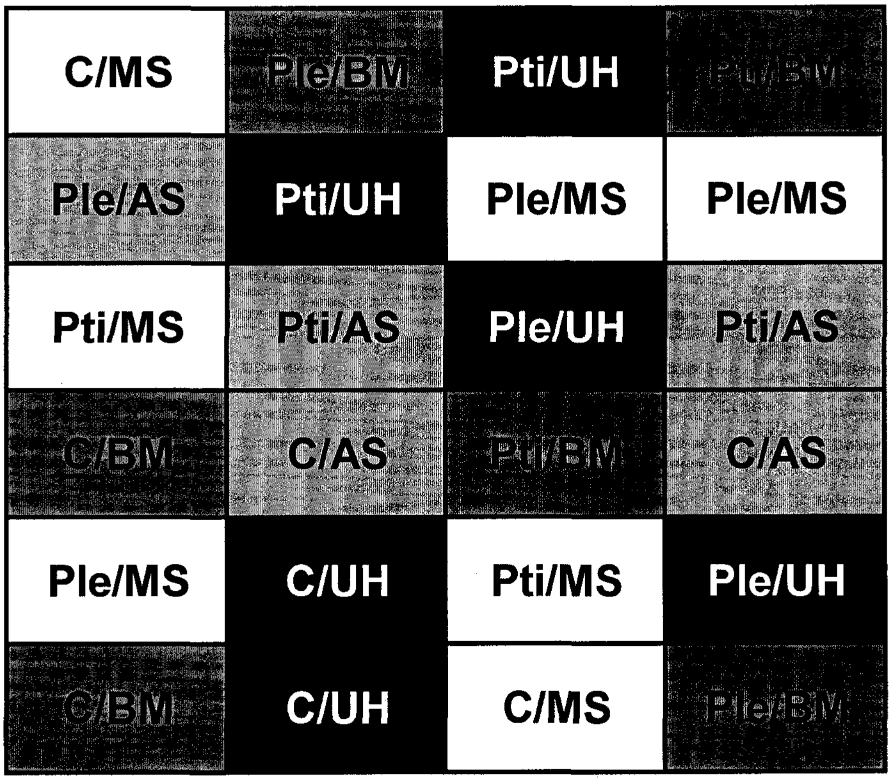


Figure 3.1 Examples of (a) small and (b) large *Pleurozium* fragments and (c) small and (d) large *Ptilium* fragments.



C/MS	Ple/BM	Pti/UH	Pti/BM
Ple/AS	Pti/UH	Ple/MS	Ple/MS
Pti/MS	Pti/AS	Ple/UH	Pti/AS
C/BM	C/AS	Pti/BM	C/AS
Ple/MS	C/UH	Pti/MS	Ple/UH
C/BM	C/UH	C/MS	Ple/BM

Figure 3.2 Diagrammatic example of a block of pots used in the small fragment experiment showing one restricted randomized arrangement of treatment combinations. Arrangements were different in each block. Abbreviations refer to treatment combinations of fragment species and substrate and are defined as follows: Ple = *Pleurozium schreberi*, Pti = *Ptilium crista-castrensis*, AS = ash, BM = burned moss, MS = mineral soil, UH = unburned humus, C = blank.

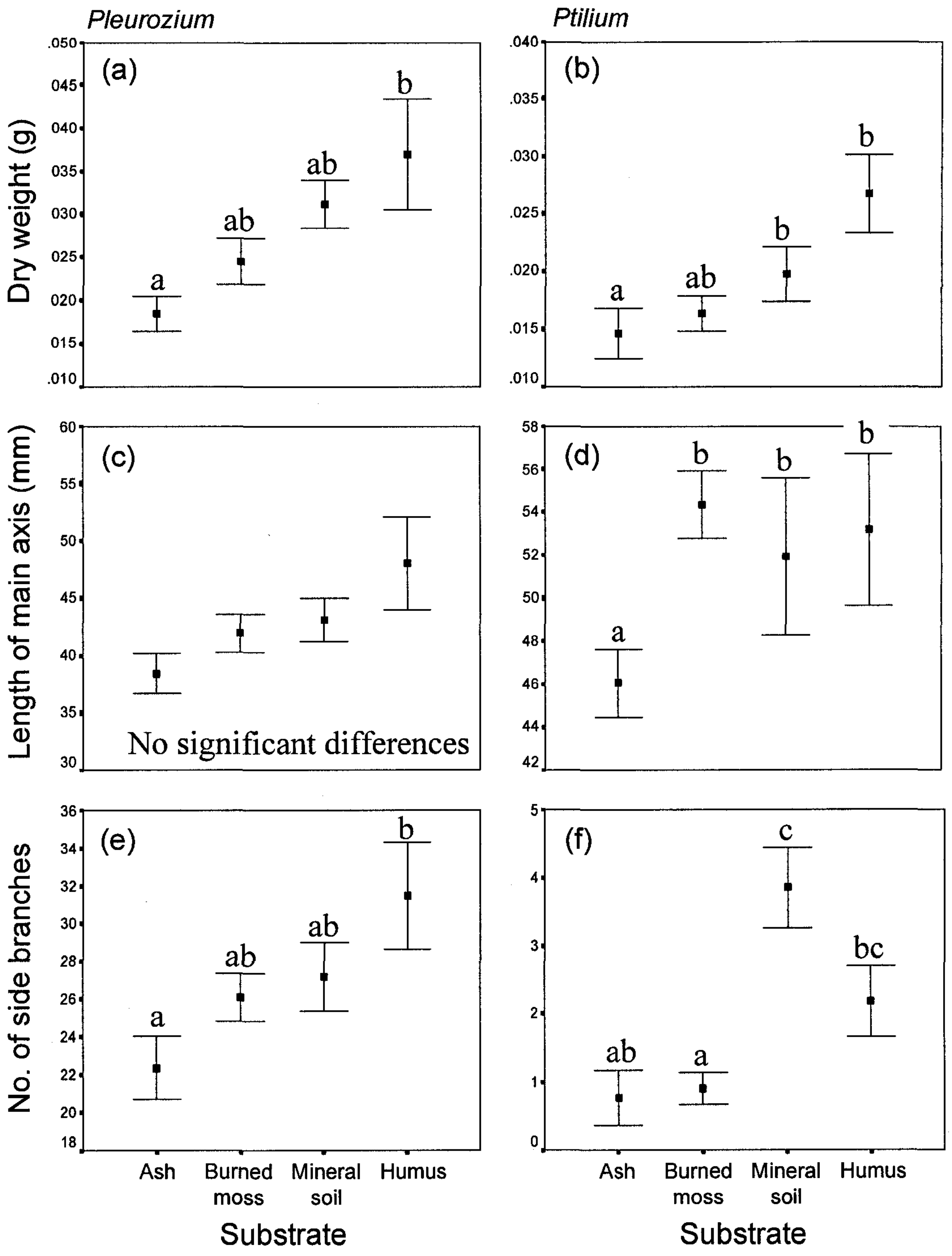


Figure 3.3 Means (± 1 SE) of dry weight (a,b), length of main axis (c,d) and number of side branches (e,f) for large *Pleurozium* and *Ptilium* fragments recorded three months after fragments were placed in an unburned spruce stand. Lower case letters indicate significant differences between treatments.

Table 3.1 Summary statistics for fragments sown in the small fragment experiment described in Chapter 3. Substrate abbreviations are as follows: AS = ash, BM = burned moss, MS = mineral soil and UH = unburned humus.

Stand	Substrate	No. of fragments sown (*N*)	Number recovered	Number alive	Percent recovered	Percent found alive[a]	Weighted prop. found alive (%)[b]
Pleurozium schreberi							
GRN1	AS	10	5	0	50.0	N/A	N/A
	BM	10	8	7	80.0	87.5	70.0
	MS	10	10	7	100.0	70.0	70.0
	UH	10	7	3	70.0	42.9	30.0
GRN2	AS	10	7	1	70.0	14.3	10.0
	BM	10	7	6	70.0	85.7	60.0
	MS	10	6	5	60.0	83.3	50.0
	UH	10	8	6	80.0	75.0	60.0
GRN3	AS	10	10	2	100.0	20.0	20.0
	BM	10	10	5	100.0	50.0	50.0
	MS	10	8	5	80.0	62.5	50.0
	UH	10	10	6	100.0	60.0	60.0
Ptilium crista-castrensis							
GRN1	AS	10	9	0	90.0	N/A	N/A
	BM	10	6	0	60.0	N/A	N/A
	MS	10	6	0	60.0	N/A	N/A
	UH	10	6	0	60.0	N/A	N/A
GRN2	AS	10	4	0	40.0	N/A	N/A
	BM	10	4	0	40.0	N/A	N/A
	MS	10	6	0	60.0	N/A	N/A
	UH	10	3	1	30.0	33.3	10.0
GRN3	AS	10	10	0	100.0	N/A	N/A
	BM	10	7	0	70.0	N/A	N/A
	MS	10	9	0	90.0	N/A	N/A
	UH	10	8	0	80.0	N/A	N/A

[a] Percent found alive is the percentage of recovered fragments that were found with living tissue.

[b] Calculation of weighted proportions is explained in Chapter 3.

Table 3.2 Initial and final mean pHs of the four experimental substrates (± one standard deviation).

	Substrate			
	Ash	Burned moss	Mineral soil	Unburned humus
Small fragment experiment				
Initial	10.4 ± 0.3	5.4 ± 0.2	6.2 ± 0.1	4.7 ± 0.2
GRN1 Final	7.4 ± 0.1	5.5 ± 0.2	6.1 ± 0.1	5.7 ± 0.2
GRN2 Final	7.1 ± 0.2	6.3 ± 0.3	6.1 ± 0.1	5.9 ± 0.3
GRN3 Final	7.3 ± 0.2	6.1 ± 0.2	6.0 ± 0.0	6.0 ± 0.2
Large fragment experiment				
Initial	9.5 ± 0.3	4.6 ± 0.4	6.0 ± 0.4	5.8 ± 0.4
GRN2 Final	7.5 ± 0.1	4.9 ± 0.3	6.2 ± 0.3	4.6 ± 0.2

Chapter 4: Short-term survival and growth of gametophyte fragments of *Pleurozium schreberi* (Brid.) Mitt. and *Ptilium crista-castrensis* (Hedw.) De Not. of different sizes under early successional conditions

Ecological succession can be defined as a process of change in the composition and structure of a species assemblage over time (Gurevitch et al. 2002). This process generally involves a combination of changes in the relative abundance and a series of local colonization and extinction events. For example, in post-fire succession in boreal white spruce (*Picea glauca* (Moench) Voss) forests, many vascular plant species (e.g. *Cornus canadensis* L., *Mertensia paniculata* (Ait.) G. Don., *Rubus ideaus* L., *Populus tremuloides* Michx., *Populus balsamifera* L. and *Picea glauca*) appear early in succession and can still be found in mid to late successional stages. In contrast, many boreal bryophytes that are common in mature white spruce forests are absent in early successional stages, and vice versa.

The pleurocarpous boreal feather mosses *Pleurozium schreberi* and *Ptilium crista-castrensis* (hereafter referred to as *Pleurozium* and *Ptilium*) show a distinct temporal trend in abundance in white spruce-dominated boreal forests in Alberta, Canada. In a 2004 survey of bryophytes in three unburned white spruce stands near the boundary of the 2001 Chisholm Fire, *Pleurozium* and *Ptilium* were found to be among the most widespread species on the forest floor, whereas they were not found in burned stands in the first three years of succession (Chapter 2). These findings are consistent with literature reports that indicate that although *Pleurozium* and *Ptilium* are frequent on the forest floor of mature to old growth white spruce forests, they are not usually found in studies of the earliest stages of post-fire succession (see, for example, O'Toole and Synnott 1971; Rowe and Scotter 1973; Viro 1974; Hobbs and Gimingham 1984; Foster 1985; Gloaguen 1990; Maltby et al. 1990; Thomas et al. 1994; Esposito et al. 1999).

Two hypotheses that may explain the absence of *Pleurozium* and *Ptilium* from early successional stages are: (i) habitat intolerance; and (ii) dispersal limitation (Fig. 1.1). Habitat intolerance is suggested by the contrast in environmental conditions between early successional stages and those in which *Pleurozium* and *Ptilium* are abundant. There is no tree canopy in the earliest stages of post-fire succession to create shade; studies have found reduced growth in late successional mosses as a result of high light intensity and evaporation stress (Busby et al. 1978; Longton and Greene 1979). Substrates also differ between early and late successional stages. Fires consume humus on the soil surface, exposing mineral soil. They can also leave a layer of ash, charred fine woody debris and duff (Ahlgren 1960; Viro 1974; Flinn and Wein 1977; Van Wagner 1983; Schimmel and Granstrom 1996; Ne'eman et al. 2004; Certini 2005). Charred and mineral substrates can have an alkaline pH and contain potentially toxic ions (Lloyd 1971; Brown 1982; Thomas et al. 1994; Kellner and Weibull 1998; Ne'eman et al. 2004; Mandre et al. 2006). Feather mosses are indicative of acidic, organic substrates (Ringius and Sims 1997). The dispersal limitation hypothesis is based on the rarity of sexual reproduction in *Pleurozium* and *Ptilium*. Research has shown that gametophyte fragments of these species have the potential to act as propagules following short-distance dispersal in mature forests (Longton and Greene 1979;

Myrmael 1993; Kershaw et al. 1994; Kimmerer 1994; Frego 1996; Rydgren et al. 1998; Rydgren and Økland 2001; Huttunen 2003). Little is known about the long distance dispersal of vegetative fragments, although previous studies have identified several potential vectors, including slugs (Kimmerer and Young 1995), snowmelt (McDaniel and Miller 2000), deer and wild boar (Heinken et al. 2001).

The habitat intolerance hypothesis can be tested by sowing propagules under conditions they would encounter early in succession. If they survive, it would disprove the habitat intolerance hypothesis and support dispersal limitation. Research described in Chapter 3 showed that vegetative fragments of *Pleurozium* and *Ptilium* could grow on some early successional substrates. This chapter describes studies of survival and growth under high levels of exposure in recently burned forests and different hydration regimes. It was beyond the scope of this study to examine propagule survival at different stand ages so we tested survival in two-year old burned forest stands that represent conditions at a very early stage of succession. We also restricted this study to survival and growth of fragments because we could easily observe changes in their condition and recover them at the end of the study. Although the ability of fragments to establish new colonies has been demonstrated in principle (Longton and Greene 1979; Mishler and Newton 1988; Myrmael 1993; Frego 1996; Frego and Carleton 1995; Jones and Rosentreter 2006), it does not necessarily follow that all fragments make equally effective diaspores. The findings of the study described in Chapter 3 suggest that the ability of a fragment to survive and grow may be a function of species and fragment size.

To test this hypothesis, we looked at survival and growth of different sized fragments in field and growth chamber experiments.

In this chapter we address the following questions: (i) are *Pleurozium* and *Ptilium* absent from recently burned forests because they are intolerant of exposure and moisture stress; and (ii) does establishment potential differ among fragments of different sizes.

Materials and Methods

Field experiment

Study sites

We set up the field experiment in 2003 in four burned white spruce forest stands in north-central Alberta. The stands were burned in the Chisholm Fire, which took place south-east of Lesser Slave Lake, Alberta, in 2001. We refer to them as BRN1, BRN2, BRN3, and BRN4 based on their geographical location. Further details are given in Chapter 2.

Study species

Details of the study species are provided in Chapter 3.

Preparation of fragments

In June 2003 we collected living gametophyte material of *Pleurozium* and *Ptilium* from a *Picea mariana*/*Picea glauca* stand in north-central Alberta.

Fragments produced from this material were of three sizes: large, small and miniature. We use these terms only to convey the relative sizes of the fragments. We created large and small fragments using the methods described in Chapter 3 (Fig. 3.1). Miniature fragments (Fig. 4.1) were formed by shredding gametophyte material in a coffee grinder. We chose these sizes because we assumed that they fall within the natural range of fragment sizes for these species. Furthermore, we expected that differences in size and morphology would provide different advantages and disadvantages in terms of establishment potential.

Experimental protocol (field experiment)

The field experiment was set up in July 2003. Five blocks of replicates were prepared in each of the study stands. In each block, we removed a *ca.* 1 m^2 area of soil to a depth of 2 cm and replaced it with organic humus collected from two unburned stands. We used this approach minimize confounding effects of exposure and substrate. We then placed a plastic mesh frame, from which we had removed 16 10 cm × 10 cm squares of mesh (arranged in 4 rows of 4), over the humus and pinned it down with plastic pegs (Fig. 4.2). One large or small fragment or approximately 12 mm^3 of miniature was placed in each of 12 squares in each block. We left four squares (blanks) without fragments to see whether unsown gametophytes of the study species emerged from the substrate. Each block contained two replicates of each species/fragment size combination so that if one fragment was lost there would be another from which data could be collected (Fig. 4.2). To ensure that treatments were not clustered in a block, we allocated them to squares using a restricted randomised design. We tied every large and small fragment to a bent plastic-coated aluminium paper clip using cotton thread and inserted the clip into the soil to keep the fragment in place. For each miniature replicate, we collected material in the plastic stopper from the end of a ballpoint pen and scattered it around the centre of the replicate. Miniature fragments were not anchored to the soil because they were generally less than 3 mm in length.

We placed one block in the centre of a 2500 m^2 area previously marked out for species surveys (Chapter 2) and the other four blocks at four locations around the central block and at least 5 m away from it. Ostensibly each of these four blocks was placed at locations N, S, E and W of the centre but we haphazardly determined the specific distance and direction of each block by hurling a tennis ball.

Data collection

In August 2003, 2004 and 2005 we recorded how many fragments we found and how many of these had living gametophyte tissue. We used the latter variable as a proxy for survival. Living tissue cannot be reliably differentiated from dead tissue visually (Bates 1979) so we assumed that green tissue and brown tissue that was not shriveled was alive. For each treatment combination, we calculated survivorship as a weighted proportion using the formula $(A_{\mathrm{sp}.i}/R_{\mathrm{sp}.i}) \times (R_{\mathrm{sp}.i}/S_{\mathrm{sp}.i})$ where

A is the number of recovered fragments of species i (sp$i$) that were alive,

R is the number of fragments of species i that were recovered, and

S is the number of fragments of species i that were sown.

The proportion of recovered fragments found alive was weighted by the proportion of sown fragments that were recovered (see Chapter 3 for an explanation).

In 2005 we recovered all fragments from the field and measured fragment condition as either: (i) the length of green tissue on *Ptilium* fragments; or (ii) the number of living branches of any order on *Pleurozium* fragments (hereafter referred to as amount of living material or ALM). We assumed that fragments in better condition (i.e. with more living material) had a higher chance of survival and used different measures for each species because of differences in their morphology.

In each large fragment we also measured environmental variables that might affect fragment condition. These were the percentage cover of bryophytes other than fragments, vascular plant cover, litter cover, median litter depth and depth of existing bryophyte carpets, pH and gravimetric soil moisture (GSM). Bryophyte cover was recorded by overlaying a mesh grid comprised of 36 1 cm^2 squares over each replicate and counting the percentage of squares that were greater than 50% covered. We used the same protocol to record litter (i.e. leaf and herbaceous litter and fine woody debris) and vascular plant cover. The median depths of litter and bryophyte carpets were measured in any replicate where cover was greater than 50%. Otherwise, we assumed that the effects of these variables was negligible and recorded them zero. We estimated soil pH using litmus paper and converted it to an H^+ concentration by raising pH to the tenth power. GSM was measured using the method described in Kalra and Maynard (1991). Details are given in Chapter 2.

