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Bryophyte community structure in a high boreal poor fen in Northern Alberta, Canada

by

Roisín Catherine Mulligan ©

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

in

Environmental Biology and Ecology

Department of Biological Sciences

Edmonton, Alberta

Spring 2002

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled *Bryophyte community structure in a high boreal poor fen in Northern Alberta, Canada* submitted by Roisín Catherine Mulligan in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Environmental Biology and Ecology.

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"*Strax efter begynte myrar, som mest stodo under vatten, dem måste vi gå en hel mil, tänk med vad möda; vart steg stod upp til knäs..... Hela denna lappens land var mest myra, hinc vocavi Styx. Aldrig kan prästen så fult, där detta ej är fulare.*"

"Shortly afterwards we began the muskegs, which mostly stood under water; these we had to cross for miles; think with what misery, every step up to our knees. The whole of this land of the Lapps was mostly muskeg, *hinc vocavi* Styx. Never can the priest describe such Hell, because it is no worse.

CAROLUS LINNAEUS 1732
After a field trip from Uppsala to Lapland

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This thesis is dedicated in loving memory of
Dr. Patrick Joseph Mulligan, M.D.
(1926-1993)

who told me I could do and be anything

who took me: golfing, to the beach, snow shoeing, fishing, to hockey games
who taught me how to play poker, to win at Scrabble, to make curry
who moved the whole family across the country because I was sick
who paid attention, who paid tuition
who taught me right from wrong
and to study, study, study

I miss his love, encouragement, dark sense of humour and smile every day

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Abstract

The underlying mechanisms behind the distribution of four focal bryophytes was examined in a high boreal poor fen 90 km south of Fort McMurray, Alberta. The importance of competitive interactions, habitat preference and regeneration capability to the existing community matrix was examined using transplant investigations and growth studies.

Sphagnum angustifolium has a very wide ecological amplitude. It is partially limited by habitat preference but competition and establishment do not locally limit this species. Dispersal is also probably not an inhibiting factor since *Sphagnum angustifolium* readily colonised many establishment tubs in which it was not planted. The very broad fundamental niche of *Sphagnum magellanicum* in this peatland is partially limited by habitat in that *S. magellanicum* cannot survive in the driest habitats. Further, *Sphagnum magellanicum* is likely not competitively excluded from any habitats but it is limited in its ability to colonise bare peat surfaces from asexual gametophytic fragments. *Sphagnum fuscum* is not limited by habitat as it can survive in all habitats, but the factors which prohibit this species full occupation of its fundamental niche are still not completely understood. The mature gametophytes of *Sphagnum fuscum* may be competitively excluded from the hollow habitats in this peatland by *S. magellanicum*. Establishment ability also likely plays an important role as *Sphagnum fuscum* appears to have a very narrow and specific regeneration niche which does not include postfire bare peat. The very narrow realised niche of

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Pleurozium schreberi in this peatland is the result of several restrictions. *Pleurozium schreberi* is competitively inferior to the Sphagna and therefore competitive exclusion is likely a factor. *Pleurozium schreberi* is also limited by habitat in that it can only survive in dry and shaded habitats, but it is quite capable of establishment on bare peat from gametophytic fragments.

Measurement of bryophyte growth was a method central to this thesis and many other examinations of bryophyte response to abiotic and biotic factors. Despite this importance, the weight that is actually gained or lost by the experimental shoots themselves is rarely measured, thus potentially leading to high experimental error. Therefore, an existing (but rarely used) method was modified, calibrated and field-tested in a back transplant experiment to allow for prediction of initial dry weight from moist weight of the experimental shoots.

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ACKNOWLEDGEMENTS

This saga began with Mrs. Kamal Saini who first fostered my interest in biology at Centennial Secondary School in Belleville, Ontario. At Trent University in Peterborough, Ontario I continued my biological pursuits with an interest in human anatomy and animal physiology. Through a twist of fate, I begrudgingly found myself taking terrestrial plant ecology because it was the only course that fit into my schedule. Within a month, I was captivated by the magnificent *Acer saccharum* Marsh. -*Fagus grandifolia* Ehrh. forest on the Trent Canal drumlin which towered over me in an almost omnipotent manner. I knew that botany was my soul.

This love was mentored and nurtured by the Trent botanists whose enthusiasm was contagious. I thank Dr. Roger Jones for teaching me the significance, magnificence and beauty of all things with chlorophyll, for helping me acquire my first botanical job and for reminding me that sometimes I was "my own worst enemy". I also thank Professor Christine Maxwell for introducing me to the splendour and importance of phycology, for refining my seminar skills and for unknowingly, showing me how to teach. To Dr. Katherine Frego I extend my gratitude for: her "dictionary of unnecessary words", her passion for plants, giving me my second job in botany and introducing me to bryology. I also thank Kate for her continued involvement in my academic career and for assistance and advice with several chapters of this thesis.

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I thank my co-advisors, Dennis Gignac and Mark Dale and my committee members, J.C. Cahill and Vic Lieffers for their contributions to this thesis. I thank Dennis for intellectual advice, financial support and that quirky sense of humour that has continued to surprise me over the years. I thank Mark for stepping into what was a difficult situation in my 5th year to enable me to finish this project; for financial support, encouragement, and suggesting statistical solutions when there appeared to be none. I thank J.C for reading rough drafts, statistical advice and his open door that I took advantage of many times. I am grateful to Vic for his advice and staunch support that did not go unnoticed.

This study was funded by Natural Sciences and Engineering Research Council operating grants to Dennis Gignac and Mark Dale and a Circumpolar/Boreal Alberta Grant to myself. Funding to myself from the Challenge Grants in Biodiversity Program, Department of Biological Sciences, University of Alberta, and the Alberta Conservation Association is also recognised with gratitude.

Graduate school is a long, tough road which was smoothed for me by the support, love, friendship and companionship of my fellow student slaves. I thank Ilka Bauer, David Beilman, Dr. Natalie Cleavitt, Dr. Stefanie Zaklan, Selena Smith, John Brzustowski, and Dr. Ranessa Cooper for their strong shoulders, eager ears and perpetual barrage of advice on all topics academic or otherwise. I am also grateful to Louise McBain, Dorothy Fabijan, Dr. Sean Graham and Maggie Haag who have, in various ways, made my time here better.

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I thank Johanne Berger and Line Blackburn for short term field and/or laboratory assistance and the staff and management at Mariana Lakes Lodge for assistance of all types over the years. I appreciate my gardens for their endless hours of mind-clearing solitude and joy, and Dennis and Teene Stashko for being the best neighbours ever! To my dearest friend and former field companion Renée Amyotte I extend my love and gratitude: thanks for putting up with me, the project, the weather, the bugs and the bears.

I also recognise the eternal love and support of my gang of friends from public and secondary school including Annalisa VanElsywk, Melany Scharley, Susan Green, Kimberley Ann Williams, Gary Crabbe and Krista Simmons. May you have all found your true place in this world and thanks for just being you. We may never have that commune we've always joked about, but we'll always have each other. I love you all.

I thank *mon amour* Arthur R. Chabot who has been at my side for most of this long journey. I thank him for his love, extreme patience, understanding and nursing care. I'm sorry about all the late nights, the events I missed, and for not always being a pleasant person to be around lately. I promise you will rediscover the person you met 6.5 years ago, once you finally pry me from this keyboard.

Lastly, I thank my family for their ongoing emotional, intellectual and financial support. I adore my furry pseudo-offspring Meaghan and Sarafina whose constant cuddly comfort is always welcome. I thank my mother for showing me how to swim, how to drive, how to cook, how to sew, and virtually anything else that I needed to know. I thank her for creating "Chicken pox

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school", for taking me everywhere including: the ballet, the symphony, the theatre, Open Houses, piano lessons, medical appointments, and sports practice etc. And I thank her for insisting that there were "no limits" on what I could achieve and where I could go in life. I thank her for finally accepting that I am destined to be a "Doctor of Plants" even though, yes mum it's true, I probably could have done neuro-surgery by now! I thank my womb mate, Stephen Patrick, for sharing: the couch for Saturday morning cartoons, his birthday, Ben, the skating pond, our friends and himself so much with me. I guess I can forgive him for sequestering all the nutrients *in vivo*, if he can forgive me for telling him that there was no Santa Clause.

Yes, it's true, there really is no Santa Clause.

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IV. BRYOPHYTE COMMUNITY STRUCTURE IN A HIGH BOREAL POOR FEN III: THE IMPORTANCE OF ESTABLISHMENT ABILITY, REGENERATION NICHE INTERACTIONS AND FACILITATION SUCCESSION cont'd

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Figure **Page**

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List of Abbreviations

ANG	*Sphagnum angustifolium* C. Jens. ex Russ.
AUL	*Aulacomnium palustre* (Hedw.) Schwaegr.
BL	Bleak Lake
BUNS	bundle sizes
CER	*Ceratodon purpureus* (Hedw.) Brid.
CL	Calling Lake
CN	Conklin
CON	control (no fragments)
CTKL	cut to known length
ddf	denominator degrees of freedom
DBG	Devonian Botanic Garden
DTW	depth to water table
FUS	*Sphagnum fuscum* (Schimp.) Klinggr.
G-force	gravitational force
K_{corr}	corrected conductivity
LB	Lac La Biche
LEP	*Leptobryum pyriforme* (Hedw.) Wils.
ln	natural logarithm
M_1	calculated initial dry weight (or length)
M_2	final dry weight (or length)
MAE	mean absolute error
MAG	*Sphagnum magellanicum* Brid.
MAR	*Marchantia polymorpha* L.
MIX	mix (all species gametophytic fragments)
ML	Mariana Lake
ndf	numerator degrees of freedom
NPAR1WAY	non parametric one way analysis of variance
p. rand.	p value from the randomisation test
P_A	mean growth of the phytometer grown with itself
PLE	*Pleurozium schreberi* Brid.
P_N	growth of the phytometer with shoots of neighbour N
POH	*Pohlia nutans* (Hedw.) Lindb.
POL	*Polytrichum* spp.
PTI	*Ptilium crista-castrensis* (Hedw.) De. Not.
R^2	Regression coefficient
RCP	relative competitive performance
RGR	relative growth rate
rpm	rotations per minute
s.e.	standard error
t	T-test value
TRT	treatment
µs/cm	micro siemens per centimetre
YC	young colonisers too small or too crowded to identify
×	interaction

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List of Abbreviations found only in the Appendix

Sphagna

Sph. aus.	*Sphagnum australe* Mitt
Sph. ang.	*Sphagnum angustifolium* C. Jens. *ex* Russ
Sph. aur	*Sphagnum auriculatum* var. *inundatum*
Sph. aus	*Sphagnum austinii* Sull.
Sph. bal.	*Sphagnum balticum* (Russ.) C. Jens.
Sph. cap.	*Sphagnum capillifolium* (Ehrh.) Hedw.
Sph. capc.	*Sphagnum capillaceum* (Weiss) Schrank
Sph. com.	*Sphagnum compactum* DC. *in* Lam. & DC.
Sph. con.	*Sphagnum contortum* Schultz
Sph. cri.	*Sphagnum cristatum* Hampe
Sph. cus.	*Sphagnum cuspidatum* Ehrh. *ex* Hoffm.
Sph. falc.	*Sphagnum falcatulum* (Russow) Limpr.
Sph. fal.	*Sphagnum fallax* (Klinggr.) Klinggr.
Sph. fim.	*Sphagnum fimbriatum* Wils. *in* Wils. & Hook.
Sph. fla.	*Sphagnum flavicomans* (Card.) Warnst.
Sph. fle.	*Sphagnum flexuosum* Dozy & Molk.
Sph. fus.	*Sphagnum fuscum* (Schimp.) Klinggr.
Sph. hen.	*Sphagnum henryense* Warnst.
Sph. imb.	*Sphagnum imbricatum* Hornsch. Ex Russ.
Sph. lin.	*Sphagnum lindbergii* Schimp. *in* Lindb.
Sph. mag.	*Sphagnum magellanicum* Brid.
Sph. nem.	*Sphagnum nemoreum* Scop.
Sph. mac.	*Sphagnum macrophyllum* Brid. var. *floridanum* Aust.
Sph. maj.	*Sphagnum majus* (Russ.) C. Jens.
Sph. pac.	*Sphagnum pacificum* Flatb.
Sph. pal.	*Sphagnum palustre* L.
Sph. pap.	*Sphagnum papillosum* Lindb.
Sph. plu.	*Sphagnum plumulosum* Röll
Sph. por.	*Sphagnum portoricense* Hampe
Sph. pul.	*Sphagnum pulchrum* (Lindb. *ex* Braithw.) Warnst.
Sph. rec.	*Sphagnum recurvum* P. Beauv.
Sph. rip.	*Sphagnum riparium* Angstr.
Sph. rub.	*Sphagnum rubellum* Wils.
Sph. rus.	*Sphagnum rusowii* Warnst.
Sph. spp.	Sphagna of unknown specific epithets
Sph. squ.	*Sphagnum squarrosum* Crome
Sph. str.	*Sphagnum strictum* Sull.
Sph. sub.	*Sphagnum subsecundum* Nees *in* Strum
Sph. sub.	*Sphagnum subnitens* Russ. & Warnst. *in* Warnst.
Sph. ten.	*Sphagnum tenellum* (Brid.) Bory
Sph. tri.	*Sphagnum trinitense* C. Müll.
Sph. war.	*Sphagnum warnstorfii* Russ.

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Abbreviations of non-Sphagna bryophytes

And. dep.	*Andreaea depressinervis* Cardot
Ano. ros.	*Anomodon rostratus* (Hedw.) Schimp.
Aul. pal.	*Aulacomnium palustre* (Hedw.) Schwaegr.
Bar. spp.	*Barbula* of unknown specific epithets
Bar. con.	*Barbula convuluta* Hedw.
Bar. hor.	*Barbula hornschuchiana*
Bar. ung.	*Barbula ungiculata* Hedw.
Bra. aus.	*Brachythecium austrosalebrosum* (C. Müll) Ochyra
Bra. rut.	*Brachythecium rutabulum* (Hedw.) B.S.G.
Bry. spp.	*Bryum* of unknown specific epithets
Bry. arg.	*Bryum argenteum* Hedw.
Bry. bic.	*Bryum bicolor* Dicks
Bry. ery.	*Bryum erythrocarpum*
Bry. gem.	*Bryum gemmilucens* Wilcz. & Demar.
Bry. cap.	*Bryum capillare* Hedw.
Bry. rad.	*Bryum radiculosum* Brid.
Bry. tor.	*Bryum torquescens* B.S.G.
Cal. cus.	*Calliergonella cuspidata* (Hedw.) Loeske
Cal. sph.	*Calypogeia sphagnicola* (H. Arnell *et* J. Perss.) Warnst. *et* Loeske
Cam. ser.	*Camptothecium sericeum* = *Homalothecium sericeum* (Hedw.) Schimp *in* B.S.G
Cam. spp.	*Campylium* of unknown specific epithets
Cam. ste.	*Campylium stellatum* (Hedw.) C. Jens.
Cat. und.	*Catharinea undulata* (Hedw.) Web. & Mohr
Cep. div.	*Cephaloziella divaricata* (Sm.) Schiffn.
Cep. loi.	*Cephalozia loitelsbergeri* Schiffn.
Cep. lun.	*Cephalozia lunulifolia* (Dum.) Dum.
Cer. pur.	*Ceratodon purpureus* (Hedw.) Brid.
Cla. Flu.	*Cladopodiella fluitans* (Nees) Joerg.
Cra. com.	*Cratoneuron commutatum* (Hedw.) Roth
Cte. mol.	*Ctenidium molluscum* (Hedw.) Mitt.
Dic. cer.	*Dicranella cerviculata* (Hedw.) Schimp.
Dic. fla.	*Dicranum flagellare* Hedw.
Dic. maj.	*Dicranum majus* Sm.
Dic. pol.	*Dicranum polysetum* Sw.
Dic. sco.	*Dicranum scoparium* Hedw.
Dic. und.	*Dicranum undulatum* Brid.
Did. acu.	*Didymodon acutus* (Brid.) Saito
Did. fal.	*Didymodon fallax* (Hedw.) Zand.
Dit. fle.	*Ditricum flexicaule* (Schwaegr.) Hampe
Dit. pal.	*Ditrichum pallidum* (Hedw.) Hampe
Dre. adu.	*Drepanocladus aduncus* (Hedw.) Warnst.

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Abbreviations of non-Sphagna bryophytes cont'd

Dre. exa.	*Drepanocladus exannulatus* (B.S.G.) Warnst.
Dre. unc.	*Drepanocladus uncinatus* (Hedw.) Warnst.
Ent. fas.	*Entoshodon fasicularis* (Hedw.) C. Müll
Euc. ver.	*Eucladium verticillatum* (Brid.) B.S.G.
Eur. pra.	*Eurhynchium praelongum* (Hedw.) Schimp *in* B.S.G.
Fis. cri.	*Fissidens cristatus* Wils. ex Mitt.
Fis. inc.	*Fissidens incurvus* Starke en Röhl
Fon. dur.	*Fontinalis duriaei* Schimp.
Fun. hyg.	*Funaria hygrometrica* Hedw.
Gym. rec.	*Gymnostomum recurvirostrum* Hedw.
Hom. lut.	*Homalothecium lutescens* (Hedw.) Robins
Hyl. spl.	*Hylocomium splendens* (Hedw.) B.S.G.
Hyp. cup.	*Hypnum cupressiforme* Hedw.
Hyp. cupl.	*Hypnum cupressiforme* var. *lacunosum* Brid.
Hyp. imp.	*Hypnum imponens* Hedw.
Hyp. jut.	*Hypnum jutlandicum* Holmen & Warncke
Hyp. plu.	*Hypnum plumaeforme* Wils.
Iso. myo.	*Isothecium myosuroides* Brid.
Jun. inf.	*Jungermannia infusca* (Steph.) Amak.
Kur. pau.	*Kurzia pauciflora* (Dicks.) Grolle
Leu. alb.	*Leucobyrum albidum* (Brid.) Lindb.
Leu. gla.	*Leucobryum glaucum* (Hedw.) Aongstr. ex Fr.
Mni. aff.	*Mnium affine* Bland ex Funck
Myl. ano.	*Mylia anomala* (Hook.) S. Gray
Nec. pum.	*Neckera pumila* Hedw.
Ort. lin.	*Orthodontium lineare* Schwägr.
Odo. den.	*Odontoschisma denudatum* (Nees) Dumort.
Pla. asp.	*Plagiochila asplenioides* (L.) Dumort.
Pla. max.	*Plagiomnium maximoviczii* (Lindb.) T.J. Kop.
Pla. und.	*Plagiomnium undulatum* (Hedw.) T.J. Kop
Pla. rep.	*Platygyrium repens* (Brid.) B.S.G.
Ple. sch.	*Pleurozium schreberi* (Brid.) Mitt.
Poh. spp.	*Pohlia* of unknown specific epithets
Pol. alp.	*Polytrichum alpestre* Hoppe
Pol. com.	*Polytrichum commune* Hedw.
Pol. for.	*Polytrichum formosum* Hedw.
Pol. jun.	*Polytrichum juniperinum* Hedw.
Pol. str.	*Polytrichum strictum* Brid.
Pot. spp.	*Pottia* of unknown specific epithets
Pot. sta.	*Pottia starkeana* (Hedw.) C. Müll
Pre. qua.	*Preissia quadrata* (Scop.) Nees
Pse. hor.	*Pseudocrossidium hornschuchianum* (K.F. Schultz.) Zander
Pse. pur.	*Pseudoscleropodium purum* (Hedw.) Fleisch
Pte. ova.	*Pterygoneurum ovatum* (Hedw.) Dix.

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Abbreviations of Non-Sphagna bryophytes cont'd

Pti. cil.	*Ptilidium ciliare* (L.) Hampe
Pti. cri.	*Ptilium crista-castrensis* (Hedw.) De Not.
Rac. can.	*Rhacomitrium canescens* (Hedw.) Brid.
Rac. mic.	*Rhacomitrium microcarpon* (Hedw.) Brid.
Rhy. rip.	*Rhynchostegium ripariodes* (Hedw.) Card.
Rhy. lor.	*Rhytidiadelphus loreus* (Hedw.) Warnst.
Rhy. squ.	*Rhytidiadelphus squarrosus* (Hedw.) Warnst.
Rhy. tri.	*Rhytidiadelphus triquetrus* (Hedw.) Warnst.
Rhy. rug.	*Rhytidium rugosum* (Hedw.) Kindb.
Sco. sco.	*Scorpidium scorpioides* (Hedw.) Limpr.
Sem. ori.	*Semibarbula orientalis* (F. Weber) Wijk & Margad.
Spl. amp.	*Splachnum ampullaceum* Hedw.
Spl. lut.	*Splachnum luteum* Hedw.
Syn. can.	*Syntrichia caninervis* = *Tortula caninervis* Mitt.
Syn. ine.	*Syntrichia inermis* = *Tortula inermis* (Brid.) Mont.
Tet. pel.	*Tetraphis pellucida* Hedw.
Tet. ang.	*Tetraplodon angustatus* (Hedw.) B.S.G.
Tet. mni.	*Tetraplodon mnioides* (Hedw.) B.S.G.
Tha. alo.	*Thamnobryum alopecurum* (Hedw.) Nieuwl.
Thu. del.	*Thuidium delicatulum* (Hedw.) B.S.G.
Thu. tam.	*Thuidium tamariscinum* (Hedw.) B.S.G.
Tom. nit.	*Tomenthypnum nitens* (Hedw.) Loeske
Tor. lat.	*Tortula latifolia* Bruch ex C.J. Hartm.
Tor. tor.	*Tortella tortuosa* Hedw.
Tre. lon.	*Trematodon longicollis* Michx.
Tri. bra.	*Trischostronum brachydontium* Bruch.
Tri. cri.	*Trichostomum crispulum* Bruch.
War. exa.	*Warnstorfia exannulata* (Schimp. *in* B.S.G.) Loeske

Lichens

Cla. ran.	*Cladonia rangiferina* (L.) Wigg
Cla. squ.	*Cladonia squamosa* (Scop.) Hoffm.
Cet. isl.	*Cetraria islandica* (L.) Ach.
Lec. gra.	*Lecidea granulosa* (Hoffm.) Ach.
Mic. tur.	*Micarea turfosa* (Massal.) Du Rietz

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Angiosperms and gymnosperms

And. pol.	*Andromeda polifolia* L.
Cal. vul.	*Calluna vulgaris* (L.) Hull
Car. lim.	*Carex limosa* L.
Car. oli.	*Carex oligosperma* Michx.
Cha. cal.	*Chamaedaphne calyculata* (L.) Moench
Dro. ang.	*Drosera anglica* Huds.
Dro. rot.	*Drosera rotundifolia* L.
Emp. nig.	*Empetrum nigrum* L.
Era. mul.	*Eragrostis multicaulis* Steud.
Eri. ang.	*Eriophorum angustifolium* Honck.
Eri. spi.	*Eriophorum spissum* Fern.
Eri. vag.	*Eriophorum vaginatum* L.
Fim. dic.	*Fimbristylis dichotoma* (L.) Vahl.
Hyd. pan.	*Hydrangea paniculata*
Kal. pol.	*Kalmia polifolia* Wang.
Mis. sin.	*Miscanthus sinensis*
Oxy. mic.	*Oxycoccus microcarpus* Turcz.
Pin. str.	*Pinus strobus* L.
Rub. cha.	*Rubus chamaemorus* L.
Sci. ces.	*Scirpus cespitosus* L.
Vac. oxy.	*Vaccinium oxycoccus* L.
Vac. uli.	*Vaccinium uliginosum* L.

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Chapter 1- Introduction

Scope of and rationale for the research

Crum (1972) defined four factors that could restrict the niche dimensions of bryophytes: i) absence of suitable habitat, ii) climatic effects, iii) competition, and iv) failure to disperse and or establish. This thesis explores the underlying mechanisms behind the observed distribution of four focal bryophytes (*Sphagnum fuscum* (Schimp.) Klinggr., *S. angustifolium* C. Jens. ex Russ., *S. magellanicum* Brid., *Pleurozium schreberi* (Brid.) Mitt.) and two secondary species (*Aulacomnium palustre* (Hedw.) Schwaegr. and *Ptilium crista-castrensis* (Hedw.) De Not.) in a high boreal poor fen (peatland) in Northern Alberta, Canada. The importance of competitive interactions, habitat preference, and regeneration capability to the existing community are examined using transplant and growth investigations. Further, a literature review of 80 bryophyte growth studies raised some serious concerns regarding the potential inaccuracy of current methods. In order to address these concerns, an existing, yet highly under-used, weight growth method was revised and tested with the study species.

The small number of empirical investigations that have examined niche relationships in boreal bryophytes have provided valuable insight into the community structure, but they have mostly been conducted in bog, rich fen and forest habitats. The relative importance of niche dynamics to the ecological amplitude of poor fen bryophytes, particularly *Sphagnum angustifolium*, remains largely unexplored.

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The importance of boreal bryophyte communities

Bryophytes are often ignored as integral components of the landscape as their small size and taxonomically troublesome reputation perpetuate the falsehood of their insignificant role in global ecological processes. Contrary to this notion, bryophytes are encountered in almost all land and many freshwater habitats. They dominate the ground layer vegetation of most boreal communities and are the primary producers in many northern ecosystems (Hayward and Clymo 1982; Van Cleve *et al.* 1983; Longton 1984; During and van Tooren 1987). For example, Van Cleve *et al.* (1983) estimated that moss production in Alaskan *Picea mariana* (Mill) BSP. forests equalled that of trees and exceeded that of the foliage by 3:1. Bryophytes are also critical to nutrient cycling and water retention in these northern habitats (Skre *et al.* 1983; Chapin *et al.* 1987; Price *et al.* 1997).

One ecosystem where bryophytes dominate the ground layer vegetation is boreal peatlands. A peatland is a wetland where the water table is at or near the surface and peat accumulation is ≥ 40 cm (Zoltai 1988). Canada has the largest area of peatlands in the world accounting for 12% of the total land surface (Terasmae 1977; Zoltai 1988). In Alberta, peatlands cover about 21% of land area (Zoltai 1988). Boreal peatlands are classified as either bogs or fens based on hydrology. Bogs are ombrotrophic, receiving all nutrients from precipitation and dust, while fens are minerotrophic due to geogenous input from water which has been in contact with mineral soil. Fens are further subdivided along a poor to rich gradient based on the number of indicator species and nutrient status. The ground

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layer vegetation in bogs and poor fens is dominated by *Sphagnum* (the peat mosses).

The dominance by this single genus facilitates its control of ecological processes over vast expanses of the boreal landscape. *Sphagnum* accomplishes this by acidifying the environment through cation exchange. This makes the environment more suitable for *Sphagnum* spp. and less hospitable for any potential competitors. *Sphagnum* is also irrefutably the most economically important bryophyte genus because of its dense carbon store, antiseptic nature and remarkable water holding capacity. Large dead hyaline cells enable Sphagna to hold 10 to 40 times their dry weight in water (Proctor 1982). This capability accounts for its use in baby diapers (historical), menstrual napkins, oil spill booms and horticultural amendments (Leverin 1943; Hennezel and Coupal 1972; Miller 1981). This absorbency, coupled with its natural antiseptic properties, made *Sphagnum* an invaluable substitute for cotton in surgical dressings during WWI (Nichols 1918). Peat also remains an important fuel in some areas.

Bryophyte peatland species distribution is controlled by four main gradients: wet to dry, ombrotrophic to minerotrophic, mire margin to mire expanse, and open to shaded (Gignac and Vitt 1990; Gerdol 1995; Nicholson and Gignac 1995). Depth to water table is often recognised as the most important gradient (Hayward and Clymo 1983; Rydin 1987; Gignac *et al.* 1991; van der Molen *et al.* 1992; Gerdol 1995; Bragazza and Gerdol 1996; Grosvernier *et al.* 1997; Bragazza 1997; Schipperges and Rydin 1998) because it exerts a major influence on water chemistry and decomposition dynamics (Damman 1978; Rydin 1993a).

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The depth to water table gradient is characterised by the species that only grow on hummocks or in hollows. Hummock species inhabit the areas farthest from the water table, while hollow species occur at the base of the hummock in areas where the water table is very close to the surface. The ombrotrophic to minerotrophic gradient may be equally important depending on the peatland under investigation and the study location (Andrus 1986; Gignac and Vitt 1990; Gignac 1992). Climate may override water table effects and chemical gradients on a regional scale (Gignac 1992).

Introduction to the study site

The study site (Figs. 1-1a, b) is a continental boreal peatland near Mariana Lake, in northeastern Alberta (55° 55' N, 111° 58' W), Canada (Fig. 1-2). The climate is boreal cold with a mean annual temperature of 0.2°C and mean annual precipitation of 464.7 mm recorded at the nearest weather station located approximately 90 km north in Fort McMurray (Environment Canada 1990). The peatland is part of a mire complex with three distinct physiognomic sections: a poor fen area with a ground layer dominated by *Sphagnum angustifolium* and *Carex* spp. (Fig. 1-3), a small, non-wooded ombrotrophic area dominated by *S. fuscum* and ericaceous shrubs (Fig. 1-4), and wooded bog islands characterised by stunted *Picea mariana* with an understory of *Pleurozium schreberi*, *S. fuscum*, *S. angustifolium*, *Rubus chamaemorus* L., *Rhododendron groenlandicum* (Oeder) Kron and Judd, and *Smilacina trifolia* (L.) Desf. (Fig. 1-5).

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Introduction to the study species

Sphagnum angustifolium (Fig. 1-6) is a fast growing hollow-inhabiting species that exhibits very wide niche breadth in acidic, wet peatlands throughout western Canada (Gignac 1993). Depth to water table may limit the distribution of *Sphagnum angustifolium*, while climate and surface water chemistry are considered non-limiting factors (Gignac *et al.* 1991). In this peatland, *Sphagnum angustifolium* occurs commonly in the wooded bog islands, and sporadically, as isolated shoots, in the non-wooded (*S. fuscum*) area.

Sphagnum magellanicum is a widespread poor fen species, typically found on the sides of large hummocks in poor fens and bogs. *Sphagnum magellanicum* (Fig. 1-7) exhibits great ecological amplitude particularly with respect to water table and surface water chemistry gradients (Gignac 1992; Bragazza 1997). In this peatland, *Sphagnum magellanicum* is found in all areas; however, it is most abundant in the poor fen and wooded bog islands.

Sphagnum fuscum is a widespread species with very broad ecological amplitude throughout western Canada in bogs, poor and moderate-rich fens (Gignac 1993). *Sphagnum fuscum* forms its own substrate in the form of densely packed hummocks, which are separated from the water table by 20 to 70 cm (Nicholson and Gignac 1995). In this peatland, *Sphagnum fuscum* occurs commonly in the bog islands, and sporadically on isolated hummocks in the poor fen section.

Pleurozium schreberi (Fig. 1-8) is a common boreal forest moss (Longton and Greene 1979; Longton 1985; Frego and Carleton 1995) which also forms a

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potentially important, yet often ignored, component of the bryophyte vegetation in many peatlands. This species exhibits wide niche breadth in western Canadian peatlands with a range extending from bogs to moderate-rich fens (Gignac 1992). In peatlands, *Pleurozium schreberi* reaches its maximum abundance at 30 cm above the water table where it usually occurs above the Sphagna (Gignac 1993). In this peatland, *Pleurozium schreberi* is found exclusively in the bog islands.

Ptilium crista-castrensis (Fig. 1-8) is a boreal forest floor inhabitant which is not usually included in peatland studies because it is generally absent. In this peatland, *Ptilium crista-castrensis* is restricted to two very small patches, both of which are shaded by young *Picea mariana*. Despite its limited distribution, *Ptilium crista-castrensis* was included in some investigations because its presence was interesting and unexpected.

Aulacomnium palustre is a common acrocarpous moss in continental western Canadian peatlands (Gignac *et al.* 1991) that grows on hummock tops with *Sphagnum fuscum* and *Polytrichum strictum* Brid. Its distribution in this peatland is precisely as just described. *Aulacomnium palustre* is also a frequent component of the bryophyte flora in disturbed areas. In this peatland the typical position of the study species along the hollow-hummock water table gradient is noted in Fig. 1-9.

Historical background of plant ecology

Early biologists such as Carolus Linnaeus (1707-1778) and Charles Darwin (1809-1882) collected essentially everything (including bryophytes), with the

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primary objective of describing and naming organisms. These endeavours lead to the desire to also classify the surroundings of these organisms, and ultimately to the founding of the science of ecology (from the Greek word *oikos* meaning house). Early plant ecologists such as Friedrich Humboldt (1769-1859), Johannes Warming (1841-1924), and Henry Cowles (1869-1939) continued taxonomic pursuits at the species level but also began classifying the groups of plants which grew together.

One such group of plants is the "community", a concept first defined in 1855 by Svetzov (Carpenter 1962) in a purely zoological sense and later botanically broadened by Clements (1905). The "modern" definition of the community as all the plants and animals in a given area is credited to Phillips (1931) and Shelford (1932). One type of community, the association, is an outdated term first coined by Humboldt in the early 19th century. The acceptance of the association by the International Botanical Congress in 1910 fuelled a heated argument and divided early plant ecologists into two schools of thought. Frederick Clements (1916) believed that vegetation was organised into discrete associations of species which differed sharply from adjacent associations of different species. In contrast, Henry Gleason (1926, 1936) postulated that the change in species abundance along environmental gradients was so gradual that it was not possible to divide the vegetation into discrete associations. Although these heretic notions were initially disregarded and Gleason branded an "ecological outlaw", their contribution to plant ecology was eventually recognised in 1953 as Gleason was honoured as an Eminent Ecologist by the Ecological Society of America (Barbour *et al.* 1987).

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At a broader level of classification is the ecosystem, a term defined by Sir Arthur Tansley (1935, 1939) as all the species in a community plus all of the abiotic factors in that given area. In a visionary statement Tansley (1935:299) reminded us of the synergism of ecology when he wrote "though the organisms may claim our primary interest, ... we cannot separate them from their special environment, with which they form one physical system."

Plant community ecology quickly evolved into a major body of knowledge as the global description of habitats continued. Early literature was rife with nomenclatural discrepancies as terminology was refined, rewritten, refuted, and reinvented (Braun-Blanquet 1933; Tansley 1935). Many would argue that the present situation is no better, if not worse, owing to the exponential increase in plant ecologists and the terminology they claim to be "fixing". Bryophyte ecology began in much the same manner as vascular plant ecology, in that most studies were descriptive. The main difference between the two fields is that bryophyte ecology is still really in its infancy as quantitative investigations have only recently (in the past 30 years) become prevalent. As a result, the autecology of most bryophyte groups remains poorly understood. For this reason, it is important to pursue bryoecological investigations.

The post WWII era brought a renewed interest in more objective and quantitative methods of delineating plant communities. The pioneering work of J. T. Curtis included such important phytosociological tools as nearest individual, point-centred and random pairs methods and ordination (Curtis and McIntosh 1951; Cottam and Curtis 1956; Bray and Curtis 1957). Similarly influential were

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the contributions of R. H. Whittaker (1920-1980) who designed classification schemes, and developed gradient analysis and quadrat methods for calculation of species richness and diversity (Whittaker 1962, 1967; Shmida 1984). The wide acceptance of these methods allowed for more detailed analyses and easier cross-referencing of results.

Models of community structure and niche theory

Now that plant ecologists had the tools to quantitatively describe the vegetation of a given area, the next task was to determine the processes behind the observed patterns (Watt 1947). This delineation is not usually attributable to a single factor, but a combination of biotic and abiotic factors. These factors are often described within the concept of the ecological niche. Although largely mis-credited to Grinnell (1917) for his California thrasher studies, the term niche was first used in the ecological sense (in the English literature) with respect to ladybeetle colour patterns by Johnson (1910). Classic niche (and competition) theories were designed for and originally tested with mobile organisms, and did not encompass important botanical factors as age, size, spatial structure or density dependent mortality (Silvertown and Law 1987). "Modern" niche theory is primarily ascribed to Hutchinson (1957, 1959) who attempted to explain the coexistence of many species of plants and animals in one area. Hutchinson envisioned an n-dimensional hypervolume inclusive of all abiotic factors (light, moisture, temperature etc.) within which a particular species may potentially exist in the absence of biotic influences such as predation, competition etc. This

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fundamental niche is usually contracted into a smaller, realised niche due to these interactions.

The only way to describe the fundamental niche of a species in the field is experimentally, by transplanting it into habitats in which it does not typically grow. Vascular plant reciprocal transplant investigations have described ecotype adaptation in *Carex exilis* (Santelmann 1991), life history differences in *Ranunculus lingua* (Johansson 1994), competition between tidal and pasture grasses (Streever and Genders 1997), and demography in *Stipa leucotricha* (Fowler and Clay 1995).

Bryophyte transplant studies are not as common as other growth experiments (Rydin 1997a; Slack 1997). Despite this, several transplant investigations have focussed on niche relationships (for reviews of bryophytes and niche theory see Slack 1982, 1990, 1997). For example, Frego and Carleton (1995) used reciprocal transplants to eliminate habitat partitioning as the driving force behind the spatial pattern of four boreal forest species, and Kooijman (1993) documented the importance of habitat preference in an examination of species replacement in Dutch rich fens. The peatland investigations of Rydin (1985, 1993a) and others have indicated that hollow-inhabiting Sphagna are excluded from hummock habitats in bogs due to their inferior ability to transport and hold water. Hollow habitats have been demonstrated to be within the fundamental niches of hummock species in bog habitats (Clymo and Reddaway 1971; Hayward and Clymo 1983; Rydin and McDonald 1985; Rydin 1986, 1987), but the reasons behind the exclusion of these species from hollow habitats are not yet fully understood

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(Rydin 1993b). While these investigations have resulted in significant advances in our understanding of peatland bryophyte community structure, most have occurred in ombrotrophic situations with *Sphagnum fuscum* (Schimp.) Klinggr., *S. rubellum* Wils., *S. balticum* (Russ.) C. Jens., and *S. tenellum* (Brid.) Brid. (Clymo and Reddaway 1971; Rydin 1985, 1986, 1993b).

One of the most-studied community interactions is competition: defined as the negative influence of one individual on another that share a resource in short supply. Competition has been recognised and contemplated since the days of Malthus, Darwin, and DeCandolle who wrote that plants were "at war" with each other (1820 *in* Clements *et al.* 1929). In the early part of the 20th century empirical investigations were uncommon in 1929 when Clements *et al.* summarised the literature. Notable exceptions were Clements (1905) who examined forbs, Montgomery's (1912) studies with *Triticum* spp. and *Hordeum* spp., and Tansley's (1917) *Galium* spp. investigations. Another early competition tenet is the now largely defunct competitive exclusion principle. This theory, which loosely states that complete competitors cannot coexist, is often incorrectly attributed to Gause (1934) who demonstrated the concept with *Paramecium* populations. However, Gause merely confirmed a theory earlier pondered by Darwin (1859) and described by Grinnell (1904).

The competitor is one of the three life strategies in Grime's (1977) classification model. In this scheme, bryophytes as a group are classified as ruderals and stress tolerators, but not as competitors. Later work by During (1979) and Grime *et al.* (1990) adapted this original classification scheme for

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bryophytes and documented four main strategies. "Fugitive" bryophytes (such as *Funaria hygrometrica* Hedw.) are acrocarpous, short-lived species with high spore production that colonise unpredictable, short-term habitats. "Colonists" (e.g. *Aulacomnium palustre* and *Ceratodon purpureus* (Hedw.) Brid.) are relatively short-lived acrocarps which colonise unpredictable, long-lived habitats. "Shuttle species" (e.g. *Tetraplodon mnioides* (Hedw.) Brid.) have varying degrees of reproductive effort and life span and colonise predictable habitats such as forest floor gaps, and tree trunks etc. "Perennial stayers", such as *Sphagnum* spp. and *Pleurozium schreberi*, colonise long-lived, predictable habitats using large spores and high asexual reproductive effort. Grime *et al.* (1990) defended the exclusion of the competitive life strategy from their classification by distinguishing between the ability of moss (such as *Sphagnum* sp.) to compete for resources and its ability to physically dominate the landscape. In other words, the dominance of *Sphagnum* spp. in boreal wetlands has nothing to do with competition, but rather its ability to retain resources in habitats which are inhospitable to superior competitors. One consequence of the reverence paid to these classification schemes is the virtual dearth of bryophyte competition investigations. Bryophyte competition studies have only become prevalent in the literature in the past ten years (Appendix A). These studies indicate that competition between bryophytes may be just as important as it is between vascular plants, and that bryophytes compete mostly with each other for space (Marino 1991; Rydin 1995, 1997a,b; Slack 1997).

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Other studies have indirectly documented bryophyte competition (Luken 1985; Kenkel 1988; Økland 1990; Gignac 1992, 1993; Kooijman and Bakker 1995), and some have suggested that the distribution of *Sphagnum* species along the hollow-hummock gradient may illustrate a competitive hierarchy (Økland 1990; Gignac 1992, 1993). One community where several bryophyte competition studies have been conducted is the boreal peatland. Preliminary results concluded that hummock species were competitively excluded from hollow habitats (Rydin 1986, 1987). Later results indicated that these mosses differed very little in competitive ability (Rydin 1993 a,b) and after 11 years, the hummock species *Sphagnum fuscum* was not competitively excluded from the hollow habitats in any of 8 replicates (Rydin 1993b). The mechanisms that preclude *Sphagnum fuscum* from inhabiting what is clearly part of its fundamental niche are still not clear.

The importance of secondary succession in shaping vascular (Connell and Slayter 1977; Grime 1977; Tilman 1985; Huston and Smith 1987; Gleeson and Tilman 1994) and bryophyte (Luken *et al.* 1985; Klinger 1990, 1996) communities is irrefutable. However, the existence of a true climax (or equilibrium) community (Clements 1936) is quite debatable. Some (During 1979; Slack 1990) propose that boreal mire ecosystems are mostly in equilibrium due to the large niche overlap of the species. Others, (Luken 1985; Andrus 1986; Økland 1990) recognise the ubiquitous role of stochastic events and the gaps in vegetation that they create, and postulate that peatland bryophyte communities are likely to follow one of the non-equilibrium coexistence theories. These non-equilibrium coexistence models attempt to incorporate the myriad of confounding

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factors which may potentially interact to produce a mature community (Silvertown and Law 1987; During and van Tooren 1990). Some of these factors which are likely important include limiting resources (*sensu* Tilman 1985), habitat heterogeneity, spatial-temporal variability, niche partitioning and colonisation ability.

One explanation for the absence of *Sphagnum fuscum* from its full fundamental niche (Mulligan and Gignac 2001) could lie in its ability (or inability) to reproduce in the regeneration niche following disturbance. Grubb (1977) defined the regeneration niche as the set of conditions required by a plant in order to successfully propagate and establish the next generation. In many bryophytes, asexual reproduction via gametophytic fragments and dichotomous forking is believed to be the primary propagation mechanism (Hayward and Clymo 1982; Clymo and Duckett 1986; Newton and Mishler 1994). Several investigations have suggested that partitioning within the regeneration niche may be the key to understanding species distribution in some mature bryophyte communities (Watson 1981; Slack 1982, 1997; Rydin 1997a,b). Despite this recognition, empirical studies of bryophyte regeneration are few, and this is another area where quantitative investigation has really just begun (Li and Vitt 1994, 1995; Frego 1996; Campeau and Rochefort 1996; Kimmerer and Young 1996; Lavoie and Rochefort 1996; Bugnon *et al.* 1997; Ferland and Rochefort 1997; Nelson *et al.* 1998; Cleavitt 2001, 2002). These studies have documented the importance of gaps in the regeneration of boreal forest bryophytes and the great variation in the regeneration ability of peatland mosses. Recently, the

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importance of local recruitment limitation (a lack of competitively superior juveniles permits the persistence of competitively inferior species) in the maintenance of species diversity has been recognised as potentially a "universal feature of sessile species" (Tilman 1999:496). The potential importance of this theory to bryophyte communities is unknown and many questions remain, but boreal peatlands present an excellent opportunity to pursue establishment investigations because they are so well-studied.

