EFFECTS OF MANAGEMENT AND DISTURBANCE REGIMES ON EARLY LIFE HISTORY PROCESSES OF BALSAM FIR (*Abies balsamea* (L.) MILL.)

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Effects of management and disturbance regimes on early life history processes of balsam fir (*Abies balsamea* (L.) Mill.).

By

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Abstract

Balsam fir relies on disturbance events to create canopy gaps into which advance regeneration can grow. To determine the factors responsible for the failure of balsam fir forest regeneration in Eastern Newfoundland, various components of the early reproductive processes were compared among various combinations of management and disturbance regimes (Protected-intact canopy; Protected-open canopy; Cut block-domestic; and Cut block-commercial). Pollen availability and viability, seed production and quality, seedling emergence and survivorship were examined within each management/disturbance regime. The results indicate that reproduction of balsam fir in this ecoregion is not limited by the availability or quality of pollen, but in part by reduced numbers of female cone producing trees within insect disturbed and selectively cut stands. Protected intact canopy and domestic cutting blocks contained the highest proportions of optimal seedbed, the lowest levels of herbivory, and therefore the highest densities of juveniles. Disturbance regime is directly linked with the early reproductive processes of balsam fir. Therefore, to implement sustainable forest management, natural disturbance patterns must be more closely mimicked to ensure survival of early life history stages.

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Introduction and Overview

The boreal forest is naturally fragmented by both wetlands and disturbances. Rowe (1961) referred to the boreal forest as a "disturbance forest", as it relies on fire, windstorms, and insect outbreaks for self-perpetuation (Sprugel and Bormann, 1981). Unlike regeneration in black spruce (*Picea mariana* (Mill.) B.S.P.) and many other boreal species that co-evolved with fire as a major disturbance, regeneration in balsam fir (*Abies balsamea* (L.) Mill.) often coincides with insect outbreaks and windthrows, which conserve advance regeneration as a seedling bank (Elliott-Fisk, 2000). The boreal forest is also increasingly disturbed by small-scale domestic cutting and larger-scale commercial logging operations.

During the past 10 years, there has been a decrease in balsam fir advance regeneration in many areas of the North Shore Forest Ecoregion of Newfoundland, Canada. The problem is particularly acute in areas that are currently experiencing and/or have experienced insect outbreaks and selective cutting during the past 10-20 years (S. Avery, pers. comm. 2001; R. Power, pers. comm. 2001). To compound the problem, moose (*Alces alces americana* Clinton), an introduced herbivore in Newfoundland, targets the advanced regeneration of younger balsam fir. This herbivore reduces the number and health of juvenile balsam fir, which are necessary for stand replacement.

These combinations of disturbance pressures will eventually affect the density and number of mature balsam fir (Greene *et al.*, 1999). Balsam fir is the dominant tree species in the eastern boreal forest and imparts considerable timber, wildlife, and conservation value to stands where it occurs. For example, one of the key factors associated with the decline in Newfoundland marten (*Martes americana atrata*) is the loss of late successional-forests due to logging (Bissonette *et al.*, 1989; Thompson, 1991; Buskirk, 1992).

Staff at Terra Nova Nation Park, a protected area in the ecoregion, are concerned that inadequate regeneration of mature balsam fir stands on the landscape will have a cascading effect (a process of replacement of species (Begon *et al.*, 1990)) on this ecoregion, further reducing the "ecological integrity" of the park (Power, 2000). Their mandate commits to protect, as a first priority, the natural and cultural heritage of our special places and ensure that they remain healthy and whole.

Staff at the Newfoundland and Labrador Department of Forest Resources and Agrifoods and the Department of Environment and Conservation (Parks and Natural Areas Division and Inland Fish and Wildlife Division) are similarly concerned that the balsam fir component of this forest will be reduced or eliminated, which would lead to a reduction in landscape level biodiversity. Their mandate is "to maintain the long term health of forest ecosystems, while providing ecological, economic and cultural opportunities for the benefit of present and future generations" (Newfoundland and Labrador Forest Management Strategy, 2003).

Most of the cut areas on the island are left to regenerate naturally post cutting. Balsam fir is an economically important species and is used in provincial paper mills and constitutes 40% of the pulp used to make paper. Balsam fir has also been used locally for domestic uses such as home building and heating since Newfoundland was inhabited. Forest management in Newfoundland is increasingly being challenged to justify sustainability of cutting practices and the effects of clearcutting, intensive forestry and landscape fragmentation on forest biodiversity (Harrison *et al.*, unpub.). For these reasons, it must be ensured that balsam fir regenerate properly and are not hampered by introduced species and poorly managed forest cutting practices.

Life Cycle Approach to Understanding Forest Regeneration

The life history of balsam fir is linked with disturbance. Accordingly, my approach to determine where regenerative difficulties exist addressed how management and disturbance regimes affect early life history processes in the species. Although the recruitment dynamics of balsam fir post seedling establishment have been studied extensively (Côté and Bélanger, 1991; Osawa, 1994; Morin and Laprise, 1997; Parent *et al.*, 2003), much less is known about the earlier reproductive processes of balsam fir with respect to disturbance (Greene *et al.*, 1999). I studied pollination, seed production, seedling emergence success and first year survivorship of seedlings. By following these processes within various management and disturbance regimes, I attempted to isolate where problems exist and suggest management strategies to increase natural regeneration of balsam fir.

Pre-dispersal Processes: Pollination and Seed Production

Early barriers to conifer regeneration may occur during pollination. Human activities disturb forests worldwide, but the impact of reduced tree densities and number on pollen transfer in wind-pollinated trees is poorly understood (Knapp *et al.*, 2001). Reproduction in some populations of wind-pollinated trees has at times been pollen limited. Knapp *et al.* (2001) examined the relationship between seed production and local density of flowering conspecific species in blue oak (*Quercus douglasii* Hook. Arn.). They reported that fragmentation and thinning of blue oak stands may reduce pollen availability and limit reproduction through reduced acorn production in this wind-pollinated species.

Although most wind-pollinated trees produce copious amounts of pollen (Whitehead, 1983), and pollen may be present at considerable distances from the source individual (Caron and Leblanc, 1992), pollen concentrations have been found to drop off sharply with increasing distance from the source (Wright, 1952; Gleaves, 1973; Levin and Kerster, 1974). The movement of pollen between mates and the dispersal of seeds are the two main mechanisms of gene movement in seed plants (Hamrick and Nason, 1996). For this reason, it is important to include the disruption of pollen movement due to disturbance as a factor when examining reduced natural regeneration. A pollination barrier can lead to additional genetic isolation, reproductive failure and ultimately the demise of species (Koenig and Ashley, 2003).

Lack of pollination has been found to be a major constraint in seed production in most conifers (Owens, 1995). Unsuccessful pollination has been cited as one of the major sources of nonviable seeds in Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) (Singh and Owens, 1981) and Sitka spruce (*Picea sitchensis* (Bong.) Carr.) (Owens and Molder, 1985). It is likely that most of the flat, nonviable seeds frequently reported in conifers result from the lack of pollination associated with low pollen density (Smith *et al.*, 1990) and viability (Elliot, 1979). Therefore, fragmentation, as a result of disturbance, may lead to reduced pollen availability and reduced seed set. This in turn may result in reduced seed rain and low advance regeneration density.

Post-dispersal Processes: Seedling Emergence Success and Survivorship

Despite its potential importance, there is a general lack of knowledge concerning the levels of seed and seedling predation in the boreal forest and the factors regulating it (Nystrand and Granström, 2000). Low seed rain can also be caused by pre-dispersal seed predation (Zasada *et al.*, 1992; Willson, 1983). In the boreal forest, pre-dispersal predation of conifer seeds begins in the canopy with various coneworm species (Spruce Coneworm (*Dioryctria reniculelloides* Mutuura and Munroe), Spruce Cone Maggot (*Hylemya abietis* Huckett)), red squirrel (*Tamiasciurus hudsonicus* (Erxleben)), Red Crossbills (*Loxia curvirostra* Linnaeus 1758), White-winged Crossbills (*L. leucoptera* Gmelin 1789), and Pine Grosbeaks (*Pinicola enucleator* Linnaeus 1758). Once the seed has fallen to the ground, post-dispersal predation of seeds by small mammals and mortality due to fungus further decreases seed number (Zasada *et al.*, 1992). Upon emergence, seedlings can be lost to predation by slugs (Nystrand and Granstöm, 1997), voles, and mice.

Disturbance also affects canopy closure, which controls relative humidity, amount of solar radiation, and soil composition (Elliott-Fisk, 2000). Thus, disturbance may be an important factor in determining seedling emergence success. These biotic and abiotic components of the environment may be affected by disturbance and form an ecological filter that determines seedling emergence success as well as first year survivorship.

Seedling success in balsam fir forests depends on seedbed availability (Place, 1955; Logan, 1969). By altering the relative availability of various seedbed types and light, disturbance and associated levels of fragmentation further control seedling emergence and survivorship.

Study Species

Balsam fir is one of the most important trees comprising the eastern boreal forest. Balsam fir occurs at its eastern range limit in Newfoundland. Its distribution runs from Hudson Bay and Alberta to Newfoundland and Labrador, southward to Massachusetts and Pennsylvania and along the Alleghenies (Wodehouse, 1959; Burns and Honkala, 1990; Farrar, 1995). It is an integral component of the boreal ecosystem in Newfoundland and is the most abundant tree species on the island (Newfoundland and Labrador Forest Management Strategy, 2003). Because balsam fir is a dominant species in this boreal forest, it plays an important role in ecosystem function.

Balsam fir is monoecious and begins to form male strobelli and release pollen at approximately 15 years of age. Pollen is released between the end of May and late June (Wodehouse, 1959; Schopmeyer, 1974). Balsam fir is aenemophilous (wind-pollinated) and produces copious amounts of pollen (Pielou, 1988).

True firs are generally considered to be moderate to poor cone producers and have a long juvenile period when no seed cones are produced, as seed production begins between the ages of 20 and 30 years. Cones are restricted to the upper few whorls of branches in the crown except when trees grow in open areas or at edges, at which time cones can be found in the upper one third of the tree (Owens and Morris, 1998). Seed production has been shown to increase with tree age and hierarchical position within the canopy (Morris, 1951).

Balsam fir produces mast seed crops approximately every two to four years (Morris, 1951; Ghent, 1958; Schopmeyer, 1974). However, a mast year in the North Shore Forest Ecoregion of Newfoundland has not occurred in the past 10 years (S. Avery, pers. comm. 2001). Within the boreal forest, the percentage of high-quality germinable seeds is often low due to frequent infestations by cone and seed insects (Hedlin, 1974; Hedlin *et al.*, 1980). Also, during any one year seed productivity may be limited by inadequate pollination (Morris, 1951). The cones break up soon after maturing in late August and release their seed between September and November (Liu, 1971; Owens and Morris, 1998). Seeds are wind dispersed and the effective seeding distance is restricted by the relatively large seed size and the fact that the seeds tend to fall with their bracts (Burns and Honkala, 1990). Balsam fir does not maintain a persistent soil seed bank, as seeds are viable for only one year (Frank and Stafford, 1970; Thomas and Wein, 1985).

Balsam fir seedlings establish mainly from mid-June to mid-July. Seedlings are able to withstand dense shade, although their growth rate can increase rapidly when they are released from light suppression (Ghent, 1958).

Study Region

This study was conducted in boreal-coniferous forest in eastern Newfoundland, Canada (Figure1.1). The study sites are located at the eastern edge of the North Shore Forest

Ecoregion of Newfoundland, which is a narrow coastal zone (20-25 km wide) from the Bonavista Peninsula to the base of the Great Northern Peninsula (Damman, 1983). Tree species in these forests consist mainly of balsam fir and black spruce. Within the North Shore Forest, the climate, soil, and disturbance regimes match the optima for balsam fir (Burns and Honkala, 1990).

Most elevations are less than 130m (Damman, 1983) and the soil underlying study sites are podzols (Power, 2000). The growing season is approximately 150 days. Observed annual rainfall is between 900 and 1200mm (75% of which falls as rain) and the mean summer temperature is approximately 12.6°C (Power, 2000). The North Shore Forest Ecoregion is considered the driest region of Newfoundland with actual moisture deficits caused by high summer temperatures (Damman, 1983).

Disturbance Descriptions

In areas of two different forest management approaches, Terra Nova National Park (protected) and Forest Management District 2 (commercial and domestic cutting), two disturbances were studied. Within the protected management regime two progressive natural disturbances were examined. Within the cutting area, two anthropogenic disturbances were examined. All sites are dominated by balsam fir and have experienced multiple disturbances to some degree including insect defoliation (Deichman, 1982), windthrow, and human cutting. However, no sites appear to have been burned (S. Avery, pers. comm. 2001; R. Power, pers. comm. 2001).

Protected sites with intact canopy (PI) were those defined as experiencing small-scale gap formation through windthrows and were represented by two sites: Hall's Beach (HB) and Dark Hole Brook Forestry Resource Road (DHB). These sites are relatively undisturbed, unbroken stands with scattered wind-throws and dense advance regeneration. DHB, while part of the commercial forest and not in the protected area, had not been cut at the time of the study and was added to the PI category because representative, intact-canopy sites in the park were few and difficult to access.

Characteristic of intact stands, the forest floor at both sites was an almost continuous moss community, comprised mostly of hypnaceous mosses with intermittent patches of sphagnaceous and dicranaceous mosses. Small snags created by blowdowns and logs and stumps at various states of decay occurred throughout, covered by mosses in many cases. The canopy at both sites was almost entirely closed and understory plants included *Clintonia borealis* (Ait.) Raf., *Gaultheria hispidula* (L.) Muhl., *Linnaea borealis* L.. Very few shrubs occurred, creating a very open, cool, and shaded understory.

Protected sites with canopy disturbances (PO) were defined as those having experienced larger scale defoliation from insect disturbances, followed by canopy break-up. This category was represented by two sites: Blue Hill (BH) and Bread Cove Brook (BRCO). Located within Terra Nova National Park and unaffected by cutting since the 1950s, both sites, experienced eastern spruce budworm (*Choristoneura fumiferana* (Clem.)) and hemlock looper (*Lambdina fiscellaria fiscellaria* Guenee) disturbances that began in the early 1970s (Blais, 1983). The majority of balsam fir communities in Terra Nova National Park were affected to some degree by budworm (Deichman, 1982) and by previous cutting (MacEachern, 2001). The insect outbreak patterns mirror those that develop in other eastern Canadian boreal forests (Power, 2000) and are a natural phenomenon in the fir-spruce forests of eastern North America (Blais, 1981). The specific study sites contained large amounts of coarse woody debris, both standing and fallen trees and branches. No trees remained to form a live canopy, and as a result, an open, generally warm and dry forest floor existed at both BH and BRCO during summer months. The landscape was scattered with mature white spruce (*Picea glauca* (Moench) Voss). Balsam fir recruitment appeared low. Advance balsam fir regeneration had been repeatedly browsed by moose and appeared stout and stunted. The ground cover consisted of grasses, common raspberry (*Rubus idaeus* L.), hairy plumboy (*Rubus pubescens* Raf.), and small patches of moss, mostly dicranaceous and hypnaceous mosses.

Areas managed for domestic cutting (CD) were defined as those having experienced traditional cutting, which entails wood being cut by hand from small plots (~5 m^2), creating gaps in the canopy similar to natural disturbance. Such areas were represented by only one un-replicated site, Deep Bight River (DBR). Patches were cut in a progressive way at DBR, to allow forest regeneration near communities that depend on wood as fuel. In domestic cutting areas, as in DBR, trees were most often removed from the forest during the winter, thereby reducing the physical disturbance of the seedbed and advance regeneration. DBR resembled at time of sampling, a mature, intact stands with a dense balsam fir canopy, broken by small cut plots and scattered, blown-down trees. The forest floor was cool and moist and consisted of a continuous moss carpet comprised almost entirely of hypnaceous mosses. Very few shrubs occurred. However, mountain maple (*Acer spicatum* Lam.) and northern wild raisin (*Viburnum cassinoides* L.) were found at the edges of the cut plots.

Areas managed for commercial cutting (CC), included specifically those that had experienced selective cutting as a result of lack of enforcement of forestry regulations. These areas were previously very common on the Bonavista Peninsula and were typically cut by small commercial operations, which selected high-value trees from all age and size classes, both high and low quality, ultimately producing an uneven-aged forest. Two sites in this category, Bunyan's Cove (BUCO) and Lethbridge (LETH), were essentially "high-graded"; large, high-quality trees were cut from previously even-aged stands in a repetitive way, leaving stands of low-vigor individuals (Smith, 1996). Over time this practice can greatly reduce genetic quality and diversity (Smith, 1996). The balsam fir forest at these sites was less dense than in the other categories, with slash and stumps throughout the understory. The forest floor was dry and moss covered. Balsam fir recruitment was low and existing advance regeneration had been repeatedly browsed by moose, resulting in a stout and stunted appearance for the replacement forest.

Objectives of this thesis

In this thesis I examine the relationship between management and disturbance regimes, and the early regeneration requirements of balsam fir. The objectives of this thesis are: 1) to determine how management and disturbance regime affects the pre-dispersal reproductive processes of pollination and seed production; and 2) to determine how disturbance regime affects the post-dispersal seedling emergence and survivorship.