Growth chamber experiment

Substrate collection and preparation

Four substrates were used in this study: ash (AS), burned moss (BM), mineral soil (MS) and unburned humus (UH). Details on how these were collected are given in Chapter 2. We measured the initial mean pH of each substrate when the experiment began, 96 days later and at the end of the study (284 days).

Experimental design

For each of the four substrate treatments, we filled 576 6.25 × 6.25 cm square plastic pots to a depth of around 7.5 cm with one of the experimental substrates. When filling pots, we attempted to maintain the vertical profile of BM and MS and we removed any bryophyte material that was already present. To test for interactions between moisture level and substrate, we set up 'high moisture' and 'low moisture' treatments. Pots in the former were placed in trays without drainage holes and watered weekly. This protocol ensured that all substrates remained moist. Pots in the low moisture treatment were placed in trays with drainage holes and watered bi-weekly so that pots could dry out. We allocated 72 pots of each substrate to the high moisture treatment and the other 72 to the low moisture treatment (72 × 4 substrates × 2 species = 576).

Pots were arranged in trays in 9 rows of 4 (Fig. 4.3). Each moisture treatment consisted of 8 trays (8 trays × 36 pots per tray = 288 pots). To avoid clustering, we allocated substrate treatments to positions within trays using a restricted randomised design. Within each moisture treatment, fragments of each species were placed in 144 pots (144 pots per species / 4 substrates = 36 pots per substrate). We further subdivided the 36 pots of each species-substrate combination by fragment size (12 pots per fragment size). Fragments were anchored in pots using the method described in the field experiment protocol.

After 96 days, fragments on AS appeared to be dead. To confirm this, we transferred 12 large *Pleurozium* fragments to fresh pots containing UH, watered these pots weekly and observed the fragments for 176 days. Six of the removed fragments were replaced in the original AS replicates by new large *Pleurozium* fragments and six were replaced by clumps of *Ceratodon purpureus*. The latter was used to test whether a ruderal species with a tolerance for a wide range of substrates and pHs could survive on the AS used in this study.

All trays were covered with clear plastic lids to reduce evaporation. In an attempt to simulate lighting conditions under a tree canopy, we taped a green plastic sheet cut from a green recycling bag to the top and sides of each lid. Trays were then placed in a growth chamber with settings that approximated a mild summer day in north-central Alberta: day temperature 24°C, night temperature 10 °C; photoperiod 15 h (06.00 - 21.00 h), light intensity 250 mE s^{-1} m^{-2}. Trays were thoroughly wetted with distilled water from above on the first day of the experiment and we watered them again after 37 days, when some replicates had dried out. Thereafter, those in the high moisture treatment were watered every 6-8 days and those in the low moisture treatment were watered every 13-15 days.

Data collection

After 284 days we recorded the presence or absence of fragments in each pot and the presence of new growth. The number of new shoots was recorded from 53 days onwards on large fragments and at the final count date (284 days) on all fragments. New shoots were easily identifiable because they were bright green and morphologically different from existing shoots. Because the total number of fragments in each miniature replicate was unknown, this variable was recorded as the number of new shoots per replicate pot.

For each treatment combination, the frequency of fragments with new growth was calculated as a weighted proportion using the formula $(N_{\mathrm{sp}.i}/R_{\mathrm{sp}.i}) \times (R_{\mathrm{sp}.i}/S_{\mathrm{sp}.i})$, where

N is the number of recovered fragments of species i (sp$i$) that had new growth,

R is the number of fragments of species i that were recovered, and

S is the number of fragments of species i that were sown.

The proportion of recovered fragments found alive was weighted by the proportion of sown fragments that were recovered (see Chapter 3 for an explanation).

To assess whether some substrates dried out faster than others, we recorded the number of replicates that were either wet or dry every 6 to 8 days between 53 and 123 days (except between 95 and 109 days). We used these data to estimate the mean proportion of replicates of each substrate that dried out over the course of the experiment.

Statistical analysis (field experiment)

We used stepwise forward conditional logistic regression (SPSS v. 11.5, SPSS Inc. 2002) to test whether fragment survival varied with species, fragment size, study site or species × fragment size interactions. All variables were entered as dummy variables. Because we could not see miniature fragments in the field with the naked eye after one growing season, we assumed that they were present in all miniature replicates in which humus had not been washed out by rain. Where a replicate was less than 50% covered with humus, we assumed that it contained no miniature fragments. Furthermore, we counted miniature fragments as growing in all relevant replicates in which a viable gametophyte of the appropriate species was recovered. This probably led to overestimation of the survival of miniature fragments because some of those counted as alive may have been previously present in the humus.

We also used stepwise forward conditional logistic regression (SPSS v. 11.5, SPSS Inc. 2002) to test whether the survival of large fragments could be predicted from species, study site, vascular plant cover, bryophyte cover, litter cover, depth of any existing bryophyte carpet, litter depth, GSM or H^+ concentration (SPSS v. 11.5; SPSS Inc. 2002). Stepwise linear regression (SPSS v. 11.5, SPSS Inc. 2002) was used to determine whether ALM could be predicted from environmental variables using the equation,

$$Y = \beta_1 + \beta_{ss}ss + \beta_{vp}vp + \beta_{bc}bc + \beta_{lc}lc + \beta_{dc}dc + \beta_{ld}ld + \beta_{sm}sm + \beta_H H + \varepsilon$$

where ss is study site

vp is vascular plant cover

bc is bryophyte cover

lc is litter cover

dc is depth of any existing bryophyte carpet

ld is litter depth

sm is gravimetric soil moisture,

and *H* is H^+ concentration

We entered study sites as dummy binary variables and all other variables were natural log transformed to produce normalised residuals from the regression.

Statistical analysis (growth chamber experiment)

We used stepwise forward conditional logistic regression to test whether fragment size, species, moisture treatment and substrate were useful for predicting the presence of new growth at 284 days. We entered each level of all variables as dummy binary variables and included all possible two-way interactions.

To test whether moisture treatment, fragment size and substrate affected the number of new shoots per fragments at 284 days, we compared treatments using multiple response permutation procedure (MRPP) with Euclidean distances in PC-ORD for Windows version 4.41 (MjM Software Design 2005). MRPP is a non-parametric method that compares groups on the basis of mathematical distances between sampling units. For details see Chapter 3.

Results

Field experiment

Fragment survival

Fig. 4.4 shows trends in the proportion of fragments that were found and the weighted proportion of fragments that were found alive over the study period. We found that the proportion of fragments found declined over the three years of the study for all fragment sizes, but these declines were less than for the weighted proportion of fragments found alive, particularly for small and miniature *Ptilium* fragments.

Table 4.1 shows results of the logistic regressions testing factors affecting survival. Large fragment size and a *Pleurozium* × small fragment interaction were significant predictors in the final model ($\chi^2 = 134.25$, df = 2; $P<0.001$). The model correctly predicted 86.1% of cases:

$$\text{Predicted logit}\ (\text{survival}_{\text{all sizes}}) = 1.678 - (4.204 \times \text{large}) + (1.890\ [\textit{Pleurozium} \times \text{small}])$$

Over four times as many large fragments survived as small or miniature fragments and the weighted proportion of large fragments that survived was similar when compared between species. More than ¾ of surviving small fragments were from *Pleurozium*. Summary statistics are given in Table 4.2.

The only significant predictor of the survival of large fragments was bryophyte cover ($\chi^2 = 5.75$, df = 1; $P = 0.016$). According to the model, fragments had a greater chance of survival at high bryophyte covers. The model correctly predicted 80.0% of cases:

$$\text{Predicted logit}\ (\text{survival}_{\text{large}}) = 0.524 + (0.021 \times \text{bryophyte cover})$$

Fragment condition (ALM)

Significant predictors of ALM on *Pleurozium* fragments were GSM, bryophyte cover and the site BRN1. The model (-1.437 + (0.520 × GSM) + (0.210 × bryophyte cover) - (0.497 × BRN1) explained 55.0% of the variance and was significant at $P < 0.001$ (SE = 0.36, $F_{3,26} = 12.80$). Only GSM was a significant predictor of ALM for *Ptilium* fragments. The model (0.994 + (0.650 × GSM)) explained 14.8% of the variance and was significant at $P < 0.001$ (SE = 1.08, $F_{1,24} = 5.33$). Summary statistics for the environmental variables used in the linear regression model are given in Table A.7 in the Appendix.

Of the 80 replicates in which no fragments were sown, we found 8.8% that contained *Pleurozium* gametophytes and 7.5% that contained *Ptilium* gametophytes.

Growth chamber experiment

Probability of producing new growth

No fragments grew on AS in the experiment so we excluded this substrate from our analyses. Large fragments that had been removed from AS replicates after

96 days and transplanted onto UH had not produced new growth after 176 days. Transplanted clumps of *Ceratodon* remained green but did not grow substantially over the same period. One tray in the low moisture treatment was damaged during the experiment we excluded the replicates in this from the analyses.

Results of the logistic regression model predicting new growth at 284 days are given in Table 4.1. Two factors and three interactions were significant in the model ($\chi^2 = 170.98$, df = 5; $P<0.001$), which correctly predicted 81.5% of cases:

$$\text{Predicted logit (growth)} = -1.427 - (2.658 \times \text{species}) + (2.794 \times [\text{moisture treatment} \times \text{MS}]) + (1.930 \times [\text{species} \times \text{large}]) + (1.558 \times \text{large}) - (0.885 \times [\text{small} \times \text{BM}])$$

Fewer *Ptilium* fragments than *Pleurozium* fragments produced new growth, regardless of moisture treatment and fragment size (Tables 4.3 and 4.4 in the Appendix). Across both species and moisture treatments the percentage of large fragments that grew (57%) was more than twice that of small fragments (26%) and over three times that of miniature fragments (17%). New growth was recorded on over four times as many large *Ptilium* fragments as small *Ptilium* fragments (50% c.f. 12%) and only one miniature *Ptilium* fragment had new growth. Differences among fragment sizes were less pronounced in the high moisture treatment than the low moisture treatment and the growth of small and miniature fragments was more likely under high moisture conditions than low moisture (high moisture: large 76%, small 38%, miniature 28%; low moisture: large 35%, small 11%, miniature 9%). In the high moisture treatment, growth of fragments of all sizes was less likely to be found on MS than on the organic substrates but in the low moisture treatment there was little difference among substrates. All small and miniature fragments that grew on MS were *Pleurozium* fragments.

Number of shoots per fragment at 284 days

We used only *Pleurozium* data to test for differences among treatments in the number of shoots per fragment because only four *Ptilium* fragments produced new shoots. Results of MRPP tests are given in Table 4.6. Significantly more *Pleurozium* fragments produced new growth in the high moisture treatment than the low moisture treatment ($T = -6.410$, $\delta_{\text{observed}} = 0.435$, $A = 0.037$, $P = 0.001$). The number of shoots per fragment did not differ among substrates in either moisture treatment but there were differences among fragment sizes within substrate treatments (Fig. 4.4). Large fragments produced significantly more shoots than small fragments on all substrates in the high moisture treatment but only on UH in the low moisture treatment. There were no differences between small and miniature fragments in either moisture treatment. In the high moisture treatment miniature fragments produced significantly fewer shoots than large fragments on UH but these fragment sizes did not differ on other substrates.

Substrate pH and hydration status

Table 4.5 gives the trends in H^+ concentration for the four substrates. In both moisture treatments, initial and final H^+ concentrations were highest in BM and UH. Acidity increased in all substrates except BM, which showed an increase in pH after

96 days and a decrease between 84 days and 289 days to levels similar to initial values.

After 53 days we found that 4.8% of BM replicates and 3.6% of UH replicates were dry in the high moisture treatment. After 60 days that number had declined to 12% for both treatments and no replicates of any treatment were dry from 74 days onwards. In the low moisture treatment all substrates had dry replicates at every count date and the proportion was generally highest for BM and UH. The final means of all count dates for the low moisture treatment were UH 49% of pots, BM 40% and MS 9%.

Trends in shoot production among substrates (growth chamber experiment)

Fig. 4.5 shows the trends in the mean number of shoots per fragment for large *Pleurozium* fragments between 38 and 284 days. This value differed little among substrates up to 123 days in the high moisture treatment. Thereafter it increased for fragments on UH, remained constant for those on BM and decreased on MS. In the low moisture treatment the final mean number of shoots per fragment was similar on UH and MS but the trend differed between these substrates. On MS it approximated a logistic growth curve with a rapid increase between 60 and 95 days. On UH it increased at a largely constant rate between 81 and 284 days. On BM the mean number of shoots per fragment remained at less than one throughout.

Discussion

A decline in the health of feather mosses following exposure has been reported by Johnston (1977); Jeglum (1984; both cited in Kershaw et al. 1994); Busby et al. (1978) and Aksamit and Irving (1984). Their findings were attributed to radiation damage, high temperatures or evaporation stress and indicate that feather mosses are intolerant of exposed habitats. This could explain their absence from early successional stages after fire. However, the results of this study do not support that hypothesis. Gametophyte fragments of *Pleurozium* and *Ptilium* survived in exposed study sites for three years and in a growth chamber some fragments produced growth on substrates that periodically dried out. Nonetheless, the survival, health and growth of fragments appeared to be influenced by several factors. Fragment survival and health was a function of bryophyte cover, fragment size and species, while growth differed among species and was affected by moisture regime and substrate.

Fragment survival

Fragments were more likely to survive in replicates with higher cover of early successional bryophytes. Bryophyte cover was also as a significant variable in a linear regression model that predicted the number of side shoots on *Pleurozium* fragments (i.e. fragment health); some *Pleurozium* fragments had a higher frequency of side shoots when bryophyte cover was high than all fragments in replicates where cover was low. These results reflect either (i) a facilitation effect of bryophyte cover on fragment survival and health; or (ii) the positive effect of a covariate on both bryophyte cover and fragment survival. Although no specific data is available on moisture levels in acrocarpous moss carpets, it seems likely that the microclimate in the spaces between gametophyte stems is cooler and more moist than that in open spaces (Parker et al. 1997). Given the poikilohydric nature of bryophytes, such conditions may increase the chances of survival of fragments in moss patches in exposed stands. If larger moss patches provide a more favourable environment than smaller patches, this could explain the positive association between bryophyte cover and both survivorship and ALM on *Pleurozium* fragments. Area may not be the most important functional feature of moss patches in this context, though. We found that bryophyte patch depth was significantly positively correlated with bryophyte cover. Although not significant in models predicting survival and health, patch depth may have increased the probability of fragment survival if (i) favourable environmental conditions within moss patches were intensified in deeper patches; or (ii) deeper patches more completely surrounded fragments. The predictive power of patch depth may have been underestimated in the logistic regression model because depth was recorded only in replicates with greater than 50% bryophyte cover.

Bryophyte cover was also correlated with litter cover, litter depth, H^+ concentration and GSM. None of these was a significant predictor of fragment survival, although GSM was a predictor of fragment condition for *Pleurozium* fragments. We expected higher values of GSM to increase the probability of fragment survival based on the theory that fragments would remain hydrated for longer on moist soils. This hypothesis was not supported by the results of this study, though. Among the study sites, BRN1 had the highest mean GSM value (Table A.7) and some experimental blocks were found to be periodically flooded. Despite this, survivorship was not highest in this site when considered regardless of species (Table 4.2). The weighted proportion of *Ptilium* fragments that were found alive in BRN1 was 90%, compared with 50% for *Pleurozium*. Several studies have reported deleterious effects of saturation on *Pleurozium* (Busby et al. 1978; Kershaw et al. 1994; Mulligan 2002). Prolonged saturation may explain some of the mortality in BRN1, while the increased number of side shoots in fragments in replicates with a higher GSM could be a positive effect of hydration below saturation levels.

Survival and growth differences among species and fragment sizes

Differences between fragment sizes were consistent with those found in the study in Chapter 3. Smaller fragments were less likely to survive in the field than large fragments, regardless of species (Fig. 4.4) and less likely to produce growth in the growth chamber, regardless of moisture treatment (Tables 4.3 and 4.4). Furthermore, the number of shoots per fragment increased with fragment size regardless of substrate and moisture treatment (Figs. 4.5). We suggest that large fragments have more physiological reserves, greater moisture retention capacity and consequently higher resilience during wetting-drying cycles. Such cycles are likely to be frequent and extreme in burned sites during summer months. The results of the small fragment experiment in Chapter 3 also indicated an interaction between species and fragment size; small *Ptilium* fragments were less likely to survive than small *Pleurozium* fragments. That finding was upheld by the results of this study. The weighted proportion of small *Ptilium* fragments that we found alive in the field was 4.0%, compared with 18.0% of small *Pleurozium* fragments (Table 4.2). There were no differences between species for miniature fragments but evaluating results for miniature fragments is problematic because we were rarely able to positively identify them in the field. Nonetheless, our findings suggest that larger fragments of *Ptilium* are more likely to contribute to post-fire recolonisation than smaller fragments.

Frego (1996) concluded that *Pleurozium* was likely to maintain its dominance of a feather moss community on the forest floor of upland black spruce forests partly because of this species produces abundant fragments. The results of our study suggest that species-specific differences in fragment viability may also contribute to the dominance of *Pleurozium*. *Pleurozium* may establish more new colonies from fragments than *Ptilium* because a larger range of fragment sizes and parts of the *Pleurozium* gametophyte have the potential to grow. Taken together with the findings of Frego (1996), this may partly explain why *Pleurozium* is often more common than *Ptilium* in old growth white spruce forests.

In the growth chamber, *Ptilium* fragments rarely produced new shoots, most of the growth being protonemata, and the shoots that were produced were morphologically different from those seen in the field. This could indicate a reaction to the experimental protocol. In the growth chamber new shoots were thin, erect and lacking the side shoots perpendicular to the main axis that characterise this species. It seems unlikely that a substrate-related factor was responsible because these responses were recorded across all substrates. The morphological difference may have been related to the quality of light falling on the fragments. The use of green plastic on the trays was meant to simulate light filtered through a tree canopy, but that light may have been critically different from what feather mosses would encounter in nature. *Pleurozium* fragments did not show morphological differences between new and existing shoots, which may indicate that *Ptilium* has a different tolerance pattern from *Pleurozium* for light spectrum and intensity.

Differences in growth among moisture treatments and substrates

The results of the study described in Chapter 3 did not support the hypothesis that *Pleurozium* and *Ptilium* fragments were intolerant of burned and mineral substrates. Fragments grown on these substrates in closed canopy forests did not show significantly reduced survival and growth. One limitation of that study was this it did not test for negative interactions between substrate and exposed conditions. The results of the growth chamber experiment here indicate that such interactions may occur with organic substrates if they dry out. Fragments on BM and UH performed poorly in the low moisture treatment compared with the high moisture treatment (Fig. 4.5, Tables 4.3 and 4.4). This response could have been due to a combination of (i) reduced moisture availability; and (ii) wicking away of moisture from the fragment by the substrate when dry. If these findings hold under field conditions, negative effects of exposure on survival may be compounded on inorganic substrates.