The models of Connell and Slayter (1977) which describe the mechanisms of three types of secondary succession have also been examined with respect to their suitability to bryophyte communities. The tolerance model states that any species (including those that occur later) may colonise a disturbed site, and that these colonists do not affect later recruitment. The inhibition model is similar to the tolerance model except that the colonists create conditions inhospitable for other species and persist, preventing further succession, until they are removed by another major disturbance. The facilitation model suggests that only early successional species may colonise a disturbed area. These colonists alter the site so that it is more suitable for later successional species. Most bryophyte communities likely follow the tolerance model and some may exhibit inhibition succession, but evidence for facilitation is meagre (Foster 1985; During and van Tooren 1987; Rydin 1997a).

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Measurement of growth in bryophytes

Accurate determination of bryophyte growth is important because it is usually the criterion by which the response to, and significance of, experimental manipulation is determined. This is true in this thesis because growth measurements are critical to the transplant studies. The methods of determining bryophyte growth are both diverse and numerous (Clymo 1970; Russell 1984, 1988). A review of 80 bryophyte growth investigations (Appendix B) revealed 9 different methods based on length and 3 for weight. This inconsistent methodology presents difficulties with respect to experimental design, data interpretation and comparison (Rieley *et al.* 1979; Wielgolaski *et al.* 1981; Hanslin 1999). Although the importance of measuring both length and weight has been demonstrated (Clymo 1970; Rincon 1988; Rincon and Grime 1989), this review also revealed that weight is often ignored as a growth component.

When weight was measured, most (85%) investigations extrapolated it from measurements of shoot elongation (Lindholm and Vasander 1990; Potter *et al.* 1995; Zechmeister 1995; Fowbert 1996), or from groups of "similar" shoots (Chapman 1965; Furness and Grime 1982; Rincon 1988; Li *et al.* 1992; Kooijman and Bakker 1993; Jauhiainen *et al.* 1994). The recently reported uncoupling of length and weight in some bryophytes (Rincon and Grime 1989; Jauhiainen *et al.* 1997; Hanslin 1999) questions the accuracy of these extrapolations. This serious concern resulted in the testing (with the study species) and refinement of the Mankiewicz (1987) weight method to facilitate its use with small groups of shoots.

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Thesis objectives

The overall objectives of this thesis are: (i) to determine quantitatively the importance of competition, habitat preference, and establishment ability to the bryophyte community structure in the peatland, (ii) to discuss these interactions within the context of current niche theory, and (iii) to determine whether these processes are analogous to those already described for ombrotrophic species.

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Literature Cited

Andrus, R.E. 1986. Some aspects of *Sphagnum* ecology. Canadian Journal of Botany **64**:416-426.

Barbour, M.G., Burk, J.H., and Pitts, W.D. 1987. Terrestrial plant ecology, 2nd edition. The Benjamin/Cummings Publishing Company Inc., Menlo Park, California.

Bragazza, L. 1997. *Sphagnum* niche diversification in two oligotrophic mires in the southern Alps of Italy. The Bryologist **100**:507-515.

Bragazza, L. and Gerdol, R. 1996. Response surfaces of plant species along water-table depth and pH gradients in a poor mire on the southern Alps (Italy). Annales Botanici Fennici **33**:11-20.

Braun-Blanquet, B. 1933. Phytosociological nomenclature. Ecology **14**:315-317.

Bray, J. R. and Curtis, J.T. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs **27**:325-349.

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Bugnon, J.-L., Rochefort, L., and Price, J.S. 1997. Field experiment of *Sphagnum* reintroduction on a dry abandoned peatland in Eastern Canada. Wetlands **17**:513-517.

Campeau, S. and Rochefort, L. 1996. *Sphagnum* regeneration on bare peat surfaces: field and greenhouse experiments. Journal of Applied Ecology **33**:599-608.

Carpenter, J.R. 1962. An ecological glossary. Hafner Publishing Company, New York.

Chapman, S.B. 1965. The ecology of Coom Rigg Moss, Northumberland. III. Some water relations of the bog system. Journal of Ecology **53**:371-384.

Chapin, F.S. III, Oechel, W.C., Van Cleve, K., and Lawrence, W. 1987. The role of mosses in the phosphorus cycling of an Alaskan black spruce forest. Oecologia **74**: 310-315.

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Cleavitt, N. 2001. Disentangling moss species limitations: the role of physiologically based substrate specificity for six species occurring on substrates with varying pH and percent organic matter. The Bryologist **104**:59-68.

Cleavitt, N. 2002. Relating rarity and phylogeny to the autecology of mosses: A comparative study of three rare-common species pairs in the Front Ranges of Alberta, Canada. Ph.D. Dissertation, University of Alberta, Edmonton, Alberta, Canada.

Clements, F.E. 1905. Research methods in ecology. University Publishing Company, Lincoln, Nebraska.

Clements, F.E. 1916. Plant succession: analysis of the development of vegetation. Carnegie Institution of Washington Publication **242**:1-512.

Clements, F.E. 1936. Nature and structure of the climax. Journal of Ecology **24**:252-284.

Clements, F.E., Weaver, J.E., and Hanson, H.C. 1929. Plant competition. Carnegie Institute of Washington, Washington, D.C.

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Clymo, R. S. 1970. The growth of *Sphagnum*: methods of measurement. Journal of Ecology **58**:13-49.

Clymo, R.S. and Reddaway, E.J.F. 1971. Productivity of *Sphagnum* (bog-moss) and peat accumulation. Hydrobiologia **12**:181-192.

Clymo, R.S. and Duckett, J.G. 1986. Regeneration of *Sphagnum*. New Phytologist **102**: 589-614.

Connell, J.H. and Slatyer, R.O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. The American Naturalist **111**:1119-1144.

Cottam, G. and Cutris, J.T. 1956. The use of distance measures in phytosociological sampling. Ecology **37**: 451-460.

Crum, H. 1972. The geographic origins of the mosses of North America's eastern deciduous forest. Journal of the Hattori Botanical Laboratory **35**:269-298.

Curtis, J. T. and McIntosh, R.P. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology **32**:476-498.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Damman, A.W.H. 1978. Distribution and movement of elements in ombrotrophic peat bogs. Oikos **30**:480-495.

Darwin, C. 1859. On the origin of the species by means of natural selection. J. Murray, London.

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

During, H.J. and van Tooren, B.F. 1987. Recent developments in bryophyte population ecology. Trends in Ecology and Evolution **2**:89-93.

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

Environment Canada. 1990. Canadian climate normals 1960-1990. Environment Canada, Ottawa.

Ferland, C. and Rochefort, L. 1997. Restoration techniques for *Sphagnum*-dominated peatlands. Canadian Journal of Botany **75**:1110-1118.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

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.

Fowbert, J.A. 1996. A experimental study of growth in relation to morphology and shoot water content in maritime Antarctic mosses. New Phytologist **82**:97-114.

Fowler, N.L. and Clay, K. 1995. Environmental heterogeneity, fungal parasitism and the demography of the grass *Stipa leucotricha*. Oecologia (Heidelb) **103**:55-62.

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

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

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Gause, G.F. 1934. The struggle for existence. Williams & Wilkins, Baltimore, Md.

Gerdol, R. 1995. Community and species-performance patterns along an alpine poor-rich mire gradient. Journal of Vegetation Science **6**: 175-182.

Gignac, L.D. 1992. Niche structure, resource partitioning, and species interactions of mire bryophytes relative to climatic and ecological gradients in western Canada. The Bryologist **95**:406-418.

Gignac, L.D. 1993. Distribution of *Sphagnum* species, communities, and habitats in relation to climate. Advances in Bryology **5**:187-222.

Gignac, L.D. and Vitt, D.H. 1990. Habitat limitations of *Sphagnum* along climatic, chemical and physical gradients in mires of Western Canada. The Bryologist **93**:7-22.

Gignac, L.D., Vitt, D.H., Zoltai, S.C. and Bayley, S.E. 1991. Bryophyte response surfaces along climatic, chemical and physical gradients in peatlands of Western Canada. Nova Hedwigia **53**:27-71.

Gleason, H.A. 1926. The individualistic concept of the plant association. Bulletin of the Torrey Botanical Club **53**:7-26.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Gleason, H.A. 1936. The individualistic concept of the plant association. American Midland Naturalist **21**:92-110.

Gleeson, S.K. and Tilman, D. 1994. Plant allocation, growth rate and successional status. Functional Ecology **8**:543-550.

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

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

Grinnell, J. 1904. The origin and distribution of the Chestnut-backed chickadee. The Auk **21**:364-382.

Grinnell, J. 1917. The niche-relationships of the California thrasher. The Auk **34**:427-433.

Grosvernier, P., Matthey, Y., and Buttler, A. 1997. Growth potential of three *Sphagnum* species in relation to water table level and peat properties with implications for their restoration in cut-over bogs. Journal of Applied Ecology **34**: 471-483.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

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

Hanslin, H.M. 1999. Seasonal dynamics of biomass increase and shoot elongation in five co-occurring boreal forest bryophytes. Journal of Bryology **21**:5-15.

Hayward, P.M. and Clymo, R.S. 1982. The ecology of *Sphagnum*. *In* Bryophyte ecology. *Edited by* A.J.E. Smith. Chapman and Hall, London, U.K. pp. 229-289.

Hayward, P.M. and Clymo, R.S. 1983. The growth of *Sphagnum*: experiments on, and simulation of, some effects of light flux and water-table depth. Journal of Ecology **71**:645-663.

Hennezel, F. and Coupal, B. 1972. Peatmoss- a natural absorbent for oil spills. The Canadian Mining and Metallurgical Bulletin **65**:51-53.

Huston, M. and Smith, T. 1987. Plant succession: life history and competition. The American Naturalist **130**:168-198.

Hutchinson, G.E. 1957. Concluding remarks. Cold Spring Harbour Symposia on Quantitative Biology **22**:415-427.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Hutchinson, G.E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? The American Naturalist **93**:145-159.

Jauhiainen, J., Vasander, H., and Silvola, J. 1994. Response of *Sphagnum fuscum* to N deposition and increased CO_2. Journal of Bryology **18**:83-95.

Jauhiainen, J., Silvola, J., Tolonen, K., and Vasander, H. 1997. Response of *Sphagnum fuscum* to water levels and CO_2 concentration. Journal of Bryology **19**:391-400.

Johansson, M.E. 1994. Life history differences between central and marginal populations of the clonal aquatic plant *Ranunculus lingua*: a reciprocal transplant experiment. Oikos **70**:65-72.

Johnson, R.H. 1910. Determinate evolution in the color pattern of the lady-beetles. Papers of the Station for Experimental Evolution No. 15. The Carnegie Institution of Washington, Washington, D.C.

Kenkel, N.C. 1988. Spectral analysis of hummock-hollow pattern in a weakly minerotrophic mire. Vegetatio **78**: 45-52.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Kimmerer, R.W. and Young, C.C. 1996. Effects of gap size and regeneration niche on species coexistence in bryophyte communities. Bulletin of the Torrey Botanical Club **123**:16-24.

Klinger, L.F. 1990. Global patterns in community succession. I. Bryophytes and forest decline. Memoirs of the Torrey Botanical Club **24**:1-50.

Klinger, L.F. 1996. The myth of the classic hydrosere model of bog succession. Arctic and Alpine Research **28**:1-9.

Kooijman, A.M. 1993. On the ecological amplitude of four mire bryophytes: a reciprocal transplant experiment. Lindbergia **18**: 19-24.

Kooijman, A.M. and Bakker, C. 1993. Causes of the replacement of *Scorpidium scorpioides* by *Calliergonella cuspidata* in eutrophicated rich fens. II. Experimental studies. Lindbergia **18**:123-130.

Kooijman, A.M. and Bakker, C. 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.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Lavoie, C. and Rochefort, L. 1996. The natural revegetation of a harvested peatland in southern Quebec: A spatial and dendroecological analysis. Ecoscience **3**:101-111.

Leverin, H.A. 1943. Peat moss or *Sphagnum* moss. Its use in agriculture industry and in the home. Canadian Department of Mines and Resources Publication **809**:1-10, Ottawa, Canada.

Lindholm, T. and Vasander, H. 1990. Production of eight species of *Sphagnum* at Surisuo mire, southern Finland. Annales Botanica Fennici **27**:145-157.

Li, Y., Glime, J.M., and Liao, C. 1992. Responses of two interacting *Sphagnum* species to water level. Journal of Bryology **17**:59-70.

Li, Y. and Vitt, D.H. 1994. The dynamics of moss establishment: temporal responses to nutrient gradients. The Bryologist **97**:357-364.

Li, Y. and Vitt, D.H. 1995. The dynamics of moss establishment: temporal responses to a moisture gradient. Journal of Bryology **18**:677-687.

Longton, R.E. 1984. The role of bryophytes in terrestrial ecosystems. Journal of the Hattori Botanical Laboratory **55**:147-163.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Longton, R.E. 1985. Reproductive biology and susceptibility to air pollution in *Pleurozium schreberi* (Brid.) Mitt. (Musci) with particular reference to Manitoba, Canada. Monographs in Systematic Botany from the Missouri Botanical Garden **11**:51-69.

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

Luken, J.O. 1985. Zonation of *Sphagnum* mosses: interactions among shoot growth, growth form and water balance. The Bryologist **88**:374-379.

Luken, J.O., Billings, W.D., and Peterson, K.M. 1985. Succession and biomass allocation as controlled by *Sphagnum* in an Alaskan peatland. Canadian Journal of Botany **63**:1500-1507.

Mankiewicz, P.S. 1987. The low pressure field porometer: a new, low cost technique for characterising external capillary water conduction in whole colonies of bryophytes and other small plants. The Bryologist **90**:253-262.

Marino, P.C. 1991. Competition between mosses (Splachnaceae) in patchy habitats. Journal of Ecology **79**: 1031-1046.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Miller, N.G. 1981. Bogs, bales and BTU's: a primer on peat. Horticulture **59**:38-45.

Montgomery, E.G. 1912. Competition in cereals. Nebraska Agriculture Experimental Station Bulletin **127**:3-22.

Mulligan, R.C. and Gignac, L.D. 2001 Bryophyte community structure in a boreal poor fen: reciprocal transplants. Canadian Journal of Botany **79**:404-411.

Nelson, M.A., Alspach, P.A., and Klinac, D. 1998. Effects of light and diaspore type on the regeneration and growth of two *Sphagnum* species collected from two New Zealand locations. Journal of Bryology **20**:17-25.

Newton, A.E. and Mishler, B.D. 1994. The evolutionary significance of asexual reproduction in mosses. Journal of the Hattori Botanical Laboratory **76**: 127-145.

Nichols, G.E. 1918. The *Sphagnum* moss and its use in surgical dressings. Memoirs of the New York Botanical Garden **19**:203-220.

Nicholson, B.J. and Gignac, L.D. 1995. Ecotope dimensions of peatland bryophyte indicator species along gradients in the Mackenzie River Basin, Canada. The Bryologist **98**:437-451.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Økland, R.H. 1990. A phytoecological study of the mire Northern Kisselbergmosen, SE Norway. III. Diversity and habitat niche relationships. Nordic Journal of Botany **10**:191-220.

Phillips, J. 1931. The biotic community. Journal of Ecology **19**:1-24.

Potter, J.A., Press, M.C., Callaghan, T.V., and Lee, J.A. 1995. Growth responses of *Polytrichum commune* and *Hylocomium splendens* to simulated environmental change in the sub-arctic. New Phytologist **131**:533-541.

Price, A.G., Dunham, K., Carleton, T., and Band, L. 1997. Variability of water fluxes through the black spruce (*Picea mariana*) canopy and feather moss (*Pleurozium schreberi*) carpet in the boreal forest of Northern Manitoba. Journal of Hydrology **196**: 310-323.

Proctor, M.C.F. 1982. Physiological ecology, water relations, light and temperature responses, carbon balance. *In* Bryophyte ecology. *Edited by* A.J.E. Smith. Chapman and Hall, London, U.K. pp. 333-381.

Rieley, J.O., Richards, P.W., and Bebbington, D.L. 1979. The ecological role of bryophytes in a north Wales woodland. Journal of Ecology **67**:497-527.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Rincon, E. 1988. Effect of initial shoot size on growth rates of five British grassland bryophytes. The Bryologist **91**:219-222.

Rincon, E. and Grime, J.P. 1989. An analysis of seasonal patterns of bryophyte growth in a natural habitat. Journal of Ecology **77**:447-455.

Russell, S. 1984. Growth measurement in bryophytes: a case study. Journal of the Hattori Botanical Laboratory **56**:147-157.

Russell, S. 1988. Measurement of bryophyte growth 1. Biomass (harvest) techniques. *In* Methods in Bryology. *Edited by* J.M. Glime. Hattori Botanical Laboratory, Nichinan. pp. 249-257.

Rydin, H. 1985. Effect of water level on desiccation of *Sphagnum* in relation to surrounding Sphagna. Oikos **45**:374-379.

Rydin, H. 1986. Competition and niche separation in *Sphagnum*. Canadian Journal of Botany **64**:1817-1824.

Rydin, H. 1987. Microdistribution of *Sphagnum* species in relation to physical environment and competition. Symposia Biologica Hungarica **35**:295-304.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Rydin, H. 1993a. Mechanisms of interactions among *Sphagnum* species along water-level gradients. Advances in Bryology **5**:153-185.

Rydin, H. 1993b. Interspecific competition between *Sphagnum* mosses on a raised bog. Oikos **66**:413-423.

Rydin, H. 1995. Effects of density and water level on recruitment, mortality and shoot size in *Sphagnum* populations. Journal of Bryology **18**: 439-453.

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

Rydin, H. 1997b. Competition between *Sphagnum* species under controlled conditions. The Bryologist **100**:302-307.

Rydin, H. and McDonald, A.J.S. 1985. Tolerance of *Sphagnum* to water level. Journal of Bryology **13**:571-578.

Santelmann, M.V. 1991. Influences on the distribution of *Carex exilis*: an experimental approach. Ecology **72**:2025-2037.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Schipperges. B. and Rydin. H. 1998. Response of photosynthesis of *Sphagnum* species from contrasting microhabitats to tissue water content and repeated desiccation. New Phytologist **140**:677-684.

Shelford. V.E. 1932. Basic principles of classification. Ecology **13**:105-120.

Silvertown. J. and Law. R. 1987. Do plants need niches? Some recent developments in plant community ecology. Trends in Ecology and Evolution **2**:24-26.

Skre. O.. Oechel. W.C.. and Miller. P.M. 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. 1982. Bryophytes in relation to ecological niche theory. Journal of the Hattori Botanical Laboratory **52**:199-217.

Slack. N.G. 1990. Bryophytes and ecological niche theory. Botanical Journal of the Linnean Society **104**:187-213.

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

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Shmida, A. 1984. Whittaker's plant diversity sampling method. Israel Journal of Botany **33**:41-46.

Streever, W.J. and Genders, A.J. 1997. Effect of improved tidal flushing and competitive interactions at the boundary between salt marsh and pasture. Estuaries **20**:807-818.

Tansley, A.G. 1917. On competition between *Galium saxatile* L. (*G. hercynicum* Weig.) and *Galium sylvestre* poll. (*G. asperum* Schreb.) on different types of soil. Journal of Ecology **5**:173-179.

Tansley, A.G. 1935. The use and abuse of vegetational concepts and terms. Ecology **16**:284-307.

Tansley, A.G. 1939. The plant community and the ecosystem. Journal of Ecology **27**:513-530.

Terasmae, J. 1977. Postglacial history of Canadian muskeg. *In* Muskeg and the Northern Environment in Canada. *Edited by* N.W. Radforth and C.O. Brawner. University of Toronto Press, Toronto, Canada. pp. 9-29.

Tilman, D. 1985. The resource-ratio hypothesis of plant succession. The American Naturalist **125**:827-851.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Tilman, D. 1999. Diversity by default. Science **283**:495-496.

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

van der Molen, P.C., Schalkoort, M., and Smit, R. 1992. Hummock-hollow complexes on Clara bog, Co. Offaly, Ireland. *In* Hummock-hollow complexes on Irish raised bogs a palaeo/actuo ecological approach of environmental and climate change. *Edited by* P.C. van der Molen, University of Amsterdam, Amsterdam, The Netherlands. pp. 117-173.

Watson, M.A. 1981. Patterns of microhabitat occupation of six closely related species of mosses along a complex altitudinal gradient. Ecology **62**:1067-1078.

Watt, A.S. 1947. Pattern and process in the plant community. Journal of Ecology **35**:1-22.

Whittaker, R.H. 1962. Classification of natural communities. Botanical Review **28**:1-239.

Whittaker, R.H. 1967. Gradient analysis of vegetation. Biological Reviews **42**:207-264.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Wielgolaski, F.E., Bliss, L.C., Svoboda, J., and Doyle, G. 1981. Primary production of tundra. *In* Tundra ecosystems. *Edited by* L.C. Bliss, O.W. Heal, and Moore, D. Cambridge University Press, Cambridge, U.K. pp. 187-225.

Zechmeister, H.G. 1995. Growth rates of five pleurocarpous moss species under various climatic conditions. Journal of Bryology **18**:455-468.

Zoltai, S.C. 1988. Wetland environments and classification. *In* Wetlands of Canada. *Co-ordinated by* C.D.A. Rubec. Polyscience, Montreal, P.Q. Canada. pp. 1-26

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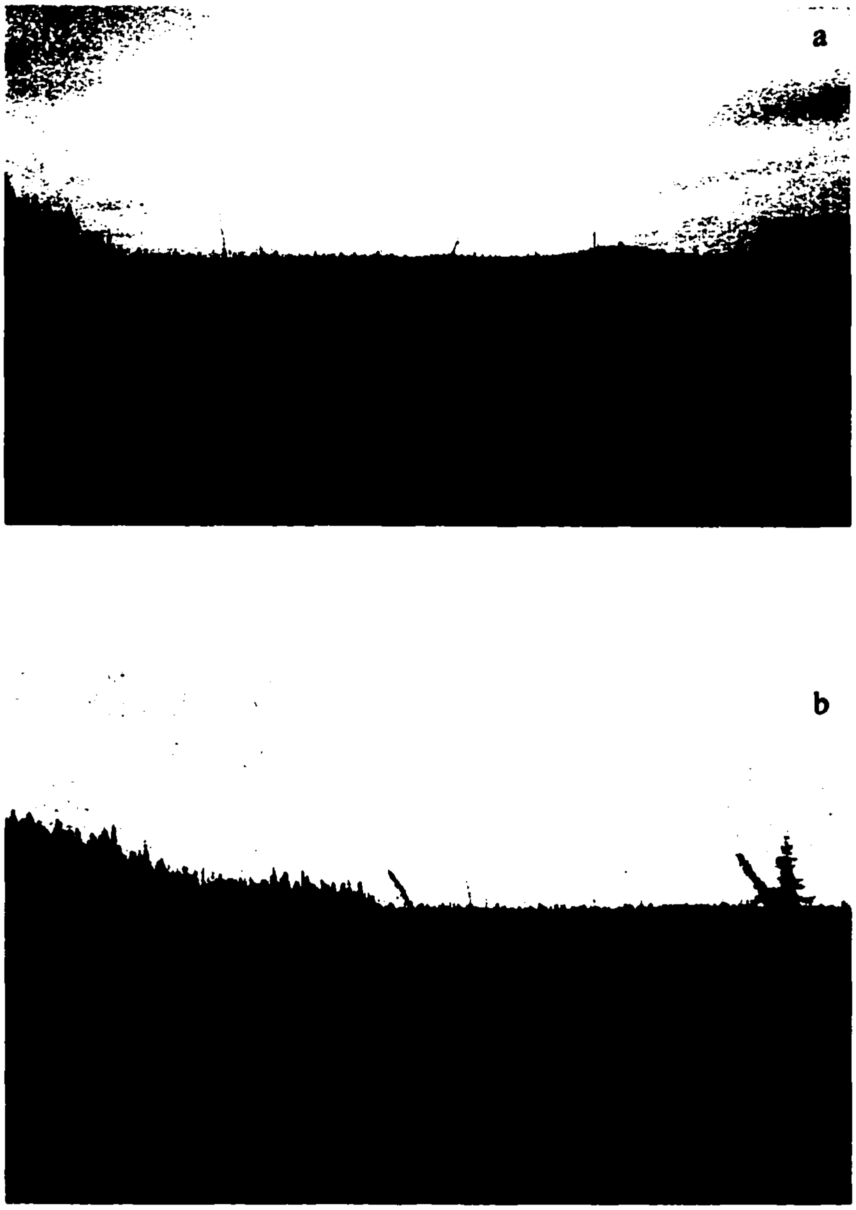

Figs. 1a & b- The Mariana Lake peatland complex showing the open nature of the peatland with *Carex* spp., *Eriophorum* spp. and a few young *Picea mariana*.

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Fig. 2- Map showing the location of Mariana Lake (★) in the province of Alberta. Canada.

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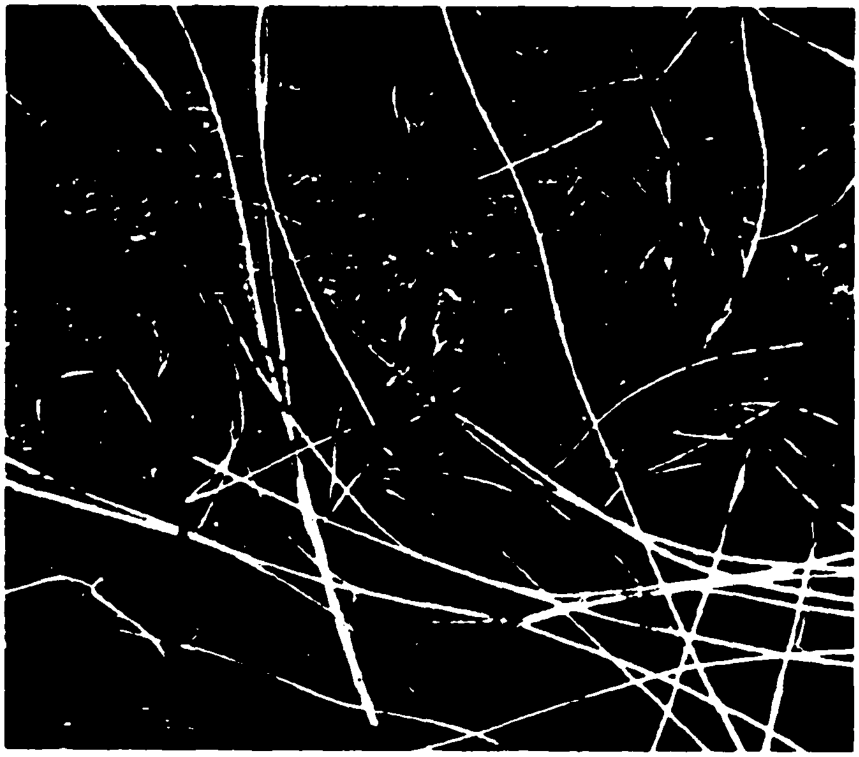

Fig. 1-3 The poor fen area of the peatland complex with *Sphagnum angustifolium*, Ericaceous shrubs and *Carex* spp.

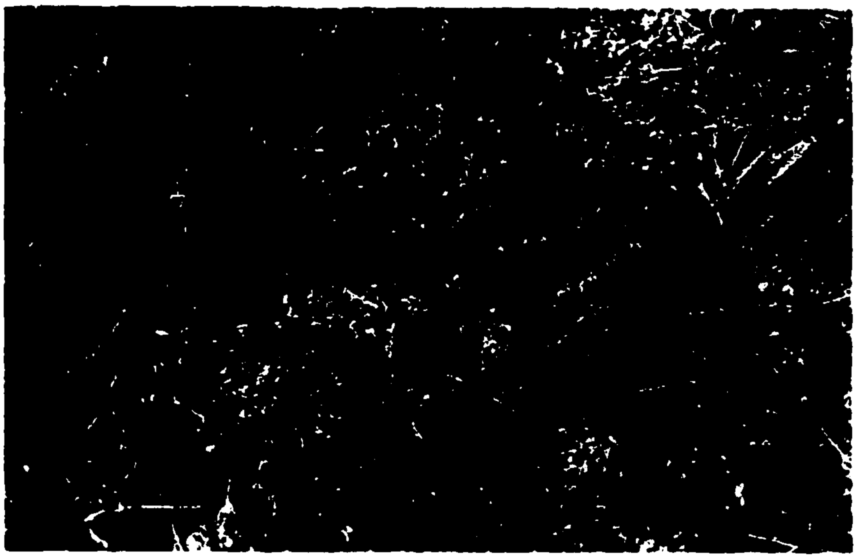

Fig. 1-4 The ombrotrophic *Sphagnum fuscum* area with Ericaceous shrubs. Note some shrubs were removed during weeding, so shrub cover is atypical for this area.

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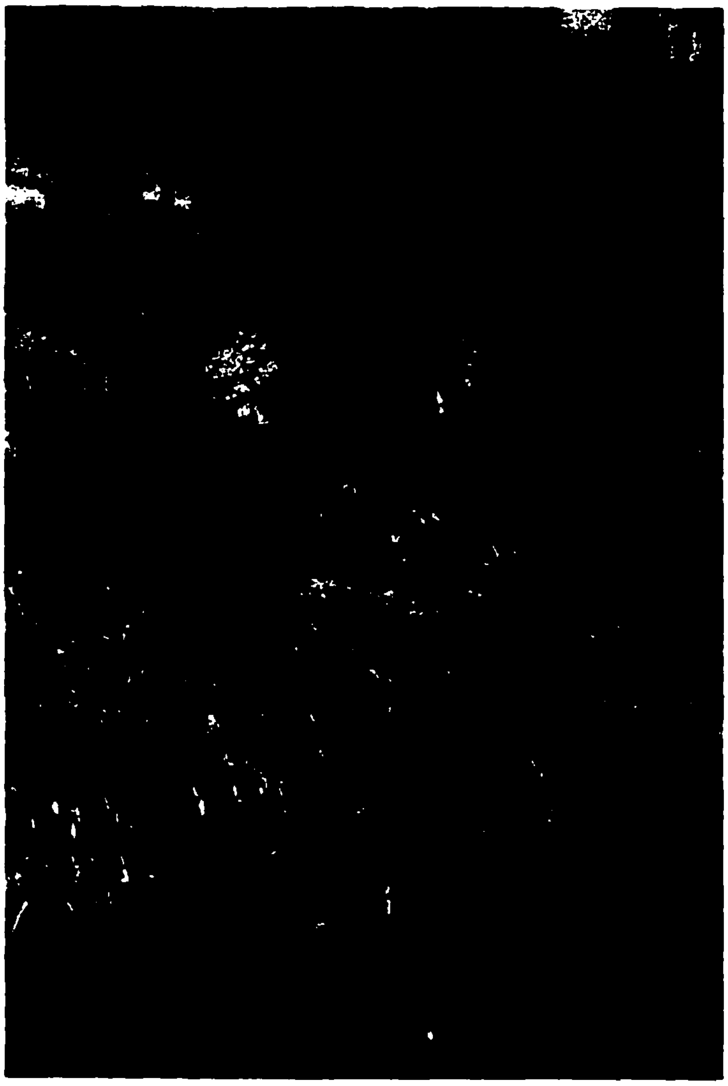

Fig. 1-5 **The bog island in the Mariana Lake peatland complex showing stunted *Picea mariana* and *Sphagnum fuscum*.**

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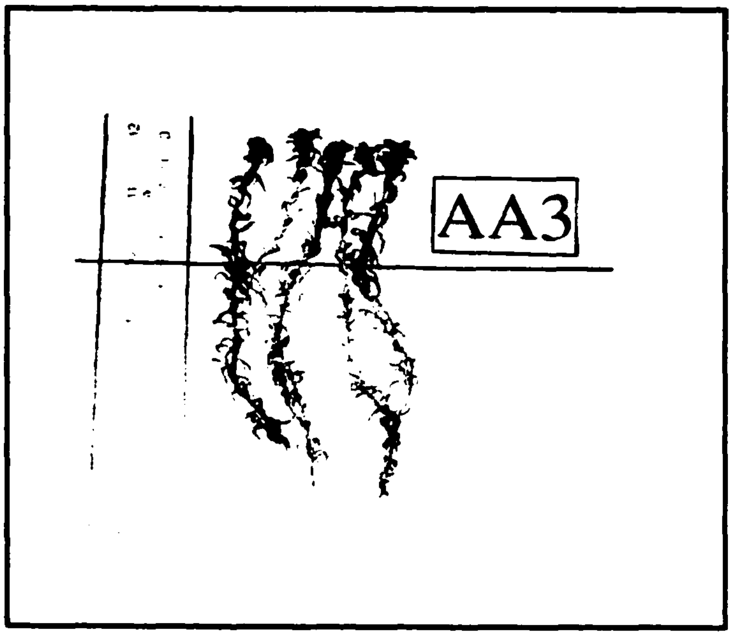

Fig. 1-6 *Sphagnum angustifolium* gametophytes (that were reciprocally transplanted into *S. angustifolium*) illustrate the slender, delicate nature of these plants. The red line is at 5 cm.

Fig. 1-7 *Sphagnum magellanicum* gametophytes are large, robust and red.

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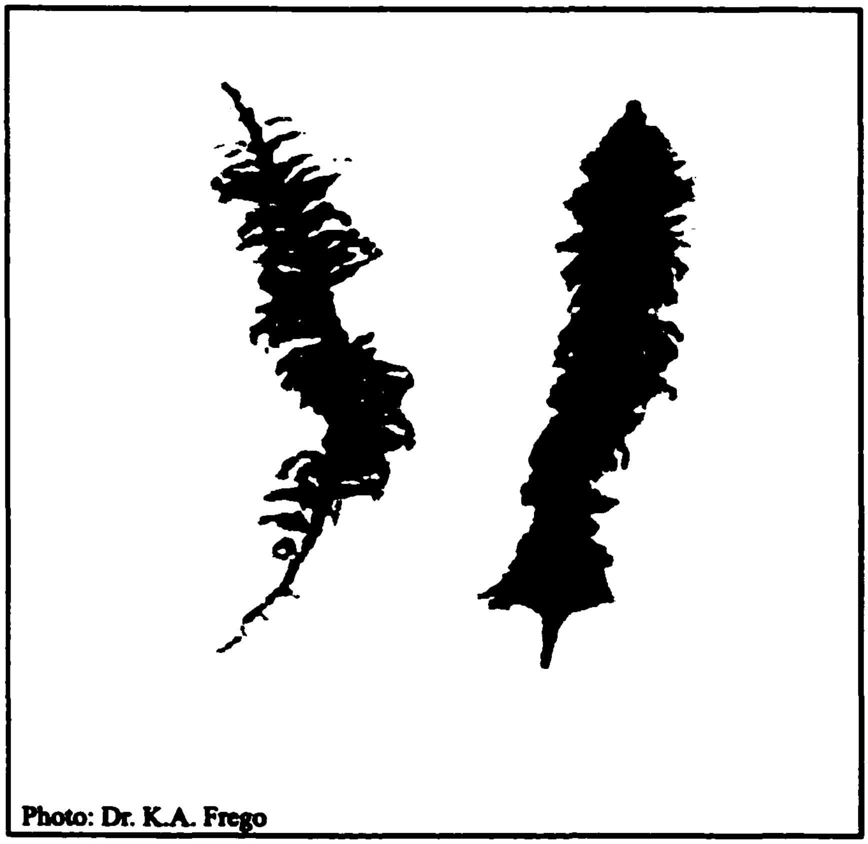

Fig. 1-8 *Pleurozium schreberi* (left) is a pleurocarpous feather moss with a distinctive red stem. *Ptilium crista-castrensis* (right)is also a pleurocarpous feather moss with strongly falcate-secund leaves.

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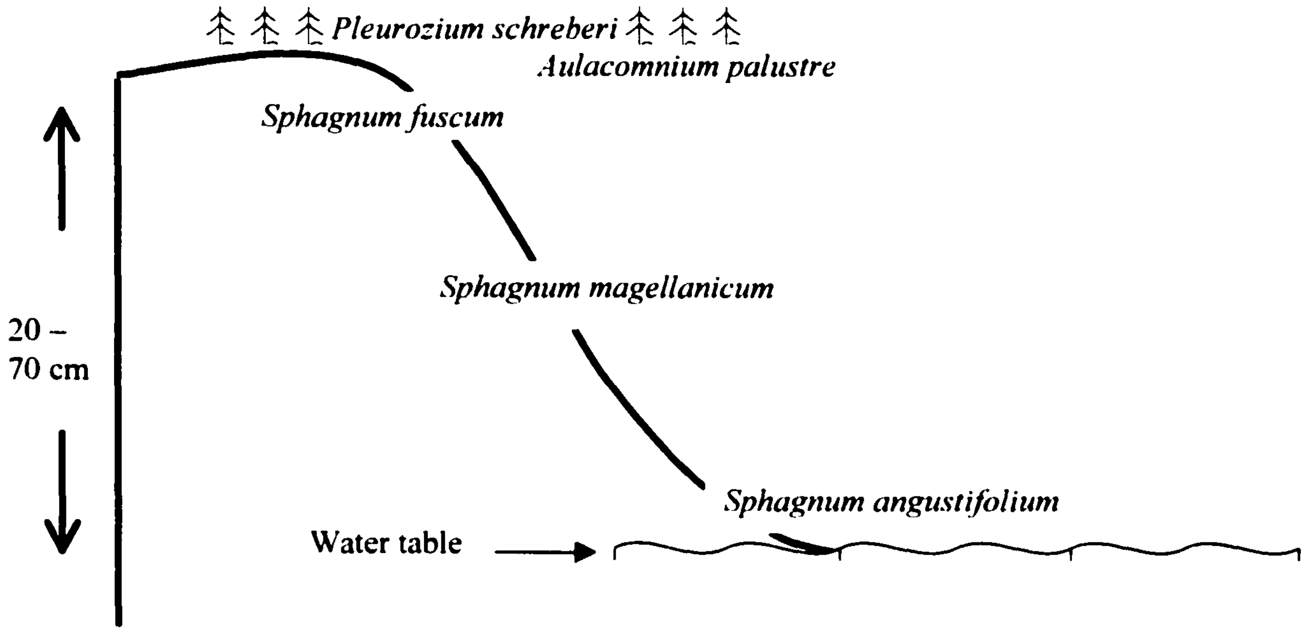

Fig. 1-9 Simplified representation of the distribution of the study species along the hollow-hummock gradient.

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Chapter 2- Bryophyte community structure in a boreal poor fen: reciprocal transplants

Introduction

Modern ecological theory defines the fundamental niche as an n-dimensional hypervolume inclusive of all abiotic factors (light, moisture, temperature etc.) within which a particular species may potentially exist in the absence of biotic influences (Hutchinson 1957). In reality, the fundamental niche is contracted into a smaller, realised niche due to factors such as competition and predation. The realised niche is usually quantified as niche breadth or overlap and there exist several formulae for this purpose (see Glime *et al.* 1987 for a review of techniques used with bryophytes). The fundamental niche is not usually quantified (see, however, Rydin 1987; Wang 1995) but instead described, since the formulae for niche breadth and overlap rely on distribution and abundance numbers not obtainable with a hypothetical or assumed construct (Malanson 1997).

The only way to accurately describe the fundamental niche of a species in the field is experimentally, by transplanting it into habitats in which it does not typically grow. Vascular plant reciprocal transplant investigations have described

A version of this chapter has been published. Mulligan, R.C. and Gignac, L.D. 2001. Bryophyte community structure in a boreal poor fen: reciprocal transplants. Canadian Journal of Botany 79:404-411.

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ecotype adaptation in *Carex exilis* (Santelmann 1991), life history differences in *Ranunculus lingua* (Johansson 1994), competition between tidal and pasture grasses (Streever and Genders 1997), and demography in *Stipa leucotricha* (Fowler and Clay 1995). Bryophyte transplant studies are not as common as other growth investigations (Rydin 1997; Slack 1997). Despite this, several transplant investigations have focussed on niche relationships. For example, Frego and Carleton (1995) used reciprocal transplants to eliminate habitat partitioning as the driving force behind the spatial pattern of four boreal forest species. Kooijman (1993) documented the importance of habitat preference in an examination of species replacement in Dutch rich fens. Further, the results of a long term examination of competition among ombrotrophic Sphagna by Rydin (1986, 1993a) suggest that *Sphagnum* species may be similar in competitive ability. This supports the theory that symmetrical competition occurs between closely related taxa (Keddy 1989), and questions the applicability of the competitive exclusion principle to mature bryophyte populations (Slack 1990, 1997).

Peatland bryophyte species distribution is controlled by four main gradients: wet to dry, ombrotrophic to minerotrophic, mire margin to mire expanse, and open to shaded (Sjörs 1950; Gignac and Vitt 1990). Depth to water table is often recognised as the most important gradient within individual peatland sites (Hayward and Clymo 1983; Rydin 1987; Gignac *et al.* 1991), as it exerts a major influence on water chemistry and decomposition dynamics (Damman 1978; Rydin 1993a). Hummock species inhabit the areas farthest from the water table,

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while hollow species occur at the base of the hummock in areas where the water table is very close to the surface. Past investigations have indicated that hollow Sphagna are excluded from hummock habitats in bogs due to their inferior ability to transport and hold water (Clymo and Hayward 1982; Rydin 1985, 1993a). Hollow habitats have been demonstrated to be within the fundamental niches of hummock species in bog habitats (Clymo and Reddaway 1971; Hayward and Clymo 1983; Rydin and McDonald 1985; Rydin 1986, 1987), but the reasons behind the exclusion of those species from hollow habitats are not yet fully understood (Rydin 1993a).

While these investigations have resulted in important advances in our understanding of peatland bryophyte community structure, most have occurred in ombrotrophic situations with *Sphagnum fuscum* (Schimp.) Klinggr., *S. rubellum* Wils., *S. balticum* (Russ.) C. Jens., and *S. tenellum* (Brid.) Brid. (Clymo and Reddaway 1971; Rydin 1985, 1986, 1993b). Therefore, the applicability of these generalisations to poor fen peatlands is unknown and the potential ecological amplitude of poor fen bryophytes remains unexplored.

In this study, reciprocal transplants were used to describe the tolerance ranges and habitat limitations of three Sphagna and one feathermoss, *Pleurozium schreberi* (Brid.) Mitt., in a poor fen with respect to depth to water table, surface water chemistry, and shade. These tolerance ranges approximate the fundamental niches of these species within this peatland. The Sphagna are *Sphagnum angustifolium* (C. Jens. ex Russ.) (Section *Cuspidata*), *S. magellanicum* Brid. (Section *Sphagnum*), and *S. fuscum* (Section *Acutifolia*). This is the first

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investigation to experimentally examine the niche dimensions of both a feather moss and *Sphagnum* species, particularly *S. angustifolium* in a poor fen habitat.

The objectives of this study are a) to determine whether the study species can grow in each others' habitats, b) to describe the tolerance ranges of the study species with respect to depth to water table, surface water chemistry and shade, and c) to explain the distribution of these mosses in the poor fen.

Materials and Methods

Study site and species

The study site is a continental boreal peatland near Mariana Lake, in northeastern Alberta (55° 55' N, 111° 58' W), Canada. The climate is boreal cold with a mean annual temperature of 0.2°C and mean annual precipitation of 464.7 mm recorded at the nearest weather station located approximately 90 km north in Fort McMurray (Environment Canada 1990). The peatland is part of a mire complex with three distinct physiognomic sections: a poor fen area with a ground layer dominated by *Sphagnum angustifolium* and *Carex* spp., a small, non-wooded ombrotrophic area dominated by *S. fuscum* and ericaceous shrubs, and wooded bog islands characterised by stunted *Picea mariana* (Mill.) BSP, *S. fuscum*, *Pleurozium schreberi*, *S. angustifolium* and such angiosperms as *Rubus*

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chamaemorus L., *Rhododendron groenlandicum* (Oeder) Kron & Judd, and *Smilacina trifolia* (L.) Desf.