These objectives were accomplished using two approaches. First, I examine the pre-dispersal fitness components of regeneration by determining male and female cone production, pollen viability and availability, seed production and quality, and pre-dispersal seed predation levels among disturbances (Chapter 1). Secondly, I investigate post-dispersal fitness components of fir regeneration, comparing the distributions of available seedbeds in the various disturbance regimes, comparing seedling mortality from biotic and abiotic sources in experimental seeding of balsam fir into various seedbeds and determining natural densities of advance regeneration (Chapter 2).

References

Begon, M., Harper, J.L., and Townsend, C.R. 1990. Ecology: Individuals, Populations and Communities. Second Edition. Blackwell Scientific Publications, Boston.

Bissonette, J.A., Fredrickson, R.J., and Tucker, B.J. 1989. Pine marten: a case for landscape level management. Transactions of the North American Wildlife and Natural Resources Conference. 54: 89-101.

Blais, J.R. 1981. Mortality of balsam fir and white spruce following a spruce budworm outbreak in the Ottawa River Watershed in Quebec. Canadian Journal of Forest Research 11: 620-629.

Blais, J.R. 1983. Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. Canadian Journal of Forest Research 13: 539-547.

Burns, R.M., and Honkala, B.H. 1990. Silvics of North America. Volume 1, Conifers. Forest Service, United States Department of Agriculture. Agriculture Handbook 654. Washington, D.C.

Buskirk, S.W. 1992. Conserving circumboreal forests for martens and fishers. Conservation Biology 6: 318-320.

Caron, G.E., and Leblanc, R. 1992. Pollen contamination in a small black spruce seedling seed orchard for three consecutive years. Forest Ecology and Management 53: 245-261.

Côté, S., and Bélanger, L. 1991. Variations de la régénération préétablie dans les sapinières boréales en fonction de leurs caractéristiques écologiques. Canadian Journal of Forest Research 21: 1770-1795.

Damman, A.W.H. 1983. An ecological subdivision of the island of Newfoundland, Monographs in Biology 48, Pp. 163-206 *In*: G.R. South, Dr. W. Junk, eds. Biogeography and Ecology of the Island of Newfoundland, The Hague.

Deichman, K.H. 1982. Terms of reference-evolution of the spruce budworm infested forest of Terra Nova National Park. Unpublished Parks Canada report.

Elliot, D.L. 1979. The current regenerative capacity of the northern Canadian trees, Keewatin, N.W.T., Canada: some preliminary observations. Arctic Alpine Research 11: 243-251.

Elliot-Fisk, D.L. 2000. The taiga and boreal forest. Pp. 40-73 *In* M.G. Barbour and W.D. Billings, eds. North American Terrestrial Vegetation Second Edition. Cambridge University Press.

Farrar, J.L. 1995. Trees in Canada. Fitzhenry and Whiteside Ltd., Markham, Ont., and Canadian Forest Service, Natural Resources Canada, Ottawa, Ont. Pp. 81-94.

Frank, R.M., and Stafford, L.O. 1970. Lack of viable seeds in the forest floor after clearcutting. Journal of Forestry 68: 776-778.

Ghent, A.W. 1958. Studies of regeneration in forest stands devastated by the spruce budworm. II. Age, height, growth, and related studies of balsam fir seedlings. Forest Science 4: 135-146.

Gleaves, J.T. 1973. Gene flow mediated by wind-borne pollen. Heredity 31: 355-366.

Greene, D.F., Zasada, J.C., Sirois, L., Kneeshaw, D., Morin, H., Charron, I., and Simard, M.J. 1999. A review of the regeneration dynamics of North American boreal forest tree species. Canadian Journal of Forest Research 29: 824-839

Hamrick, J.L., and Nason, J.D. 1996. Consequences of gene flow in plants. Pp. 203-236 *In* O.E. Rhodes Jr., R.K. Chesser, and M.H. Smith, eds. Population Dynamics in Ecological Space and Time. University of Chicago Press, Chicago.

Harrison, D., Hearn, B., and Fuller, A. 2001. Landscape thresholds and response to fragmentation by endangered Newfoundland Marten. Unpublished.

Hedlin, A.F. 1974. Cone and seed insects of British Columbia. Environment Canada Canadian Forest Service Information Report BC-X-90.

Hedlin, A.F., Yates, H.O., III, Tovar, D.C., Ebel, D.H., Koerber, T.W., and Merkel, E.P. 1980. Cone and seed insects of North American conifers. Environment Canada, Canadian Forestry Service.

Knapp, E.E., Goedde, M.A., and Rice, K.J. 2001. Pollen-limited reproduction in blue oak: implications for wind pollination in fragmented populations. Oecologia 128: 48-55.

Koenig, W.D., and Ashley, M.V. 2003. Is pollen limited? The answer is blowin' in the wind. Trends in Ecology and Evolution. 18: 157-159.

Levin, D.A., and Kerster, H.W. 1974. Gene flow in seed plants. Evolutionary Biology 7: 139-220.

Liu, T.,-S. 1971. A Monograph of the Genus *Abies.* Department of Forestry, College of Agriculture, National Taiwan University. Taipei, Taiwan.

Logan, K.T. 1969. Growth of tree seedlings as affected by light intensity. IV. Black spruce, white spruce, balsam fir, and eastern white cedar. Can. Dep. Fish. For. Canadian Forest Service Publication 1256.

MacEachern, A. 2001. Natural Selections: National Parks in Atlantic Canada, 1935-1970. McGill-Queen's University Press.

Morin, H., and Laprise, D. 1997. Seedling bank dynamics in boreal balsam fir forests. Canadian Journal of Forest Research 27: 1442-1451.

Morris, R.F. 1951. The effects of flowering on the foliage production and growth of balsam fir. Forestry Chronicle 27: 40-57.

Newfoundland and Labrador Forest Management Strategy. 2003. Department of Forest Resources and Agrifoods, Government of Newfoundland and Labrador.

Nystrand, O., and Granström, A. 1997. Forest floor moisture controls predator activity on juvenile seedlings of *Pinus sylvestris*. Canadian Journal of Forest Research 27: 1746-1752.

Nystrand, O., and Granström, A. 2000. Predation on *Pinus sylvestris* seeds and juvenile seedlings in Swedish boreal forest in relation to stand disturbance by logging. Journal of Applied Ecology 37: 449-463.

Osawa, A. 1994. Seedling response to forest canopy disturbance following a spruce budworm outbreak in Maine. Canadian Journal of Forest Research 24: 850-859.

Owens, J.N. 1995. Constraints to seed production: temperate and tropical forest trees. Tree Physiology 15: 477-484.

Owens, J.N., and Molder, M. 1985. The reproductive cycles of the true firs. B.C. Ministry of Forests, Forestry Branch, Research Division, Victoria, B.C.

Owens, J.N., and Morris, S.J. 1998. Factors affecting seed and cone development in Pacific silver fir (*Abies amabilis*). Canadian Journal of Forest Research 28: 1146-1163.

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

Pielou, E.C. 1988. The world of the Northern Evergreens. Comstock Publishing Associates. London.

Place, I.C.M. 1955. The influence of seed-bed conditions on the regeneration of spruce and balsam fir. Canadian Department of Northern Affairs and Natural Resources Forestry Branch Bulletin 117.

Power, R. 2000. Terra Nova National Park Vegetation Management Plan 2000-2004. Heritage Canada, Parks Canada Agency.

Rowe, J.S. 1961. Critique of some vegetational concepts as applied to forests in northwestern Alberta. Canadian Journal of Botany 39: 1007-1017.

Schopmeyer, C.S. 1974. Seeds of woody plants in the United States. U.S. Department of Agriculture Forest Service Handbook 450. U.S. Government Printing Office, Washington, D.C.

Singh, H., and Owens, J.N. 1981. Sexual reproduction of Englemann spruce (*Picea englemanii*). Canadian Journal of Botany 59: 793-810.

Smith, D.M. 1996. The Practice of Silviculture: Applied Forest Ecology. John Wiley and Sons, New York.

Smith, C.C., Hamrick, J.L., and Kramer, C.L. 1990. The advantage of mast years for wind pollination. American Naturalist 136: 154-166.

Sprugel, D.G., and Bormann, F.H. 1981. Natural disturbance and the steady state in high-altitude balsam fir forests. Science 211: 390-393.

Thomas, P.A., and Wein, R.W. 1985. Delayed emergence of four conifer species on postfire seedbeds in eastern Canada. Canadian Journal of Forest Research 15: 727-729.

Thompson, I.D. 1991. Could marten become the spotted owl of eastern Canada? Forestry Chronicle 67: 136-140.

Whitehead, D.R. 1983. Wind pollination: some ecological and evolutionary perspectives. Pp. 97-108 *In*: Real L., ed. Pollination Biology. Academic Press, London.

Willson, M.F. 1983. Plant Reproductive Ecology. John Wiley and Sons. New York.

Wodehouse, R.D. 1959. Pollen grains and their structure, identification, and significance in science and medicine. Hafner Publishers Co. New York.

Wright, J.W. 1952. Pollen dispersion of some forest trees (Research paper 46). United States Department of Agriculture. Forest Service. Northeastern Forest Experiment Station, Upper Darby.

Zasada, J.C., Sharik, T.L., and Nygren, M. 1992. The reproductive process in boreal forest trees. *In*: H.H. Shugart, R. Leemans, and G.B. Bonan, eds. A Systems Analysis of the Global Boreal Forest. Cambridge University Press, Cambridge.

Co-Authorship Statement

All manuscripts in this thesis were co-authored with Dr. Luise Hermanutz and Dr. Brian McLaren. In all instances I was the principal contributor to project design and proposal, implementation of the field research component, analysis of the data and manuscript preparation.

Each of the following chapters will be submitted as a separate manuscript for publication. Consequently, there is necessary repetition between the general introduction and chapters.

Chapter 1. Do disturbance and management regimes affect wind pollinated trees? A study of early reproductive processes in balsam fir.

1.1 Introduction

The effect of disturbance on early reproductive processes such as pollen transfer (Knapp *et al.*, 2001), fertilization efficiency, and pre-dispersal seed predation in wind-pollinated trees is poorly understood. The efficiency of pollen transfer between plants is often dependant on stand structure, species composition, and population density (Antonovics and Levin, 1980). However, research on tree populations to date has focused almost solely on insect-pollinated species (Knapp *et al.*, 2001). This knowledge gap is surprising considering that boreal forests worldwide have evolved under conditions of natural disturbance, which play a major role in determining forest structure and species composition (Henry and Swan, 1974).

In addition to natural disturbance, human activities, such as forestry also cause disturbance. Therefore, it is becoming increasingly more important to understand the relationship between disturbance and the early reproductive processes of common, wind-pollinated, boreal trees. Forests are subject to increasing fragmentation due to large-scale commercial cutting and lack of natural regeneration. As stands and individuals become more isolated as a result of disturbance, it is possible that at some point insufficient pollen dispersal may limit fertilization and seed production. This has the potential to lead to genetic isolation and further reproductive failure as observed in some temperate forests (Knapp *et al.*, 2001; Sork *et al.*, 2002; Koenig and Ashley, 2003).

During the past decade, there has been a decrease in balsam fir regeneration in the North Shore Forest Ecoregion in Newfoundland, Canada. Unlike black spruce (*Picea mariana* (Mill.) B.S.P.), which relies on fire disturbances to regenerate, balsam fir (*Abies balsamea* (L.) Mill.) is better adapted to insect outbreaks and wind events that allow advance regeneration and layering (Blais, 1983; Elliott-Fisk, 2000; Morin *et al.*, 1993). Because the production and retention of a dense advanced regeneration is critical to the growth and persistence of balsam fir stands, its reduction could suggest serious problems in regenerative ability. This paper examines whether early reproductive processes are affected by disturbance and management regimes, and if so, at what stage in the production of advance regeneration these obstructions occur. Understanding how recruitment is affected by disturbance is essential in today's managed landscapes.

Four disturbance types were examined in two management regimes: an area protected from most large-scale human disturbance (Terra Nova National Park) and an area managed for cutting (Forest Management District 2-Crown Land). Protected sites with intact canopy (PI) are expected to have high pollen availability and seed production, resulting in adequate seed rain. Protected sites with canopy disturbances (PO), such as defoliating insect infestations, are expected to have lower pollen availability and seed production because of a reduced tree density and vigor. Areas managed for cutting that closely mimic natural disturbances with intact canopy, such as domestic cutting sites (CD), are also expected to contain high pollen availability and subsequently adequate seed production. Areas managed for commercial cutting (CC), specifically selective cutting, are expected to have lower pollen availability and seed rain, because they contain fewer trees and fewer dominant male and female cone producing trees.

In this study, we examined the effects of management and disturbance regime on the early reproductive processes of balsam fir. Our objective was to determine where the impediment to natural regeneration for balsam fir is occurring. Both male (male cone production, pollen viability, pollen availability) and female (female cone production, seed production and quality, pre-dispersal seed predation) reproductive components were measured and compared among management and disturbances regimes.

1.2 Methods

Study Species: The Reproductive Biology of Balsam Fir

Balsam fir is one of the most important trees in forests in boreal and northeastern regions of the northeastern United States and southeastern Canada. It is an integral component of the boreal ecosystem in Newfoundland and Labrador and it is the most abundant tree species on the island (Damman, 1983; Newfoundland and Labrador Forest Management Strategy, 2003).

Balsam fir is monoecious (Frank, 1990) and begins to form male strobelli and release pollen at approximately 15 years of age. The species is aenemophilous and pollen is released between the end of May and late June (Frank, 1990). Seed production begins between the ages of 20 and 30 years (Bakuzis and Hansen, 1965). Mast years normally occur every 2-4 years (Ghent, 1958; Schopmeyer, 1974). However, a mast year in the North Shore Forest Ecoregion of Newfoundland has not occurred in the past 10 years (S.

Avery, pers. comm. 2001; R. Power, pers. comm. 2001). Cones break up soon after maturing in late August and seeds are disseminated by the wind in September through November (Liu, 1971; Owens and Morris, 1998). The effective seeding distance is restricted by the relatively large seed size and the fact that the seeds tend to fall with the bracts (Burns and Honkala, 1990). The percentage of high-quality germinable seeds is often low due to frequent infestation by cone and seed insects (Hedlin, 1974; Hedlin *et al.*, 1980). Balsam fir does not produce a persistent soil seedbank (Frank and Stafford, 1970). In a healthy, regenerating stand, seedling establishment is closely correlated with seed production in the previous year (Parent *et al.*, 2003).

Study Sites

Fieldwork was conducted during May – September of 2001 and 2002 at seven sites in both Terra Nova National Park (TNNP- 404 km^2) (54° 00' W, 48° 30' N) and adjacent Forest Management District 2 (4221 km^2), which are representative of the easternmost section of the continent-wide belt of the boreal forest zone (Rowe, 1972). Sites were chosen both inside and outside of the park (Figure 1.1) to capture both protection and cutting management strategies as well as natural and anthropogenic disturbance regimes in balsam fir dominated forests. The North Shore Forest Ecoregion was selected for its variety of accessible disturbance regimes, and specific study sites were selected where observations of insufficient canopy replacement is occurring in fir dominated stands (Hermanutz and McLaren, unpublished data, 2001).

Management and Disturbance Regimes

Two management strategies were examined - *Protected* from further human disturbance (in TNNP); and *managed for cutting* (in Forest Management District 2-Crown Land) (Table 1.1). Within each of these management regimes, two disturbances were studied - *Protected*: intact canopy (PI) experiencing small-scale gap formation through windthrows, and canopy openings (PO) experiencing larger scale defoliating insect disturbances; and *Cutting*: domestic cutting (CD) experiencing traditional cutting practices, which entails wood being cut by hand from small plots (~5 m^2) and commercial selective cutting (CC), which selects trees from all age and size classes, both high and low quality, to produce an uneven-aged forest.

All selected sites were dominated by balsam fir and in the past have experienced multiple disturbances including insect defoliation (Deichman, 1982), windthrow, and human cutting. However, no sites appeared to have been burned. In the present study, sites were chosen to represent current dominant disturbance and management regimes.

Stand Description

Predominant disturbance type, time of disturbance and stand age was determined from tree increment cores and knowledge of local foresters (S. Avery, pers. comm. 2001; R. Power, pers. comm. 2001)(Table 1.1).

Male Reproductive Components

A) Male Cone Production

In a comparison of potential pollen availability among sites, all balsam fir within one 1250 m^2 plots were surveyed for the presence of male cones through visual inspection with binoculars with the exception of one PO site (Blue Hill, TNNP), which had no standing trees.

B) Pollen Viability

Pollen viability was assessed at 2 sites: Dark Hole Brook Forestry Resource Road (PI) and Deep Bight River (CD). Two samples from two branches on opposite sides of each tree were collected from 30 and 24 trees respectively on June 2nd and 4th respectively, 2002, during the peak pollen period. Pollen was extracted by gently tapping the collected branch tip on a microscope slide. Each sample contained pollen from approximately five male cones. The percentage of viable grains within` the first 200 pollen encountered was calculated using Alexander stain (Alexander, 1980).

C) Pollen Availability

At each site, five 1 m tall, pollen-collecting platforms were set up 5 m apart in a straight line to compare availability of pollen. Pollen was trapped in 15 mm plastic petri dishes sprayed with Tangle Trap®. The dishes were replaced every 2 days to prevent pollen saturation from the first week of June until the first week of July during both 2001 and 2002. The total number of pollen grains per plate was counted using a microscope under 40X. A one-way analysis of variance was conducted to determine if there was a difference in pollen counts between years and to determine if there was a significant difference in pollen availability among four disturbance regimes. The residuals were checked to determine if they were normal, homogeneous and independent using

NSCORES, histograms, and by comparing residuals to fitted residual, and residuals to the residual lag.