At the end of the experiment the weighted proportion of fragments with new growth on MS was lower than that on BM and UH in the high moisture treatment, as was the number of shoots per fragment (Fig. 4.5). The number of shoots per fragment also declined after 123 days due to the death of new shoots on fragments on MS (Fig. 4.6). These results could be explained by a negative interaction between MS and high soil moisture content. This interaction may be due to poor drainage in MS replicates. Mineral soil was composed of fine particles and a film of water was visible on the surface of this substrate in high moisture treatment replicates. Fragments might therefore have experienced negative effects from saturation. If *Pleurozium* has a lower tolerance to saturation than *Ptilium*, the proportion of large *Pleurozium* fragments that produced new growth should be lower than that of *Ptilium*. Moreover, small and miniature fragments should be more severely affected than large fragments because a greater proportion of the fragment will be saturated. Results were consistent with the first prediction; in the high moisture treatment, small and miniature fragments on MS were much less likely to produce new growth relative to large fragments than those on BM and UH (Table 4.3). No small and miniature *Ptilium* fragments grew on MS, so the second prediction can only be evaluated on the basis of results for large fragments. These results do not support the prediction because a higher proportion of large *Pleurozium* fragments than large *Ptilium* fragments produced new growth on MS. This result may be misleading, however, because due to the branching pattern of large *Pleurozium* fragments, little of the fragment surface was in contact with the substrate.

We were surprised by the extreme toxicity of AS in the growth chamber experiment. The pH of AS was higher than that of any of the other substrates throughout the experiment but initial and final values were similar to those recorded in the field experiment described in Chapter 3 (Table 4.4). Factors other than pH, such as high concentrations of oxides and hydroxides, might explain the toxicity of this substrate. This issue is further discussed in Chapter 3.

Conclusions

The feather mosses *Pleurozium schreberi* and *Ptilium crista-castrensis* are common in late successional moss communities in boreal spruce forests but absent from the bryophyte assemblage in recently burned forests. Our study involved a test of the hypothesis that vegetative propagules of these species were intolerant of the effects of exposure in burned forests. This hypothesis was not supported by the results of field and growth chamber experiments, although survivorship was reduced and growth was less likely to occur under conditions where moisture was limited. Our study also showed that there were significant differences among species and fragment sizes in survivorship and the probability of producing new growth. Large, branched fragments that included the main axis of the original gametophyte branch were significantly more successful than small side shoots or shredded pieces of leaf and stem. Small and miniature *Ptilium* fragments were rarely recovered alive in a field experiment and *Ptilium* fragments of all sizes were much less likely than those of *Pleurozium* to produce new shoots in the growth chamber. Shoot growth on *Ptilium* and *Pleurozium* fragments was morphologically different in the growth chamber from that observed in the field, which might have been due to unsuitable lighting conditions. Fragments were most likely to grow on UH and least likely to grow on ash and wet mineral soil.

Literature Cited

Ahlgren, C.E. 1960. Some effects of fire on reproduction and growth of vegetation in northeastern Minnesota. Ecology **41**: 431-445.

Aksamit, S.E. and F.D. Irving. 1984. Prescribed burning for lowland black spruce regeneration in northern Minnesota. Canadian Journal of Forest Research. **14**: 107-113.

Bates, J.W. 1979. The relationship between physiological vitality and age in shoot segments of *Pleurozium schreberi* (Brid.) Mitt. Journal of Bryology 10: 339-351.

Brown, D.H. 1982. Mineral nutrition. Pages 383-344 *in* A.J.E Smith, editor. Bryophyte Ecology. Chapman and Hall, New York, USA.

Busby, J.R., L.C. Bliss and C.D. Hamilton. 1978. Microclimate control of growth rates and habitats of the boreal forest mosses, *Tomenthypnum nitens* and *Hylocomium splendens.* Ecological Monographs **48**: 95-110.

Certini, G. 2005. Effects of fire on properties of forest soils: a review. Oecologia **143**: 1-10.

Coates, K.D., S. Haeussler, S. Lindeburgh, R. Pojar and A.J. Stock. 1994. Ecology and Silviculture of Interior Spruce in British Columbia. Forest Resource Development Report. Forestry Canada and British Columbia Ministry of Forests, Victoria, British Columbia.

Esposito A, S. Mazzoleni and S. Strumia. 1999. Post-fire bryophyte dynamics in Mediterranean vegetation. Journal of Vegetation Science **10**: 261-268.

Flinn, M.A. and R.W. Wein. 1977. Depth of underground plant organs and theoretical survival during fire. Canadian Journal of Botany **55**: 2550-2554.

Foster, D.R. 1985. Vegetation development following fire in *Picea mariana* (black spruce)-*Pleurozium* forests of south-eastern Labrador, Canada. Journal of Ecology **73**: 517-534.

Frego, K.A. 1996. Regeneration of four boreal bryophytes: colonization of experimental gaps by naturally occurring propagules. Canadian Journal of Botany **74**: 1937-1942.

Frego, K.A. and T.J. Carleton. 1995. Microsite tolerance of four bryophytes in a mature black spruce stand: reciprocal transplants. The Bryologist **98**: 452-458.

Gloaguen, J.C. 1990. Post-burn succession on Brittany heathlands. Journal of Vegetation Science **1**: 147-152.

Gurevitch, J., S.M. Scheiner and G.A. Fox. 2002. The Ecology of Plants. Sinauer Associates, Sunderland, Massachusetts, USA.

Hobbs, R.J. and C.H. Gimingham. 1984. Studies on fire in Scottish Highland communities II: post-fire vegetation development. Journal of Ecology **72**: 585-610.

Huttunen, S. 2003. Reproduction of the mosses *Pleurozium schreberi* and *Pohlia nutans* in the surroundings of copper smelters at Harjavalta, S.W. Finland. Journal of Bryology **25**: 41-47.

Jeglum, J.K. 1984. Strip cutting in shallow-soil upland black spruce near Nipigon, Ontario. Information Report OX-359. Forestry Canada Ontario Region, Sault Saint Marie, Ontario.

Johnston, W.F. 1977. Black spruce in the north central states. General Technical Report NC-34. U.S. Dept. of Agriculture, Forest Service, North Central Forest Experiment Station. St. Paul, Minnesota.

Jones, P.R. and R. Rosentreter. 2006. Gametophyte fragment growth of three common desert mosses on artificial and natural substrates. The Bryologist **109**: 166-172.

Kellner, O. and H. Weibull. 1998. Effects of wood ash on bryophytes and lichens in a Swedish pine forest. Scandinavian Journal of Forest Research Supplement **2**: 76-85.

Kershaw, M., R. Wiltshire and C. Hollstedt. 1994. Critical silvics of feathermoss as related to vegetation management. VMAP Technical Report No. 94-03. Vegetation Management Alternatives Program, Ministry of Natural Resources, Ontario.

Kimmerer, R.W. 1994. Ecological consequences of sexual versus asexual reproduction in *Dicranum flagellare* and *Tetraphis pellucida*. The Bryologist **97**: 20-25.

Lloyd, P.S. 1971. Effects of fire on the chemical status of herbaceous communities of the Derbyshire Dales. Journal of Ecology **59**: 261-273.

Longton, R.E. and S.W. Greene. 1979. Experimental studies of growth and reproduction in the moss *Pleurozium schreberi* (Brid.) Mitt. Journal of Bryology **10**: 321-338.

Maltby, E., C.J. Legg and M.C.F. Proctor. 1990. The ecology of severe moorland fire on the North York Moors: effects of the 1976 fires, and subsequent surface and vegetation development. Journal of Ecology **78**: 490-518.

Mandre M., H. Parn and K. Ots. 2006. Short-term effects of wood-ash on the soil and the lignin concentration and growth of *Pinus sylvestris* L. Forest Ecology and Management **223**: 349-357.

Mishler, B.D. and A.E. Newton. 1988. Influences of mature plants and desiccation on germination of spores of gametophytic fragments of *Tortula.* **15**: 327-342.

Mulligan, R.C. 2002. Bryophyte community structure in a high boreal poor fen in Northern Alberta, Canada. PhD thesis, University of Alberta, Edmonton, Alberta.

Myrmael, A. 1993. Regeneration studies of five spruce, *Picea abies*, forest bryophytes. Lindbergia **18**: 7-18.

Ne'eman, G., S. Goubitz, and R. Nathan. 2004. Reproductive traits of *Pinus halepensis* in the light of fire - a critical review. Plant Ecology **171**: 69-79.

O'Toole, M.A. and D.M. Synnott. 1971 The bryophyte succession on blanket peat following calcium carbonate, nitrogen, phosphorous and potassium fertilizers. Journal of Ecology **59**: 121-126.

Parker, W.C., S.R. Watson, and D.W. Cairns. 1997 The role of hair-cap mosses (*Polytrichum* spp.) in natural regeneration of white spruce (*Picea glauca* (Moench) Voss). Forest Ecology and Management **92**: 19-28.

Rowe, J.S. and G.W. Scotter. 1973. Fire in the boreal forest. Quaternary Research **3**: 444-464.

Rydgren, K., R.H. Økland and T. Økland. 1998. Population biology of the clonal moss *Hylocomium splendens* in Norwegian boreal spruce forests. 4. Effects of experimental disturbance. Oikos **82**: 5-19.

Rydgren, K. and R.H. Økland. 2001. Sporophyte production in the clonal moss *Hylocomium splendens*: the importance of shoot density. Journal of Bryology **23**: 91-96.

Schimmel, J. and A. Granstrom. 1996. Fire severity and vegetation response in the boreal Swedish forest. Ecology **77**: 1436-1450.

SPSS Inc. 2002. SPSS Base 11.0 for Windows User's Guide. SPSS Inc., Chicago, Illinois.

Thomas, P.A., M.C.F. Proctor and E. Maltby. 1994. The ecology of severe moorland fire on the North York Moors: chemical and physical constraints on moss establishment from spores. Journal of Ecology **82**: 457-474.

Van Wagner, C.E. 1983. Fire behaviour in northern coniferous forests and shrublands. Pages 65-80 *in* R.W. Wein, and D.A. MacLean, editors. The Role of Fire in Northern Circumpolar Ecosystem. John Wiley and Sons, New York, USA.

Viro, P.J. Effects of forest fire on soil. Pages 7-46 *in* T.T. Kozlowski and C.E. Ahlgren, editors. Fire and Ecosystems. Academic Press, New York, USA.

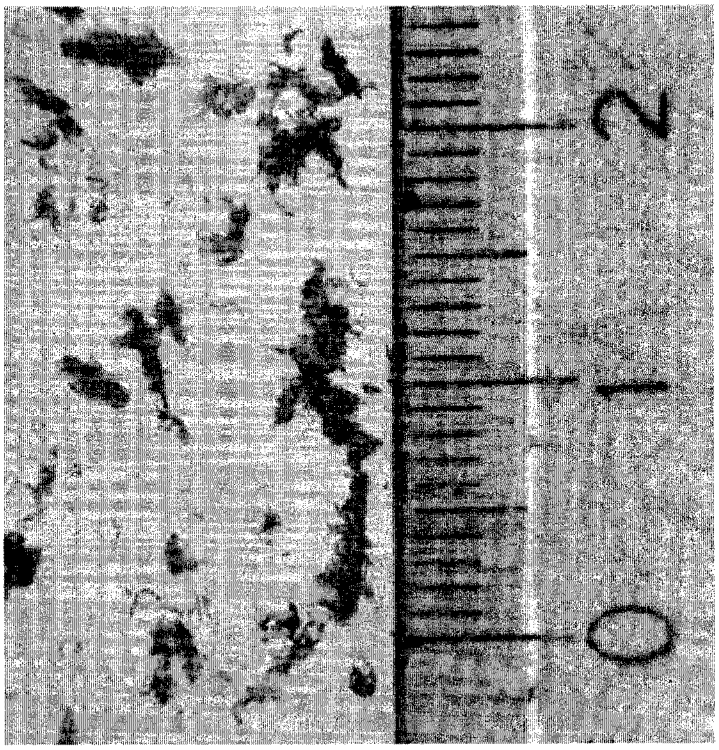
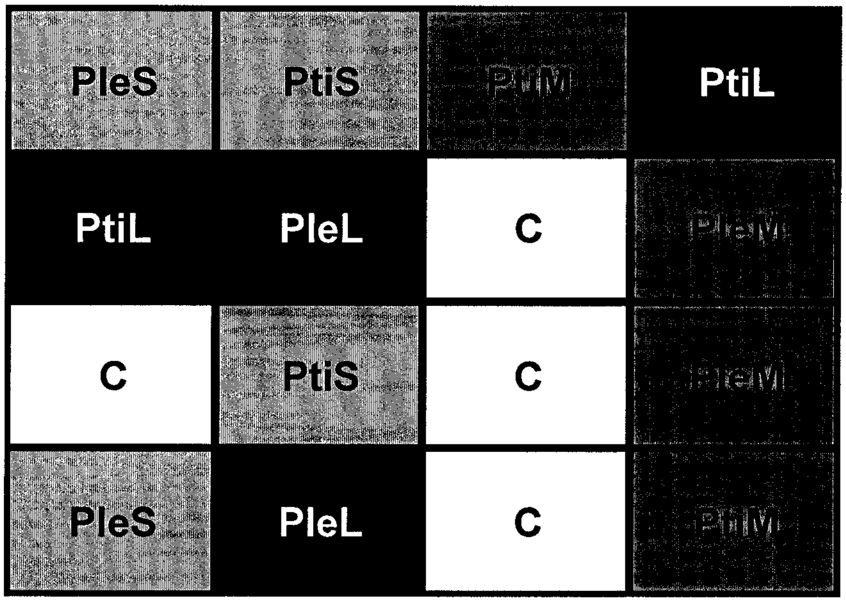
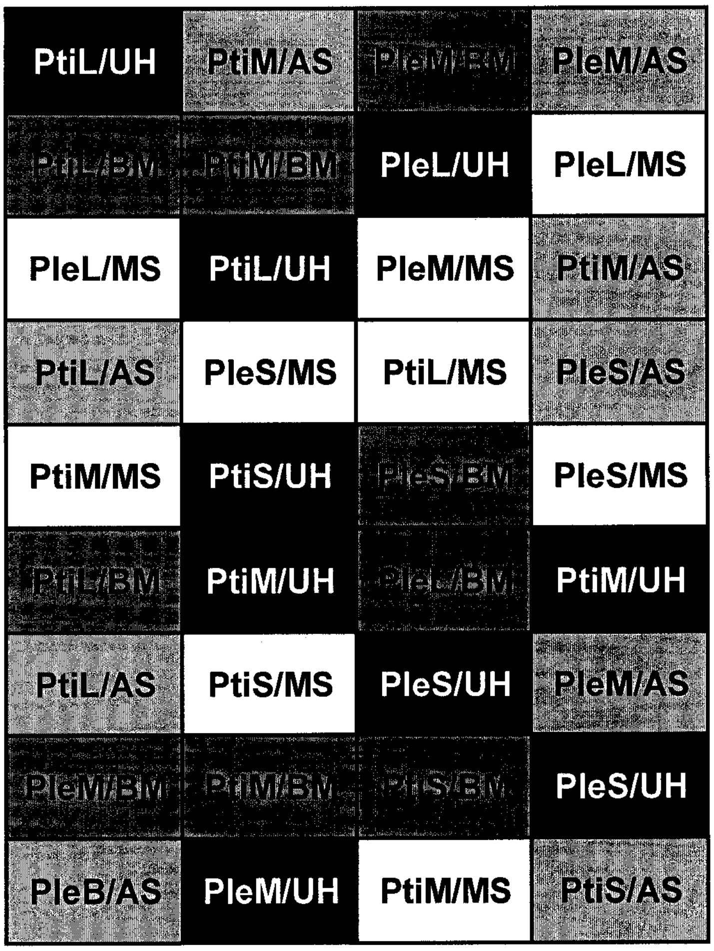


Figure 4.1 Miniature *Ptilium* fragments.



PleS	PtiS	PtiM	PtiL
PtiL	PleL	C	PleM
C	PtiS	C	PleM
PleS	PleL	C	PtiM

Figure 4.2 Examples of an experimental block in the field experiment (top) and a restricted randomized arrangement of treatment combinations within a block (bottom). Abbreviations refer to treatment combinations of fragment species and fragment size and are defined as follows: Ple = *Pleurozium schreberi*, Pti = *Ptilium crista-castrensis*, L = large, S = small, M = miniature and C = blank (no fragment).



PtiL/UH	PtiM/AS	PleM/BM	PleM/AS
PtiL/BM	PtiM/BM	PleL/UH	PleL/MS
PleL/MS	PtiL/UH	PleM/MS	PtiM/AS
PtiL/AS	PleS/MS	PtiL/MS	PleS/AS
PtiM/MS	PtiS/UH	PleS/BM	PleS/MS
PtiL/BM	PtiM/UH	PleL/BM	PtiM/UH
PtiL/AS	PtiS/MS	PleS/UH	PleM/AS
PleM/BM	PtiM/BM	PtiS/BM	PleS/UH
PleB/AS	PleM/UH	PtiM/MS	PtiS/AS

Figure 4.3 Example layout of a block for the growth experiment showing one restricted randomized arrangement of treatment combinations. Arrangements were different in each tray. Abbreviations refer to treatment combinations of fragment species, fragment size and substrate and are defined as follows: Ple = *Pleurozium schreberi*, Pti = *Ptilium crista-castrensis*, L = large, S = small, M = mulch and C = blank, AS = ash, BM = burned moss, MS = mineral soil, UH = unburned humus.

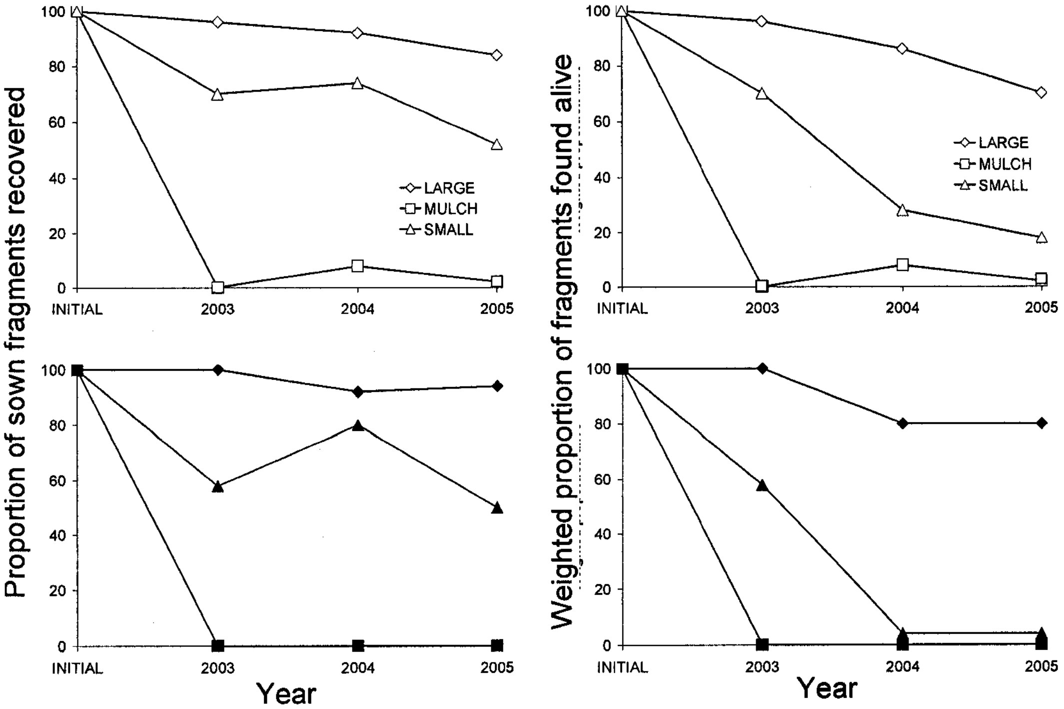


Figure 4.4 Trends over three years in (left) the proportion of fragments of three sizes that were recovered in field plots and (right) the weighted proportion of recovered fragments that were found alive. Initial data represent the proportion at the time of sowing (July 2003). Counts took place in August 2003, 2004 and 2005.