Sphagnum angustifolium is a fast growing hollow species that exhibits very wide niche breadth in acidic, wet peatlands throughout western Canada (Gignac 1993). Depth to water table may limit the distribution of *Sphagnum angustifolium*, while climate and surface water chemistry are considered non-limiting factors (Gignac *et al.* 1991). In this peatland, *Sphagnum angustifolium* occurs commonly in the wooded bog islands, and sporadically, as isolated shoots, in the non-wooded (*S. fuscum*) area. *Sphagnum magellanicum* is a widespread poor fen species typically found on the sides of large hummocks in poor fens and bogs. *Sphagnum magellanicum* exhibits great ecological amplitude particularly with respect to water table and surface water chemistry gradients (Gignac 1992; Bragazza 1997). In this peatland, *Sphagnum magellanicum* is found in all areas, but it is most abundant in the poor fen and wooded habitats. *Sphagnum fuscum* is a widespread species with very broad ecological amplitude throughout western Canada in ombrotrophic, poor fen, and moderate-rich fen peatlands (Gignac 1993). *Sphagnum fuscum* forms its own substrate in the form of densely packed hummocks, which are separated from the water table by 20 to 70 cm (Nicholson and Gignac 1995). In this peatland, *Sphagnum fuscum* occurs commonly in the wooded habitat, and sporadically on isolated hummocks in the poor fen section. *Pleurozium schreberi* is a common boreal forest moss (Longton and Greene 1979; Longton 1985) that also forms a potentially important, yet often disregarded, component of the bryophyte vegetation in many peatlands. This

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species exhibits wide niche breadth in western Canadian peatlands with a range extending from bogs to moderate-rich fens (Gignac 1992). In peatland situations, *Pleurozium schreberi* reaches its maximum abundance at 30 cm above the water table where it usually occurs above the Sphagna (Gignac 1992). In this peatland, *Pleurozium schreberi* is found exclusively in the wooded habitat.

The distribution of the study species along the wet to dry gradient (from wet to dry) in this peatland is *Sphagnum angustifolium*, *S. magellanicum*, *S. fuscum*, and *Pleurozium schreberi*. Nomenclature follows Ireland *et al.* (1987) for bryophytes and Kron and Judd (1990) for *Rhododendron groenlandicum*. Nomenclature for all other vascular plants follows Moss (1983).

Water chemistry and environmental variables

Electrical conductivity and pH were measured with portable meters once at each transplant location at the end of the experiment. In areas where 2 to 4 transplants occurred in the immediate vicinity (within 1 m) of one another, one measurement for each parameter was taken. Conductivity was corrected for hydrogen ions and temperature (20°C) following Sjörs (1950). Water samples were taken four or five times per habitat at the end of the study, collected in small polyethylene acid-washed bottles (3% HCl), filtered through #42 Whatman filter paper, and acidified with 1 ml HCl in 24 ml water. Mineral element concentrations (Mg^{++}, Ca^{++}, P, Na^{+}, and K^{+}) were measured with argon plasma spectrophotometry. Depth to water table was measured from small manually dug holes or natural depressions at each transplant location at the end of the experiment. Shade was

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assessed visually as the percent cover of overstory shrubs and trees at diameter at breast height and recorded once per transplant location at the end of the experiment. Shading by other vascular plants was considered inconsequential as transplant locations with minimal herbaceous cover were selected. The collection of environmental data only at the end of the experiment could be an avenue for criticism as some variables (e.g. depth to water table) fluctuate seasonally or temporally. However, this was deemed acceptable since the authors have conducted research in this peatland for over 5 years and are very familiar with "typical' values.

Transplant experiment

In June 1998, 25 transplant plugs 17 cm in diameter and approximately 20 cm in length were removed from homogeneous areas representing typical habitats for each of the four species. The plugs were cut from the moss carpet using a metal stovepipe. The central 25 shoots of each plug (a "shoot bundle") were extracted, cut to 5 cm in length, soaked in deionized water for 20 minutes and rotated 20 times in a standard plastic salad spinner with an inner diameter of 21 cm and a 3:1 gear ratio. The shoots were spun at a speed of 190 rotations per minute to generate a force of approximately 40 times gravity. The salad spinner acts as a centrifuge to permit starting from a standardised water content. Each shoot bundle was weighed on a Mettler PE 3600 scale and the weight recorded as moist weight. The bundles were tied with orange nylon thread and reinserted into the transplant plugs. The transplant plugs containing the shoot bundles were

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randomly inserted into the holes created by the stovepipe. The transplants were not concentrated in plots in order to reduce potential losses from ungulate trampling. Some transplants were grouped together in areas where large expanses of suitable habitat were available.

Each species was transplanted into its own habitat (controls) and the three habitats of the other species. Each treatment was replicated five times for a total of 100 transplants. In areas subjected to periodic flooding (e.g., *Sphagnum angustifolium* habitat) thin u-shaped metal rods were inserted through the transplant plug about 10 cm down to prevent them from floating away.

In June 1999, the transplant plugs were harvested and carefully teased apart. The centre shoot bundles were removed, air dried for 3 days and the dried at 30°C for 24 hours. The shoots were weighed and the weight recorded as final dry weight. Final dry weight was subtracted from initial predicted dry weight to give change in dry weight reported per 25-shoot bundle. Initial dry weight was predicted from initial moist weight (Mankiewicz 1987) using regression equations as in Frego and Carleton (1995), and van der Hoeven *et al.* (1998). The shoots were rehydrated and measured to assess change in shoot length which was calculated as total final length per 25 shoot bundle minus total initial length per bundle (25 shoots × 5 cm = 125 cm per bundle). Dichotomous forking of individual Sphagna was measured from the capitulum of the new shoot to the base where it arose from the parent plant. Forking was recorded separately and included in total final length.

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Health of the transplanted shoots

The health of the transplanted shoots was assessed visually on a scale of 1-5 based on appearance (Table 2-1). Shoots that were in excellent health and exhibited no morphological abnormalities were rated 5, while completely black shoots that appeared dead were rated 1. Shoot colour (interpreted to be chlorosis in the case of degradation), shoot disintegration, and stress-induced morphological changes such as branch loss and etiolation were the criteria used to determine the health ratings.

Tolerance Ranges

Tolerance ranges of the species for depth to water, shade, pH, K_{corr}, Ca^{++}, and Mg^{++} were determined as follows. For the purposes of this study we define tolerance as the ability of the plant to exhibit good growth as outlined in Table 2-1. A species was defined as tolerating a habitat if a) its mean health rating was $\geq$ 3 and b) its mean growth in length and weight in that habitat were not significantly different from its mean growth in length and weight in its own habitat. By default, a species' tolerance range also includes its own habitat.

Statistical Analyses

Statistical analyses were conducted with SAS statistical packages (SAS Institute 1989). All growth data were subjected to a one way Analysis of Variance (ANOVA) using Procedure (Proc.) GLM (general linear model). Tukey's test was used for post hoc mean separations. The environmental variables did not

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fully meet ANOVA assumptions and were tested with a nonparametric ANOVA analogue, the Kruskal-Wallis test and Dunn's mean separation test (Zar 1996) using Excel (Microsoft 1997). Stepwise regressions were used to determine the relationship between the environmental variables and the changes in growth that occurred.

Results

Water chemistry and environmental variables

Magnesium, calcium, phosphorus, potassium, and sodium concentrations did not differ significantly among habitats (Table 2-2). Mean pH was significantly higher in the *Sphagnum angustifolium* habitat when compared to the *S. magellanicum* habitat (Table 2-2). In the remaining habitats, mean pH ranged from 4.10 in the *Sphagnum fuscum* area to 4.13 in the *Pleurozium schreberi* area. Mean corrected conductivity (K_{corr}), which ranged from 13.2 *µs*/cm in the *Sphagnum fuscum* area to 17.3 µs/cm in the *Pleurozium schreberi* habitat (Table 2-2), did not differ significantly. Mean depth to water table did not differ significantly between the species in the two wet habitats (*Sphagnum angustifolium* compared to *S. magellanicum*) or the two dry habitats (*S. fuscum* compared to *Pleurozium schreberi*) (Table 2-2). Mean depth to water table was significantly higher in the *Sphagnum fuscum* and *Pleurozium schreberi* habitats when they were compared to the *S. angustifolium* and *S. magellanicum* areas.

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Mean percent cover (shade) was significantly higher in the dry habitats compared with the wet areas (Table 2-2).

Growth of the transplanted shoots

Sphagnum angustifolium grew as well in the *S. magellanicum* habitat as in its own (Fig. 2-1). Growth in length and weight of *Sphagnum angustifolium* was significantly affected by depth to the water table (Table 2-3). Growth was significantly greater in the wetter habitats (*Sphagnum angustifolium* and *S. magellanicum*) than in the drier ones (*S. fuscum* and *Pleurozium schreberi*) (Fig. 2-1).

Growth in length and weight of *Sphagnum magellanicum* (Fig. 2-1) was greatest in the *S. angustifolium* habitat, while its performance in its own habitat was intermediate. Depth to water table had a significant influence on growth in both weight and length of *Sphagnum magellanicum* (Table 2-3). Growth in length and weight of *Sphagnum magellanicum* was significantly lower in the *Pleurozium schreberi* habitat.

There was no significant difference for growth in length or weight of *Sphagnum fuscum* (Fig. 2-1) in any of the four habitats. The growth of *Sphagnum fuscum* was not significantly affected by any of the variables examined (Table 2-3).

Growth in length of *Pleurozium schreberi* (Fig. 2-1) was greatest in its own habitat, but growth in weight was greatest in the *Sphagnum angustifolium* habitat. Growth of *Pleurozium schreberi* was significantly lower in the *Sphagnum fuscum*

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habitat. Depth to water table had a significant influence on growth in weight of *Pleurozium schreberi* (Table 2-3).

Health of the transplanted shoots

The transplanted shoots were healthiest in their own habitats (Table 2-4). The health of some species in certain habitats was particularly poor. For example, the health of *Pleurozium schreberi* in the *Sphagnum angustifolium* area was rated as 2. *Sphagnum angustifolium* performed only slightly better (2.1) in the *Pleurozium schreberi* (Fig. 2-2a) and *S. fuscum* (Fig. 2-2b) habitats. In general, the Sphagna were not healthy in the *Pleurozium schreberi* habitat.

Tolerance Ranges

Fig. 2-3 illustrates tolerance ranges of the study species within this peatland. Broad overlap between all Sphagna is particularly evident with respect to K_{corr}, Ca^{++}, pH, and Mg^{++} gradients. Depth to water table and shade show some partitioning since *Sphagnum angustifolium* is tolerant of a much narrower range than *S. fuscum* or *S. magellanicum*. The restricted ecological amplitude exhibited by *Pleurozium schreberi* is reflected in its tolerance ranges, which are particularly narrow for depth to water table, pH, and Mg^{++}.

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Discussion

In this peatland, differences in water chemistry among habitats were minimal (Table 2-2) and did not have a significant influence on growth of the transplanted mosses. The surface water chemistry of bogs and poor fens is typically low in concentrations of important mineral elements (e.g. Ca^{++}, Mg^{++}, and K^{+}) and nutrients (e.g. N and P) (Pakarinen and Tolonen 1977; Damman 1978; Gignac 1989). Mire surface water chemistry can limit species distribution with pH, conductivity, and calcium being most important (Gignac 1989).

As the n-dimensional nature of Hutchinson's niche suggests, it is impossible to measure every potential niche factor and it is possible (but unlikely) that an unmeasured niche factor may play a role in the bryophyte community structure in this peatland. Therefore, for the purposes of this study we define habitat limitation as: restricted by the tolerance range of the adult gametophyte for the nine variables measured in this peatland.

Depth to water table is the only measured environmental variable significantly related to growth of the study species (Table 2-3). The potential distribution of *Sphagnum angustifolium* is limited to areas with lower water tables such as the *S. magellanicum* habitat. Despite these limitations, the potential ecological amplitude of *Sphagnum angustifolium* in this peatland is

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quite broad (Fig. 2-3). Therefore, habitat limitation is not the sole factor that has structured its distribution.

The upper limit of *Sphagnum angustifolium* and other species in Section *Cuspidata* on the water table gradient is set by a combination of physiological intolerance to desiccation (van der Molen *et al.* 1992; Rydin 1993a; Schipperges and Rydin 1998) and absence of morphological specialisation for water retention. These mosses lack the well developed pendent branches and dense canopies that enable hummock Sphagna to retain and transport water efficiently (Clymo and Hayward 1982; Jauhiainen *et al.* 1997; Slack 1997). The desiccation exhibited by *Sphagnum angustifolium* in the hummock habitats in this peatland (Fig. 2-2) indicates that the physiological intolerance of hollow species to drier conditions which has been documented in ombrotrophic peatlands, is also applicable in poor fens.

Sphagnum magellanicum is partially limited by habitat, in that it cannot survive in the driest (*Pleurozium schreberi*) habitat. *Sphagnum magellanicum* shoots transplanted into this habitat appeared desiccated (Fig. 2-4) and were missing branches and capitula. Despite these limitations, *Sphagnum magellanicum* exhibits wide tolerance (Fig. 2-3) within *S. angustifolium* and *S. fuscum* habitats and its present distribution in this peatland is not wholly the result of habitat restrictions.

In this peatland, the differences in abiotic factors among the habitats do not significantly affect the growth of *Sphagnum fuscum* (Table 2-3). Further, the ability of this species to live in all sampled habitats (Figs. 2-1, 2-5, 2-6) is

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reflected in its very broad tolerance ranges for all variables examined in this study (Fig. 2-3). The distribution of *Sphagnum fuscum* cannot be explained by habitat restriction; it must be the result of other factors. For *Sphagnum fuscum* to occupy hollow habitats (without experimental manipulation), it would have to invade a mature moss canopy of either a slope species (*S. magellanicum* in this peatland) or a hollow species (*S. angustifolium* in this peatland). Therefore, either adult *Sphagnum fuscum* plants cannot compete with *S. magellanicum* and/or *S. angustifolium*, or the vegetative diaspores of *S. fuscum* cannot become established amongst the mature canopies of the other two Sphagna. Another possibility, that *Sphagnum fuscum* could establish in small gaps but not persist as adult plants, is unlikely because of its limited ability to regenerate from asexual diaspores (Li and Vitt 1995; Mulligan unpublished data). Further, the ability of *Sphagnum fuscum* to tolerate all habitats sampled in this peatland indicates that its broad tolerance to water level, documented in ombrotrophic peatlands and growth chamber studies (Clymo and Reddaway 1971; Rydin and McDonald 1985; Rydin 1986, 1993a,b; Grosvernier *et al.* 1997; Jauhiainen *et al.* 1997), is also exhibited in poor fen situations. Thus, the supposition that hollow habitats are within the fundamental niches of bog hummock species may be extended to include poor fens.

Pleurozium schreberi is the species most restricted by habitat in this study, as its tolerance range (Fig. 2-3) includes only its own current habitat. The apparent success of *Pleurozium schreberi* in the *Sphagnum angustifolium* habitat (Fig. 2-1) is misleading. Despite a mean increase in weight, which was greater than that in

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its own habitat (Fig. 2-1), the *Pleurozium schreberi* shoots were brown and black with small amounts of green remaining only at the shoot apices. Chlorophyll loss and reduced photosynthesis have been reported in *Pleurozium schreberi* grown under adverse conditions of combined increased light intensity and high water tables (Busby *et al.* 1978; Longton and Greene 1979). The growth of *Pleurozium schreberi* in this habitat was likely a stress response, although it is interesting that only weight was affected.

It may be necessary to view the results of a short-term investigation such as this one with caution, as short-term responses in bryophyte transplant investigations have been reversed over the long term (e.g. Rydin 1993a). Although the growth of *Pleurozium schreberi* in the *Sphagnum angustifolium* habitat was unexpected, its condition was such that its survival was extremely unlikely. Though a longer investigation may have clarified other trends, the consistency of the remaining results with longer term investigations in ombrotrophic situations strongly suggests that the short-term trends exhibited are analogous with long term patterns.

In conclusion, this investigation documents that generalisations regarding the behaviour of hummock and hollow species, particularly with respect to the depth to water gradient, are similar in bogs and poor fens. The presence of water flow and different minerotrophic status in poor fens do not affect the behaviour of the species. These generalisations include the exclusion of hollow species from hummock habitats, attributed to their inferior water retention and transport

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capacity, and the inclusion of hollow habitats within the fundamental niches of hummock specie

Within the range of environmental conditions in the fen, depth to water table was the most important factor regulating species distribution as it exerted a significant influence on the growth of all species investigated, except *Sphagnum fuscum*. *Pleurozium schreberi* exhibited the narrowest fundamental niche, indicating that its present distribution is partially the result of habitat limitation, i.e. *Pleurozium schreberi* is restricted to its present habitats because it cannot grow in the other habitats. The fundamental niches of *Sphagnum angustifolium* and *S. magellanicum* are quite broad, and their distributions in this peatland are the result of a combination of habitat limitation and other factors beyond the scope of this study. The fundamental niche of *Sphagnum fuscum* is very broad, as it was able to grow in all habitats examined in this peatland, i.e. it is not excluded from the other habitats because of an inability to survive there. The reasons behind the restriction of *Sphagnum fuscum* to its realised niche, particularly its exclusion from hollow habitats, are still not fully understood, but it is speculated that a combination of competition and establishment ability are involved. Overall, the bryophyte community structure in this peatland is only partially explained by habitat limitation on the nine axes examined. Other factors such as establishment and dispersal are likely important, as are temporal and spatial variation and stochastic disturbance.

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Summary

The ability of four boreal bryophytes (*Sphagnum angustifolium* C. Jens ex Russ., *Sphagnum fuscum* (Schimp.) Klinggr., *Sphagnum magellanicum* Brid. and *Pleurozium schreberi* (Brid.) Mitt.) to live in each others' habitats was examined in a one year reciprocal transplant experiment conducted in a poor fen peatland in Northern Alberta, Canada. Growth in length was determined by measuring shoot elongation, and growth in dry weight was determined by subtracting final dry weight from initial predicted dry weight. Species tolerance ranges, which approximate to fundamental niches, were determined by the significant differences in growth among the species. Stepwise regression analyses indicated that depth to water was the most important factor for all species except *Sphagnum fuscum*. *Pleurozium schreberi* exhibited the narrowest potential distribution, indicating that its present distribution is partially the result of habitat limitation. Although *Sphagnum magellanicum* and *Sphagnum angustifolium* exhibited wide potential ecological amplitude, the distributions of these species are partially limited by habitat. *Sphagnum fuscum* was able to grow in all habitats and its distribution is not limited by any of the habitat factors measured.

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Literature Cited

Bragazza, L. 1997. *Sphagnum* niche diversification in two oligotrophic mires in the southern Alps of Italy. The Bryologist **100**:507-515.

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

Clymo, R.S., and Reddaway, E.J.F. 1971. Productivity of *Sphagnum* (bog-moss) and peat accumulation. Hydrobiologia **12**:181-192.

Clymo, R.S., and Hayward, P.M. 1982. The ecology of *Sphagnum*. *In* Bryophyte Ecology. *Edited by* A.J.E. Smith. Chapman and Hall, London. pp. 229-289.

Damman, A.W.H. 1978. Distribution and movement of elements in ombrotrophic peat bogs. Oikos **30**:480-495.

Environment Canada. 1990. Canadian climate normals 1960-1990. Environment Canada, Ottawa.

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Fowler, N.L., and Clay, K. 1995. Environmental heterogeneity, fungal parasitism and the demography of the grass *Stipa leucotricha*. Oecologia (Heidelb) **103**:55-62.

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

Gignac, L.D. 1989. Mineral content of mire surface water and hummock-forming *Sphagnum* species in peatlands of western Canada. Lindbergia **15**:151-160.

Gignac, L.D. 1992. Niche structure, resource partitioning, and species interactions of mire bryophytes relative to climatic and ecological gradients in Western Canada. The Bryologist **95**:406-418.

Gignac, L.D. 1993. Distribution of *Sphagnum* species, communities, and habitats in relation to climate. Advances in Bryology **5**:187-222.

Gignac, L.D., and Vitt, D.H. 1990. Habitat limitations of *Sphagnum* along climatic, chemical, and physical gradients in mires of western Canada. The Bryologist **93**:7-22.

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Gignac, L.D., Vitt, D.H., Zoltai, S.C., and Bayley, S.E. 1991. Bryophyte response surfaces along climatic, chemical, and physical gradients in peatlands of western Canada. Nova Hedwigia **53**:27-71.

Glime, J.M., Slack, N.G., and Meston, C.L. 1987. A comparison of the Levins' and Freeman-Tukey niche width measures for bryophytes in an Adirondack stream. Symposia Biologica Hungarica **35**:457-466.

Grosvernier, P., Matthey, Y., and Buttler, A. 1997. Growth potential of three *Sphagnum* species in relation to water table level and peat properties with implications for their restoration in cut-over bogs. Journal of Applied Ecology **34**:471-483.

Hayward, P.M., and Clymo, R.S. 1983. The growth of *Sphagnum*: experiments on, and simulation of, some effects of light flux and water-table depth. Journal of Ecology **71**:845-863.

Hutchinson, G.E. 1957. Concluding remarks. Cold Spring Harbour Symposia on Quantitative Biology **22**:415-427.

Ireland, R.R., Brassard, G.R., Schofield, W.B., and Vitt, D.H. 1987. Checklist of the mosses of Canada. II. Lindbergia **13**:1-62.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Jauhiainen, J., Silvola J., Tolonen, K., and Vasander, H. 1997. Response of *Sphagnum fuscum* to water levels and CO_2 concentration. Journal of Bryology **19**:391-400.

Johansson, M.E. 1994. Life history differences between central and marginal populations of the clonal aquatic plant *Ranunculus lingua*: a reciprocal transplant experiment. Oikos **70**:65-72.

Keddy, P. 1989. Competition. Chapman and Hall, London, U.K.

Kooijman, A.M. 1993. On the ecological amplitude of four mire bryophytes: a reciprocal transplant experiment. Lindbergia **18**: 19-24.

Kron, K.A. and Judd, W.S. 1990. Phylogenetic relationships within the Rhodoreae (Ericaceae) with specific comments on the placement of *Ledum*. Systematic Botany **15**:57-68.

Li, Y. and Vitt, D.H. 1995. The dynamics of moss establishment: temporal responses to a moisture gradient. Journal of Bryology **18**: 677-687.

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Longton, R.E. 1985. Reproductive biology and susceptibility to air pollution in *Pleurozium schreberi* (Brid.) Mitt. (Musci) with particular reference to Manitoba, Canada. Mongraphs in Systematic Botany from the Missouri Botanical Garden **11**:51-69.

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

Malanson, G.P. 1997. Simulated responses to hypothetical fundamental niches. Journal of Vegetation Science **8**:307-316.

Mankiewicz, P.S. 1987. The low pressure field porometer: a new, low cost technique for characterizing external capillary water conduction in whole colonies of bryophytes and other small plants. The Bryologist **90**:253-262.

Microsoft, 1997. Microsoft excel 97. Microsoft Corporation, Santa Rosa, California.

Moss, E.H. 1983. Flora of Alberta 2nd edition, revised by John G. Packer. University of Toronto Press, Toronto.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Nicholson, B.J., and Gignac, L.D. 1995. Ecotope dimensions of peatland bryophyte indicator species along gradients in the Mackenzie River Basin, Canada. The Bryologist **98**:437-451.

Pakarinen, P., and Tolonen, K. 1977. On the growth-rate and dating of surface peat. Suo **28**:19-24.

Rydin, H. 1985. Effect of water level on desiccation of *Sphagnum* in relation to surrounding Sphagna. Oikos **45**:374-379.

Rydin, H. 1986. Competition and niche separation in *Sphagnum*. Canadian Journal of Botany **64**:1817-1824.

Rydin, H. 1987. Microdistribution of *Sphagnum* species in relation to physical environment and competition. Symposia Biologica Hungarica **35**:295-304.

Rydin, H. 1993a. Interspecific competition between *Sphagnum* mosses on a raised bog. Oikos **66**:413-423.

Rydin, H. 1993b. Mechanisms of interactions among *Sphagnum* species along water-level gradients. Advances in Bryology **5**:153-185.

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

Rydin, H., and McDonald, A.J.S. 1985. Tolerance of *Sphagnum* to water level. Journal of Bryology **13**:571-578.

Santelmann, M.V. 1991. Influences on the distribution of *Carex exilis*: an experimental approach. Ecology **72**:2025-2037.

SAS Institute. 1989. SAS/STAT user's guide, version 6, fourth edition. SAS Institute Inc., Cary, N.C., U.S.A.

Schipperges, B. and Rydin, H. 1998. Response of photosynthesis of *Sphagnum* species from contrasting microhabitats to tissue water content and repeated desiccation. New Phytologist **140**:677-684.

Sjörs, H. 1950. On the relation between vegetation and electrolytes in North Swedish mire waters. Oikos **2**:241-258.

Slack, N.G. 1990. Bryophytes and ecological niche theory. Botanical Journal of the Linnean Society **104**:187-213.

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

Streever, W.J., and Genders, A.J. 1997. Effect of improved tidal flushing and competitive interactions at the boundary between salt marsh and pasture. Estuaries **20**:807-818.

van der Hoeven, E.C., Korporaal, M., and van Gestel, E. 1998. Effects of simulated shade on growth, morphology and competitive interactions in two pleurocarpous mosses. Journal of Bryology **20**:301-310.

van der Molen, P.C., Schalkoort, M., and Smit, R. 1992. Hummock-hollow complexes on Clara bog, Co. Offaly, Ireland. *In* Hummock-hollow complexes on Irish raised bogs a palaeo/actuo ecological approach of environmental and climate change. *Edited by* van der Molen, P.C. University of Amsterdam, Amsterdam, The Netherlands. pp. 117-173.

Wang, J. 1995. The models of niche and their application. Ecological Modelling **80**:279-291.

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Zar, J.H. 1996. Biostatistical analysis 3rd edition. Prentice Hall, New Jersey, U.S.A.

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Table 2-1 Criteria used to determine health rating of shoots transplanted into the Mariana Lake peatland

Score	Rating	Criteria
5	Excellent	No chlorosis, branch/leaf loss, or shoot breakage, morphology typical
4	Very good	No chlorosis or shoot breakage. Shoots slightly less robust than normal in terms of capitula (if Sphagna) and branches.
3	Good	Some chlorosis and branch/leaf loss. No shoot breakage.
2	Poor	Most shoots chlorotic; typical colour retained at shoot apex only. Branch/leaf loss substantial. Some *Sphagnum* missing capitula. Some shoots broken; etiolation in *Pleurozium*
1	Very poor	Shoots black, cholorophyll at shoot apices of a few shoots only. Many *Sphagnum* missing capitula, many shoots broken.

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Table 2-2 Means of elemental concentrations (mg l^{-1}), pH, corrected conductivity (K_{corr})(μs/cm), depth to water table (DTW) (cm), and shade (% cover of overstory trees and shrubs) ± s.e. for each transplant habitat in the Mariana Lake peatland. Means with the same letter do not differ significantly by variable ($p<0.05$). Means for pH calculated by converting to antilog. Statistical tests for pH conducted on raw data. ANG = *Sphagnum angustifolium*, MAG = *S. magellanicum*, FUS = *S. fuscum*, PLE = *Pleurozium schreberi*.

Habitat	Ca^{++}	Mg^{++}	K^{+}	P	Na^{+}	pH	K_{corr}	DTW	% Cover
ANG	1.16±0.2a	0.23±0.03b	0.33±0.1a	0.06±0.03a	1.51.51±0.1a	4.18±0.03a	13.4±0.9a	10.6± 0.5a	4.0±1.1a
MAG	1.34±0.1a	0.31±0.07b	0.20±0.1a	0.03±0.02a	1.29±0.2a	4.03±0.08b	17.8±3.5a	13.7± 1.0a	13.9±2.9a
FUS	1.11±0.1a	0.20±0.02b	0.52±0.1a	0.08±0.02a	1.26±0.2a	4.10±0.03ab	13.2±0.9a	23.5±2.5b	25.2±3.1b
PLE	1.38±0.2 a	0.31±0.05b	0.54±0.3a	0.04±0.01a	1.47±0.1a	4.13±0.03ab	17.3±2.6a	23.4±1.2b	23.2±1.5b

Table 2-3 Stepwise regression analyses for the relationships between growth in length and weight (dependent variables) of the study species, and depth to water table (DTW), corrected conductivity (K_{corr}), shade, and pH. Bold values significant $p<0.05$.

Species	**Variable**	**LENGTH**		**WEIGHT**	
		F	**p>F**	**F**	**p>F**
S. angustifolium	DTW	**24.66**	0.0001	**17.30**	0.0008
	K_{corr}	1.8446	0.1945	0.3898	0.5424
	Shade	0.0642	0.8035	0.9615	0.3435
	pH	1.3528	0.2630	0.2646	0.6150
S. magellanicum	DTW	**8.6170**	0.0166	**3.2315**	0.1024
	K_{corr}	0.0189	0.8942	0.4084	0.5387
	Shade	4.2926	0.0720	0.2865	0.6055
	pH	0.0310	0.8646	0.7616	0.4055
S. fuscum	DTW	0.3544	0.5611	0.4146	0.5300
	K_{corr}	0.0935	0.7642	1.4200	0.2532
	Shade	0.0028	0.9583	0.5543	0.4689
	pH	0.5391	0.4749	3.0416	0.1031
P. schreberi	DTW	0.4223	0.5304	**13.481**	0.0037
	K_{corr}	0.0002	0.9901	0.0524	0.8236
	Shade	0.4566	0.5145	0.8952	0.3664
	pH	0.9920	0.3428	0.0660	0.8025

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Table 2-4 Mean health rating ± s.e. of the shoot bundles of the study species (n=5) transplanted in the Mariana Lake peatland after one year. The health of the mosses was assessed visually based on appearance on a scale of 1-5, with 5 being excellent and 1 being very poor. Bold values represent the highest rank for each species. ANG = *S. angustifolium*, MAG = *S. magellanicum*, FUS = *S. fuscum*, PLE = *Pleurozium schreberi*.

	Habitat			
Species	ANG	MAG	FUS	PLE
S. angustifolium	**4.8 ± 0.1**	3.6 ± 0.2	2.9 ± 0.4	2.1 ± 0.3
S. magellanicum	3.7 ± 0.3	**4.9 ± 0.1**	3.0 ± 0.1	2.5 ± 0.3
S. fuscum	3.9 ± 0.1	3.4 ± 0.1	**4.6 ± 0.3**	3.8 ± 0.2
P. schreberi	2.0 ± 0.1	2.8 ± 0.1	3.6 ± 0.1	**5.0 ± 0.0**

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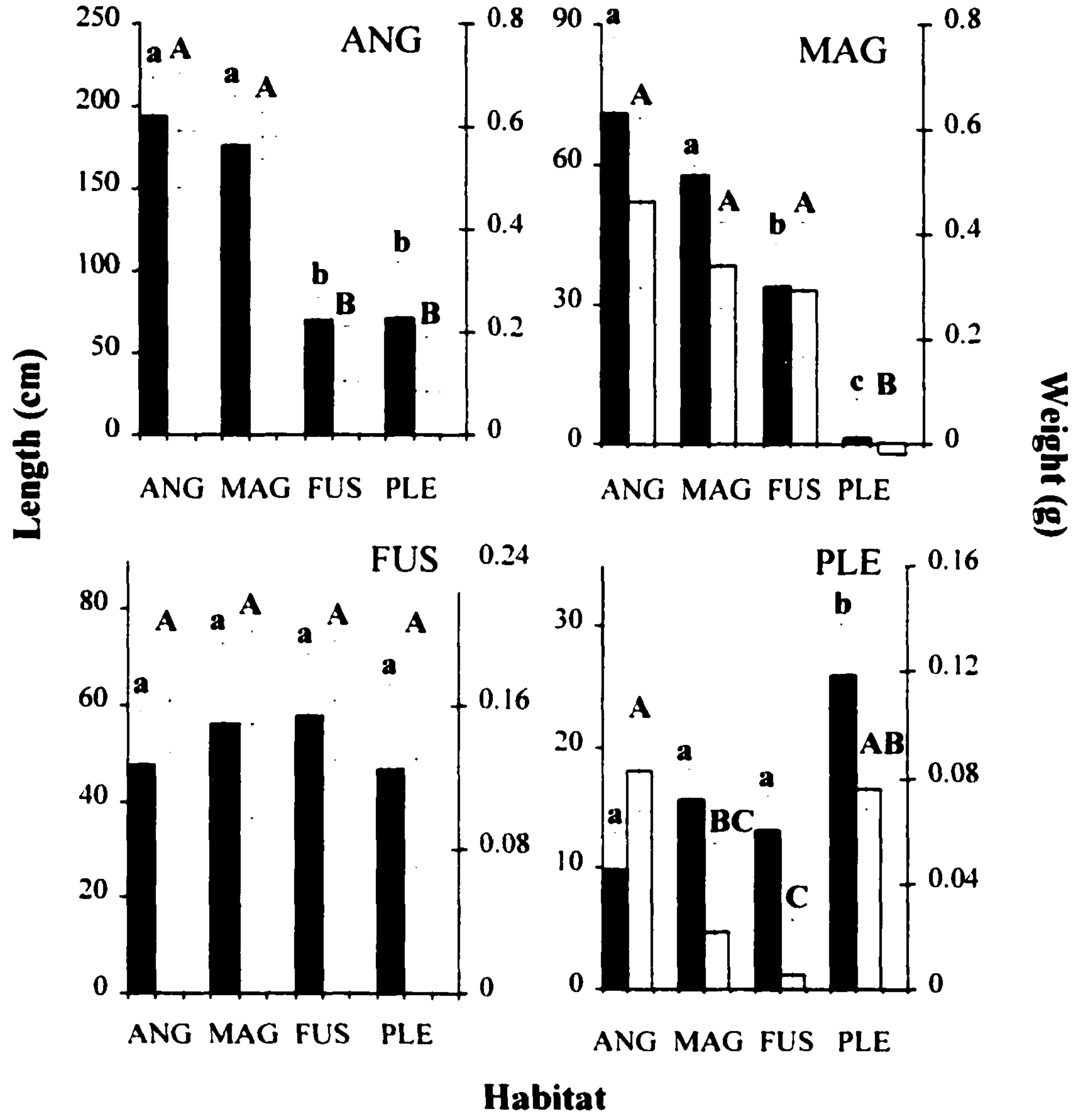

Fig. 2-1 Mean increase in length (grey bars) and weight (white bars) ± s.e. of 25 shoot bundles of the mosses transplanted in the peatland after one year (n = 5). Means with the same letter and case size are not significantly different, $p<0.05$ based on ANOVA (general linear model). ANG = *S. angustifolium*, MAG = *S. magellanicum*, FUS = *S. fuscum*, PLE = *Pleurozium schreberi*.

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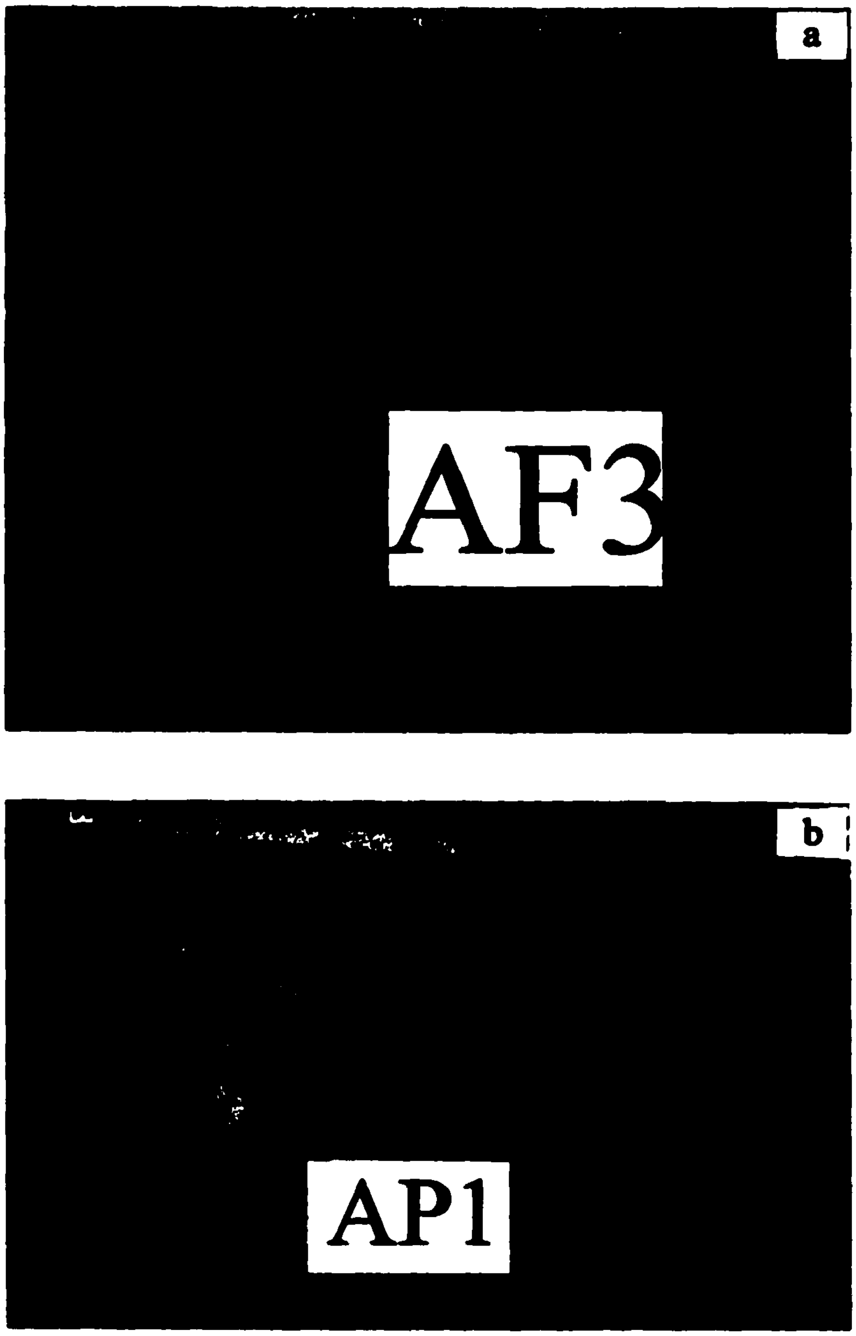

Fig. 2-2 ***Sphagnum angustifolium*** **exhibits desiccation and chlorosis after living in the** ***Sphagnum fuscum*** **(a) and** ***Pleurozium schreberi*** **(b) habitats for one year.**

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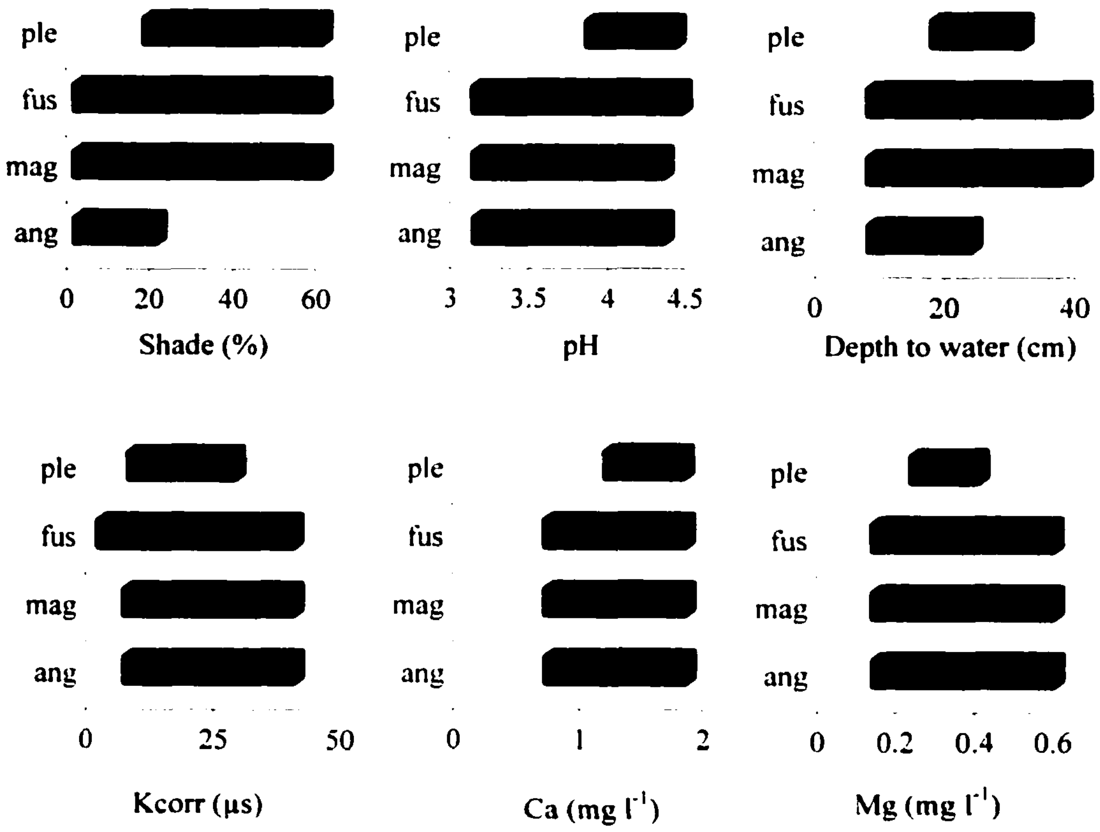

Fig. 2-3 The tolerance ranges of the mosses transplanted in the Mariana Lake peatland after one year presented by niche factor. The tolerance range of a species includes habitats where its mean growth is not significantly different than its mean growth in its own habitat, and the mean health of the transplanted species is ≥ 3 (good). ANG = *Sphagnum angustifolium*, MAG = *S. magellanicum*, FUS = *S. fuscum*, PLE = *Pleurozium schreberi*.

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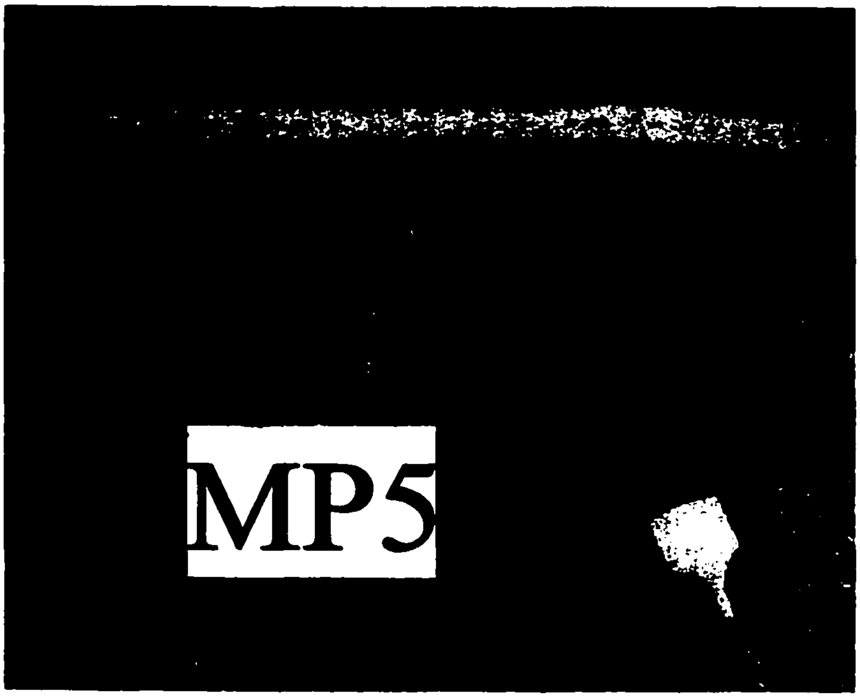

Fig. 2-4 *Sphagnum magellanicum* was not healthy in the *Pleurozium schreberi* habitat.

Fig. 2-5 *Sphagnum fuscum* successfully lived in the *Sphagnum magellanicum* habitat.