Female Reproductive Components

A) *Female Cone Production*

In a comparison of female cone production among sites, all balsam fir within one 1250 m^2 plots were surveyed for the number of living trees and the number that produced female cones through visual inspection with binoculars with the exception of one PO site (Blue Hill, TNNP), which had no standing trees.

B) Seed set and Seed quality

In an examination of seed production and quality, individual female cones (n= 1133) were collected from all sites with cones during the first week of September 2001 and 2002. Individual cones were bagged to examine variation among trees in all characters. The cones were examined externally for insect damage. Cones were then allowed to air dry, and filled seeds were separated and counted. Internal insect damage was noted. The seeds from each cone were weighed together to the ±0.01mg.

A linear regression tested for a significant difference in the number of seeds per cone between years. If no difference existed between years, the data were pooled. Residuals were tested as outlined above.

In a test of differences in seed quality and quantity among disturbances, a one-way analysis of variance compared number of seeds per cone, mean dry cone weight, and mean dry seed weight among disturbances. Residuals were examined as outlined above.

C) Pre-dispersal Seed Predation

To determine the impact of pre-dispersal insect predation on seed output, the percentage of cones damaged internally by insects was calculated for each disturbance type. Whether the frequency of insect damaged cones is influenced by disturbance regime was tested with a Poisson response variable G-statistic (SAS, 1999).

1.3 Results

Male Reproductive Components

A) Male Cone Production

Protected, intact stands (n=75) and CD (n=84) plots contained the highest numbers of trees with male cones (Figure 1.2). PO (n=9) had very few living trees and consequently very few trees producing pollen.

B) Pollen Viability

Pollen viability was greater than 95% at both sites tested. Of the 49,256 pollen grains examined, the mean viability ranged from 92.1 - 100%.

C) Pollen Availability

As there was no significant difference in pollen counts per plate found between years ($F_{[2,107]}=1.3$, $p=0.234$), 2001 and 2002 data were pooled. Residuals were found to be normal, homogenous, and independent. Hall's Beach was not included in the analysis due to inaccessibility of the site during pollen dispersal.

Pollen availability was not significantly different among management nor disturbance regimes ($F_{[2,107]}$=2.06, p=0.111) (Figure 1.3). Residuals were normal, homogenous, and independent.

Female Reproductive Components

A) Seed Production and Seed Quality

There was no significant difference in the mean number of seeds per cone between 2001 and 2002 ($F_{[1,1132]}$=7.67, p=0.006), so the two years' data were pooled. Residuals were normal, homogenous, and independent.

Significant differences occurred in mean number of seeds per cone ($F_{[3,1132]}$ =23.4, p<0.001), mean dry cone weight ($F_{[3,1132]}$=21.43, p<0.0001), and mean dry seed weight ($F_{[3,1132]}$=26.88, p<0.0001) among disturbances (Table 1.2). The cones and seeds within CC were the heaviest and also contained the highest number of seeds per cone among disturbances. Residuals were normal, homogeneous, and independent.

B) Pre-dispersal Seed Predation

The percentage of cones damaged internally by cone insects was high at all sites. However, the frequency of cones internally damaged by insects is significantly related to management and disturbance regime (G=2245.79; df=1132; p<0.0001). Commercially cut stands contained the highest percentage of cones with internal insect damage (66%), followed by PI (55%) and CD (44%). There were no cones accessible in the PO to collect and examine.

1.4 Discussion

Management and disturbance regimes differentially affect the early reproductive processes of balsam fir. Contrary to evidence in other North American forest types (Knapp *et al.*, 2001; Koenig and Ashley, 2003), our results indicate that disturbance does not limit availability of pollen in balsam fir in the North Shore Forest Ecoregion of Newfoundland. Differences in the density of female cone producing trees and pre-dispersal seed predation by cone insects among disturbances and management regimes may have larger impacts on reducing the reproductive output during early stages of the balsam fir life history process than previously documented.

Forests are managed for many reasons; to protect representative portions of various ecosystem types and to enable sustainable, cutting-based industries. However, all stands we investigated were affected by various types and intensities of disturbance, from small localized tree blow-downs to larger-scale insect defoliations. Even protected, unbroken stands are fragmented by water bodies, wetlands, and elevated areas. Recent research (Knapp *et al.*, 2001) addresses the possibility that as forest stands become more isolated, the potential exists for a population's size to decline to the point where some individuals receive insufficient pollen. Our results indicate that balsam fir reproduction in the North Shore Forest Ecoregion is not limited by the availability of pollen. Pollen from wind pollinated trees has been assumed to be abundant and travel long distances, which facilitates extensive gene flow (Koenig and Ashley, 2003). Despite large differences in the mean densities of trees with male cones, pollen counts were not significantly different among management and disturbance regimes. Because neither pollen availability nor viability was found to be low in the years examined, these factors do not appear to influence the level of and size of advance regeneration. Our results further support the suggestion that pollen from distant as well as local pollen sources play a significant role in pollination (Dong and Wagner, 1994; Epperson and Allard, 1989; Hamrick and Godt, 1990; Latta and Mitton, 1997; Latta *et al.*, 1998), as fragmentation due to disturbance appears to have little effect on pollen availability. This suggests that wind pollinated boreal trees have evolved to "cope" with highly fragmented landscapes. These ecosystems may show some resilience to disturbance with respect to pollen availability (Scheffer *et al.*, 2001).

The movement of pollen between mates and the dispersal of seeds are the two main mechanisms of gene movement in seed plants (Hamrick and Nason, 1996). However, the seeds of wind-dispersed conifers are not expected to move as far as pollen because of their considerably greater mass (Latta *et al.*, 1998). Therefore, local seed production may be an important limiting factor affecting the regeneration of balsam fir. In this study, large differences exist in the number of trees producing female cones among management and disturbance regimes. Differences in cone production among management and disturbance regimes are not discussed in other studies. Because seed does not disperse as far as pollen due to its larger size, seed rain may be limited at commercially cut and protected, open canopy sites. Seed rain within these areas is known to be very low. Hermanutz and McLaren (unpublished data) compared seed rain among 14 sites within the North Shore Forest Ecoregion and found seed rain to be ~0.0014 seeds per m^2 over 4 years compared with Houle and Payette's (1991) calculation of balsam fir seed rain during a mast year to be 92.5 seeds per m^2 and 0 seeds per m^2 during a non-mast year. This supports the observations that a masting event has not occurred in the North Shore Forest during this time.

Although statistically significant differences exist in cone and seed characteristics, such as seed number and cone size, among management and disturbance regimes, these differences may not be large enough to be biologically significant or detectable at the landscape level. Any small difference in seed number and size was overshadowed by larger differences in female cone production. In this way, even though heavily fragmented stands (for example commercially cut stands) produced the largest cones with the largest number of seeds per cone, these sites still experienced low seed rain due in part to the limited number of female, cone-producing trees.

Other than inadequate pollination, one of the most important constraints to seed production in the genus *Abies* is insect infestation (Owens and Morris, 1998). The percentage of high quality germinable seeds is often low due to frequent infestations by cone and seed insects (Hedlin, 1974; Hedlin *et al.*, 1980). Cone insects damaged approximately half of cones in all sites. The percentage of cones with internal insect damage was highest in CC stands (66%) followed by PI (55%) and CD (44%). The frequency of cones damaged by insects was significantly influenced by management and disturbance regimes. Owens and Morris (1998) also found that the major cause of seed loss in Amabilis fir (*Abies amabilis* [Doug] ex. Loud) was due to insect infestations. As in our study, these counts were made from fully developed cones and did not include the many seed cones totally destroyed during development. Like Owens and Morris (1998), we found most of the insect damaged cones dried and disintegrated at about the time of fertilization. As a result, they were not available for cone collection and analysis. Our observations and results support the Owens and Morris (1998) hypothesis that the importance of insect infestations to the potential seed crop is much higher than reported measured percentages indicate.

Squirrels are a major vertebrate cone predator (Halvorson, 1986) and are known to decimate the cone crops of numerous North American conifers (Hurley *et al.*, 1987). The red squirrel (*Tamiasciurus hudsonicus* (Erxleben)) is the only squirrel in Newfoundland and was first introduced in 1963 (Payne, 1976). Squirrels were first documented as a mass consumer of black spruce cones in 1986 near the base of the Great Northern Peninsula (West, 1986) and in Central Newfoundland during the summers of 2001-2003 (K. Tulk, unpublished data, 2003). Finley (1969) suggested that the red squirrel is capable of harvesting an entire cone crop from various conifers, at least in poor or moderate seed years. West (1989) concluded that in years with small cone crops, the proportion of cones per tree removed by squirrels varied from 15 to 64%, by the end of August, and from 64 to 96% by October on black spruce. Red squirrel densities in Terra Nova National Park and surrounding areas are estimated at between 0.23 and 0.50 squirrels per hectare (K. Lewis, unpublished data, 2004). West (1989) suggested that at densities as low as 2 squirrels/ha, these cone predators may have a significant effect on the availability of mature cones in a year with a small cone crop, but not necessarily in years when cone crops are large, as in a mast year. In this way, the lack of a mast year in over a decade, combined with increased cone predation by the cone insects and the growing population of red squirrel in central and coastal Newfoundland forests may help explain insufficient natural regeneration of balsam fir observed in some areas of the North Shore Forest Ecoregion.

Pre-dispersal seed predation is one of the factors thought to select for masting (Janzen, 1971; Silvertown, 1980; Kelly, 1994). During a masting event, higher proportions of seed escape predation due to predator satiation (Houle, 1999; Koenig and Ashley, 2003). The lack of a mast year for approximately 10 years in the North Shore Forest Ecoregion (S.Avery, pers.comm. 2001; R. Power, pers.comm. 2001) may exacerbate the heavy pre-dispersal seed predation by both cone insects and the red squirrel.

Disturbance-induced fragmentation is within the environmental variation experienced during life history of balsam fir. These results show that management and disturbance regime directly and indirectly affect the early reproductive processes of balsam fir. The success of early reproductive processes is cumulative and the product of male and female cone production, pollen viability and availability, and pre-dispersal seed predation by cone insects and red squirrel.

Pollen from distant sources may supplement local pollen, as no differences were found in pollen availability among management and disturbance regimes. This suggests that the cause of reduced recruitment in this ecoregion is not due to lack of fertilization, and pollination processes may not be particularly sensitive to changes in management and disturbance regimes.

Female cone production is important as seed rain is local and not from distant sources due to the large size of balsam fir seed (Latta *et al.*, 1998). In areas where advance regeneration is greatly reduced due to heavy moose browsing or is destroyed by cutting methods, female cone production is essential to produce local seed and allow regeneration, as balsam fir do not have a persistent seedbank. Pre-dispersal seed predation by cone insects is related to management and disturbance regime and greatly (>50%) reduces seed production in all management and disturbance regimes. In this way, the reduction of female cone producing trees compounded by pre-dispersal seed predation by both cone insects and red squirrel will further reduce regenerative potential and may explain the low observed seed rain (Hermanutz and McLaren, unpublished data) and the lack of young cohorts post-disturbance in PO (insect disturbed sites) and CC (selectively cut sites).

Sporadic observations are insufficient for planning management strategies (Caron and Powell, 1989). Determination of the variation in numbers of seed and pollen cones, and changes in numbers with tree age and loss to predation, and cone-crop intervals are need for managing sustainable, naturally regenerating stands.

1.5 References

Alexander, M.P. 1980. A versatile stain for pollen, fungi, yeast, and bacteria. Stain Technology 55: 13-18.

Antonovics, J., and Levin, D.A. 1980. The ecological and genetic consequences of density-dependant regulation in plants. Annual Review of Ecology and Systematics 11: 411-452.

Bakuzis, E.V., and Hansen, H.L. 1965. Balsam fir: A Monographic Review. The University of Minnesota Press, Minneapolis, MN.

Blais, J.R. 1983. Trends in the frequency, extent and severity of spruce budworm outbreaks in eastern Canada. Canadian Journal of Forest Research 13: 539-547.

Burns, R.M., and Honkala, B.H. 1990. Silvics of North America. Volume 1, Conifers. Forest Service, United States Department of Agriculture. Agriculture Handbook 654. Washington, D.C.

Caron, G.E., and Powell, G.R. 1989. Patterns of seed-cone and pollen-cone production in young *Picea mariana* trees. Canadian Journal of Forest Research 19: 359-364.

Damman, A.W.H. 1983. An ecological subdivision of the island of Newfoundland, Monographs in Biology 48, Pp. 163-206 *In*: G.R. South, Dr. W. Junk, eds. Biogeography and Ecology of the Island of Newfoundland, The Hague.

Deichman, K.H. 1982. Terms of reference-evolution of the spruce budworm infested forest of Terra Nova National Park. Unpublished Parks Canada report.

Dong, J., and Wagner, D.B. 1994. Paternally inherited chloroplast polymorphism in *Pinus*: estimation of diversity and population subdivision and tests of disequilibrium with a maternally inherited mitochondrial polymorphism. Genetics 136: 1187-1194.

Elliot-Fisk, D.L. 2000. The taiga and boreal forest. Pp. 40-73 *In* M.G. Barbour and W.D. Billings, eds. North American Terrestrial Vegetation Second Edition. Cambridge University Press.

Epperson, B.K., and Allard, R.W. 1989. Spatial autocorrelation analysis of the distribution of genotypes within populations of lodgepole pine. Genetics 121: 840-858.

Finley, R.B., Jr. 1969. Cone caches and middens of *Tamiasciurus* in the Rocky Mountain region. University of Kansas Museum of Natural History Miscellaneous Publications. No. 51.

Frank, R.M. 1990. *Abies balsamea* (L.) Mill. Balsam fir. Silvics of North America. Vol. 1. Conifers (eds. R.M. Burns and B.H. Honkala), pp. 26-35. Agricultural Handbook 654. USDA Forest Service. Washington, DC.

Frank, R.M., and Stafford, L.O. 1970. Lack of viable seeds in the forest floor after clearcutting. Journal of Forestry 68: 776-778.

Ghent, A.W. 1958. Studies of regeneration in forest stands devastated by the spruce budworm. II. Age, height, growth, and related studies of balsam fir seedlings. Forest Science. 4: 135-146.

Halvorson, C.H. 1986. Influence of vertebrates on conifer seed production. *In* Proceedings-Conifer Tree Seed in the Inland Mountain West Symposium, August 5-6, 1985, Missoula, MT. United States Department of Agriculture Forest Service Intermountain Research Station, Odgen, UT. USDA Forest Service General Techniques Report INT-203.

Hamrick, J.L., and Godt, M.J.W. 1990. Allozyme diversity in plant species. Pp. 43-63 *In* A.H.D. Brown, M.T. Clegg, A.L. Kahler, and B.S. Wier, eds. Plant Population Genetics, Breeding and Genetic Resources. Sinauer, Sunderland, M.A.

Hamrick, J.L., and Nason, J.D. 1996. Consequences of gene flow in plants. Pp. 203-236 *In* O.E. Rhodes Jr., R.K. Chesser, and M.H. Smith, eds. Population Dynamics in Ecological Space and Time. University of Chicago Press, Chicago.

Hedlin, A.F. 1974. Cone and seed insects of British Columbia. Environment Canada and Canadian Forest Service Information Report BC-X-90.

Hedlin, A.F., Yates, H.O., III, Tovar, D.C., Ebel, D.H., Koerber, T.W., and Merkel, E.P. 1980. Cone and Seed Insects of North American Conifers. Environment Canada, Canadian Forestry Service.

Henry, J.D., and Swan, J.M.A. 1974. Reconstructing forest history from live and dead plant material-an approach to the study of forest succession in south west New Hampshire. Ecology 55: 772-783.

Houle, G. 1999. Mast seeding in *Abies balsamea*, *Acer saccharum* and *Betula alleghaniensis* in an old growth, cold temperate forest of north-eastern North America. Journal of Ecology 87: 413-422.

Houle, G., and Payette, S. 1991. Seed dynamics of *Abies balsamea* and *Acer saccharum* in a deciduous forest of northeastern North America. American Journal of Botany 78: 895-905.

Hurley, T.A., Yeatman, C.W., and Robertson, R.J. 1987. Maturity and viability of seed from squirrel-cut pine cones. Forestry Chronicles 63: 268-271.

Janzen, D.H. 1971. Seed predation by animals. Annual Review of Ecology and Systematics 2: 465-492.

Kelly, D. 1994. The evolutionary ecology of mast seeding. Trends in Ecology and Evolution 9: 465-470.

Knapp, E.E., Goedde, M.A., and Rice, K.J. 2001. Pollen-limited reproduction in blue oak: implications for wind pollination in fragmented populations. Oecologia 128: 48-55.

Koenig, W.D., and Ashley, M.V. 2003. Is pollen limited? The answer is blowin' in the wind. Trends in Ecology and Evolution 18: 157-159.

Latta, R.G., and Mitton, J.B. 1997. A comparison of population structure across four classes of gene marker in limber pine. Genetics 146: 1153-1163.

Latta, R.G., Linhart, Y.B., Fleck, D., and Elliot, M. 1998. Direct and indirect estimates of seed versus pollen movement within a population of ponderosa pine. Evolution 52: 61-67.