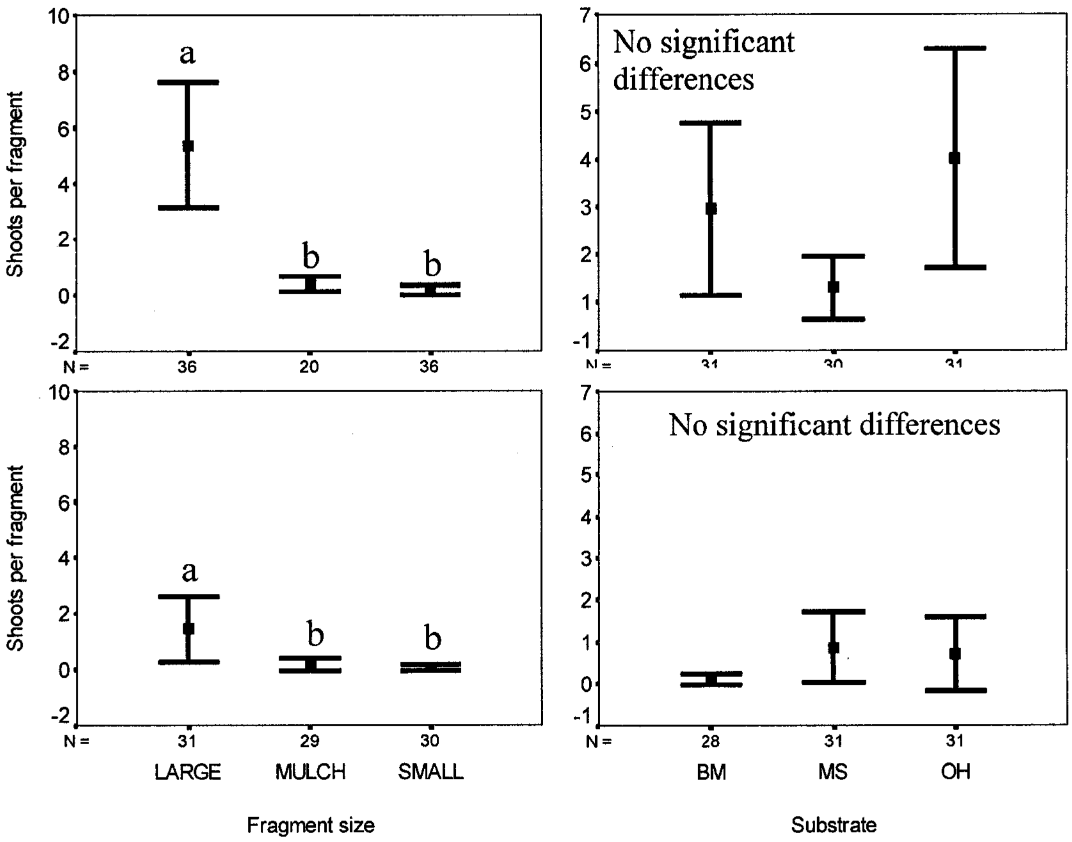


Figure 4.5 Mean number of shoots per fragment (± 95% CI) for *Pleurozium* fragments in the high moisture treatment (top) and low moisture treatment (bottom) among different fragment sizes (left) and substrates (right). Lower case letters indicate significant differences between treatments. Substrate abbreviations are as follows: BM = burned moss, MS = mineral soil, and OH = unburned humus.

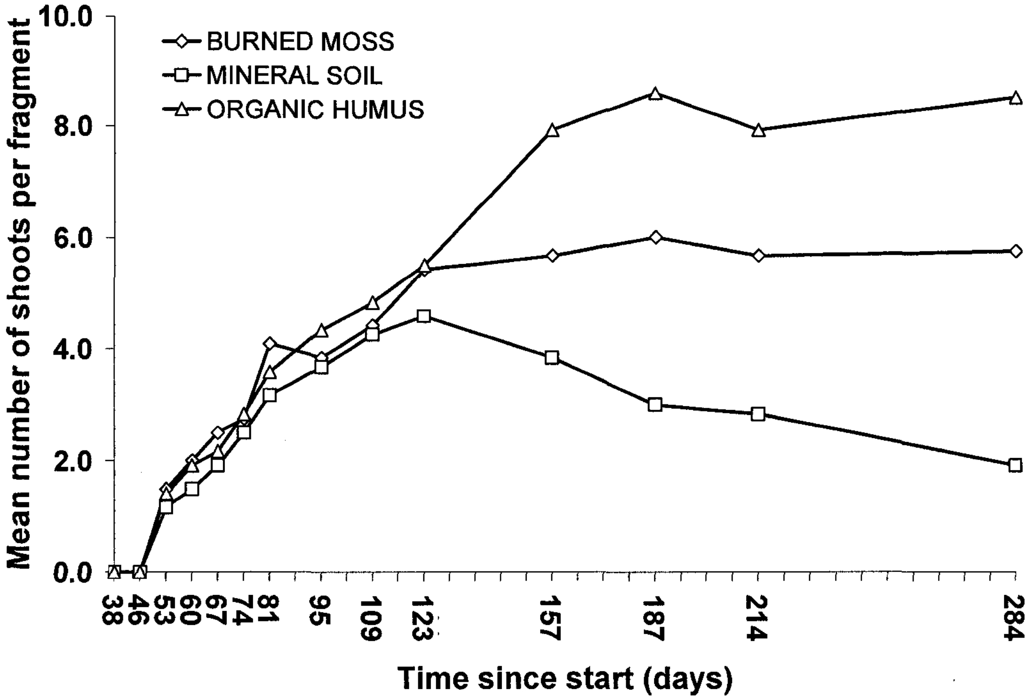


Figure 4.6 Trends in the number of shoots per fragment on large *Pleurozium* fragments on three substrates between 38 and 284 days after fragments were placed in a growth chamber under high moisture. Time since start is given only for those count dates on which data were recorded. A constant rate of change is assumed between dates.

Table 4.1 Results of forward conditional stepwise logistic regressions testing for significant predictors of survival (field experiment) and growth (growth chamber experiment) for large, small and miniature fragments of *Pleurozium schreberi* and *Ptilium crista-castrensis*.

Variable	Slope	SE	*Z*=	*P*-value	Odds Ratio
Field experiment, all fragment sizes					
Large fragment	-4.204	0.469	-8.964	<0.001	0.015
Pleurozium × small fragment	1.890	0.552	3.424	0.001	6.618
Field experiment, large fragments					
Bryophyte cover	0.028	0.015	1.867	0.064	1.028
Growth chamber experiment					
Ptilium	-2.658	0.466	-5.704	<0.001	0.070
Large fragment	1.558	0.385	4.047	<0.001	4.751
High moisture × MS	2.794	0.350	7.982	<0.001	16.340
Large fragment × *Ptilium*	1.930	0.610	3.163	0.002	6.886
BM × small fragment	-0.885	0.380	-2.330	0.020	0.413

Table 4.2 Summary statistics for fragments sown in the field experiment described in Chapter 4, showing the proportion of replicates in which fragments were found, the proportion of recovered fragments that were alive and growth measures. Calculation of weighted proportions is explained in Chapter 3.

Stand	Fragment size	No. of fragments sown (*N*)	Number recovered	Number alive	Percent recovered	Percent found alive[a]	Weighted prop. found alive (%)[b]
Pleurozium schreberi							
BRN1	Large	10	7	5	70.0	71.4	50.0
	Small	10	5	0	50.0	N/A	N/A
	Miniature	10	10	0	100.0	N/A	N/A
BRN2	Large	10	9	9	90.0	100.0	90.0
	Small	10	5	3	50.0	60.0	30.0
	Miniature	10	10	0	100.0	N/A	N/A
BRN3	Large	10	9	8	90.0	88.9	80.0
	Small	10	4	2	40.0	50.0	20.0
	Miniature	10	10	2	100.0	20.0	20.0
BRN4	Large	10	9	5	90.0	55.6	50.0
	Small	10	5	2	50.0	40.0	20.0
	Miniature	10	1	0	10.0	N/A	N/A
Ptilium crista-castrensis							
BRN1	Large	10	9	9	90.0	100.0	90.0
	Small	10	4	0	40.0	N/A	N/A
	Miniature	10	10	1	100.0	10.0	10.0
BRN2	Large	10	10	8	100.0	80.0	80.0
	Small	10	4	0	40.0	N/A	N/A
	Miniature	10	10	0	100.0	N/A	N/A
BRN3	Large	10	9	6	90.0	66.7	60.0
	Small	10	5	1	50.0	20.0	10.0
	Miniature	10	10	1	100.0	10.0	10.0
BRN4	Large	10	9	7	90.0	77.8	70.0
	Small	10	5	0	50.0	N/A	N/A
	Miniature	10	4	1	40.0	25.0	10.0

[a] Percent found alive is the percentage of recovered fragments that were found with living tissue.

[b] Calculation of weighted proportions is explained in Chapter 3.

Table 4.3 Summary statistics for fragments sown in the high moisture treatment in the growth chamber experiment described in Chapter 4. Substrate abbreviations are as follows: AS = ash, BM = burned moss, MS = mineral soil and UH = unburned humus.

Fragment size	Substrate	No. of fragments sown (*N*)	Number recovered	Number with new growth	Percent recovered	Percent with new growth[a]	Weighted prop. found alive (%)[b]
Pleurozium schreberi							
Large	AS	6	6	0	100.0	0.0	0.0
	BM	12	12	9	100.0	75.0	75.0
	MS	12	12	9	100.0	75.0	75.0
	UH	12	12	12	100.0	100.0	100.0
Small	AS	6	6	0	100.0	0.0	0.0
	BM	12	12	10	100.0	83.3	83.3
	MS	12	12	1	100.0	8.3	8.3
	UH	12	12	9	100.0	75.0	75.0
Miniature	AS	12	12	0	100.0	0.0	0.0
	BM	12	7	6	58.3	85.7	50.0
	MS	12	6	1	50.0	16.7	8.3
	UH	12	7	5	58.3	71.4	41.7
Ptilium crista-castrensis							
Large	AS	6	6	0	100.0	0.0	0.0
	BM	12	12	8	100.0	66.7	66.7
	MS	12	12	5	100.0	41.7	41.7
	UH	12	12	12	100.0	100.0	100.0
Small	AS	6	6	0	100.0	0.0	0.0
	BM	12	12	2	100.0	16.7	16.7
	MS	12	12	0	100.0	0.0	0.0
	UH	12	12	5	100.0	41.7	41.7
Miniature	AS	12	12	0	100.0	0.0	0.0
	BM	12	8	0	66.7	0.0	0.0
	MS	12	11	0	91.7	0.0	0.0
	UH	12	8	1	66.7	12.5	8.3

[a] Percent with new growth is the percentage of recovered fragments that were found with new growth.

[b] Calculation of weighted proportions is explained in Chapter 3.

Table 4.4 Summary statistics for fragments sown in the low moisture treatment in the growth chamber experiment described in Chapter 4. Substrate abbreviations are as follows: AS = ash, BM = burned moss, MS = mineral soil and UH = unburned humus.

Fragment size	Substrate	No. of fragments sown (*N*)	Number recovered	Number with new growth	Percent recovered	Percent with new growth[a]	Weighted prop. found alive (%)[b]
Pleurozium schreberi							
Large	AS	10	10	0	100.0	N/A	N/A
	BM	9	9	3	100.0	33.3	33.3
	MS	11	11	5	100.0	45.5	45.5
	UH	11	11	5	100.0	45.5	45.5
Small	AS	10	10	0	100.0	N/A	N/A
	BM	10	10	1	100.0	10.0	10.0
	MS	11	10	3	90.9	30.0	27.3
	UH	10	10	2	100.0	20.0	20.0
Miniature	AS	10	10	0	100.0	N/A	N/A
	BM	11	9	1	81.8	11.1	9.1
	MS	10	10	2	100.0	20.0	20.0
	UH	10	10	2	100.0	20.0	20.0
Ptilium crista-castrensis							
Large	AS	10	10	0	100.0	N/A	N/A
	BM	11	11	4	100.0	36.4	36.4
	MS	10	10	2	100.0	20.0	20.0
	UH	11	11	3	100.0	27.3	27.3
Small	AS	11	11	0	100.0	N/A	N/A
	BM	10	10	1	100.0	10.0	10.0
	MS	10	10	0	100.0	N/A	N/A
	UH	11	11	0	100.0	N/A	N/A
Miniature	AS	11	11	0	100.0	N/A	N/A
	BM	11	9	0	81.8	N/A	N/A
	MS	11	10	0	90.9	N/A	N/A
	UH	10	10	0	100.0	N/A	N/A

[a] Percent with new growth is the percentage of recovered fragments that were found with new growth.

[b] Calculation of weighted proportions is explained in Chapter 3.

Table 4.5 Mean substrate pH values recorded at the beginning of the growth chamber experiment and after 84 and 284 days.

Time	*n*	Ash	Burned moss	Mineral soil	Unburned humus
High moisture treatment					
Initial	6	9.0	4.3	5.6	4.6
84 days	6	7.7	5.5	5.8	5.0
284 days (final)	8	7.8	4.7	5.5	4.2
Low moisture treatment					
Initial	6	9.0	4.3	5.6	4.6
84 days	6	8.6	5.0	5.5	5.2
284 days (final)	8	8.1	4.5	5.3	4.2

Table 4.6 Results of pairwise comparisons using multiple response permutation procedure (with Euclidean distances) testing for the effect of fragment size on the number of shoots per fragment after 284 days in a growth chamber. Only differences among *Pleurozium* fragments were tested and only significant differences between treatments are shown.

Substrate	Contrast	T-statistic	Observed d	A	*P*-value
High moisture					
Burned moss	Large v Small	-3.757	0.493	0.160	0.010
Mineral soil	Large v Small	-6.152	0.322	0.298	0.001
Unburned humus	Large v Small	-2.305	0.619	0.112	0.034
	Large v Mulch	-5.054	0.533	0.202	0.002
Low moisture					
Unburned humus	Large v Small	-2.567	0.292	0.132	0.027

Chapter 5: Burned feather mosses as a biological legacy of low severity fires in Alberta's boreal spruce (*Picea* spp.) forests*

Franklin et al. (2002) coined the term 'biological legacies' to describe the remains of living organisms left by disturbances. Using the example of snags and remnant old-growth trees, Franklin et al. (2002) and Keeton and Franklin (2005) showed that biological legacies can be important structural components of *Pseudotsuga meziesii* forests in the U.S. Pacific Northwest following disturbance because they provide services to other biota. Forest fires in the boreal ecosystem also leave biological legacies. These can include the burned remains of feather mosses, which are left on the forest floor after low severity fires in mature spruce (*Picea* spp.) forests.

Burned feather moss carpets are largely composed of the remains of the perennial pleurocarpous mosses *Pleurozium schreberi* (Brid.) Mitt., *Hylocomium splendens* (Hedw.) BSG and *Ptilium crista-castrensis* (Hedw.) De Not.. They reflect the high cover of these species on the forest floor prior to disturbance. Feather moss carpets can range from less than 10 cm to more than 50 cm in depth (Bonan and Shugart 1989). Burning chars the upper layers, while lower layers are left intact. Therefore, burned moss carpets retain the structural features of living carpets and may have similar impacts. For example, living feather moss carpets can be unsuitable seedbeds because roots of seedlings that germinate within the upper layers may not reach the underlying soil and could experience nutrient deficiency and drought (Aksamit and Irving 1984; Coates et al. 1994; Steijlen et al. 1995;

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* This study was devised and supervised by the author and carried out as a BIOL 499 research project by an undergraduate student, Nyja Thordarson, in the Department of Biological Sciences at the University of Alberta. Data were re-analysed by the author prior to compiling this chapter.

Hörnberg et al. 1997; Ringius and Sims 1997; Zackrisson et al. 1997; Hanssen 2003). Germinants that do fall through to the soil surface will have to survive shading by the moss material above (During and van Tooren 1990; Hörnberg et al. 1997).

There is considerably variability in the regeneration niches of plant species and their capacity to tolerate stress (Grubb 1977; Grime 1977). To the extent that it constitutes a stressful environment, burned moss may exert selective pressure upon the establishment potential and spatial distribution of plant species by excluding them from locations where it is present. If the recruitment of tree species, in particular, is inhibited by burned moss, effects on canopy composition could be long lasting (Morneau and Payette 1989; Johnson 1995). This would have implications for forest management and biota that depend upon the presence of particular species.

As part of a broader research project investigating the successional ecology of *Pleurozium schreberi* and *Ptilium crista-castrensis* in the boreal forests in Alberta, Canada, we carried out a laboratory experiment to assess the impact of burned feather moss on the germination, short-term survival and growth of selected tree species and forbs. Our objective was to test the hypothesis that feather mosses can influence succession in the vascular plant community in early successional stages because vascular plant species differ in their ability to tolerate burned moss at the seed and seedling stage.

Materials and Methods

Study species

We chose four vascular plant species (two trees and two forbs) for this study on the basis that they are common in central Alberta and seeds were readily obtainable: *Larix laricina* (Du Roi), *Picea glauca* (Moench) Voss, *Petasites palmatus* and *Linum lewisii* Pursh.

Petasites palmatus (Asteraceae) is a common herbaceous perennial in boreal wetlands, muskegs and damp forests (Moss 1996). This species can appear soon after a stand-replacing fire, growing in moist open soil and burned-over *Sphagnum* hummocks (personal observation). Although rhizomatous, it produces abundant light achenes with thin pappus hairs from composite white inflorescences. *Petasites* seeds were collected from wild plants in the fall of 2002.

Linum lewisii (Linaceae) is a non-clonal herbaceous perennial of open boreal forest and dry grassland (Moss 1996). It can be a valuable forage species for deer and birds and may be useful for erosion control (USDA 2007). *Linum* seeds were provided by McKenzie Seeds, a retail seed supplier in Brandon, Manitoba.

Picea glauca (Pinaceae) is extensively harvested in the boreal region for pulp and lumber (Nienstaedt and Zasada 1990). It has also been used for the re-vegetation of coal mine spoils in Alberta (Watson et al. 1980). Seeds of *Picea glauca* were removed from cones collected from a single tree in a garden in Edmonton, Alberta, in the fall of 2002.

Larix laricina (Pinaceae) has been used in the remediation of coal mine spoils and sand tailings in Alberta (Watson et al. 1980). It is not a major commercial timber species (Uchytil 1991a). It is a shade-intolerant tree commonly found alongside *Picea mariana* (Mill.) BSP. in muskegs and other stands with a high water table (Bonan and Shugart 1989; Uchytil 1991a; Beckingham and Archibald 1996). *Larix laricina* seeds were provided for this experiment by the Alberta Tree Improvement and Seed Centre.

Substrate collection

Three substrates were used in this study, burned feather moss (BM), mineral soil (MS) and unburned humus (UH). All were collected in October 2002 from a *Picea mariana* stand burned in 2002 in the House River Fire in north-central Alberta. Collection of BM and MS is described in Chapter 3. Humus was collected from beneath BM.

Survival and growth experiment

Short-term seedling survival was compared among *Larix laricina*, *Picea glauca* and *Petasites palmatus* (we later added *Linum lewisii* for the germination study based on the results for *Petasites* in the survival study). We pregerminated seeds of each species in 60 mm Petri plates on a sheet of Whatman #1 filter paper moistened with 2 ml distilled water. Germination was defined as the emergence of the radical tip from the testa. We prepared 20 pots of each of the substrates for the tree species but only seven pots of each substrate were prepared for *Petasites* because of the limited number of seeds that germinated.