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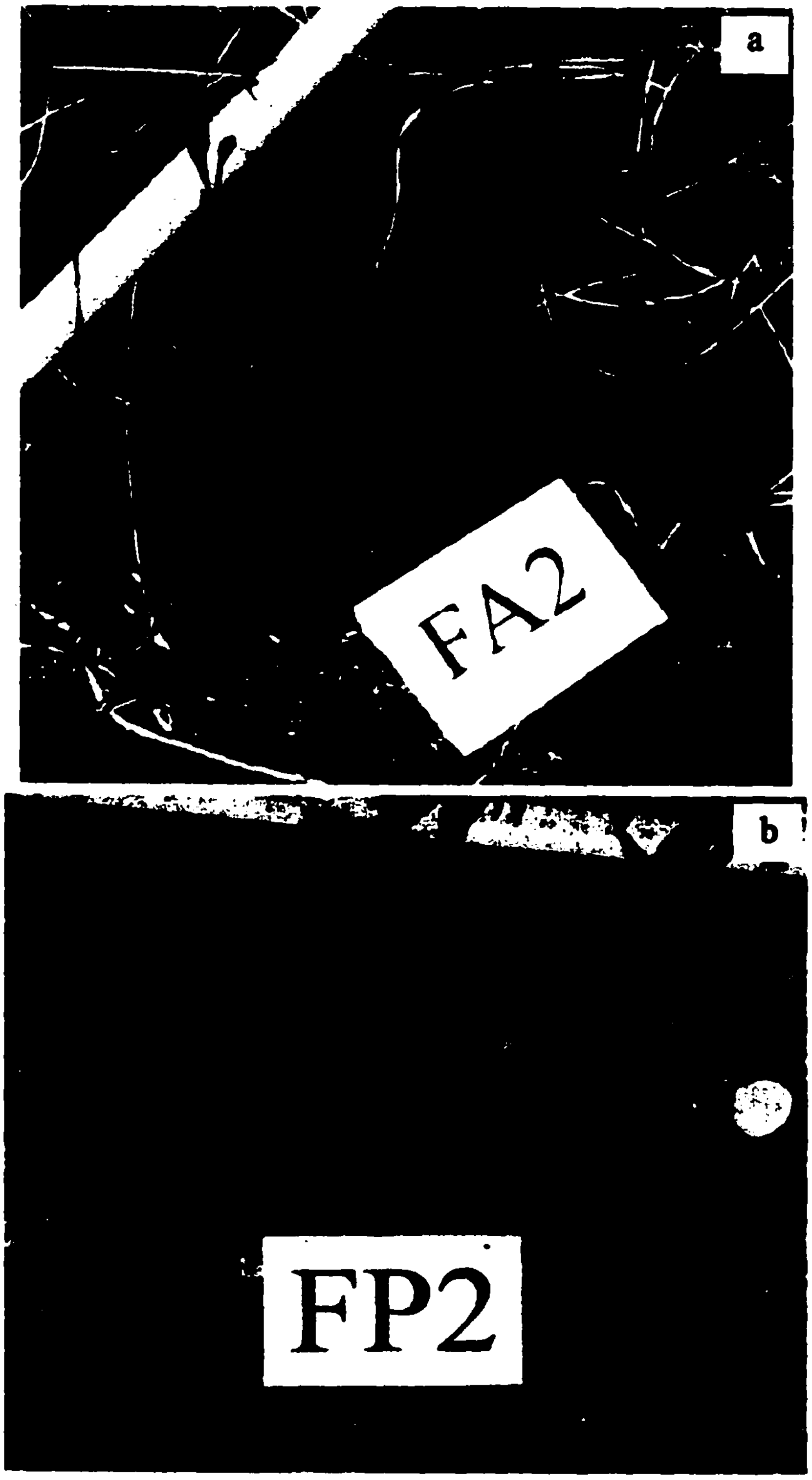

Fig. 2-6 ***Sphagnum fuscum*** **successfully lived in the** ***Sphagnum angustifolium*** **(a) and** ***Pleurozium schreberi*** **(b) habitats.**

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Chapter 3- Bryophyte community structure in a boreal poor fen II: interspecific competition among five mosses

Introduction

Despite being second only to the angiosperms in number of species (Crosby 1980), bryophytes are poorly understood and often ignored as an integral component of the landscape. This is not surprising, given their size and reputation as taxonomically troublesome organisms, however the bryophytes that dominate the boreal forest floor are critical to primary production, nutrient cycling, and water retention (Skre *et al.* 1983; Chapin *et al.* 1987; Carleton and Read 1991; Price *et al.* 1997). Similarly, the *Sphagnum* (peat) mosses that dominate the ground layer vegetation of many boreal peatlands are the main primary producers in these areas (Longton 1984; Andrus 1986; During and van Tooren 1987; Gerdol 1995). Further, as bryophytes react relatively quickly to subtle changes in their environment at microscales, they are valuable indicator species for pollutants and climate change (Gorham 1988, 1991; Gignac *et al.* 1998).

A version of this chapter has been accepted for publication. Mulligan, R.C. and Gignac, L.D. 2002. Bryophyte community structure in a boreal poor fen II: interspecific competition among five mosses. Canadian Journal of Botany: in press

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In Grime's (1977) classification, bryophytes as a group are classified as ruderals and stress tolerators. As such, bryophyte competition has received little attention until recently (During and van Tooren 1990; Økland 1994; Bates 1998), and transplant experiments are quite rare (Rydin 1997a). This is unfortunate as bryophytes make excellent material for competition studies. The virtual absence of herbivory (Longton 1992) precludes confusion between the effects of herbivory and competition, and the lack of true roots facilitates relatively easy manipulation and excludes belowground competition as an additional factor. Although the number of empirical studies remains low and much evidence is indirect, bryophyte competition experiments are currently much more common than a decade ago, and it appears that bryophyte-bryophyte competition may be just as important as that between vascular plants, in some communities (Rydin 1997a). These studies indicate that bryophytes compete mostly with each other (Rydin 1997a), however; competition for nutrients between bryophytes and higher plants has been documented (Chapin *et al.* 1987; Svensson 1995). Studies of bryophyte-bryophyte competition suggest that competition is primarily for space (Marino 1991; Rydin 1995, 1997a; Slack 1997), but competition for light (van der Hoeven *et al.* 1998) and nutrients (Twenhöven 1992) also occurs. As suggested by Rydin, it is time to move beyond simply testing for the existence of competition among bryophytes to examine the mechanisms involved and relative importance of these interactions in bryophyte communities.

The intensity of competition can be reported and measured in various ways. Competitive effect is the ability of a plant to suppress the growth of its

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neighbours. Competitive response is the ability to evade or tolerate repression, and competitive ability is the sum of competitive effect and response. A competitive hierarchy is a network wherein marked differentiation of competitive ability allows for species ranking. In a completely transitive competitive hierarchy all species of higher rank outcompete all species of lower rank (Keddy and Shipley 1989). More commonly, at least one species of lower rank outcompetes one or more species of a higher rank and such reversals of rank form an intransitive pattern.

There are numerous controversial issues in angiosperm competition theory. Two of the more unresolved points are: (i) whether the intensity of competitive interactions shifts with productivity changes (Tilman 1977, 1985; Grime 1979; Keddy 1989; Grace 1991; Goldberg *et al.* 1999), and (ii) what, if any, plant traits confer a competitive advantage (Grace 1990; Bengtsson *et al.* 1994; Goldberg 1996). Despite these issues, recent angiosperm studies have documented general, although not unanimous, acceptance of the following points: (i) competition is an important mechanism in many plant communities (Connell 1983; Schoener 1983; Goldberg and Barton 1992; Bengtsson *et al.* 1994), (ii) when two individuals compete, one individual usually enjoys a disproportionate advantage (Keddy 1989; Shipley and Keddy 1994), (iii) congeners and other closely related organisms are often similar in competitive ability (Goldberg and Werner 1983; Shmida and Ellner 1984; Goldberg 1987; Keddy 1989), (iv) competitive hierarchies exist in many communities (Keddy and Shipley 1989; Goldberg and Landa 1991; Shipley 1993; Nernberg and Dale 1997; Rosch and van Rooyen

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1997), (v) these hierarchies are often concordant among different habitats and indicator species (Goldberg and Landa 1991; Keddy *et al.* 1994; Rosch and van Rooyen 1997), and (vi) the size of the organism is often important to the outcome, with larger organisms enjoying an advantage over smaller ones (Connell 1983; Schoener 1983; Goldberg and Landa 1991; Bengtsson *et al.* 1994; Gaudet and Keddy 1988; Schwinning and Weiner 1998).

The applicability of these "higher plant" tenets to bryophytes has not been examined. We should not assume that theories developed for and tested with vascular plants are applicable to bryophytes, just as we cannot infer the suitability of animal principles to plant populations. Some of the most important differences between bryophytes and angiosperms which would be important to the mechanisms behind competitive interactions include water relations (Dilks and Proctor 1979; Proctor 1982, 1990), and bryophytes' gametophyte-dominated life cycle and predominantly asexual reproduction (Clymo and Duckett 1986; Shaw 1992; Newton and Mishler 1994).

One community where several bryophyte competition studies have been conducted is the boreal peatland. Bog and poor fen peatlands consist of a rolling micro-landscape of hummocks and hollows. Hummock species inhabit the areas farthest from the water table, while hollow species occur at the base of the hummock in areas where the water table is very close to the surface. Differences in pH, conductivity, evapotranspiration and depth to water table along the hummock-hollow gradient create distinct microhabitats that are generally inhabited by different species of *Sphagnum*.

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A long-term study of competitive interactions among several Sphagna initially concluded that hummock species were excluded from the hollows due to competition (Rydin 1986, 1987). Later results indicated that these mosses differed very little in competitive ability (Rydin 1993 a,b) and after 11 years, the hummock species *Sphagnum fuscum* (Schimp.) Klinggr. was not competitively excluded from the hollow habitats in any of 8 replicates (Rydin 1993a). The mechanisms which preclude *Sphagnum fuscum* from inhabiting what is clearly part of its fundamental niche (Mulligan and Gignac 2001) are not clear.

Other studies have produced indirect evidence of competition (Luken 1985; Kenkel 1988; Økland 1990; Gignac 1992, 1993; Kooijman and Bakker 1995), and some (Økland 1990; Gignac 1992, 1993) have suggested that the distribution of Sphagna along the hummock-hollow gradient may illustrate a competitive hierarchy. While these studies provide valuable insight into the importance of competition in structuring peatland bryophyte communities, they have all been conducted in ombrotrophic bogs or rich fens (Kooijman and Bakker 1995). The competitive interactions of poor fen species, particularly *Sphagnum angustifolium* C. Jens. ex Russ., remains largely unexplored.

In this study, we used *Aulacomnium palustre* (Hedw.) Schwaegr. as a phytometer to examine the competitive ability of three Sphagna (*Sphagnum angustifolium*, *S. fuscum*, and *S. magellanicum* Brid.), and two feather mosses (*Pleurozium schreberi* (Brid.) Mitt. and *Ptilium crista-castrensis* (Hedw.) De Not.) in two habitats of a poor fen in Northern Alberta, Canada. A phytometer is a common indicator species that is grown with the study species. The ability of

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the study species to repress the growth of the phytometer provides an indication of their competitive effect. For example, if *Aulacomnium palustre* increases in weight and length when grown with *Sphagnum fuscum*, but decreases when transplanted into *S. angustifolium*, then *S. angustifolium* has more competitive ability than *S. fuscum*, in this instance. *Aulacomnium palustre* was chosen as the phytometer because it is not closely related to any of the study species and it occurs in both habitats examined. Also, the growth habit of *Aulacomnium palustre* allowed for shoot elongation measurements that would be more straightforward than some other bryophytes (eg. *Sphagnum*). Phytometer use has never been reported with bryophytes but they have been used to document competitive hierarchies in wetland herbaceous communities (Keddy and Shipley 1989; Wilson and Keddy 1986; Keddy *et al.* 1994; Gaudet and Keddy 1995), community-level competition in ephemeral grassland species (Rosch and van Rooyen 1997), and as a primary means of testing productivity-competition relationships in old field and wetland communities (Wilson and Tilman 1991, 1993; Twolan-Strutt and Keddy 1996; Cahill 1999). This is the first field examination of competition between poor fen bryophytes and the first concurrent investigation of competition in both *Sphagnum* and feather mosses.

The primary objectives of this study are: i) to determine the competitive effect of the study species in two habitats, ii) to determine whether this pattern illustrates a competitive hierarchy, and iii) to determine if the hierarchy is concordant between the two habitats. Secondary objectives of this investigation are to ascertain whether competitive interactions between poor fen bryophytes are

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analogous to those documented for ombrotrophic species and to comment on the applicability of plant competition theory derived from angiosperms to bryophytes.

Materials and Methods

Study site and species

The study site is a continental high boreal peatland near Mariana Lake, in northeastern Alberta (111° 58' W longitude, 55° 55' N latitude), Canada. The peatland is part of a mire complex with three distinct areas. *Sphagnum angustifolium* and *Carex* spp. dominate the ground layer in the poor fen area. *Sphagnum fuscum* and ericaceous shrubs dominate a small non-wooded section that also has scattered young *Picea mariana* (Mill.) B.S.P. The wooded bog islands are characterised by stunted *Picea mariana*, *Pleurozium schreberi*, *Sphagnum fuscum*, *Sphagnum angustifolium*, and angiosperms such as *Rubus chamaemorus* L., *Rhododendron groenlandicum* (Oeder) Kron and Judd, and *Smilacina trifolia* (L.) Desf. For detailed information on the study site and the study species (except *Ptilium crista-castrensis* and *Aulacomnium palustre*) see the first paper in this series (Mulligan and Gignac 2001).

Ptilium crista-castrensis is a boreal forest floor moss (Frego and Carleton 1995) which is largely confined to the surrounding forest in this study area. Nonetheless, very small patches of both feather mosses occur in both the poor fen

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and non-wooded habitats where they are always shaded by young *Picea mariana*. *Aulacomnium palustre* is a common acrocarpous species in continental western Canadian peatlands (Gignac *et al.* 1991) which grows on hummock tops with *Sphagnum fuscum* and *Polytrichum strictum* Brid. Its distribution in this peatland is precisely as described above.

Nomenclature follows Anderson (1990) for *Sphagnum*, Ireland *et al.* (1987) for all other bryophytes, Kron and Judd (1990) for *Rhododendron groenlandicum*, and Moss (1983) for all other plants.

Transplant experiment

Two transplant plots (total) were set up using a Latin Square design (Fig. 3-1) in the non-wooded (*Sphagnum fuscum*-dominated) (Fig. 3-2) and wooded (bog island) habitats in August 1995. The plots were selected on the basis of the following criteria: bryophyte species homogeneity, flatness, and paucity of angiosperms in order to reduce the influence of microtopography and shading. Twelve transplant plugs, 7.5 cm in diameter and approximately 20 cm in length, were removed from typical habitats for each of the five study species using a PVC plastic coring device or Exacto™ knives. The central 5 shoots of each plug were extracted, discarded and replaced with five healthy, unbranched shoots of *Aulacomnium palustre* (a "phytometer bundle" Fig. 3-3). The shoots of *Aulacomnium palustre* were cut to 3 cm in length, soaked in deionized water for 20 minutes (to ensure standardised moisture content) and rotated 20 times in a standard plastic salad spinner with an inner diameter of 21 cm at a speed of 190

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rotations per minute (rpm). Each phytometer bundle was weighed on a Mettler PE 3600 scale and the weight recorded as moist weight. The bundles were tied with thread, labelled with an aluminum tag and inserted into the large transplant plugs (neighbours) which were reinserted into the moss mat at level height. Six 7.5 cm back transplants of *Aulacomnium palustre* containing a phytometer bundle of *A. palustre* were also included in each plot.

The transplanted phytometer shoots were harvested after 23 months in July 1997. Some bundles were lost due to ungulate trampling and avian interference. In other cases, a few phytometer bundles were recovered with less than 5 shoots. The reason behind the shoot loss was unclear but animal interference was suspected (Fig. 3-2). The most prudent analyses were conducted, in that only intact bundles were included. Shoot elongation (length) was determined by subtracting original length (5 shoots x 3 cm = 15 cm) from total final length and reported as mean shoot growth of the phytometer per neighbour species. Branching was noted and included in final length. The shoots were air dried for 3 days and placed in a Cenco heater at 30°C for 24 hours to complete the drying. The shoots were weighed and the weight recorded as final dry weight. Final dry weight was subtracted from initial predicted dry weight to give change in dry weight reported per 5-shoot bundle. Initial dry weight was predicted from initial moist weight (Mankiewicz 1987; Mulligan *et al.* in press) with R^2=0.67 using regression equations as in Frego and Carleton (1995) and van der Hoeven *et al.* (1998). Growth in length and weight was converted to relative growth rate (RGR) (Harper 1977) as follows:

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$$[1] \qquad RGR = \frac{\ln(M_2) - \ln(M_1)}{t_2 - t_1}$$

where ln = natural logarithm, M_2 = final dry weight (or length), M_1 = calculated initial dry weight (or initial length), t_2-t_1 = the length of the experiment in days. The ability of the neighbour species to suppress the growth of the phytometer was calculated as relative competitive performance (RCP) following Keddy *et al.* (2000) as:

$$[2] \qquad RCP = \frac{P_A - P_N}{P_A} \times 100$$

where P_A = the mean growth (in length or weight) of the phytometer grown with its own neighbours and P_N is the mean growth (in length or weight) of the phytometer grown with shoots of neighbour N.

Water chemistry and environmental variables

A perforated PVC pipe well, inserted to height even with the moss carpet at each plot, was used to take depth to water table measurements and extract water chemistry samples. Depth to water table was measured twice during August 1995 and three times in 1996 (June, August and September) and 1997 (May, June

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and July). Water samples were taken once per year (1995, 1996, 1997), collected in small polyethylene acid-washed bottles (3% HCl), filtered through #42 Whatman filter paper, and acidified with 1 ml HCl in 24 ml water. Mineral element concentrations (Mg^{++}, Ca^{++}, P, Na^{+}, and K^{+}) were measured with argon plasma spectrophotometry. Conductivity was measured with a portable Hanna meter (HI 8033) and corrected for hydrogen ions and temperature (to 20°C) following Sjörs (1950). A Fisher pH/temp meter 119 and litmus paper were used to determine pH. Measurements were taken twice in 1995 and three times each in 1996 and 1997. In order to reduce the effect of angiosperms and conifer seedlings on growth of the transplants, plots were weeded at least every six weeks during the growing seasons. A portable wooden boardwalk system (Fig. 3-4).was used during set up and weeding to reduce disturbance to the transplant areas.

Statistical analyses

All statistical analyses were conducted with SAS statistical packages (SAS Institute 1989). Proc Univariate was used to test for normality and Proc Mixed (Littell *et al.* 1996) was used to run ANOVA for the effects of habitat and species on relative growth in weight and length of the phytometer. A significant species effect indicates the presence of a competitive hierarchy (Keddy *et al.* 2000). Tukey's test was used for post hoc mean separations. Some of the environmental parameters did not fully meet ANOVA assumptions and these were analysed with a nonparametric ANOVA analogue, the Mann-Whitney U test (Zar 1996).

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Differences in competitive ranks of the species between the two habitats were tested with the Mann-Whitney U test. A significant difference in competitive ranks indicates that the competitive rankings are not concordant between the two habitats. Simple linear regression was used to determine if a relationship existed between growth in length and weight of the phytometer in the two habitats. A non-significant relationship between these two parameters could be further evidence of the uncoupling of length and weight which has been recently reported for several bryophytes (Rincon and Grime 1989; Jauhiainen *et al.* 1997; Hanslin 1999).

Results

Change in mean relative growth of the phytometer shoots

ANOVA for treatment (neighbour species) effects on mean relative growth rates were significant for both length and weight (Table 3-1). The site effect was significant for length only and the site × treatment interaction was not significant in either case (Table 3-1).

When grown with *Sphagnum magellanicum* the phytometer grew very poorly in both habitats (Fig. 3-5), losing weight and length in the non-wooded habitat. The performance of *Aulacomnium palustre* was intermediate when grown with *Sphagnum fuscum* and *S. angustifolium* and very good with the feather moss neighbours (Fig. 3-5). In the wooded habitat, mean RGR in length of

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Aulacomnium palustre with *Sphagnum* neighbours was significantly lower than its performance with the feather mosses. In the non-wooded habitat mean RGR in length and weight of the phytometer with *S. magellanicum* and *S. fuscum* was significantly lower than its growth with *Ptilium crista-castrensis* (Fig. 3-5). There were no significant differences in mean RGR expressed as weight in the wooded habitat. There were no significant differences in competitive ranks for any species in the two habitats.

Relative competitive performance of the study species

Treatment (neighbour species) effects on mean relative competitive ability were significant for both length and weight parameters (Table 3-3). Site did not have a significant effect, nor was there a site × treatment interaction (Table 3-3).

Sphagnum magellanicum exhibited strong competitive effect measured as relative competitive performance in both habitats (Fig. 3-6). Mean competitive performance of *Sphagnum magellanicum* was significantly greater than that of *Ptilium crista-castrensis* in all combinations except weight in the wooded habitat. The competitive performance of *Sphagnum fuscum* in the non-wooded area was 78% for length and 22% for weight (Fig. 3-6). *Sphagnum angustifolium* exhibited very low competitive performance in the wooded habitat and none in the *Sphagnum fuscum* habitat. *Pleurozium schreberi* and *Ptilium crista-castrensis* did not show evidence of competitive suppression in either habitat (Fig. 3-6). The trends in competitive performance between length and weight are identical for the non-wooded habitat (Fig. 3-6, Table 3-4). In the wooded area,

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length and weight reacted slightly differently with a reversal in ranks of *Sphagnum fuscum* and *S. angustifolium* in length and in ranks of *Pleurozium schreberi* and *Ptilium crista-castrensis* in weight (Fig. 3-6, Table 3-4).

The relationship between length and weight

The relationship between increase in dry weight and shoot elongation was significant for the non-wooded (R^2 =0.27; p<0.013) and wooded habitats (R^2 = 0.26; p<0.015).

Water chemistry and environmental variables

Depth to water table was the only environmental variable to differ significantly between the two habitats. Depth to water table in the non-wooded area (5.58 cm) was significantly lower ($t_{(0.001, 8)}$ = 6.04) than in the wooded habitat (20.4 cm) (Table 3-2).

Discussion

This investigation documents the existence of a competitive hierarchy with feather mosses as subordinates to the Sphagna. This corroborates the indirect evidence of Gignac (1992) and Bragazza and Gedol (1996) who concluded that *Sphagnum* spp. are generally better competitors in bogs and poor fens than non-

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Sphagna. It is likely that the limited distributions of *Pleurozium schreberi* and *Ptilium crista-castrensis* are the result of both competitive exclusion by Sphagna and habitat limitation as *P. schreberi* was limited to only its own habitat in a reciprocal transplant study in this peatland (Mulligan and Gignac 2001). The lack of competitive effect of the feather mosses suggest that they actually facilitated phytometer growth. This facilitation may have occurred because the feather mosses would not exert the allelopathic influence on the phytometer that has been documented for Sphagna. *Sphagnum* mosses have remarkable cation exchange capacity wherein they sequester the minute levels of nutrients present and release H^+ ions. This interference competition acidifies the environment, making it less hospitable to most other plants, thus ensuring the proliferation of *Sphagnum* over vast areas of the landscape (Clymo and Hayward 1982; Clymo 1984; van Breeman 1995).

Competitive hierarchies could be relevant to *Sphagnum*-dominated communities because the close proximity of gametophytes to one another provides great potential for interspecific interaction (Økland 1990), and asymmetric (*sensu* Keddy 1989) interactions appear to be much more common than symmetric ones (Connell 1983). Conversely, as the proportion of asymmetrical interactions is thought to be lowest in communities with very closely related species (Keddy 1990), competition amongst poor fen Sphagna could be largely symmetrical as reported for ombrotrophic Sphagna (Rydin 1993a, 1997b).

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The competitive hierarchy in this peatland is not completely transitive (*cf* Keddy and Shipley 1989; Shipley and Keddy 1994) as two reversals in rank order occur (Table 3-4). Reversals are believed to be common in competitive hierarchies (Connell 1983; Herben and Krahulec 1990) as rank can vary with density (Zamfir and Goldberg 2000), water availability (Fowler 1982) and frequency of stochastic events. Further, the ubiquity of disturbance in plant communities, the importance of gap dynamics, and the prevalence of reversals suggest that complete transivity would likely be the exception and not the rule. Interestingly, the bryophytes in this study contravene an assumption of competitive hierarchy theory which assumes that competitive abilities are negatively correlated with fundamental niche width, i.e. the width of the fundamental niche is a predictor of competitive ability (Keddy 1989). Mulligan and Gignac (2001) documented very wide fundamental niches for the Sphagna in this peatland and a very narrow range for *Pleurozium schreberi* (*Ptilium crista-castrensis* was not in the study). Therefore, the competitive hierarchy theory may not be predictive for these bryophytes as suggested for angiosperms (Keddy 1989).

The similarity in water chemistry and environmental parameters between the two habitats (Table 3-1) likely contributes to their similar RGR and RCP trends, as habitat factors are very important to determination of species rankings. The significant difference in depth to water table (Table 3-1) likely explains the significant site effect for length (Table 3-2) as *Aulacomnium palustre* should

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perform better in the wooded habitat where the lower water table level is closer to that of the realised niche of this species (Gignac *et al.* 1991).

The closeness in competitive performance trends between the two habitats coupled with the concordance in competitive rankings (Table 3-4), indicates that these bryophytes have a similar intensity of competitive effect in the two habitats examined. This does not necessarily imply that these findings would be concordant with those in another type of wetland or a different habitat within this peatland. In fact, a third phytometer plot was set up in the very wet *Sphagnum angustifolium* habitat in 1995. Unfortunately, very high water levels (the plants were submerged most of the growing seasons) resulted in the complete overgrowth of all phytometer bundles. Since the shoots of *Aulacomnium palustre* all appeared dead, these data were discarded, but this does illustrate the potential for a different outcome depending on habitat.

It is not known whether growth in length or weight is more important to competitive effect in bryophytes. Since the relationship between increase in shoot elongation and increase in dry weight is not as strong as previously assumed (Jauhiainen *et al.* 1997; Hanslin 1999; Mulligan *et al.* in press) it is preferable to measure both parameters. This study corroborates this uncoupling of length and weight in mosses. Although regressions exploring the relationship of increases in length to increases in weight were significant, the fit is not very strong for either habitat. Angiosperm studies have documented a strong correlation between growth in dry weight and seed set (fitness) and between height and dry weight (Casper and Cahill 1996). Since mire bryophytes

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reproduce primarily through asexual gametophytic fragments and dichotomous forking (During and van Tooren 1987; Slack 1997), features which facilitate spore production are unlikely to be important to their fitness. Spore production may, however be important to fitness for fugitive and colonist species such as *Funaria hygrometrica* Hedw. Fitness, *per se*, has not been examined in bryophytes but it is likely that morphological and physiological factors which confer water retention and or desiccation tolerance, or establishment ability could be important. Traits which confer fitness in bryophytes are also very likely to differ between species of different life strategies (see During 1992).

On a strictly statistical basis, the lack of significant differences in RCP between these Sphagna corroborates Rydin's (1993a) findings that competitive effect is similar among Sphagna. This study cannot directly comment on the strength of competitive effect between the neighbour species as pairwise comparisons were not made and all comparisons are made with reference to the phytometer. However, the very high between-replicate variability exhibited by these data (and other bryophyte growth studies i.e. Pakarinen 1978; Rydin 1986, 1993a, 1997b; Twenhöven 1992; Zamfir and Goldberg 2000) indicates that their true biological significance may be masked by "noise". The suppression of growth of the phytometer by *Sphagnum magellanicum* (Fig. 3-5) and its high RCP (Fig. 3-6) strongly suggests that it is a competitive species (*cf* Økland 1990). Interestingly, it is also the largest bryophyte in this study (Mulligan *et al.* in press).

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The competitive effect of *Sphagnum magellanicum* may help elucidate one of the most perplexing phenomena in recent *Sphagnum* ecology. *Sphagnum fuscum* (and other hummock Sphagna) can survive high water levels in ombrotrophic (Clymo and Reddaway 1971; Andrus 1986; Rydin 1986, 1993a, b) and poor fen (Mulligan and Gignac 2001) peatlands, and growth chamber investigations (Grosvernier *et al.* 1997; Jauhiainen *et al.* 1997), yet these mosses are almost never found in hollow habitats. For *Sphagnum fuscum* to grow in the hollows without the manipulation of an investigator, it would have to move down the hummock side through *S. magellanicum*. Therefore, *Sphagnum fuscum* may be absent from the hollows due to competitive interactions with *S. magellanicum*. This suggestion deserves a corollary though, as it is difficult to imagine that *Sphagnum fuscum* would be dispersal limited over such a short distance. It is obviously not impossible for the diaspores of *Sphagnum fuscum* to arrive at the hollow habitat, but they are unable to establish amongst the mature canopy of the hollow species and the adult individuals cannot get through the "*magellanicum* wall." This seems plausible since *Sphagnum fuscum* has been found growing in hollow habitats in oceanic peatlands from which *S. magellanicum* was absent (Gignac, personal communication). Many studies have suggested that competition in the regeneration niche (pre-emptive competition) may be the key to understanding the coexistence of some bryophytes, and the importance of "who gets there first" cannot be discounted (Watson 1981; Slack 1982, 1997; Rydin 1986, 1987, 1993a, b, 1997a, b; Li and Vitt 1994, 1995; Frego 1996).

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Bryophytes are an extremely diverse group of organisms which employ a wide range of life strategies (During and van Tooren 1990; Grime *et al.* 1990; During 1992). On the narrow basis of this investigation and the limited number of empirical studies the following generalisations may be made: (i) competition is an important interaction in some bryophyte communities (Kosiba and Sarosiek 1991; Marino 1991; Glime and Iwatsuki 1997; Zamfir and Goldberg 2000), (ii) concordant competitive hierarchies exist in some bryophyte communities (Table 3-4; Marino 1991; Zamfir and Goldberg 2000) and (iii) the size of the organism may be important (this study).

In conclusion, many aspects of bryophyte competition theory are analogous to higher plant tenets. For example, this study documents the existence of a competitive hierarchy with *Sphagnum* mosses being competitively superior to the feather mosses. In addition, the biological significance of these data suggest that *Sphagnum magellanicum* is a competitive species that hinders mature individuals of *S. fuscum* from occupying their full fundamental niche. Future research with boreal bryophytes, specifically population-level studies and regeneration niche interactions, is necessary. Although we are beginning to understand community structure in well-studied boreal habitats, the literature is virtually non-existent for most bryophyte species and competitive interactions within and among these groups should also be examined.

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Summary

A possible competitive hierarchy among five boreal bryophytes (*Sphagnum angustifolium*, *Sphagnum fuscum*, *Sphagnum magellanicum*, *Ptilium crista-castrensis*, and *Pleurozium schreberi*) was examined in a two-year transplant experiment conducted in two habitats of a poor fen in Northern Alberta, Canada, using a sixth moss (*Aulacomnium palustre*) as a phytometer. Change in relative growth rate in length and weight (competitive effect), indicated the existence of a hierarchy in this peatland wherein the feather mosses are subordinates to the Sphagna. Relative competitive performance, which was calculated relative to the growth of the phytometer in monoculture, indicated that *Sphagnum magellanicum* exhibited the greatest competitive effect. *Sphagnum magellanicum* may be a strong competitor and partially inhibit *S. fuscum* from occupying its full fundamental niche. *Sphagnum fuscum* and *S. angustifolium* have low competitive ability in the habitats studied in this peatland. The feather mosses did not demonstrate competitive effect and may have facilitated growth of the phytometer.

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Literature Cited

Anderson, L.E. 1990. A checklist of *Sphagnum* in North America North of Mexico. The Bryologist **93**: 500-501.

Andrus, R.E. 1986. Some aspects of *Sphagnum* ecology. Canadian Journal of Botany **64**: 416-426.

Bates, J.W. 1998. Is 'life-form' a useful concept in bryophyte ecology? Oikos **82**: 223-237.

Bengtsson, J., Fagerström, T., and Rydin, H. 1994. Competition and coexistence in plant communities. Trends in Ecology and Evolution **9**: 246-250.

Bragazza, L. and Gerdol, R. 1996. Response surfaces of plant species along water-table depth and pH gradients in a poor mire on the southern Alps (Italy). Annales Botanici Fennici **33**: 11-20.

Cahill, J.F. Jr. 1999. Fertilization effects on interactions between above- and belowground competition in an old field. Ecology **80**: 466-480.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Casper, B.B. and Cahill, J.F. Jr. 1996. Limited effects of soil nutrient heterogeneity on populations of *Abutilon theophrasti* (Malvaceae). American Journal of Botany **83**:333-341.

Chapin, F.S. III, Oechel, W.C., Van Cleve, K., and Lawrence, W. 1987. The role of mosses in the phosphorus cycling of an Alaskan black spruce forest. Oecologia **74**: 310-315.

Clymo, R.S. 1984. *Sphagnum* dominated peat bog: a naturally acid ecosystem. Philosophical Transactions of the Royal Society of London B. **305**: 487-498.

Clymo, R.S. and Hayward, P.M. 1982. The ecology of *Sphagnum*. *In* Bryophyte Ecology. *Edited by* A.J.E. Smith. Chapman and Hall, London, U.K. pp. 229-289.

Clymo, R.S. and Reddaway, E.J.F. 1971. Productivity of *Sphagnum* (bog-moss) and peat accumulation. Hydrobiologica **12**: 181-192.

Clymo, R.S. and Duckett, J.G. 1986. Regeneration of *Sphagnum*. New Phytologist **102**: 589-614.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Connell, J.H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. The American Naturalist **122**: 661-696.

Crosby, M.R. 1980. The diversity and relationships of mosses: an inquiry into the biology of mosses based upon a symposium sponsored by the Pacific Section, Botanical Society of America. *In* Mosses of North America. Proceedings of a symposium sponsored by the Pacific Section, Botanical Society of America Pacific Division. *Edited by* R.J. Taylor and A.E. Leviton. American Association for the Advancement of Science, San Francisco, California. pp. 115-129.

Dilks, T.J.K. and Proctor, M.C.F. 1979. Photosynthesis, respiration and water content in bryophytes. New Phytologist **82**: 97-114.

During, H.J. 1992. Ecological classification of bryophytes and lichens. *In* Bryophytes and lichens in a changing environment. *Edited by* J.W. Bates and A.M. Farmer. Oxford Science Publications, Oxford, U.K. pp. 1-31.

During, H.J. and van Tooren, B.F. 1987. Recent developments in bryophyte population ecology. Trends in Ecology and Evolution **2**: 89-93.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

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

Fowler, N. 1982. Competition and coexistence in a North Carolina grassland. III. Mixtures of component species. Journal of Ecology **70**: 77-92.

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

Gaudet, C.L. and Keddy, P.A. 1988. A comparative approach to predicting competitive ability from plant traits. Nature **334**: 242-243.

Gaudet, C.L. and Keddy, P.A. 1995. Competitive performance and species distribution in shoreline plant communities: A comparative approach. Ecology **76**: 280-291.

Gerdol, R. 1995. Community and species-performance patterns along an alpine poor-rich mire gradient. Journal of Vegetation Science **6**: 175-182.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Gignac, L.D. 1992. Niche structure, resource partitioning, and species interactions of mire bryophytes relative to climatic and ecological gradients in western Canada. The Bryologist **95**: 406-418.

Gignac, L.D. 1993. Distribution of *Sphagnum* species, communities, and habitats in relation to climate. Advances in Bryology **5**: 187-222.

Gignac, L.D., Vitt, D.H., Zoltai, S.C., and Bayley, S.E. 1991. Bryophyte response surfaces along climatic, chemical and physical gradients in peatlands of Western Canada. Nova Hedwigia **53**: 27-71.

Gignac, L.D., Nicholson, B.J., and Bayley, S.E. 1998. The utilization of bryophytes in bioclimatic modeling: predicted northward migration of peatlands in the Mackenzie River Basin, Canada, as a result of global warming. The Bryologist **101**: 572-587,

Glime, J.M. and Iwatsuki, Z. 1997. Niche partitioning of plant taxa associated with geothermal vents at Wakoto, Hokkaido, Japan. Journal of the Hattori Botanical Laboratory **82**: 123-141.

Goldberg, D.E. 1987. Neighborhood competition in an old-field plant community. Ecology **68**: 1211-1223.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Goldberg, D.E. 1996. Competitive ability: definitions, contingency and correlated traits. Philosophical Transactions of the Royal Society of London B. **351**: 1377-1385.

Goldberg, D.E. and Werner, P.A. 1983. Equivalence of competitors in plant communities: A null hypothesis and a field experimental approach. American Journal of Botany **70**: 1098-1104.

Goldberg, D.E. and Landa, K. 1991. Competitive effect and response: hierarchies and correlated traits in the early stages of competition. Journal of Ecology **79**: 1013-1030.

Goldberg, D.E. and Barton, A.M. 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. The American Naturalist **139**: 771-801.

Goldberg, D.E., Rajaniemi, T., Gurevitch, J., and Stewart-Oaten, A. 1999. Empirical approaches to quantifying interaction intensity: competition and facilitation along productivity gradients. Ecology **80**: 1118-1131.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Gorham, E. 1988. Canada's peatlands: their importance for the global carbon cycle and possible effects of "greenhouse" climatic warming. Transactions of the Royal Society of Canada **3**: 21-23.

Gorham, E. 1991. Northern peatlands: role in the carbon cycle and probable responses to global warming. Ecological Applications **1**: 182-195.

Grace, J.B. 1990. On the relationship between plant traits and competitive ability. *In* Perspectives on plant competition. *Edited by* J.B. Grace and D. Tilman. Academic Press, New York. pp. 51-66.

Grace, J.B. 1991. A clarification of the debate between Grime and Tilman. Functional Ecology **5**: 583-587.

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

Grime, J.P. 1979. Plant strategies and vegetation processes. Wiley, New York.

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

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Grosvernier, P., Matthey, Y., and Buttler, A. 1997. Growth potential of three *Sphagnum* species in relation to water table level and peat properties with implications for their restoration in cut-over bogs. Journal of Applied Ecology **34**: 471-483.

Hanslin, H.M. 1999. Seasonal dynamics of biomass increase and shoot elongation in five co-occurring boreal forest bryophytes. Journal of Bryology **21**: 5-15.

Harper, J.L. 1977. Population biology of plants. Academic Press, Oxford.

Herben, T. and Krahulec, F. 1990. Competitive hierarchies, reversals of rank order and the de Wit approach: are they compatible? Oikos **58**: 254-256.

Ireland, R.R., Brassard, G.R., Schofield, W.B., and Vitt, D.H. 1987. Checklist of the mosses of Canada II. Lindbergia **13**: 1-62.

Jauhiainen, J., Silvola J., Tolonen, K., and Vasander, H. 1997. Response of *Sphagnum fuscum* to water levels and CO_2 concentration. Journal of Bryology **19**: 391-400.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Keddy, P.A. 1989. Competition. Chapman and Hall, Suffolk, U.K.

Keddy, P.A. 1990. Competitive hierarchies and centrifugal organization in plant communities. *In* Perspectives on plant competition. *Edited by* J.B. Grace and D. Tilman. Academic Press, San Diego, California. pp. 265-290.

Keddy, P.A. and Shipley, B. 1989. Competitive hierarchies in herbaceous plant communities. Oikos **54**: 234-241.

Keddy, P.A., Twolan-Strutt, L., and Wisheu, I.C. 1994. Competitive effect and response rankings in 20 wetland plants: Are they consistent across three environments? Journal of Ecology **82**: 635-643.

Keddy, P.A., Gaudet, C.L., and Fraser, L.H. 2000. Effects of low and high nutrients on the competitive hierarchy of 26 shoreline plants. Journal of Ecology **88**: 413-423.

Kenkel, N.C. 1988. Spectral analysis of hummock-hollow pattern in a weakly minerotrophic mire. Vegetatio **78**: 45-52.

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Kooijman, A.M. and Bakker, C. 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.

Kosiba, P. and Sarosiek, J. 1991. Competition between mosses *Catharinea undulata* (L.) Web. et. Mohr. and *Mnium affine* Bland. Ekologia Polska **39**: 377-389.

Kron, K.A. and Judd, W.S. 1990. Phylogenetic relationships within the Rhodoreae (Ericaceae) with specific comments on the placement of *Ledum*. Systematic Botany **15**: 57-68.

Li, Y. and Vitt, D.H. 1994. The dynamics of moss establishment: temporal responses to nutrient gradients. The Bryologist **97**: 357-364.

Li, Y. and Vitt, D.H. 1995. The dynamics of moss establishment: temporal responses to a moisture gradient. Journal of Bryology **18**: 677-687.

Littell, R.C., Milliken, G.A., Stroup, W.W., and Wolfinger, R.D. 1996. SAS system for mixed models. SAS Institute Inc., Cary, N.C.

Longton, R.E. 1984. The role of bryophytes in terrestrial ecosystems. Journal of the Hattori Botanical Laboratory **55**: 147-163.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Longton, R.E. 1992. The role of bryophytes and lichens in terrestrial environments, pp. 32-76. *In* Bryophytes and lichens in a changing environment. *Edited by* J.W. Bates and A.M. Farmer. Oxford Scientific Publications, Claredon Press, Oxford, U.K.

Luken, J.O. 1985. Zonation of *Sphagnum* mosses: interactions among shoot growth, growth form and water balance. The Bryologist **88**: 374-379.

Mankiewicz, P.S. 1987. The low pressure field porometer: a new, low cost technique for characterizing external capillary water conduction in whole colonies of bryophytes and other small plants. The Bryologist **90**:253-262.

Marino, P.C. 1991. Competition between mosses (Splachnaceae) in patchy habitats. Journal of Ecology **79**: 1031-1046.

Moss, E.H. 1983. Flora of Alberta 2nd edition. University of Toronto Press, Toronto.

Mulligan, R.C. and Gignac, L.D. 2001 Bryophyte community structure in a boreal poor fen: reciprocal transplants. Canadian Journal of Botany **79**:404-411.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Mulligan, R.C., Gignac, L.D., Amyotte, R.C., and Frego, K.A. 2002. Determination of bryophyte growth: a weight method allowing for transplant of small groups of shoots. Journal of Bryology: in press.

Nernberg, D. and Dale, M.R.T. 1997. Competition of five native prairie grasses with *Bromus inermis* under three moisture regimes. Canadian Journal of Botany **75**: 2140-2145.

Newton, A.E. and Mishler, B.D. 1994. The evolutionary significance of asexual reproduction in mosses. Journal of the Hattori Botanical Laboratory **76**: 127-145.

Økland, R.H. 1990. A Phytoecological study of the mire Northern Kisselbergmosen, SE Norway. III. Diversity and habitat niche relationships. Nordic Journal of Botany **10**: 191-220.

Økland, R.H. 1994. Patterns of bryophyte association at different scales in a Norwegian boreal spruce forest. Journal of Vegetation Science **5**: 127-138.

Pakarinen, P. 1978. Production and nutrient ecology of three *Sphagnum* species in southern Finnish raised bogs. Annales Botanici Fennici **15**: 15-26.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Price, A.G., Dunham, K., Carleton, T., and Band, L. 1997. Variability of water fluxes through the black spruce (*Picea mariana*) canopy and feather moss (*Pleurozium schreberi*) carpet in the boreal forest of Northern Manitoba. Journal of Hydrology **196**: 310-323.

Proctor, M.C.F. 1982. Physiological ecology, water relations, light and temperature responses, carbon balance. *In* Bryophyte ecology. *Edited by* A.J.E. Smith. Chapman and Hall, London, U.K. pp. 333-381.

Proctor, M.C.F. 1990. The physiological basis of bryophyte production. Botanical Journal of the Linnean Society **104**: 61-77.

Rincon, E. and Grime, J.P. 1989. An analysis of seasonal patterns of bryophyte growth in a natural habitat. Journal of Ecology **77**: 447-455.

Rosch, H. and van Rooyen, M.W. 1997. Competitive effect and response of ten Namaqualand ephemeral plant species at two nutrient levels. South African Journal of Botany **63**: 210-215.

Rydin, H. 1986. Competition and niche separation in *Sphagnum*. Canadian Journal of Botany **64**: 1817-1824.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Rydin, H. 1987. Microdistribution of *Sphagnum* species in relation to physical environment and competition. Symposia Biologica Hungarica **35**: 295-304.

Rydin, H. 1993a. Interspecific competition between *Sphagnum* mosses on a raised bog. Oikos **66**: 413-423.

Rydin, H. 1993b. Mechanisms of interactions among *Sphagnum* species along water-level gradients. Advances in Bryology **5**: 153-185.