Liu, T.,-S. 1971. A Monograph of the Genus *Abies*. Department of Forestry, College of Agriculture, National Taiwan University. Taipei, Taiwan.

Morin, H., Laprise, D., and Bergeron, Y. 1993. Chronology of spruce budworm outbreaks in the Lake Duparquet region, Abitibi, Quebec. Canadian Journal of Forest Research 23: 1497-1506.

Newfoundland and Labrador Forest Management Strategy. 2003. Department of Forest Resources and Agrifoods, Government of Newfoundland and Labrador.

Owens, J.N., and Morris, S.J. 1998. Factors affecting seed and cone development in Pacific silver fir (*Abies amabilis*). Canadian Journal of Forest Research 28: 1146-1163.

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

Payne, N.F. 1976. Red squirrel introduction to Newfoundland. Canadian Field Naturalist 90: 60-64.

Rowe, J.S. 1972. The Forest Regions of Canada. Canadian Forestry Service, Ottawa.

SAS Institute Inc. Copyright (c) 1999. Proprietary Software Version 8 (TS MO), Cary, NC., USA.

Scheffer, M., Carpenter, S., Foley, J.A., Folkes, C., and Walker, B. 2001. Catastrophic shifts in ecosystems. Nature 413: 591-596.

Schopmeyer, C.S. 1974. Seeds of Woody Plants in the United States. Handbook 450. United States Department of Agriculture Forest Service. Washington, DC.

Silvertown, J.W. 1980. The evolutionary ecology of mast seeding in trees. Biological Journal of Linnean Society 14: 235-250.

Sork, V.L. Davis, F.W., Smouse, P.E., Apsit, V.J., Dyer, R.J., Fernandez, M.J.F., and Kuhn, B. 2002. Pollen movement in declining populations of California valley oak, *Quercus lobata*: where have all the fathers gone? Molecular Ecology 11: 1657-1668.

West, R.J. 1986. Seasonal incidence of cone pests of black spruce in Newfoundland. Canadian Forest Service Newfoundland Forest Research Center Information Report N-X-244.

West, R.J. 1989. Cone depletions by the red squirrel in black spruce stands in Newfoundland: implications for commercial cone collection. Canadian Journal of Forest Research 19: 1207-1210.

Table 1.1: Study site disturbance characteristics including time of disturbance and stand age prior and post disturbance. (S. Avery, pers. comm. 2001; R. Power, pers. comm. 2001) (*Management Regime: P=Protected; C=Cut block) (Disturbance Regime: I=intact canopy; O=open canopy; D=domestic cutting; C=commercial cutting)*

Management Regime	**Disturbance Regime**	**Site Name**	**Predominant disturbance type**	**Time of Last Disturbance**	**Stand Age before Disturbance**	**Current Stand Age**	**Advance regeneration density per m^2**
P	I	Hall's Beach	Small-scale windthrows	N/A	N/A	60-80	2.26
P	I	Dark Hole Brook	Small-scale windthrows	N/A	N/A	60-80	4.42
P	O	Blue Hill	Insect defoliation	Late 1970's	40-60	N/A	0
P	O	Bread Cove Brook	Insect defoliation	Late 1970's	40-60	60-80	0.2
C	D	Deep Bight River	Domestic cutting	Ongoing for hundreds of	10-80	10-80	2.96

				years			
C	C	Bunyan’s Cove	Selective cutting	1980’s	60-80	60-80	0.21
C	C	Lethbridge	Selective cutting	1980’s	60-80	60-80	0.18

Table 1.2: Mean cone measurements ±SE for cones collected in 2001 and 2002 by management / disturbance regime. Significant differences among disturbance regimes were found for each character. (No cones were present in PO)

(PI=protected, intact canopy; PO=protected, open canopy; CD=cut block, domestic; CC= cut block, commercial)

Management/ Disturbance Regime (N = number of cones)	**Mean Number of seeds per cone**	**Mean Dry Cone Weight (g)**	**Mean Dry Seed Weight (g)**
PI N = 554	249.01 ± 51.70	5.92 ± 1.40	1.86 ± 0.62
PO N = 0	N/A	N/A	N/A
CD N = 271	225.30 ± 69.10	6.03 ± 1.60	1.84 ± 0.78
CC N = 308	256.60 ± 56.30	6.58 ± 1.40	2.21 ± 0.79

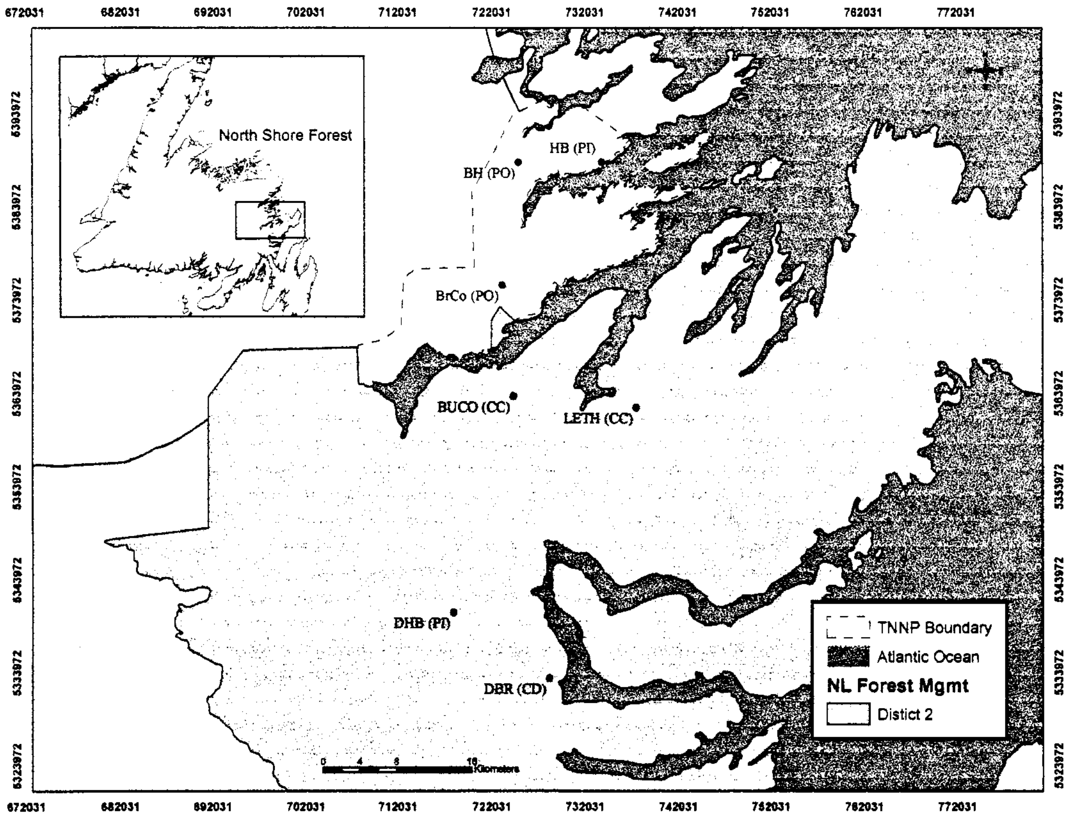

Figure 1.1: Map of study sites within the North Shore Forest Ecoregion, indicating management and disturbance regimes. *(Management/Disturbance Regimes: PI=protected, intact canopy; PO=protected, open canopy; CD=Cutting block, domestic; CC=cutting block, commercial) (Site names: HB=Hall's Beach; BH=Blue Hill; BRCO=Bread Cove Brook; BUCO=Bunyan's Cove Forestry Access Road; LETH=Lethbridge; DHB=Dark Hole Brook Forestry Resource Road; DBR=Deep Bight River)*

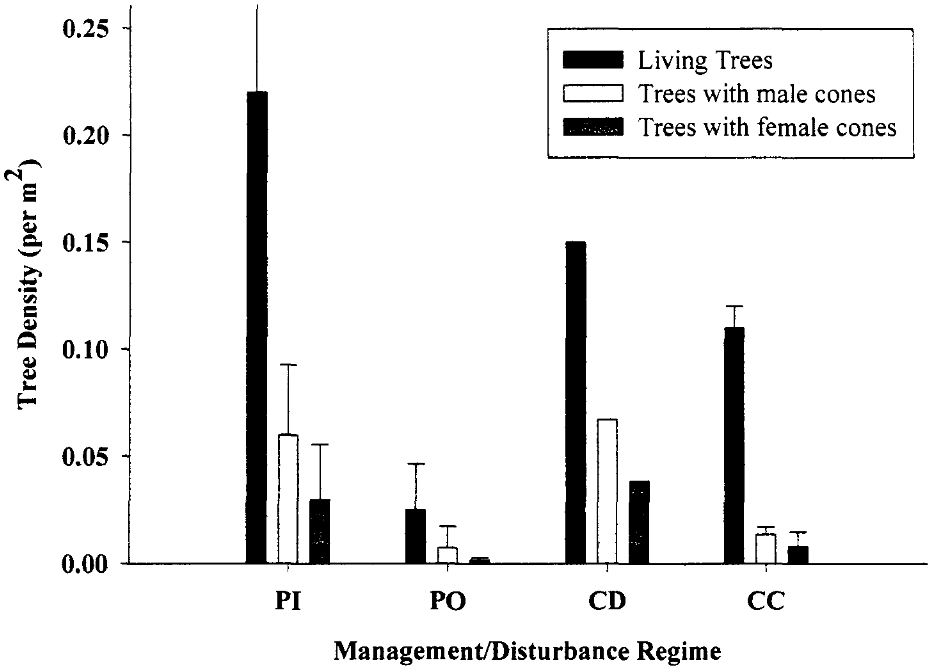

Figure 1.2: Mean ± SE total density of living trees, trees with male cones present, and trees with female cones present per m^2 within each management/disturbance regime. *(PI=protected, intact canopy; PO=protected, open canopy; CD=cut block, domestic; CC= cut block, commercial)*

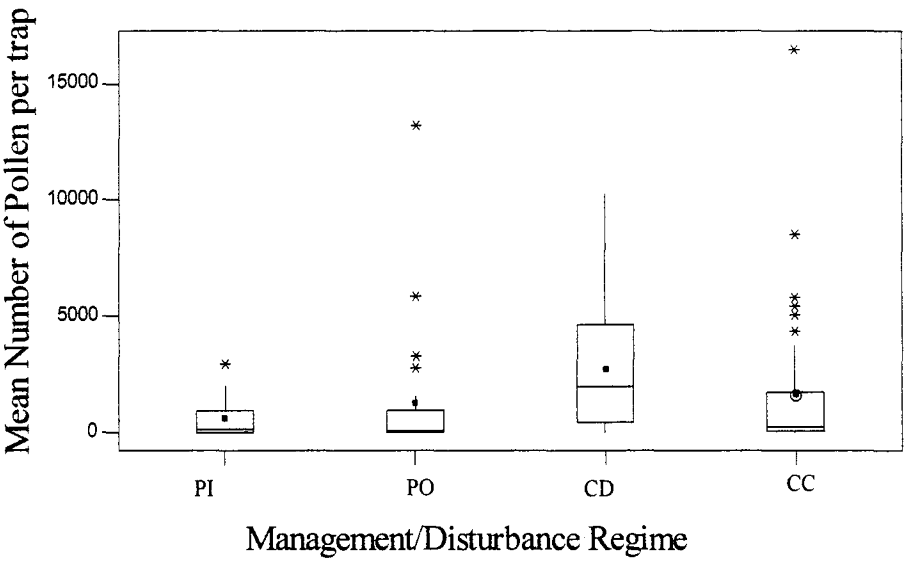

Figure 1.3: Box plot of mean number of pollen grains per trap by management/disturbance regime including all pollen measurements between the first week of June and the first week of July pooling 2001 and 2002 field seasons. Means are indicated by solid circles. *(PI=protected, intact canopy; PO=protected, open canopy; CD=cut block, domestic; CC= cut block, commercial)(Hall's Beach is excluded)*

Chapter 2. Comparing post seed dispersal reproductive processes in balsam fir among management and disturbance regimes in Newfoundland's boreal forest.

2.1 Introduction

The boreal forest is a disturbance-driven ecosystem (Rowe, 1961; Elliott-Fisk, 2000). Balsam fir (*Abies balsamea* (L.) Mill.) is a 'gap replacement' species and relies on disturbance events such as insect outbreaks and wind events to create canopy gaps into which juveniles, known as 'advance regeneration', develop from the understory (Spurr and Barnes, 1980). The production of a dense advance regeneration is essential for post-disturbance balsam fir forest regeneration (Spurr and Barnes, 1980; Blais, 1983; Morin *et al.*, 1993), in part because balsam fir propagules do not form a persistent seedbank (Olmstead and Curtis, 1947). Although the factors affecting recruitment dynamics of balsam fir post seedling establishment have been studied extensively (Côté and Bélanger, 1991; Osawa, 1994; Morin and Laprise, 1997; Parent *et al.*, 2003), much less is known about the earlier reproductive processes of balsam fir and how they relate to disturbance (Greene *et al.*, 1999). This knowledge gap is surprising considering that boreal forests worldwide have evolved under conditions of natural disturbance, and are increasingly affected by disturbance created by human activities, both of which play a major role in determining forest structure and species composition (Henry and Swan, 1974; Spurr and Barnes, 1980).

Seedling survivorship in balsam fir forests is known to depend on seedbed and light availability (Place, 1955; Vázina and Péch, 1964; Logan, 1969; Côté and Bélanger, 1991; Kneeshaw and Bergeron, 1996; Parent *et al.*, 2003; Simard *et al.*, 2003). Initial seedling survival is inversely proportional to organic depth, and then declines as follows: moss covered logs> moss> needle litter> broad leaf litter (Knapp and Smith, 1982; Bonan and Shugart, 1989; Harmon and Franklin, 1989; Bartlett *et al.*, 1991; Côté and Bélanger, 1991; Nakamura, 1992; Szewczyk and Szwagrzyk, 1996). McLaren and Janke (1996) found that germination rates are higher on broadleaf than needle litter but that subsequent survivorship is higher on needles.

Although seedling predation is known to affect forest regeneration, factors regulating conifer seedling predation in boreal forests are unknown (Nystrand and Granström, 1997). Conifer seedlings are at considerable risk of predation during the first few weeks after germination in the boreal forest (Lehto, 1957; McVean, 1961; Yli-Vakkuri, 1961; Kielland-Lund, 1963). Levels of herbivory due to specific seedling predator taxa have not been estimated in any previous studies, but slugs (mainly *Arion* spp.) have been assumed to be among the most important seedling consumers (Nystand and Granström, 1997).

During the past decade, observations have shown a considerable lack of balsam fir recruitment in the North Shore Forest Ecoregion in Newfoundland, Canada (S. Avery, pers. comm. 2001; R. Power, pers. comm. 2001; Hermanutz and McLaren, unpub. data). This paper attempts to determine if natural balsam fir regeneration is impeded during the post-seed-dispersal processes of emergence and first-year survival by experimentally investigating the role of disturbance in the regeneration dynamics of balsam fir.

Understanding how recruitment is affected by disturbance is essential in today's managed landscapes.

Four disturbance types will be examined within the two management regimes. One area of the North Shore Forest Ecoregion has been protected from further human disturbance since the 1950s when Terra Nova National Park was created. A second area is managed for cutting as Forest Management District 2. The disturbance types within these two areas include protected sites with intact canopy (PI), which experience small-scale disturbances such as windfalls. This level of disturbance leaves the forest canopy predominantly intact and an expected understory of high balsam fir seedling emergence and survivorship (Spurr and Barnes, 1980). Protected sites with open canopy (PO), due to current defoliating insect infestations, are expected to have dense older advance regeneration as they have been released from their canopy for many years (Morin *et al.*, 1993). Areas managed for cutting that closely mimic natural disturbances by reducing damage to seedbed as well as conserving advance regeneration, such as domestically cut sites (CD), should also contain dense advance regeneration. Areas managed for commercial cutting (CC) specifically selective cutting, are expected to have reduced densities of advance regeneration due to seedbed disturbance experienced during the cutting process.

In this study, we examined the effects of management and disturbance regime on the early reproductive processes of seedling emergence success and survivorship of balsam fir. Our objective is to determine where the impediment to natural regeneration for balsam fir is occurring. To accomplish this we: (1) compared seedling emergence success and survivorship in both natural and experimentally seeded plots; (2) identified and ranked the impact of seedling predators; and (3) measured seedbed composition and availability, critical physical factors (soil moisture and temperature), and seedling predation levels among management and disturbance regimes.

2.2 Methods

Study Site

Fieldwork was conducted during May – September of 2001 and 2002 at seven sites in both Terra Nova National Park (TNNP- 404 km^2) (54° 00' W, 48° 30' N), and adjacent Forest Management District 2 (4221 km^2), which are representative of the easternmost section of the continent-wide belt of the boreal forest zone (Rowe, 1972). Sites were chosen both inside and outside of the park (Figure 2.1) to capture both protection and cutting management strategies as well as natural and anthropogenic disturbance regimes in balsam fir dominated forests. The North Shore Forest Ecoregion was selected for its variety of accessible disturbance regimes, and specific study sites were selected where observations of insufficient canopy replacement is occurring in fir dominated stands (Hermanutz and McLaren, unpublished data; S. Avery, pers. comm. 2001).