In each pot, we placed randomly selected pre-germinated seeds at eight evenly spaced locations around the perimeter and 10 mm from the edge and we placed two additional seeds either side of the centre of the pot approximately 20 mm apart. Transplanting occurred over the period of one week and we transplanted all seeds in each on the same day.

Pots were randomly arranged in flats, placed in a growth chamber and watered every three days. We rearranged flats after watering. After four, 10 and 14 weeks, we recorded survival of each transplanted seedling as a binary variable (1 = Alive, 0 = Dead). We only counted seedlings with green leaves as alive. At 14 weeks, we measured the stem length and the above-ground biomass of surviving seedlings and calculated a mean for each pot containing two or more seedlings. Root length and total biomass could not be measured because we could not extract roots from BM. After we had removed the seedlings, the pH of 7 randomly selected pots of each substrate was recorded and converted to an H^+ concentration. A mean H^+ concentration was calculated from this data and converted back to a pH value.

Germination study

To compare germination rates, we distributed substrates evenly among 1,296 16 cm^2 pots (432 pots per substrate). When we were filling pots, we attempted to maintain the vertical structure of BM and MS. We placed filled pots in flats in blocks of six (two rows of three pots per block), each block containing only one substrate treatment.

In each of 144 pots of each substrate we sowed four seeds of a single species. Pots were arranged such that a row of three pots in a block contained one species, and the adjacent row contained a different species. *Linum lewisii* pots were adjacent to those containing *Petasites palmatus*, and *Larix laricina* was next to *Picea glauca*. We then randomly distributed blocks among 12 trays and placed these in a growth chamber. Conditions in the growth chamber were intended to approximate a mild summer day in north-central Alberta: day temperature 24°C, night temperature 10°C; day length 15 hours; light intensity: 250 mE s^{-1} m^{-2}.

We watered trays were watered with distilled water at the start of the experiment and covered them with plastic to maintain humidity. Watering was repeated once a week thereafter. Units were re-randomized among trays after each watering. The number of new germinants of each species was recorded every second day. Where possible, we defined germination as the appearance of a radicle, but in the BM treatment watering had the potential to displace seeds out of sight into lower layers. In those cases, we counted a seed as germinated if a seedling emerged from the substrate. We assumed that seeds had not germinated if no seedling emerged. We stopped counting when no further germination was recorded over seven days.

Data analysis

We compared survival among species, substrates, pots and sowing dates at 14 weeks using a general linear mixed model (GLMM) with a binomial distribution in the GLIMMIX procedure (SAS Version 9.1.3, SAS Institute Inc. 2006). Main and interaction effects were calculated for two fixed effects: species and substrate. A species × substrate interaction nested within pot was entered as a random factor.

We compared mean height and mean dry weight among substrates within species using analysis of covariance (ANCOVA) in SPSS version 11.5 (SPSS Inc. 2002). Because there was the potential for greater competition in pots with more survivors, we included the number of seedlings in a pot at 14 weeks as a covariate. The homogeneity of variances was confirmed for all tests using Levene's statistic (Zar 1996). The distribution of the data for *Picea* seedlings on MS was non-normal for both variables (Shapiro-Wilks test, untransformed data: $P = 0.027$ for mean height and 0.029 for dry weight) and data transformation resulted in greater divergences from a normal distribution. Nevertheless, we used the ANCOVA because this method can be robust to non-normal distributions and allowed for the inclusion of the covariate (SPSS Inc. 2002). We used Bonferroni *post hoc* tests to identify significant pairwise comparisons.

Stepwise binary logistic regression (SPSS version 11.5, SPSS Inc. 2002) was used to test whether substrates species and interactions between substrates and species were good predictors of germination. We entered substrates and species as dummy indicator variables and performed post hoc pairwise Pearson chi-squared tests in SPSS to identify significant differences between substrates within species and between tree species within substrates. Frequency of germinants was the dependent variable.

Results

Survival

Figure 5.1 shows trends in survival on the experimental substrates. After 4 weeks, survival of *Petasites palmatus* was 16% on MS, 10% on BM and 6% on UH. After 10 weeks, seedlings were alive only on MS and survival had declined to 14%. No *Petasites* seedlings were alive on any substrate at 14 weeks. Almost half of all *Larix* seedlings on BM were dead after 4 weeks and the mortality rate increased between 4 and 10 weeks. In contrast, more than half of all *Picea* seedlings were alive on all substrates at 14 weeks. Mortality rate decreased after 4 weeks and again after 10 weeks on both BM and UH.

The GLMM showed that survival at 14 weeks was significantly related to species ($F_{1,\ 108} = 12.46$, $P < 0.001$) and substrate ($F_{2,\ 108} = 11.24$, $P < 0.001$) and there was a significant species × substrate interaction ($F_{2,\ 108} = 9.78$, $P < 0001$). Survival of *Larix* seedlings was significantly higher on UH than on MS and significantly lower overall than survival of *Picea* seedlings. There were no significant differences between substrates for *Picea*.

Growth

Differences among substrates in final mean height and mean dry weight are shown in Fig. 5.2. The number of seedlings in a pot was not a significant covariate for either species but substrate was significant in the model for *Larix laricina* seedlings for mean height ($F_{2,\,46} = 11.36$, $P < 0.001$) and mean dry weight ($F_{2,\,46} = 31.42$, $P < 0.001$). Mean height and mean dry weight of *Larix* seedlings were significantly higher on UH than on both BM (SE = 1.77, $t = -2.93$, $P = 0.005$) and MS (SE = 1.41, $t = -4.75$, $P<0.001$). There were no significant differences among substrates in the mean height of *P. glauca* seedlings but substrate was a significant factor in the model for mean dry weight ($F_{2,\,53} = 10.13$, $P < 0.001$). Mean dry weight of *Picea* seedlings was significantly higher on UH than on both BM (SE = 0.001, $t = -4.43$, $P<0.001$) and MS (SE = 0.001, $t = -2.90$, $P<0.005$).

Germination

Petasites failed to germinate on any of the substrates. *Larix laricina* (SE: 0.124, $Z = -7.242$, $P<0.001$, odds ratio 0.408) and UH (SE: 0.122, $Z = 5.230$, $P<0.001$, odds ratio 1.893) were significant predictors of germination in the logistic regression model ($\chi^2 = 80.885$, df = 2; $P<0.001$). The model correctly predicted 59.3% of cases.

$$\text{Predicted logit (germ.)} = 0.271 - (0.898 \times \textit{Larix}) + (0.638 \times \text{UH})$$

Summary statistics for germination are given in Table 5.1. Results of pairwise goodness of fit tests are given in Tables 5.2 and 5.3. Germination of *Larix* seeds was significantly lower on UH than on MS and significantly fewer *Linum* seeds germinated on UH than on any other substrate (Table 5.2). The germination of *Larix* was higher than that of *Linum* and *Picea* on all substrates (Table 5.3).

Substrate pH

The final mean pH values of MS, BM and UH were 4.63, 4.54 and 4.32, respectively.

Discussion

Forest fires can leave a variety of biological legacies (*sensu* Franklin and MacMahon 2000). Attention has previously focussed on snags and fallen trees (Franklin and MacMahon 2000; Franklin et al. 2002; Keeton and Franklin 2005) but these are not the only organic structures left by disturbances that are biologically important. Other biological legacies include woody debris, which provides habitat for arthropods and affects the chemical properties of forest soils (Klinka et al 1995; Niwa et al. 2001), and living feather mosses left by clear-cutting (Nguyen-Xuan et al. 2000). Forest fires can also leave biological legacies in the form of incompletely combusted feather moss carpets. Our study has shown that seedlings of vascular plant species vary in their tolerance of BM and indicated that BM on the forest floor can influence community composition and structure.

Germination

We found that seeds of the study species were just as likely to germinate on BM as on other substrates (Fig. 5.3). Given the highly porous structure of BM and the tendency for it to dry out in warm weather under natural conditions (personal observation), this result was unexpected. *Larix laricina*, in particular, favours a moist seed bed (Duncan 1954) and we expected it to show a reduced germination rate on BM. A possible explanation for better than expected germination on this substrate is that regular watering of pots kept BM moist. In addition, the depth of material in pots was less than the thickness of BM carpets in the field. We made this compromise to limit the possibility that seeds would become unobservable. Together with the bright overhead lighting, this could have made it less likely that seeds would fall to a depth where light was insufficient for germination.

The germination rate of *Larix laricina* exceeded 50% on all substrates (Table 5.1), which is relatively high compared to rates reported in the literature. Duncan (1954) reported rates between 30% and 60% under laboratory conditions and cited other studies that found rates of between 10% and 85% and an average rate of 47%. This may have been a result of highly favourable hydration conditions in the growth chamber. Germination of *L. laricina* requires moist organic humus or mineral soil (Duncan 1954; Johnston 1990). Frequent watering of pots in this study ensured that all substrates were continuously moist, which might have provided optimal conditions for germination. Furthermore, the pH of all substrates was within the range of 4.5 to 7.6 that was found by Duncan (1954) to favour good germination, although that author concluded that pH was probably not a limiting factor for *L. laricina* seeds.

In contrast to *Larix*, *Picea glauca* showed germination rates at the low end of the range quoted in the literature. Maximum germination was 53% on BM, which is close to the value of 61% recorded by Caron et al. (1990) for seeds stored for six weeks and 62% for pre-chilled seeds stored for two weeks. Nonetheless, this rate was low compared with the values of 94.7% recorded in the same study for pre-chilled seeds stored for six weeks. Safford (1974; cited in Uchytil (1991b)) gave germination rates for *Picea glauca* of 50% to 70% and Kolotelo (1994) recorded rates of over 80% under different soaking and stratification treatments. Coates et al. (1994) state that spruce seeds require no special treatment to break dormancy but stratification and exposure to light can increase germination rates. Seeds were not stored or treated to break dormancy in this study, which may explain the relatively low germination rate. *P. glauca* seeds have shown high germination on a range of organic and mineral substrates (Charron and Greene 2002; Awada et al. 2004), which is consistent with the lack of differences in germination rate among substrates in this study.

The high mortality rate of *Petasites* seedlings may have been due to difficulties in transplanting seedlings. Seedlings were extremely fragile and radicles often became detached from the cotyledons when pre-germinated seeds were being transferred to pots from Petri Plates. Although seedlings were discarded when we noticed this, some damage may have gone unnoticed. The failure of *Petasites* to germinate on any substrate suggests that rhizomes are more important for the post-fire regeneration of this species.

Seedling survival and short-term growth

Burned feather moss was a poor substrate for seedlings of *Larix laricina*. Almost 50% of the pre-germinated *Larix* seeds that were transplanted onto BM died within four weeks. Eighty percent were dead after 14 weeks (Fig. 5.1). High mortality in the first few weeks after germination is a feature of this species (Duncan 1954; Johnston 1990). Duncan (1954) found that only 30% of seedlings growing in field plots were surviving after one year, only 6% survived two years and only 3.5% survived for three growing seasons. The same author reported 40% mortality for *L. laricina* seedlings in the first five to six weeks since germination. In our study, survivorship of *L. laricina* seedlings on BM had declined to 20% after only 14 weeks, which was less than half that of seedlings surviving on other substrates after the same period was (Fig. 5.1). Common causes of seedling mortality in *L. laricina* include damping off, mechanical injury and drought (Duncan 1954). Damping-off can be caused by pathogenic fungi such as *Fusarium* spp. and encouraged by moist conditions (Coates et al. 1994). Given that we kept the substrates continuously moist in our study, the risk of damping off may have been elevated. However, the roots of *L. laricina* seedlings may still have dried out in the gaps between moss stems. Duncan (1954) reported that roots of seedling tamaracks rarely exceed three-quarters of an inch in the first few weeks of growth and may be vulnerable to drought. In this study BM did not hold moisture and may have elevated seedling roots above the soil. Therefore, drought may have contributed to the high mortality rate on BM.

The mortality of *Pic*ea glauca seedlings was highest in the first four weeks but did not exceed 27% on any substrate (Fig. 5.1). Mortality rates over a similar period could not be found in the literature for comparison but other studies show high mortality in the earliest phase of seedling growth. Purdy et al. (2002) reported that less than 3% of *Picea glauca* seeds sown in mixedwood boreal forest stands survived to become one-year-old germinants, but survival was much higher in subsequent years. Similar results were reported in field sowing experiments by Charron and Greene (2002), who found that the stage from abscised seed to the end of the first summer accounted for 63 to 100% of all deaths. Causes of seedling mortality in spruce include desiccation, heat injury, flooding, frost, competition with other vegetation, animal damage and pathogenic fungi (Coates et al. 1994). As with *Larix*, *Picea* seedlings may have suffered some mortality in this study as a result of fungus-induced damping off.

If dry weight provides a good measure of short-term growth, BM appears to be a sub-optimal substrate for the growth of both *Picea glauca* and *Larix laricina.* In addition to retaining little moisture, this substrate might not provide a suitable environment for the growth of mycorrhizal fungi, which are essential for optimum growth of tree species in boreal forest soils (Van Cleve et al. 1983; Boormann and Sidle 1990; Paré et al. 1993). On BM the mean height of *Larix* seedlings was *c.* 9 mm less than that of *P glauca* seedlings. Mean above-ground dry weight was also lower, but the magnitude of the difference was less. This could indicate that *P.*

glauca has a higher tolerance for BM than *L. laricina*. *Picea* seedlings can tolerate a variety of mineral and organic seedbeds and mature trees can be found growing under a range of moisture regimes in Alberta (Beckingham and Archibald 1996). In contrast, *Larix laricina* is characteristic of wetter substrates in bogs and fens (Beckingham and Archibald 1996).

Effects of burned moss on secondary succession

Early stages in secondary succession often have the highest species richness, with high contributions from seed dispersed species (Ahlgren 1960; Shafi and Yarranton 1973; Rowe and Scotter 1973; Abrams and Dickmann 1982; Chipman and Johnson 2002). If BM carpets are widespread on the forest floor and influence regeneration from seed, they may also affect the diversity and composition of early successional plant communities and the rate of regeneration. The wet forests and muskegs where *Larix* is found alongside *Picea mariana* can have a high cover of *Pleurozium schreberi* (Foster 1985; Johnston and Elliott 1996; Boudreault et al. 2002; Bonan and Shugart 1989). These are among the habitats least likely to burn with high intensity (Rowe and Scotter 1973; van Wagner 1983; Uchytil 1991a). Our results suggest that *Larix* will be less likely to recolonise after fire in those areas where the remains of *Pleurozium* and other feather mosses are incompletely combusted. The dispersion of individual trees that do establish might partly reflect patchiness in the post-fire distribution of BM carpets. As a shade-intolerant species, *Larix* must also grow at a competitive rate early in succession in order to claim a place in the tree canopy. If growth is stunted in BM, most seedlings of *Larix* that do become established may die later as a result of shading by species that are more tolerant of BM. A longer term experiment is necessary to show whether the height difference between *Picea* and *Larix* seedlings that was found on BM in the study would be maintained.

In stands where feather moss remains are widespread, early successional stages may contain a relatively high proportion of species that regenerate from rhizomes and other underground organs. Schimmel and Granstrom (1996) found that seed-dispersing species tended to be increasingly dominant as depth of burn increased in Swedish forests, whereas rhizomatous species that were dominant in the pre-fire vegetation were relatively abundant after low severity fires. In the stand from which we collected substrates, we observed that the most abundant species present one year after fire were *Ledum groenlandicum* Oeder, *Rosa acicularis* Lindl. and *Cornus canadensis* L. (personal observation). All grow rapidly after fire from structures that survive underground (personal observation; Ahlgren 1960; Rowe and Scotter 1973; Morneau and Payette 1989). In a burned *Picea mariana* stand within the boundaries of the same fire, *Picea glauca* seedlings were found to be restricted to depressions where burned moss was not present (personal observation). Absent from both sites were several species that were recorded after a similar period since fire in stands where no BM was present, such as *Geranium bicknellii* L., *Dracocephalum parviflorum* Nutt. and *Corydalis* spp. All of these species establish after fire primarily or exclusively from seed (Rowe and Scotter 1973; Abrams and Dickman 1982; Johnston and Elliott 1996; Schimmel and Granstrom 1996). Early successional bryophytes, such as *Ceratodon purpureus*

(Hedw.) Brid., *Funaria hygrometrica* Hedw. and *Leptobryum pyriforme* (Hedw.) Wils. were also uncommon in site where BM was collected and were most frequent in patches of mineral soil. These species are common in burned forests where the forest floor is comprised of mineral substrates (Chapter 2, Morneau and Payette 1989; Maltby et al. 1990; Schimmel and Granstrom 1996; Nguyen-Xuan et al. 2000).

Management considerations

Management strategies for biological legacies have so far focussed on living and dead trees in disturbed forest stands (Franklin and MacMahon 2000; Franklin et al. 2002; Keeton and Franklin 2005). Our findings show that BM carpets also require attention. The removal of burned moss remains from the soil surface may lead to more rapid and spatially homogeneous growth of early successional forest vegetation. This will not be appropriate in all circumstances, though. The eradication of any biological legacy will impact other biota (Franklin et al. 2002; Keeton and Franklin 2005). Legacies must be kept intact if the objective is to maintain their ecosystem functions. This is true for BM carpets regardless of whether they inhibit regeneration of some plant species. Longer term field studies of the impacts of BM carpets should yield data of value to forest managers in the boreal zone where secondary succession is an unavoidable management consideration and emulation of natural disturbance is a priority.

Conclusions

We tested the potential for burned feather moss carpets to influence the establishment of vascular plant species by comparing the germination of *Larix laricina*, *Picea glauca*, *Linum lewisii* and *Petasites palmatus* on mineral soil, unburned humus and the burned remains of feather mosses in a growth chamber experiment. Germination did not differ between substrates. Survival of *Larix laricina* seedlings on burned feather moss was significantly lower than that of *Picea* seedlings on any substrate and *Larix* seedlings on all other substrates. Mean height and dry weight of *Larix* seedlings was significantly higher on humus than on mineral soil and burned feather moss but did not differ significantly between substrates for *Picea*. Our results suggest that burned moss can mediate the establishment of plant species from seed. Specific effects will vary among species, which could influence the species composition and spatial structure of forest stands throughout succession.

Literature Cited

Abrams, M.D. and D.I. Dickman. 1982. Early revegetation of clear-cut and burned jack pine sites in northern lower Michigan. Canadian Journal of Botany **60**: 946-954.

Ahlgren, C.E. 1960. Some effects of fire on reproduction and growth of vegetation in northeastern Minnesota. Ecology **41**: 431-445.

Aksamit, S.E. and F.D. Irving. 1984. Prescribed burning for lowland black spruce regeneration in northern Minnesota. Canadian Journal of Forest Research **14**: 107-113.

Awada, T., G.M. Henebry, R.E. Redmann and H. Sulistiyowati. 2004. *Picea glauca* dynamics and spatial pattern of seedlings regeneration along a chronosequence in the mixedwood section of the boreal forest. Annals of Forest Science **61**: 789-794.

Beckingham, J.D. and J. Archibald, 1996. Field Guide to Ecosites of Northern Alberta. Special Report 5. Natural Resources Canada, Canadian Forest Service, Northwest Region, Northern Forestry Center, Edmonton, Alberta.

Bonan, G.B. and H.H. Shugart. 1989. Environmental factors and ecological processes in boreal forests. Annual Review of Ecology and Systematics **20**: 1-28.