Rydin, H. 1995. Effects of density and water level on recruitment, mortality and shoot size in *Sphagnum* populations. Journal of Bryology **18**: 439-453.

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

Rydin, H. 1997b. Competition between *Sphagnum* species under controlled conditions. The Bryologist **100**: 302-307.

SAS Institute Inc. 1989. SAS/STAT user's guide, version 6. SAS Institute Inc., Cary, N.C.

Schoener, T.W. 1983. Field experiments on interspecific competition. American Naturalist **122**: 240-285.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Schwinning, S. and Weiner, J. 1998. Mechanisms determining the degree of size asymmetry in competition among plants. Oecologia **113**: 447-455.

Shaw, A.J. 1992. The evolutionary capacity of bryophytes and lichens. *In* Bryophytes and lichens in a changing environment. *Edited by* J.W. Bates and A.M. Farmer. Claredon Press, Oxford, U.K. pp. 362-380.

Shipley, B. 1993. A null model for competitive hierarchies in competition matrices. Ecology **74**: 1693-1699.

Shipley, B. and Keddy, P.A. 1994. Evaluating the evidence for competitive hierarchies in plant communities. Oikos **69**: 340-345.

Shmida, A. and Ellner, S. 1984. Coexistence of plant species with similar niches. Vegetatio **58**: 29-55.

Sjörs, H. 1950. On the relation between vegetation and electrolytes in north Swedish mire waters. Oikos **2**: 241-258.

Skre, O., Oechel, W.C., and Miller, P.M. 1983. Moss leaf water content and solar radiation at the moss surface in a mature black spruce forest in central Alaska. Canadian Journal of Forest Research **13**: 860-868.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Slack, N.G. 1982. Bryophytes in relation to ecological niche theory. Journal of the Hattori Botanical Laboratory **52**: 199-217.

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

Svensson, B.M. 1995. Competition between *Sphagnum fuscum* and *Drosera rotundifolia*: a case of ecosystem engineering. Oikos **74**: 205-212.

Tilman, D. 1977. Resource competition between planktonic algae: an experimental and theoretical approach. Ecology **58**: 338-348.

Tilman, D. 1985. The resource ratio hypothesis of succession. The American Naturalist **125:** 827-852.

Twenhöven, F.L. 1992. Competition between two *Sphagnum* species under different deposition levels. Journal of Bryology **17**: 71-80.

Twolan-Strutt, L. and Keddy, P. 1996. Above- and belowground competition intensity in two contrasting wetland plant communities. Ecology **77:** 259-270.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

van Breemen, N. 1995. How *Sphagnum* bogs down other plants. Trends in Ecology and Evolution **10**: 270-275.

van der Hoeven, E.C., Korporaal, M., and van Gestel, E. 1998. Effects of simulated shade on growth, morphology and competitive interactions in two pleurocarpous mosses. Journal of Bryology **20**: 301-310.

Watson, M.A. 1981. Patterns of microhabitat occupation of six closely related species of mosses along a complex altitudinal gradient. Ecology **62**:1067-1078.

Wilson, S.D. and Keddy, P.A. 1986. Species competitive ability and position along a natural stress/disturbance gradient. Ecology **67:** 1236-1242.

Wilson, S.D. and Tilman, D. 1991. Components of plant competition along an experimental gradient of nitrogen availability. Ecology **72**: 1050-1065.

Wilson, S.D. and Tilman, D. 1993. Plant competition and resource availability in response to disturbance and fertilization. Ecology **74**: 599-611.

Zamfir, M. and Goldberg, D.E. 2000. The effect of initial density on interactions between bryophytes at individual and community levels. Journal of Ecology **88**: 243-255.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Zar, J.H. 1996. Biostatistical analysis 3rd edition. Prentice Hall, New Jersey, U.S.A.

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Table 3-1 Means of elemental concentrations (mg l^{-1}), pH, corrected conductivity (K_{corr})(µs/cm) and depth to water table (DTW) (cm) ± s.e. for each habitat in the Mariana Lake peatland. Means with the same letter do not differ significantly by variable. *** significant $p < 0.001$. Means for pH calculated by converting to antilog. Statistical tests for pH conducted on raw data.

Habitat	**Ca^{++}**	**Mg^{++}**	**K^{+}**	**P**	**Na^{+}**	**pH**	**K_{corr}**	**DTW**
Non-wooded	1.14±0.1a	0.18±0.03a	0.48±0.1a	0.07±0.02a	1.48±0.3a	4.33±0.29a	22.58±7.5a	5.58±1.0a***
Wooded	1.31±0.1a	0.26±0.04a	0.49±0.2a	0.05±0.02a	1.58±0.3a	4.26±0.01a	18.00±4.8a	20.4±2.3b***

Table 3-2 Analysis of variance for fixed effects of habitat (SITE) and species (TRT), on relative growth rates of weight (regular font) and length (bold font) of the phytometer *Aulacomnium palustre* when grown with various neighbour species after two years in the Mariana Lake, Alberta poor fen. × = interaction; ndf = numerator degrees of freedom; ddf = denominator degrees of freedom F = F value, p = probability. * df was adjusted with Satterthwaite's approximation to correct for multiple error terms.

SOURCE	**ndf**	**ddf**	**F**	**p**
SITE	1	34	2.74	0.1071
TRT	4	34	4.65	0.0042
SITE × TRT	4	34	2.58	0.0548
SITE	**1**	**34**	**0.15**	**0.7010**
TRT	**4**	**34**	**18.40**	**0.0001**
SITE × TRT	**4**	**34**	**2.42**	**0.0673**

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Table 3-3 Analysis of variance for fixed effects of habitat (SITE) and species (TRT) on relative competitive performance expressed as weight (regular font) and length (**bold font**) of the phytometer *Aulacomnium palustre* when grown with various neighbour species after two years in the Mariana Lake, Alberta poor fen. × = interaction; ndf = numerator degrees of freedom; ddf = denominator degrees of freedom F = F value. p = probability.

SOURCE	**ndf**	**ddf**	**F**	**p**
SITE	1	34	2.74	0.1071
TRT	4	34	4.65	0.0042
SITE × TRT	4	34	2.58	0.0548
SITE	**1**	**34**	**0.15**	**0.7010**
TRT	**4**	**34**	**18.40**	**0.0001**
SITE × TRT	**4**	**34**	**2.42**	**0.0673**

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Table 3-4 Competitive rank of the study species in *Sphagnum fuscum* and bog island habitats in the Mariana Lake, Alberta poor fen peatland. Competitive rank is derived from the percent ability of the study species to suppress the growth of the phytometer, *Aulacomnium palustre*. Competitive reversals in bold.

	LENGTH		WEIGHT	
Species	**on-ooded**	**ooded**	**Non-wooded**	**Wooded**
S. magellanicum	1	1	1	1
S. fuscum	2	**3**	2	2
S. angustifolium	3	**2**	3	3
Pleurozium schreberi	4	4	4	**5**
Ptilium crista-castrensis	5	5	5	**4**

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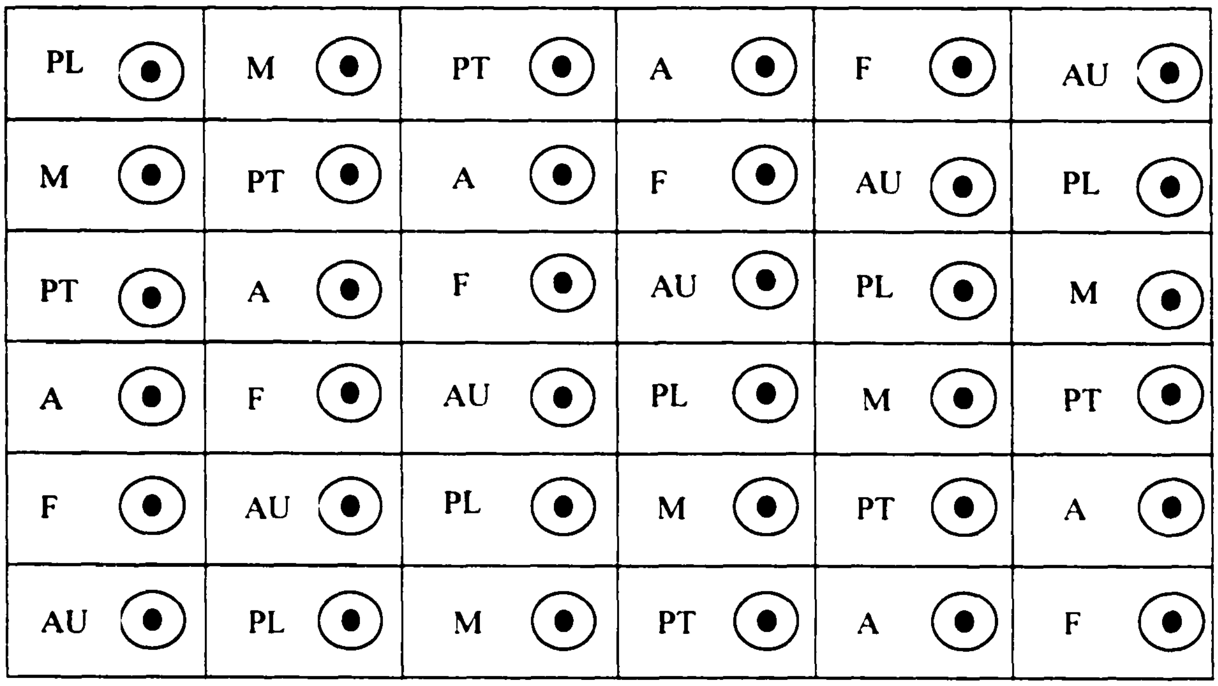

PL ⦿	M ⦿	PT ⦿	A ⦿	F ⦿	AU ⦿
M ⦿	PT ⦿	A ⦿	F ⦿	AU ⦿	PL ⦿
PT ⦿	A ⦿	F ⦿	AU ⦿	PL ⦿	M ⦿
A ⦿	F ⦿	AU ⦿	PL ⦿	M ⦿	PT ⦿
F ⦿	AU ⦿	PL ⦿	M ⦿	PT ⦿	A ⦿
AU ⦿	PL ⦿	M ⦿	PT ⦿	A ⦿	F ⦿

Fig. 3-1 The Latin square design used in the transplant plot set up. The large, unfilled circles are transplant plugs of the neighbour species (abbreviated to the immediate left). The small filled circles are the phytometer bundles of *Aulacomnium palustre*. There was one large plot like this in each of the two habitats (wooded and non-wooded) examined. PL = *Pleurozium schreberi*, M = *Sphagnum magellanicum*, A = *S. angustifolium*, F= *S. fuscum*, AU = *Aulacomnium palustre*.

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Fig. 3-2 The transplant plot in the non-wooded habitat showing avian interference (tags removed), and the PVC well.

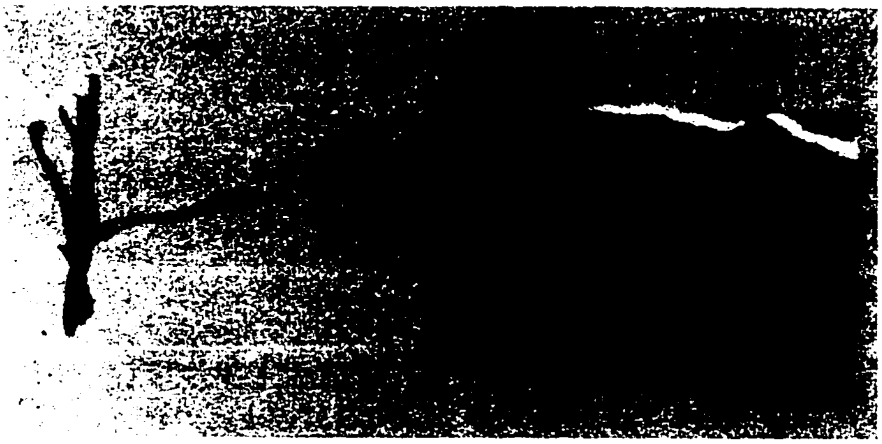

Fig. 3-3 A phytometer bundle of 5 shoots of *Aulacomnium palustre* showing orange thread and aluminum tag.

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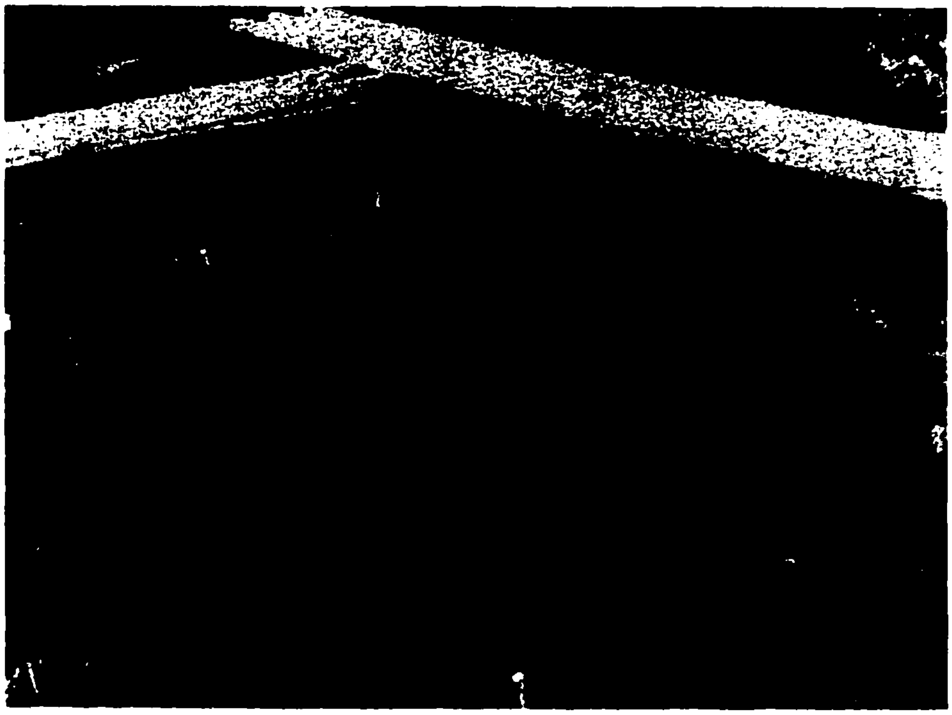

Fig. 3-4 Plot set up in 1995 showing the portable wooden boardwalk used to reduce trampling to the transplant plots during weeding and data collection.

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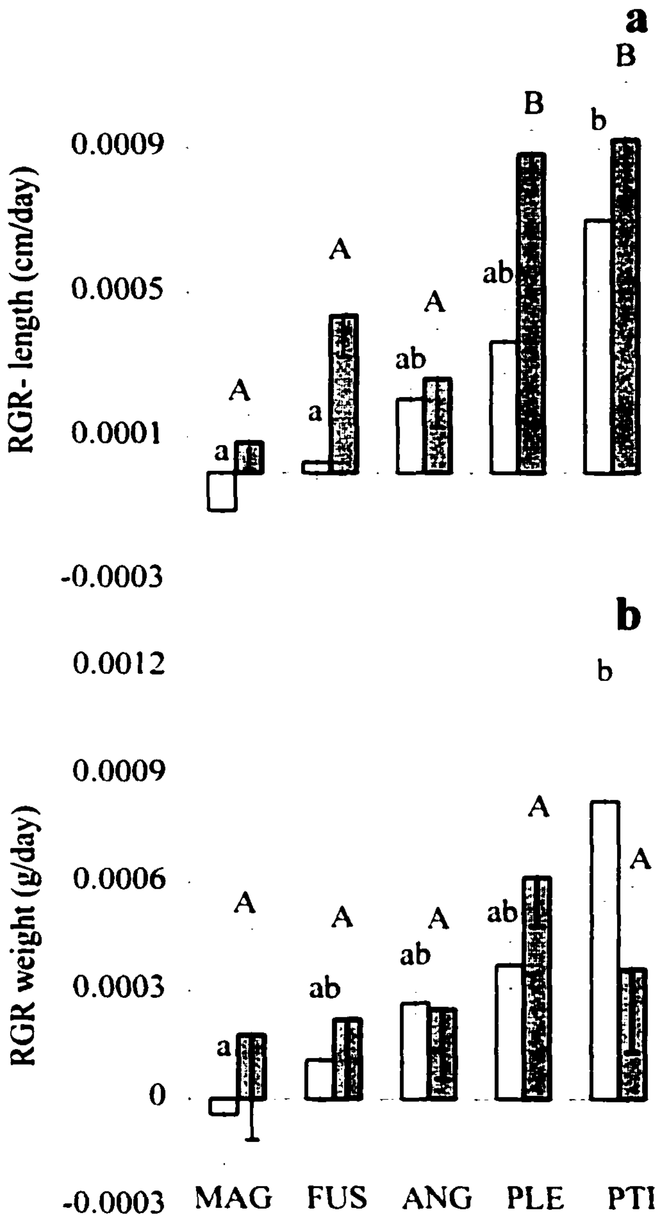

Fig. 3-5 Mean relative growth rate (RGR) in length (a) and weight (b) of the phytometer *Aulacomnium palustre* after two years with various neighbour species in non-wooded (stippled bars) and wooded (open bars) habitats in the Mariana Lake poor fen. MAG = *Sphagnum magellanicum*, FUS = *S. fuscum*, ANG = *S. angustifolium*, PLE = *Pleurozium schreberi*, PTI = *Ptilium crista-castrensis*. Means with the same letter and case size do not differ significantly ($p<0.0025$).

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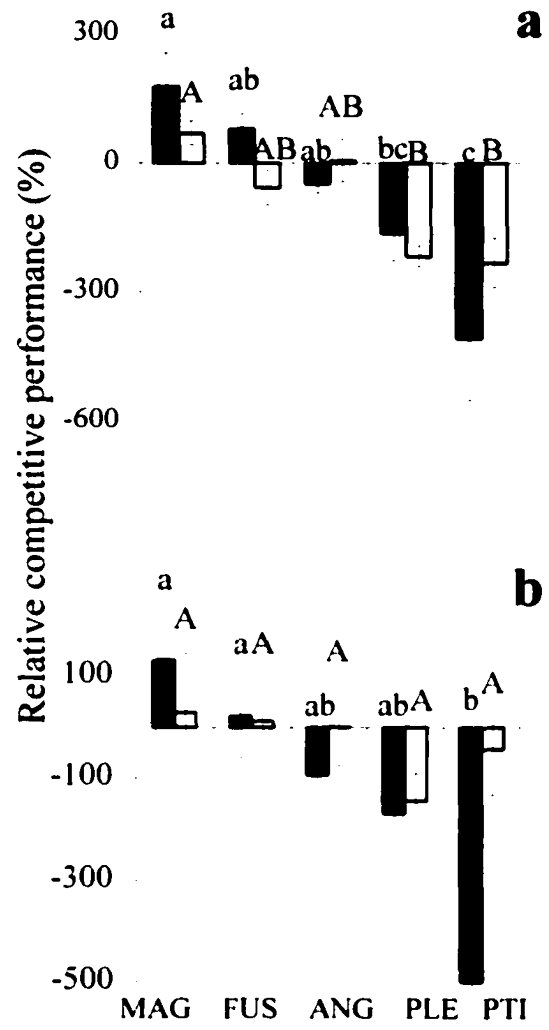

Fig. 3-6 Mean relative competitive performance expressed as percent ability to suppress the growth in length (a) and weight (b) of the phytometer *Aulacomnium palustre* by various neighbour species after two years in non-wooded (grey bars) and wooded (white bars) habitats in the Mariana Lake poor fen. MAG = *Sphagnum magellanicum*, FUS = *S. fuscum*, ANG = *S. angustifolium*, PLE = *Pleurozium schreberi*, PTI = *Ptilium crista-castrensis*. Means with the same letter and case size do not differ significantly ($p<0.0025$).

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Chapter 4- Bryophyte community structure in a high boreal poor fen III: the influence of establishment ability, regeneration niche interactions and facilitation succession

Introduction

Secondary succession, the revegetation of land following disturbance, is a long recognised cornerstone of ecological theory (Cooper 1913; Clements 1916; Gleason 1917; Tansley 1920; Crocker and Major 1955). Despite this, the potential significance of regeneration niche interactions was not formally recognised until 1947 (Watt). Watt's theories were quantitatively examined by Harper (1977) and broadened by Grubb (1977) who defined the regeneration niche as the environmental conditions which will facilitate the replacement of one adult plant by a mature plant of the following generation. In an attempt to apply the competitive exclusion principle to plant communities, Grubb (1977) postulated that differentiation in the regeneration niche could explain the existence of multiple species that appeared to be occupying the same niche. The importance of this succession phase to species diversity in angiosperm

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communities has been investigated in several habitats (Tilman 1993; Špacková *et al.* 1998; Fortin *et al.* 1999; Roy *et al.* 2000).

The possibility that regeneration niche interactions may be equally important to bryophyte communities has been recently recognised (Slack 1990, 1997; Rydin 1997; Cleavitt 2001, 2002). Bryophytes are particularly well suited for regeneration investigations as asexual reproduction from gemmae, dichotomous branching and gametophytic fragments are believed to be the most common method of propagation in many species (Clymo and Duckett 1986; During and van Tooren 1987; Newton and Mishler 1994). As such, there have been many studies, mostly examining asexual regeneration, in the last ten years.

Revegetation by bryophytes during secondary succession has been studied for a variety of disturbances. Post-fire revegetation has been examined in several habitats including: boreal and deciduous forests, waste ground, fields and heathlands (Southorn 1976; Foster 1985; Clément and Touffet 1990; De Las Heras *et al.* 1990). Other types of disturbances that have been examined are: regeneration in small naturally occurring and artificially created forest gaps, fallen logs, trailside trampling and oil field contamination (Studlar 1983; Nakamura 1987; Thomas *et al.* 1994; McAlister 1995; Frego 1996; Kimmerer and Young 1996; Maksimenko *et al.* 1997).

Most of these studies document a strikingly consistent flora in the communities they describe. Bryophyte pioneer communities are dominated by acrocarpous, colonist and fugitive species (*sensu* During 1979) which are relatively short-lived and have high sexual reproductive effort (O'Toole and

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Synnott 1971; Southorn 1976; Foster 1985; During *et al.* 1987; Bremer and Ott 1990; Jonsson 1993; Thomas *et al.* 1994). These colonists include *Funaria hygrometrica* Hedw., *Ceratodon purpureus* (Hedw.) Brid., *Brachythecium rutabulum* Hedw. B.S.G., *Pohlia* spp., *Bryum* spp., and *Polytrichum* spp. The pioneer species are eventually followed by perennial stayers (*sensu* During 1979) such as *Pleurozium schreberi* Brid., *Sphagnum* spp. and *Leucobryum glaucum* (Hedw.) Angstr. Perennial stayers may be acrocarpous or pleurocarpous and largely rely on vegetative reproduction for propagation.

The post-disturbance revegetation of peatlands by bryophytes has recently attracted much interest. Most studies have focussed on the regeneration of *Sphagnum* on peatlands that have been harvested for horticultural purposes. This harvesting removes most of the peat deposit and leaves a dry, hostile environment which usually does not return to its former wetland state (Ferland and Rochefort 1997). The potential usefulness of several *Sphagnum* species to the revegetation of abandoned, harvested peatlands has been examined in many investigations (O'Toole and Synnott 1971; Elling and Knighton 1984; Smart *et al.* 1989; Meade 1992; Salonen 1992; Salonen *et al.* 1992; Campeau and Rochefort 1996; Lavoie and Rochefort 1996; Bugnon *et al.* 1997; Ferland and Rochefort 1997; Grosvernier *et al.* 1997; LaRose *et al.* 1997; Jauhiainen 1998; Nelson *et al.* 1998; Rochefort and Bastien 1998). In addition, Li and Vitt (1994, 1995) examined the effect of moisture and nutrients on the ability of several bryophytes to colonise sterile, bare peat surfaces. These studies document generally good success with Section *Cuspidata* species and mixed results with species from Sections

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Sphagnum and *Acutifolia* (Li and Vitt 1994, 1995; Money 1995; Rochefort *et al.* 1995; Campeau and Rochefort 1996; Nelson *et al.* 1998).

Fire, as an initiator of secondary succession in peatlands, has received much less attention than peat harvesting. Kuhry (1994) used stratigraphic analyses to calculate a 1150 year fire rotation for Western Canadian peatlands. It appears that, unlike peat harvesting, most peatland fires are not severe enough to significantly alter long term (> 30 years) vegetation patterns (Jasieniuk and Johnson 1982; Kuhry 1994).

In this investigation, the ability of six boreal bryophytes to establish from gametophytic fragments on natural burnt peat medium over two years in peatland and botanic garden settings was examined. The species were *Sphagnum fuscum* (Schimp.) Klinggr., *S. angustifolium* C. Jens. ex Russ., *S. magellanicum* Brid., *Pleurozium schreberi* (Brid.) Mitt., *Ptilium crista-castrensis* (Hedw.) De Not. and *Aulacomnium palustre* (Hedw.) Schwaegr. The objectives of this study were i) to determine the ability of each species to establish in the absence of introduced neighbours, ii) to determine the effect of regeneration niche competition on establishment ability, and iii) to discuss the role of the regeneration niche in the community dynamics of the mature bryophyte populations in this peatland.

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Materials and Methods

Study Site

The study site is a continental boreal peatland near Mariana Lake, in Northeastern Alberta (55° 55' N, 111° 58' W), Canada. The climate is boreal cold with a mean annual temperature of 0.2°C and mean annual precipitation of 464.7 mm recorded at the nearest weather station located in Fort McMurray approximately 90 km north (Environment Canada 1990). The peatland is part of a mire complex with three distinct physiognomic sections: the largest area is a poor fen with a ground layer dominated by *Sphagnum angustifolium* and *Carex* spp., and the two smaller areas are a small, non-wooded ombrotrophic area dominated by *S. fuscum* and ericaceous shrubs, and wooded bog islands characterised by stunted *Picea mariana* (Mill.) BSP., *Pleurozium schreberi*, *S. fuscum*, *S. angustifolium* and such angiosperms as *Rubus chamaemorus* L., *Rhododendron groenlandicum* (Oeder) Kron & Judd, and *Smilacina trifolia* (L.) Desf.

Establishment experiment

In June 1996 burnt peat was collected from a burn site 41 km north of Mariana Lake, Alberta. The 132,678 ha fire burned from May 28 until July 10, 1995 (Alberta Environment 1996). The site was covered with charred stunted trees (likely *Picea mariana*), and had some hollows of *Sphagnum* Section *Cuspidata* that had not burned. Blocks measuring approximately 40 × 30 × 15 cm were cut

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from the blackened peat where there was no apparent colonisation. The peat was transported to the Devonian Botanic Garden (DBG), near Edmonton, Alberta, where it was separated into two distinct layers. The first layer was approximately 5 cm deep and was composed of dark black charcoal with *Pleurozium schreberi* remnants. The second layer consisted of approximately 8 cm of grey ash with partially decomposed *Sphagnum* spp. remnants. The two layers were homogenised separately in a recently cleaned soil mixer and placed into rectangular clear plastic Rubbermaid tubs (39.5 × 26.5 × 13.5 cm) in the same order and approximate thickness as the peat arrived (i.e. 5 cm of the first layer was placed on top of 8 cm of the second layer). Prior to receiving the peat, each tub was punctured with 12 water percolation holes (5 mm in diameter) and lined with a 31 × 47 cm sheet of grey fibreglass window screening to prevent invasion of other plants through the holes.

Shoots of *Sphagnum angustifolium*, *S. fuscum*, *S. magellanicum* and *Pleurozium schreberi* were collected from the Mariana Lake fen and *Aulacomnium palustre* was collected from a fen close to the burn site. *Ptilium crista-castrensis* shoots were gathered from the upland boreal forest surrounding the fen. All plants appeared healthy and, since the objective of the study was to determine the ability of the study species to regenerate asexually, plants with sporophytes were discarded. The plants were cleaned with deionized water to remove any contamination (such as other bryophytes or mineral soil), and cut to known length of 5 cm for *Sphagnum* and 3 cm for the others. They were then air-dried for 72 hours and chopped into 2 - 4 mm fragments (Fig. 4-1) using a Black

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and Decker coffee grinder. There were eight treatments, abbreviated as follows: *Aulacomnium palustre* (AUL), *Sphagnum angustifolium* (ANG), control with no fragments (CON), *S. fuscum* (FUS), *S. magellanicum* (MAG), all species (MIX), *Pleurozium schreberi* (PLE) and *Ptilium crista-castrensis* (PTI). All tubs except CON received 45 cm^3 of fragments (whether single species or mixed) which were sprinkled evenly across the entire tub and moistened with deionised water. The removal of a problematic, phenotypically plastic variant of *Sphagnum angustifolium* from the study resulted in the MIX tubs receiving an extra 6.4 cm^3 of *S. angustifolium* fragments.

Forty tubs were placed in the Mariana Lake poor fen in a hummocky, non-wooded area adjacent to a bog island. The tubs were placed in hummock sides along three north-south transects that were 9 m apart. A knife was used to create depressions in the hummocks. In order to align the top of the tubs with the top of the moss mat, the depressions were intentionally cut a bit shallower than the dimensions of the tub to allow for them to sink into the peat. The tubs were inserted randomly into the depressions at approximately 3 - 5 m intervals depending on the availability of suitable hummocks. Only one tub was inserted into each hummock. In order to mimic the natural hummock slope, a spirit level was used to place the tubs on 30° angles (following Li and Vitt 1994) and the tubs were all aligned to face west. The distribution of tubs in the Mariana Lake peatland was as follows: individual tubs of fragments: 6 species × 4 replicates = 24; mixed tubs (all species) 1 × 4 replicates = 4; and 12 controls (no fragments); total tubs = 40.

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In order to mitigate potential losses due to animal interventions, the entire experiment was replicated in a screened-in outdoor enclosure at the DBG. The methodology was similar except for the following: the plastic tubs were placed in 185.5 × 87 × 12 cm plastic trays which were filled with sterile water (reverse osmosis), acidified to pH 4 - 4.7 using 10 mL 6M HCl, stabilised with 50 mL of Tris. HCl buffer and placed on 30^0 angles. Because only 4 control tubs were used, the total number of tubs at this site was 32.

Monitoring and measurement of environmental parameters

The tubs were weeded of angiosperm invaders at least twice each growing season. Electrical conductivity and pH were measured at both sites at least twice per growing season using portable Hanna meters and pH paper. The Tris. HCl buffer was not strong enough to buffer pH during rainfall events, therefore, after one year, the buffer was abandoned and the pH was left to fluctuate. Also at this time, the trays at the DBG were cleaned out to remove debris and fresh water (treated as before except without the HCl) was added. With the exception of this cleaning, the water level at the DBG was left to fluctuate naturally and the tubs were randomly rotated every two months during the growing seasons.

After one growing season, the tubs were mapped using a wire mesh with 216 2 × 2 cm square grid cells. The grid was placed snugly into each tub and the percent cover of all bryophytes in each cell was determined visually. Juvenile plants that were either too crowded or young to identify were designated as "young colonists". *Leptobryum pyriforme* (Hedw.) Wils., *Ceratodon purpureus*

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(Hedw.) Brid. and *Pohlia nutans* (Hedw.) Lindb. were identified from sporophyte-producing plants. The tubs were mapped again in August 1998 using the same method and species categories (Table 4-1). In order to remove edge effects, data from the three top and bottom rows and the four columns closest to the tub side edges were discarded. These data were discarded because the patterns of growth in these rows clearly showed this edge effect. As a result, data from 96 of the original 216 cells were analysed.

In July 1998 the burn site was revisited to document the revegetation. Large areas were still black and uncolonised. Twelve peat blocks (40 × 25 × 10 cm) were extracted at 5 m intervals along two north-south running transects located within 10 m of the original collection site. The bryophyte flora was described using the following relevée method. Three to five small (2 × 2 cm to 5 × 5 cm) patches were selectively chosen to represent different bryophytes and removed from each block. The bryophyte flora from each patch was identified and recorded until no new species were added. Nomenclature follows Ireland *et al.* (1987) for mosses, Schuster (1966) for hepatics and Moss (1983) for all vascular plants except *Rhododendron groenlandicum* (Kron and Judd 1990).

Statistical Analyses

Overall Frequency (All Species) The percent cover data were converted to presence/absence for each species in each of the 96 cells. These data were expressed as percent total frequency per species per tub. In order to balance the design, data from the extra CON tubs from Mariana Lake were randomly

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removed and thus data from only 4 of the original 12 tubs were analysed. Zeros were entered for all species that did not grow in all treatments regardless of whether they were planted (sown) or not. Periods were entered for missing tubs as per SAS specifications. Data were tested for normality using Proc Univariate (SAS Institute 1989) and they did not meet ANOVA assumptions. Proc GLM (SAS Insitute 1989) was used to run MANOVA parametrically. A restricted randomisation test (with species held constant) was run in SAS. The F value (as opposed to the SS) was used for the test because it considers all factors (and interactions) and is considered the more powerful option of the two.

Frequency of Planted Species Mean frequencies of the planted species (in only the tubs in which they were planted) were analysed by site with a non-parametric ANOVA analogue, the Kruskal-Wallis test using Proc NPAR1WAY in SAS (SAS Institute 1989). Mean separations on these data were conducted with Dunn's test (Zar 1996) for tied ranks and unequal sample sizes which was programmed into Excel (Microsoft 1997).

Frequency of Unplanted Species Voluntary recruitment was analysed similarly, in that all data from the six unplanted species was used but only data from volunteer occurrences of planted species such as *Sphagnum angustifolium*, *S. magellanicum* and *Aulacomnium palustre* were analysed. Since it was not possible to determine the exact designation of the young colonisers group, these data were included with voluntary recruitment. A Kruskal-Wallis test was performed with Proc NPAR1WAY (SAS Institute 1989) and mean separations on

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these data were calculated by hand with Nemenyi's test (Zar 1996) for tied ranks and equal sample sizes.

Environmental Data Conductivity was corrected for hydrogen ions and temperature (20°C) following Sjörs (1950). The conductivity and pH data were analysed with the Wilcoxon rank-sum test in SAS (SAS Institute 1989).

Results

Planted (sown) species

Aulacomnium palustre, *Sphagnum angustifolium* and *Pleurozium schreberi* regenerated at Mariana Lake with high mean relative frequency. *Ptilium crista-castrensis* exhibited medium establishment success and the two other Sphagna did not regenerate (Fig. 4-2). *Sphagnum fuscum* did not grow in any tub of any treatment at Mariana Lake. *Sphagnum magellanicum* did not grow in its own tubs, but it was found in very small amounts (mostly in year two) in the MIX, PLE, PTI, CON and FUS treatments.

The pattern was very similar at the DBG (Fig. 4-2). *Aulacomnium palustre* exhibited a mean total frequency that was significantly higher than all other species (Fig. 4-2). *Sphagnum angustifolium*, *Pleurozium schreberi* and *Ptilium crista-castrensis* regenerated with intermediate success and were significantly different from all others. *Sphagnum fuscum* and *S. magellanicum* did not

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regenerate in any tub of any treatment and thus, had mean frequencies that were significantly lower than all others.

All species both sites

Overall, the randomisation test indicated that all factors and interactions were highly significant (Table 4-2). Mean total frequency at the DBG (49.92%) was significantly higher than at Mariana Lake (20.96 %) (Table 4-3). The significance of year is evident as the unplanted species increased in frequency between years one and two partially at the expense of the planted species (Fig. 4-3). Seven tubs were lost due to animal activity: two tubs at the DBG and five at Mariana Lake. Most tubs were aggressively dug up by animals (possibly coyotes) and one was destroyed by ungulate trampling. In order to conduct the most prudent analyses, only data from tubs which survived both years were analysed.

Voluntary recruitment

Some sown species (particularly *Aulacomnium palustre* but to a lesser extent *Sphagnum angustifolium* and *S. magellanicum*) also appeared in treatments in which they were not introduced. Other unplanted species were *Leptobryum pyriforme* (Hedw.) Wils., *Ceratodon purpureus*, *Marchantia polymorpha* L., *Polytrichum* spp., *Dicranum undulatum* Brid. and *Pohlia nutans* (Hedw.) Lindb. (Table 4-1). Additional voluntary species that were identified after the end of the study were *Didymodon fallax* (Hedw.) Zand., *Bryum* cf. *capillare* Hedw.,

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Calliergonella cuspidata (Hedw.) Loeske and *Funaria hygrometrica* (Table 4-1). These species were included in the young colonist category.

The voluntary species separated into three categories (very frequent, intermediately frequent and infrequent) that were fairly consistent between the two sites (Fig. 4-4). *Polytrichum* spp., *Ceratodon purpureus* and the young colonists exhibited mean total frequencies that were significantly higher than all other species (Fig. 4-4). *Aulacomnium palustre* and *Leptobryum pyriforme* demonstrated intermediate frequency, and *Dicranum undulatum*, *Marchantia polymorpha* and *Pohlia nutans* were infrequent.

Flora of the original burn site

Vascular plants included *Rhododendron groenlandicum* (Oeder) Kron & Judd, *Epilobium angustifolium* L., *Picea mariana*, *Smilacina trifolia* (L.) Desf., *Chamaedaphne calyculata* (L.) Moench and *Arctostaphylos uva-ursi* (L.) Spreng. The bryophyte flora consisted of *Ceratodon purpureus*, *Polytrichum* spp., *Plagiomnium* sp., *Tomenthypnum nitens* (Hedw.) Loeske, *Funaria hygrometrica*, *Marchantia polymorpha* and *Aulacomnium palustre*. There was one very small specimen of *Sphagnum* Section *Acutifolia*. No *Pleurozium schreberi* or *Ptilium crista-castrensis* was evident.

Environmental data

Mean pH at the DBG (6.77 ± 0.13) was significantly higher than at Mariana Lake (4.95 ± 0.43) (Wilcoxon W = 861.00, $p<0.0001$). Mean corrected conductivity at

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the DBG (280.87 ± 8.39 µs/cm) was significantly higher than at Mariana Lake (71.21 ± 5.23 µs/cm) (Wilcoxon W = 861.00, p<0.0001).

Discussion

The significant difference between the two sites is likely a function water chemistry differences. The higher pH and K_{corr} at the DBG (compared to the peatland) would be more suitable for the growth of most of the non-Sphagna (Gignac *et al.* 1991). For example, *Ptilium crista-castrensis* had mean total frequencies of 5.36 ± 2.55 at Mariana Lake and 28.75 ± 6.16 at the DBG. Similarly, these water chemistry differences also likely contributed to the differences in growth of *Aulacomnium palustre* which had mean total frequencies of 3.56 ± 0.81 and 27.46 ± 6.40 at Mariana Lake and 37.55 ± 3.64 and 83.72 ± 3.33 at the DBG as volunteer and planted species, respectively.

The success of *Sphagnum angustifolium* in all treatments, years and sites is consistent with other examinations of regeneration of this species and other species of Section *Cuspidata* (Li and Vitt 1994, 1995; Rochefort *et al.* 1995; Campeau and Rochefort 1996; Grosvernier *et al.* 1997). Further, its appearance

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as an unplanted species in several other treatments demonstrates its excellent dispersal abilities. In fact, Grosvernier *et al.* (1997) suggested that *Sphagnum fallax* (also from Section *Cuspidata*) establishes like a r-selected species and later switches to a K-selected strategy.

The prolific growth of *Aulacomnium palustre* (Fig. 4-5) is not surprising given its strong regenerative capabilities and wide nutrient tolerance (Gignac *et al.* 1991; Li and Vitt 1994, 1995; Wassen and Joosten 1996). The appearance of this species in almost every tub at both sites confirms that it is a very good coloniser.

Sphagnum magellanicum and *S. fuscum* are very common, widespread continental Sphagna (Gignac 1992), and their virtual inability to establish on bare peat (Figs. 4-6 and 4-7, respectively) is perplexing but consistent with Li and Vitt (1994, 1995). The complete absence of *Sphagnum magellanicum* from the DBG where there was no propagule source, its inability to colonise in its own tubs at Mariana Lake and its appearance in several tubs in which it was not planted, strongly suggest that its occurrences were the result of sexual reproduction. Therefore, sexual reproduction may be more important for *Sphagnum magellanicum* than current theory (Clymo and Duckett 1986) suggests.

The performance of *Sphagnum magellanicum* and *S. fuscum* is not consistent with that reported by Campeau and Rochefort (1996) who successfully grew both species from fragments in the field. This discrepancy is likely due to the plastic shade cloth used. It appears that *Sphagnum fuscum* is unable to regenerate under field conditions without this added protection. Rochefort *et al.* (1995) also

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successfully grew *Sphagnum magellanicum* (*S. fuscum* was not part of the study) in the field. Other factors possibly responsible for the discrepancies in regeneration success are fragment size and desiccation tolerance. Although Campeau and Rochefort (1996) reported no statistically significant fragment size effect, their fragments (5, 10 and 20 mm) were much larger than those in this study or in Li and Vitt (1995). Further, the importance of using larger (5 - 25 mm) diaspores with the capitulum still attached has been documented for some species including *Sphagnum fuscum* (Campeau and Rochefort 1996; Nelson *et al.* 1998). This is, however, a rather artificial propagation method as fragments of that size, especially with the capitulum attached, would not disperse very far in nature. The coffee grinder used in this study created small fragments (Fig. 4-1) that did not have the capitulum attached.

Another factor was likely desiccation. During the second growing season the fragments encountered drought conditions at both sites. By May 1998 the water level in the peatland had fallen by approximately 20 cm. Sagot and Rochefort (1996) reported that desiccation delays *Sphagnum* fragment establishment and Grosvernier *et al.* (1997) noted that *S. magellanicum* and *S. fuscum* would be less suitable for revegetation trials because their fragments are less adapted to desiccation than those of *Sphagnum fallax*. Therefore, the regeneration niches of *Sphagnum fuscum* and *S. magellanicum* may be very different from that of their adult plants as colony structure is crucial to desiccation tolerance in this genus (Nelson *et al.* 1998).

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It is not possible to ascertain whether the unplanted species grew from the buried diaspore bank or the aerial diaspore rain, but their prevalence at both sites and virtual absence from the mature community, points to facilitation succession as an important mechanism in the development of mature peatland bryophyte communities. For example, it appears that some species, e.g. *Sphagnum fuscum* and *S. magellanicum* require some sort of mature canopy for invasion. Indeed, *Ceratodon purpureus*, *Pohlia nutans* and *Polytrichum* spp. have been found overtopped 20-40 years postfire (Thomas *et al.* 1994). Therefore, although diaspore banks (and their colonist constituents) are acknowledged as common components of the revegetation of commonly disturbed or ephemeral habitats, it is now evident that they may also play an important role in the revegetation of more stable ecosystems such as the boreal forest (Jasieniuk and Johnson 1982; Jonsson 1993) and peatlands (Kuhry 1994; this study). Contrary to Rydin (1997), who contends that most bryophytes likely follow the tolerance model (*c.f.* Connell and Slayter 1977), this study suggests an important role for facilitation succession in peatland bryophyte communities.

Ptilium crista-castrensis and *Pleurozium schreberi* (Fig. 4-8) successfully established in all treatments in which they were planted at both sites. Despite this, feather mosses are not typical components of the early post-fire bryophyte flora in boreal areas (Foster 1985).

A very interesting trend existed between the two years. The planted species such as *Sphagnum angustifolium*, *Pleurozium schreberi* and *Ptilium crista-castrensis* were able regenerate on the burnt peat medium but they mostly lost

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ground in the second year to the unplanted colonists (Fig. 4-4). Although some of the increase in volunteers over this period and the concomitant decline in the young colonists as the result of a better ability to identify the latter in year two, there is still a substantial increase in these (planted) species. Also, it must be assumed that some of the young colonists grew into planted species. Both Sphagna and the feather mosses are categorised as perennial stayers (*sensu* During 1979) or K-selected species (Slack 1982) as they reproduce primarily vegetatively in long-term, potentially stable ecosystems. The decline of these bryophytes (between the two years) is because they lack physiological and morphological adaptations for surviving in an open, bare and hostile environment such as would occur post-fire. The adaptations of the fugitive and colonist bryophytes that permit their proliferation in these disturbed areas include compact growth forms, low age at first reproduction, and high sexual reproductive effort through the production of large quantities of small, long lived spores (During 1979). The post-fire establishment of pleurocarpous mosses and leafy liverworts occurs much later in secondary succession after the fugitives and colonists decline (Southorn 1976; De Las Heras *et al.* 1990; Jonsson 1993).