The North Shore Forest Ecoregion is a narrow coastal zone (20-25 km wide) that runs from the Bonavista Peninsula to the base of the Great Northern Peninsula (Damman, 1983), and is dominated by balsam fir and black spruce (*Picea mariana* (Mill.) B.S.P.). Elevation is less than 130m (Damman, 1983) and the soil underlying study sites are podzols (Power, 2000). The growing season is approximately 150 days. Observed annual rainfall is between 900 and 1200mm (75% of which falls as rain) and the mean summer temperature is approximately 12.6EC (Power, 2000). The North Shore Forest Ecoregion is considered the driest region of Newfoundland with actual moisture deficiencies caused by high summer temperatures (Damman, 1983).

Management and Disturbance Regimes

Two management strategies were examined - *Protected* from further human disturbance; and *managed for cutting* (Figure 2.1; Table 2.1). For each of these management regimes, two disturbances were studied - *Protected*: intact canopy (PI) experiencing small-scale gap formation through windthrows, and canopy openings; (PO) experiencing larger scale defoliating insect disturbances; and *Cutting*: domestic cutting (CD) experiencing traditional cutting practices, which entails wood being cut by hand from small plots (~5 m^2), and commercial selective cutting (CC), which selects trees from all age, size and quality classes, producing an uneven-aged forest. However, these stands were 'high-graded'; large, dominant trees were cut in a repetitive way.

All selected sites were dominated by balsam fir and in the past have experienced multiple disturbances including insect defoliation, windthrow, and cutting. No sites appeared to have burned (S. Avery, pers. comm. 2001; R. Power, pers. comm. 2001). Although each site has experienced various past disturbances, the study sites were chosen to represent current dominant disturbance and management regimes. DHB, while part of a forest managed for its timber resource, has not been cut and is added to the PI category because representative, intact-canopy sites within the park are few and difficult to access.

Stand Description

Predominant disturbance type, time of disturbance, and stand age were determined from tree increment cores and knowledge of local foresters (S. Avery, pers. comm. 2001; R. Power, pers. comm. 2001)(Table 2.1). Balsam fir density was determined by counting the total number of standing living trees within randomly chosen 1250 m^2 plots at each site (Table 2.1). It was not possible to generate digital fragmentation indices due to the ocean boundaries which naturally fragment this ecoregion.

Seedbed Inventory

The quantity of each seedbed type available at each disturbance was determined by establishing six 25m line transects haphazardly at each disturbance using a measuring tape. The occurrence of each potential seedbed type, which included all substrate types encountered on the forest floor, was measured along each transect and used to derive the percentage of each seedbed type available at each site. Seedbed types were classified following McLaren and Janke (1996): Hypnaceous moss; Sphagnum moss; Dicranaceous moss; Exposed rock; Mineral soil; Coniferous litter; Deciduous litter; Mixed litter (approximately 50% of each coniferous and deciduous); Living root; Living Log; Fresh fallen log (could not penetrate with a pencil); Decaying log; Fresh stump; Decaying stump. Other seedbed types classified included: grasses, *Cladina* spp., water, and lycopodium.

Minitab for Windows 13.31 was used to analyze these data. A one way ANOVA was completed to determine if there was a significant difference in number of seedbed types present/available among management/disturbance regimes. The residuals were checked to determine if they were normal, homogeneous, and independent using NSCORES, histograms, and comparison of residuals to fitted residuals, and residuals to the residual lag. Percentage of area covered by each seedbed type for each management and disturbance regime was calculated for each sample. The three most predominant seedbed types for each management and disturbance regime and site were determined.

Seedling Survey

In order to determine the density of naturally emerging seedlings within each management and disturbance regime, 400 random - 1m^2 quadrats were surveyed for juvenile balsam fir seedlings at each site. Juvenile seedlings were defined as any unbranched balsam fir with only one growing tip under 30cm. When a balsam fir seedling was encountered, its height was measured, and presence of browsing and the seedbed type that it was currently growing in was noted. Relative levels of browsing among disturbance regimes and seedbed types that contained the highest density of naturally occurring seedlings were assessed.

Seedling density, percentage of seedlings browsed and proportion of seedlings that were new germinants (as of 2002) were determined for each by management and disturbance regime. The proportion of seedlings encountered per seedbed type was calculated.

Seedling Aging

A sample of seedlings (N= 265) was collected from all sites during the summer of 2002. These seedlings were aged following the method of Kneeshaw and Claveau (2001). A one-way ANOVA was used to determine if there was a significant difference in the number of bud scars, and therefore age, among sites and management and disturbance regimes. The residuals were checked as outlined above. These data were also used to determine when the last masting event occurred at these sites.

Experimental Seeding

At each site, during the first week of June, three 25 cm^2 plots were established in each of three moss categories; dicranaceous, hypnaceous, and sphagnaceous. The plots were prepared by removing all deciduous leaf litter and plants. Balsam fir seed from the Wooddale Provincial Tree Nursery was planted every 5 cm^2 using a quadrat so that each plot had 25 seeds. Adjacent to each plot was a 25 cm^2 unseeded control plot, which was prepared in the same manner. Each site also had a vermiculite control plot, which was set up by removing the moss in a 25 cm^2 area and replacing it with vermiculite. This type of control was established to allow comparison of abiotic variables such as soil moisture (McLaren and Janke, 1996).

The seedling emergence plots were monitored weekly from the second week of June until the first week of November when they became snow covered during 2001 and

2002. Newly emerged seedlings were marked with fluorescent pink toothpicks. Emergence, growth and fate, as well, in 2002, notes as to probable cause of death were recorded. Each source of mortality had specific methods of seedling destruction, enabling unambiguous assignment of fate. Voles clipped seedlings at the base, cleanly severing the stem. Slugs, were often observed on the seedlings and on subsequent visits, the seedling was either dead or severely damaged. Slime trails as well as slug "scoughing" on the remains of the seedling were considered clear evidence of slug herbivory. Drought caused the seedling to desiccate and the remaining dried seedling would remain intact on site. "Other herbivory" was recorded when the seedling was exhumed by the herbivore or completely eaten leaving no clues as to which seedling predator was responsible. All seedling damage observed could be attributed to one of these classes, which were based on observations.

Throughout the summer and fall during 2001 and 2002 the plots were monitored weekly for soil moisture and temperature. Soil moisture was measured using a Delmhurst Soil Moisture Tester (Model KS-1) with gypsum probes buried at 7.5-10 cm deep in the plot for the duration of the field season. Seedlings were excavated to determine the depth of the roots. Probes were buried at that depth (7.5-10 cm) to determine soil moisture available to seedling roots. One probe was buried within each moss plot at all sites, totaling 70 probes. Probes were buried at that depth to determine soil moisture conditions experienced by the roots of balsam fir seedlings. Resistance in Ohms was measured giving relative moisture readings among sites. Soil temperature

(^{o}C) was measured using a Barnant Thermocouple Thermometer (Type K) at a depth of 10 cm.

Seedling emergence success among disturbances was examined using a binary logistic regression of the General Linear Model. Binary logistic regression was used to investigate the relationship between the response variable (success or failure of emergence) and multiple explanatory variables that were both categorical and continuous (SAS, 1999). The full model included all main effects (disturbance, site, year, seedbed, soil moisture, soil temperature) and their interactions. Using a Pearson correlation, many variables were found to be insignificant and were removed. There were many significant interaction terms and consequently the main effects could not be examined within this model (Sokal and Rohlf, 1995). For the main effects, each disturbance was examined separately. The relationship between seedling emergence success and seedbed type was then examined within each disturbance regime separately using binary logistic regressions. Residuals were examined as outlined above. The proportion of successful seedling emergence was calculated for each seedbed type within each disturbance regime and then ranked.

Seedling emergence and first-year survival were related to soil moisture and differences in soil moisture were tested among disturbance regimes and seedbed types. Binary logistic regressions were used to determine if soil moisture was related to seedling emergence and a one-way ANOVA was performed to compare among disturbance regimes. Finally, within each disturbance, to determine if soil moisture was significantly different among seedbed types, one-way ANOVAs were performed. In all cases, the residuals were examined as outlined above.

Actual seedling emergence and mortality for each disturbance were calculated as the proportion of seedlings that died of drought, slug damage, vole herbivory or other herbivory with the data collected in 2002.

2.3 Results

Seedbed Inventory

No significant differences in the number of seedbed types present among management and disturbance regimes occurred (Table 2.2; p=0.139, df=6, n=7). Residuals were normal, homogenous, and independent. Seedbed types ranged from 17 (PO) to a low of 12 (PI) with CD (13) and CC (16) intermediate.

The dominant seedbed type across all sites was hypnaceous moss, ranging from 30.83% in CC to 78.01% in PI (Table 2.2). Deciduous leaf litter was the second dominant seedbed type in PO (20.85%) and CC (27.96%). Sphagnum moss (13.09%) and mixed litter (9.49%) were the second dominant seedbed types in PI and CD respectively.

Seedling Survey

Both PI and CD sites had high seedling densities (Figure 2.2; 3.2/m^2 and 3.0/m^2 respectively) compared to the PO and CC stands which had very low seedlings densities (0.1/m^2 and 0.2/m^2 respectively).

The highest level of seedling herbivory occurred in areas of insect disturbances (PO), where 12.8% of seedlings had been browsed (Figure 2.2), followed by CC (8.3%), CD (6.2%), and PI (5.9%).

The number of seedlings assessed during the 2002 survey were sorted into "new germinants" (seedlings that have germinated during the past year) or "older unbranched seedlings" (seedlings that are larger and show multiple annual growth scars but remain unbranched) by management and disturbance regime (Figure 2.3). Search effort varied among disturbances (PI = 210m^2; PO = 400m^2; CD = 193m^2; CC = 400m^2). More seedlings were found in PI and CD than PO and CC. Seedlings were found on 8 of the 18 seedbed types present. The seedbed types with the highest density of seedlings across all disturbances were hypnaceous moss, mixed litter, and coniferous litter (Table 2.2). In all disturbance regimes, the seedbed type with the highest percentage of seedlings was hypnaceous moss. Mixed litter contained the second highest percentage of seedlings within PO (7.69%), CD (7.29%), and CC (31.01%) sites. The second-highest percentage of seedlings in PI and PO were found in coniferous litter (3.27%) and mixed litter (7.69%) respectively.

Seedling Aging

There was no significant difference in number of bud scars, and therefore age, among sites ($p=0.754$, $F=0.53$, $df=260$) or disturbances ($p=0.453$, $F=0.88$, $df=260$) (Figure 2.4). Residuals were normal, homogenous, and independent. The average age of seedlings was 6.2±1.2 years ($N=265$), suggesting that the last mast year was 1996.

Experimental Seeding

In 2001 no seedlings emerged in any control plot at any site. In 2002 only one seedling emerged in one control plot at one site. External recruitment was therefore considered to be negligible in both years.

Emergence was synchronous across all disturbance types, commencing in week 4 (first week of July). In 2001 and 2002, 3075 seeds were planted; six hundred and eighty nine emerged (22.4%) and of those that emerged 357 (51.8%) survived their first growing season. PI stands experienced the highest proportion of seedling emergence, followed by those in PO and CC (Figure 2.7). The proportion that survived in each disturbance was constant. Approximately 50% of seedlings survived their first growing season (PI (52%); PO (57%); CD (56%); CC (46%)). Over-winter survival was low; 6.3, 2.7, and 4.0 percent of seedlings survived within PO, CD, and CC respectively. Over-winter mortality was not measured in PI sites due to lack of access to boats in early spring as the snow receded.

The final binary logistic regression model examining seedling emergence included both main effects (disturbance and seedbed type) and interactions (disturbance and seedbed and soil moisture; seedbed and soil moisture and soil temperature; soil moisture and soil temperature) (Table 2.3). Residuals were normal, homogeneous, and independent. Due to the presence of significant interaction effects, the main effects were analyzed separately by disturbance using binary logistic regression.

Seedling emergence is significantly different among disturbance regimes (G=123.092, df=3, p<0.0001). Residuals were normal, homogeneous, and independent. The highest proportion of seedling emergence was recorded in PI stands (0.38), followed by PO (0.18), and CC (0.17), and trailed by CD (0.07). Seedling emergence was significantly different among seedbed types in all disturbances except CD (Table 2.4). Seedling emergence for each seedbed type ranked differently among disturbances (Figure 2.5). There was also a significant difference in seedling emergence in vermiculite plots among disturbance regimes (G=41.172, df=3, p<0.0001). The highest proportion of seedling emergence in vermiculite plots occurred in PI (0.57), followed by CD (0.36), PO (0.25), and CC (0.16). The emergence in the vermiculite control plots followed the same emergence trend as in moss plots, with the exception of CD. CD experienced the lowest emergence among the moss plots, and the second highest emergence in the vermiculite control plot. These results confirm the initial hypothesis that PI would have the highest emergence, followed by CD, which closely mimic PI stands.

Soil moisture was not directly related to seedling emergence for any disturbance regime (PI: G=0.277; df=1; p=0.598; PO: G=0.952; df=1; p=0.329; CD: G=0.007; df=1; p=0.934; CC: G=0.205; df=1; p=0.651). Soil moisture was also not significantly different among disturbance regimes (Figure 2.6; F=1.04; df=103; p=0.378) or among seedbed types within a disturbance regime (PI: F=1.93, df=33, p=0.162; PO: F=1.34, df =26, p=0.281; CD: F=1.26, df=12, p=0.324; CC: F=1.10, df=29, p=0.346). Residuals were normal, homogenous, and independent in all these cases.

Herbivory was the main cause of seedling mortality during summer, and was responsible for the death of 95.6% of seedlings across all sites, while drought was responsible for only 4.4% of seeding mortality (Figure 2.8). Herbivory due to small mammals such as mice and voles was highest at PI (96.4%), CD (90.9%), and CC (92.1%) sites and slightly lower at PO stands, in which they were responsible for 65.7% of the mortality. Death due to slugs was highest within PO (28.6%) followed by CD (9.0%), CC (2.6%), and PI (1.4%). Slugs were found to play a role in conifer seedling herbivory and were responsible for 13 of 158 (8.2%) seedling deaths. Non-native slugs, including *Arion hortensis*, *Arion subfuscus*, and *Limax maximus*, were observed browsing balsam fir seedlings at all sites.

Mortality began during week 6 (third week of July) in all disturbances. However, each source of mortality varied temporally. Mortality caused by drought occurred during weeks 8 through 11 (August) and mortality due to herbivory occurred during weeks 6 through 16 (third week of July to first week of October).

Differential mortality was not based on soil moisture variation among disturbance regime or seedbed type. It is suspected that soil moisture is highly variable among and within years, and may contribute to increased seedling mortality in drier years. In contrast, herbivory was the cause of 96% of seedling deaths, and differed among disturbance regimes.

2.4 Discussion

Management and disturbance regimes affect the early reproductive processes of seedling emergence and survivorship in balsam fir. Seedling emergence varies significantly among disturbance regimes, as a result of variation in herbivory levels. Herbivory levels are also linked with disturbance regime, in part as a result of invasions of non-native species that browse advance regeneration at all life history stages and alter regeneration dynamics. Cutting practices that destroy advance regeneration and degrade seedbed further impede natural regeneration. Small scale, traditional cutting practices as they were studied in this area appear to promote natural regeneration by mimicking natural disturbance through small gap creation.

The distribution of conifer seedlings has been related to the distribution of specific seedbeds (Day, 1964; Knapp and Smith, 1982; Christy and Mack, 1984; Bartlett *et al.*, 1991; Côté and Bélanger, 1991; St. Hilaire and Leopold, 1995; Anderson and Winterton, 1996; McLaren and Janke, 1996; Cornett *et al.*, 1997; Simard *et al.*, 1998). Logging alters forest composition through the differential removal of one species and/or the leaving of another (Spurr and Barnes, 1980). In the North Shore Forest Ecoregion the removal of spruce and fir have resulted in an increase in residual tolerant hardwoods such as trembling aspen, paper birch, and mountain maple. This effect influences seedbed composition by increasing the amount and depth of deciduous leaf litter. Deciduous litter, especially in combination with poorly decomposed fibrous mor, is a poor seedbed for balsam fir (Bakuzis and Hansen, 1965). Our study supported this, as no seedlings were found on deciduous litter in either of the PO and CC disturbances, although this type represented over 20% of available seedbeds. Many other studies have found that deciduous litter had reduced conifer seedling densities (McLaren and Janke, 1996;

Kneeshaw and Bergeron, 1996; Côté and Bélanger, 1991; Simard *et al.*, 2003). Place (1952, 1955) found that almost any kind of fresh litter constitutes poor seedbed and that more than 15 centimeters of undecomposed litter is limiting to the germination and survival of balsam fir seedlings.

The survey of naturally occurring seedlings revealed that they were found in the highest density in hypnaceous moss, mixed litter, and coniferous litter. Short mosses are often cited as important seedbed (Harmon *et al.*, 1986; Côté and Bélanger, 1991; McLaren and Janke, 1996; Cornett *et al.*, 1997; Simard *et al.,* 1998). However, the amount of each seedbed available by disturbance did not correspond with seedling density, thereby identifying suitable and unsuitable seedbed types. For example, within mature, intact (PI) and domestic cutting stands (CD), hypnaceous moss constituted the highest proportion of available seedbed (78% and 71%). It also had the highest densities of naturally occurring, older seedlings (3.2 and 3.0 seedlings per m^2), the majority (91% and 76%) of which were found on hypnaceous moss. Although seedling emergence success was not consistently higher on hypnaceous moss in the experimental seedlings, it does appear that longer-term survival is greater on hypnaceous moss.