Boormann, B.T. and R.C. Sidle. 1990. Changes in productivity and distribution of nutrients in a chronosequence at Glacier Bay National Park. Alaska. Journal of Ecology **78**: 561-578.

Boudreault, C., Y. Bergeron, S. Gauthier and P. Drapeau. 2002. Bryophyte and lichen communities in mature to old-growth stands in eastern boreal forests of Canada. Canadian Journal of Forest Research **32**: 1080-1093.

Caron, G.E., B.S.P. Wang and H.O. Schooley. 1990. Effect of tree spacing, cone storage and prechilling on germination of *Picea glauca* seed. Forestry Chronicle 66: 388-392.

Charron, I. and D.F. Greene. 2002. Post-wildfire seedbeds and tree establishment in the southern mixedwood boreal forest. Canadian Journal of Forest Research **32**: 1607-1615.

Chipman, S.J. and E.A. Johnson. 2002. Understory vascular plant species diversity in the mixedwood boreal forest of western Canada. Ecological Applications **12**: 588-601.

Coates, K.D., S. Haeussler, S. Lindeburgh, R. Pojar and A.J. Stock. 1994. Ecology and Silviculture of Interior Spruce in British Columbia. Forest Resource Development Report. Forestry Canada and British Columbia Ministry of Forests, Victoria, British Columbia.

Duncan, D.P. 1954. A study of some of the factors affecting the natural regeneration of tamarack (*Larix laricina*) in Minnesota. Ecology **35**: 498-521.

During, H.J. and B.F. van Tooren. 1990. Bryophyte interactions with other plants. Botanical Journal of the Linnean Society **104**: 79-98.

Foster, D.R. 1985. Vegetation development following fire in *Picea mariana* (black spruce)-*Pleurozium* forests of south-eastern Labrador, Canada. Journal of Ecology **73**: 517-534.

Franklin, J.F. and J.A. MacMahon. 2000. Message from a mountain. Science. **288**: 1183-1185.

Franklin, J.F., T.A. Spies, R. Van Pelt, A.B. Carey, D.A. Thornburgh, D.R. Berg, D.B. Lindenmayer, M.E. Harmon, W.S. Keeton, D.C. Shaw, K. Bible and J. Chen. 2002. Disturbance and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management **155**: 399-423.

Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. American Naturalist **111**: 1169-1194.

Grubb, P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biological Reviews **52**: 107-145.

Hanssen, K.H. 2003. Natural regeneration of *Picea abies* on small clear-cuts in SE Norway. Forest Ecology and Management **180**: 199-213.

Johnston, W. F. 1990. *Larix laricina* (Du Roi) K. Koch tamarack. Pages 141-151 *in* R. Burns and B.H. Honkala, technical coordinators. Silvics of North America. Volume 1. Conifers. Agriculture Handbook 654. U.S. Department of Agriculture, Forest Service, Washington, DC, USA.

Johnson, D., L. Kershaw, A. MacKinnon and J. Pojar. 1995. Plants of the Western Boreal Forest and Aspen Parkland. Lone Pine Publishing and the Canadian Forest Service, Edmonton, Canada.

Johnston, M.H. and J.A. Elliott. 1996. Impacts of logging and wildfire on an upland black spruce community in northwestern Ontario. Environmental Monitoring and Assessment **39**: 283-297.

Keeton, W.S. and J.F. Franklin. 2005. Do remnant old-growth trees accelerate rates of succession in mature Douglas-fir forests? Ecological Monographs **75**: 103-118.

Klinka, K., L.M. Lavkulich, Q. Wang and M.C. Feller. 1995. Influence of decaying wood on chemical properties of forest floors and surface mineral soils: a pilot study. Annals of Forest Science **52**: 523-533.

Kolotelo, D. 1994. Response of interior spruce to extended stratification. From Seed and Seedling Extension Topics Volume 7. Cone and Seed Improvement Program, British Columbia Ministry of Forests Seed Centre.

Maltby, E., C.J. Legg and M.C.F. Proctor. 1990. The ecology of severe moorland fire on the North York Moors: effects of the 1976 fires, and subsequent surface and vegetation development. Journal of Ecology **78**: 490-518.

Morneau, C. and S. Payette. 1989. Postfire lichen-spruce woodland recovery at the limit of the boreal forest in northern Quebec. Canadian Journal of Botany **67**: 2770-2782.

Moss, E.H. 1996. Flora of Alberta. 2nd Edition. Revised by J.G. Packer. University of Toronto Press, Toronto, Canada.

Nguyen-Xuan, T., Y. Bergeron, D. Simard, J.W. Fyles and D. Paré. 2000. The importance of forest floor disturbance in the early regeneration patterns of the boreal forest of western and central Quebec: a wildfire versus logging comparison. Canadian Journal of Forest Research **30**: 1353-1364.

Nienstaedt, H. and J.C. Zasada. 1990 *Picea glauca* (Moench) Voss white spruce. Pages 204-226 *in* R. Burns and B.H. Honkala, technical coordinators. Silvics of North America. Volume 1. Conifers. Agriculture Handbook 654. U.S. Department of Agriculture, Forest Service, Washington, DC, USA.

Niwa, C.G., R.W. Peck and T.R. Torgersen. 2001. Soil, litter and coarse woody debris habitats for arthropods in eastern Oregon and Washington. Northwest Science **75**: 141-147.

Paré, D., Y. Bergeron and C. Camiré. 1993. Changes in the forest floor of Canadian southern boreal forest after disturbance. Journal of Vegetation Science **4**: 811-818.

Ringius, G.S. and R.A. Sims. 1997. Indicator Plant Species in Canadian Forests. Canadian Forest Service, Ottawa, Canada.

Rowe J.S., and G.W. Scotter. 1973. Fire in the boreal forest. Quaternary Research **4**: 444-464.

Safford, L.O. 1974. *Picea* A. Dietr. Spruce. Pages 587-597 *in* Schopmeyer, C.S., ed. Seeds of woody plants in the United States. Agricultural Handbook 450. U.S. Department of Agriculture Forest Service, Washington D.C.

SAS Institute Inc. 2006. SAS 9.1.3 Help and Documentation, SAS Institute Inc. 2000-2004, Cary, North Carolina.

Schimmel, J. and A. Granstrom. 1996. Fire severity and vegetation response in the boreal Swedish forest. Ecology **77**: 1436-1450.

Shafi, M.I. and G.A. Yarranton. 1973. Diversity, floristic richness and species evenness during a secondary (post-fire) succession. Ecology **54**: 897-902.

SPSS Inc. 2002. SPSS Base 11.0 for Windows User's Guide. SPSS Inc., Chicago, Illinois.

Steijlen, I., M-C. Nilsson and O. Zackrisson. 1995. Seed regeneration of Scots pine in boreal forest stands dominated by lichen and feather moss. Canadian Journal of Forest Research **25**: 713-723.

Uchytil, R. J. 1991a. *Larix laricina.* In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Accessed March 22, 2006 at: http://www.fs.fed.us/database/feis/

Uchytil, R. J. 1991b. *Picea glauca.* In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Accessed July 29, 2007 at: http://www.fs.fed.us/database/feis/

USDA NRCS 2007. *The PLANTS database*. Version: 030211. <http://plants.usda.gov>. National Plant Data Center, Baton Rouge, Louisiana, USA.

Van Cleve, K., L.K. Oliver, R. Schlentner, L.A. Viereck and C.T. Dyrness. 1983. Productivity and nutrient cycling in taiga forest ecosystems. Canadian Journal of Forest Research **13**: 747-766.

Watson, L. E., R. W. Parker and D. F. Polster. 1980. Manual of Species Suitability for Reclamation in Alberta. Vol. II: Forbs, Shrubs and Trees. Report No. RRTAC 80-5, 541P. Alberta Land Conservation and Reclamation Council, Edmonton, Alberta, Canada.

Zackrisson, O., M-.C. Nilsson, A. Dahlberg and A. Jäderlund. 1997. Interference mechanisms in conifer-Ericaceae-feathermoss communities. Oikos **78**: 209-220.

Zar, J.H. 1984. Biostatistical Analysis. 2nd Edition. Prentice-Hall, Inc., Englewood Cliffs, New Jersey, USA.

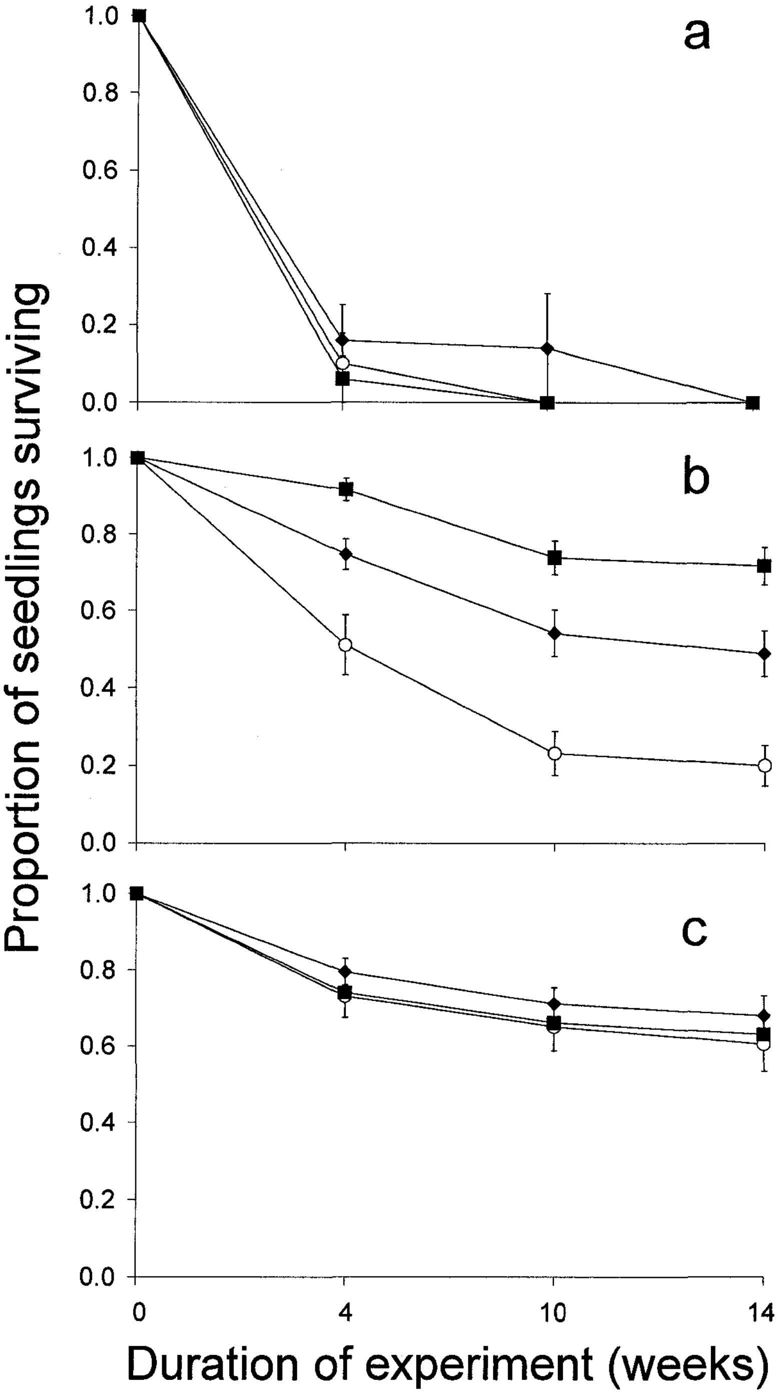

Figure 5.1 Mean proportion of seedlings sown (± 1 SE) of (a) *Petasites palmatus*, (b) *Larix laricina* and (c) *Picea glauca* that were surviving on burned feather moss (○), mineral soil (◆) and unburned humus (■) at four count dates.

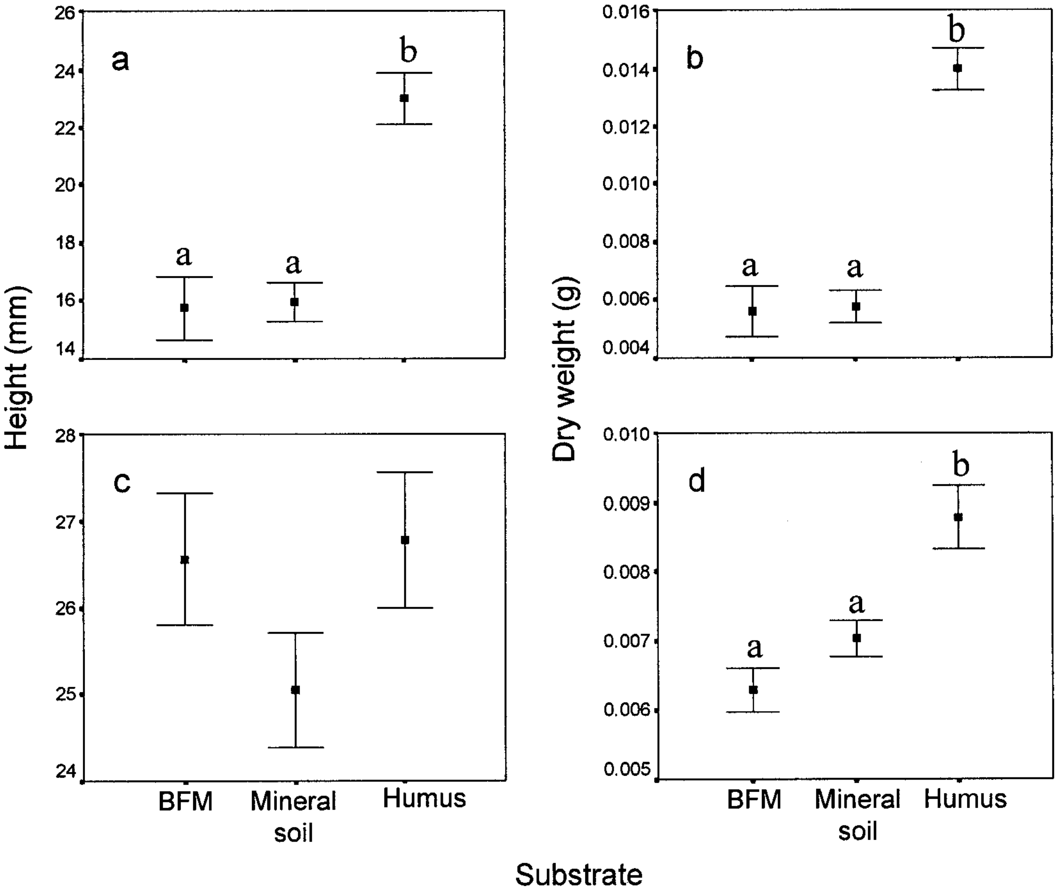

Figure 5.2 Final mean height and mean dry weight (± 1 SE) of *Larix laricina* (a, b) and *Picea glauca* (c, d) seedlings on burned feather moss (BM), mineral soil and unburned humus 14 weeks after they were transplanted. Lower case letters indicate significant differences between treatments.

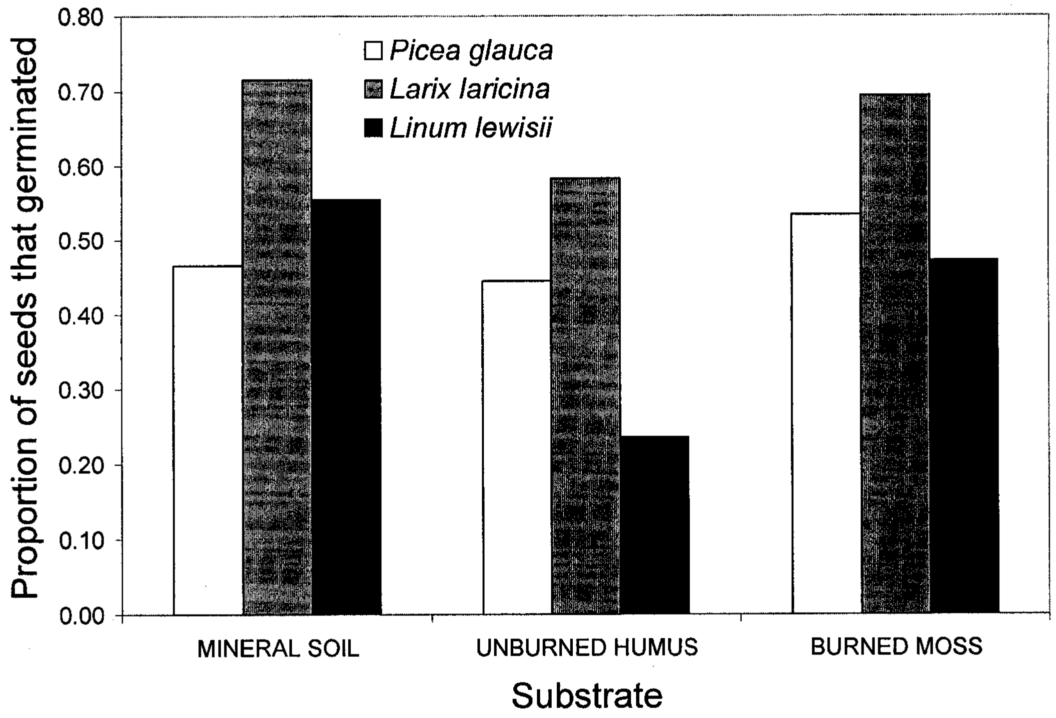

Figure 5.3 Total proportion of seeds of *Picea glauca*, *Larix laricina* and *Linum lewisii* that germinated on mineral soil, burned moss and unburned humus.

Table 5.1 Summary statistics for germination of *Picea glauca*, *Larix laricina*, *Linum lewisii* and *Petasites palmatus* in a growth chamber. Substrate abbreviations are as follows: BM = burned moss, MS = mineral soil and UH = unburned humus.

Species	Substrate	No. of seeds sown (*N*)	Number germinated	Percent germination
Picea glauca	BM	144	77	53.5
	MS	144	67	46.5
	UH	144	64	44.4
Larix laricina	BM	144	100	69.4
	MS	144	103	71.5
	UH	144	84	58.3
Linum lewisii	BM	144	68	47.2
	MS	144	80	55.6
	UH	144	34	23.6
Petasites palmatus	BM	144	0	N/A
	MS	144	0	N/A
	UH	144	0	N/A

Table 5.2 Results of pairwise goodness-of-fit tests on the effects of substrate on germination rate of *Larix laricina, Linum lewisii* and *Picea glauca* after 14 weeks in a growth chamber. Substrate abbreviations are defined as follows: burned moss (BM), mineral soil (MS), and unburned humus (UH).

	Larix laricina		*Linum lewisii*		*Picea glauca*	
Comparison	Chi-square statistic	*P*-value	Chi-square statistic	*P*-value	Chi-square statistic	*P*-value
BM v MS	0.067	0.796	1.682	0.195	1.125	0.289
BM v UH	3.386	0.066	16.531	<0.001	2.001	0.157
MS v UH	4.941	0.026	29.401	<0.001	0.056	0.813

Table 5.3 Results of pairwise goodness-of-fit tests on the effects of species (*Linum lewisii*, *Larix laricina* and *Picea glauca*) on germination rate on burned moss, mineral soil and unburned humus after 14 weeks in a growth chamber.