In conclusion, this investigation corroborates other studies which have documented the ability of Section *Cuspidata* Sphagna (*Sphagnum angustifolium*, in this study) to easily regenerate on bare peat surfaces. *Pleurozium schreberi* and *Ptilium crista-castrensis* successfully established at both sites. The planted K-selected species declined between years at both sites, probably because they lack the morphological and physiological specialisation of the unplanted r-

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selected species. These adaptations enable the r-selected species to regenerate and increase in number and this gives them an advantage in the regeneration niche.

Sphagnum fuscum was not able to colonise in any treatment at either site. The small size and susceptibility of the fragments of this species to desiccation may be contributing factors. It is also possible that *Sphagnum fuscum* fragments have very particular regeneration niche requirements which were not met by the conditions in this study. These requirements may include facilitation by a canopy of colonist and fugitive bryophytes. *Sphagnum magellanicum* did not regenerate at the DBG site and appeared in very small numbers, in treatments in which it was not planted, at Mariana Lake. This suggests that *Sphagnum magellanicum* likely appeared via sexual reproduction and perhaps this method of propagation is more important for this species than previously believed. The regeneration of *Sphagnum magellanicum* may have also been inhibited by desiccation and the small fragments used. *Aulacomnium palustre* exhibited the highest establishment success and this is attributed to its colonist life strategy.

Prolific growth of unplanted fugitive and colonist species such as *Ceratodon purpureus*, *Polytrichum* spp. and *Leptobryum pyriforme* document the importance of these species to postfire succession in peatlands and suggests a more important role for facilitation succession in bryophyte populations than current theory suggests.

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Summary

The ability of six boreal bryophytes (*Sphagnum angustifolium*, *S. fuscum*, *S. magellanicum*, *Pleurozium schreberi*, *Ptilium crista-castrensis* and *Aulacomnium palustre*) to establish from gametophytic fragments on natural burnt peat medium in peatland and botanic garden settings over two years was examined. *Sphagnum fuscum* did not regenerate in any treatment at either site and its present distribution in the peatland may be the result of past facilitation by colonist bryophytes. *Sphagnum magellanicum* failed to grow at the botanic garden or in its own treatments at the peatland and its appearance in other treatments at the peatland suggests colonisation via sexual diaspores. Further, this study suggests that the regeneration niches for these Sphagna are very different than the realised niches of the mature plants.

Sphagnum angustifolium regenerated with good success in all treatments at both sites and appeared via sexual or asexual diaspores in many other treatments. *Pleurozium schreberi* and *Ptilium crista-castrensis* grew successfully in all tubs in which they were planted. *Aulacomnium palustre* established with high frequency at both sites as a planted and unplanted species. Prolific growth of unplanted acrocarpous colonist and fugitive bryophytes suggests an important role for facilitation succession in bryophyte peatland communities following fire. Between the two years of the study the unplanted, r-selected colonists increased in frequency partially at the expense of the planted K-selected species and this

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decline is attributed to an absence of specialisation in the latter for expansion in hostile post-fire habitats.

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Literature Cited

Alberta Environment. 1996. FP48 Fire history database 1983-95. Provincial Forest Fire Center, Forest Protection Division, Land and Forest Service, Edmonton, Alberta.

Bremer, P. and Ott, E.C.J. 1990. The establishment and distribution of bryophytes in the woods of the IJsselmeerpolders, The Netherlands. Lindbergia **16**:3-18.

Bugnon, J.-L., Rochefort, L. and Price, J.S. 1997. Field experiment of *Sphagnum* reintroduction on a dry abandoned peatland in eastern Canada. Wetlands **17**:513-517.

Campeau, S. and Rochefort, L. 1996. *Sphagnum* regeneration on bare peat surfaces: field and greenhouse experiments. Journal of Applied Ecology **33**:599-608.

Cleavitt, N. 2001. Disentangling moss species limitations: the role of physiologically based substrate specificity for six species occurring on substrates with varying pH and percent organic matter. The Bryologist 104:59-68.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Cleavitt, N. 2002. Relating rarity and phylogeny to the autecology of mosses: A comparative study of three rare-common species pairs in the Front Ranges of Alberta, Canada. Ph.D. Dissertation, University of Alberta, Edmonton, Alberta, Canada.

Clément, B. and Touffet, J. 1990. Plant strategies and secondary succession on Brittany heathlands after severe fire. Journal of Vegetation Science **1**:195-202.

Clements, F.E. 1916. Plant succession. Carnegie Institution of Washington Publication. Carnegie Institution of Washington, Washington, D.C.

Clymo, R.S. and Duckett, J.G. 1986. Regeneration of *Sphagnum*. New Phytologist **102**:589-614.

Connell, J.H. and Slayter, R.O. 1977. Mechanisms of succession in natural communities and their roles in community stability and organization. The American Naturalist **111**:1119-1144.

Cooper, W.S. 1913. The climax forest of Isle Royale, Lake Superior, and its development. Botanical Gazette **55**:1-44.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Crocker, R.L. and Major, J. 1955. Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. Journal of Ecology **43**:427-448.

De Las Heras, J., Guerra, J. and Herranz, J.M. 1990. Bryophyte colonization of soils damaged by fire in south-east Spain. Journal of Bryology **16**:275-288.

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

During, H.J. and van Tooren, B.F. 1987. Bryophyte interactions with other plants. Botanical Journal of the Linnean Society **104**:79-98.

During, H.J., Brugues, M., Cros, R.M. and Lloret, F. 1987. The diaspore bank of bryophytes and ferns in the soil in some contrasting habitats around Barcelona, Spain. Lindbergia **13**:137-149.

Elling, A.E. and Knighton, M.D. 1984. *Sphagnum* moss recovery after harvest in a Minnesota bog. Journal of Soil and Water Conservation **39**:209-211.

Environment Canada. 1990. Canadian climate normals 1960-1990. Environment Canada, Ottawa.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Ferland, C. and Rochefort, L. 1997. Restoration techniques for *Sphagnum*-dominated peatlands. Canadian Journal of Botany **75**:1110-1118.

Fortin, M.-J., Payette, S. and Marineau, K. 1999. Spatial vegetation diversity index along a postfire successional gradient in the northern boreal forest. Ecoscience **6**:139-148.

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.

Gignac, L.D. 1992. Niche structure, resource partitioning, and species interactions of mire bryophytes relative to climatic and ecological gradients in Western Canada. The Bryologist **95**:406-418.

Gignac, L.D., Vitt, D.H., Zoltai, S.C. and Bayley, S.E. 1991. Bryophyte response surfaces along climatic, chemical, and physical gradients in peatland of western Canada. Nova Hedwigia **53**:27-71.

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Gleason, H.A. 1917. The structure and development of the plant community. Bulletin of the Torrey Botanical Club **44**:463-481.

Grosvernier, P., Matthey, Y. and Buttler, A. 1997. Growth potential of three *Sphagnum* species in relation to water level and peat properties with implications for their restoration in cut-over bogs. Journal of Applied Ecology **34**:471-483.

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

Harper, J.L. 1977. Population biology of plants. Academic Press, Oxford, U.K.

Ireland, R.R., Brassard, G.R., Schofield, W.B. and Vitt, D.H. 1987. Checklist of the mosses of Canada II. Lindbergia **13**:1-62.

Jasieniuk, M.A. and Johnson, E.A. 1982. Peatland vegetation organization and dynamics in the western subarctic, Northwest Territories, Canada. Canadian Journal of Botany **60**:2581-2593.

Jauhiainen, S. 1998. Seed and spore banks of two boreal mires. Annales Botanici Fennici **35**:197-201.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Jonsson, B.G. 1993. The bryophyte diaspore bank and its role after small-scale disturbance in a boreal forest. Journal of Vegetation Science **4**:819-826.

Kimmerer, R.W. and Young, C.C. 1996. Effect of gap size and regeneration niche on species coexistence in bryophyte communities. Bulletin of the Torrey Botanical Club **123**:16-24.

Kron, K.A. and Judd, W.S. 1990. Phylogenetic relationships within the Rhodoreae (Ericaceae) with specific comments on the placement of *Ledum*. Systematic Botany **15**:57-68.

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

LaRose, S., Price, J. and Rochefort, L. 1997. Rewetting of a cutover peatland: hydrologic assessment. Wetlands **17**:416-423.

Lavoie, C. and Rochefort, L. 1996. The natural revegetation of a harvsted peatland in southern Quebec: a spatial and dendroecological analysis. Ecoscience **3**:101-111.

Li, Y. and Vitt, D.H. 1994. The dynamics of moss establishment: temporal responses to nutrient gradients. The Bryologist **97**:357-364.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Li, Y. and Vitt, D.H. 1995. The dynamics of moss establishment: temporal responses to a moisture gradient. Journal of Bryology **18**:677-687.

Maksimenko, O.E., Chervyakov, N.A., Karkishko, T.I. and Glotov, N.V. 1997. Dynamics of reestablishment of vegetation in an anthropogenically disturbed Sphagnum bog in the territory of an oil field in the Middle Ob region. Russian Journal of Ecology **28**:211-215.

McAlister, S. 1995. Species interactions and substrate specificity among log-inhabiting bryophyte species. Ecology **76**:2184-2195.

Meade, R. 1992. Some early changes following the rewetting of a vegetated cutover peatland surface at Danes Moss, Cheshire, U.K., and their relevance to conservation management. Biological Conservation **61**:31-40.

Microsoft, 1997. Microsoft Excel 97. Microsoft Corporation, Santa Rosa, California.

Money, R.P. 1995. Re-establishment of a *Sphagnum*-dominated flora on cut-over lowland raised bogs. *In* Restoration of temperate wetlands. *Edited by* Wheeler, B.D., Shaw, S.C., Foijt, W.J. and Robertson, R.A. John Wiley and Sons Ltd.

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Moss, E.H. 1983. Flora of Alberta 2nd Ed. Revised by John G. Packer. University of Toronto Press, Toronto.

Nakamura, T. 1987. Bryophyte and lichen succession on fallen logs and seedling establishment in *Tsuga-Abies* forest of central Japan. Symposia Biologica Hungarica **35**:485-495.

Nelson, M.A., Smale, P.E., Alspach, P.A. and Klinac, D. 1998. Effects of light and diaspore type on the regeneration and growth or two *Sphagnum* species collected from two New Zealand locations. Journal of Bryology **20**:17-25.

Newton, A.E. and Mishler, B.D. 1994. The evolutionary significance of asexual reproduction in mosses. Journal of the Hattori Botanical Laboratory **76**:127-145.

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

Rochefort, L., Gauthier, R. and Lequéré, D. 1995. *Sphagnum* regeneration-toward an optimisation of bog restoration. *In* Restoration of temperate wetlands. *Edited by* Wheeler, B.D., Shaw, S.C., Foijt, W.J. and Robertson, R.A. John Wiley and Sons, New York.

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Rochefort, L. and Bastien, D.F. 1998. Réintroduction de sphaignes dans une tourbière exploitée: évaluation de divers moyen de protection contre la dessiccation. Ecoscience **5**:117-127.

Roy, V., Ruel, J.-C. and Plamondon, A.P. 2000. Establishment, growth and survival of natural regeneration after clearcutting and drainage on forested wetlands. Forest Ecology and Management **129**:253-267.

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

Sagot, C. and Rochefort, L. 1996. Tolérance des Sphaignes à la dessiccation. Cryptogamie, Bryologie et Lichénologie **17**:171-183.

Salonen, V. 1992. Effects of artificial plant cover on plant colonization of a bare peat surface. Journal of Vegetation Science **3**:109-112.

Salonen, V., Penttinen, A. and Särkkä, A. 1992. Plant colonization of a bare peat surface: population changes and spatial patterns. Journal of Vegetation Science **3**:113-118.

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SAS Institute. 1989. SAS/STAT User's Guide. Version 6. Fourth Edition. SAS Institute Inc., Cary. N.C., U.S.A.

Schuster. R.M. 1966. The Hepaticae and Anthocerotae of North America East of the hundredth meridian. Columbia University Press. New York.

Sjörs. H. 1950. On the relation between vegetation and electrolytes in North Swedish mire waters. Oikos **2**:241-258.

Slack. N.G. 1982. Bryophytes in relation to ecological niche theory. Journal of the Hattori Botanical Laboratory **52**:199-217.

Slack. N.G. 1990. Bryophytes and ecological niche theory. Botanical Journal of the Linnean Society **104**:187-213.

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

Smart. P.J.. Wheeler. B.D. and Willis. A.J. 1989. Revegetation of peat excavations in a derelict raised bog. New Phytologist **114**:733-748.

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Špacková, I., Kotorová, I. and Lepš, J. 1988. Sensitivity of seedling recruitment to moss, litter and dominant removal in an oligotrophic wet meadow. Folia Geobotanica **33**:17-30.

Southorn, A.L.D. 1976. Bryophyte recolonization of burnt ground with particular reference to *Funaria hygrometrica* I. Factors affecting the pattern of recolonization. Journal of Bryology **9**:63-80.

Studlar, S.M. 1983. Recovery of trampled bryophyte communities near Mountain Lake, Virginia. Bulletin of the Torrey Botanical Club **110**:1-11.

Tansley, A.G. 1920. The classification of vegetation and the concept of development. Journal of Ecology **8**: 118-149.

Thomas, P.A., Proctor, M.C.F. and Maltby, E. 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. 1993. Species richness of experimental productivity gradients: how important is colonization limitation? Ecology **74**:2179-2191.

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Wassen, M.J. and Joosten, J.H.J. 1996. In search of a hydrological explanation for vegetation changes along a fen gradient in the Biebrza Upper Basin (Poland). Vegetatio **124**: 191-209.

Watt. A.S. 1947. Pattern and process in the plant community. Journal of Ecology **35**:1-22.

Zar, J.H. 1996. Biostatistical analysis 3rd edition. Prentice Hall, New Jersey, U.S.A.

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Table 4-1 Flora of regeneration experiment including Mariana Lake, DBG and original burn sites. Only species that were quantified are abbreviated.

Category	**Description (if applicable)**	**Abbreviation**
Leptobryum pyriforme		LEP
Pohlia nutans		POH
Ceratodon purpureus		CER
Polytrichum spp.	*Polytrichum commune* and *P. strictum*	POL
Marchantia polymorpha		MAR
Young colonists	Colonisers too young to identify	YC
Calliergonella cuspidata		
Didymodon fallax		
Funaria hygrometrica		
Tomenthypnum nitens		
Bryum cf. *capillare*		

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Table 4-2 The results of multiple analysis of variance (general linear model) of the effect of year, site, treatment (trt) and species (spp) on relative frequency of planted and volunteer species at both sites run paramterically (first four columns) and with a restricted randomisation test (last column) based on F value. × = interaction, DF = degrees of freedom, SS = sum of squares, F = F value, p = probability, p rand. = probability from randomisation test.

Source	DF	SS	F	p	p rand.
Year	1	1394.53	10.78	0.0011	<0.0001
Site	1	90698.29	701.33	<0.0001	<0.0001
Trt	7	3460.89	3.82	0.0004	<0.0001
Spp	12	589398.35	379.80	<0.0001	<0.0001
Year × site	1	1790.74	13.85	0.0002	<0.0001
Year × spp	12	41757.98	26.91	<0.001	<0.0001
Year × trt	7	1829.21	2.02	0.0497	<0.0001
Site × spp	12	157610.68	101.56	<0.001	<0.0001
Site × trt	7	769.35	0.85	0.5460	<0.0001
Trt × spp	84	71194.11	6.55	<0.001	<0.0001
Year × site × trt	7	387.55	0.43	0.8851	<0.0001
Year × site × spp	12	39709.05	25.59	<0.001	<0.0001
Year × trt × spp	84	12822.36	1.18	0.1343	<0.0001
Site × trt × spp	84	24361.68	2.24	<0.001	<0.0001
Year×site×trt×spp	84	8479.54	0.78	0.9261	<0.0001
Error	1118	144583.88			

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Table 4-3 The results of Kruskal-Wallis non-parametric analysis of variance of relative frequency (both years combined) of planted (bold font) and volunteer (regular font) species (main effect) at DBG (Devonian Botanic Garden) and ML (Mariana Lake) sites. The significant tests indicate that the regeneration capability of the species differed when they were divided into these (planted and unplanted) categories. Mean separations were conducted with Dunn's and Nemenyi tests. DF = degrees of freedom, SS = sum of squares, MS = mean square, F = F value, p = probability.

Site	Source	DF	SS	MS	F	p>F
DBG	**Among**	**5**	**74815.41**	**04963.08**	**59.38**	**0.0001**
	Within	**89**	**22427.04**	**251.99**		
ML	**Among**	**5**	**14134.05**	**2826.81**	**11.36**	**0.0001**
	Within	**80**	**19918.00**	**248.98**		
DBG	Within	7	430018.23	61431.18	133.6	0.0001
	Among	480	220717.68	459.83		
ML	Within	7	123352.29	17621.76	125.7	0.0001
	Among	576	80757.11	140.20		

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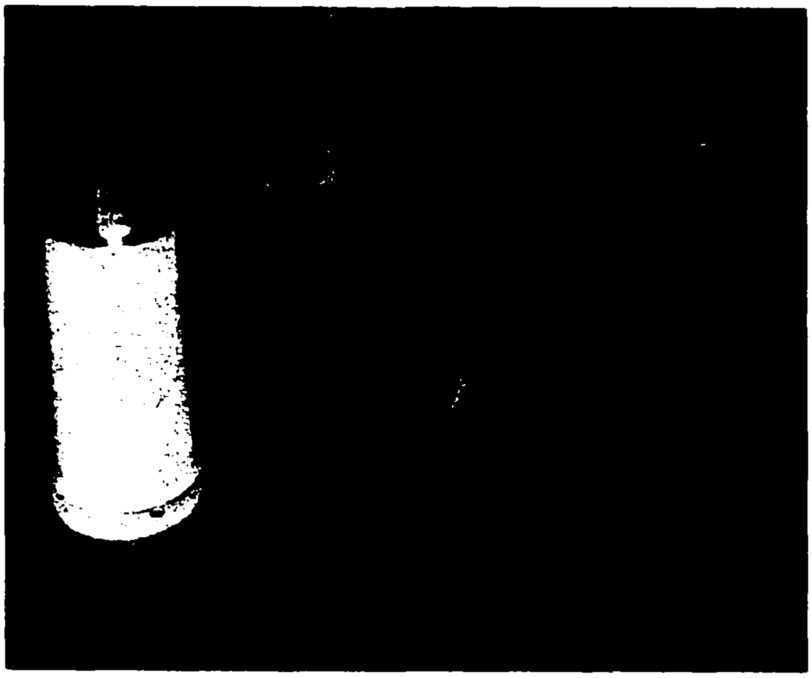

Fig. 4-1 The coffee grinder and the gametophytic fragments (*Aulacomnium palustre* in this case) created by it.

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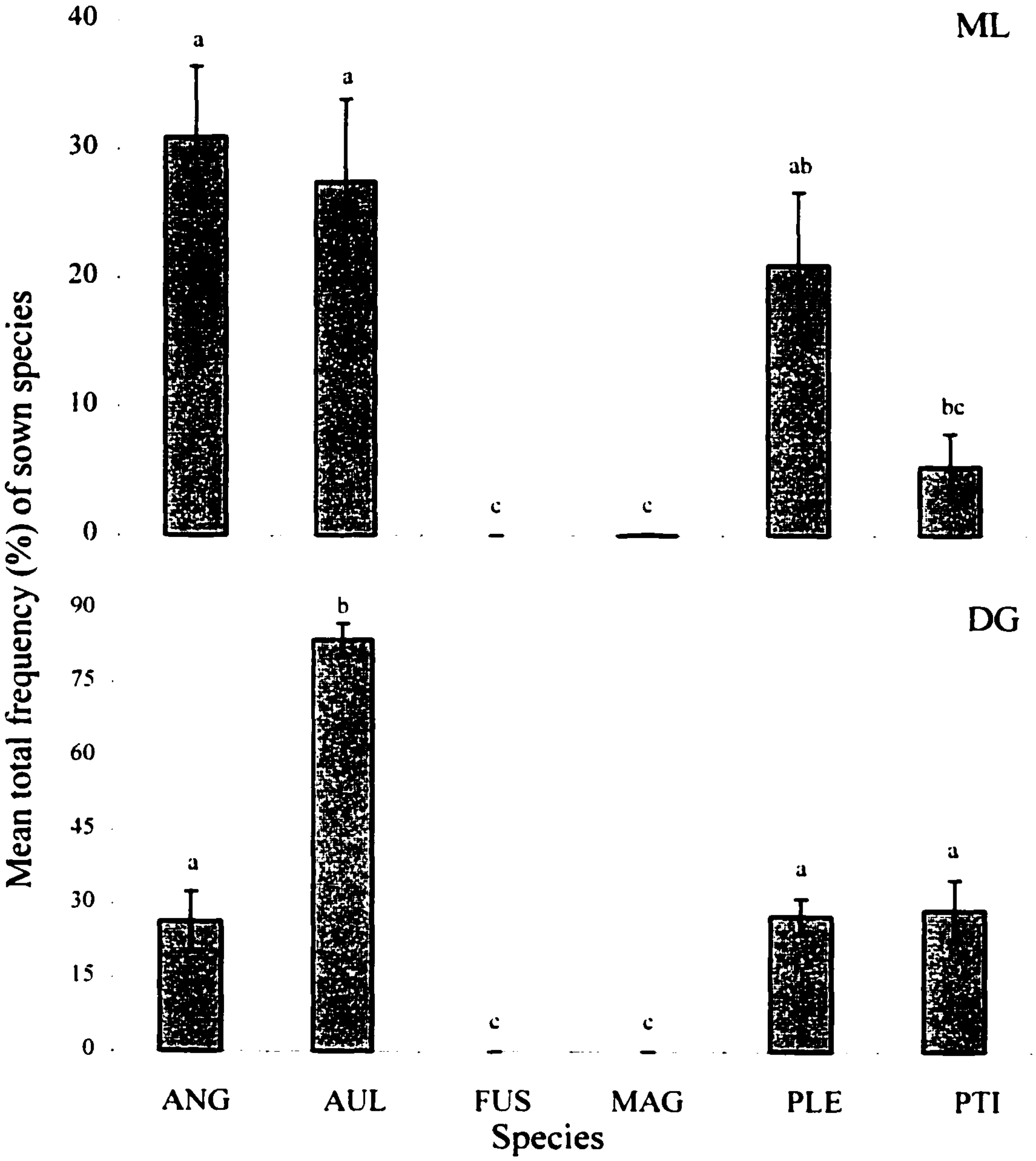

Fig. 4-2 Mean relative frequency (%) of planted (sown) species from the tubs in which they were sown at Mariana Lake (ML) and Devonian Botanic Garden (DBG) sites. Means with the same letter do not differ significantly at $p<0.05$. ANG = *Sphagnum angustifolium*, FUS = *S. fuscum*, MAG = *S. magellanicum*, AUL = *Aulacomnium palustre*, PLE = *Pleurozium schreberi*, PTI = *Ptilium crista-castrensis*.

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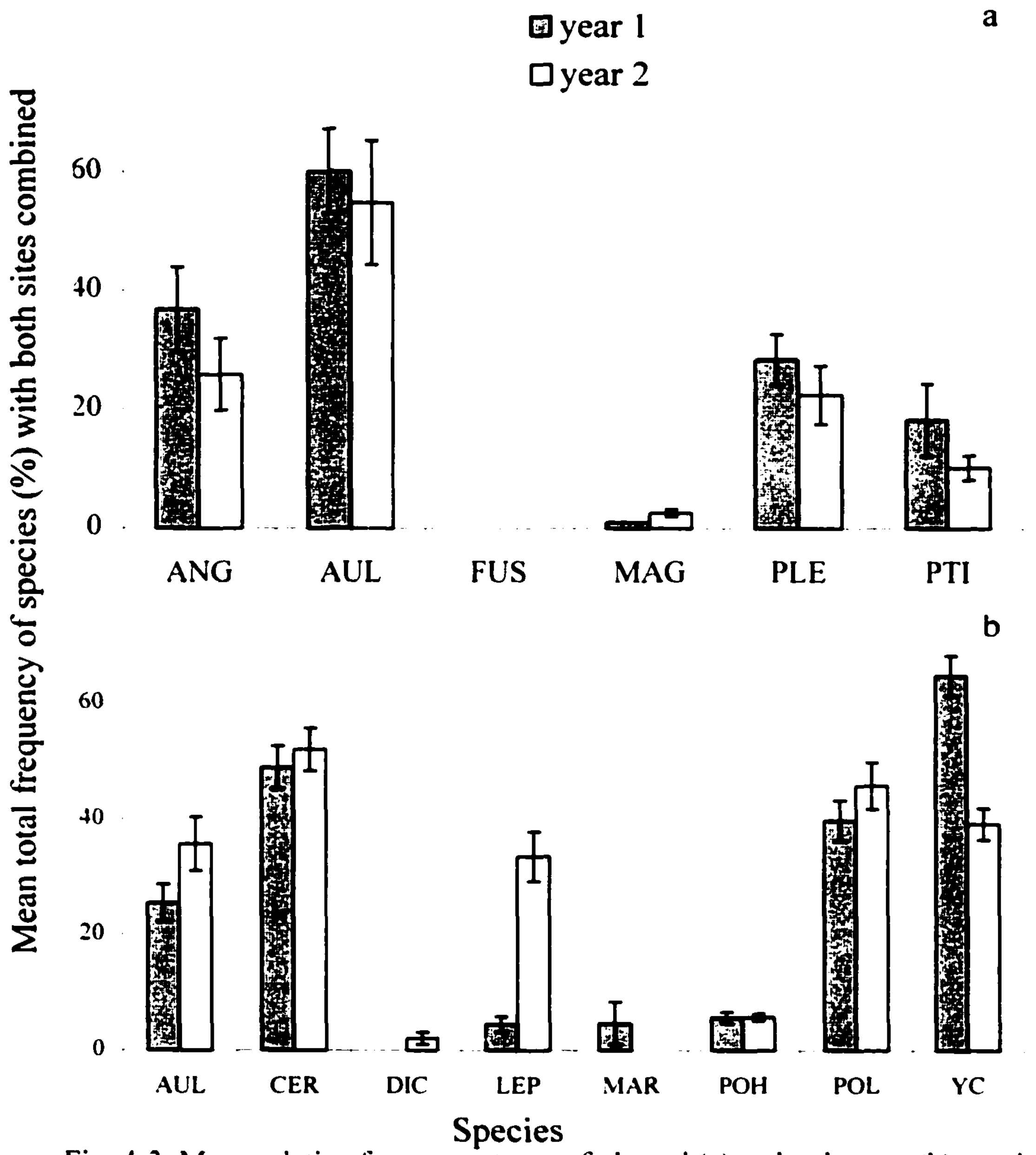

Fig. 4-3 Mean relative frequency ± s.e. of planted (a) and volunteer (b) species at the Mariana Lake and Devonian Botanic Garden sites (combined) from year one (grey bars) and year two (white bars). ANG = *Sphagnum angustifolium*. FUS = *fuscum*, MAG = *S. magellanicum*, AUL = *Aulacomnium palustre*, PLE = *Pleurozium schreberi*, PTI = *Ptilium crista-castrensis*. For other abbreviations see Table 4-1.

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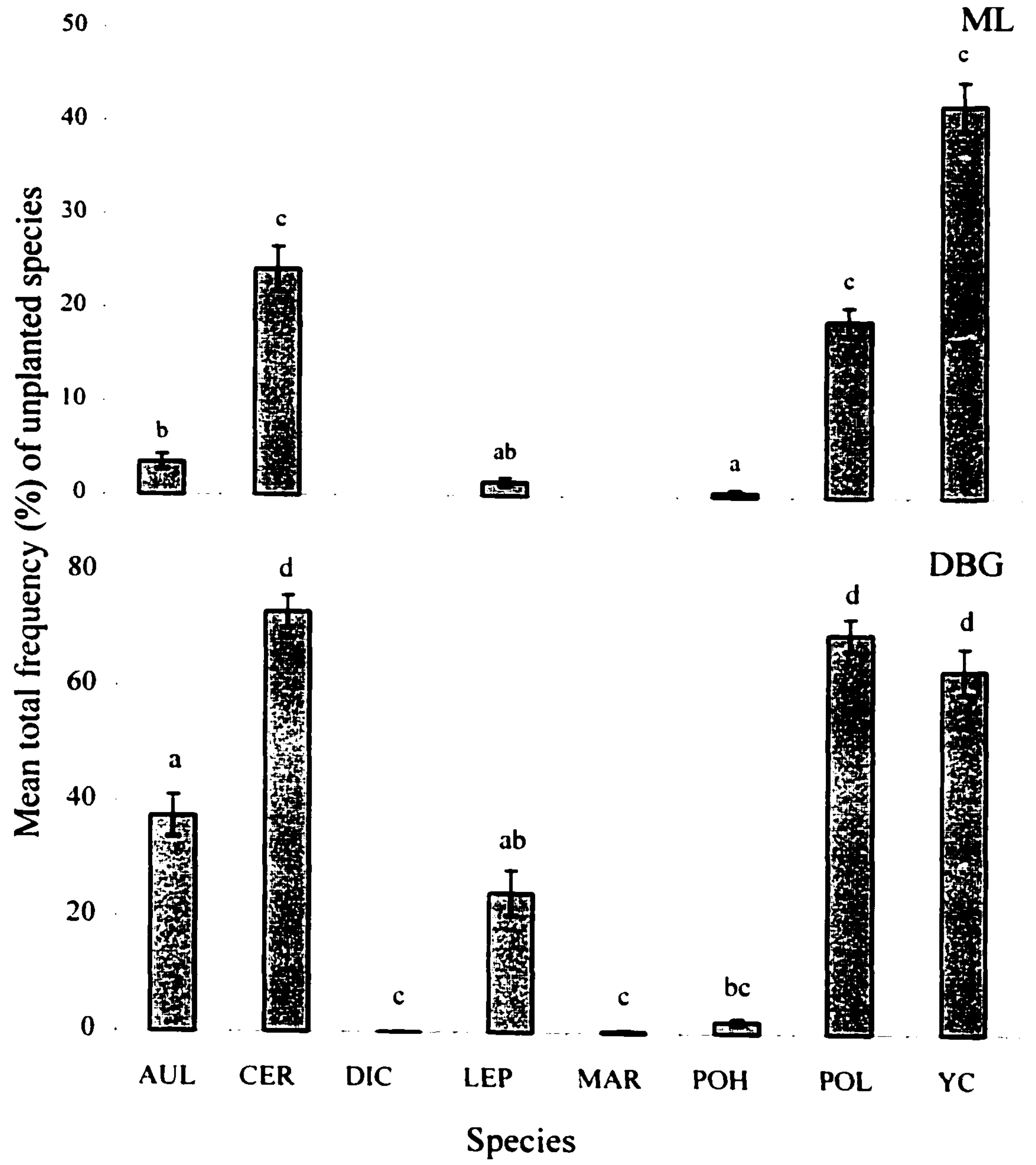

Fig. 4-4 Mean relative frequency (%) of volunteer species at Mariana Lake (ML) and Devonian Botanic Garden (DBG) sites. Means with the same letter do not differ significantly at $p<0.05$. For other abbreviations see Table 1.

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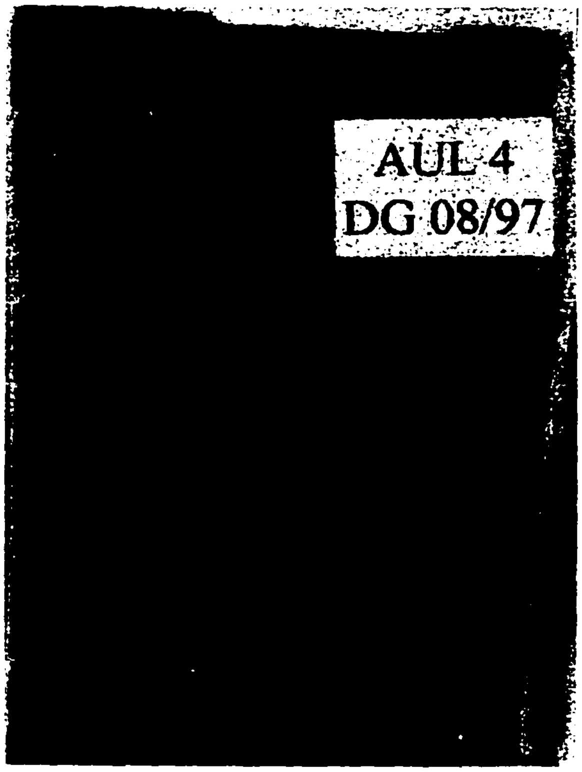

Fig. 4-5 Regeneration tub of *Aulacomnium palustre* illustrates the prolific growth of this colonist and growth of the volunteers.

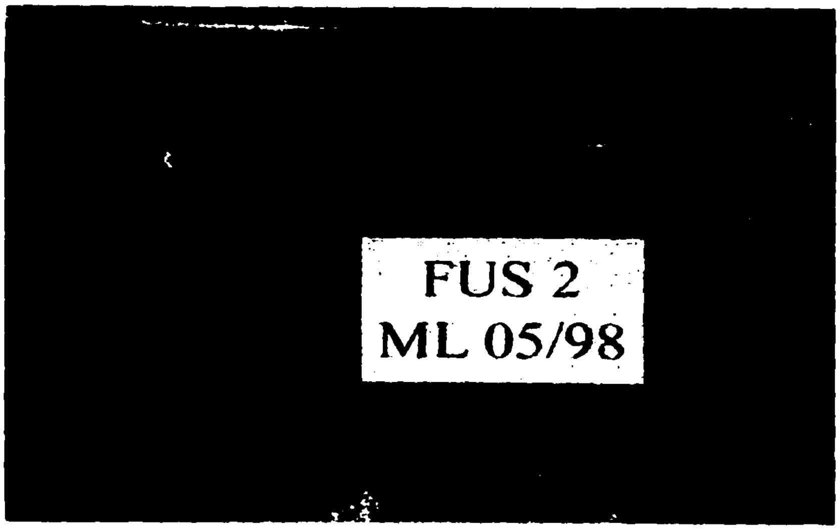

Fig. 4-6 *Sphagnum fuscum* failed to grow in any treatment or site. The *Sphagnum* in this tub from Mariana Lake is *S. angustifolium*.

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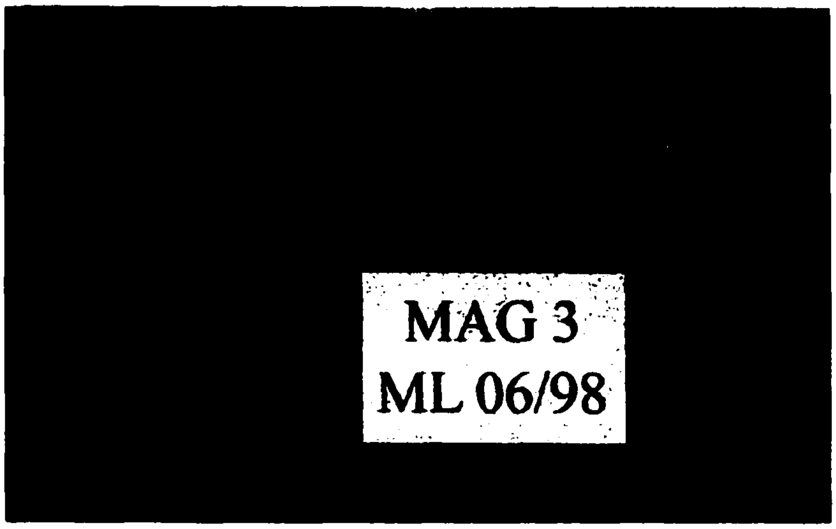

Fig. 4-7 ***Sphagnum magellanicum*** **did not regenerate in any tub at either site. The** ***Sphagnum*** **in this tub from Mariana Lake is** ***S. angustifolium.***

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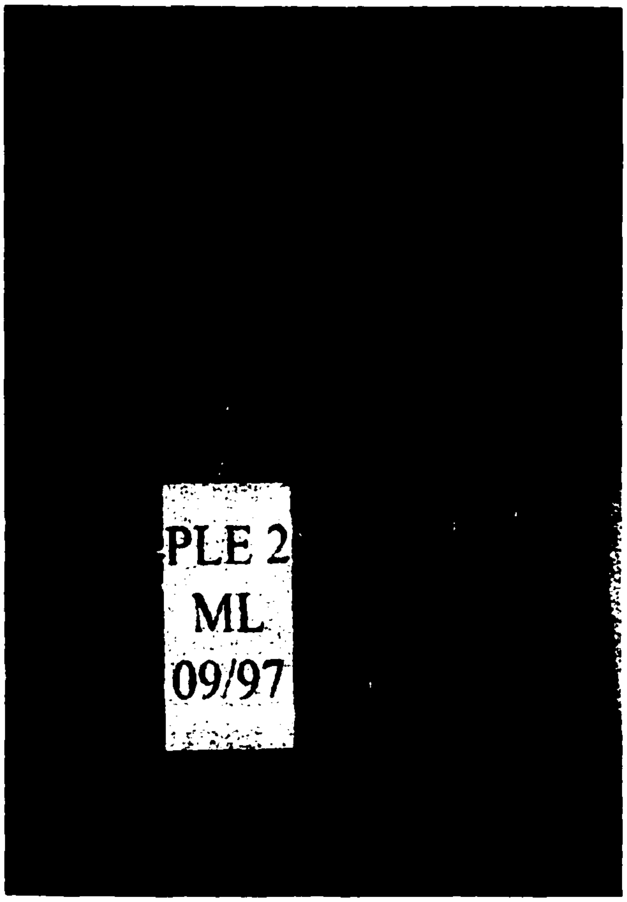

Fig. 4-8 *Pleurozium schreberi* regenerated with good success.

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Chapter 5- Determination of bryophyte growth: a weight method allowing for transplant of small groups of shoots

Introduction

Accurate determination of bryophyte growth is important because it is usually the criterion by which the response to, and significance of, experimental manipulation is determined. For example, bryophyte growth studies have been used to delineate species' responses to important abiotic factors such as light (Hayward and Clymo 1983; Rincon 1993), nutrients (Li *et al.* 1993; Gerdol *et al.* 1998), water (Clymo 1973; Fowbert 1996) and temperature (Furness and Grime 1982; Potter *et al.* 1995). In boreal forest species, growth responses are important as these mosses play critical roles in primary production, nutrient cycling and water retention (Skre *et al* 1983; Oechel and Van Cleve 1986; Carleton and Read 1991; Price *et al.* 1997). In peatland bryophytes, growth rates are necessary to determine global carbon pool contribution, construct accurate climate change models, calculate yield

A version of this chapter has been accepted for publication. Mulligan, R.C., Gignac, L.D., Amyotte, R.C. and Frego, K.A. 2002. Determination of bryophyte growth: a weight method allowing for transplant of small groups of shoots. Journal of Bryology: in press.

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potential and develop restoration methods for harvested peatlands (Gorham 1994; Ferland and Rochefort 1997; Gignac *et al.* 1998; Stokes *et al.* 1999).

The methods of determining bryophyte growth are both numerous and diverse (Clymo 1970; Russell 1984, 1988). A review of 80 bryophyte growth investigations revealed nine methods for measuring length and three for weight. This lack of methodological uniformity presents difficulties with respect to experimental design, data interpretation and data cross-referencing (Rieley *et al.* 1979; Wielgolaski *et al.* 1981; Hanslin 1999). Furthermore, 35% of reviewed investigations relied solely on elongation, i.e. change in shoot length, as a growth parameter. Although the importance of measuring both length and weight has been demonstrated (Clymo 1970; Rincon 1988; Rincon and Grime 1989), weight is often overlooked in bryophyte growth studies, as its direct measurement is particularly challenging.

When weight was measured, most (85%) investigations used one of two extrapolation methods. Weight may be extrapolated from measurements of shoot elongation, i.e., the shoots are cut to a known length at the beginning of the investigation and new growth is cut and weighed directly at the end of the study (Lindholm and Vasander, 1990; Potter *et al.* 1995; Zechmeister 1995; Fowbert 1996). The accuracy of this procedure is questionable as the relationship between growth in length and weight is much weaker than previously assumed for some acrocarpous, pleurocarpous and *Sphagnum* species (Rincon and Grime 1989; Jauhiainen *et al.* 1997; Hanslin 1999).

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Weight may also be extrapolated from shoots external to the investigation. As it is impossible to obtain initial oven dry weight without mortality, this weight is often estimated from groups of "similar" shoots (Chapman 1965; Furness and Grime 1982; Rincon 1988; Li *et al.* 1992; Kooijman and Bakker 1993; Jauhiainen *et al.* 1994). This is a procedure which must be used with caution because moss gametophytes of the same species cut to the same length can exhibit high variability in weight, which may result in imprecise estimates (Clymo 1970; Clymo and Hayward 1982; Russell 1988). For example, Clymo (1970) noted that the coefficient of variation for weights of *Sphagnum magellanicum* plants cut to 5 cm in length was 37% (n = 20).

A method that does not rely on estimates from either length increase or "similar" shoots uses linear regression to estimate initial dry weight from air-dried shoots (Hanslin 1999). One problem with this method is the possibility that air-drying may negatively impact growth and survival of the shoots. Although no negative effects on the study species were noticed by Hanslin (1999), pre-trial tests indicated a strong negative effect on *Sphagnum girgensohnii* and the author cautioned that the method may not be suitable for species from more mesic and hydric habitats.

A method that circumvents the potential difficulties of all these methods is to estimate dry weight from the moist experimental shoots. This procedure does not kill the plants and the moist shoots may then be transplanted or

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otherwise manipulated. Moist weight is rarely used in bryophyte growth experiments, accounting for only 5% of studies (Shimizu *et al.* 1984; van der Hoeven *et al.* 1998; Sastad *et al.* 1999). In addition, Frego and Carleton (1995) adapted Mankiewicz's (1987) moist weight technique to quantify growth of 10-cm diameter colonies of four boreal forest bryophytes.

Mankiewicz (1987) used a salad spinner as a centrifuge to remove all available water from external capillary spaces. Most ectohydric bryophytes with unistratose leaves exhibit a poikilohydric habit wherein water is both lost and gained easily and rapidly through external capillary transfer. The external water comprises most of the water by volume of the plants (Dilks and Proctor 1976; Busby and Whitfield 1978; Hedderson and Longton 1996). Centrifugation standardises the hydration such that the plants are in a state of equilibrium. Simple linear regression is used to estimate initial dry weight of colonies from the weight of moist spun colonies.

In this investigation, the Mankiewicz (1987) method was modified and field-tested to facilitate its use with small groups of bryophytes (as opposed to colonies). The study species include one acrocarpous moss, *Aulacomnium palustre* (Hedw.) Schwaegr.; two pleurocarpous feather mosses, *Pleurozium schreberi* (Brid.) Mitt. and *Ptilium crista-castrensis* (Hedw.) De Not.; and three Sphagna: *Sphagnum angustifolium* (Russ.) C. Jens (Section *Cuspidata*), *S. magellanicum* Brid. (Section *Sphagnum*) and *S. fuscum* (Schimp.) Klinggr. (Section *Acutifolia*).

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The objective of this investigation is to offer bryophyte ecologists a uniform, field-tested weight determination method appropriate for use with a variety of mosses including wetland species. This is achieved in a sequence of steps: (1) determination of the number of revolutions required to bring groups of shoots to a standardised moisture content, and its relationship to the number of shoots in the group; (2) calibration of the relationship between moist and dry weights; (3) test of the accuracy of the calibration, using new shoots from the populations for which the relationship was derived; (4) field-test of the accuracy of the calibration by using it to measure growth in a transplant experiment; (5) investigation of the robustness of the method by testing it on shoots from a range of different populations.