The results of the experimental seeding illustrate that some seedbed types experience higher seedling emergence success. This differs from the results of the seedling survey, which indicates suitable seedbed types for seedling survivorship. These results confirm Simard *et al.* (1998) who found that small *Abies* seedlings (0-5cm; <5 yr) were associated with moss and leaf and needle litter, while taller seedlings (> 5cm; ca. 5-12 yr) were mostly associated with moss. Because high mortality during the first five years can obscure early seedbed associations, analysing the distribution of older seedlings can help determine seedbeds truly safe for regeneration (Schupp, 1995). Hypnaceous, dicranaceous, and sphagnaceous mosses are all suitable seedbeds for emergence, but differ in providing a safe site for survival during the seedling life history stage.

Few studies examine the association between individual bryophyte species and tree seedlings, or the role of individual bryophyte species on seed germination or seedling establishment (St. Hilaire and Leopold, 1995). However, McLaren and Janke (1996) also found that hypnaceous moss had the highest seedling emergence. Duchesneau and Morin (1999) found that sphagnum moss and decaying wood were the most favourable seedbeds for balsam fir establishment. Our results do not support these results; in the seedling survey, sphagnum moss was found to have a lower density of seedlings even when more predominant on the forest floor than other seedbed types.

The juvenile seedling survey found that unbroken stands had the highest seedling densities, followed by fuel wood cut plots. Insect disturbances and selective cuts had much lower naturally occurring seedling densities. These results support a New Brunswick study where Dixon and Place (1952) investigated spruce and fir reproduction in a stand clearcut 8 years previously and in an intact stand. Under the canopy, in the uncut stand, survival ranged from 30 to 180 seedlings per m^2, whereas in the clearcut area, reproduction averaged only 10-30 seedlings per m^2. Hughes and Bechtel (1997) examined fir regeneration in regenerating clearcuts and intact stands to determine the extent to which disturbance size affected stem densities and distributions. They found that regeneration of fir in clearcuts (0.8-5.3 stems per m^2) was only 6-20% of regeneration in corresponding intact forests (14 stems per m^2). In our study, advance regeneration density within intact stands was 2.26 seedlings per m^2 with only 0.2 seedlings per m^2 within commercially cut stands. They attributed the low stem densities in highly fragmented sites to low seed density. All of our sites had very low balsam fir seed rain, 0.0014 per m^2 (Hermanutz and McLaren, unpublished data) which may also explain the low density of balsam fir seedlings observed at our sites.

Differences in seedling density are suspected to be due in part to other biotic and abiotic factors associated with management and disturbance regime. Parent *et al.* (2003) stated that variations in seed production will likely modulate seedling abundance, and that although the contributions of masting events are acknowledged, there is little empirical evidence to support the idea in balsam fir stands.

Contrary to all other studies concerning balsam fir seedling survivorship and soil moisture (Bakuzis and Hansen, 1965; Place, 1955), in our study there was no differential seedling mortality due to soil moisture. Soil moisture was not significantly different among disturbance regimes and did not affect seedling emergence as a main effect in our study. However, soil moisture does have interactive effects with disturbance, seedbed type, and soil temperature. In work completed by Place (1955), it was found that weather largely governed the success of balsam fir reproduction. He found that in New Brunswick, rain in June and July is of special importance and that the day-to-day weather is most important on very wet or very dry sites and is usually of much greater importance in the open than under vegetation. This will create regeneration challenges following cutting practices that fully expose seedbeds to desiccation and yet require natural regeneration.

Seedling mortality was approximately 50% during the first growing season, and increased over-winter to >90%. Place (1955) found that seedlings germinating after mid-July seldom survive the following winter. Simard *et al.* (2003) also found that most conifer seedlings die as seeds or seedlings within five years after dispersal.

Herbivory by native and introduced species of both the new germinants and juvenile seedlings plays a key role in the regeneration dynamics of balsam fir and consequent forest structure in the North Shore Forest Ecoregion. In 2002, herbivory by voles and/or mice caused approximately 96% of seedling mortality. It is not necessary that a species be either added or eliminated in order to greatly alter forest structure and function. Change in the abundance of a species may also have a considerable effect (Spurr and Barnes, 1980). Many herbivores such as moose (*Alces alces*), snowshoe hare (*Lepus americanus*), and approximately four species of mouse, lemming and vole have been introduced during the past 200 years to add to the single native meadow vole (*Microtus pennsylvanicus*) (J. Maunder, pers. comm., 2003). The Newfoundland wolf (*Canis lupus*) was extirpated in the early 20th century. Carnivore and herbivore densities can affect forest structure by influencing the density and composition of tree seedlings during regeneration in forest fragments (Cadenasso and Pickett, 2000).

Moose are often seen as primarily browsers of balsam fir advance regeneration at the sapling stage, and take large proportion of that biomass (S. Avery, pers. comm. 2001; Power, 2000). However, other smaller herbivores such as voles, mice and slugs are primarily seedling predators (Zasada *et al.*, 1992), most of which have also been introduced to the island of Newfoundland (J. Maunder, pers. comm., 2003). In this way, they also play a significant role in the destruction of balsam fir advance regeneration, but through the destruction of seedlings at an earlier life history stage than moose. Introduced species may cause an enhanced and unpredictable change in the regeneration dynamics of plants on the island of Newfoundland.

Slug predation is dependent on forest floor moisture levels that are dictated by weather changes (Nystrand and Granström, 1997), which in turn are affected by disturbance regime through variations in canopy cover. Slugs affect balsam fir regeneration dynamics by consuming new germinants and are responsible for 8.2% of seedling mortality due to herbivory. This suggests that damage to plants is very important just after seedling emergence, but is less important as seedling's mature (Byers and Bierlein, 1982; Charlton, 1978). For this reason, slugs are an important introduced species on the island of Newfoundland. There is only one native slug to Newfoundland (*Deroceras laeve* Müller 1774 ; Family Limacidae), yet there are now 13 slug species currently established on the island (Maunder, 1985). These seedling predators have moved beyond human settlements and into more remote and natural landscapes where they can potentially alter the regeneration dynamics of plants (Goudie, 1997). Slugs may function as "ecosystem architects" by altering tree seedling densities. Unlike mice and voles, nothing is known about their ecosystem level affects.

The reduced masting frequency in this region was unexpected as balsam fir normally produces large amounts of seed every 2 to 3 years (Morris, 1951; Ghent, 1958;

Schopmeyer, 1974). The lack of juvenile balsam fir within this ecoregion is a result of a combination of cascading factors that begin with low seed rain resulting from high level of pre-dispersal seed predation (Ch 1), high levels of seedling herbivory, which is further aggravated by cutting practices that destroy the seedbed and advance regeneration.

Disturbance is directly linked with the regeneration dynamics of balsam fir through its impact on both the abiotic and biotic conditions a seed and seedling experiences. Soil moisture, suitable seedbed availability, and herbivory are all linked closely with disturbance regime.

The production and retention of advance regeneration is critical in natural balsam fir forest regeneration. In forests disturbed by defoliating insects, heavy browsing of all life history stages including new germinants and older juvenile seedlings, by moose, mice, voles, and even slugs have additive effects on the forests ability to regenerate. Areas being commercially cut through practices such as high grading are also experiencing regeneration failure, while traditional wood harvesting methods, which mimic natural disturbances, are not. High grading creates large gaps in the canopy, increases poor seedbed types such as deciduous leaf litter, and finally destroys advance regeneration. Disturbance regime is directly linked with seedling success and persistence. For sustainable forest management, natural disturbance patterns must be more closely mimicked to ensure survival of early life history stages.

2.5 References

Anderson, L.J., and Winterton, A.J. 1996. Germination as a determinant of seedling distributions among natural substrates in *Picea engelmannii* (Pinaceae) and *Abies lasiocarpa* (Pinaceae). American Journal of Botany 83: 112-117.

Bakuzis, E.V., and Hansen, H.L. 1965. Balsam fir, *Abies balsamea* (Linnaeus) Miller: a monographic review. The University of Minnesota Press, Minneapolis.

Bartlett, R.M., Reader, R.J., and Larson, D.W. 1991. Multiple controls of cliff-edge distribution patterns of *Thuya occidentalis* and *Acer saccharum* at the stage of seedling recruitment. Journal of Ecology 79: 183-197.

Blais, J.R. 1983. Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. Canadian Journal of Forest Research 13: 539-547.

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

Byers, R.A., and Bierbein, D.L. 1982. Feeding preferences of three slugs species in the laboratory. Melsheimer Entomology Series 32: 5-11.

Cadenasso, M.L., and Pickett, S.T.A. 2000. Linking forest edge structure to edge function: mediation of herbivore damage. Journal of Ecology 88: 31-44.

Charlton, J.F.L. 1978. Slugs as a possible cause of establishment failure in pasture legumes oversown in boxes. New Zealand Journal of Experimental Agriculture 6: 313-317.

Christy, E.J., and Mack, R.N. 1984. Variation in demography of juvenile *Tsuga heterophylla* across the substratum mosaic. Journal of Ecology 72: 75-91.

Cornett, M.W., Reich, P.B., and Puettmann, K.J. 1997. Canopy feedbacks and microtopography regulate conifer seedling distribution in two Minnesota conifer-deciduous forests. Écoscience 4: 353-364.

Côté, S., and Bélanger, L. 1991. Variations de la régénération préétablie dans les sapiniéres boréales en fonction de leurs caractéristiques écologiques. Canadian Journal of Forest Research 21: 1770-1795.

Damman, A.W.H. 1983. An ecological subdivision of the island of Newfoundland, Monographs in Biology 48, Pp. 163-206 *In*: G.R. South, Dr. W. Junk, eds. Biogeography and Ecology of the Island of Newfoundland, The Hague.

Day, R.J. 1964. The microenvironments occupied by spruce and fir regeneration in the Rocky mountains. Department of Forestry, Canadian Forest Resources Branch Contribution 576.

Dixon, A.C., and Place, I.C.M. 1952. The influence of microtopography on survival of spruce and fir reproduction. Canadian Department of Resources and Development, Silviculture Leaflet No. 68.

Duchesneau, R., and Morin, H. 1999. Early seedling demography in balsam fir seedling banks. Canadian Journal of Forest Research 29: 1502-1509.

Elliott-Fisk, D.L. 2000. The Taiga and Boreal Forest *In*: M.G. Barbour and W.D. Billings, eds. North American Terrestrial Vegetation Second Edition. Cambridge University Press.

Ghent, A.W. 1958. Studies of regeneration in forest stands devastated by the spruce budworm. II Age, height, growth, and related studies of balsam fir seedlings. Forest Science 4: 135-146.

Greene, D.F., Zasada, J.C., Sirois, L., Kneeshaw, D., Morin, H., Charron, I., and Simard, M., -J. 1999. A review of the regeneration dynamics of North American boreal forest tree species. Canadian Journal of Forest Research 29: 824-839.

Goudie, J.E. 1997. Slug populations (Mollusca: Gastropoda) in commercial balsam fir, *Abies balsamea*, forests in western Newfoundland. Honours Dissertation. Memorial University of Newfoundland.

Harmon, M.E., and Franklin, J.F. 1989. Tree seedlings on logs in *Picea-Tsuga* forests in Oregon and Washington. Ecology 70: 48-59.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K., Jr., and Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15: 133-302.

Henry, J.D., and Swan, J.M.A. 1974. Reconstructing forest history from live and dead plant material-An approach to the study of forest succession in south west New Hampshire. Ecology 55:772-783.

Hughes, J.W., and Bechtel, D.A. 1997. Effect of distance from forest edge on regeneration of red spruce and balsam fir in clearcuts. Canadian Journal of Forest Research 27: 2088-2096.

Kielland-Lund, J.J. 1963. Noen faktorer som påvirker spireresultatet for gran [Summary: Some factors affecting spruce germination results]. Tidsskr. Skogbruk. 71: 58-78.

Knapp, A.K., and Smith, W.K. 1982. Factors influencing understory seedling establishment of Englemann spruce (*Picea engelmanni*) and subalpine fir (*Abies lasiocarpa*) in southeast Wyoming. Canadian Journal of Botany 60: 2753-2761.

Kneeshaw, D.D., and Bergeron, Y. 1996. Ecological factors affecting the abundance of advance regeneration in Quebec's southwestern boreal forest. Canadian Journal of Forest Research 26: 888-898.

Kneeshaw, D.D., and Claveau, Y. 2001. Effects of adventitious roots on age determination in balsam fir regeneration. Canadian Journal of Forest Research 31: 1292-1295.

Lehto, J. 1957. Tutkimuksia männyn luontaisesta uudistumisesta Etelä-Soumen kangasmailla [Summary: Studies on the natural reproduction of Scots pine on the upland soils of southern Finland]. Acta Forestalia Fennica 66: 101-106.

Logan, K.T. 1969. Growth of tree seedlings as affected by light intensity. IV. Black spruce, white spruce, balsam fir, and eastern white cedar. Canadian Dep. Fish. For. Canadian Forest Service Publication 1256.

Maunder, J.E. 1985. A guide to identifying Newfoundland slugs. Curatorial Reports of the Newfoundland Museum. Natural History Series No. 1. Newfoundland Museum, Historic Resources Division, Department of Culture, Recreation, and Youth, Government of Newfoundland and Labrador.

McLaren, B.E., and Janke, R.A. 1996. Seedbed and canopy cover on balsam fir seedling establishment in Isle Royale National Park. Canadian Journal of Forest Research 26: 728-793.

McVean, D.N. 1961. Experiments on the direct sowing of Scots pine. Empirical Forestry Review 40: 217-227.

Minitab 2000. Statistical software for windows version 13.31. Minitab Inc.

Morin, H., and Laprise, D.1997. Seedling bank dynamics in boreal balsam fir forests. Canadian Journal of Forest Research 27: 1442-1451.

Morin, H., Laprise, D., and Bergeron, Y. 1993. Chronology of spruce budworm outbreaks in the Lake Duparquet region, Abitibi, Quebec. Canadian Journal of Forest Research 23: 1497-1506.

Morris, R.F. 1951. The effects of flowering on the foliage production and growth of balsam fir. Forestry Chronicle 27: 40-57.

Nakamura, T. 1992. Effect of bryophytes on survival of conifer seedlings in subalpine forests of central Japan. Ecological Research 7: 155-162.

Nystrand, O., and Granström, A. 1997. Forest floor moisture controls predator activity on juvenile seedlings of *Pinus sylvestris*. Canadian Journal of Forest Research 27: 1746-1752.

Olmstead, N.W., and Curtis, J.D. 1947. Seeds of the forest floor. Ecology 28: 49-52.

Osawa, A. 1994. Seedling response to forest canopy disturbance following a spruce budworm outbreak in Maine. Canadian Journal of Forest Research 24: 850-859.

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

Place, I.C.M. 1952. Comparative growth of spruce and fir seedlings in sandflats. Canadian Department of Resources and Development, Silviculture Leaflet No. 64.

Place, I.C.M. 1955. The influence of seed-bed conditions on the regeneration of spruce and balsam fir. Canadian Department of Northern Affairs and Natural Resources Forestry Branch Bulletin 117

Power, R. 2000. Terra Nova National Park Vegetation Management Plan 2000-2004. Heritage Integrity. Parks Canada.

Rowe, J.S. 1961. Critique of some vegetational concepts as applied to forests in northwestern Alberta. Canadian Journal of Botany 39: 1007-1017.

Rowe, J.S. 1972. Forest regions of Canada. Canadian Forest Service Publication 1300

SAS Institute Inc. Copyright (c) 1999. Proprietary Software Version 8 (TS MO), Cary, NC., USA.

Schopmeyer, C.S. 1974. Seeds of woody plants in the United States. United States Department of Agriculture, Forest Service Handbook 450. United States Goverment Printing Office, Washington, DC.

Schupp, E.W. 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. American Journal of Botany 82: 399-409.

Simard, M-.J., Bergeron, Y., and Sirois, L. 1998. Conifer seedling recruitment in a southeastern Canadian boreal forest: the importance of substrate. Journal of Vegetation Science 9: 575-582.

Simard, M-.J., Bergeron, Y., and Sirois, L. 2003. Substrate and litterfall effects on conifer seedling survivorship in southern boreal stands of Canada. Canadian Journal of Forest Research 33: 672-681.

Sokal, R.R., and Rohlf, J.F. 1995. Biometry: the principles and practice of statistics in biological research. W.H. Freeman and Company, New York.

Spurr, S. H., and Barnes, B.V. 1980. Forest Ecology. John Wiley and Sons, Inc. Pp.687

St. Hilaire, L.R., and Leopold, D.J. 1995. Conifer seedling distribution in relation to microsite conditions in a central New York forested minerotrophic peatland. Canadian Journal of Forest Research 25: 261-269.

Szewczyk, J., and Szwagrzyk, J. 1996. Tree regeneration on rotten wood and on soil in old-growth stands. Vegetatio 122: 37-46.

Vázina, P.E., and Péch, G. 1964. Solar radiation beneath conifer canopies in relation to crown closure. Forest Science 10: 443-451.