	Burned moss		Mineral soil		Humus	
Comparison	Chi-square statistic	*P*-value	Chi-square statistic	*P*-value	Chi-square statistic	*P*-value
Larix v *Picea*	7.095	0.008	17.587	<0.001	5.018	0.025
Larix v *Linum*	13.729	<0.001	7.254	0.007	34.471	<0.001
Picea v *Linum*	0.889	0.346	2.001	0.587	13.008	<0.001

SUMMARY AND GENERAL CONCLUSIONS

In the first three years of succession after the 2001 Chisholm Fire in north-central Alberta, Canada, the bryophyte species composition of burned *Picea glauca*-dominated forest stands was almost entirely different from that of unburned stands near the fire boundary. *Ceratodon purpureus* was the dominant species in the burned sites and *Bryum argenteum, Bryum caespiticium*, *Funaria hygrometrica* and *Leptobryum pyriforme* were also common. The feather mosses *Pleurozium schreberi*, *Hylocomium splendens* and *Ptilium crista-castrensis* were the dominant species in two of the unburned sites, whereas *Plagiomnium* spp. and *Brachythecium* spp. were abundant in the third (Table 2.1).

Ceratodon purpureus, *Bryum caespiticium*, *Leptobryum pyriforme* and *Marchantia polymorpha* were found in one unburned site on mineral soil exposed by a fallen tree.

Although we found different moss communities in early and late successional forests, it does not necessarily follow that these communities represent contrasting ends of a successional trajectory. However, the consistency between these communities and those found at similar stages of succession in other studies implies that in the burned study sites a transition will occur from one community to the other. Nevertheless, it seems unlikely that this transition will happen directly. None of the most common species in the unburned sites were found in species surveys in the burned sites (Chapter 2) and the findings of empirical studies in Chapters 3 and 4 support the hypothesis that *Pleurozium schreberi* and *Ptilium crista-castrensis* are dispersal limited. Vegetative fragments of these species were significantly more likely to be successful if they were relatively large. By virtue of their size large fragments may be less readily dispersed than small fragments. If that is so, widespread establishment of *Pleurozium* and *Ptilium* species will be delayed. Other research suggests that several of the species that were found in the burned sites will decline in abundance within the first few years of succession, possibly too soon to be replaced directly by feather mosses. Therefore, it seems unlikely that competition with vigorous perennial mosses is an important factor in the decline of pioneer species.

Given the abundance of *Populus* sp. in our burned study sites, it is probable that succession in these sites will follow a trajectory in which intermediate successional stages are characterized by a deciduous canopy. In such stands, moss cover on the forest floor is typically low, probably due to the high amounts of leaf litter (personal observation). It follows that acrocarpous species will be intolerant of burial by litter because their upright growth form does not readily permit them to exploit gaps that allow them to reach the light. In contrast, pleurocarpous species, such as *Pleurozium*, *Ptilium*, *Hylocomium splendens* and *Brachythecium* sp., may be able to grow between litter layers until they can an open site. Thus, the build up of litter may be a contributing factor in the decline of early successional species and may keep moss cover low until species tolerant of litter cover become widely established.

According to the results of the experiments described in Chapter 3, many of the vegetative fragments produced by *Ptilium* may not be viable propagules.

Smaller *Ptilium* fragments had low reproductive potential, which may help to explain why *Pleurozium* and *Hylocomium splendens* are often more abundant than *Ptilium* in old spruce stands. However, the dispersal potential of large *Ptilium* fragments may be greater than that of large *Pleurozium* fragments if their falcate secund morphology increases the chances of them attaching to the bodies of animals. Moreover, *Ptilium* gametophytes produce globular leaf clusters that could have reproductive significance. In terms of overall reproductive potential, these may compensate somewhat for the low viability of small *Ptilium* fragments.

Defining establishment from moss fragments

Assessing the establishment potential of vegetative fragments of *Pleurozium* and *Ptilium* is complicated because no definition of establishment has been established for this context. A review of the literature produced no unequivocal criteria for establishment in general, but some features are consistently suggested. These include survival over a defined period, the achievement of a permanent (and usually stationary) position within a community and an increase in biomass (see, for example, Keever 1957; Hassel and Soderström 1999; Delach and Kimmerer 2002; Sundberg and Rydin 2002; Jones and del Moral 2005; Brown et al. 2006; Chauhan et al. 2006; Fulbright et al. 2006; Jankju-Borzelabad and Griffiths 2006; Raffl et al. 2006; Ward et al. 2006). Using these criteria to define establishment of *Pleurozium* and *Ptilium* from fragments is problematic because it is not known (i) the length of time for which fragments of these species remain viable; and (ii) how fragments would obtain a permanent position. Protonemata and rhizoids may provide some anchorage, we never found these on fragments in our field experiments.

For this study, survival, fragment condition (ALM) and fragment growth were used as proxies for establishment potential because we assumed that higher values of these variables reflected greater resilience and more resilient fragments were more likely to grow into new colonies. The extent to which this is true must be tested using a longer term study. Survival is clearly essential for establishment, but there may be no positive correlation between establishment potential and either condition or amount of growth. Indeed, the fragments that survive the longest may be those that conserve resources under stressful conditions rather than expend them by growing. Further studies are necessary to determine (a) whether fragments can survive for long enough in recently burned stands to grow into new colonies, and (b) what characteristics increase establishment potential. Fragment size would appear to be a component of the answer to (b) but other factors, such as the amount of time fragments have been detached from source material, may also be important.

A model of post-fire recolonization by Pleurozium *and* Ptilium

Recolonisation of burned forests by *Pleurozium* and *Ptilium* is likely to involve a combination of processes. Fig. 6.1 shows hypothetical modes of colonization by *Pleurozium* and *Ptilium* during post-fire succession. These are (i) through growth of propagules in the diaspore bank; (ii) through regeneration of burned material; (iii) from immigrant propagules dispersed into the fire interior in one or more dispersal episodes; and (iv) through encroachment at the fire boundaries. Experiments that test the longevity of fragments and spores in the diaspore bank are necessary to test hypothesis (i). Hypothesis (ii) has not been tested explicitly. BM was not found to regenerate in this study or the study described in Chapter 3 but this author has seen examples of what appear to be regeneration of Pleurozium from burned material in a *Picea mariana* burned in the House River Fire in northern Alberta. The contribution of hypothesis (iii) to recolonisation depends on the number of viable spores dispersed over long distances and the frequency of dispersal episodes involving fragments. The dispersal limitation hypothesis rests on the assumptions that spores are rare and vegetative fragments are not readily dispersed long distances. This may be an oversimplification because the long distance dispersal potential of fragments is likely to be influenced by several factors, including species and fragment size. The model described in hypothesis (iv) begins when one or more fragments is dispersed a short distance into the burned area from a colony outside the burn. Some of these fragments grow to a sufficient size that they produce a second 'generation' of fragments. Some of these new fragments may be dispersed a short distance further into the burned area and the process is repeated. Dispersal limitation and the results given in Chapters 2 and 3 of this thesis provide no objections to this hypothesis. If establishment potential increases with fragment size and large fragments are less likely to be dispersed long distances, this model may represent an important mode of recolonisation.

Some effects of mosses on succession in the vascular plant community

The last study described in this thesis (Chapter 5) showed that burned moss material left as a legacy of fire could have affects upon the structure of the vascular plant community. Because feather mosses are perennials, they can form thick carpets on the floor of old spruce forests. Other researchers have shown positive and negative effects of these carpets on vascular plant establishment and growth (Steijlen et al. 1995; Nilsson et al. 1996; Hörnberg at al. 1997; Zackrisson et al. 1997; Kuuluvainen and Juntunen 1998; Kotorová and Lepš 1999; Hanssen 2003; Parent et al. 2003; Sedia and Ehrenfeld 2003; Van der Wal and Brooker 2004). These effects may persist after the fire if the carpets are burned but not destroyed, and they might have long term impacts on canopy composition and structure. The results of our growth chamber experiment suggest that *Larix laricina* will be uncommon in the regenerating canopy of stands that contain a high abundance of burned moss because the survival of *L. laricina* seedlings on this substrate is poor. *Larix laricina* is a major component of several wet ecosite phases in Alberta (Beckingham and Archibald 1996). Because fire severity is generally lower under wet conditions (Van Wagner 1983; Larsen 1997) these phases are more likely to retain burned feather moss. As a result, *Larix*-dominated stands might show a change in ecosite phase after a fire. *Picea glauca* seedlings were not significantly affected by burned feather moss material in a growth chamber experiment.

Seedlings performed poorly on burned feather moss probably because they were elevated above the soil surface and they experienced severe water stress in this rapidly draining material. If this occurs in nature, sites with abundant burned feather moss might show delayed or different successions from those with little burned moss even when their pre-and post-fire conditions are otherwise similar. Colonisation by a variety of vascular plants that establish from seed may be inhibited and bryophytes may also find the dry, blackened surfaces of the moss carpet unfavourable.

Future research

The long term nature of forest succession ensures that any single study can focus on only a few aspects of the process. The scope of the research described in this thesis was further limited by the restricted time available for collecting data from field surveys and experiments. The use of a chronosequence approach can allow for the study of various possible stages within a succession, but this was not possible here due to the limited number of white spruce-dominated stands at intermediate successional stages in Alberta and lack of time to conduct surveys. As a result of these limitations, several questions raised by this research require further attention. Testing the ability of shade and litter to suppress the growth of ruderal mosses would clarify the role of these factors in the decline of the early successional moss community and may give a more precise indication of the timing of this decline. The relative importance of long distance dispersal and short distance dispersal events for recolonisation by feather mosses might be clarified by research into potential vectors of vegetative diaspores. In particular, the possibility that fragments are transported on the bodies of large mammals that forage in early successional sites requires further study. Some other key issues that have not been addressed in detail in this research include the importance of spores in the dispersal of late successional mosses and the possible benefits of falcate-secund morphology for dispersal. Further research in these topics should clarify the relative importance of sexual and asexual reproductive strategies for the regeneration of *Pleurozium schreberi* and *Ptilium crista-castrensis*. Meanwhile, studies of the significance of living and burned moss carpets for the establishment and growth of a wide range of vascular plants would show the extent to which mosses can influence community structure and succession in the vascular plant community at different successional stages.

Literature Cited

Beckingham, J.D. and J. Archibald, 1996. Field Guide to Ecosites of Northern Alberta. Special Report 5. Natural Resources Canada, Canadian Forest Service, Northwest Region, Northern Forestry Center, Edmonton, Alberta.

Brown, C.S., A.F. Mark., G.P. Kershaw and K.J.M. Dickinson. 2006. Secondary succession 24 years after disturbance of a New Zealand high-alpine cushionfield. Arctic, Antarctic, and Alpine Research **38**: 325–334.

Chauhan, B.S., G. Gill and C. Preston. 2006. Seedling recruitment pattern and depth of recruitment of 10 weed species in minimum tillage and no-till seeding systems. Weed Science **54**: 658–668.

Delach, A and R.W. Kimmerer. 2002. The effect of *Polytrichum piliferum* on seed germination and establishment on iron mine tailings in New York. The Bryologist **105**: 249-255.

Fulbright, T.E., J.A. Ortega-Santos, A. Lozano-Cavazos, and L.E. Ramírez-Yanez. 2006. Establishing vegetation on migrating inland sand dunes in Texas. Rangeland Ecology and Management **59**: 549-556.

Hanssen, K.H. 2003. Natural regeneration of *Picea abies* on small clear-cuts in SE Norway. Forest Ecology and Management **180**: 199-213.

Hassel, K. and L. Soderström. 1999. Spore germination in the laboratory and spore establishment in the field in *Pogonatum dentatum* (Brid.) Brid. Lindbergia **24**: 3-10.

Hörnberg, G., M. Ohlson and O. Zackrisson. 1997. Influence of bryophytes and microrelief conditions on *Picea abies* seed regeneration patterns in boreal old-growth swamp forests. Canadian Journal of Forest Research **27**: 1015-1023.

Jankju-Borzelabad, M. and H. Griffiths. 2006. Competition for pulsed resources: an experimental study of establishment and coexistence for an arid-land grass. Oecologia **148**: 555-563.

Jones, C.C. and R. del Moral. 2005. Effects of microsite conditions on seedling establishment on the foreland of the Coleman Glacier, Washington. Journal of Vegetation Science **16**: 293-300.

Keever, C. 1957. The establishment of *Grimmia laevigata* on bare granite. Ecology **38**: 422-429.

Kotorová, I. and J. Lepš. 1999. Comparative ecology of seedling recruitment in an oligotrophic wet meadow. Journal of Vegetation Science **10**: 175-186.

Kuuluvainen, T. and P. Juntunen. 1998. Seedling establishment in relation to microhabitat variation in a windthrow gap in a boreal *Pinus sylvestris* forest. Journal of Vegetation Science **9**: 551-562.

Larsen, C.P.S. 1997. Spatial and temporal variations in boreal forest fire frequency in northern Alberta. Journal of Biogeography **24**: 663-673.

Nilsson, M.-C.., I. Steijlen and O. Zackrisson. 1996. Time restricted seed regeneration of Scots pine in sites dominated by feather moss after clear-cutting. Canadian Journal of Forest Research **26**: 945-953.

Parent, S., M-J. Simard, H. Morin and C. Messier. 2003. Establishment and dynamics of the balsam fir seedling bank in old forests of northeastern Quebec. Canadian Journal of Forest Research **33**: 597-603.

Raffl, C., M. Mallaun, R. Mayer and B. Erschbamer. 2006. Vegetation succession pattern and diversity changes in a glacier valley, central Alps, Austria. Arctic, Antarctic, and Alpine Research **38**: 421–428.

Sedia, E.G. and J.G. Ehrenfeld. 2003. Lichens and mosses promote alternate stable plant communities in the New Jersey Pinelands. Oikos **100**: 447-458.

Steijlen, I, M-C. Nilsson and O. Zackrisson. 1995. Seed regeneration of Scots pine in boreal forest stands dominated by lichens and feather moss. Canadian Journal of Forest Research **25**: 713-723.

Sundberg, S. and H. Rydin. 2002. Habitat requirements for establishment of *Sphagnum* from spores. Journal of Ecology **90**: 268-278.

Van der Wal, R. and R.W. Brooker. 2004. Mosses mediate grazer impacts on grass abundance in Arctic ecosystems. Functional Ecology **18**: 77-86.

Van Wagner, C.E. 1983. Fire behaviour in northern coniferous forests and shrublands. Pages 65-80 *in* R.W. Wein, and D.A. MacLean, editors. The Role of Fire in Northern Circumpolar Ecosystem. John Wiley and Sons, New York, USA.

Ward, J.P. 2006. Water requirements for emergence of buffelgrass (*Pennisetum ciliare*). Weed Science **54**: 720–725.

Zackrisson, O., M-C. Nilsson, A. Dahlberg and A. Jäderlund. 1997. Interference mechanisms in conifer-Ericaceae-feathermoss communities. Oikos **78**: 209-220.

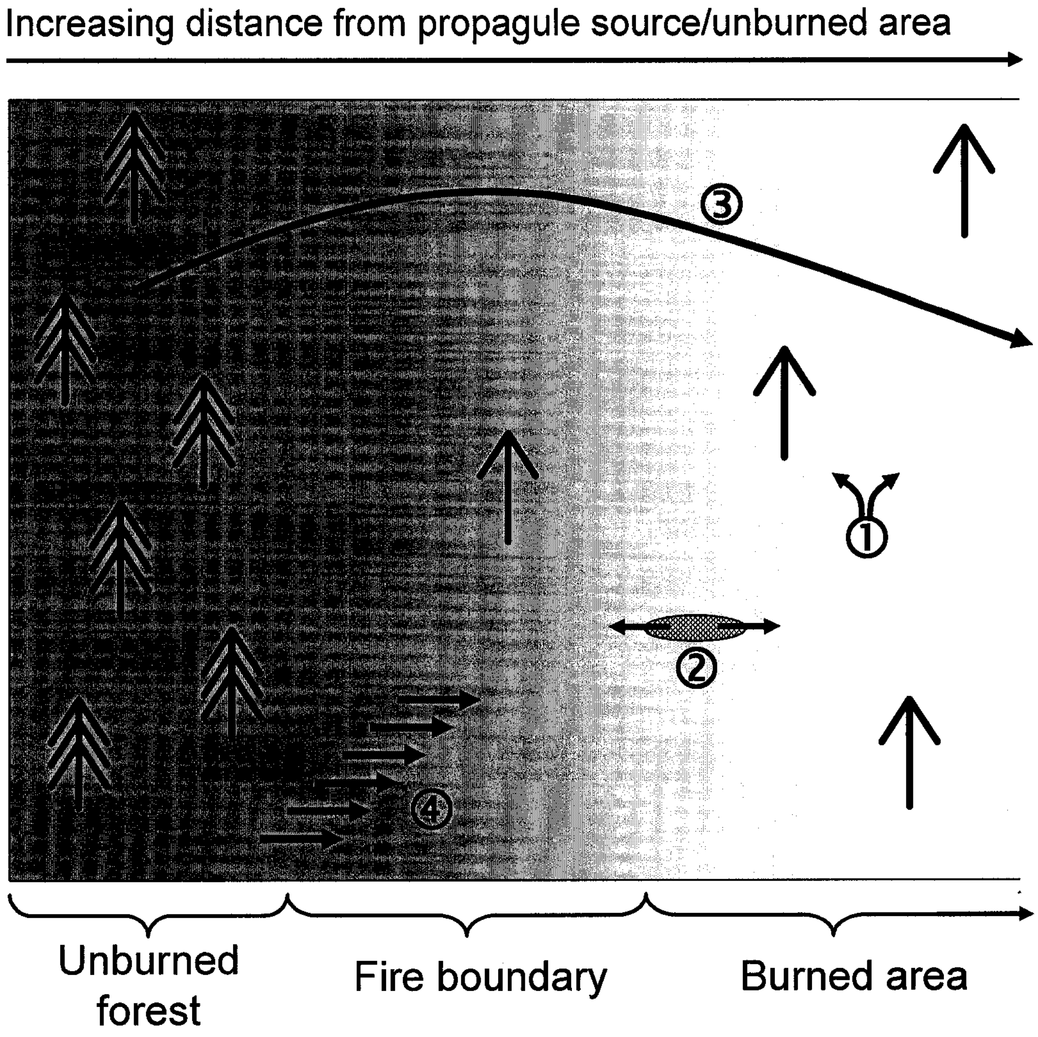

Figure 6.1 Diagrammatic illustration of hypotheses for recolonisation of burned areas by feather mosses: (1) through growth of propagules in the diaspore bank; (2) through regeneration of burned material; (3) from immigrant propagules dispersed into the fire interior in one or more dispersal episodes; and (4) through encroachment at the fire boundaries.

APPENDIX

Table A.1 Results of MRPP analyses testing for differences between years in quadrat-level values of moss cover and environmental variables recorded in BRN1. Pairwise tests are given if a three-way comparison was significant. NS indicates that no pairwise comparisons were significant for that variable.