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Materials and Methods

Description of the method

Bundle size and rotation level. Healthy shoots of the study species were collected from a mixed mire complex near Mariana Lake, Alberta, Canada 55° 57'N, 112 ° 01' 30"W during June 1998 and refrigerated at 3°C until used. Gametophytes were cut to equal length (50 mm), except for *Aulacomnium palustre*, which was cut to 30 mm. Shoots were grouped as "shoot bundles" of 5, 10, 15, 20 or 25, saturated in distilled water and spun at 12 levels (1, 2, 3, 4, 5, 10, 15, 20, 25, 30, 40, and 50 rotations). The shoots were spun at a speed of 190 rotations per minute in a standard plastic salad spinner with an inner diameter of 21 cm to generate a force of approximately 40 times gravity. The salad spinner had a 3:1 gear ratio meaning that each complete rotation of the handle spun the inner basket three times. After spinning, the shoots were immediately weighed on a Mettler PE 3600 scale. The shoot bundles were rehydrated after each rotation level. For example, a shoot bundle was cut, hydrated, spun once, weighed, rehydrated and then spun twice, etc. It was therefore possible to record the weight decrease in order to determine how many revolutions were necessary to remove all available external water from the shoots.

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Repeated measures analysis of variance (SPSS Inc. 1993) was used to determine the significance of within subject (rotation number) and between subject (bundle size and species) effects and interactions. Tukey's multiple comparison test (Zar 1996) was used for mean separations, and to determine the rotation level at which each species and bundle size reached equilibrium ("cut-off point"). The cut-off point was defined as the first occurrence of a non-significant pairwise comparison providing that the coefficient of variation of the remaining means was <5%. For example, if the first non-significant pairwise comparison was between spins four and five, then spin four was the cut-off point providing that the coefficient of variation of the means of spins 5-12 was <5%. Simple linear regression (SAS Institute 1989) between cut-off point and mean initial weight of the shoot bundles was used to determine the relationship between these variables.

The relationship between moist weight and actual dry weight. New shoots were collected, stored and cut as previously described, with the exception that only 25-shoot bundles were used. This bundle size was chosen for further analyses as it exhibited less damage in the salad spinner and would be easier to recover in the field. Over 4500 shoots were used: 25 shoots per bundle × 30 replicate bundles × six species. Shoot bundles were saturated in distilled water, spun 20 times, and immediately weighed, with weight recorded as moist weight. The shoots were air dried for a minimum of 48 hours to give

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actual dry weight. Some species e.g. *Sphagnum magellanicum* were dried for 96 hours. Simple linear regressions (SAS Institute 1989) between moist weight and actual dry weight were used to determine the relationship between these variables.

Accuracy of the method

The relationship between actual and predicted dry weights. In order to determine the accuracy of the method, an additional ten new shoot bundles per species were prepared as before. Dry weights were predicted by inserting the moist weight value into the regression, and comparing the result to actual dry weight after 48-96 hours of air drying. Mean absolute error (MAE), which was used as a measure of accuracy, was calculated as:

$$\frac{|\text{predicted dry weight (g)} - \text{actual dry weight (g)}|}{\text{actual dry weight (g)}} \times 100\ \% \qquad [1]$$

Field-testing. The method was tested with shoots of *Sphagnum angustifolium*, *S. fuscum*, *S. magellanicum* and *Pleurozium schreberi* in a back transplant experiment (i.e. *S. angustifolium* transplanted into *S. angustifolium*) in the Mariana Lake peatland (Mulligan and Gignac 2001). The experiment, conducted from June 1998 to June 1999, used transplant plugs measuring 17 cm diameter and approximately 20 cm in length. The

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plugs were cut from homogeneous areas representing typical habitats for each species using a metal stovepipe. The central 25 shoots of each plug were extracted, cut to 50 mm in length, soaked in distilled water for 20 minutes and rotated 20 times in the salad spinner. Each shoot bundle was weighed to give moist weight. The bundles were tied with orange nylon thread and reinserted into the transplant plugs. The transplant plugs (containing the shoot bundles) were inserted into the holes created by the stovepipe. Growth as length was determined by measuring shoot elongation, calculated as total final length per 25 shoot bundle minus total initial length per bundle (25 shoots × 5 cm = 125 cm per bundle). Growth as dry weight was determined by subtracting final dry weight from initial predicted dry weight. Predicted initial dry weights were obtained from regression equations as previously outlined.

The growth measured as both length and weight of the transplanted shoots was compared to that of groups of 25 untransplanted shoots. The latter were samples of each species obtained within 1 m of each transplanted plug, with growth first determined as elongation using annual (innate) growth markers (Russell 1984, 1988) from June 1998 until June 1999. Annual growth markers occur due to seasonal influences which result in differences in leaf size, branching, and sporophyte production (Russell 1988). These markers are convenient for measuring annual growth of bryophytes in temperate, boreal and arctic climates. Three samples of each species were removed from the immediate vicinity of each control transplant plug (e.g.

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Sphagnum fuscum transplanted into *S. fuscum* habitat) for growth marker analysis.

Growth of untransplanted *Sphagnum angustifolium* was determined from stem markers which are distinct bends in the stem (Fig. 5-1) due to the weight of the snow from the preceding winter (Russell 1988; Jappinen and Hotanen 1990). Twenty-five shoots of each species were cut for each of the three replicates. The gametophytes were air-dried for 3 days and placed in a Cenco heater at 30°C for 24 hours of final drying, after which they were weighed immediately.

In autumn apical growth of *Sphagnum magellanicum* slows with shortening day lengths. Internode lengths shorten and branches become crowded to produce distinct clumps (Fig. 5-2) (Hayward and Clymo 1982). Growth of untransplanted *Sphagnum magellanicum* from June 1998 until June 1999 was determined with these branch markers using the same procedure followed for the bend markers on *S. angustifolium*.

Changes in branching pattern and pigmentation have been used as growth markers for *Sphagnum fuscum* (Pakarinen and Tolonen 1977; Belyea and Warner 1994). No growth markers were evident on *Sphagnum fuscum* in the present study, however, isolated gametophytes of *Sphagnum magellanicum* may be found throughout *S. fuscum*. *Sphagnum* species growing in close proximity must maintain the same growth rate (i.e. maintain their capitula at the same level) in order to prevent the effects of etiolation (in the case of

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slower growth) or desiccation (in the case of faster growth) (Hayward and Clymo 1983; Rydin 1993a, b). Since *Sphagnum magellanicum* must increase in length as the same rate as *S. fuscum* to retain its presence on the hummock, *S. fuscum* growth rates can be deduced from the measurable growth of *S. magellanicum*. *Sphagnum magellanicum* shoots growing in the *S. fuscum* hummock were removed and their growth determined using these markers.

Dry weight was also determined. New gametophyte tissue (growth) was cut off three replicates groups of 25 shoots of each species, air-dried for 72 hours, placed in a Cenco heater at 30°C for 24 hours of final drying and immediately weighed. The student's *t*-test was used to determine significant differences between growth in length and weight of the transplanted vs. untransplanted specimens.

It was not possible to determine the transplanting effect for *Pleurozium schreberi*. The annual occurrence of perichaetia and/or perigonia (Longton 1985) and changes in branching patterns (Zechmeister 1995) have been used as growth markers for this species in the past, however success of this approach has been limited. Further, the *Pleurozium schreberi* in this study exhibited no discernible annual branching patterns and the occurrence of sex organs was too sporadic to permit their use.

Robustness of the method

The robustness of the method was tested with shoots from four other locations

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in Alberta, Canada (Fig. 5-3). Robustness is the ability of the method to predict initial dry weight from moist weight for other populations of the same species without building another regression equation. Shoots of *Sphagnum fuscum*, *S. angustifolium*, *Ptilium crista-castrensis*, and *Pleurozium schreberi* were treated as previously outlined with the exception that these shoots were air dried for 72 hours and then oven dried at 30°C in a Cenco heater. The original regression equations were used to predict initial dry weight from moist weight. Initial predicted dry weights were compared with actual dry weights using MAE as a measure of accuracy.

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Results

Bundle size, rotation level and regression analyses

The greatest water loss occurred during the first five rotation levels (1, 2, 3, 4, 5) (Fig. 5-4). Hydration of all bundle sizes of *Aulacomnium palustre* levelled off very quickly, after only one or two turns of the salad spinner. *Sphagnum fuscum*, *S. angustifolium* and *Pleurozium schreberi* lost water quickly, usually reaching equilibrium after four or five spins (Fig. 5-4). *Ptilium crista-castrensis* and *Sphagnum magellanicum* lost water slowly and typically required between 10 and 20 spins to reach equilibrium (Fig. 5-4). Cut-off point was significantly dependent on mean initial moist weight ($R^2 = 0.55$, $p < 0.001$). Dry weight was significantly dependent on moist weight for all species ($p < 0.001$) with R^2 values ranging from 0.89 for *Sphagnum magellanicum* to 0.99 for *S. angustifolium* (Fig. 5-5). The effects of rotation level (time), species (trt), bundle size (bundsize) and all possible interactions on moist weight were highly significant ($p < 0.001$) (Table 5-1). Multiple comparisons of species effect indicated that the mean moist weights of *Sphagnum magellanicum* and *Aulacomnium palustre* were significantly different from all others (Fig. 5-6).

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Accuracy and robustness of the method

The accuracy of the method to predict initial dry weight from moist weight, as indicated by MAE, ranged from 90-98% (Table 5-2). For all species except *Sphagnum magellanicum*, *t*-tests revealed no significant difference in growth measured as length or weight (Fig. 5-7) between shoots that were back-transplanted into their own habitats and untransplanted shoots (i.e. growth measured using annual markers). Transplanted shoots of *Sphagnum magellanicum* grew significantly less than untransplanted shoots in both length (2.32 ± 0.75 cm vs 6.81 ± 1.52 cm) and weight (0.34 ± 0.16 g vs. 0.99 ± 0.31 g) respectively (Fig. 5-7). The robustness of the method, as indicated by MAE, was highly variable and ranged from 65-99% (Table 5-3).

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Discussion

Water movement in bryophytes occurs via four pathways: hydroids (the internal water conduction cells in some species e.g. *Polytrichum*), cell walls, cell to cell, or external capillary spaces (Proctor 1982). Most bryophytes, including all in this study, are ectohydric, with water conduction occurring primarily through external capillary spaces (Romanov 1968; Busby and Whitfield 1978; Hayward and Clymo 1982). External water is loosely held in large spaces (150-1500 µm in *Sphagnum*) between leaves, branches, stems and individual gametophytes (Hayward and Clymo 1982). The majority of remaining water is internal and held more tightly in smaller intracellular spaces (1.5 –15 µm in *Sphagnum*) in hyaline cells and pores (Hayward and Clymo 1982). The rate of water loss rate results from a complex synergy of physiological, morphological and environmental factors including: the number, size and configuration of external capillary and internal spaces; special features such as hair tips, papillae, lamellae, and rhizoids; and depth to water table, boundary layer resistance, and windspeed (Proctor 1982, 1990). The number, size and configuration of spaces is further dependent on such features as colonial structure, growth form, branch architecture, shoot density and leaf size and shape. Unfortunately, quantitative data regarding the size of external capillary spaces is very sparse (see, however, Hayward and Clymo

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1982). In this investigation, the force applied by the salad spinner was sufficient to empty only the larger, external capillary spaces such as those between branches and leaves.

It is not surprising that rotation level significantly affected moisture content (Table 5-1), i.e. that weight declined with additional spins until the equilibrium point was reached. However, the success of this method clearly requires that the minimum number of spins for the particular volume and species being tested, and the G-force generated by the particular salad spinner be reached.

The significant differences in moist weight among species (Table 5-1) are a function of both relative shoot size and initial water contents. Based on these characteristics, species fall into three categories with different patterns of water loss (Fig. 5-4). *Aulacomnium palustre*, the smallest moss tested, lost water very rapidly. This is consistent with its small size (low dry weight) and flat leaves, which are less effective for water retention because they lack the reservoir effect created by concave leaves. *Ptilium crista-castrensis* and *Sphagnum magellanicum* lost water slowly, presumably because their large size (Fig. 5-6) confers greater water holding capacity. Mosses of intermediate dry and moist weights, i.e. *Sphagnum fuscum*, *S. angustifolium* and *Pleurozium schreberi*, lost water at an intermediate rate. The greater water holding capacity of *Ptilium crista-castrensis* over *Pleurozium schreberi*, was noted by Busby and Whitfield (1978), and is presumably conferred by its

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strongly falcate secund leaves which create smaller spaces than the loosely imbricate leaves of *P. schreberi*.

It is generally believed that colony structure affects the rate of water loss (Proctor 1982, 1990; Silvola and Aaltonen 1984; Schipperges and Rydin 1998). In their natural colonial form, species with more compact colony structure, such as *Aulacomnium palustre*, *Sphagnum fuscum* and *S. magellanicum* should lose water more slowly than the feather mosses and *S. angustifolium* which grow in loose tufts or mats. Based on the dense packing of gametophytes and well-developed pendent branches in hummock-inhabiting Sphagna, which provide smaller external capillary spaces and hence superior water-holding capacity (Rydin 1985; Gerdol *et al.* 1996; Grosvernier *et al.* 1997; Jauhiainen *et al.*1998), *Sphagnum angustifolium* should lose water faster than the hummock-forming species (*S. fuscum* and *S. magellanicum*). For some mosses, bundles of 25 shoots behaved as one would predict their colonies would, i.e. *Sphagnum angustifolium* and *Pleurozium schreberi* lost water rapidly and *S. magellanicum* lost water slowly, however bundles of the others did not exhibit water loss patterns that would be expected from their colonial characteristics. Combined with the significant relationship between moist weight and rotation level needed to reach equilibrium, this study indicates that shoot size and the anatomical and morphological characteristics of individual shoots may have a greater combined effect on water retention than colonial architecture. Therefore,

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some of the traditional water-relations differences between these species were lost through manipulation, in removing shoots to form bundles and/or in the artificial environment of the salad spinner which separated shoots. Clymo (1973) documented reduced growth in *Sphagnum* shoots due to handling, with damage increasing as the frequency of handling episodes increased. Even careful handling can disrupt capillary bonds with longer capillary bonds such as those in *Sphagnum papillosum* (Section *Sphagnum*) being more susceptible to breakage (Hayward and Clymo 1982). This breakage likely explains the transplanting effect noted for *Sphagnum magellanicum* (Fig. 5-7), which is very similar in size and branch architecture to *S. papillosum*. A similar effect was also noted in a reciprocal transplant study (Mulligan and Gignac 2001) where *Sphagnum magellanicum* performed better in the wetter *S. angustifolium* habitat than in its own. Evidence of transplanting effect, which we attribute to disruption of capillary bonds by handling, suggests that special caution should be exercised if species of Section *Sphagnum* are to be transplanted. The absence of a transplanting effect for all other species tested in this investigation illustrates the suitability of the moist weight method for field use, specifically for transplant studies.

The very strong relationship between dry and moist weight (i.e. equilibriated moisture content) for all species was expected and has been reported in other studies. For example, this relationship has been documented for *Pleurozium schreberi* (R^2= 0.87) and *Ptilium crista-castrensis* (R^2= 0.54),

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Calliergonella cuspidata (R^2=0.99) and *Rhytidiadelphus squarrosus* (R^2=0.98), and *Sphagnum angustifolium* (R^2=0.92), (Frego 1994, van der Hoeven *et al.* 1998; Sastad *et al.* 1999, respectively). The documentation of this relationship validates the prediction of initial dry weight from initial moist weight.

As expected, bundle size significantly affected moist weight (Table 5-1). Since all bundle sizes reacted differently to the spinning treatment (data not shown), prospective investigators should carefully select the bundle size most appropriate to their experimental design. It should be noted that bundle size may affect the relationship between moist and dry weight as the R^2 for 5 shoots of *Aulacomnium palustre* was only 0.67 (Mulligan unpublished data).

The accuracy of the method to predict initial dry weight from initial moist weight was impressive, with MAE for all species < 10% (Table 5-2). The accuracy of the method with specimens from other locations was less impressive, as the robustness of the method was highly variable. This variability is likely caused by differences in growth rates. Considerable between-location variation in growth and habitat-specific genotypic variation and phenotypic plasticity have been documented for some *Sphagnum* spp. and *Pleurozium schreberi* (Clymo 1970; Baxter *et al.* 1989; Wachowiak-Zielinska and Zielinski 1995; Sastad *et al.* 1999). Therefore, it is recommended that all samples tested with this method be obtained from the same population, preferably within the same growing season.

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In conclusion, the moist weight growth determination method is a highly accurate and inexpensive technique for weight measurement of small groups of bryophytes. The robustness of the method was variable, suggesting caution in the use of material from outside the study location for which the predictive equation is calibrated. It is important for investigators wishing to use this method to conduct pre-trial experiments in order to ascertain the water-relations of the specific populations of each bryophyte species to be examined. Although the efficacy of this method has been demonstrated for the species in this study, other mosses may require slightly different treatment. This method may not be suitable for endohydric species which generally do not transplant well due to their internal conduction (e.g., *Polytrichum* spp.).

The method, which is appropriate for use in laboratory and field studies including transplant experiments, may be used with a variety of different species and growth forms. Such versatility illustrates its potential for widespread use, which may facilitate greater use of weight as a growth parameter in future investigations. Moreover, the method allows for circumvention of some of the potentially inaccurate bryophyte weight growth methods in current use.

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Summary

A review of 80 bryophyte growth studies revealed that change in dry weight is a measurement that is often ignored or extrapolated, either from "similar" shoots that are external to the investigation or from increases in shoot elongation. The weight that is actually gained or lost by the experimental shoots themselves is rarely measured, thus potentially leading to high experimental error. In order to address this concern, an existing (although rarely utilised) method was modified, calibrated and field-tested in a back transplant experiment to allow for prediction of initial dry weight from moist weight of the experimental shoots. Centrifugation with a salad spinner was used to bring the moisture contents of small groups of saturated shoots of pleurocarpous (*Pleurozium schreberi*, *Ptilium crista-castrensis*), acrocarpous (*Aulacomnium palustre*) and *Sphagnum* (*Sphagnum angustifolium*, *S. magellanicum* and *S. fuscum*) mosses to equilibrium. Regression analyses, which indicated highly significant relationships between dry and moist weight for all species, were used to predict dry weight from moist weight. The accuracy of the method was calculated as mean absolute error and ranged from 90-98% depending on the species. The robustness of the moist weight method, tested with populations from four other locations, was highly variable, ranging from 65-96%. The method is versatile, inexpensive and potentially applicable for widespread use.

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Literature Cited

Baxter, R., Emes, M.J. and Lee, J.A. 1989. Effects of the bisulphite ion on growth and photosynthesis in *Sphagnum cuspidatum*. New Phytologist **111**:457-462.

Belyea, L.R. and Warner, B.G. 1994. Dating of the near-surface layer of a peatland in northwestern Ontario, Canada. Boreas **23**:259-269.

Busby, J.R. and Whitfield, D.W.A. 1978. Water potential, water content, and net assimilation of some boreal forest mosses. Canadian Journal of Botany **56**:1551-1558.

Carleton, T.J. and Read, D.J. 1991. Ectomycorrhizas and nutrient transfer in conifer–feather moss ecosystems. Canadian Journal of Botany **69**:778-785.

Chapman, S.B. 1965. The ecology of Coom Rigg Moss, Northumberland. III. Some water relations of the bog system. Journal of Ecology **53**:371-384.

Clymo, R.S. 1970. The growth of *Sphagnum*: methods of measurement. Journal of Ecology **58**:13-49.

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Clymo, R.S. 1973. The growth of *Sphagnum*: some effects of environment. Journal of Ecology **61**:849-869.

Clymo, R.S. and Hayward, P.M. 1982. *Sphagnum* Ecology. *In* Bryophyte ecology. *Edited by* A.J.E. Smith. Chapman and Hall, London. pp 229-289.

Dilks, T.J.K. and Proctor, M.C.F. 1976. Effects of intermittent desiccation on bryophytes. Journal of Bryology **9**:249-264.

Ferland, C. and Rochefort, L. 1997. Restoration techniques for *Sphagnum*-dominated peatlands. Canadian Journal of Botany **75**:1110-1118.

Fowbert, J.A. 1996. A experimental study of growth in relation to morphology and shoot water content in maritime Antarctic mosses. New Phytologist **82**:97-114.

Frego, K.A. 1994. Factors influencing the local distribution of four bryophyte species in mature upland black spruce forest. Ph.D. thesis. Department of Botany, University of Toronto, Ontario, Canada.

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

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

Gerdol, R., Bonora, A., Gualandri, R. and Pancaldi, S. 1996. CO_2 exchange, photosynthetic pigment composition, and cell ultrastructure of *Sphagnum* mosses during dehydration and subsequent rehydration. Canadian Journal of Botany **74**:726-734.

Gerdol, R., Bonora, A., Marchesini, R., Gualandri, R. and Pancaldi, S. 1998. Growth response of *Sphagnum capillifolium* to nighttime temperature and nutrient level: mechanisms and implications for global change. Arctic and Alpine Research **30**:388-395.

Gignac LD, Nicholson BJ, Bayley SE. 1998. The utilization of bryophytes in bioclimatic modeling: predicted northward migration of peatlands in the Mackenzie River Basin, Canada, as a result of global warming. The Bryologist **101**:572-587.

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Gorham, E. 1994. The future of research in Canadian peatlands: a brief survey with particular reference to global change. Wetlands **14**:206-215.

Grosvernier, P., Matthey, Y. and Buttler, A. 1997. Growth potential of three *Sphagnum* species in relation to water table level and peat properties with implications for their restoration in cut-over bogs. Journal of Applied Ecology **34**:471-483.

Hanslin, H.M. 1999. Seasonal dynamics of biomass increase and shoot elongation in five co-occurring boreal forest bryophytes. Journal of Bryology **21**:5-15.

Hayward, P.M. and Clymo, R.S. 1982. Profiles of water content and pore size in *Sphagnum* and peat, and their relation to peat bog ecology. Proceedings of the Royal Society of London B **215**:299-325.

Hayward, P.M. and Clymo, R.S. 1983. The growth of *Sphagnum*: experiments on, and simulation of, some effects of light flux and water-table depth. Journal of Ecology **71**:845-863.

Hedderson, T.A. and Longton, R.E. 1996. Life history variation in mosses: water relations, size and phylogeny. Oikos **77**:31-43.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

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

Jauhiainen, J., Vasander, H. and Silvola, J. 1994. Response of *Sphagnum fuscum* to N deposition and increased CO_2. Journal of Bryology **18**:83-95.

Jauhiainen, J., Silvola, J., Tolonen, K. and Vasander, H. 1997. Response of *Sphagnum fuscum* to water levels and CO_2 concentration. Journal of Bryology **19**:391-400.

Jauhiainen, J., Wallen, B. and Malmer, N. 1998. Potential NH_4^+ and NO_3^- in seven *Sphagnum* species. New Phytologist **138**:287-293.

Kooijman, A. and Bakker, C. 1993. Causes of the replacement of *Scopidium scorpioides* by *Calliergonella cuspidata* in eutrophicated rich fens. II. Experimental studies. Lindbergia **18**:123-130.

Lindholm, T. and Vasander, H. 1990. Production of eight species of *Sphagnum* at Surisuo mire, southern Finland. Annales Botanica Fennici **27**:145-157.

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Li, Y., Glime, J.M. and Liao, C. 1992. Responses of two interacting *Sphagnum* species to water level. Journal of Bryology **17**:59-70.

Li, Y., Glime, J.M. and Drummer, T.D. 1993. Effects of phosphorus on the growth of *Sphagnum magellaniucm* Brid. and *S. papillosum* Lindb. Lindbergia **18**:25-30.

Longton, R.E. 1985. Reproductive biology and susceptibility to air pollution in *Pleurozium schreberi* (Brid.) Mitt. (Musci) with particular reference to Manitoba, Canada. Monographs in Systematic Botany from the Missouri Botanical Garden **11**:51-69.

Mankiewicz, P.S. 1987. The low pressure field porometer: a new, low cost technique for characterising external capillary water conduction in whole colonies of bryophytes and other small plants. The Bryologist **90**:253-262.

Mulligan, R.C. and L.D. Gignac. 2001. Bryophyte community structure in a boreal poor fen: reciprocal transplants. Canadian Journal of Botany **79**:404-411.

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Oechel, W.C., Van Cleve, K. 1986. The role of bryophytes in nutrient cycling in the taiga. *In*:. Forest ecosystems in the Alaskan taiga a synthesis of structure and function. *Edited by* K. Van Cleve, F.S. Chapin III, P.W. Flanagan, L.A. Viereck and C.T. Dyrness. Springer-Verlag, New York. pp. 121-137.

Pakarinen, P. and Tolonen, K. 1977. Regional survey of heavy metals in peat mosses (*Sphagnum*). Ambio **6**: 38-40.

Potter, J.A., Press, M.C., Callaghan, T.V., and Lee, J.A. 1995. Growth responses of *Polytrichum commune* and *Hylocomium splendens* to simulated environmental change in the sub-arctic. New Phytologist **131**:533-541.

Price, A.G., Dunham, K., Carleton, T., and Band, L. 1997. Variability of water fluxes through the black spruce (*Picea mariana*) canopy and feather moss (*Pleurozium schreberi*) carpet in the boreal forest of Northern Manitoba. Journal of Hydrology **196**:310-323.

Proctor, M.C.F. 1982. Physiological ecology: water relations, light and temperature responses, carbon balance. *In*: Bryophyte ecology. *Edited by* A.J.E. Smith. Chapman and Hall, London. pp. 333-382.

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Proctor, M.C.F. 1990. The physiological basis of bryophyte production. Botanical Journal of the Linnean Society **104**:61-77.

Rieley, J.O., Richards, P.W., and Bebbington, D.L. 1979. The ecological role of bryophytes in a north Wales woodland. Journal of Ecology **67**:497-527.

Rincon, E. 1988. Effect of initial shoot size on growth rates of five British grassland bryophytes. The Bryologist **91**:219-222.

Rincon, E. 1993. Growth responses of six bryophyte species to different light intensities. Canadian Journal of Botany **71**:661-665.

Rincon, E., and Grime, J.P. 1989. An analysis of seasonal patterns of bryophyte growth in a natural habitat. Journal of Ecology **77**:447-455.

Romanov, V.V. 1968. Hydrophysics of bogs. Israel Program for Scientific Translations, Jerusalem, Israel.

Russell, S. 1984. Growth measurement in bryophytes: a case study. Journal of the Hattori Botanical Laboratory **56**:147-157.

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Russell, S. 1988. Measurement of bryophyte growth 1. Biomass (harvest) techniques. *In*: Methods in bryology. *Edited by* J.M. Glime. Hattori Botanical Laboratory, Nichinan. pp. 249-257.

Rydin, H. 1985. Effects of density and water level on recruitment, mortality and shoot size in *Sphagnum* populations. Journal of Bryology **18**:439-453.

SAS Institute Inc. 1989. SAS/STAT user's guide, version 6, fourth edition, volume 2. SAS Institute Inc., Cary, N.C., U.S.A.

Sastad, S.M., Pedersen, B., Digre, K. 1999. Habitat-specific genetic effects on growth rate and morphology across pH and water-table level gradients within a population of the moss *Sphagnum angustifolium* (Sphagnaceae). American Journal of Botany **86**:1687-1698.

Schipperges, B., and Rydin, H. 1998. Response of photosynthesis of *Sphagnum* species from contrasting microhabitats to tissue water content and repeated desiccation. New Phytologist **140**:677-684.

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Shimizu, H., Takeuchi, Y., Satake, K., and Totsuka, T. 1984. Growth and photosynthesis of a moss *Plagiomnium maximoviczii* (Lindb.) Kop. (1) effects of light intensity. Journal of the Hattori Botanical Laboratory **56**:159-166.

Silvola, J., and Aaltonen, H. 1984. Water content and photosynthesis in the peat mosses *Sphagnum fuscum* and *S. angustifolium*. Annales Botanici Fennici **21**:1-6.

Skre, O., Oechel, W.C., and Miller, P.M. 1983. Moss leaf water content and solar radiation at the moss surface in a mature black spruce forest in central Alaska. Canadian Journal of Forest Research **13**:860-868.

SPSS Inc. 1993. SPSS for windows: advanced statistics, release 6.0. SPSS Inc., Chicago, U.S.A.

Stokes, J.R., Alspach, P.A., and Stanley, C.J. 1999. Effect of water table on the growth of three New Zealand *Sphagnum* species: implications for *S. cristatum* management. Journal of Bryology **21**:25-29.

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van der Hoeven, E.C., Korporaal, M., van Gestel, E. 1998. Effects of simulated shade on growth, morphology and competitive interactions in two pleurocarpous mosses. Journal of Bryology **20**:301-310.

Wachowiak-Zielinska, M., and Zielinski, R. 1995. Genetic variation of the haploid moss *Pleurozium schreberi* (Musci, Hylocomiaceae) from Poland. Fragmenta Floristica *et* Geobotanica **40**:417-423.

Wielgolaski, F.E., Bliss, L.C., Svoboda, J., and Doyle, G. 1981. Primary production of tundra. *In* Tundra Ecosystems. *Edited by* L.C. Bliss, O.W. Heal, and D. Moore. Cambridge University Press, Cambridge, U.K. pp. 187-225.

Zar, J.H. 1996. Biostatistical analysis 3rd edition. Prentice Hall, New Jersey, U.S.A.

Zechmeister, H.G. 1995. Growth rates of five pleurocarpous moss species under various climatic conditions. Journal of Bryology **18**:455-468.

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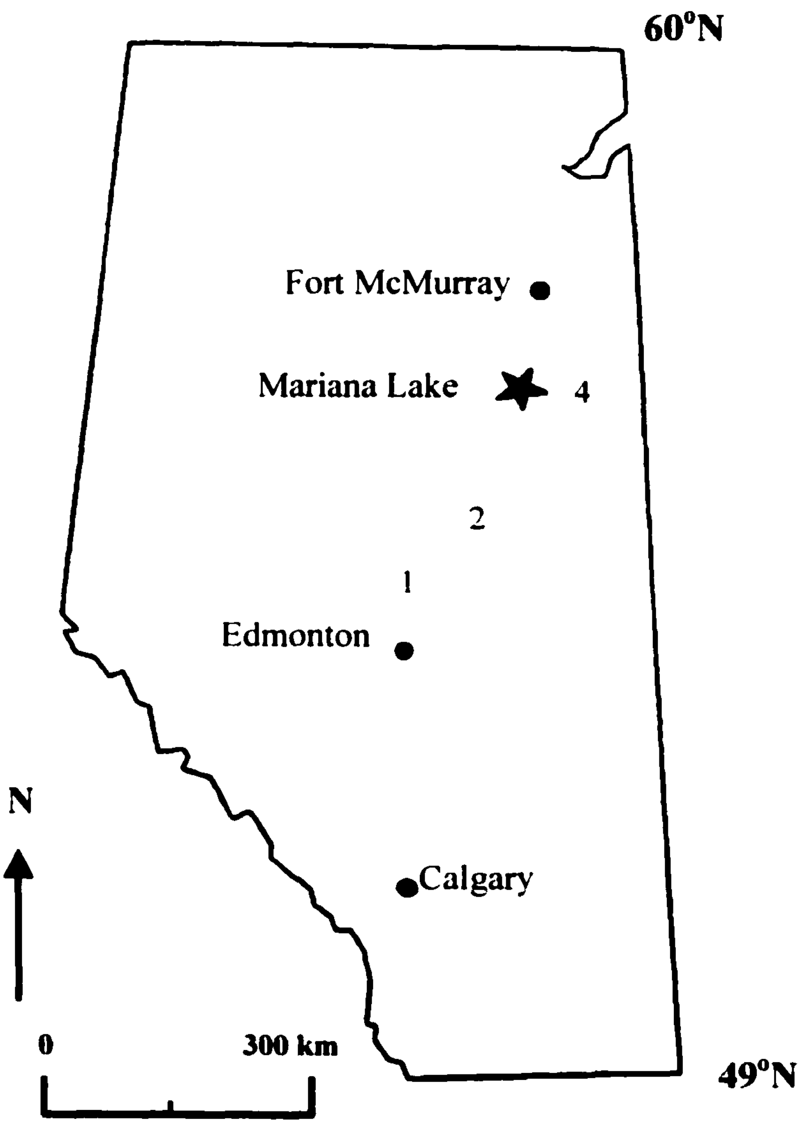

Fig. 5-1 The location of the Mariana Lake peatland in Alberta, Canada, and other peatlands where material was collected to test the robustness of the moist weight growth method. 1= Bleak Lake, 2 = Lac La Biche, 3 = Calling Lake, 4 = Conklin.

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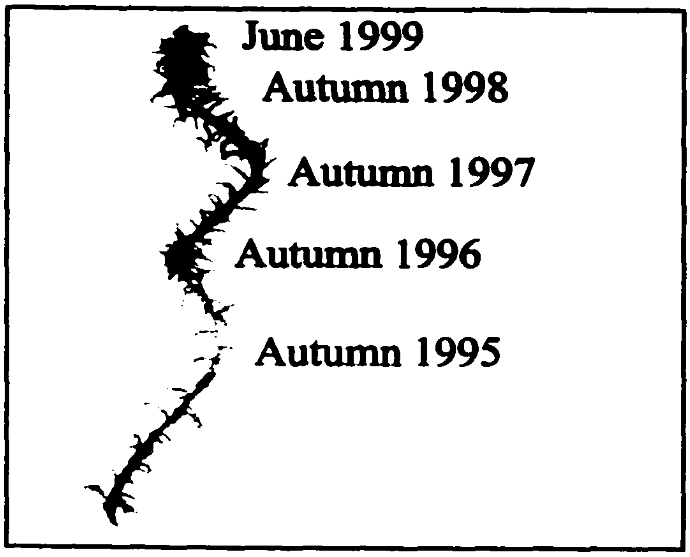

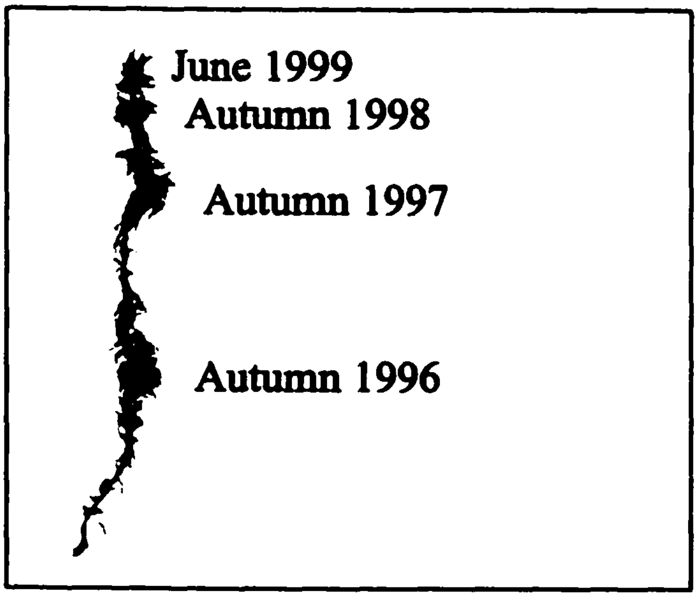

Fig. 5-2 **_Sphagnum angustifolium_ (top) showing annual bend growth markers.**
Fig. 5-3 **_Sphagnum magellanicum_ (bottom) with annual branch markers.**

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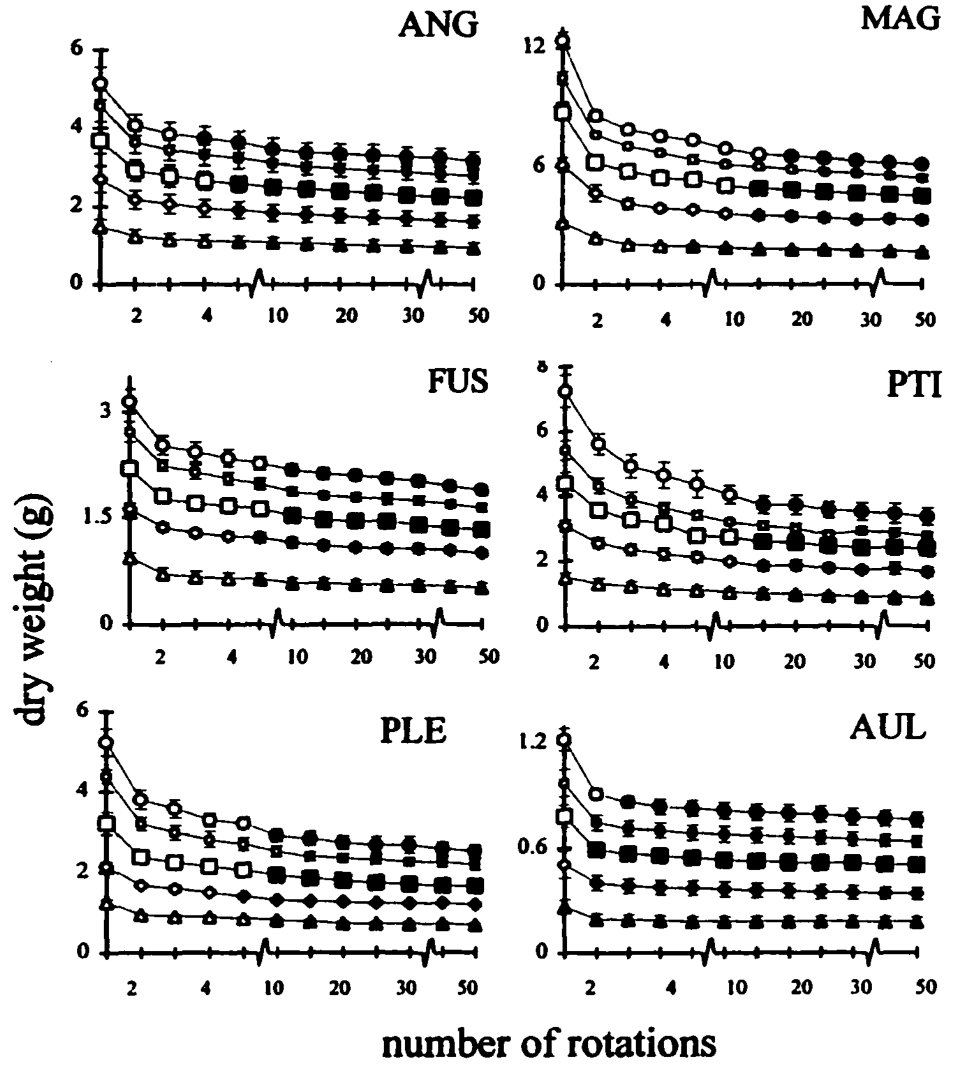

Fig. 5-4 Mean change in moist weight ± standard error of 5 (▲), 10 (◆), 15 (■), 20 (▪), and 25 (●) shoot bundles of *Sphagnum angustifolium* (ANG), *Sphagnum magellanicum* (MAG), *Sphagnum fuscum* (FUS), *Pleurozium schreberi* (PLE), *Ptilium crista-castrensis* (PTI) and *Aulacomnium palustre* (AUL) from the Mariana Lake peatland after various rotations (1, 2, 3, 4, 5, 10, 15, 20, 25, 30, 40, 50) in the salad spinner. The point at which each species and bundle size reaches equilibrium is indicated by a change in the data marker from open to filled. Equilibrium rotation level was defined as the first occurrence of a non-significant ($p > 0.005$) pairwise comparison providing that the coefficient of variation of the remaining means was <5%.

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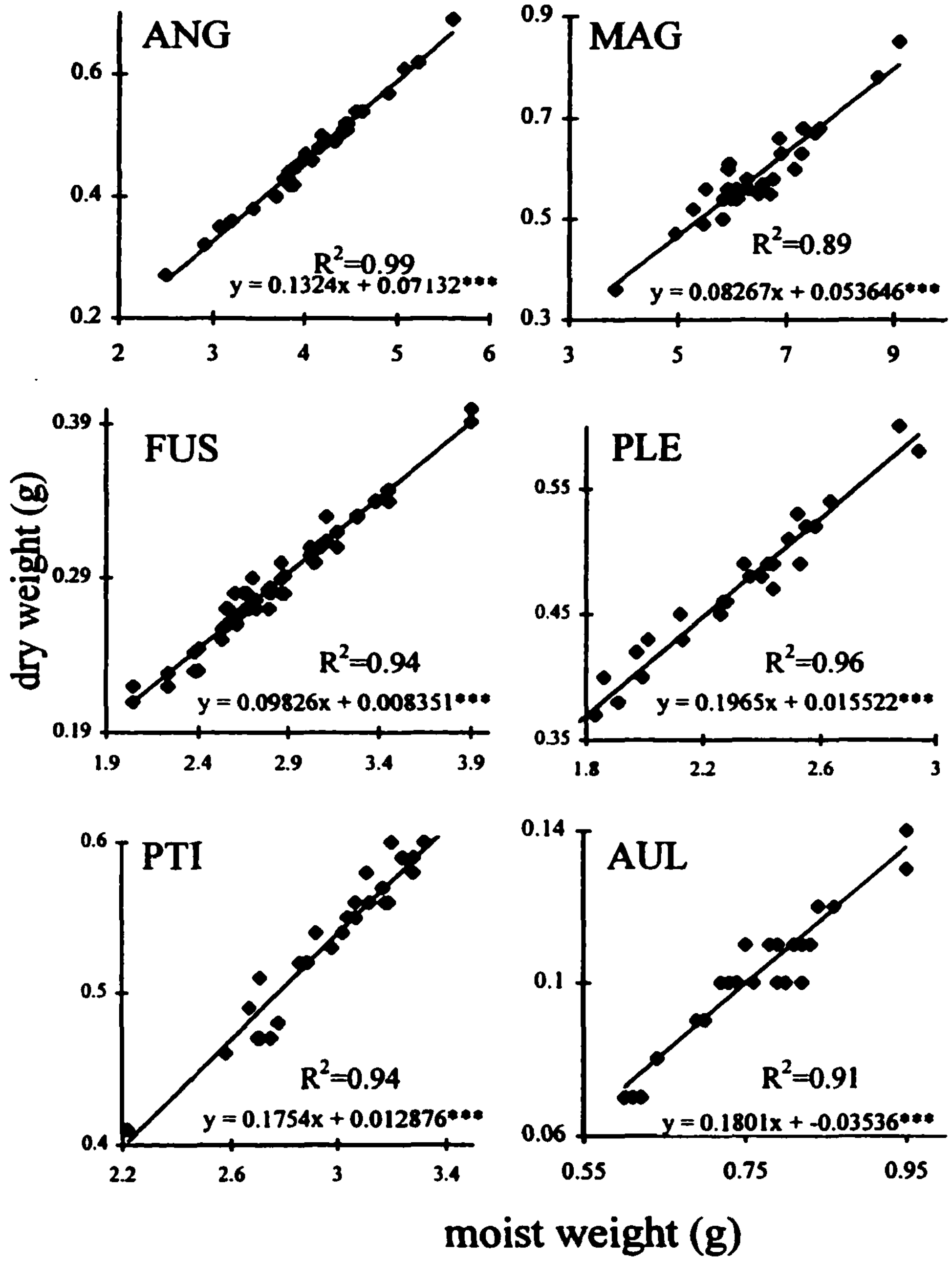

Fig. 5-5 The relationship between mean dry and moist weight of *Sphagnum angustifolium* (ANG), *Sphagnum magellanicum* (MAG), *Sphagnum fuscum* (FUS), *Pleurozium schreberi* (PLE), *Ptilium crista-castrensis* (PTI) and *Aulacomnium palustre* (AUL) from the Mariana Lake peatland is illustrated by regression analyses. *** highly significant at $p<0.001$.