Yli-Vakkuri, P. 1961. Kokeellisia tutkimuksia taimien syntymisetsä ja ensi kehityksestä kuusikoissa ja männiköissä [Summary: Experimental studies on the emergence and initial development of tree seedlings in spruce and pine stands]. Acta Forestalia Fennica 75: 111-122.

Zasada, J.C., Sharik, T.L., and Nygren, M. 1992. The reproduction processes in boreal forest trees. *In*: H.H. Shugart, R. Leemans, and G.B. Bonan, eds. A Systems Analysis of the Global Boreal Forest. Cambridge University Press, Cambridge.

Table 2.1: Study site disturbance characteristics including time of disturbance and stand age prior and post disturbance. (S. Avery, pers. comm. 2001; R. Power, pers. comm. 2001) *(Management Regime: P=Protected; C=Cut block) (Disturbance Regime: I=intact canopy; O=open canopy; D=domestic cutting; C=commercial cutting)*

Management Regime	**Disturbance Regime**	**Site Name**	**Predominant Disturbance Type**	**Time of Last Disturbance**	**Stand Age Before Disturbance**	**Current Stand Age**	**Living Balsam Fir Density (per m^2)**
P	I	Hall's Beach	Small-scale windthrows	N/A	N/A	60-80	0.16
P	I	Dark Hole Brook	Small-scale windthrows	N/A	N/A	60-80	0.28
P	O	Blue Hill	Insect defoliation	Late 1970's	40-60	N/A	0
P	O	Bread Cove Brook	Insect defoliation	Late 1970's	40-60	60-80	0.05
C	D	Deep Bight River	Domestic cutting	Ongoing for hundreds of	10-80	10-80	0.15

				years			
C	C	Bunyan’s Cove	Selective cutting	1980’s	60-80	60-80	0.08
C	C	Lethbridge	Selective cutting	1980’s	60-80	60-80	0.14

Table 2.2: Percentage of each seedbed type present in each management/disturbance regime and percentage of seedlings encountered per seedbed type by disturbance regime. *(Top 3 most predominant bolded in each category)*

(PI=protected, intact canopy; PO=protected, open canopy; CD=cut block, domestic; CC= cut block, commercial)

	PI		PO		CD		CC	
Seedbed Type	Seedbed Available (%)	Seedbed hosting seedlings (%)	Seedbed Available (%)	Seedbed hosting seedlings (%)	Seedbed Available (%)	Seedbed Hosting Seedlings (%)	Seedbed Available (%)	Seedbed hosting seedlings (%)
hypnaceous moss	**78.01**	**90.63**	**46.89**	**83.33**	**70.62**	**76.23**	**30.83**	**38.61**
dicranaceous moss	0.87	**2.37**	1.98	2.56	2.73	2.85	5.82	8.86
sphagnaceous moss	**13.09**	1.81	0.93	0.00	0.41	3.65	0.06	0.00
decaying log	2.21	0.11	**19.67**	**3.85**	4.03	0.00	9.00	0.00
decaying stump	0.21	0.11	0.29	0.00	0.37	2.22	0.58	0.00
fresh stump	0.00		0.00		0.23		0.05	
fresh log	0.23		0.78		2.11		2.96	
deciduous litter	1.25	0.11	**20.85**	2.56	4.15	1.11	**27.96**	8.86
coniferous litter	0.22	**3.27**	0.37	0.00	**4.47**	**6.66**	5.46	**12.66**
mixed litter	**2.73**	1.58	3.24	**7.69**	**9.49**	**7.29**	**15.21**	**31.01**
exposed rock	0.00		0.28		0.08		0.43	
mineral soil	0.44		0.69		0.82		0.40	
grass	0.00		3.25		0.00		0.47	
living root	0.03		0.09		0.05		0.11	
living log	0.00		0.04		0.39		0.00	
cladina	0.00		0.31		0.00		0.00	
water	0.00		0.03		0.00		0.40	
lycopodium	0.00		2.54		0.00		0.00	

Table 2.3: Binary logistic regression output for factors affecting seedling emergence success in completed final model.

Source	**Deviance**	**DF**	**Chi-Square**	**Pr>ChiSq**
Intercept	843.2766			
Disturbance	636.0156	3	207.26	<0.0001
Seedbed	558.5027	3	77.51	<0.0001
Disturbance*Seedbed	474.5896	9	83.91	<0.0001
Soil Moisture*Disturbance	442.6729	4	31.92	<0.0001
Soil Moisture*Seedbed	385.1030	3	57.57	<0.0001
Soil Temperature*Seedbed	356.6271	4	28.48	<0.0001
Soil Moisture*Soil Temperature	329.4119	1	27.22	<0.0001

Table 2.4: Summary of binary logistic regressions to determine if seedling emergence success is significantly different among seedbed types within each management/disturbance regime. *(PI=protected, intact canopy; PO=protected, open canopy; CD=cut block, domestic; CC= cut block, commercial)*

	PI	PO	CD	CC
Δ G	14.865	62.785	4.128	9.477
DF	2	2	2	2
P value	0.001	>0.0001	0.127	0.009
Decision	Significant	Significant	Not significant	Significant

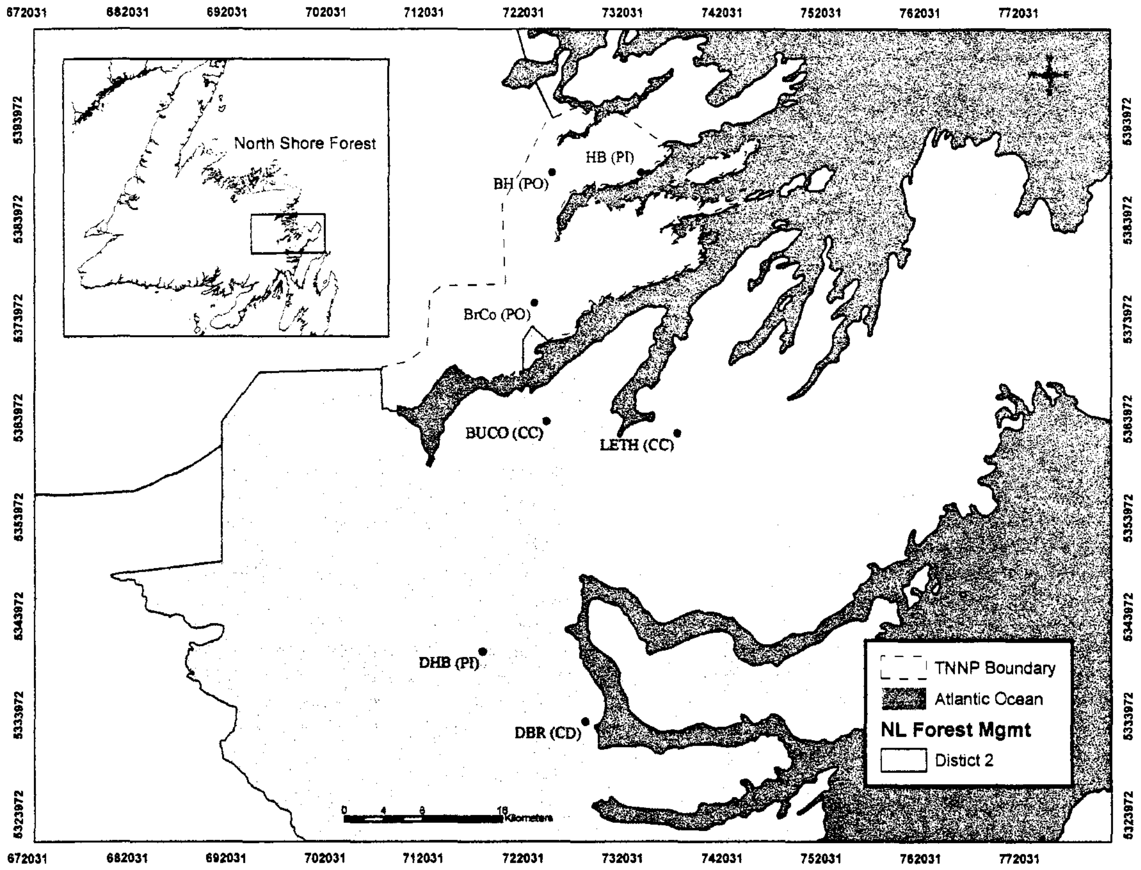

Figure 2.1: Map of study sites within the North Shore Forest Ecoregion, indicating management and disturbance regimes. *(Management/Disturbance Regimes: PI=protected, intact canopy; PO=protected, open canopy; CD=Cutting block, domestic; CC=cutting block, commercial) (Site names: HB=Hall's Beach; BH=Blue Hill; BRCO=Bread Cove Brook; BUCO=Bunyan's Cove Forestry Access Road; LETH=Lethbridge; DHB=Dark Hole Brook Forestry Resource Road; DBR=Deep Bight River)*

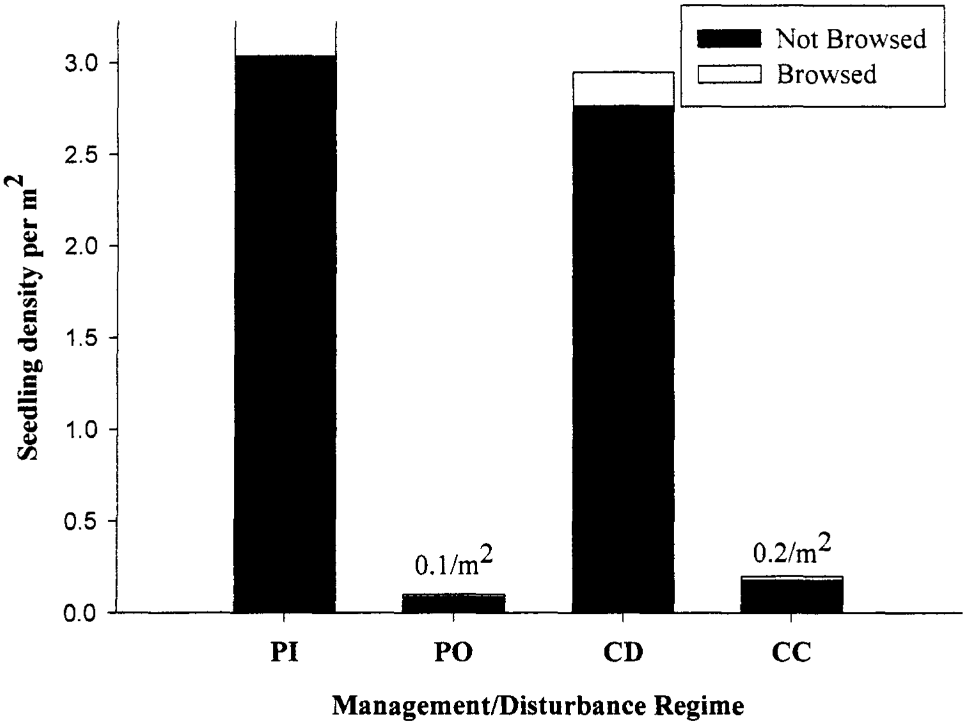

Figure 2.2: Naturally occurring juvenile seedling density showing proportion of seedlings browsed and not browsed by slugs, voles, and mice in each management /disturbance regime. *(PI=protected, intact canopy; PO=protected, open canopy; CD=cut block, domestic; CC= cut block, commercial)*

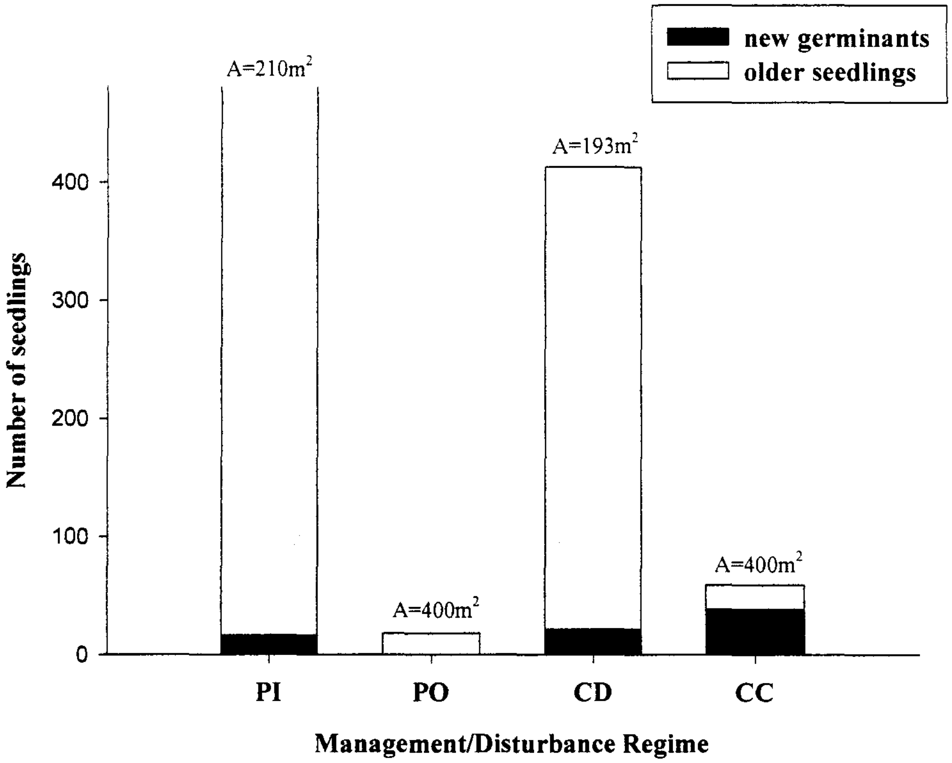

Figure 2.3: Total number of seedlings found during the 2002 surveys that were new germinants or older unbranched seedlings by management/disturbance regime. Area searched (A) given above columns *(PI=protected, intact canopy; PO=protected, open canopy; CD=cut block, domestic; CC= cut block, commercial)*

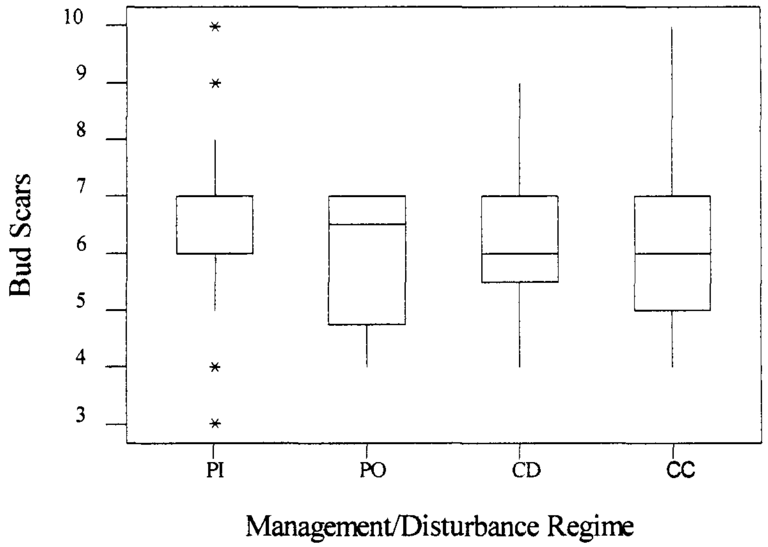

Figure 2.4: Boxplot of budscars (age) per seedling by management/disturbance regime. *(PI=protected, intact canopy; PO=protected, open canopy; CD=cut block, domestic; CC= cut block, commercial)*

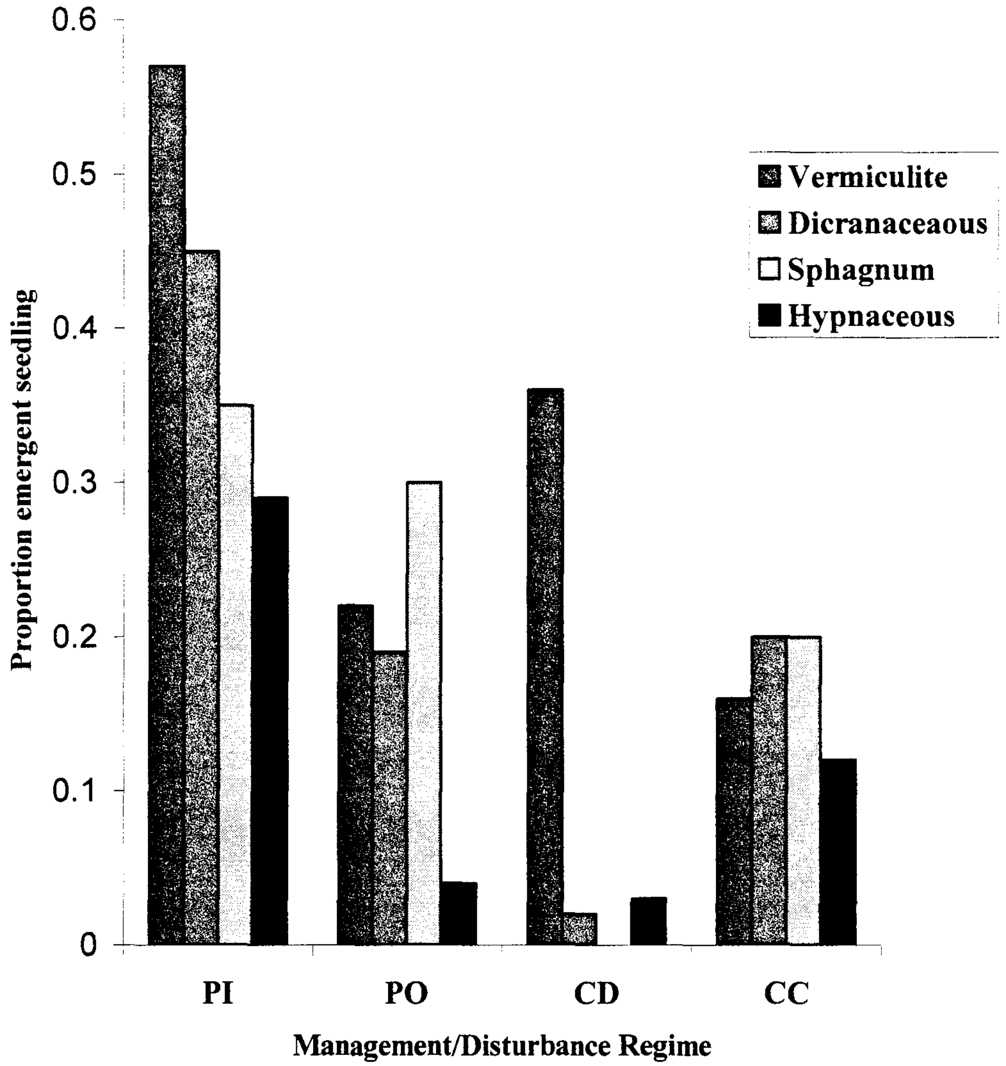

Figure 2.5: Proportion of seedling emergence for each seedbed type within each management/disturbance regime. *(PI=protected, intact canopy; PO=protected, open canopy; CD=cut block, domestic; CC= cut block, commercial)*