Group	Contrast	T-statistic	Observed ♦	A	*P*-value
Percent cover and species richness of mosses					
Total moss cover	NS	N/A	N/A	N/A	N/A
Bryum argenteum	2002-2003	-28.714	0.216	0.340	<0.001
	2003-2004	0.607	0.381	-0.029	0.680
	2002-2004	-24.143	0.226	0.285	<0.001
Bryum caespiticium	2002-2003	0.725	0.353	-0.005	0.755
	2003-2004	-2.106	0.371	0.066	0.042
	2002-2004	-5.489	0.334	0.039	0.001
Ceratodon purpureus	2002-2003	-6.407	0.376	0.044	0.001
	2003-2004	-2.622	0.316	0.066	0.027
	2002-2004	-1.487	0.366	0.010	0.083
Funaria hygrometrica	NS	N/A	N/A	N/A	N/A
Leptobryum pyriforme	2002-2003	-0.056	0.542	0.001	0.314
	2003-2004	-4.170	0.457	0.169	0.008
	2002-2004	-3.194	0.518	0.036	0.018
Polytrichum juniperinum	NS	N/A	N/A	N/A	N/A
Abiotic variables					
Forb cover	NS	N/A	N/A	N/A	N/A
Shrub cover	2002-2003	-3.423	0.618	0.024	0.012
	2003-2004	0.959	0.555	-0.023	0.875
	2002-2004	-3.301	0.613	0.024	0.013
LLHL cover	2002-2003	-19.544	0.448	0.184	<0.001
	2003-2004	-0.026	0.390	0.001	0.374
	2002-2004	-22.843	0.438	0.206	<0.001
Marchantia polymorpha cover	NS	N/A	N/A	N/A	N/A

Table A.2 Results of MRPP analyses testing for differences between years in quadrat-level values of moss cover and environmental variables recorded in BRN3. Pairwise tests are given if a three-way comparison was significant. NS indicates that no pairwise comparisons were significant for that variable.

Group	Contrast	T-statistic	Observed ♦	A	*P*-value
Percent cover and species richness of mosses					
Total moss cover	2002-2003	-15.753	0.399	0.091	<0.001
	2003-2004	0.369	0.289	-0.010	0.520
	2002-2004	-23.061	0.390	0.133	<0.001
Bryum argenteum	2002-2003	-2.270	0.501	0.028	0.040
	2003-2004	-4.846	0.449	0.200	0.005
	2002-2004	-1.500	0.474	0.019	0.079
Bryum caespiticium	2002-2003	-6.934	0.516	0.074	0.001
	2003-2004	-0.853	0.351	0.025	0.145
	2002-2004	-9.770	0.515	0.100	<0.001
Ceratodon purpureus	2002-2003	-19.891	0.385	0.126	<0.001
	2003-2004	0.730	0.320	-0.021	0.787
	2002-2004	-19.872	0.389	0.124	<0.001
Funaria hygrometrica	NS	N/A	N/A	N/A	N/A
Leptobryum pyriforme	2002-2003	-2.033	0.174	0.022	0.049
	2003-2004	-0.171	0.526	0.006	0.281
	2002-2004	-10.486	0.196	0.115	<0.001
Polytrichum juniperinum	2002-2003	0.709	0.149	-0.008	1.000
	2003-2004	-0.408	0.382	0.016	0.230
	2002-2004	-4.943	0.183	0.052	0.005
Moss species richness	2002-2003	-2.919	0.325	0.023	0.020
	2003-2004	-0.411	0.196	0.011	0.245
	2002-2004	-5.133	0.310	0.041	0.002
Abiotic variables					
Forb cover	2002-2003	-4.017	0.443	0.025	0.006
	2003-2004	0.254	0.163	-0.007	0.471
	2002-2004	-4.059	0.441	0.025	0.006
Shrub cover	2002-2003	-1.403	0.599	0.012	0.088
	2003-2004	0.641	0.630	-0.018	0.699
	2002-2004	-4.161	0.595	0.036	0.007
LLHL cover	2002-2003	-14.474	0.573	0.116	<0.001
	2003-2004	0.862	0.264	-0.024	0.819
	2002-2004	-16.226	0.566	0.130	0.000
Marchantia polymorpha cover	2002-2003	-0.487	0.559	0.005	0.210
	2003-2004	0.525	0.665	-0.017	0.614
	2002-2004	-3.030	0.559	0.027	0.020

Table A.3 Site-level values of selected environmental variables recorded in four boreal white spruce stands (BRN1 to BRN4) burned in the Chisholm Fire in north-central Alberta. Data were collected in 2003, two years after the fire. Cover values and GSM are the means of 15 quadrats (± one standard deviation), litter depth is the modal category from 15 quadrats (categories were 0-10 mm, 11-20 mm and >20 mm), richness is the total number of unique species, DBH is the mean of 15 spruce trees (selected as the nearest tree to each quadrat) and tree density was calculated as the mean of the number of trees in three randomly chosen 10.0 m × 16.7 m subplots.

Variable	Study site			
	BRN1	BRN2	BRN3	BRN4
Mean litter cover (%)	71.60 ± 28.79	67.00 ± 26.68	65.00 ± 20.96	53.47 ± 25.21
Modal litter depth (mm)	0 -10	0 -10	0 -10	0 -10
Mean bryophyte cover (%)	29.94 ± 21.79	25.56 ± 21.61	37.44 ± 20.57	5.21 ± 13.19
Bryophyte richness	8	7	7	5
Mean forb cover (%)	98.20 ± 38.77	143.73 ± 54.92	54.33 ± 25.60	25.20 ± 31.93
Forb richness	18	13	13	12
Mean shrub cover (%)	39.20 ± 38.06	24.47 ± 40.76	14.80 ± 19.77	26.00 ± 23.93
Shrub richness	5	8	4	5
Mean GSM (%)	55.79 ± 10.68	55.02 ± 14.46	42.10 ± 11.34	8.09 ± 5.58
Mean DBH (cm)	13.39 ± 6.29	29.16 ± 10.33	29.05 ± 9.88	15.64 ± 10.36
Mean tree density (no. of trees/m^2)	0.24 ± 0.07	0.11 ± 0.04	0.08 ± 0.02	0.17 ± 0.02

Table A.4 Stand-level values of selected environmental variables recorded in late successional boreal white spruce (*Picea glauca*) stands near the boundaries of the Chisholm Fire in north-central Alberta. Data were collected in 2004, three years after the fire. For each stand cover values are the means of 15 quadrats (± one standard deviation), litter depth is the modal category from 15 quadrats (categories were 0-10 mm, 11-20 mm and >20 mm), GSM is the mean of 10 randomly selected quadrats, richness is the total number of unique species, DBH is the mean of 15 spruce trees (selected as the nearest tree to each quadrat) and tree density was calculated as the mean of the number of trees in three randomly chosen 10.0 m × 16.7 m subplots

Variable		Study site	
	GRN1	GRN2	GRN3
Mean litter cover (%)	79.60 ± 17.82	86.60 ± 10.68	83.80 ± 13.31
Modal litter depth (mm)	> 20	> 20	> 20
Mean bryophyte cover (%)	28.30 ± 17.16	19.26 ± 9.88	32.97 ± 23.52
Bryophyte richness	15	12	11
Mean forb cover (%)	81.53 ± 29.43	28.00 ± 27.69	59.93 ± 35.04
Forb richness	23	15	20
Mean shrub cover (%)	47.80 ± 35.09	46.13 ± 37.09	26.40 ± 17.76
Shrub richness	9	11	10
Mean GSM (%)	69.79 ± 12.24	67.03 ± 6.56	68.47 ± 11.15
Mean DBH (cm)	48.98 ± 15.59	33.87 ± 7.60	31.87 ± 10.81
Mean tree density (no. of trees/m^2)	0.05 ± 0.03	0.05 ± 0.00	0.06 ± 0.01

Table A.5 Forbs recorded in burned and unburned white spruce stands in and around the 2001 Chisholm Fire in Alberta, Canada, during the first, second and third growing seasons (2002 – 2004) after the fire.

	Burned sites								Unburned sites		
	2002		2003				2004		2004		
Species	BRN1	BRN3	BRN1	BRN2	BRN3	BRN4	BRN1	BRN3	GRN1	GRN2	GRN3
Forbs											
Achillea millefolium	-	-	-	-	-	-	-	-	M	M	-
Actaea rubra	-	-	-	M	-	-	-	-	-	M	M
Aralia nudicaulis	-	0.97	-	0.20	0.20	1.00	M	0.07	12.53	5.07	12.80
Aster ciliolatus	2.22	0.04	4.73	2.00	-	0.07	1.07	M	0.53	1.67	2.27
Aster conspicuus	0.16	-	-	-	0.67	0.07	0.20	-	M	0.20	-
Aster puniceus	-	-	-	-	-	-	-	-	-	-	M
Athyrix felix-femina	-	-	-	-	-	-	-	-	6.20	-	-
Caltha palustris	-	-	-	M	-	-	-	-	-	-	-
Campanula rotundifolia	-	-	-	-	-	M	-	-	-	-	-
Chenopodium capitatum	-	-	-	-	-	M	-	-	-	-	-
Cinna latifolia	-	-	-	-	-	-	-	-	-	-	M
Circaea alpina	-	-	-	-	-	-	-	-	0.60	-	-
Cirsium arvense	-	-	-	M	-	-	M	-	-	-	-
Coptis trifolia	-	-	-	-	-	-	-	-	-	-	M
Cornus canadensis	2.71	5.66	2.53	1.47	7.00	5.27	3.00	2.53	4.13	2.87	6.73
Corydalis aurea	3.76	-	-	-	-	-	-	-	-	-	-
Cystopteris fragilis	-	-	-	-	-	-	-	-	0.20	-	-
Delphinium glaucum	-	-	-	M	-	-	-	-	-	-	-
Disporum trachycarpum	-	-	-	-	-	-	-	0.07	M	-	M
Dracocephalum parviflorum	-	0.04	-	-	-	M	-	-	-	-	-
Epilobium angustifolium	9.86	16.65	5.53	52.53	34.47	0.20	7.27	34.40	-	-	-
Epilobium glandulosum	5.70	-	5.20	6.40	3.40	-	-	1.73	-	-	M
Equisetum arvense	49.17	0.85	34.73	62.33	-	0.27	22.13	0.20	0.47	M	2.60
Equisetum pratense	7.11	-	11.60	16.00	-	M	3.67	M	-	-	-
Equisetum scirpoides	62.63	-	26.73	-	-	-	26.13	-	-	-	-
Equisetum sylvaticum	0.32	0.08	-	0.27	0.20	-	M	0.13	15.40	M	1.47
Fragaria virginiana	-	-	-	M	-	-	M	M	M	M	0.87
Galium boreale	1.66	0.32	0.40	0.80	-	1.33	-	M	M	0.13	1.87
Galium triflorum	-	-	-	M	-	-	M	-	0.73	0.07	M
Gentiana amarella	-	-	-	-	-	-	M	-	-	-	-
Geranium bicknellii	0.48	32.93	0.20	0.27	0.33	M	0.20	0.27	-	-	-
Geum aleppicum	-	-	-	-	-	-	M	-	-	-	-
Geum rivale	-	-	-	M	-	-	-	-	-	-	-
Goodyera repens	-	-	-	-	-	-	-	-	-	0.07	-
Gymnocarpum dryopteris	-	-	-	-	-	-	-	-	1.73	1.73	M
Halenia deflexa	-	-	0.07	-	-	-	-	-	-	-	-
Hieracium umbellatum	-	-	-	M	-	M	M	0.33	-	-	M
Impatiens capensis	-	-	-	0.20	-	-	-	0.60	12.47	-	M
Lathyrus ochroleuceus	-	-	0.13	-	-	-	0.60	0.07	M	M	2.07
Lilium philadelphicum	-	-	-	-	-	-	M	-	-	-	-
Linnaea borealis	-	-	-	-	-	-	M	M	-	-	-
Lycopodium annotinum	-	-	-	-	-	-	-	0.60	0.13	M	0.07
Lycopodium complanatum	-	-	-	-	-	-	0.60	1.20	1.20	M	1.33
Lycopodium obscurum	-	-	-	-	-	-	0.60	1.20	1.20	M	1.13

Values are percent cover estimates from quadrat surveys and M indicates species recorded only during meanders; dashes indicate that species were not found.

The survey protocol was changed between 2002 and 2003; details are given in the text.

Table A.5 (cont.) Forbs recorded in burned and unburned white spruce stands in and around the 2001 Chisholm Fire in Alberta, Canada, during the first, second and third growing seasons (2002 – 2004) after the fire.

	Burned sites								Unburned sites		
	2002		2003				2004		2004		
Species	BRN1	BRN3	BRN1	BRN2	BRN3	BRN4	BRN1	BRN3	GRN1	GRN2	GRN3
Forbs (cont.)											
Maianthemum canadense	0.12	0.69	0.27	M	0.13	M	-	-	0.87	1.07	0.87
Melilotus alba	-	-	-	-	-	-	-	M	-	-	-
Mertensia paniculata	0.85	0.77	0.53	1.00	-	-	-	M	1.87	5.67	2.07
Mitella nuda	-	-	-	0.27	-	-	-	-	0.93	2.60	1.33
Monoses uniflora	-	-	-	-	-	-	-	-	M	-	-
Oplopanax horridus	-	-	-	-	-	-	-	-	-	-	M
Parnasia palustris	-	-	-	-	-	-	M	-	-	-	-
Petasites frigidus	-	-	-	-	-	-	-	M	-	-	-
Petasites palmatus	0.93	1.37	0.87	M	0.60	0.93	0.07	1.47	0.07	0.93	1.53
Petasites vitifolius	-	-	-	-	-	-	0.20	-	-	-	-
Potentilla norvegica	-	-	-	-	-	-	-	M	-	-	-
Pyrola asarifolia	-	-	-	-	-	-	-	-	M	-	M
Rubus pubescens	14.26	4.36	4.13	M	1.93	1.40	3.40	2.07	5.87	5.40	10.60
Senecio paupercaulis	0.16	-	-	-	0.20	-	0.40	-	-	-	-
Smilacina stellata	-	-	-	-	-	-	-	-	-	-	M
Sonchus arvensis	-	-	-	M	-	-	-	-	-	-	-
Sonchus asper	-	-	-	-	-	-	M	M	-	-	-
Taraxacum officianale	0.36	-	0.20	M	-	M	0.33	0.07	-	-	-
Trientalis borealis	-	-	-	-	0.07	-	-	0.60	1.47	M	1.07
Trifolium hybridum	-	-	-	M	-	-	M	M	-	-	-
Urtica dioica	0.20	-	-	M	-	-	M	-	-	-	M
Vicia americana	2.95	0.04	0.27	M	-	-	0.60	1.20	1.20	M	0.60
Viola canadensis	-	-	-	-	-	-	-	-	-	-	M
Viola sp.	0.24	0.08	0.07	-	-	M	0.00	0.60	1.07	0.27	1.33
Graminoids											
Calamagrostis canadensis	-	-	-	M	-	-	M	M	M	-	-
Carex sp.	0.40	-	-	-	-	8.47	M	M	-	-	-
Dactylis glomerata	-	-	-	-	-	-	-	M	-	-	-
Deschampsia flexusoa	-	-	-	-	-	-	M	-	-	-	-
Elymus innovatus	-	-	-	-	-	M	M	M	-	-	-
Unidentified	-	4.93	-	-	5.13	3.40	0.07	5.13	10.67	0.27	7.33

Values are percent cover estimates from quadrat surveys and M indicates species recorded only during meanders; dashes indicate that species were not found.

The survey protocol was changed between 2002 and 2003; details are given in the text.

Table A.6 Trees and shrubs recorded in burned and unburned white spruce stands in and around the 2001 Chisholm Fire in Alberta, Canada, during the first, second and third growing seasons (2002 – 2004) after the fire.

	Burned sites								Unburned sites		
	2002		2003				2004		2004		
Species	BRN1	BRN3	BRN1	BRN2	BRN3	BRN4	BRN1	BRN3	GRN1	GRN2	GRN3
Trees and shrubs											
Abies balsamea	-	-	-	-	-	-	<0.01	0.60	5.07	28.53	M
Alnus sp.	-	-	-	-	-	M	M	-	-	M	-
Amelanchier alnifolia	-	-	-	-	-	-	-	-	M	M	M
Betula papyrifera	-	-	-	M	-	M	-	M	0.33	M	-
Cornus stolonifera	-	-	-	M	-	-	-	-	-	M	-
Ledum groenlandicum	-	-	-	-	-	-	-	-	-	M	3.93
Linnaea borealis	-	-	-	-	-	2.80	-	-	0.33	0.93	1.80
Lonicera dioica	-	-	-	0.40	-	-	-	M	M	M	0.47
Lonicera involucrata	-	-	-	M	-	-	4.67	M	4.40	7.67	1.87
Picea glauca	0.04	-	-	-	-	-	-	-	M	2.33	M
Picea mariana	-	-	-	-	-	-	-	-	-	-	M
Pinus banksiana	-	-	-	-	-	0.07	-	M	-	-	-
Populus balsamifera	1.86	-	2.93	4.20	0.87	1.87	15.93	7.40	M	0.27	0.13
Populus tremuloides	13.54	0.32	27.00	4.27	-	17.67	10.53	1.00	M	0.20	0.27
Ribes glandulosum	-	-	-	-	-	-	M	-	M	-	M
Ribes lacustre	-	-	-	0.20	-	-	-	-	M	M	M
Ribes oxycanthoides	-	-	-	2.00	-	-	M	-	1.40	-	M
Ribes triste	-	-	-	-	-	-	M	-	M	1.07	0.20
Rosa acicularis	1.17	6.59	3.27	3.53	9.93	3.60	8.07	5.73	6.00	0.60	14.27
Rubus idaeus	0.24	2.26	4.47	9.67	3.00	2.80	<0.01	1.07	28.40	0.13	M
Salix monticola	-	-	-	M	-	-	M	M	-	-	-
Salix sp.	3.03	0.73	1.53	-	-	-	2.20	1.60	-	-	-
Sambucus racemosa var. *pubens*	-	-	-	-	-	-	-	-	-	-	M
Shepherdia canadensis	-	-	-	-	-	-	M	-	-	M	-
Sorbus aucuparia	-	-	-	-	-	-	-	-	M	-	-
Sorbus scopulina	-	-	-	-	-	-	-	-	-	-	M
Symphoricarpus albus	-	-	-	0.20	-	-	M	M	M	M	-
Vaccinium myrtilloides	-	-	-	-	-	M	-	-	-	-	-
Vaccinium vitis-idaea	-	-	-	-	-	-	-	-	-	M	0.40
Viburnum edule	-	0.57	-	M	1.00	-	-	-	1.40	1.80	3.07
Viburnum opulus	0.12	-	-	-	-	-	<0.01	0.60	-	2.60	-

Values are percent cover estimates from quadrat surveys and M indicates species recorded only during meanders; dashes indicate that species were not found.

The survey protocol was changed between 2002 and 2003; details are given in the text.

Table A.7 Stand-level mean values for the environmental variables (± 1 standard deviation) measured in the field experiment described in Chapter 4.

Study site	N	Mean vascular plant cover (%)	Mean bryophyte cover (%)	Mean litter cover (%)	Mean litter depth (mm)	Mean depth of bryophyte carpet (mm)	Mean gravimetric soil moisture (%)	Mean H+ concentration (ppm)
BRN1	14	6.17 ± 3.77	89.88 ± 18.73	22.22 ± 17.23	0.07 ± 0.27	13.79 ± 6.40	65.20 ± 13.40	7.47E-08 ± 3.10E-08
BRN2	17	6.41 ± 4.74	50.51 ± 37.20	34.15 ± 28.61	1.88 ± 4.28	3.88 ± 5.06	55.14 ± 13.41	1.80E-07 ± 2.86E-07
BRN3	14	6.37 ± 4.11	38.29 ± 31.32	22.82 ± 12.62	0	2.36 ± 3.77	39.98 ± 9.90	1.75E-05 ± 1.03E-05
BRN4	11	1.31 ± 2.25	33.59 ± 29.30	36.11 ± 22.87	1.73 ± 3.10	0.55 ± 0.82	10.76 ± 8.96	2.16E-05 ± 1.54E-05