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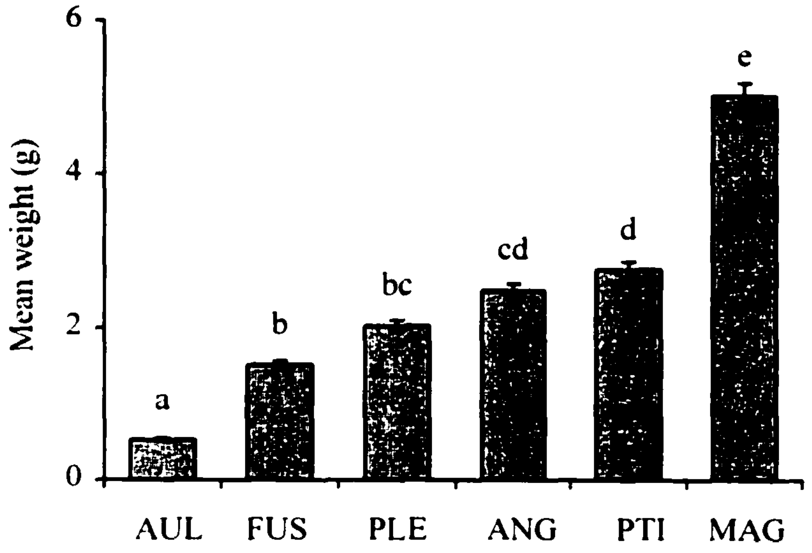

Fig. 5-6 Mean separations of species effect expressed as mean moist weight (g) ± standard error and based on Tukey's multiple comparison test ($p<0.05$, N =15) for *Aulacomnium palustre* (AUL), *Sphagnum fuscum* (FUS), *Pleurozium schreberi* (PLE), *Sphagnum angustifolium* (ANG), *Ptilium crista-castrensis* (PTI) and *Sphagnum magellanicum* (MAG) tested for the moist weight growth determination method.

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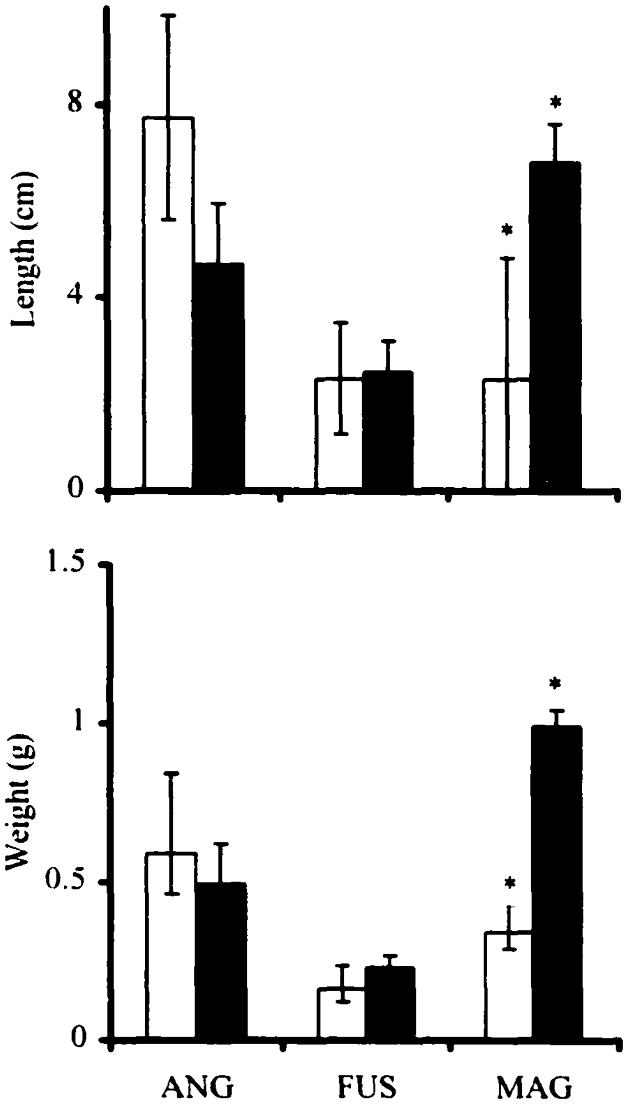

Fig. 5-7 Mean growth in length (cm) and weight (g) ± standard deviation after one year of transplanted (open bars) and untransplanted (stippled bars) 25 shoot bundles of *Sphagnum angustifolium* (ANG), *Sphagnum fuscum* (FUS) and *Sphagnum magellanicum* (MAG) from the Mariana Lake peatland. * significant at $p<0.05$ based on Student's *t*-test.

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Table 5-1 Repeated measures analysis of variance of the effects of salad spinner rotation level (TIME), species (SP), and bundle sizes (BUNS) on moist weights of *Sphagnum angustifolium*, *Sphagnum magellanicum*, *Sphagnum fuscum*, *Pleurozium schreberi*, *Ptilium crista-castrensis*, and *Aulacomnium palustre* tested for the Mariana Lake moist weight growth method. Within subject effect in bold; between-subject effects in regular font. × = interaction; df = degrees of freedom; SS = sum of squares; MS = mean square; F = F value, p = probability. * df was adjusted with the Huynh-Feldt Epsilon because the data failed Mauchly's test of sphericity.

SOURCE	**df**	**SS**	**MS**	**F**	**p**
TIME	**4.6***	**205.2**	**44.4**	**1637.2**	
TIME × SP	**18.9***	**108.4**	**5.9**	**216.2**	**.000**
TIME × BUNS	**18.5***	**40.9**	**2.2**	**81.6**	**.000**
TIME × SP × BUNS	**74.0***	**21.1**	**0.29**	**10.5**	**.000**
Error (TIME)	**231.1***	**6.3**	**0.003**		
Intercept	1	5067.5	5067.5	8185.1	.000
SP	4	2057	514.3	830.6	.000
BUNS	4	792	198.0	319.8	.000
SP × BUNS	16	300.6	18.8	30.3	.000
Error	50	31.0	0.62		

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Table 5-2 The accuracy of the Mariana Lake moist weight growth determination method for *Sphagnum angustifolium* (ANG), *Aulacomnium palustre* (AUL), *Sphagnum fuscum* (FUS), *Sphagnum magellanicum* (MAG), *Pleurozium schreberi* (PLE) and *Ptilium crista-castrensis* (PTI) is illustrated by the relationship between mean actual and predicted dry weights ± standard error (s.e.), which is expressed as mean absolute error (MAE) ± s.e. Sp. = species, acc. = accuracy

Sp.	Actual dry weight (g) ± s.e.	Predicted dry weight (g) ± s.e.	MAE (%) ± s.e.	% acc.
ANG	0.58 ± 0.02	0.62 ± 0.01	8.69 ± 1.78	91
FUS	0.36 ± 0.06	0.39 ± 0.06	9.97 ± 3.26	90
MAG	0.58 ± 0.02	0.58 ± 0.02	1.98 ± 0.61	98
AUL	0.10 ± 0.004	0.10 ± 0.004	3.23 ± 0.78	97
PLE	0.51 ± 0.03	0.54 ± 0.04	3.68 ± 0.78	96
PTI	0.52 ± 0.02	0.51 ± 0.02	3.34 ± 0.44	97

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Table 5-3 The robustness of the Mariana Lake moist weight growth determination method for *Sphagnum angustifolium* (ANG), *Sphagnum fuscum* (FUS), *Pleurozium schreberi* (PLE) and *Ptilium crista-castrensis* (PTI), is illustrated by the relationship between mean actual and predicted dry weights ± standard error (s.e.), which is reported as percent mean absolute error (MAE) ± s.e., acc. = accuracy, Sp. = species The method was tested with shoots from the following locations in Alberta, Canada: Bleak Lake (BL), Calling Lake (CL), Lac La Biche (LB), and Conklin (CN), n =10 for all.

Sp.	Location: latitude longitude	Actual dry wt (g)± s.e.	Predicted dry wt (g)±s.e.	MAE (%) ± s.e.	% acc.
ANG	BL 54°40'N 113°28'W	0.56±0.02	0.62±0.02	10.3±1.9	90
ANG	CL 55°15'N 113°20'W	0.55±0.01	0.57±0.02	2.7±1.6	97
FUS	BL 54°40'N 113°28'W	0.33±0.01	0.27±0.01	19.7±1.8	80
FUS	CL 55°15'N 113°20'W	0.38±0.02	0.38±0.01	1.2±0.9	99
FUS	LB 54°46'N 111°58'W	0.39±0.01	0.45±0.01	15.5±1.3	84
FUS	CN 55°38'N 111°05'W	0.45±0.01	0.39±0.01	12.9±1.2	87
PLE	CL 55°15'N 113°20'W	0.40±0.02	0.54±0.02	34.8±2.8	65
PLE	CL 55°15'N 113°20'W	0.41±0.03	0.53±0.04	28.4±2.2	72
PLE	CL 55°15'N 113°20'W	0.49±0.04	0.60±0.05	22.7±1.6	77
PTI	CL 55°15'N 113°20'W	0.45±0.02	0.58±0.02	30.3±1.6	70
PTI	CL 55°15'N 113°20'W	0.45±0.02	0.55±0.02	24.7±0.9	75

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Chapter 6- Summary and conclusions

The mature bryophyte communities in the Mariana Lake peatland are the result of a synergy of abiotic and biotic factors complicated by the stochasticity that is ubiquitous in nature. This thesis documents the importance of three of these: habitat preference, competition and establishment ability. They are significant in different ways, to different species (Table 1), and at different intensities, but they have all interacted to produce the extant community. Further, these investigations document that generalisations regarding the behaviour of hummock and hollow species, particularly with respect to the depth to water gradient, are similar in bogs and poor fens. The presence of water flow and different minerotrophic status in poor fens do not affect the behaviour of the species. These generalisations include the exclusion of hollow species from hummock habitats, attributed to their inferior water retention and transport capacity, and the inclusion of hollow habitats within the fundamental niches of hummock species. Despite the narrow geographical scale of this thesis, the generalisations it documents may have much wider implications. This is because the distribution of Sphagna along the hummock-hollow gradient is generally consistent across the circumpolar range of boreal peatlands, with species from Section *Acutifolia* inhabiting hummock habitats and species from Section *Cuspidata* growing in hollows.

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The reciprocal transplant study describes the fundamental niches of the study species and documents the importance of habitat limitation to the distribution of all species except *Sphagnum fuscum*. Within the range of measured environmental conditions in the fen, depth to water table was the most important factor regulating species distribution because it exerted a significant influence on the growth of all species investigated, except *Sphagnum fuscum*. The potential distribution of *Sphagnum angustifolium* is limited to areas with lower water tables such as the *S. magellanicum* habitat. The upper limit of *Sphagnum angustifolium* and other species in Section *Cuspidata* on the water table gradient is set by a combination of physiological intolerance of desiccation (van der Molen *et al.* 1992; Rydin 1993; Schipperges and Rydin 1998) and absence of morphological specialisation for water retention. The desiccation exhibited by *Sphagnum angustifolium* in the hummock habitats in this peatland indicates that the physiological intolerance of hollow species to drier conditions, which has been documented in ombrotrophic peatlands, is also found in poor fens. The potential ecological amplitude of *Sphagnum angustifolium* in this peatland is still very broad and habitat limitation is not the sole factor that has structured its distribution. *Sphagnum magellanicum* is partially limited by habitat, in that it cannot survive in the driest (*Pleurozium schreberi*) habitat. Despite this, *Sphagnum magellanicum* exhibits wide tolerance including the *S. angustifolium* and *S. fuscum* habitats and its present distribution in this peatland is not wholly the result of direct habitat restrictions. *Pleurozium schreberi* exhibited the narrowest fundamental niche, indicating that its present distribution is partially

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restricted by habitat limitation, i.e. *P. schreberi* is restricted to its present habitats because it cannot grow in the other habitats. The fundamental niche of *Sphagnum fuscum* is very broad, and it was able to grow in all habitats examined in this peatland, i.e. it is not excluded from the other habitats because of an inability to survive there. Nonetheless, the realised niche of *Sphagnum fuscum* in this peatland is quite narrow and it is never found in hollow habitats.

One explanation for the inability of *Sphagnum fuscum* to inhabit its full fundamental niche is competitive exclusion from hollow habitats by *Sphagnum angustifolium*. This does not appear to be the case, though, because the competition investigation revealed that *Sphagnum fuscum* and *S. angustifolium* have low competitive ability in the habitats studied in this peatland. This study did indicate the existence of a competitive hierarchy wherein the feather mosses are subordinates to the Sphagna. The feather mosses did not demonstrate competitive effect and may have facilitated growth of the phytometer by ameliorating the allelopathic effect of the acidity created by the Sphagna. On a strictly statistical basis, the results of this chapter support Rydin's (1993) findings that competitive ability differs very little between Sphagna. However, the true significance of these data may be masked by noise from the high between replicate variability.

Sphagnum magellanicum exhibited the greatest competitive effect and this species may be a strong competitor, acting to inhibit *S. fuscum* from occupying the full range of its fundamental niche. For *Sphagnum fuscum* to grow in the hollows without the manipulation of an investigator, it would have to move down

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the hummock side through *S. magellanicum*. Therefore, *Sphagnum fuscum* may be absent from the hollows due to competitive interactions with *S. magellanicum*. This theory deserves a corollary, however, because it is difficult to imagine that *Sphagnum fuscum* would be dispersal limited over such a short distance. It is obviously not impossible for the diaspores of *Sphagnum fuscum* to arrive at the hollow habitat, but they are unable to establish amongst the mature canopy of the hollow species and the adult individuals cannot get through the "*magellanicum* wall." This seems plausible because *Sphagnum fuscum* has been found growing in hollow habitats in oceanic peatlands from which *S. magellanicum* was absent (Gignac, L.D. personal communication).

If, as suspected, the diaspores of *Sphagnum fuscum* cannot establish among a mature canopy of *S. angustifolium* plants, then how does this species regenerate after a major disturbance like fire? Questions like this are prevalent in recent bryophyte ecology papers as bryologists realise that regeneration niche interactions have been virtually ignored. This is rapidly changing, particularly if studies of the suitability of *Sphagnum* spp. for the revegetation of abandoned, harvested peatlands are considered.

This thesis documents that the study species differ widely in their ability to regenerate from gametophytic fragments. *Pleurozium schreberi* and *Ptilium crista-castrensis* can easily establish on bare peat when gametophytic fragments are introduced. *Sphagnum angustifolium* was very successful in the tubs in which it was planted and it also appeared in many other treatments, presumably from asexual or sexual diaspore colonisation. *Sphagnum magellanicum* did not grow

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at all at one site and it appeared only in very small amounts in treatments in which it was not planted but only at the Mariana Lake site. The occurrence of these plants is likely attributable to sexual reproduction from the local spore source and this method of reproduction may be more important to this species than previously believed. *Sphagnum fuscum* did not regenerate at either site in any treatment. This may have partially been a function of desiccation and/or the small fragment size used. Successful regeneration of *Sphagnum fuscum* from fragments on bare peat has only been reported once (Campeau and Rochefort 1996). In their study, *Sphagnum fuscum* was grown from larger fragments with the capitulum attached that were shaded by a plastic cloth. Therefore, it seems that large (10-25 mm) fragments and shade are necessary for regeneration. Further, it is suspected that the regeneration niche of *Sphagnum fuscum* is very narrow.

Aulacomnium palustre exhibited the highest colonisation success. It was present in almost every tub at both sites. This is consistent with other regeneration studies of this species (Li and Vitt 1994) and with its "colonist" life strategy. Prolific growth of unplanted fugitive and colonist species such as *Ceratodon purpureus*, *Polytrichum* spp. and *Leptobryum pyriforme* documented their importance to peatland postfire succession and suggests a more important role for facilitation succession in these populations than currently believed. It was very interesting that the planted K-selected species (*Sphagnum angustifolium*, *Pleurozium schreberi* and *Ptilium crista-castrensis*) declined between years one and two at both sites, while most of the unplanted species

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increased in frequency over this same period. The planted species could not successfully expand in the regeneration niche because they lack the morphological and physiological adaptations necessary for proliferation that are characteristic of colonist species.

A central method in this thesis has been the measurement of bryophyte growth. Accurate determination of bryophyte growth is important because it is usually the criterion by which the response to, and significance of, experimental manipulation is determined. A review of 80 bryophyte growth studies revealed that change in dry weight is a measurement that is often ignored or extrapolated, either from "similar" shoots that are external to the investigation or from increases in shoot elongation. The weight that is actually gained or lost by the experimental shoots themselves is rarely measured, thus potentially leading to high experimental error. In order to address this concern, an existing (although rarely used) method (Mankiewicz 1987) was modified, calibrated and field-tested in a back transplant experiment to allow for prediction of initial dry weight from moist weight of the experimental shoots. The accuracy of the method was calculated as mean absolute error and ranged from 90-98% depending on the species. The robustness of the moist weight method, tested with populations from four other locations, was highly variable, ranging from 65-96%. This suggests caution in the use of material from outside the study location for which the predictive equation is calibrated. It is important for investigators wishing to use this method to conduct pre-trial experiments in order to ascertain the water-relations of the specific populations of each bryophyte species to be examined.

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Although the efficacy of this method has been demonstrated for the species in this study, other mosses may require slightly different treatment. This method may not be suitable for endohydric species which generally do not transplant well due to their internal conduction (e.g. *Polytrichum* spp.). The method is versatile, inexpensive and potentially applicable for widespread use, which may facilitate greater use of weight as a growth parameter in future investigations. Moreover, the method allows for circumvention of some of the potentially inaccurate bryophyte weight growth methods in current use.

The limitations of this thesis

The short-term nature of the investigations in this thesis may be a concern as short-term trends in *Sphagnum* ecology studies (e.g. Rydin 1986) have been reversed over the long term (11 years) (Rydin 1993). Although a longer study may have clarified some of the trends, the consistency of the results with investigations in ombrotrophic peatlands suggests that the short term studies were adequate for the purposes of this thesis.

Two potentially important factors which were beyond the scope of this thesis are dispersal and climate. Although the role of dispersal in bryophytes is very poorly understood at this time, its potential significance cannot be discounted. The regeneration study indirectly examined dispersal, by documenting the excellent colonisation ability of *Sphagnum angustifolium* and *Aulacomnium palustre* as volunteers in some of the treatments. Climate could not be considered as all studies occurred in Continental areas, but the importance

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of climate in the structuring of Western Canadian peatlands was described by Gignac (1992).

Future research with boreal bryophytes, specifically population-level studies and molecular work, is necessary. The phenotypic plasticity exhibited by *Sphagnum angustifolium* in this study should also be investigated. Although we are beginning to understand community structure in these well-studied boreal habitats, the inability of *Sphagnum fuscum* to establish in hollow habitats is still unclear and should be investigated. One easy way to accomplish this would be to cut a swath through the *Sphagnum magellanicum* on the side of the hummock and see if *S. fuscum* is able to disperse into the hollow with competition from *S. magellanicum* removed.

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Literature Cited

Campeau, S. and Rochefort, L. 1996. *Sphagnum* regeneration on bare peat surfaces: field and greenhouse experiments. Journal of Applied Ecology **33**:599-608.

Gignac, L.D. 1992. Niche structure, resource partitioning, and species interactions of mire bryophytes relative to climatic and ecological gradients in Western Canada. The Bryologist **95**:406-418.

Li, Y. and Vitt, D.H. 1994. The dynamics of moss establishment: temporal responses to nutrient gradients. The Bryologist **97**:357-364.

Mankiewicz, P.S. 1987. The low pressure field porometer: a new, low cost technique for characterizing external capillary water conduction in whole colonies of bryophytes and other small plants. The Bryologist **90**:253-262.

Rydin, H. 1986. Competition and niche separation in *Sphagnum*. Canadian Journal of Botany **64**:1817-1824.

Rydin, H. 1993. Interspecific competition between *Sphagnum* mosses on a raised bog. Oikos **66**:413-423.

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Schipperges, B. and Rydin, H. 1998. Response of photosynthesis of *Sphagnum* species from contrasting microhabitats to tissue water content and repeated desiccation. New Phytologist **140**:677-684.

van der Molen, P.C., Schalkoort, M., and Smit, R. 1992. Hummock-hollow complexes on Clara bog, Co. Offaly, Ireland. *In* Hummock-hollow complexes on Irish raised bogs a palaeo/actuo ecological approach of environmental and climate change. *Edited by* van der Molen, P.C. University of Amsterdam, Amsterdam, The Netherlands. pp. 117-173.

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Table 1- A summary of the influence of the probable limitations to the realised niches of the study species as revealed by the thesis investigations. Numbers in parentheses refer to the relevant chapter. ✓ = yes, ✖ = no, ? = not tested.

Species	Habitat (2) Preference	Competition (3)	Establishment (4)
S. angustifolium	✓	✖	✖
S. magellanicum	partially	✖	✓
S. fuscum	✖	maybe	✓
Ple. schreberi	✓	✓	✖
Ptil. cris.-cast.	✓	✓	✖

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Appendix A

Table 1A- Summary of bryophyte competition literature as of June 2000. For abbreviations see abbreviation list.

Author	Year	Journal	Habitat	Field	Growth Chamber	Other	Species	Methods	Conclusions
Twenhoven	1992	Journal of Bryology	Bog	✓			Sph. fal., Sph. mag..	Fertiliser-length, weight % frequency	Sph. fal. is a competitor Sph. mag. is a stress-tolerator
Rydin	1997	The Bryologist	Bog		✓		Sph. fus., Sph. bal., Sph. ten.	Relative cover	Variability less but still present Sphagna differ little in their competitive ability
Rydin	1987	Symposia Biologica Hungarica	Bog	✓			Sph. rub. Sph. ten., Sph. fus., Sph. bal.	Transplant (% cover)	In hollows competition important but priority of colonization may also be important. More study is necessary
Rydin	1993	Oikos	Bog	✓			Sph. bal., Sph. ten., Sph. fus.	Transplant (% cover)	High variability; difference in competitive ability between Sphagna is small
Li *et al.*	1992	Journal of Bryology	Poor fen		✓		Sph. mag., Sph. pap.	Competitive ability, response to H_2O level, H_2O holding	Sph. mag. better competitor than Sph. pap. for water, also evidence of protoco-operation.
Rydin	1995	Journal of Bryology	Bog	✓	✓		Sph. fus., Sph. ten., Sph. bal.	Effect of H_2O level & density on shoot size-shoots grown in beakers	Shoots increase in area more via increase in capitulum area rather than increase in shoot #; -recruitment decreases with area
Rydin	1986	Canadian Journal of Botany	Bog	✓			Sph. fus., Sph. rus., Sph. bal., Sph. ten., Sph. cus.	Change in area	Difference in competitive ability small but competition not excluded as important. Establishment may be more important
Malmer *et al.*	1994	Folia Geobotan. Phytotax-onomica	Peatlands				*Sphagnum* spp. & vascular plants (eg. Dro. rot.)	interactions between Sphagna and vasculars in peatlands	Vasculars & Sphagna stress tolerant; maybe pre-emptive competition with Sphagna usurping mineral nutrients
Kooijman & Bakker	1995	Journal of Ecology	Mesotrophic & eurtrophic fens		✓		Sph. squ., Sph. sub., Sco. sco., Cal. cus.	Replacement series	Indirect evidence of competitive interactions which may have affected species replacement

Table 1A- Summary of bryophyte competition literature cont'd.

Author	Year	Journal	Habitat	Field	Growth chamber	Other	Species	Methods	Conclusions
Soro *et al*	1999	Journal of Vegetation Science	Bog	✓			Sph. ang., Sph. fus., Sph. rub, Sph. ten., Sph. lin., Sph. bal., Sph. cus., And. pol., Cal. vul., Emp. nig., Sph. ten., Rub. cha., Vac. oxy., Vac. uli.	% cover; niche overlap	Largest. niche breadth: Sph. rub. >Sph. fus. >Sph. bal.>Sph. ten. >Sph. cus. # species/plot > undisturbed
Kenkel	1988	Vegetatio	Poor fen	✓			Cha. cal., Car. lim., Kal. pol., Oxy. mic., Eri. ang., Eri. spi., Sph. cus., Sph. nem., Sph. mag., Sph. fus.	Spatial examination (% cover) with implications for competition	Niche partitioning -strong deviation from random -indirect evidence that competition may be important
Gignac	1992	The Bryologist	Various peatland	✓			Aul. pal., Cam. ste. Hyl. spl, Ple. sch., Tom. nit., Sph. ang., Sph. aus., Sph. cus., Sph. fus., Sph. lin., Sph. mag. Sph. pap. Sph. rub., Sph. ten., Sph. war.	Niche breadth & overlap	Habitat partitioning evident Niche shifts indirect evidence of competitive hierarchy Sphagna > than non-Sphagna, lawn/carpet Sphagna > than hummock
Kosiba & Sarosiek	1991	Ekologia Polska	Botanic Garden			✓	Cat. und., Mni. aff.	Length, density, weight	Negative correlation between increase in density of Cat. Und. & that of Mni. aff., Cat. Und. strong competition
Bragazza & Gerdol	1996	Annales Botanici Fennici.	Poor fen	✓			Sph. mag., Sph. fal., Sph. com., Sph. cap., Sph. rus., Sph. sub., Drep. spp., Pol. spp.	Response surfaces based on distribution along gradient.	DTW most important gradient -No clear habitat partitioning -indirect evidence Sphagna better competitors than other mosses
Watson	1981	Ecology	Many	✓			Pol. com., Pol. jun, Pol. pil. etc.	Examination of realised niches along altitudinal gradient	Evidence for competition weak. Other interactions at other stages may be important, eg. competition in the regeneration niche

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Table 1A- Summary of bryophyte competition literature cont'd.

Author	**Year.**	**Journal**	**Habitat**	**Field**	**Growth chamber**	**Other**	**Species**	**Methods**	**Conclusions**
McAlister	1995	Ecology	Deciduous forest		✓		Leu. alb., Ano. ros., Pla. rep.	Replacement series- fragments on fallen logs; % cover, biomass	Niche overlap. No significant negative or positive interactions. Growth in mixture = growth in monoculture. competition LOW
Scandrett & Gimminghm	1989	Journal of Ecology	Dry heathland				Ple. sch., Hyl. spl., Hyp. jut.	Replacement series (cold frame)	Higher yields in shade than in light
van der Hoeven *et al.*	1998	Journal of Bryology	Chalk grassland			✓	Rhy. squ., Cal. cus.	Growth response to light. Cover, weight & length	No significant competitive effect
Marino	1991	Ecology	Fen	✓	✓		Tet. ang., Tet. mni., Spl. amp., Spl. lut.	Ability # shoots in mixture & alone. Area occupied	Symmetrical competition between congeners. Competitive hierarchy (significant species effect) but some were equal
Okland	1994	Journal of Vegetation Science	Boreal forest	✓			Ple. sch., Pti. cri.	Spatial patterns	Low proportion negative interaction, competition not important
Rincon & Grime	1989	Journal of Ecology	Many		✓		Bra. rut., Eur. pra., Fis. cri., Pse. pur., Tha. alo., Thu. tam.	Light manipulation; RGR	Species with > potential RGR more effective colonists. Documents his productivity competition theory
Svensson	1995	Oikos	Subarctic Bog	✓			Sph., fus., & Dro. rot.	Fertilisation-growth measurements	Competition for nutrients affects community. Sph. ten., Sph. fus. competes & wins again Sph. ten. Dro. rot. for mineral nutrients
Li & Vitt	1995	Journal of Bryology	Poor fen			✓	Aul. pal., Sph. fus., Sph. ang., Sph. mag., Pol. str.	Competition in the regeneration niche	Regeneration. niche may be more important than those in mature communities. Competition in in mature comm. not discounted.
Zamfir & Goldberg	2000	Ecology	Grass land		✓		Dic. sco., Rac. can., Hom. lut., Hyp. cup, Rhy. tri., Rhy. rug.	Effect of density on competition	Growth ⬇ with ⬆density. Competitive hierarchy concordant along abundance gradient.
Glime & Iwatsuki	1997	Journal of the Hattori. Botanical Laboratory	Geo-thermal vents	✓			Hyd. pan., Mic. sin., Hyp plu, Sph pal, Era mul, Jun inf, Tre lon, Fim dic, Odo den	Niche breadth & overlap	Bryophytes tolerant of wider conditions than angiosperms, but not usually good competitors with angiosperms for space.

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Appendix B

Table 2A- Summary of bryophyte growth studies as of June 2000. For abbreviations see abbreviation list.

Authors	Weight Method	Length Method	Species	Purpose of study
Sastad *et al.* 1999	Fresh mass- shoots kept in water saturated environment & squeezed between 2 pieces of filter paper (R^2 between wet weight & dry weight checked at end of experiment (R^2=0.92)	NA	Sph. ang.	Habitat specific genetic effects on growth rate across pH and water level gradients
Shiraishi *et al* 1996	Volumetric – capitulum corrected	Cranked wire; Point level (like cranked wire but with a plate like disc.)	Sph. ten., Sph.. pap. Sph. nem.	To foster restoration work
Li *et. al.* 1993	Dry weight of capitulum of similar specimens taken & subtracted at end	Velcro- strip	Sph. mag., Sph. pap.	Effect of phosphorus on growth
Li *et. al.* 1992	Dry weight of capitulum of similar specimens taken & subtracted at end	Velcro- strip	Sph. mag., Sph. pap.	Effect of water level on growth of interacting species
Li and Glime 1990	Dry weight of capitulum of similar specimens taken and subtracted at end	Velcro- strip	Sph. mag., Sph. pap.	Effect of nutrients on growth of *Sphagnum*
Riis and Sand-Jensen 1997	Increase in length cut off and weighed	Innate markers	Sph. sub., Dre. exa.	Effect of depth: light, temperature and CO_2 on growth
Baxter *et al.* 1989	NA	CTKL (40mm)	Sph. cus.	Effect of bisulphite on growth & photosynthesis
Austin and Wieder 1987	NA	CTKL (50 mm)	Sph. fal., Sph. hen., Sph. pul.	Effect of simulated acid precipitation on growth
Hulme and Blyth 1982	NA	CTKL (50 mm)	Sph. cus., Sph. pap., Sph.. mag., Sph. cap., Sph.. aur. var. inu.	Phenology of growth
Kooijman 1993	NA	velcro strip-TRANSPLANT	Sco.sco., Sph. con., Sph.. sub., Cam. ste., Cal. cus.	Delineation of ecological amplitude
Kooijman and Bakker 1993	Initial dry based on 30 similar plants; final dry	CTKL (50 mm)	Sco. sco., Cal.. cus., Sph.. sub., Sph. fal.	Water type, nutrients & interspecific interactions on species replacement

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Table 2A- Summary of bryophyte growth studies cont'd

Authors	**Weight Method**	**Length Method**	**Species**	**Purpose of study**
Gerdol 1995- Journal of Ecology- field	In. weight capitula 100°C-24 hr) subtracted from final mean weight	CTKL- 30 mm	Sph. fal., Sph. mag., Sph. cap.	Phenology
Gerdol 1995-Journal of Ecology- lab	In. weight capitula 100°C-24 hr) subtracted from final mean weight	CTKL- 50 mm	Sph. fal., Sph. mag., Sph. cap.	Phenology- photoperiod & temperature
Gerdol 1996	Initial capitulum weight subtracted from final mean dry weight -24 hr 100°C	CTKL-30 mm	Sph. mag.	Phenology & microhabitats
Pitkin 1975	NA	Increase in length beyond a pin inserted into bark of tree on which moss was growing measured	Hyp.cup., Pla. rep., Iso. myo., Nec. pum., Cam. ser.	Phenology
Murray *et. al.* 1989	NA	Cranked wire	Sph. spp.	Solar radiation, water
Gerdol *et. al.* 1998	In dry weight from 30 similar plants	CTKL- 30 & 50 mm	Sph. cap.	Night time temperature and nutrient level
Moore 1989	Growth measurements converted to productivity values with bulk density measurements	Cranked wire	Sph. ang., Sph. war., Sph. fus., Sph. cap.	Production of *Sphagnum* species
Aerts *et. al.* 1992	Initial dry weightfrom similar shoots	Cranked wire	Sph. bal., Sph. mag.	Nutrients & N supply
Shiraishi *et. al.* 1996	Dry weight of capitulum and stem	Cranked wire-like- "point level" metho	Sph. ten., Sph. nem., Sph. pap.	Growth & production: point level method
Lindholm 1990	NA	Reference mark outside the plant	Sph. fus.	Time, temperature and DTW
Rieley *et. al.* 1979	NA	Nets	Sph. rec.	Role of bryophytes in forest, their ability to change leachate chemical composition
Jauhiainen *et. al* 1997	Dry weight – captitulum & stem	Plastic strip & innate markers	Sph fus.	DTW, CO_2 concentration

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Table 2A- Summary of bryophyte growth studies cont'd

Authors	Weight Method	Length Method	Species	Purpose of study
Lindholm and Vasander 1990	Growth cut off and dried	Net	Sph. mag., Sph. pap., Sph. ang., Sph. fle., Sph. rip., Sph. war., Sph. fus.	Production of *Sphagnum* species
Damman 1978	Dry weight per unit of stem length- capitulum corr.	Cranked wire	Sph. mag., Sph. fus.	Distribution and movement of elements
Rochefort *et. al.* 1990	Dry weight-capitulum corr.	Cranked wire	Sph. ang., Sph. fus., Sph. mag.	Effect of acid precipitation
Rochefort and Vitt 1988	NA	Velcro strip method	Tom. nit., Sco. sco.	Effect of simulated acid precipitation
Pedersen 1975	Production values determined from growth in length	Cylinder method CTKL- 80mm	Sph. pul., Sph. pap., Sph. fal., Sph. cus., Sph. mag.	Growth in relation to climate, DTW, etc.
Rice 1995	Plants divided into stems, branches & capitula, dried separate .Absolute growth- average total growth in length × mass of branches & stems. Thus, capitulum corrected	CTKL- 30mm	Sph. mac., Sph. str., Sph. pap., Sph. por., Sph. pap., Sph. tri., Sph. rec.	Growth rates, allocation of tissues for growth
Hayward and Clymo 1983	Dry weight- capitulum corrected- new growth cut off and weighed	CTKL	Sph. cap., Sph. pap., Sph. rec.	Effect of light and water table depth on growth
Clymo & Reddaway 1971-hidrobiologica	Increase cut off & weighed- capitulum corrected	Cranked wire	Sph. rub., Sph. rec., Sph. pap., Sph. cus.	Productivity and peat accumulation
Clymo & Reddaway 1971-jecol	Increase cut off & weighed, capitulum corrected	Cranked wire	Sph. rub.	
Boatman 1977	Initial Dry similar shoots final dry based on apical 50mm of shoot.	CTKL- 50mm	Sph. cus.	Chlorophyll content, N, Mg, K

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Table 2A- Summary of bryophyte growth studies cont'd

Authors	**Weight Method**	**Length Method**	**Species**	**Purpose of study**
Clymo 1973	Dry weight capitulum corr.	CTKL- 50mm	Sph. sub. Sph. squ., Sph. plum., Sph. rec., Sph. pap., Sph. mag., Sph. cus	DTW, shade, pH, Ca, desiccation, surface roughness
Luken 1985	NA	cranked wire	Sph. mag., Sph. fus., Sph. ang.	DTW & zonation of the Sphagna
Stokes *et al.* 1999	Increase in length cut off and weighed	CTKL	Sph. cri., Sph. fal., Sph. sub.	Effect of water table on growth; implications for management
Chapman 1965	dry- similar shoots collected	CTKL- 50 mm	Sph pap., Sph. mag.	General ecology of peatland; also water relations
Brock and Bregman 1989	Dry mass estimated from similar shoots	CTKL	Sph. rec.	Periodicity of growth, productivity & decomposition
Jauhiainen *et al.* 1994	Initial dry weight of capitulum & 3cm of stem estimated from similar shoots	Plastic strip method (Lindholm)	Sph fus.	Response to N deposition and increased CO_2
Ferguson & Lee 1983	NA	CTKL- Transplant	Sph. rec., Sph. pap., Sph. mag., Sph. cap., Sph. ten., Sph. imb.	General description of growth of *Sphagnum* in that area
Press *et. al* 1986	NA	CTKL (40mm)	Sph. cus	Effect of increased atomospheric N on growth
Pakarinen 1978	Production measured	Innate markers	Sph. fus., Sph. bal., Sph. maj.	Prodcution and nutrient ecology
Longton & Greene 1969		Tagged at certain length and measured later	Ple.sch	Reproductive cycle and to discern general pattern of growth
Vitt *et. al.* 1993	Initial dry weight per mm of stem	CTKL (15-20 mm)	Sco. sco.	Effect of water chemistry on growth
Shaw *et. al.* 1991		Change in cover, so no length or weight	Cer. pur.	Effects of metal contamination on growth
Pentecost 1987	NA	Photography	Rhy. rip.	Tufa deposition, water flow
Pentecost 1987	NA	Tagged and photographed	Euc. ver & Cra. com.	Tufa deposition, water flow

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Table 2A- Summary of bryophyte growth studies cont'd

Authors	Weight Method	Length Method	Species	Purpose of study
Pentecost 1987	NA	Version of cranked wire, with plastic broom bristles	Gym. rec.	Tufa deposition, water flow & a method for identifying bryoliths is described
Tyler *et. al.* 1995	Dry weight per vessel at end of experiment	Total % cover	Bar. spp, Bry. spp., Cam. spp., Cer. pur., Dic. cer., Dit. fle., Ent. fas., Fun. hyg., Hyp. cup., Poh. spp., Pot. spp., Tor. tor., Tor. lat., Tri. bra.	Importance of phosphate to bryophyte establishment
Glime 1987	NA	CTKL (20-30 mm), some placed on Velcro strips	Fon. dur.	Effects of temperature and light on growth
Bates 1997	Initial dry weight estimated. from 20 similar shoots	NA	Bra. rut., Pse. pur.	Effect of intermittent desiccation
Vitt 1989	NA	Photography; increase in colony surface area	Rac. mic.	Patterns of growth- precipitation
Potter *et. al.* 1995	Increase in length cut off and dry weight determined	Innate markers	Pol. com., Hyl. spl.	Effects of temperature, water supply and nutrients on growth
Stark 1997	NA	Innate markers	Syn. ine.	Phenology of growth and reproductive biology
Clark *et. al.* 1998	Initial dry weight estimated from a subsample	NA	No species identified. Bryophytes separated based on growth form: mat, weft, turf, pendant, tail	Production and decomposition of epiphytic bryophytes (tropical study)
Watson 1975	NA	Innate markers	Pol. com.	Annual periodicity of growth
Shimizu *et. al.* 1984	Fresh weight determined after blotting with 10 sheets of paper towel	CTKL (20mm)	Pla. max.	Effect of light intensity on growth and photosynthesis
Stark *et. al.* 1998	NA	Innate markers	Syn. can.s	Growth rate relative to sex expression

Table 2A- Summary of bryophyte growth studies cont'd

Authors	**Weight Method**	**Length Method**	**Species**	**Purpose of study**
Sidhu & Brown 1996	Growth in length cut off and weighed (80C)	CTKL 20 mm & vertically positioned on Velcro strips in clear boxes with solution touching shoot bases	Rhy. squ.	Effect of heavy metals on shoot growth- new laboratory method
Fowbert 1996	Growth in length cut off and weighed	CTKL (10mm)	Bra. aus., Dre. unc. And. dep.	Morphology and shoot water content
Sharma & Chopra 1987	NA	Change in length measured as lead increased	Sem. ori.	Effect of lead on growth
Bates & Farmer 1990-field	NA	Tagged shoots	Ple. sch.	Effect of calcium and pH on growth
Bates & Farmer 1990-growth chamber	NA	CTKL (2mm)	Ple. sch.	Effect of calcium and pH on growth
Rochefort and Vitt 1988	NA	Velcro strip	Tom. nit., Sco.. sco.	Effect of simulated acid rain
Rincon 1993	Initial dry weight- 48 hr at 80°C- similar shoots	CTKL -15mm	Bra. rut., Thu. tam., Eur. pra., Pla. und., Psc. pur.	Effect of light intensity on growth
Rincon 1988- jbryol	Initial dry weight estimated, based on 20 similar shoots	NA	Bra. rut., Psc. pur.	Effect of herbaceous litter on growth
Rincon 1988- Bryologist	Initial dry weight estimated based on 20 similar shoots	CTKL- 3-45 mm	Bra. rut., Psc. pur., Pla. und., Thu. tam.	Effect of herbaceous litter on growth
Rieley *et. al.* 1979	Growth above nets cut off, dried & weight	Nets	Leu. gla., Rhy. lor., Ple. sch. , Pol. for., Dic. maj.	Role of bryophytes in forest, leachate chemical composition

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Table 2A- Summary of bryophyte growth studies cont'd

Authors	**Weight Method**	**Length Method**	**Species**	**Purpose of study**
Frego & Carleton 1995	Moist weight technique-regression	Shoots tagged with thread and their lengths above the thread recorded-TRANSPLANT	Ple. sch,. Dic. und., Pti.cri.	Microsite effect on growth
Zechmiester 1995	Weight reported but method not explained (?)	Petri dish method of Rincon and Grime 1989 & external marker	Ple. sch., Hyl. spl., Hyp. cup., Cte. Mol.	Effect of altitude & temperature on growth
Rincon and Grime 1989-J. Ecol-447-455	Initial dry weight from 20 similar shoots	CTKL (20mm)	Bra. rut., Pla. und., Thu. tam., Pse. pur.	Phenology
Rincon & Grime 1989-J Ecol-439-446	Initial dry from similar shoots	NA	Thu. tam., Pse. pur., Bra. rut., Eur. pra., Fis. cri., Tha. alo.	Light and plasticity
Pakarinen & Rinne 1979	NA	Innate marker	Hyl. spl., Pol. com.	Heavy metals
Pakarinen & Rinne 1979	NA	Seasonal growth pattern	Ple. sch.	Heavy metals
Pakarinen & Rinne 1979	NA	Annual increments	Dic. maj.	Heavy metals
Busby *et. al.* 1978	NA	Cranked wire	Tom. nit.	Microclimate control of growth
Busby *et. al.* 1978	Dry weight of growth segments	Innate marker	Hyl. spl.	Microclimate control of growth
Busby *et. al.* 1978	NA	Growth of current year was harvested when this could be determined	Pti. cri., Ple. sch.	Microclimate control of growth
Van der Hoeven *et. al.* 1998	Moist weight- regression analysis	CTKL- 40 mm	Rhy. squ., Cal. cus.	Effects of shade on growth and competitive interactions
Hanslin 1999	Initial dry weight based on similar shoots	CTKL (30mm)	Dic. maj., Pla. asp., Pti. cri., Rhy. lor.	Phenology

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Table 2A- Summary of bryophyte growth studies cont'd

Authors	**Weight Method**	**Length Method**	**Species**	**Purpose of study**
Longton & Greene 1979	Final weight after drying room temperature	CTKL 70mm & tied with cotton marker	Ple. sch.	Growth and reproduction- general study
Baker 1972	Growth cut off & weighed	Cranked wire	Cho. aci.	Production & decomposition
Ferguson *et. al* 1978	NA	CTKL	Sph. imb., Sph. rec., Sph. pap., Sph. ten., Sph. mag., Sph. capc.	Effect of sulphur on growth
Grigall 1985	Dry mass per unit stem length- capitulum corrected	Tagged and cranked wire	Sph. fus. Sph. mag., Sph. ang., Sph. fal.	Production
Gehrke 1998	Dry mass increase- capitulum corrected	Cranked wire	Sph. fus.	Effect of UV radiation on production
Simola 1977-J. Hat. Bot. Lab.	Dry weight- not explained	NA	Sph. fim.	Effects of heavy metals
Kooijman & Bakker 1995	Dry weight- not explained further	CTKL- 50 mm	Sco. sco., Sph. sub., Cal. cus., Sph. squ.	Role of water type & nutrients in replacement of species
Longton 1972	Growth cut off & weighed	Innate markers	Pol. alp.	Productivity, reproduction
Sonesson *et. al* 1996	Change in dry weight, but not mentioned that anything was weighed at start	Change in shoot elongation but no mention of CTKL?	Hyl. spl.	Effect of UV radiation and CO^2 on growth
Callaghan *et. al* 1997	Innate markers cut off & weighed (dry weight)	Innate markers	Hyl. spl.	Relation of climate to growth, seasonality of growth
Zechmeister 1995	Weight. of segments which grew during the period of the experiment were cut off & weighed	External markers i.e. permanent paint on shoots & petri dishes (Rincon & Grime 1989)	Ple. sch., Hyl. spl., Hyp. cup., Cte.mol.	Effect of altitude & temperature
Grosvernier *et al.* 1997	Dry initial 60°C- capitulum corrected	CTKL (50mm) and tagged with thread	Sph. fal., Sph. mag., Sph. fus.	DTW with implications for restoration on harvested peatland
Furness & Grime 1982	Initial dry weight estimated from 20 similar shoots	CTKL (25 mm)	Bra. rut.	Effect of temperature on growth