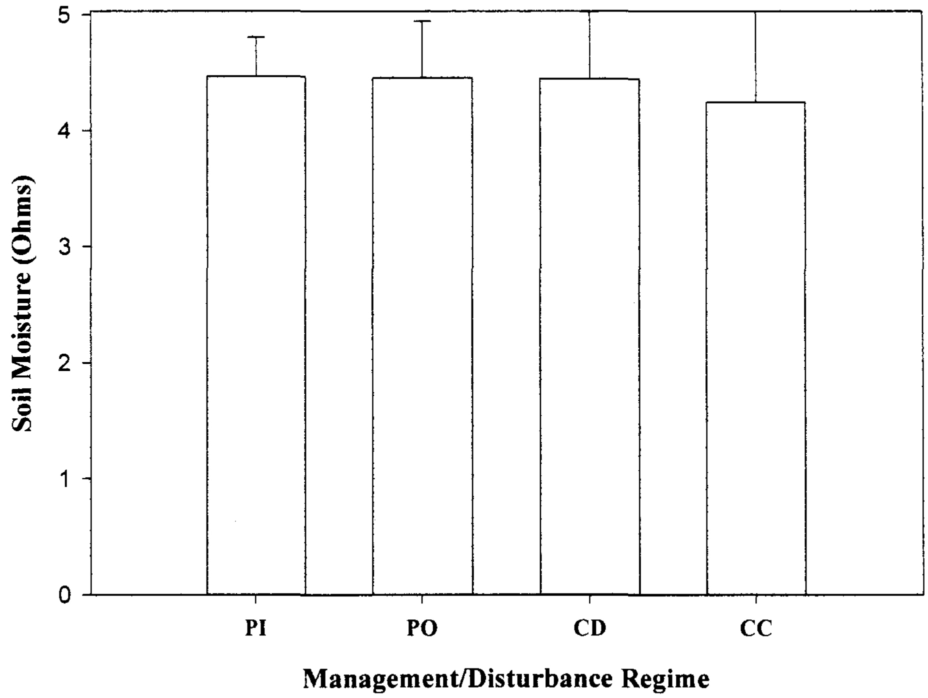

Figure 2.6: Mean soil moisture measurements taken weekly during summer and fall in 2001 and 2002 within each management/disturbance. *(PI=protected, intact canopy; PO=protected, open canopy; CD=cut block, domestic; CC= cut block, commercial)*

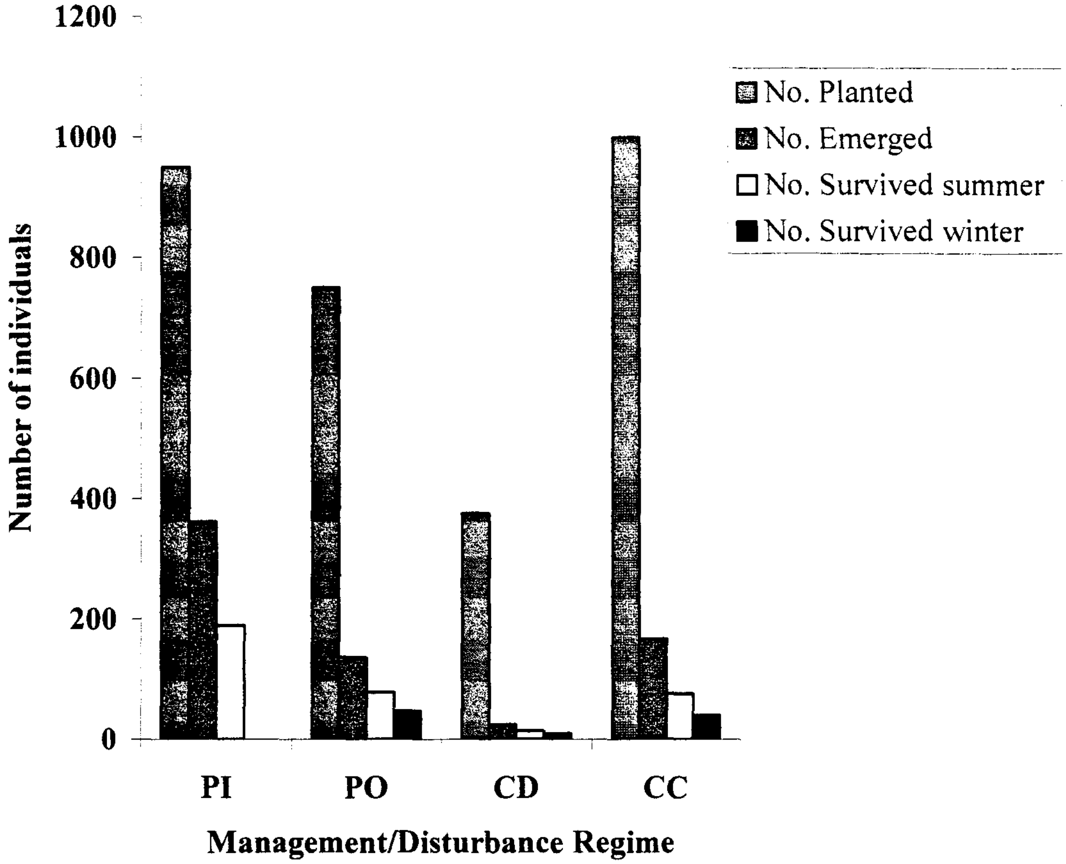

Figure 2.7: Number of seeds planted, and number of seedlings which emerged, survived the first growing season, and survived their first winter for each management/disturbance in 2001 and 2002. *(PI=protected, intact canopy; PO=protected, open canopy; CD=cut block, domestic; CC= cut block, commercial)*

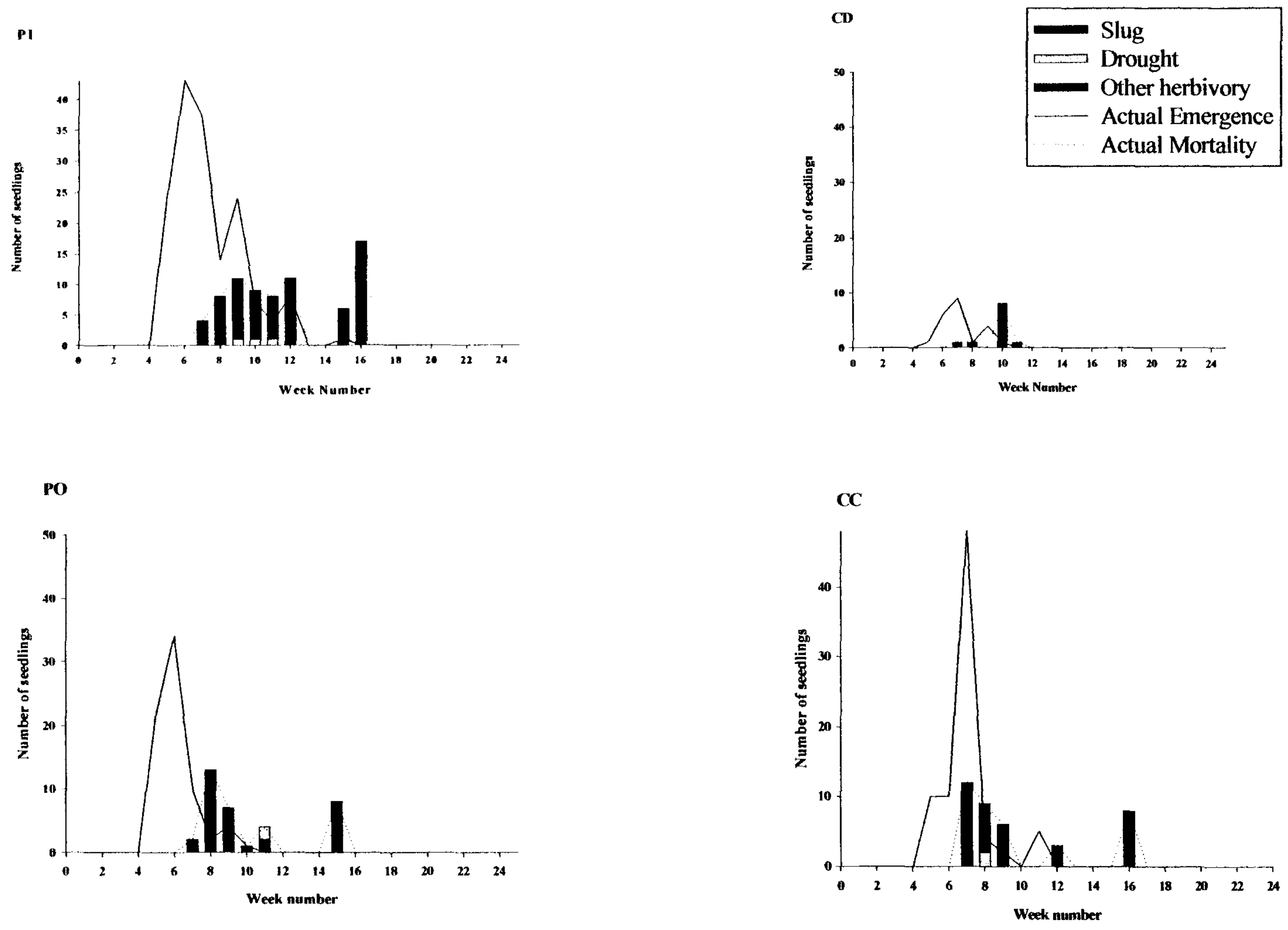

Figure 2.8: Emergence, mortality, and causes of mortality for each management/disturbance regime. *(PI=protected, intact canopy; PO=protected, open canopy; CD=cut block, domestic; CC= cut block, commercial)*

Thesis Summary and Conclusion

An observed failure in balsam fir regeneration in areas of disturbance and low cone crops in balsam fir in the North Shore Forest Ecoregion of Newfoundland initiated this study. Outcomes of this study can be used for management purposes by Parks Canada (Terra Nova National Park) and the Newfoundland and Labrador Department of Forest Resources and Agrifoods, as well as by the Parks and Natural Areas and Inland Fish and Wildlife Divisions of the Department of Environment and Conservation. Balsam fir is a dominant species in the area. Its values are both ecological and socio-economical and a decrease in its abundance or its absence would affect biodiversity and change cultural and industrial practices in the area.

High densities of moose, which browse juvenile balsam fir, as well as commercial cutting practices that reduce advance regeneration density, have been suspected causes of regeneration failure in fir. This study closely examined how management and disturbance regimes affect the early reproductive processes of balsam fir. It is an important gap to fill in our understanding of this dominant boreal species. Chapter 1 examined the pre-seed dispersal processes of pollination and seed production. Chapter 2 examined the post-seed dispersal processes of seedling emergence success and survivorship.

Pre-dispersal Process: Pollination and Seed Production

In Chapter 1, I examined the pre-dispersal fitness components of regeneration by determining male and female cone production, pollen viability and availability, seed production and quality, and pre-dispersal seed predation levels among disturbances.

Despite large differences in tree density, pollen counts were not significantly different among disturbance regimes. Pollen from distant sources may supplement local pollen in fragmented areas. Pollen does not appear to be an important factor controlling the reduced regeneration in the North Shore Forest Ecoregion.

Female cone production is necessary for natural regeneration of balsam fir for two reasons; because seed rain is local due to the large size of balsam fir seed (Burns and Honkala, 1990) and because balsam fir do not produce a persistent seedbank (Frank and Stafford, 1970). Therefore, any reduction in female cone producing trees directly reduces a stand's regenerative ability. There is an additive effect in areas where advance regeneration is greatly reduced by heavy moose browsing or is destroyed by cutting methods.

Pre-dispersal seed predation by cone insects greatly (>50%) reduces seed production in all management and disturbance regimes. Red squirrel, a mass consumer of cone crops (West, 1986; Tulk, unpublished data), also reduces seed production. However, squirrel impact on balsam fir cone crops in Newfoundland has not yet been determined. The reduction of female cone producing trees compounded by pre-dispersal seed predation by both cone insects and red squirrel may further reduce regenerative potential and may explain low seed rain (Hermanutz and McLaren, unpublished data) as well as the lack of young cohorts following disturbance in insect disturbed sites and selectively cut sites.

Post-dispersal Processes: Seedling Emergence Success and Survivorship

In Chapter 2, I investigated the post-dispersal reproductive processes of balsam fir among management and disturbance regimes by comparing the distributions of available seedbeds, determining natural densities of advance regeneration, and examining seedling mortality from biotic and abiotic sources in experimentally seeded plots.

Seedbed composition and availability differed significantly among management and disturbance regimes. Intact sites and domestic cutting sites had higher proportions of suitable seedbeds such as hypnaceous moss and coniferous litter, and also contained higher densities of juvenile balsam fir, while insect disturbed and selectively cut sites contained higher proportions of poor seedbeds such as deciduous leaf litter.

Seedling emergence success was significantly different among management and disturbance regimes, with the highest emergence success being in intact stands and those that mimic natural disturbance patterns such as domestic cutting sites. Of the approximately 50% of seedlings that die during their first year, almost all (96%) are killed by introduced herbivores such as voles, mice and slugs.

Low seed rain resulting from the reduction of female cone producing trees and high levels of pre-dispersal seed predation (Chapter 1), and followed by the reduction of suitable seedbed and high levels of seedling herbivory (Chapter 2) can explain the low density of naturally occurring juvenile balsam fir seen in the North Shore Forest Ecoregion.

Management Strategy Suggestions to Increase Natural Regeneration of Balsam fir

* Cutting techniques that minimize the destruction of advance regeneration should be promoted and utilized to allow natural regeneration of balsam fir and help reduce the time taken for stand replacement post cutting.

* “High-grading” is an unfavourable practice and is not sustainable. Natural regeneration of balsam fir at these sites is very low because this practice reduces the number of trees producing female cones and consequently reduces regenerative ability of the site. Cutting methods such as “high-grading” need to be replaced by cutting practices that mimic natural disturbances more closely such as in the domestic cutting patterns observed in this study.

* Red squirrel numbers and their predation of cones must be monitored. Their level of pre-dispersal cone predation is unknown for balsam fir in this province and is know to be significant in other boreal regions (Finley, 1969; Halvorsen, 1986; Hurley *et al.*, 1987; West, 1986). Reduction in the numbers of this introduced, non-native cone predator may need to be managed in order to allow natural regeneration of conifers, especially in this ecoregion.

*The impact of cone insects on seed rain in reducing seed by approximately half needs to be considered when calculating numbers of seed trees to leave after cutting. Size of cut blocks in areas browsed by moose is a second factor in sustainable forest management planning.

References

Burns, R.M., and Honkala, B.H. 1990. Silvics of North America. Volume 1, Conifers. Forest Service, United States Department of Agriculture. Agriculture Handbook 654. Washington, DC

Finley, R.B., Jr. 1969. Cone caches and middens of *Tamiasciurus* in the Rocky Mountain region. University of Kansas Museum of Natural History Miscellaneous Publications. No. 51. pp.233-273.

Frank, R.M., and Stafford, L.O. 1970. Lack of viable seeds in the forest floor after clearcutting. Journal of Forestry 68: 776-778.

Halvorson, C.H. 1986. Influence of vertebrates on conifer seed production. *In* Proceedings-conifer tree seed in the Inland Mountain West Symposium, August 5-6, 1985, Missoula, MT. United States Department of Agriculture Forest Service Intermountain Research Station, Odgen, UT. USDA Forest Service General Techniques Report INT-203.

Hurley, T.A., Yeatman, C.W., and Robertson, R.J. 1987. Maturity and viability of seed from squirrel-cut pine cones. Forestry Chronicles 63: 268-271.

West, R.J. 1986. Seasonal incidence of cone pests of black spruce in Newfoundland. Canadian Forest Service Newfoundland Forest Research Center Information Report N-X-244.